



Morphological tricks and blessed genitalia: rectifying the family placement of *Fijicolana tuberculata* (Opiliones: Laniatores: Zalmoxidae)

ABEL PÉREZ-GONZÁLEZ^{1,3}, PRASHANT P. SHARMA² & DANIEL N. PROUD¹

¹*División Aracnología, Museo Argentino de Ciencias Naturales, CONICET, Av. Ángel Gallardo 470, C1405DJR Buenos Aires, Argentina*

²*Department of Zoology, University of Wisconsin-Madison, Madison, WI 53706, USA*

³*Corresponding author. E-mail: abelaracno@gmail.com*

Abstract

The type specimens of *Fijicolana tuberculata* Roewer, 1963 were re-examined and the male genital morphology is illustrated and described for the first time. Despite the presence of several morphological features that are typical of Samoidae, such as the presence of scopulae on legs III and IV, genital morphology unambiguously indicates that this species belongs to the Zalmoxidae rather than to the Samoidae. *Fijicolana* Roewer, 1963 is newly synonymized with *Zalmoxis* Sørensen, 1886. However, the newly implied combination is preoccupied by *Z. tuberculatus* Goodnight & Goodnight, 1948 thus the replacement name *Zalmoxis roeweri* **nom. nov.** is proposed to avoid secondary homonymy. The definition of *Z. roeweri* **nom. nov.** is amended, and the morphology of this species is compared with other representatives of Zalmoxidae and Samoidae. We conclude that the presence of scopulae alone is not a sufficiently diagnostic characteristic for Samoidae and, therefore, correctly placing taxa into families within Samooidea + Zalmoxoidea requires additional morphological evidence (e.g. genital morphology). In light of this result, we point out that the "scopulated" Australasian samoids *Badessania metatarsalis* Roewer, 1949, *Sawaiellus berlandi* Roewer, 1949 and *Parasamoa gressitti* Goodnight & Goodnight, 1957 require re-examination in order to detect potential errors in their family placement.

Key words: Samoidae, taxonomy, scopula, penis morphology, Fiji, Melanesia

Introduction

In the highly criticized Roewerian system (e.g. Giribet & Kury 2007) the presence of a dense tarsal scopula on legs III and IV is a crucial character to recognize subfamilies (many of them since elevated to families) in Roewer's Phalangodidae concept. In this typological approach the presence of scopulae was used to separate Samoinae from Phalangoninae/Tricommatinae, Ibaloniinae from Podoctinae/Erecananinae and Acrobuniinae from Epedaninae (Roewer 1912). Adhering to this schema until his last published work, Roewer (1963) created one more monotypic genus by describing a new species from the Fiji Islands: *Fijicolana tuberculata* Roewer, 1963. This species exhibits several features typical of Samoidae (see Pérez-González & Kury 2007), such as an incrassate metatarsus III of the male and a remarkably dense tarsal scopula on legs III and IV in both sexes, key characters that led Roewer to place this taxon in the Samoinae. A re-examination of the type series of *F. tuberculata*, and in particular the study of male genital morphology, allowed us to clarify the family placement of this species, provide additional taxonomic characters, and propose nomenclatural changes.

Material and methods

Type specimens of *Fijicolana tuberculata* deposited in the SMF (Senckenberg Naturmuseum und Forschungsinstitut, Frankfurt, Germany) were examined. Other specimens used for morphological comparison are deposited in the MCZ (Museum of Comparative Zoology, Harvard University, Cambridge, USA) and in the INBIO (Instituto Nacional de Biodiversidad de Costa Rica, Santo Domingo, Heredia, Costa Rica).

Photographs of ethanol preserved specimens were taken with a Leica DFC 290 digital camera attached to a Leica M165C stereomicroscope, and different focal planes were combined using Helicon Focus Pro (www.heliconsoft.com). Male genitalia preparation followed Acosta *et al.* (2007), with temporary mounts embedded in glycerol. Male leg III was temporarily mounted and cleared in clove oil. Penis and leg III of the male were drawn using a camera lucida attached to an Olympus BH-2 compound microscope. Genitalia drawings were digitized using Corel Draw X7. Figures were edited using Photoshop CS5 or Corel Draw X7. For SEM preparation the body parts were dehydrated in a series of increasing concentrations of ethanol (85%, 90%, 95%, 100%), and air-dried before being fixed on a stub and sputter-coated. Micrographs for *Badessa ampycooides* were obtained using the protocol described in Gainett *et al.* (2014).

Taxonomy

Zalmoxidae Sørensen, 1886

Zalmoxis Sørensen, 1886

Zalmoxis Sørensen, 1886: 64 [type species: *Zalmoxis robusta* Sørensen, 1886, by subsequent designation in Roewer 1949].
Fijicolana Roewer, 1963: 223 [type species: *Fijicolana tuberculata* Roewer, 1963, by original designation] **syn. nov.**
See the remainder of the extensive synonymy in Sharma *et al.* (2011: 42–43).

Justification of synonymy. Our decision follows the same rationale proposed by Sharma *et al.* (2011), based on evidence from a molecular phylogeny which indicates that the Indo-Pacific Zalmoxidae constitute a monophyletic group (Sharma & Giribet 2012), thus disfavoring monotypic genera that would render *Zalmoxis* para- or polyphyletic. The habitus of *F. tuberculata* is zalmoxid-like, with a pyriform dorsal scutum, and remarkably similar to that of the New Caledonian species *Zalmoxis neocaledonicus* Roewer, 1912 and *Zalmoxis mendax* Sharma, 2012. Additionally, the well-marked bulla, male genital morphology, and enlarged metatarsus III are very similar to other *Zalmoxis* species (see below). The only two morphological features discordant with the most recent diagnosis of *Zalmoxis* (see Sharma *et al.* 2011) are the presence of five tarsomeres on leg IV (rather than six in typical *Zalmoxis* species) and the presence of tarsal scopulae on legs III and IV. Sharma *et al.* (2011) stated that the tarsal formula for *Zalmoxis* is 3: 5–9: 5: 6, however a re-examination of all tarsal formulae described for the species currently placed in *Zalmoxis* shows greater variation in all legs: 3–4: 4–9: 4–5: 5–6 (Table 1). The presence of five tarsomeres on leg IV, supposedly diagnostic for *Fijicolana*, is currently shared by 11 other *Zalmoxis* species (Table 1). Therefore the presence of a scopula remains as the only diagnostic feature of *Fijicolana* that would separate it from other species of *Zalmoxis*. Given that molecular evidence supports the monophyly of *Zalmoxis* in the Pacific Islands, and that scopulae on tarsi III and IV are recurrently observed in unrelated lineages (*e.g.* Ibaloniinae; Kury 2007, Sharma & Giribet 2011), the scopula alone is insufficient to support *F. tuberculata* as belonging to a genus of its own and instead is regarded as a putative autapomorphy of this species.

Zalmoxis roeweri **nom. nov.**

(Figs 1, 2A–C, 3A–E)

Fijicolana tuberculata Roewer, 1963: 223, pl. 18, figs 1–4.

Zalmoxis tuberculatus (Roewer, 1963) **comb. nov.**, by this act becoming a junior secondary homonym of *Zalmoxis tuberculatus* Goodnight & Goodnight, 1948).

Placement. Originally in the Phalangodidae: Samoinae. Here transferred to the Zalmoxidae.

Type material. Male holotype, one male and one female paratypes from MELANESIA, Fiji; SMF 9911155-RII/11155-3; examined. Remark: The paratypes are one male and one female instead of two females as stated by Roewer (1963) in the original description. The male paratype is poorly preserved and has presumably dried up in the past.

TABLE 1. Species of *Zalmoxis* with tarsomere counts that differ from the most common tarsal formula 3: 5–9: 5: 6 (deviations are shown in bold).

Species	I	II	III	IV
<i>Zalmoxis bendis</i> Sharma <i>et al.</i> , 2012	3	6	4–5	5
<i>Zalmoxis brevipes</i> (Roewer, 1949)	3	5	5	5
<i>Zalmoxis crassitarsis</i> Suzuki, 1982	3	6	5	5
<i>Zalmoxis cuspanalis</i> (Roewer, 1927)	3	6	5	5
<i>Zalmoxis dammermani</i> (Roewer, 1927)	3	5	5	5
<i>Zalmoxis derzelas</i> Sharma <i>et al.</i> , 2012	3	6	5	5
<i>Zalmoxis gebeleizis</i> Sharma <i>et al.</i> , 2012	3	6	5	5
<i>Zalmoxis kaktinsae</i> Sharma, 2012	3	4	5	5
<i>Zalmoxis lavacaverna</i> Hunt, 1993	3	5	5	5
<i>Zalmoxis mendax</i> Sharma, 2012	4	7	5	6
<i>Zalmoxis mitobatipes</i> (Roewer, 1926)	3	6	5	5
<i>Zalmoxis roeweri</i> nom. nov.	3	7	5	5
<i>Zalmoxis similis</i> Suzuki, 1982	3	6	5	5

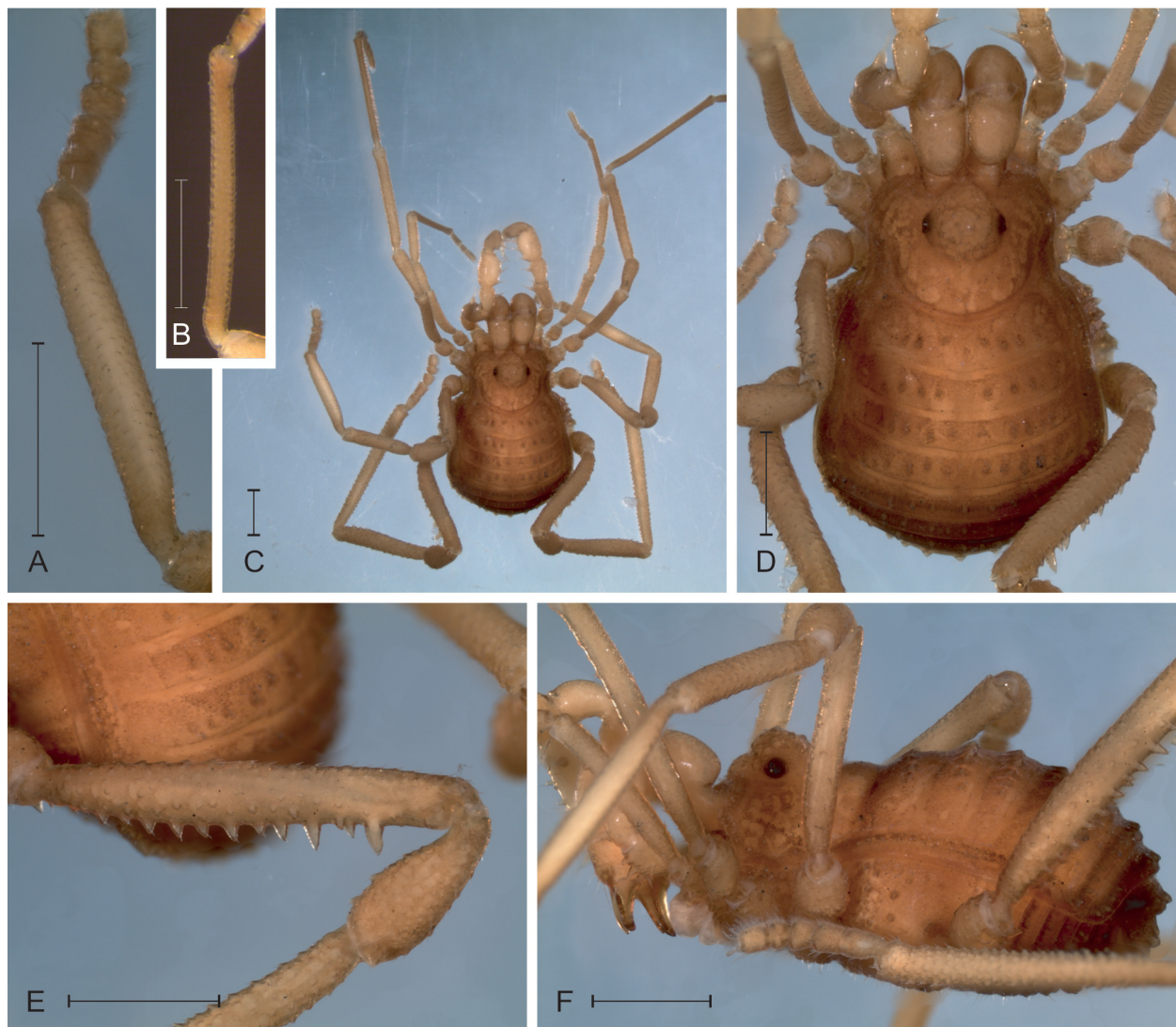


FIGURE 1. *Zalmoxis roeweri* **nom. nov.** (previously *Fijicolana tuberculata* Roewer, 1963), male holotype (A, C–F), female paratype (B). (A) left metatarsus and tarsus III, lateral view. (B) left metatarsus III, lateral view (C–D) habitus, dorsal view. (E) left femur and patella IV, lateral view. (F) habitus, lateral view. Scale bars 1 mm.

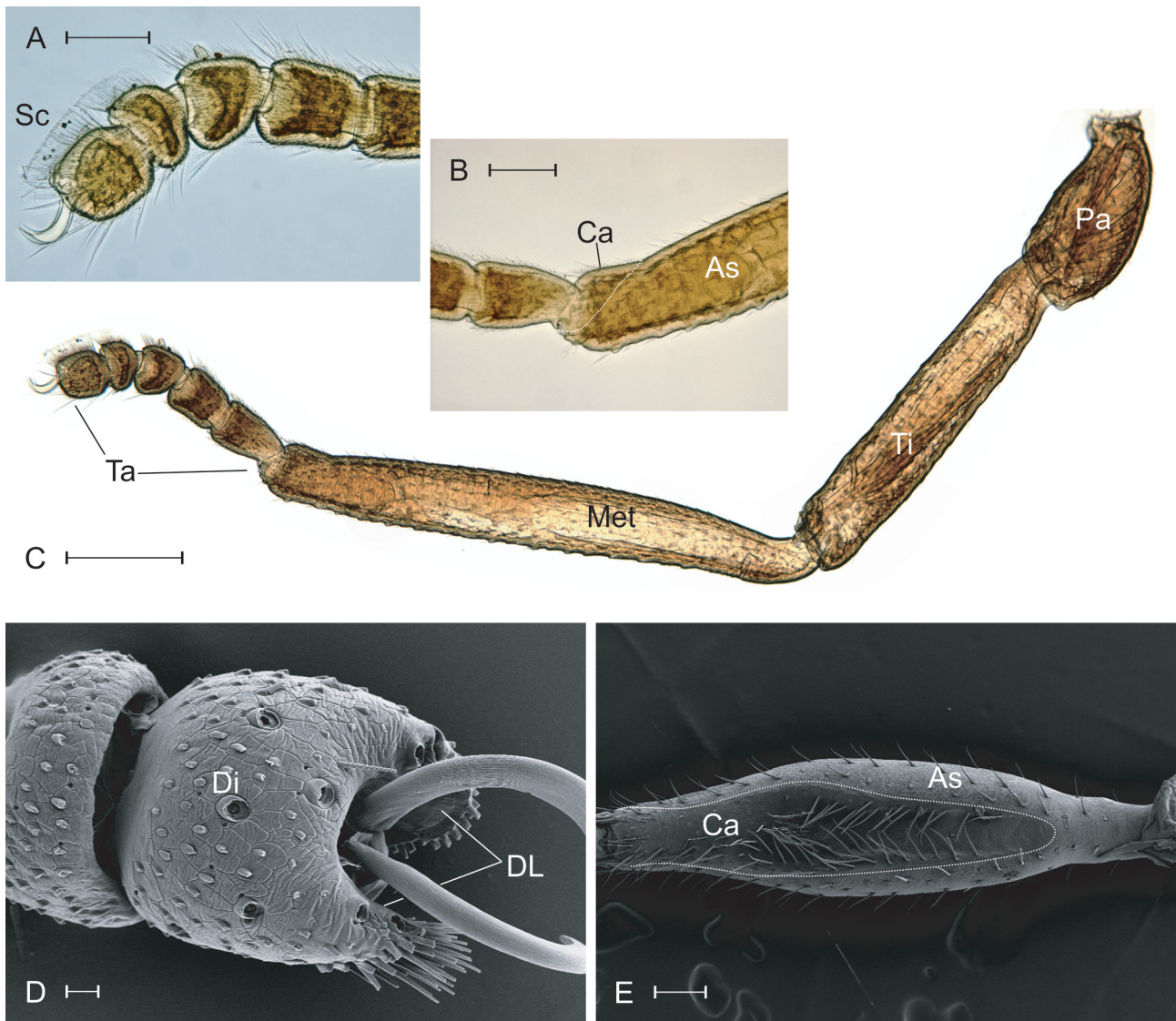


FIGURE 2. (A–C) *Zalmoxis roeweri* **nom. nov.** (previously *Fijicolana tuberculata* Roewer, 1963), male paratype. (D–E) *Badessa ampycooides* Sørensen, 1886 (Samoidae) from Fiji, male; pictures courtesy of Guilherme Gainett and Gonzalo Giribet. (A) left tarsus III, lateral view. (B) distal portion of left metatarsus III, lateral view. (C) patella to tarsus of left leg III, lateral view. (D) distitarsus III, dorsal view, setae removed. (E) metatarsus III, ventral view. Scale bars: A, B: 0.2 mm; C: 0.4 mm; D: 10 μ m; E: 100 μ m. As: astragalus; Ca: calcaneus; Di: distitarsus; DL: distitarsal lobes; Met: metatarsus; Pa: patella; Sc: scopula; Ta: tarsus; Ti: tibia.

Etymology. The new name is a patronym in honor of the German arachnologist Carl Friedrich Roewer who first studied and described this species.

Diagnosis. Distinguished from other *Zalmoxis* species by the presence of a conspicuous, dense scopula on the terminal tarsomere of legs III and IV in both sexes; five tarsomeres on leg IV; metatarsus III of males incrassate; anal operculum unarmed. Additionally, it is distinguished from *Zalmoxis derzelas* Sharma *et al.*, 2012 by larger body size and differences in armature of femur IV and male genital morphology, particularly the very wide rutrum.

Genital morphology. Penis (Figs 3A–E): Pars distalis well-defined, wider than pars basalis. Pergula and rutrum clearly distinguishable. Rutrum very wide, apically shaped like an arrowhead, only slightly wider than base (Fig. 3C). Setae above pergula arranged in three medial ventral pairs and two lateral groups of three. Dorsal-most seta in each lateral group larger than others. One pair of small setae widely separated from each other, situated ventrolaterally below pergula. Capsula externa modified into a massive stragulum, basally fused, with two small dorso-subapical projections. Capsula interna entirely concealed by stragulum (in unexpanded penis), with a long, thin stylus and two rigid, laminar, curved conductors.

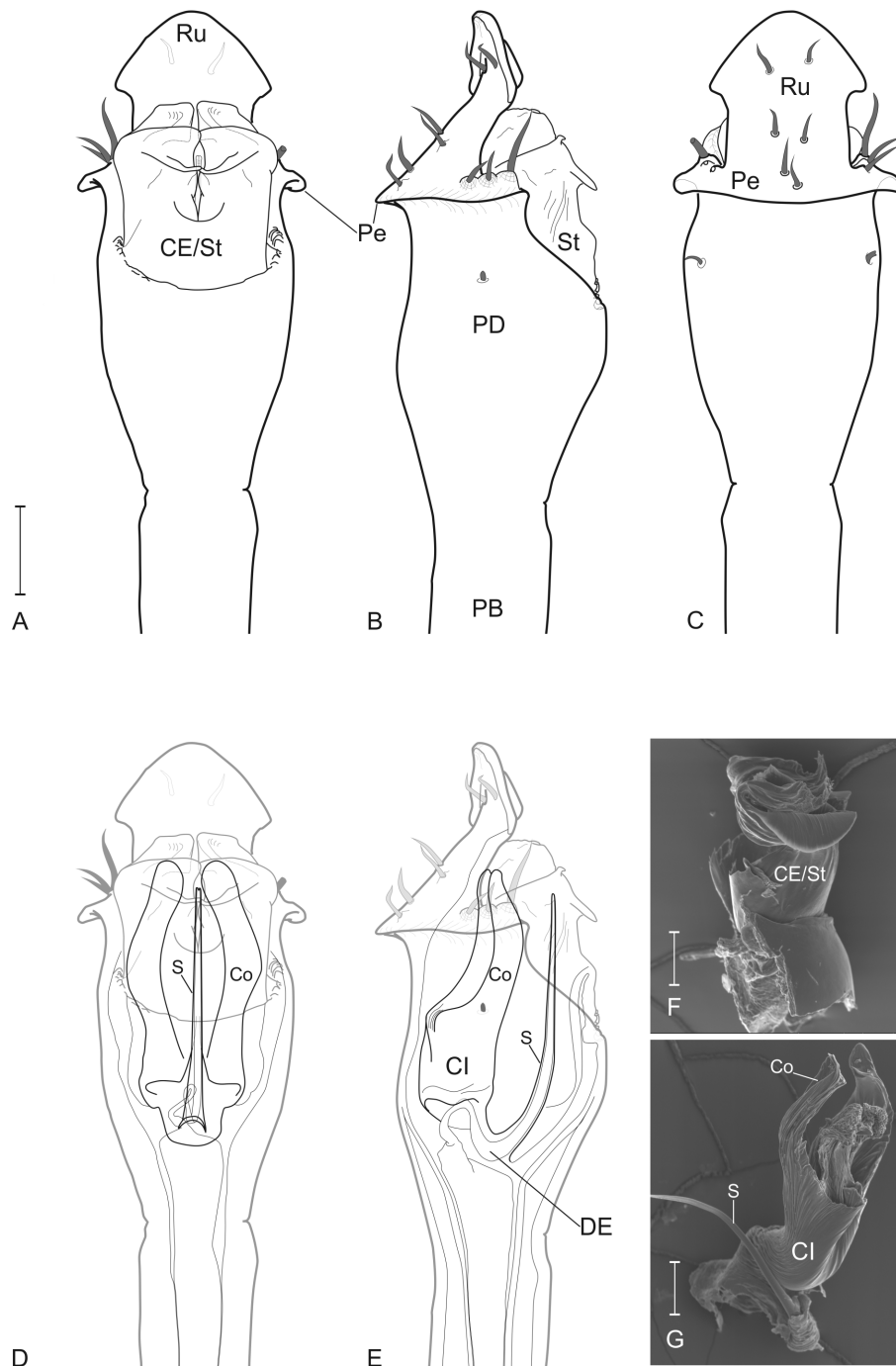


FIGURE 3. (A–E) *Zalmoxis roeweri* **nom. nov.** (previously *Fijicolana tuberculata* Roewer, 1963), penis of male paratype. (F–G) *Ethobunus zalmoxiformis* (Roewer, 1949), SEM micrographs of penis parts. (A) distal portion of penis, dorsal view. (B) same, lateral view. (C) same, ventral view. (D) same, dorsal view, showing internal morphology. (E) same, lateral view, showing internal morphology. (F) capsula externa, lateral view. (G) capsula interna, laterodorsal-apical view. Scale bars: A–E (to same scale): 100 μ m; F, G: 100 μ m. CE: capsula externa; CI: capsula interna; Co: conductor; DE: ductus ejaculatorius; PB: pars basalis; PD: pars distalis; Pe: pergula; Ru: rutrum; S: stylus; St: stragulum.

Discussion

The family Samoidae was erected by Sørensen (1886) to include four species in three genera from the Pacific Islands: *Badessa ampycoides* Sørensen, 1886, *Samoa obscura* Sørensen, 1886, *Samoa variabilis* Sørensen, 1886, and *Feretrius quadrioculatus* (L. Koch, 1865). Sørensen (1886) took great care in defining this group on the basis

of a broader morphological characterization, but he also used the presence of a tarsal scopula on legs III and IV of males as a distinctive characteristic for his new family. A careful review of the literature and an examination of some type specimens (unpublished data) indicate that these four species are closely related, and given that *Samoa* Sørensen, 1886 is the type genus of the family, these taxa represent the typical Samoidae as defined by Pérez-González & Kury (2007). It should be noted, however, that the highest samoid diversity is found in the Neotropics, and the close ties between Neotropical and Australasian samoids is supported by morphological (unpublished data) and molecular phylogenetic evidence (Sharma & Giribet 2011). The disjunct amphi-Pacific distribution of samoids is similar to that of zalmoxids, the latter of which probably arrived in Australasia by transoceanic dispersal out of the Neotropics (Sharma & Giribet 2012).

Decades after Sørensen (1886) there was a resurgence of Laniatores studies, and authors revisited the systematics of the Pacific Island samoids, adding the species: *Badessania metatarsalis* Roewer, 1949, *Sawaiellus berlandi* Roewer, 1949, *Waigeucola palpalis* Roewer, 1949, *F. tuberculata*, *Parasamoa gressitti* Goodnight & Goodnight, 1957 and *Zalmoxista australis* (Sørensen, 1886) (see Roewer 1949 and 1963, Goodnight & Goodnight 1957, Pérez-González & Kury 2007). Although Sørensen, Roewer, C. J. Goodnight and M. L. Goodnight had not recognized genital morphology as an important source of systematic characters, Sørensen was much more meticulous about detailed morphological characteristics that defined the family. The other authors were overly influenced by two features that exhibit extraordinary evolutionary convergence: the tarsal scopula and the incrassate metatarsus III exhibited by males of some species.

The male genitalia unambiguously support the inclusion of *Z. roeweri* **nom. nov.** in the Zalmoxidae. The penis morphology corresponds to the groundplan described for the family (see Kury & Pérez-González 2007) and it is very similar to other Southeast Asian and Australasian species (see Sharma 2012, Sharma *et al.* 2012). The capsula interna morphology is widely unstudied for zalmoxids, despite its potential for providing valuable diagnostic characters. We did not expand the penis of *Z. roeweri* **nom. nov.** due to the scarcity of available specimens (only two males exist in the type series), but we were able to observe the presence of two rigid and curved laminar conductors and of a long, thin stylus (Figs 3D–E). A similar morphology of the capsula interna could be observed in *Ethobunus zalmoxiformis* (Roewer, 1949) from Costa Rica (Volcán Poás National Park, Alajuela Province, 25.x.2004, A. Pérez-González, C. Viquez, J. Mata, R. Gutierrez, INBIO). Nevertheless, the capsula externa is greatly different in both species (Figs 3F–G). The presence of two laminar conductors and of a long and thin stylus is probably shared across the Zalmoxidae, but further studies are needed. Unfortunately, the genital morphology of other Fijian Zalmoxidae [*Zalmoxis insularis* (Roewer, 1949), *Zalmoxis pygmaeus* Sørensen, 1886 and *Zalmoxis robustus* Sørensen, 1886] remains unknown, thus preventing comparisons of *Z. roeweri* **nom. nov.** with the *Zalmoxis* species recorded from the islands of Fiji. External characters such as the well-marked bulla, pyriform body shape, and sexually dimorphic leg IV also support the synonymy of *Fijicolana* with *Zalmoxis*.

Two of the most remarkable (and tricky) morphological features of *Z. roeweri* **nom. nov.** are the incrassate metatarsus III (in males; Fig. 1A cf. Fig. 1B) and the scopulae on legs III and IV (in both sexes; Fig. 2A, C) because they are most commonly exhibited by members of Samooidea. After careful examination we detected that the metatarsus III of *Z. roeweri* **nom. nov.** males is only superficially similar to that of samoid harvestmen (Fig. 2E). The samooidean metatarsus III possesses a long intrusion of the astragalus by the calcaneus on the ventral surface, thus forming a very peculiar structure with glandular pores and modified setae (presumably with a secretory function, see Pérez-González & Kury 2007, Willemart *et al.* 2010; contra Šilhavý 1979 who advocates for a stridulatory function). The "samooidean type" of metatarsus III is present in *B. ampycoides*, a samoid from Fiji (Fig. 2E), but it is absent in *Z. roeweri* **nom. nov.** where the swelling is restricted to the astragalus and where there is no ventral calcaneus intrusion (Fig. 2B). This different kind of incrassate metatarsus III also occurs in other *Zalmoxis* species such as *Z. derzelas*, *Zalmoxis gebeleizis* Sharma *et al.*, 2012, and *Zalmoxis zibelthiurdos* Sharma *et al.*, 2012 (Sharma *et al.* 2012: figs 3e, 7e, 13e).

The scopulae on distitarsi of legs III and IV of *Z. roeweri* **nom. nov.** are dense and very well developed (Fig. 2A), remarkably similar to scopulae observed in samooidean taxa. We were not able to examine the legs under the scanning electron microscope, but under the compound microscope it appears that the scopula is composed of the same kind of apically enlarged setae that are present in several species of Samoidae (see Šilhavý 1979: fig. 3 and unpublished data) as well as in some other distant families (see Pinto-da-Rocha 1997: fig. 587; Rambla 1990). One major difference is present in the form of the apical surface of the distalmost tarsomere. In Samoidae the end of the distalmost tarsomere is ventrolaterally projecting forward, thus forming two lobes on which ventral scopular hairs

are situated basally. These scopulate tarsal lobes extend beyond the base of the claw, forming a deep cavity (see Šilhavý 1979: fig. 2). This kind of distitarsus morphology can be seen in the Fijian samoid *B. ampycoides* (Fig. 2D). In *Z. roeweri* **nom. nov.**, however, the distalmost tarsomere lacks such lobes (Fig. 2A).

Given that the samoid-like characteristics exhibited by *Z. roeweri* **nom. nov.** are only superficially similar to those present in samooidean harvestmen, and that they probably evolved convergently in different lineages, we conclude that the presence of a scopula is not diagnostic for Samoidae and that incrassate leg segments need to be studied and compared in greater detail than before. Additionally, when placing taxa into families belonging to the clade Samooidea + Zalmoxoidea, an examination of their genital morphology is crucial. As the presence of a scopula has been a key characteristic for family assignment in the past, a re-evaluation of poorly described samoids (in particular Australasian species) is needed to eliminate taxonomic misplacements.

We have demonstrated that the placement of species in the Samoidae on the basis of a scopula and of a slightly incrassate metatarsus III in males is problematic. The transfer of *Fijicolana* from the Samoidae to the Zalmoxidae points out only a single instance of taxonomic misplacement by early authors stemming from the highly convergent morphology of these two closely related families. We suspect that other Australasian “samoids” may also belong to the Zalmoxidae or possibly to other families. Although we have not yet examined all type specimens of the other Australasian samoids, our study casts doubt on the placement of the “scopulated” species *Badessania metatarsalis*, *Sawaiellus berlandi* and *Parasamoa gressitti*. The strongly developed basichelicerite with a well-marked bulla illustrated in the original descriptions of these species raises doubts about their current placement in the Samoidae and suggests inclusion in the Zalmoxidae. It will be necessary to carry out a detailed study of the external and genital morphology of these species. The present work, together with the recent transfer of *Waigeucola palpalis* to Podoctidae (Pérez-González 2011), improves our understanding of the systematics of Samoidae, Zalmoxidae and Podoctidae. Interestingly, this work has revealed more about Samoidae than Zalmoxidae, the latter having already been thoroughly examined across the Pacific Islands (Sharma 2012, Sharma & Giribet 2012, Sharma *et al.* 2011, 2012). We have only begun to scratch the surface as the true diversity and biogeography of Australasian Samoidae is largely unknown. Detailed studies of the remaining taxa, as well as an examination of new material collected from this region, will undoubtedly promote species discovery, and elucidate evolutionary histories and biogeographic patterns.

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References

- Acosta, L.E., Pérez-González, A. & Tourinho, A.L. (2007) Methods and techniques of study: Methods for taxonomic study. *In*: Machado, G., Pinto-da-Rocha, R. & Giribet, G. (Eds.), *Harvestmen: the biology of Opiliones*. Harvard University Press, Cambridge, pp. 494–505.
- Gainett, G., Sharma, P.P., Pinto-da-Rocha, R., Giribet, G. & Willemart, R.H. (2014) Walk it off: predictive power of appendicular characters toward inference of higher-level relationships in Laniatores (Arachnida: Opiliones). *Cladistics* 30, 120–138.
<http://dx.doi.org/10.1111/cla.12029>
- Giribet, G. & Kury, A.B. (2007) Phylogeny and biogeography. *In*: Machado, G., Pinto-da-Rocha, R. & Giribet, G. (Eds.), *Harvestmen: the biology of Opiliones*. Harvard University Press, Cambridge, pp. 62–87.
- Goodnight, C.J. & Goodnight, M.L. (1948) New phalangids from the southwest Pacific. *American Museum Novitates*, 1371, 1–14.

- Goodnight, C.J. & Goodnight, M.L. (1957) Opiliones. *Insects of Micronesia*, 3 (2), 71–83.
- Hunt, G.S. (1993) A new cavernicolous harvestman from lava tube caves in tropical Australia (Arachnida: Opiliones: Phalangodidae). *Memoirs of the Queensland Museum*, 33 (1), 217–219.
- Koch, L. (1865) Beschreibung neuer Arachniden und Myriopoden. *Verhandlungen der kaiserlich-königlichen zoologisch-botanischen Gesellschaft in Wien*, 15, 857–892.
- Kury, A.B. (2007) Podoctidae Roewer, 1912. *In*: Pinto-da-Rocha, R., Machado, G. & Giribet, G. (Eds.), *Harvestmen: the biology of Opiliones*. Harvard University Press, Cambridge, pp. 221–224.
- Kury, A.B. & Pérez-González, A. (2007) Zalmoxidae Sørensen, 1886. *In*: Pinto-da-Rocha, R., Machado, G. & Giribet, G. (Eds.), *Harvestmen: the biology of Opiliones*. Harvard University Press, Cambridge, pp. 243–246.
- Pérez-González, A. (2011) New familial assignment for two harvestman species of the infraorder Grassatores (Arachnida: Opiliones: Laniatores). *Zootaxa*, 2757, 24–28.
- Pérez-González, A. & Kury, A.B. (2007) Samoidae Sørensen, 1886. *In*: Pinto-da-Rocha, R., Machado, G. & Giribet, G. (Eds.), *Harvestmen: the biology of Opiliones*. Harvard University Press, Cambridge, pp. 224–226.
- Pinto-da-Rocha, R. (1997) Systematic review of the Neotropical family Stygnidae (Opiliones, Laniatores, Gonyleptoidea). *Arquivos de Zoologia*, 33 (4), 163–342.
<http://dx.doi.org/10.11606/issn.2176-7793.v33i4p163-342>
- Rambla, M. (1990) Les scopula des Opilions, différences avec les scopula des Araignées (Arachnida, Opiliones, Araneae). *In*: Célérier, M.L., Heurtault, J. & Rollard, C. (Eds.), *Comptes rendus du XIIème Colloque européen d'Arachnologie. Bulletin de la Société européenne d'Arachnologie*, 1 (Supplement Volume), 293–298.
- Roewer, C.F. (1912) Die Familien der Assamiiden und Phalangodiden der Opiliones-Laniatores (= Assamiden, Dampetriden, Phalangodiden, Epedaniden, Biantiden, Zalmoxiden, Samoiden, Palpipeden anderer Autoren). *Archiv für Naturgeschichte, Berlin, Abteilung A*, 78 (3), 1–242.
- Roewer, C.F. (1926) Opiliones vom Mount Maquiling auf Luzon Philippinen. *Philippine Journal of Science*, 29 (4), 545–559.
- Roewer, C.F. (1927) Weitere Weberknechte I. *Abhandlungen herausgegeben vom Naturwissenschaftlichen Verein zu Bremen*, 26 (2), 261–402.
- Roewer, C.F. (1949) Über Phalangodiden I. (Subfam. Phalangodinae, Tricommatinae, Samoinae.) Weitere Weberknechte XIII. *Senckenbergiana*, 30 (1/3), 11–61.
- Roewer, C.F. (1963) Über einige Arachniden (Opiliones und Araneae) der orientalischen und australischen Region. *Senckenbergiana Biologica*, 44, 223–230.
- Sharma, P.P. (2012) New Australasian Zalmoxidae (Opiliones: Laniatores) and a new case of male polymorphism in Opiliones. *Zootaxa*, 3236, 1–35.
- Sharma, P.P. & 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.
<http://dx.doi.org/10.1071/IS11002>
- Sharma, P.P. & Giribet, G. (2012) Out of the Neotropics: Late Cretaceous colonization of Australasia by American arthropods. *Proceedings of the Royal Society of London, B: Biological Sciences*, 279, 3501–3509.
<http://dx.doi.org/10.1098/rspb.2012.0675>
- Sharma, P.P., Buenavente, P.A.C., Clouse, R.M., Diesmos, A.C. & Giribet, G. (2012) Forgotten gods: Zalmoxidae of the Philippines and Borneo (Opiliones: Laniatores). *Zootaxa*, 3280, 29–55.
- Sharma, P.P., Kury, A.B. & Giribet, G. (2011) The Zalmoxidae (Arachnida: Opiliones: Laniatores) of the Palearctic: a catalogue of Southeast Asian and Indo-Pacific species. *Zootaxa*, 2972, 37–58.
- Šilhavý, V. (1979) New American representatives of the subfamily Samoinae (Opiliones, Phalangodidae, Arach.). *Annotationes zoologicae et botanicae*, 130, 1–27.
- Sørensen, W.E. (1886) Opiliones. *In*: Koch, L. & Keyserling, E. von (Eds.), *Die Arachniden Australiens nach der Natur beschrieben und abgebildet, vol. [Theil] 2 [of two volumes & atlas, 1871–1889], fascicle [Lieferung] 33*. Bauer & Raspe, Nürnberg, pp. 53–86, pls. 5–6.
- Suzuki, S. (1982) Contributions to the taxonomy and zoogeography of the Opiliones of the Philippines, Bismarck and Solomon Islands. With an appendix on some related species from the Moluccas and Sumatra. *Steenstrupia*, 8 (8), 181–225.
- Willemart, R.H., Pérez-González, A., Farine, J.P. & Gnaspini, P. (2010) Sexually dimorphic tegumental gland openings in Laniatores (Arachnida, Opiliones), with new data on 23 species. *Journal of Morphology*, 271 (6), 641–653.
<http://dx.doi.org/10.1002/jmor.10822>