



Zalmoxidae (Arachnida: Opiliones: Laniatores) of the Paleotropics: a catalogue of Southeast Asian and Indo-Pacific species

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Abstract

A revised catalogue of the Paleotropical Zalmoxidae including images of selected available type specimens is presented. Distribution data are provided to the best of our knowledge. The genera *Acrozalmoxis* Roewer, 1915, *Camanastus* Roewer, 1949, *Papuastus* Roewer, 1949, *Savoa* Roewer, 1949, and *Zalmoxomma* Roewer, 1949 are newly synonymized with the type genus *Zalmoxis* Sørensen, 1886. The following new combinations are established: *Zalmoxis australis*, *Zalmoxis bonka*, *Zalmoxis insularis*, *Zalmoxis maculosus*, *Zalmoxis occidentalis*, and *Zalmoxis ponapeus*. *Bogania* Forster, 1955 and *Bunofagea* Lawrence, 1959 are removed from Zalmoxidae and transferred to Phalangodidae. *Gjellerupia* Roewer, 1913 and *Spalicus* Roewer, 1949 are considered Grassatores *incertae sedis*. The incidence of preoccupied taxon names is redressed by designation of new specific epithets as follows: *Zalmoxis neoguineensis* (Roewer, 1915) is renamed *Zalmoxis thorelli*; *Zalmoxis neoguineensis* (Müller, 1917) is renamed *Zalmoxis muelleri*; *Zalmoxis neoguineensis* (Roewer, 1949) is renamed *Zalmoxis mutus*; and *Zalmoxis minima* (Roewer, 1915) is restored to *Gjellerupia minima*. *Zalmoxis pallicolor* Strand, 1910 is synonymized with *Zalmoxis armatipes* Strand, 1910. Diagnoses of genera are provided. Species richness and familial level relationships of Zalmoxidae are discussed.

Key words: Grassatores, Phalangodidae, Zalmoxoidea, *Zalmoxis*

Introduction

Of the 27 described families of Laniatores (Giribet *et al.* 2010), only two are known to occur throughout Southeast Asia, the Southwest Pacific, and the Mascarene Islands: Podoctidae Roewer, 1912 and Zalmoxidae Sørensen, 1886. A recent investigation of opilionid interfamilial relationships based on sequence data from five molecular markers supported monophyly of Zalmoxidae and its sister relationship to Fissiphalliidae Martens, 1988 (Giribet *et al.* 2010). These results accord with relationships proposed by morphological studies (Kury & Pérez-González 2002). Although interfamilial relationships of Laniatores are not conclusively resolved, there is sufficient morphological and molecular sequence data to support a distant relationship of Podoctidae and Zalmoxidae (Giribet *et al.* 2010; Sharma & Giribet 2009a), suggesting independent colonizations of Southwest Pacific islands by Opiliones.

Comprising approximately 200 species in 70 genera, Zalmoxidae are small (1.5–5 mm) Laniatores that dwell in leaf-litter or caves (Kury & Pérez-González 2007). Originally described on the basis of two species from Fiji, Zalmoxidae are presently known in the Paleotropics from the Indo-Malay Archipelago, the Philippines, New Guinea, Australia, New Caledonia, Fiji, and Micronesia (Starega 1989). They have also been described from Madagascar and the Seychelles, although it is disputed whether these species belong in Zalmoxidae (Kury & Pérez-González 2007).

The taxonomic history of Zalmoxidae and its constituent genera is replete with labyrinthine synonymies and resurrections. Some time after the description of the first "Zalmoxioidae" (Sørensen, 1886), Roewer (1912, 1923) collapsed the family into the system Phalangodidae, which has transiently harbored species of nearly all of the derived Laniatores (the infraorder Grassatores, *sensu* Kury 2003) families at some point or another. In addition,

Roewer proceeded to describe new species in a prolific, but insufficiently detailed, manner, and to place these in newly erected, often monotypic, genera (e.g., Roewer 1949a). Previously described species of *Zalmoxis* Sørensen, 1886 were also transferred to new monotypic genera (Roewer 1949a), including some that Roewer had described himself (e.g., Roewer 1912). Furthermore, Roewer made use of superficial external morphological characters (such as the number of tarsal articles and the armature of the body or appendages) to delineate generic boundaries. However, in their discussion of morphological variation in opilionids, Goodnight & Goodnight (1953) demonstrated the limited utility of characters pertaining to (1) dorsal spination, (2) leg spination, (3) tarsal formula, and (4) ocularial armature, for taxonomic purposes, with empirical examples from Laniatores species. The demonstrable variation in the characters utilized to delineate Roewerian genera discourages the retention of Roewer's generic nomenclature.

Some of Roewer's oversights were corrected by synonymy of numerous, frequently monotypic, genera with *Zalmoxis* (Goodnight & Goodnight 1957). However, this system, rapidly adopted by subsequent authors (e.g., Suzuki 1977), led to the generation of multiple preoccupied taxon names, which subsequently went uncorrected. For example, there are at present three distinct species named "*Zalmoxis neoguinensis*" and another two "*Zalmoxis minima*."

Zalmoxids remained in the subfamily Phalangodinae with unrelated taxa until the resurrection of Zalmoxidae by Staręga (1989) (Staręga used the simpler, more euphonious name with its stem based on the type genus, which accords with ICZN guidelines; Sørensen's "Zalmoxioidae" was lost in the process). In the course of the resurrection, Staręga (1989) limited Zalmoxidae to five Paleotropical genera (formerly in Phalangodinae), and designated numerous other phalangodine genera as *incertae sedis*. He later added three Mascarene Island genera to Zalmoxidae (Staręga 1992). Staręga (1989, 1992) also excluded all Neotropical genera from Zalmoxidae, but this convention was not followed (Kury, 2003). In a catalogue of the Neotropical Laniatores, Kury (2003) included a large number of formerly phalangodid species in Zalmoxidae, based largely on external characters easily recognizable without dissection (typically the extent of information available in the literature), but also on genital morphology for better studied taxa. The newly defined Zalmoxidae is characterized by the presence of a rutrum and a pergula (Kury & Pérez-González, 2007)—two structures of the divided lamina ventralis in the male genitalia—and a well developed capsula externa, called a stragulum (the shape of the stragulum is significant; an enlarged finger-like stragulum is a synapomorphic character of Fissiphalliidae Martens, 1988, the sister family of Zalmoxidae) (Kury & Pérez-González 2002). Nevertheless, similar taxonomic confusion persists among the Neotropical genera (Kury & Pérez-González 2007), resulting in numerous pending synonymies of genera and species, inclusions in Zalmoxidae, and removals from Zalmoxidae. The revision of Neotropical Zalmoxidae is part of an ongoing effort to catalog the diversity of Opiliones worldwide (Kury, work in progress). By comparison, Paleotropical Zalmoxidae have received far less taxonomic attention.

In order to begin redressing these numerous taxonomic anomalies and to synthesize a quinquilingual body of frequently obscure literature, we present a revised catalogue of the Paleotropical Zalmoxidae, including locality information and images of selected available type specimens. We largely follow the system of synonymies established by Goodnight & Goodnight (1957), correcting for preoccupation of taxon names resulting from their efforts. The present work is a requisite first step toward continued taxonomic progress and knowledge of Zalmoxidae systematics and biogeography (Sharma, work in progress).

Methods

The holotype and/or paratype specimens of selected described species were photographed using a JVC KY-F70B digital camera mounted on a Leica MZ 12.5 stereomicroscope. A series of images (from 10 to 15) was taken at different focal planes and assembled with the dedicated software package Auto-Montage Pro Version 5.00.0271 by Syncroscopy. Each specimen was photographed in dorsal view.

Locality records were compiled for all species from the taxonomic literature. Type localities are indicated by asterisks. Additional locality information, typically reflecting geopolitical changes since the original collections, or interpolated first order administrative divisions, is indicated by brackets.

Repository institutions: AMNH (American Museum of Natural History, New York), MCZ (Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA).

Taxonomy

Order Opiliones Sundevall, 1833

Suborder Laniatores Thorell, 1876

Infraorder Grassatores Kury in Giribet *et al.*, 2002

Family uncertain (Genera *incertae sedis*)

Genus *Gjellerupia* Roewer, 1913

Gjellerupia Roewer, 1913b, p. 158; 1915, p. 20; 1923, p. 107; Starega, 1989, p. 5.

Gjellerupiola [partim.]: Roewer, 1949a, p. 29.

Zalmoxis [partim.]: Goodnight & Goodnight, 1957, p. 81.

Type species. *Gjellerupia neoguineensis* Roewer, 1913, by monotypy.

Gender. Feminine.

Diagnosis. Ocularium wider than long, well displaced from anterior margin of carapace, finely granulated. Closely spaced pair of small spines under the eyes. Scutum with five clear, parallel sulci, not connected by a median longitudinal sulcus. Posterior scutum and free tergites armed with small spines. Spiracles visible. Proximal segment of chelicera with prominent bulla. Tarsal formula 3–4: 7–10: 5–7: 6–8.

Remarks. The large number of tarsal articles of these species as well as their general appearance supports placement outside Zalmoxidae, but tarsal formula has received criticism as an arbiter in systematics (Goodnight & Goodnight, 1953). While we suspect that *Gjellerupia* may be true Zalmoxidae, the brightline for inclusion in the family is the presence of the rutrum and the pergula (Kury & Pérez-González, 2007), and the genitalic morphology of these species is not known. One image of a zalmoxid penis ascribed to a *Gjellerupia* does appear in publication (Kury & Pérez-González, 2007), but this image was taken by one of the authors (A.B.K.; 1994) who later suspected the validity of the identification (it may have been a *Zalmoxis*). For the present, we maintain *Gjellerupia* as *incertae sedis* and endeavor to undertake investigation of its placement in future study.

Gjellerupia minima Roewer, 1915, restored combination

Gjellerupia minima Roewer, 1915, p. 20–21, fig. 10; 1923, p. 107–109, fig. 108–109; 1949a, p. 29.

Gjellerupiola minima: Roewer, 1949a, p. 29, fig. 43.

Zalmoxis minima: Goodnight & Goodnight, 1957, p. 81–83 [junior secondary homonym of *Zalmoxis minimus* Roewer, 1912].

Record. *Wilhelmshafen [Madang, Papua New Guinea].

Remarks. This species was originally described from a single male holotype specimen by Roewer (1915) as having a tarsal formula of 4: 7: ? : 7. Subsequently, Roewer made this species the type of the new genus *Gjellerupiola* (Roewer, 1949a), and changed the counts of the tarsalia to 3: >6: 5: 6. It is the interpretation of the authors that Roewer attempted to correct an error in the original description (Roewer, 1915; reiterated by Roewer, 1923), but did so by erecting a new monotypic genus without justification. Goodnight & Goodnight (1957) later synonymized *Gjellerupiola* with *Zalmoxis*, but neglected to designate a new specific epithet (the validity of the earlier described *Zalmoxis minima* Roewer, 1912 resulted in a preoccupation), resulting in two species with the name "*Zalmoxis minima*." We observe that this species and *Gjellerupia neoguineensis* Roewer, 1913 have similar habitus, armature and shape, suggesting that they are congeners. Consequently, we correct the homonymy by restoring *Gjellerupia minima* Roewer, 1915.

Gjellerupia neoguineensis Roewer, 1913

Gjellerupia neoguineensis Roewer, 1913b, p. 159–161; 1923, p. 108, fig. 108.

Record. *Sermowai River, elevation 400 m, near Walckenaer Bay [West Papua, Indonesia] in forest, collected 3–4 April, 1911 by K. Gjellerup.

Genus *Spalicus* Roewer, 1949

Spalicus Roewer, 1949a, p. 22; Staręga, 1989, p. 5.

Gender. Masculine.

Type species. *Spalicus oeditarsus* Roewer, 1949, by monotypy.

Diagnosis. Ocularium wider than long, unarmed, and displaced from the anterior margin of the carapace. First two transverse sulci not parallel and not connected through a median longitudinal sulcus; second transverse sulcus strongly angled posteriorly in the middle. Scutal areas 1–5, free tergites, and anal operculum unarmed. Spiracles visible. Proximal segment of chelicer without a prominent bulla. Tarsal formula 3: 7: 6: 6. Distitarsus I with two articles, distitarsus II with three articles. Male genitalia unknown.

Remarks. Originally in Phalangodidae, the general appearance of this species suggests that it could be related to Zalmoxidae, barring the absence of the bulla. Similarly, Staręga (1989) considered the placement of this genus to be obscure. It is possible that *Spalicus* is related to *Bogania*, but neither hypothesis can be tested without examining the genitalia of this species.

Spalicus oeditarsus Roewer, 1949

Spalicus oeditarsus Roewer, 1949a, p. 22–24, fig. 26 (pl. 4).

Record. *Blue Mountains [New South Wales, Australia].

Family Phalangodidae Simon, 1879

Genus *Bogania* Forster, 1955

Bogania Forster, 1955, p. 375; Staręga 1989, p. 4.

Type species. *Bogania granulata* Forster, 1955, by monotypy.

Gender. Feminine.

Diagnosis. Carapace shorter than tergal region, scutum and ocularium granulate. Ocularium removed from anterior margin of carapace. Genital operculum of male large, subtriangular, and extending anteriorly to coxae II; not enlarged in females. Legs unarmed; tarsal formula 3: 5–6: 5: 6. Male genitalia long, slender; ventral plate defined only as a distal setigerous portion of truncus; with numerous small setae and terminating in sharp or blunt process; stragulum long and tubular, stylus flagelliform and needlelike, parastylar lobe prominent; no rutrum and no pergula.

Remarks. Originally in Phalangodinae, transferred to Zalmoxidae by Staręga (1989). The absence of a rutrum and pergula, which are the defining synapomorphies for Zalmoxidae + Fissiphalliidae, indicates that *Bogania* should be removed from the former. *Bogania* should be considered as a member of Phalangodidae **new familial assignment**, based on the close similarities between the genitalic structures of *Bogania* species and true phalangodids (Cantrell, 1980).

Bogania advena Cantrell, 1980

Bogania advena Cantrell, 1980, p. 252–253, figs. 29, 33, 37.

Record. *Bulburin State Forest, Queensland, Australia, collected 1–3 April, 1972, by G.B. Monteith.

***Bogania distincta* Cantrell, 1980**

Bogania distincta Cantrell, 1980, p. 249–251, figs. 27, 31, 35.

Record. *Bunya Mountains, Queensland, Australia, collected 11–12 February, 1967, by B.K. Cantrell.

***Bogania exigua* Cantrell, 1980**

Bogania exigua Cantrell, 1980, p. 251–252, figs. 28, 32, 36.

Record. *Kenilworth State Forest, Queensland, Australia, collected 1 April, 1969, by B.K. Cantrell; Jimna State Forest, collected 5 April, 1969, by B.K. Cantrell.

***Bogania granulata* Forster, 1955**

Bogania granulata Forster, 1955, p. 375–377, figs. 40–45; Cantrell, 1980, p. 247–248.

Record. *Bogan River, New South Wales, Australia, collected August 1952 by J.W.T. Armstrong.

***Bogania neogranulata* Cantrell, 1980**

Bogania neogranulata Cantrell, 1980, p. 248–249, figs. 26, 30, 34.

Record. *The Knoll, Mt. Tamborine, Queensland, Australia, collected 11 August, 1969, by B.K. Cantrell.

Genus *Bunofagea* Staręga, 1992

Bunofagea Lawrence, 1959, p.: 82–83; Staręga, 1989, p. 5 [unavailable name, ICZN 13.3]; Staręga, 1992, p. 295.
Bunofagea Staręga, 1992: 295.

Type species. *Bunofagea gracilipes* Lawrence, 1959, by original designation.

Gender. Feminine.

Diagnosis. Ocularium placed toward the anterior margin of the carapace. Proximal segment of chelicers with shallow bulla. Legs unarmed, with leg II much longer than leg IV and three times the length of the body; tarsal formula 3: 4: 5: 6. Distitarsus I with two articles, distitarsus II with three articles. Male genitalia long, slender; ventral plate defined only as a distal tapering setigerous portion of truncus; with 4 pairs of lateral and two pair of ventrodistal small acuminate setae and one very large foliaceous seta; stragulum long and tubular, with two pairs of square terminal processes, stylus flagelliform and needlelike; no rutrum and no pergula.

Remarks. Originally in Phalangodinae, transferred to Zalmoxidae by Staręga (1992). The general appearance of this genus suggests a distant relationship to Zalmoxidae. The penis of a paratype of *Bunofagea gracilipes* has been dissected and examined by us, and it includes structures characteristic of Phalangodidae (Fig. 2); we therefore consider *Bunofagea* to be a member of Phalangodidae **new familial assignment**. Furthermore, the related monotypic Madagascan genus *Remyus* Roewer, 1949 has been included in a molecular phylogeny and subsequently transferred to Phalangodidae (Sharma & Giribet, in press), suggesting a similar placement for *Bunofagea*.

***Bunofagea gracilipes* Lawrence, 1959**

Bunofagea gracilipes Lawrence, 1959, p. 82–85, fig. 25; Staręga, 1992, p. 295.

Record. *Behara, forêt de Bevia, south Madagascar, collected August 1948 by J. Millot.

***Bunofagea remyi* Lawrence, 1959**

Bunofagea remyi Lawrence, 1959, p. 85–86, fig. 28; Staręga, 1992, p. 295.

Record. *Ambatofinandrahana, central Madagascar, collected August 1948 by J. Millot.

Family Zalmoxidae Sørensen, 1886

Zalmoxioidae Sørensen, 1886, p. 63.

Epedanidae [partim]: Loman, 1902, p. 197.

Phalangodidae [partim]: Roewer, 1912, p. 101; 1923, p. 64; Mello-Leitão, 1938, p. 136; Goodnight & Goodnight, 1943, p. 1; 1947, p. 328; 1948, p. 1; 1957, p. 81; 1983, p. 202; Šilhavý, 1979, p. 60; González-Sponga, 1987, p. 45; Suzuki, 1941, p. 98; 1969, p. 16; 1977, p. 12; 1982, p. 16; 1985, p. 261.

Gonyleptidae [partim]: Juberthie, 1970, p. 140.

Gonyleptidae Stygnoleptinae H. Soares, 1972, p. 68; Dumitrescu, p. 1976, 18; Kury, 1997, p. 2 [junior subjective synonym of Zalmoxidae Sørensen, 1886, by Kury (1997)].

Zalmoxidae Staręga, 1989, p. 4–5; 1992, p. 295; Kury & Cokendolpher, 2000, p. 142; Kury, 2003, p. 5–6, 14, 240–253, 262–263; Kury & Pérez-González, 2007, p. 243–246.

Type genus. *Zalmoxis* Sørensen, 1886.

Genus *Metazalmoxis* Roewer, 1912

Metazalmoxis Roewer, 1912, p. 135; Roewer, 1923, p. 93; Rambla, 1983, p. 11; Staręga, 1989, p. 5; 1992, p. 295.

Type species. *Metazalmoxis ferrugineus* Roewer 1912, by monotypy.

Gender. Masculine (see remarks). Specific name is accordingly emended.

Diagnosis. Scutum narrowed from the first transverse sulcus. Five transverse sulci, the first orthogonal to the longitudinal axis, the second through fifth bent into angles. Scutal areas unarmed, but with small spine on anal operculum. Coxa IV twice as wide as other coxae. Spiracles small and barely visible. Chelicers robust, with prominent bulla on proximal segment. Pedipalpal segments robust and armed. Legs robust, femur of male leg IV strongly arcuate, tibia of leg IV mostly clavate and spined. Tarsal formula 4: 8: 5: 5. Distitarsus II with three articles. Male genitalia with setose rutrum bearing two small lateral extensions; basally dilated below the pergula.

Remarks. Originally in Phalangodinae, transferred to Zalmoxidae by Staręga (1992). The name is derived from the prefix "meta-" and the preexisting genus *Zalmoxis*. In spite of the feminine form assumed by Roewer (1912), the correct gender should be masculine (see remarks under genus *Zalmoxis*).

***Metazalmoxis ferrugineus* Roewer, 1912**

Metazalmoxis ferruginea Roewer, 1912, p. 135, fig. 32; 1923, 93–94, fig. 91; Rambla, 1983, p. 11–15, fig. 1; Staręga, 1992, p. 295.

Record. *Seychelles Islands (specific locality unknown).

Genus *Zalmoxis* Sørensen, 1886

Zalmoxis Sørensen, 1886, p. 64; Thorell, 1891, p. 82–83; Roewer, 1912, p. 126–127; Müller, 1917, p. 253–254; Roewer, 1923, p. 85; Goodnight & Goodnight, 1957, p. 81; Suzuki, 1977, p. 12; Staręga, 1989, p. 4.

Chondrobunus Loman, 1902, p. 207 [junior subjective synonym of *Zalmoxis* Sørensen, 1886 by Roewer (1912); type species: *Chondrobunus granulatus* Loman, 1902, by monotypy].

Euzalmoxis Roewer, 1915, p. 15 [junior subjective synonym of *Zalmoxis* Sørensen, 1886 by Goodnight & Goodnight (1957); type species: *Euzalmoxis neoguineensis* Roewer, 1915, by monotypy].

Hoplozalmoxis Roewer, 1915, p. 18 [junior subjective synonym of *Zalmoxis* Sørensen, 1886 by Goodnight & Goodnight (1957); type species: *Hoplozalmoxis pallida* Roewer, 1915, by monotypy].

Acrozalmoxis Roewer, 1915, p. 16 [type species: *Acrozalmoxis neoguineensis* Roewer, 1915, by monotypy]. **New synonymy.**

Parazalmoxida Roewer, 1917, p. 93 [junior subjective synonym of *Zalmoxis* Sørensen, 1886 by Goodnight & Goodnight (1957); type species: *Parazalmoxida solitaria* Roewer, 1917, by monotypy].

Gjellerupia [partim.]: Roewer, 1915, 109 [junior subjective synonym of *Zalmoxis* Sørensen, 1886 by Goodnight & Goodnight (1957); type species: *Gjellerupia neoguineensis* Roewer, 1913, by monotypy].

Zalmoxilla Roewer, 1926, p. 546 [junior subjective synonym of *Zalmoxis* Sørensen, 1886 by Goodnight & Goodnight (1957); type species: *Zalmoxilla mitobatipes* Roewer, 1926, by monotypy].

Zalmoxana Roewer, 1927, p. 294 [junior subjective synonym of *Zalmoxis* Sørensen, 1886 by Goodnight & Goodnight (1957); type species: *Zalmoxana dammermani* Roewer, 1927, by monotypy].

Metagjellerupia Goodnight & Goodnight, 1947, p. 328 [junior subjective synonym of *Zalmoxis* Sørensen, 1886 by Goodnight & Goodnight (1957); type species: *Metagjellerupia jewetti* Goodnight & Goodnight, 1947, by original designation].

Foella Goodnight & Goodnight, 1948, p. 1 [junior subjective synonym of *Zalmoxis* Sørensen, 1886 by Goodnight & Goodnight (1957); type species *Foella remingtoni* Goodnight & Goodnight, 1948, by original designation].

Camanastus Roewer, 1949a, p. 20. [type species: *Camanastus insularis* Roewer, 1949, by original designation.] **New synonymy.**

Zalmoxomma Roewer, 1949a, p. 25 [type species: *Zalmoxomma occidentalis* Roewer, 1949, by original designation]; Starega, 1989, p. 4; 1992, 295. **New synonymy.**

Papuastus Roewer, 1949a, p. 26; Starega, 1989, p. 4 [type species: *Papuastus maculosus* Roewer, 1949, by original designation]. **New synonymy.**

Pygozalmoxis Roewer, 1949a, p. 28 [junior subjective synonym of *Zalmoxis* Sørensen, 1886 by Goodnight & Goodnight (1957); type species: *Zalmoxis neocaledonica* Roewer, 1912, by original designation].

Gagirius Roewer, 1949a, p. 28 [junior subjective synonym of *Zalmoxis* Sørensen, 1886 by Goodnight & Goodnight (1957); type species: *Gagirius neoguineensis* Roewer, 1949, by original designation].

Sepikusta Roewer, 1949a, p. 29 [junior subjective synonym of *Zalmoxis* Sørensen, 1886 by Goodnight & Goodnight (1957); type species: *Sepikusta armata* Roewer, 1949a, by original designation].

Linabia Roewer, 1949a, p. 29 [junior subjective synonym of *Zalmoxis* Sørensen, 1886 by Goodnight & Goodnight (1957); type species: *Zalmoxis armatipes* Strand, 1910, by original designation].

Gjellerupiola [partim.] Roewer, 1949a, p. 29 [junior subjective synonym of *Zalmoxis* Sørensen, 1886 by Goodnight & Goodnight (1957); type species: *Gjellerupiola minima* Roewer, 1949, by monotypy].

Papuodes Roewer, 1949a, p. 29 [junior subjective synonym of *Zalmoxis* Sørensen, 1886 by Goodnight & Goodnight (1957); type species: *Papuodes convexus* Roewer, 1949a, by original designation].

Savoa Forster, 1949, p. 144 [type species: *Savoa bonka* Forster, 1949, by original designation]. **New synonymy.**

Zalmoxista [partim.]: Roewer, 1949b, p. 143–144 [type species: *Zalmoxis australis* Sørensen, 1886, by original designation]. **New synonymy.**

Type species. *Zalmoxis robustus* Sørensen, 1886, by subsequent designation: Roewer (1949a: 20).

Gender. Masculine (see remarks). All specific names are accordingly emended. The names *bonka*, *insula*, *lavacaverna* and *spinicoxa* are unaltered because they are nouns in apposition.

Diagnosis. Ocularium wider than long, unarmed or tuberculate. First scutal area large, without a dividing transverse furrow. Transverse sulci distinct; first orthogonal to longitudinal axis, others angular and anteriorly concave ("V"-shaped), with exceptions. Free tergites and anal plate variably armed with spines or tubercles. Spiracles typically visible. Coxae IV larger than coxae III. Pedipalpal segments robust and spined. Tarsal formula 3, 5–9, 5, 6. Distitarsus I with two articles, distitarsus II with three articles. Male genitalia comprising a stragulum overlying the stylus. Lamina ventralis divided into distal rutrum and basal pergula, both variably bearing setae; stragulum articulated to truncus like a jackknife. Sexual dimorphism typical, but variable; male leg IV usually arcuate and with stouter spines, especially on femur IV, tibia IV and/or opisthosomal segments.

Remarks. Sørensen (1886) described the genus *Zalmoxis* to include two new species. *Z. robusta* Sørensen, 1886 and *Z. pygmaea* Sørensen, 1886. He did not choose a type species, which was acceptable before 1931, and treated the genus as feminine. Subsequently, Hirst (1912) described *Zalmoxis austerus*, treating the genus as masculine; Roewer (1912) treated *Zalmoxis* as feminine. The origin of the name is the Greek Ζάλμοξις, a Thracian male divinity. ICZN article 30.1.2. states that "a genus-group name that is or ends in a Greek word transliterated into Latin without other changes takes the gender given for that word in standard Greek dictionaries". Therefore, in

spite of the feminine form assumed by Sørensen, the correct gender should be masculine, and we follow this hereafter.

***Zalmoxis armatus* (Roewer, 1949)**

Sepikusta armata Roewer, 1949a, p. 29.

Zalmoxis armata: Goodnight & Goodnight, 1957, p. 81–83.

Record. *Sepik, New Guinea [East Sepik, Papua New Guinea].

***Zalmoxis armatipes* Strand, 1910**

Zalmoxis armatipes Strand, 1910, p. 6–7; Goodnight & Goodnight, 1957, p. 81–83.

Zalmoxis pallicolor: Strand, 1910, p. 7; Roewer, 1912, p. 129. **New synonymy.**

Gjellerupia armatipes: Roewer 1923, 109.

Gjellerupia pallicolor: Roewer, 1923, 109.

Linabia armatipes: Roewer, 1949a, 29.

Record. *Torricelli Range, elevation 690 m, New Guinea [Sandaun, Papua New Guinea].

Remarks. Strand (1910) informally suggested a species called *Zalmoxis pallicolor* Strand, 1910 from the same locality as the holotype of *Z. armatipes* Strand, 1910. His suggestion was informal and uncertain because he believed the holotype of *Z. pallicolor* Strand, 1910 could have been a juvenile of *Z. armatipes* Strand, 1910. *Z. pallicolor* Strand, 1910 was only distinguishable from *Z. armatipes* Strand, 1910 by its smaller size, pale gray color, less pronounced armature, and minor differences in the widths of the opisthosomal segments, all of which are in accordance with a juvenile (the grayish color is especially distinctive in specimens that have undergone recent molts; Townsend *et al.* 2009). Roewer (1912, 1923) also expressed uncertainty about the validity of *Z. pallicolor*, but maintained it and eventually transferred the two species to separate genera without justification. On the basis of the original descriptions, observations of juvenile stages in Zalmoxidae, and recent studies of postembryonic development in Laniatores, we consider the type of *Z. pallicolor* Strand, 1910 to be a juvenile specimen of *Z. armatipes* Strand, 1910.

***Zalmoxis aspersus* Roewer, 1949**

Zalmoxis aspersa Roewer, 1949a, p. 20, fig. 22a–e (pl. 3).

Record. *Milgrave Island [Mulgrave or Badu Island, Torres Strait, Queensland, Australia].

***Zalmoxis austerus* Hirst, 1912**

Zalmoxis austerus Hirst, 1912, p. 65–66, figs. 1, 1a (pl. 1); Müller 1917, p. 254–256, figs. 1–4.

Zalmoxis austera [emended]: Roewer, 1923, p. 89–90, fig. 86; Staręga, 1989, p. 2, figs. 5–6.

Records. *New Britain, Bismarck Archipelago [Papua New Guinea]; Sattelberg, Wilhelmshafen, New Guinea [Madang, Papua New Guinea].

Remarks. The male genitalia of this species underlaid the resurrection and redescription of Zalmoxidae *sensu* Staręga. The penis of this species became the standard for Zalmoxidae; specifically, with a lamina ventralis divided into the characteristic rutrum and pergula.

***Zalmoxis australis* (Roewer, 1949) new combination**

Camanastus australis Roewer, 1949a, p. 20, fig. 21a–d (pl. 3).

Record. *Hatzfeldhafen, [Madang, Papua New Guinea].

Remarks. Originally in Phalangodidae, **new familial assignment.** The dimensions of the bulla are not sufficient to distinguish *Camanastus* from *Zalmoxis*, and it closely resembles *Zalmoxis* in every other respect. Preliminary molecular sequence data of Paleotropical Zalmoxidae suggest that *Camanastus* is nested within *Zalmoxis*, which would render *Zalmoxis* paraphyletic (Sharma & Giribet, unpublished results). We therefore synonymize *Camanastus* with *Zalmoxis*.

***Zalmoxis bonka* (Forster, 1949) new combination**

Savoa bonka Forster, 1949, p. 145–146, figs. 10–16.

Record. *Savo Island (Solomon Islands), collected under dead branches and coconut fronds in coastal forest.

Remarks. Forster (1949) erected the monotypic genus *Savoa* on the basis of (1) the unarmed dorsal scutum (thereby distinct from *Acrozalmoxis*), and (2) the ocularial spine (thereby distinct from *Zalmoxis*). However, a number of *Zalmoxis* species have been described with ocularial spines. Furthermore, *Zalmoxis* otherwise ascribable to "Savoa" have been collected from the vicinity of the Solomon Islands that lack the ocularial spine. We therefore synonymize *Savoa* with *Zalmoxis*.

***Zalmoxis brevipes* (Roewer, 1949)**

Zalmoxana brevipes Roewer, 1949a, p. 16, fig. 11a–d (pl. 2).

Zalmoxis brevipes: Goodnight & Goodnight, 1957, p. 81–83.

Record. *Finschhafen, New Guinea [Morobe, Papua New Guinea].

***Zalmoxis cardwellensis* Forster, 1955**

(Figure 1a)

Zalmoxis cardwellensis Forster, 1955, p. 371–373, figs. 33–36.

Record. *Cardwell Range, north Queensland, Australia, from leaf-mold, collected 2 June, 1953 by T.E. Woodward.

***Zalmoxis cheesmani* (Roewer, 1949)**

Linabia cheesmani Roewer, 1949a, p. 29, fig. 42a–d (pl. 6).

Zalmoxis cheesmani: Goodnight & Goodnight, 1957, p. 81–83.

Record. *Mount Lina, New Guinea [Cyclops Mountains, West Papua, Indonesia].

***Zalmoxis convexus* (Roewer, 1949)**

Papuodes convexus Roewer, 1949a, p. 30, fig. 44a–d (pl. 6).

Zalmoxis convexus: Goodnight & Goodnight, 1957, p. 81–83.

Record. *Astrolabe-Bai, New Guinea [Astrolabe Bay, Madang, Papua New Guinea].

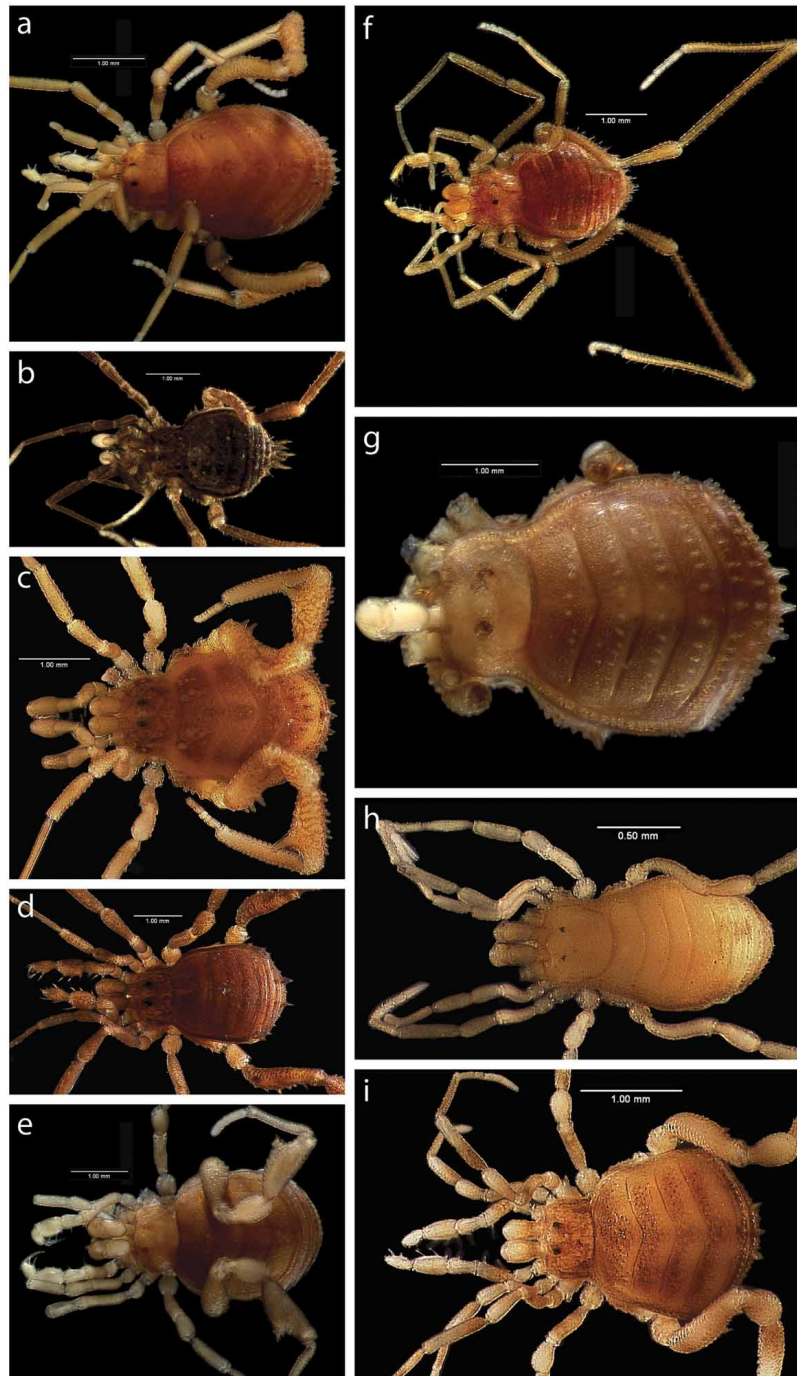


FIGURE 1. *Zalmoxis* Sørensen, 1886, (a) *Zalmoxis cardwellensis* Forster, 1955, male paratype (AMNH); (b) *Zalmoxis* cf. *cuspanalis* (MCZ); (c) *Zalmoxis darwinensis* Goodnight & Goodnight, 1948, male holotype (AMNH); (d) *Zalmoxis jewetti* (Goodnight & Goodnight, 1947), male holotype (AMNH); (e) *Zalmoxis marchei* Roewer, 1912, male holotype (MCZ); (f) *Zalmoxis mitobatipes* (Roewer, 1926), male paratype (MCZ); (g) *Zalmoxis neocaledonicus* Roewer, 1912, male holotype (MCZ); (h) *Zalmoxis remingtoni* (Goodnight & Goodnight, 1948), male holotype (AMNH); (i) *Zalmoxis tuberculatus* Goodnight & Goodnight, 1948, male paratype (AMNH).

Zalmoxis crassitarsis Suzuki, 1982

Zalmoxis crassitarsis Suzuki, 1982, p. 190–193, figs. 21–28.

Record. *Cape Hoskins, Valoga, New Britain, Bismarck Archipelago, in rainforest, collected 12 July, 1962.

***Zalmoxis cuspanalis* Roewer, 1927**

(Figure 1b)

Zalmoxis cuspanalis Roewer, 1927, p. 288, fig. 11; Suzuki, 1977, p. 3.

Record. *Mount Maquiling [also Makiling], Laguna province, Luzon (Philippines).

***Zalmoxis dammermani* (Roewer, 1927)**

Zalmoxana dammermani Roewer, 1927, p. 294–295, fig. 14.

Zalmoxis dammermani: Goodnight & Goodnight, 1957, p. 81–83.

Record. *Kendeng, elevation 1400 m, and Ongop-ongop, elevation 1850 m, Idjen, Java [Indonesia], collected February and April 1924 by Dammerman.

***Zalmoxis darwinensis* Goodnight & Goodnight, 1948, restored combination**

(Figure 1c)

Zalmoxis darwinensis Goodnight & Goodnight, 1948, p. 4–6, figs. 10–11.

Zalmoxista darwinensis: Roewer, 1949b, p. 143–144.

Record. *Darwin, Australia, collected February 9–13, 1945 by Borys Malkin.

Remarks. Roewer (1949) differentiated the genus *Zalmoxista* from *Zalmoxis* primarily on the basis of the five-segmented second tarsus, and secondarily on the visibility of the spiracle and shape of the transverse plates, i.e., sulci ("Querfürche"). None of these characters are reliable for distinguishing genera from *Zalmoxis*, singly or in combination, given the variability of *Zalmoxis* species (Goodnight & Goodnight, 1953). Three species were placed in *Zalmoxista*: *Zalmoxis australis* (Sørensen, 1886), which Roewer (1912) himself had once placed in *Zalmoxis*; *Zalmoxis darwinensis* (Goodnight & Goodnight, 1948); and *Zalmoxis tuberculatus* (Goodnight & Goodnight, 1948). Furthermore, the type species of *Zalmoxista*, *Zalmoxista australis* (Sørensen, 1886), was subsequently transferred to Samoidae (Pérez-González & Kury, 2007). Roewer's convention was not universally followed, but it was not formally addressed either. Here we return *Zalmoxista darwinensis* (Goodnight & Goodnight, 1948) and *Zalmoxista tuberculata* (Goodnight & Goodnight, 1948) to *Zalmoxis*. In addition to the aforementioned limitations in the characters used to distinguish these species from *Zalmoxis*, we observe from re-examination of the type material of these two species (ref. Fig. 1), as well as recently collected material (by P.P.S.) that *Zalmoxis darwinensis* Goodnight & Goodnight, 1948 is more closely related to *Zalmoxis cardwellensis* Forster, 1955 than to New Caledonian *Zalmoxis*, with respect to both gross morphology and molecular sequence data (Sharma, work in progress).

***Zalmoxis granulatus* (Loman, 1902)**

Chondrobunus granulatus Loman, 1902, p. 207–208, fig. 8 (pl. 9).

Zalmoxis granulata: Roewer, 1912, p. 129; 1923, 87–88, fig. 84; Müller, 1917, p. 254–255; Roewer, 1923, 87–88, fig. 84.

Record. *Ralum, Lowon, Bismarck Archipelago.

***Zalmoxis heynemani* Suzuki, 1977**

Zalmoxis heynemani Suzuki, 1977, p. 15–17, fig. 4.

Record. *Sitio Taglawio, Maco, Tacum, Davao Province, Mindanao (Philippines), collected October 1946 by H. Hoogstraal and D. Heyneman, in original forest near sea level.

***Zalmoxis insula* Forster, 1955**

Zalmoxis insula Forster, 1955, p. 373–375, figs. 37–39.

Record. *Dauan I., Torres Strait, north Queensland, Australia, collected 6 May, 1953 by E.N. Marks.

***Zalmoxis insularis* (Roewer, 1949) new combination**

Camanastus insularis Roewer, 1949a, p. 20, fig. 20a–d (pl. 3).

Record. *Fiji Is. [Fiji, Melanesia].

Remarks. Originally in Phalangodidae, **new familial assignment.** See *Zalmoxis australis*.

***Zalmoxis jewetti* (Goodnight & Goodnight, 1947)**

(Figure 1d)

Metagjellerujia jewetti Goodnight & Goodnight, 1947, p. 6–7, figs. 10–11.

Zalmoxis jewetti: Goodnight & Goodnight, 1957, p. 81–83.

Record. *Mt. Dafansero, elevation 4700 ft., Cyclops Mountains, New Guinea [West Papua, Indonesia], collected 22 April, 1945 by G.G. Jewett, Jr., in a sago palm.

***Zalmoxis kaiensis* Suzuki, 1982**

Zalmoxis kaiensis Suzuki, 1982, p. 195–197, figs. 35–37.

Record. *Kai Island, Groot Key, Molucca Islands [Indonesia], collected April 1922 by Th. Mortensen.

***Zalmoxis lavacaverna* Hunt, 1993**

Zalmoxis lavacaverna Hunt, 1993, p. 217–219, fig. 1.

Record. *Collins Two-Ten Cave, Spring Creek Station, Mt. Surprise, Queensland, Australia, collected 21 January, 1989 by M. Ashe, F.G. Howarth and H. Howe; Long Shot Cave, Spring Creek Station, Mt. Garnet, Queensland, Australia, collected 20 January 1989 by F.G. Howarth, M. Ashe, H. Hoch and D. Irvin.

***Zalmoxis lavongaiensis* Suzuki, 1985**

Zalmoxis lavongaiensis Suzuki, 1985, p. 261–262, fig. 1.

Record. *Lavongai (New Hanover), Banatam, New Britain, Bismarck Archipelago, under bark, collected 20 March, 1962 during Noona Dan Expedition.

***Zalmoxis luzonicus* Roewer, 1949**

Zalmoxis luzonica Roewer, 1949a, p. 22, fig. 23a–f (pl. 3); Suzuki, 1977, p. 3.

Record. *Mount Maquiling, Laguna Province, Luzon (Philippines).

***Zalmoxis maculosus* (Roewer, 1949) new combination**

Papuastus maculosus Roewer, 1949a, p. 26, fig. 36a–d (pl. 5).

Record. *New Guinea (specific locality unknown).

Remarks. Goodnight & Goodnight (1957) overlooked this taxon when synonymizing a large number of Roewerian genera with *Zalmoxis*. There are no characters that distinguish *Papuastus* from *Zalmoxis*. Roewer's illustrations show a very long scutal area I, egg-shaped swollen pedipalpal tibia and stigmata obliterated by a fold of the coxa IV.

***Zalmoxis marchei* Roewer, 1912**

(Figure 1e)

Zalmoxis marchei Roewer, 1912, p. 129; 1923, p. 88, fig. 85; Goodnight & Goodnight, 1957, p. 83.

Record. *Mariana Islands (specific locality unknown).

***Zalmoxis mindanaonicus* Suzuki, 1977**

Zalmoxis mindanaonica Suzuki, 1977, p. 13–14.

Zalmoxis mindanaoensis Suzuki, 1977, p. 14, fig. 3.

Record. *East slope of Mt. McKinley, elevation 3000 ft, Davao Province, Mindanao (Philippines), collected November 1, 1946 by H. Hoogstraal.

Remarks. The specific epithet may be confused with "*mindanaoensis*." This is due to an error in the original description, wherein Suzuki (1977) named this species "*Zalmoxis mindanaonica*," but referred to it as "*Zalmoxis mindanaoensis*" in the figure legend.

***Zalmoxis minimus* Roewer, 1912**

Zalmoxis minima Roewer, 1912, p. 132; 1923, p. 89.

Record. *Langemak, Sepik, New Guinea.

Remarks. The species Roewer (1912) described as *Zalmoxis minima* is smaller than, and found in a distant locality from, *Gjellerupia minima* Roewer, 1915, though both species once shared the same specific epithet.

***Zalmoxis mitobatipes* (Roewer, 1926)**

(Figure 1f)

Zalmoxilla mitobatipes Roewer, 1926, p. 546–547, fig. 1 (pl. 1).

Zalmoxis mitobatipes: Goodnight & Goodnight, 1957, p. 81–83.

Record. *Mount Maquilung, Laguna Province, Luzon (Philippines).

***Zalmoxis muelleri* new name**

Zalmoxis neoguineensis Müller, 1917, p. 253, 256–258, figs. 3–5 [junior secondary homonym of *Euzalmoxis neoguineensis* Roewer, 1915]; Roewer, 1923, p. 90, fig. 87a–b.; Goodnight & Goodnight, 1957, p. 81–83.

Gagirius neoguineensis [partim.]: Roewer, 1949a, p. 28.

Record. *Sattelberg, Wilhelmshafen, New Guinea [Madang, Papua New Guinea]; other unspecified localities in New Guinea.

Etymology. Our replacement name honors the original author of this species, Adolf Müller.

***Zalmoxis mutus* new name**

Gagirius neoguineensis Roewer, 1949a, p. 28, figs 40a–d (pl. 5) [junior secondary homonym of *Euzalmoxis neoguineensis* Roewer, 1915].

Zalmoxis neoguineensis [partim.]: Goodnight & Goodnight, 1957, p. 81.

Record. *Friedrich-Wilhelmshafen [Madang, Papua New Guinea].

Etymology. Species name comes from Latin *mutus* (= dumb), referring to the fact that it remained "silent" and undetected by subsequent authors, concealed by the taxonomic confusion of Roewer.

Remarks. Roewer (1949a) referred to a species named "*Gagirius neoguineensis* Müller, 1913" as the type of the new genus *Gagirius*, indicated "Roewer, 1923 (part)" and cited material from the Budapest Museum. This means that he decided to pick part of the type series of Müller's species and create a new one. But the specific name was kept the same, and all without clear explanation. If both genera *Euzalmoxis* and *Gagirius* are kept as junior synonyms of *Zalmoxis*, the two other species described under the name *neoguineensis* will become junior secondary homonyms of *Euzalmoxis neoguineensis* Roewer, 1915.

***Zalmoxis neobritanicus* Suzuki, 1982**

Zalmoxis neobritanica Suzuki, 1982, p. 188–190, figs. 15–20.

Record. *Yalom, New Britain, Bismarck Archipelago, in secondary growth, collected 15 May, 1962.

***Zalmoxis neocaledonicus* Roewer, 1912**

(Figure 1g)

Zalmoxis neocaledonica Roewer, 1912, p. 131–132; Roewer, 1923, p. 88–89; Goodnight & Goodnight, 1957, p. 81–83.
Pygozalmoxis neocaledonica: Roewer, 1949a, p. 28, figs. 39a–d (pl. 5).

Record. *Noumea, New Caledonia.

***Zalmoxis neoguineensis* (Roewer, 1915)**

Euzalmoxis neoguineensis Roewer, 1915, p. 16, fig. 7; Goodnight & Goodnight, 1947, p. 328.

Zalmoxis neoguineensis [partim.]: Goodnight & Goodnight, 1957, p. 81–83.

Record. *Sattelberg, Wilhelmshafen, New Guinea [Madang, Papua New Guinea].

Remarks. Goodnight & Goodnight (1957) synonymized the genus *Euzalmoxis* with *Zalmoxis*, but neglected to designate new combinations to overcome preoccupation of the other *Zalmoxis neoguineensis*. Here we have renamed or transferred all other "*Zalmoxis neoguineensis*" resulting from transfer of the species that have been treated to other genera, thereby resolving secondary homonymy.

***Zalmoxis occidentalis* (Roewer, 1949) new combination**

Zalmoxomma occidentalis Roewer, 1949a, 22, fig. 25a–e; Staręga, 1989, 1, figs 1–4; Staręga, 1992, 295.

Record. *Mauritius (specific locality unknown).

Remarks. One of numerous monotypic genera established by Roewer (1949a), there is no justification for distinguishing this genus from *Zalmoxis*, and it closely resembles other *Zalmoxis* (specifically, certain species from New Guinea) in every respect, including spination of tibia IV and the armature of the free tergites.

Zalmoxis pallidus (Roewer, 1915)

Hoplozalmoxis pallida Roewer, 1915, p. 19, fig. 9.

Zalmoxis pallida: Goodnight & Goodnight, 1957, p. 81–83.

Record. *Sattelberg, Wilhelmshafen, New Guinea [Madang, Papua New Guinea].

Zalmoxis patellaris (Roewer, 1949)

Chondrobunus patellaris Roewer, 1949a, p. 24, fig. 27a–d (pl. 4).

Zalmoxis patellaris: Goodnight & Goodnight, 1957, p. 81–83.

Record. *Finschhafen, New Guinea [Morobe, Papua New Guinea].

Zalmoxis ponapeus (Roewer, 1949) new combination, revalidated

Euzalmoxis ponapea Roewer, 1949a, p. 24, figs. 30a–d (pl. 4) [junior subjective synonym of *Parazalmoxida solitaria* Roewer, 1917, by Goodnight & Goodnight (1957), synonymy herein disclaimed].

Zalmoxis solitaria [partim.]: Goodnight & Goodnight, 1957, p. 81–83.

Record. *Ponape, Caroline Islands.

Remarks. Goodnight & Goodnight (1957) did not observe any specimens resembling what Roewer (1949b) described as *Euzalmoxis ponapea*, but nevertheless synonymized *Parazalmoxida solitaria* and *Euzalmoxis ponapea* as *Zalmoxis solitaria* on the basis of close similarities between specimens available to them from Jaluit and Ponape. The synonymy was erroneous; there are clear differences between Roewer's "*Parazalmoxida*" and "*Euzalmoxis*" from Micronesian islands (namely, differences in size, shape, and length of appendages). The Goodnights were clearly (as they themselves conceded) looking at one widespread species ("*Parazalmoxida*") and making an assumption about another within the range of the first. We resurrect *Euzalmoxis ponapea*, but follow Goodnight & Goodnight (1957) with respect to the synonymy of *Euzalmoxis* with *Zalmoxis*.

Zalmoxis pumilus (Roewer, 1949)

Euzalmoxis pumila Roewer, 1949a, p. 24, figs. 29a–d (pl. 4).

Zalmoxis pumila: Goodnight & Goodnight, 1957, p. 81–83.

Record. *Sepik, New Guinea [East Sepik, Papua New Guinea].

Zalmoxis pygmaeus Sørensen, 1886

Zalmoxis pygmaea Sørensen, 1886, p. 13–14, fig. 6; Roewer, 1923, p. 86.

Record. *Viti Levu, Fiji, Melanesia.

Remarks. Sørensen reported the collecting locality as "Polynesia, on 'Viti' island". He was referring to Viti Levu, the largest island of the Fiji and a constituent of Melanesia, not Polynesia. The holotype is a typical female

lacking sexually dimorphic armature. This species is markedly smaller than *Z. robusta*, described concurrently from Viti Levu.

***Zalmoxis remingtoni* (Goodnight & Goodnight, 1948)**

(Figure 1h)

Foella remingtoni Goodnight & Goodnight, 1948, p. 1–4, figs. 7–8.

Zalmoxis remingtoni: Goodnight & Goodnight, 1957, p. 81–83.

Record. *Seven miles south of La Foa, New Caledonia, collected 11 March, 1945 by C.L. Remington.

***Zalmoxis robustus* Sørensen, 1886**

Zalmoxis robusta Sørensen, 1886, p. 12–13, fig. 5; Roewer, 1923, p. 86; Staręga, 1989, p. 4.

Record. *Viti Levu, Fiji, Melanesia.

Remarks. Sørensen (1886) reported the collecting locality as "Polynesia, on 'Viti' island". He was referring to Viti Levu, the largest island of the Fiji and a constituent of Melanesia, not Polynesia. The holotype of *Z. robusta* is a 4.5 mm long male that bears the sexually dimorphic fourth walking leg characteristic of the genus ("Differentia sexualis armatura pedum IV forsitan demonstratur," p. 13).

***Zalmoxis sarasinorum* Roewer, 1913**

Zalmoxis sarasinorum Roewer, 1913a, p. 85; Roewer, 1923, p. 90.

Record. *Tomohon, North Sulawesi [Indonesia], collected April 1895 by Sarasin from tree moss.

Remarks. The original description of this species provided little detail, no diagnosis, and no illustrations. Examination of several undescribed morphospecies from North and West Sulawesi (Sharma & Giribet, unpublished results) suggests that the zalmoxids from this region are typical *Zalmoxis*.

***Zalmoxis savesi* (Simon, 1880)**

Mermerus savesi Simon, 1880, p. 175.

Zalmoxis savesi: Roewer, 1912, p. 129; Roewer, 1923, p. 88.

Record. *Noumea, New Caledonia.

Remarks. There are no illustrations of the species in the literature, but the original description accords unambiguously with *Zalmoxis*.

***Zalmoxis sepikus* (Roewer, 1949)**

Chondrobunus sepikus Roewer, 1949a, p. 24, figs. 28a–d (pl. 4).

Zalmoxis sepikus: Goodnight & Goodnight, 1957, p. 81–83.

Record. *Sepik, New Guinea [East Sepik, Papua New Guinea].

***Zalmoxis similis* Suzuki, 1982**

Zalmoxis similis Suzuki, 1982, p. 193–195, figs. 29–34.

Record. *Yalom, New Britain, Bismarck Archipelago, in rainforest, collected 25 April, 1962.

***Zalmoxis soerenseni* Simon, 1892**

Zalmoxis soerenseni Simon, 1892, p. 44, figs. 7–8; Roewer, 1912, p. 29; Roewer, 1923, p. 87, fig. 83a–b.

Record. *Cueva de San Mateo, Luzon (Philippines).

Remarks. This species was originally described with limited detail and illustrations. Roewer (1923) added little more information in his redescription (e.g., tarsal formula), but significantly, did not assign it to a new genus. The tarsal formula (3: 6: 5: 6) and Roewer's reluctance to devise a new system suggest that this species is a large (ca. 5 mm) typical *Zalmoxis*.

***Zalmoxis solitarius* (Roewer, 1917)**

Parazalmoxida solitaria Roewer, 1917, p. 94, fig. 1; Roewer, 1923, p. 96–97; Suzuki, 1941, p. 28, fig. 1.
Zalmoxis solitaria [partim.]: Goodnight & Goodnight, 1957, p. 81–83, fig. 5.

Record. *Jaluit Island (Marshall Islands); Mt. Nahnalaud, Mt. Kupwuriso, and Mt. Temwetemwensekir, Ponape (Caroline Islands), collected by H.S. Dybas March, 1948.

Remarks. Distinguished from "*Euzalmoxis ponapea*." See *Zalmoxis ponapeus*.

***Zalmoxis spinicoxa* Roewer, 1949**

Zalmoxis spinicoxa Roewer, 1949a, p. 22, figs. 24a–f (pl. 3).

Record. *Border of eastern Hollandia, New Guinea [Sandaun, Papua New Guinea].

***Zalmoxis thorelli* new name**

Acrozalmoxis neoguinensis Roewer, 1915, p. 17, fig. 8 [junior secondary homonym of *Euzalmoxis neoguinensis* Roewer, 1915]; Roewer, 1923, p. 93

Record. *Sattelberg, Wilhelmshafen, New Guinea [Madang, Papua New Guinea].

Remarks. The monotypic genus *Acrozalmoxis* Roewer, 1915 was distinguished from *Zalmoxis* on the basis of the armature of the ocularium, posterior scutum, and free tergites; and the shape of the transverse plates, i.e., sulci ("Querfürche"), but as Goodnight & Goodnight (1953) have demonstrated, the characters used to delimit this genus cannot be used to distinguish genera reliably, much less species (see Discussion for review of Goodnight & Goodnight, 1953). Furthermore, numerous *Zalmoxis* species described subsequent to the erection of *Acrozalmoxis* demonstrate morphological variation that encompasses the "uniqueness" of *Acrozalmoxis*, e.g., ocularial and scutal armature. Consequently, we collapse this genus into *Zalmoxis* and designate a new specific epithet due to the pre-occupation of *Zalmoxis neoguinensis*. The specific epithet honors Tord Tamerlan Teodor Thorell, who described the first two species of Zalmoxidae from New Guinea.

***Zalmoxis tuberculatus* Goodnight & Goodnight, 1948, restored combination**

(Figure 1i)

Zalmoxis tuberculata Goodnight & Goodnight, 1948, p. 6–7, fig. 10.

Zalmoxista tuberculata: Roewer, 1949b, p. 143–144.

Record. *La Foa, New Caledonia, collected March 7, 1945 by C.L. Remington.

Remarks. See *Zalmoxis darwinensis*.

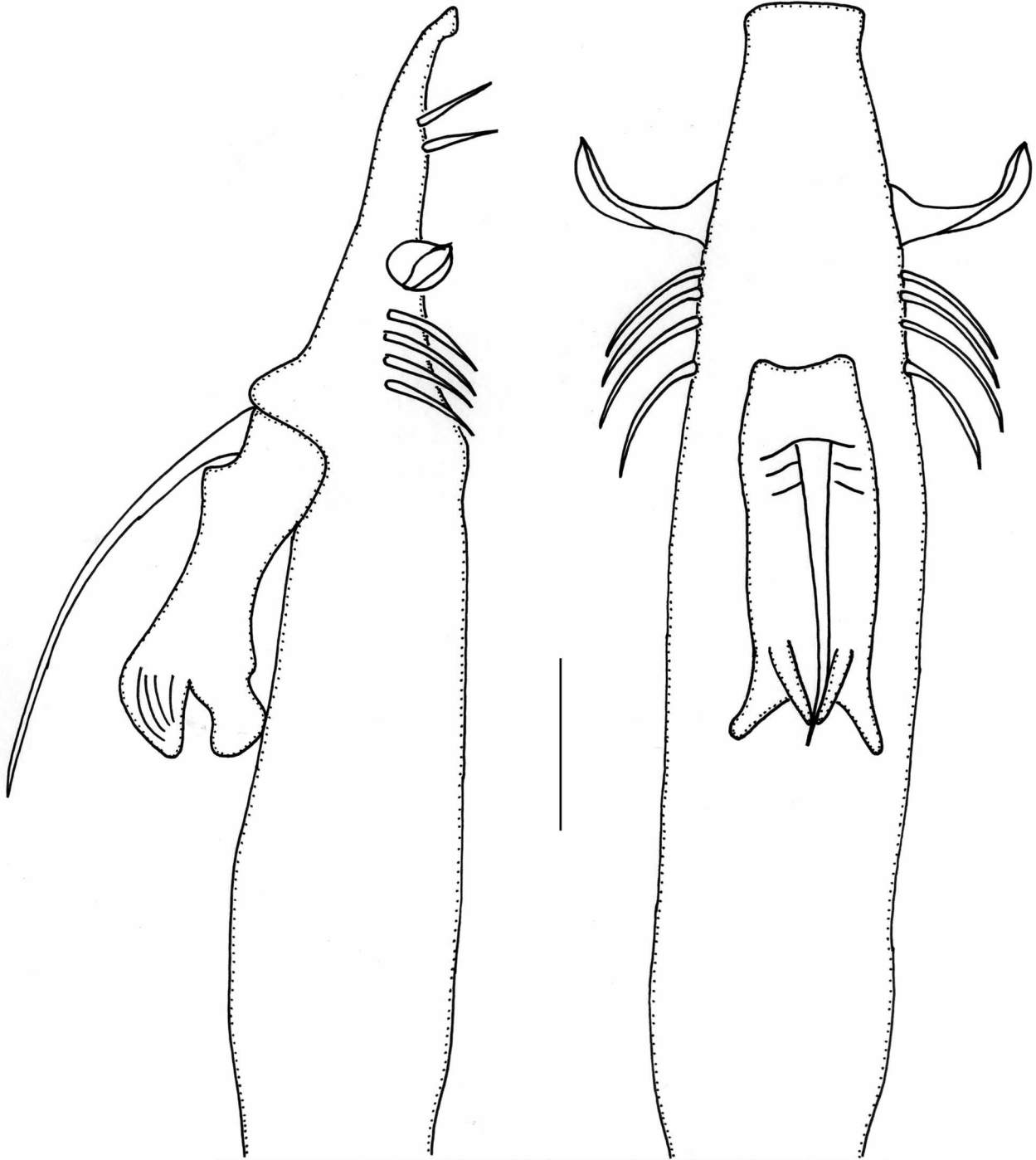


FIGURE 2. Male paratype of *Bunofagea gracilipes* Lawrence, 1959 (MNHN). Left, lateral view of penis; right, dorsal view of penis. Scale bar = 100 μ m.

Discussion

The distribution and species richness of Palearctic Zalmoxidae present a unique opportunity for biogeographical study (Figs. 3–4). However, numerous taxonomic errors and oversights have accumulated over more than a century of study, owing to uncorrected preoccupations of specific epithets, unjustified monotypic genera, and unwarranted synonymy. The present catalogue endeavors to synthesize an eclectic and increasingly obscure literature, and to correct these taxonomic errors prior to the description of new species. *A priori* definition of taxonomic entities is an essential first step to ongoing taxonomic and phylogenetic study.

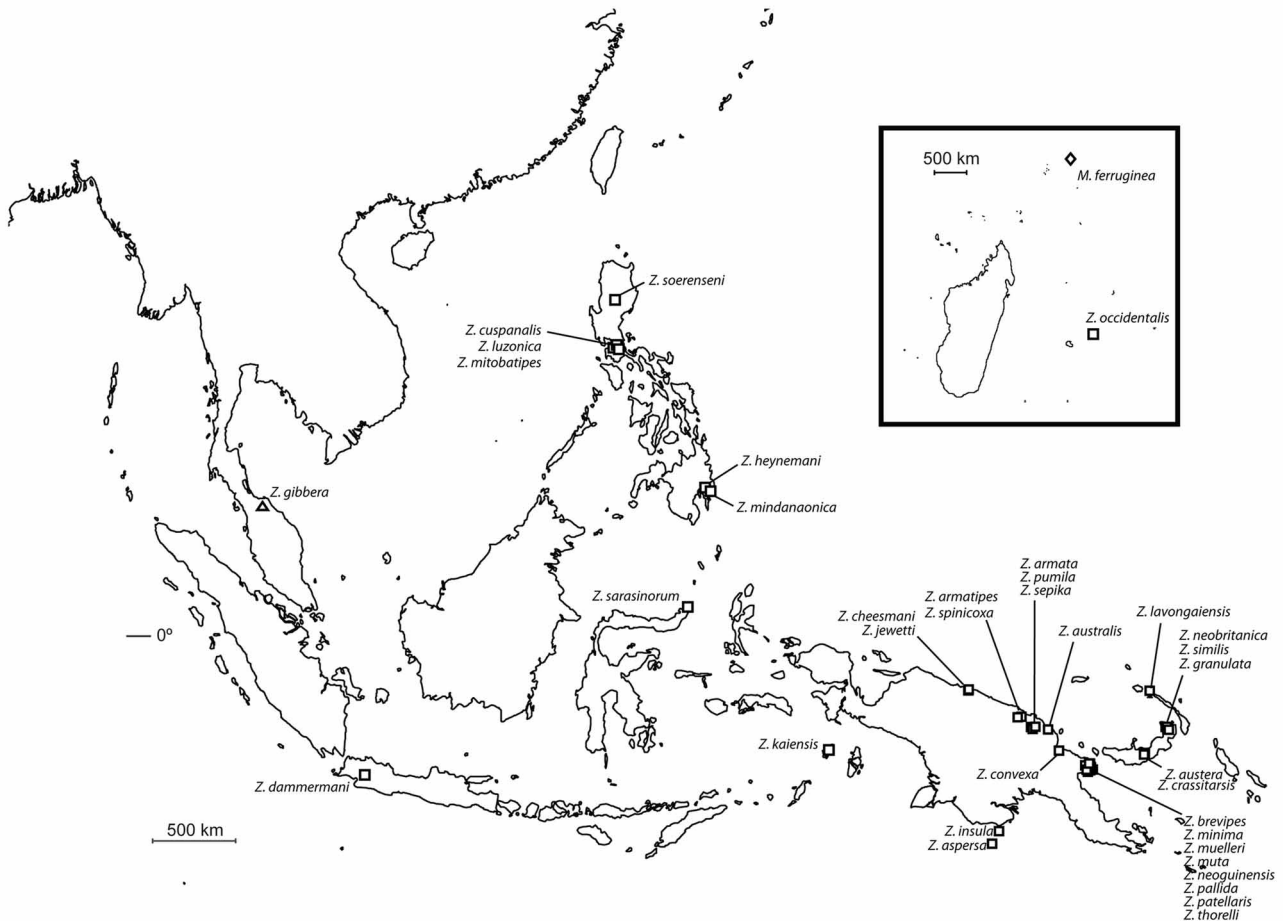


FIGURE 3. Map of Southeast Asia showing known localities for Zalmoxidae species. Inset, map of Mascarene Islands showing known localities for Indian Ocean species.

To this end, we have largely reverted to the system of synonymies established by Goodnight & Goodnight (1957), in addition to synonymizing other genera that they overlooked, based upon the Goodnights' critique of characters used to delimit opilionid genera and species (Goodnight & Goodnight, 1953). Our taxonomic action follows results from ongoing phylogenetic study of Zalmoxidae based on molecular sequence data (Sharma, work in progress; presented at the 18th International Congress of Arachnology, June 2010), which (1) indicates that the Indo-Pacific Zalmoxidae constitute a monophyletic group and (2) disfavors previously erected monotypic genera, as they render *Zalmoxis* para- or polyphyletic. Though the system of Goodnight & Goodnight (1957) was not universally adopted due to the perception of unjustified synonymies, we submit that the subdivision of Indo-Pacific Zalmoxidae into numerous genera (and without explicit justification) was itself unwarranted. There are no unambiguous morphological characters we are aware of that justify the subdivision of *Zalmoxis*.

Zalmoxidae (like Samoidae) is atypical among Laniatores, being a widespread circum-Pacific family, whereas most families (with rare exceptions of ancient groups such as Triaenonychidae; Mendes & Kury, 2008), are restricted to a single continent. The uniformity of male genitalia is remarkable, with South American and Palearctic species sharing the same underlying architecture. Following Kury & Pérez-González (2007), Zalmoxidae belongs to the superfamily Zalmoxoidea, with three other families—Fissiphallidae Martens, 1988, Icalectidae

Kury & Pérez-González, 2002, and Guasiniidae González-Sponga, 1997—which are all endemic to the Neotropics. A recent phylogeny of Opiliones placed Fissiphallidae sister to a monophyletic Zalmoxidae, with Icalectidae in turn sister to Fissiphallidae + Zalmoxidae (Giribet *et al.* 2010). These results suggest a radiation of the Paleotropical lineage out of the Neotropics, a very unusual biogeographical pattern. A previous such case in Opiliones, wherein a New Caledonian endemic lineage was found to have an ancient relationship to a Neotropical group, was considered a relict, possibly the result of a formerly pan-Gondwanan group undergoing extinction (Boyer *et al.* 2007; Sharma & Giribet, 2009b). However, the sampling of Zalmoxidae by Giribet *et al.* (2010) was limited to three species (two Neotropical and one Pacific); and the fourth member of Zalmoxoidea, Guasiniidae, was not represented, obviating an unambiguous conclusion. Consequently, the systematic validity of Zalmoxidae and the relationships within Zalmoxoidea remain largely unresolved.

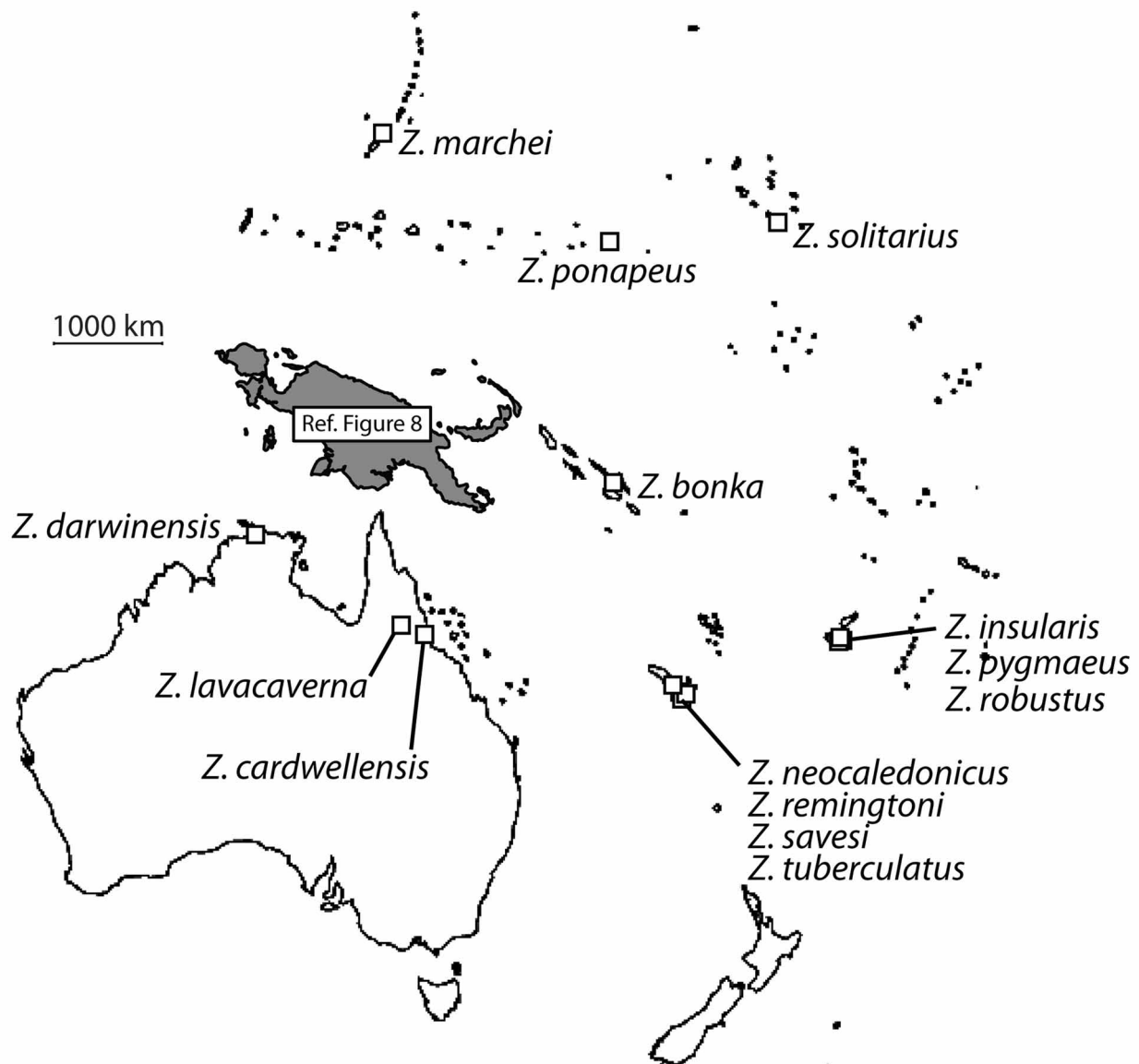


FIGURE 4. Map of the Southwest Pacific showing known localities for Zalmoxidae species. Island groups embellished for clarity.

By reason of being very small Opiliones, Zalmoxidae are often overlooked in general collections and are greatly undersampled. The number of described species of Paleotropical Zalmoxidae poorly estimates both the diversity and the biogeography of this group, as undescribed morphospecies continue to be found in new regions altogether (Hunt, 1991). Preliminary examination of undescribed material among museum collections from this region indicates that as many as 35–50 new species are available for description and study, and ongoing collecting efforts are likely to dramatically increase their known diversity. Subsequent to further taxonomic revisions, the

diversity of this family may also be expanded by transfer of previously described species. Studying this fauna could prove valuable for characterizing colonization of oceanic islands from continental sources and speciation in archipelagoes.

Acknowledgments

As with (many) previous manuscripts, we are indebted to Peter J. Schwendinger for generously providing numerous collections and hundreds of specimens from the Indo-Malay Archipelago and the Solomon Islands for study. The quality of an earlier version of this manuscript was significantly improved by comments from Abel Pérez-González, William Shear, and Nobuo Tsurusaki. Much of the undescribed material was sorted by Laura Leiben-
sperger. Miguel A. Alonso-Zarazaga clarified the gender of "*Zalmoxis*".

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