Zootaxa 5646 (3): 301–343
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5646.3.1
http://zoobank.org/urn:lsid:zoobank.org:pub:F93E30E9-21A2-4DE5-B31A-624C8A0AFE94

Reinstatement of the genus *Pseudoleiobunum* Müller, 1914 with the inclusion of a new species from Hong Kong and reallocation of the *Leiobunum maximum* species complex (Arachnida: Opiliones: Eupnoi: Sclerosomatidae)

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Abstract

The genus *Leiobunum* Koch, 1839 is extremely diverse and includes species distributed globally. Taxonomic relationships within *Leiobunum* are unclear since diagnostic features of the genus are vague and common in many other eupnoan species. The discovery of a new species in Hong Kong prompted an examination of East Asian Leiobuninae using a combination of external morphological and molecular analyses, and comparison of genital morphology and ecological features. Morphological and molecular data link this new species to the *Leiobunum maximum* superspecies. In this paper, we resurrect *Pseudoleiobunum*, the oldest genus name for *Leiobunum maximum*. We place members of the superspecies into *Pseudoleiobunum*, along with the new species *P. lutulentum* **sp. nov.**.

Key words: Harvestmen, Integrative Taxonomy, Phylogeny, Scanning Electron Microscopy

Introduction

A new species of Eupnoi harvestman was found in Hong Kong from various sites along mountain streams. The species superficially resembles Leiobuninae species of the family Sclerosomatidae, such as *Leiobunum maximum* Roewer, 1910 from southern China and Taiwan, and *Leiobunum japanense* Müller, 1914 from the Ryukyu Islands to Japanese mainland (Suzuki 1976).

The genus *Leiobunum* Koch, 1839 is one of the most diverse Sclerosomatidae genera (currently 102 described species), and is widely distributed throughout Eurasia, East Asia and North America (Kury *et al.* 2021). The relationships between *Leiobunum* species are unclear in part due to the generic and oftentimes vague diagnosis of *Leiobunum*. This issue has troubled taxonomists since the genus' establishment in the mid-19th century, with many changes and corrections made to the genus and its definition (Crawford 1992).

Tsurusaki (1985) followed up on Suzuki (1976) and re-suggested the grouping of the *Leiobunum curvipalpi* superspecies (hereafter referred to as *curvipalpe*-group), based on the morphological similarities shared by its members (See Discussion). Tsurusaki also suggested a close relationship between these species (largely found in Japan) and some North American species, such as *L. calcar* Wood, 1868 and *L. leiopenis* Davis, 1934. This close relationship was based on how the *curvipalpe*-group and the North America group of *Leiobunum* both possess non-alated penis, which is a unique trait in *Leiobunum* (Tsurusaki 1985).

However, in an extensive phylogenetic study that sequenced four nuclear and two mitochondrial gene regions from over 70 species across different families, Hedin *et al.* (2012) showed that both genera *Leiobunum* and *Nelima* Roewer, 1910 are polyphyletic. *Leiobunum* species are often more closely related to *Nelima* from the same

Accepted by J. Shultz: 10 Apr. 2025; published: 10 Jun. 2025

geographical regions (*e.g.*, East Asia or Europe) than to *Leiobunum* from other regions. The study emphasized the need for taxonomic revision of Leiobuninae in both East Asia and North America (Hedin *et al.* 2012).

In addition, Hedin *et al.* (2012) reconfirmed the suggestion of Suzuki (1976) and Tsurusaki (1985) for the superspecies groupings of East Asian *Leiobunum* species. More specifically, the study showed that Asian Leiobuninae are genetically separated into different clades, such as the *curvipalpe*-group and *maximum*-group.

Hedin *et al.* revealed classification problems within the Asian *Leiobunum* taxonomy that must be addressed, namely the separation of groups such as the *curvipalpe*-group and *maximum*-group from *Leiobunum*. Upon the discovery of a new species from Hong Kong, we begin revising Asian *Leiobunum* by resurrecting the genus *Pseudoleiobunum* to reclassify and separate the *maximum*-group from the larger *Leiobunum* genus. We support this newly resurrected genus *Pseudoleiobunum* and infer a close relationship between the *maximum*-group and the new Hong Kong species using integrative taxonomy methods (general morphology, genital morphology, phylogenetic analysis, and ecology).

Materials and methods

Collection

Specimens were caught by hand in the field, preserved immediately in 70% ethanol and stored at 4 °C in the laboratory. Hong Kong specimens were caught from four locations: Tei Tong Zai, Lantau Island (LINGU-INV72, 73, 74, 75); Tai Mo Shan (LINGU-INV50, 51, 52, 53, 57, 59, 154); Shing Mun Reservoir (LINGU-INV46, 55, 58, 60, 132, 134, 145, 146), Kowloon Peak (LINGU-INV61), Fo Tan (LINGU-INV62, 63, 64, 65) and Ma On Shan (LINGU-INV106, 107, 115, 116, 117, 118, 119) (Figure 1). All samples are housed at the Lingnan University Natural History Collection, and identified with the prefix LINGU-INV.

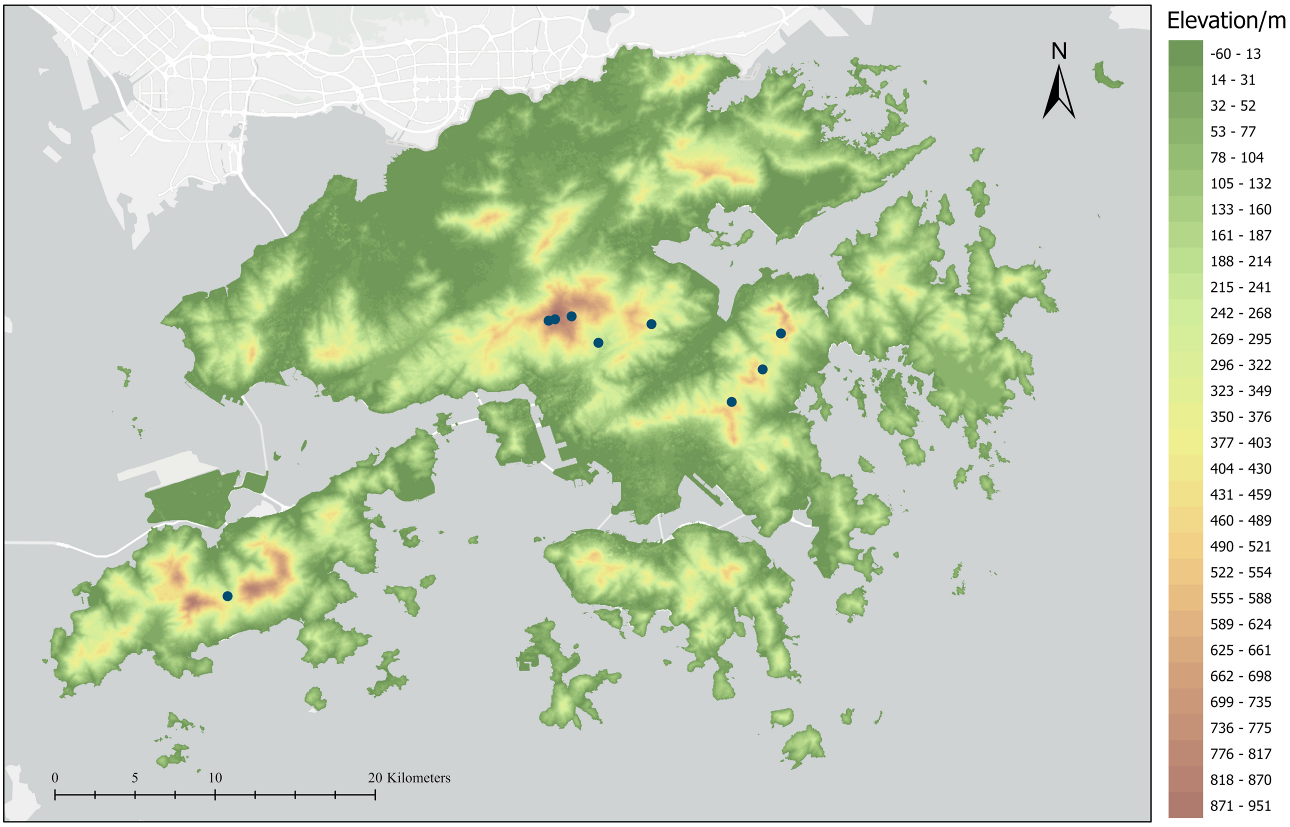

FIGURE 1. Altitudinal map of Hong Kong, China and the locations of the specimens used in this study. *Pseudoleiobunum lutulentum* **sp. nov.** were found in places with higher altitudes and higher humidity, preferably streams.

Three more specimens (*Pseudoleiobunum maximum distinctum* (LINGU-INV156), *Pseudoleiobunum japanense japonicum* (LINGU-INV155) and *Pseudoleiobunum japanense japonicum* Juvenile (LINGU-INV154)) stored in 70% ethanol were collected by Dr. Tsurusaki and used for molecular analysis (See Appendix 6).

Morphological examination

Examination procedures follow Acosta *et al.* (2007) and Lian *et al.* (2011). Specimens were examined and measured with a stereomicroscope imaging system (Leica M205 C Stereomicroscope), equipped with a DMC5400 20 Megapixel color CMOS camera (Leica Microsystems Ltd.).

To better examine and take pictures of the seminal receptacle of the female genital, we used a SAGA-SG50-SM light microscope (SAGA Optics Co., Ltd.). Pictures of the detailed genital structure were captured with the mounted AM7025X Dino-Eye Edge Digital eye-piece camera (AnMo Electronics Corporation).

All illustrations were done with the GNU Image Manipulation Program (GIMP), with highlights added manually with a pencil (Montesanto, 2015). These illustrations, measurements and photographs were taken with a mounted 4K microscopic camera and ToupView camera control software (ToupTek Photonics Co., Ltd.). All measurements are recorded in millimeters (mm).

For electron microscopy, the genitalia were processed following modified protocols of Bennett & Townsend (2013) and Proud & Townsend (2019). The genitalia were first cleaned in PE buffer solution (Qiagen). Next, the genitalia were carefully treated in a graded ethanol series (30%, 45%, 65%, 80%, 90%) for at least 30 minutes at each concentration, then placed in acetone (Tan *et al.* 2023). Upon completion, the genitalia were stored at 4 °C.

Critical point drying was performed with a critical point dryer (Leica Biosystems, EM CPD300). Genitalia were then mounted on aluminum stubs with adhesive, fixed to show the ventral, dorsal and lateral views. The genitalia were sputter-coated with gold for 50 s under 40 mA current (BAL-TEC, SCD 005). Electron microscopy was performed with a scanning electron microscope (LEO 1530 FEG).

DNA Sequencing

We conducted a phylogenetic analysis to infer the phylogenetic placement of the new species within Leiobuninae. A total of 27 samples were selected for DNA sequencing (Appendix 6). The left legs I–IV were removed and used for DNA extraction using a DNeasy® Blood and Tissue Kit (Qiagen) following the manufacturer's protocols (Tan *et al.* 2023).

Polymerase chain reaction protocols followed modified versions of Boyer *et al.* (2007), Pinto-da-Rocha *et al.* (2014), Chen & Shih (2018), Hedin *et al.* (2012) and Tan *et al.* (2023). Four loci were amplified for this study: 28S ribosomal RNA (*28S*), 16S ribosomal RNA (*16S*), 18S ribosomal RNA (*18S*) and cytochrome c oxidase subunit 1 (*COI*). Details of the PCR conditions, along with the primers used are listed in Appendix 5. PCR products were checked with gel electrophoresis and purified with the QIAquick PCR Purification Kit (Qiagen). Sequencing was performed with the ABI 3730xl System at Macrogen (Seoul, Korea).

This study builds on the genetic studies of Hedin *et al.* (2012) and Giribet *et al.* (2010), including data from the type species *Pseudoleiobunum japanense* taken from Hedin *et al.* (2012). A total of four datasets were analyzed—a dataset of each of the four individual loci and a concatenated dataset (Figs 8–9, Appendices 1–3). Sequences from the new species were aligned with the GenBank data using MUSCLE (Edgar 2004) in Geneious v11.1 (Dotmatics). Maximum Likelihood phylogenetic trees were constructed using Randomized Axelerated Maximum Likelihood (RAxML) (Stamatakis 2014). Support values for all the trees were calcualated using 1000 bootstrap pseudoreplicates. The concatenated dataset was made by combining the individually aligned datasets of *COI*, *28S*, *18S* and *16S*.

All analysis included three sequences from *P. lutulentum* **sp. nov.** (LINGU-INV53, 64, 73) and three sequences from Japanese samples: *P. japanense japonicum* (LINGU-INV154, 155), *P. maximum distinctum* (LINGU-INV156). The *COI* analysis consisted of a total of 32 sequences (Appendix 3), *18S* analysis has a total of 50 samples (Appendix 1), *28S* analysis consisted of 65 sequences (Figure 8) and the concatenated analysis included 73 sequences (Figure 9).

EF1 sequencing was also attempted but they have failed due to weak signals. However, we have included the protocols used for *EF1* loci for future reference, but phylogenetic analysis of *EF1* was not included.

Outgroups for all the analyses were chosen from the Phalangiidae, Neopilionidae and *Metopilio* groups, based on Hedin *et al.* (2012).

Taxonomy

Sclerosomatidae Simon, 1879

Leiobuninae Banks, 1893

Pseudoleiobunum **Müller, 1914**

Pseudoliobunum Müller, 1914: 95; Roewer, 1923: 923–924; Crawford, 1992: 41.
Metaliobunum Suzuki, 1940: 276; Crawford, 1992: 30.
Metaleiobunum Suzuki, 1965: 353.
Pseudoleiobunum Suzuki & Ohrui, 1972: 47; Suzuki, 1965: 193; 1976: 199–202.
Leiobunum (in part) Suzuki, 1973; 1953; 1976: 191, 204; Crawford, 1992: 26.

Type species: *Pseudoleiobunum japanense* Müller, 1914: 95.

Diagnosis. *Pseudoleiobunum* shares many of *Leiobunum*'s characteristics, but can be distinguished by having medium to large brown leathery or heavily granulated body, generally dorsoventrally flattened. The abdomen is usually truncated (more apparent in males or underfed individuals). Scutal tergite areas I–III often with one small, inconspicuous central hump (size of the hump varies greatly even amongst individuals of the same species) (Figure 2). In many individuals, the two lateral-posterior tips of the scutum elevate slightly, resembling a pair of small angled posterior armaments (such characteristic is also more apparent in underfed/male individuals, degree of scutal tip formation is highly variable between species and individuals) (Figs 2–3). Labrum generally slender and unarmed. *Pseudoleiobunum* also possesses relatively shorter legs compared to *Leiobunum*, femur I often (but not always) shorter than body (ratio of the length of femur I to body ranges from 0.66–1.6, with a mean of 1.06; for other species of East Asian *Leiobunum* and *Nelima*, the ratio ranges from 0.97–3.52, with a mean of 1.69) (Table 1 & Figure 12). The pedipalp of *Pseudoleiobunum* also possesses distomesal patellar and tibial apophysis in both males and females. In some species (*e.g.*, *P. lutulentum* **sp. nov.** and *P. maximum distinctum*), the pedipalpal tibial apophysis may be less apparent than the patella apophysis.

TABLE 1. Morphological measurements for male specimen (LINGU-INV154) and (female specimen) (LINGU-INV106) of *Pseudoleiobunum lutulentum* **sp. nov.** All measurements are in millimeters (mm).

	Trochanter	**Femur**	**Patella**	**Tibia**	**Tarsus**	**Total**
Pedipalpus	0.35	0.82	0.45	0.55	1.08	3.25
	(0.68)	(1.78)	(0.95)	(1.25)	(2.27)	(6.93)
Leg I	0.60	5.6	0.95	4.10	9.67	20.92
	(0.61)	(4.90)	(1.23)	(3.25)	(9.29)	(19.28)
Leg II	0.62	14.19	1.44	10.86	24.09	51.2
	(0.55)	(15.93)	(1.72)	(11.90)	(25.02)	(55.12)
Leg III	0.55	5.7	1.22	3.63	9.68	20.78
	(0.62)	(5.08)	(1.25)	(3.28)	(9.31)	(19.54)
Leg IV	0.55	8.4	1.31	5.36	13.87	29.49
	(0.68)	(7.37)	(1.38)	(4.73)	(13.16)	(27.32)

Etymology. Latin designation is derived from the combination of the prefix 'pseudes' (false) with the genus name *Leiobunum* (Crawford 1992).

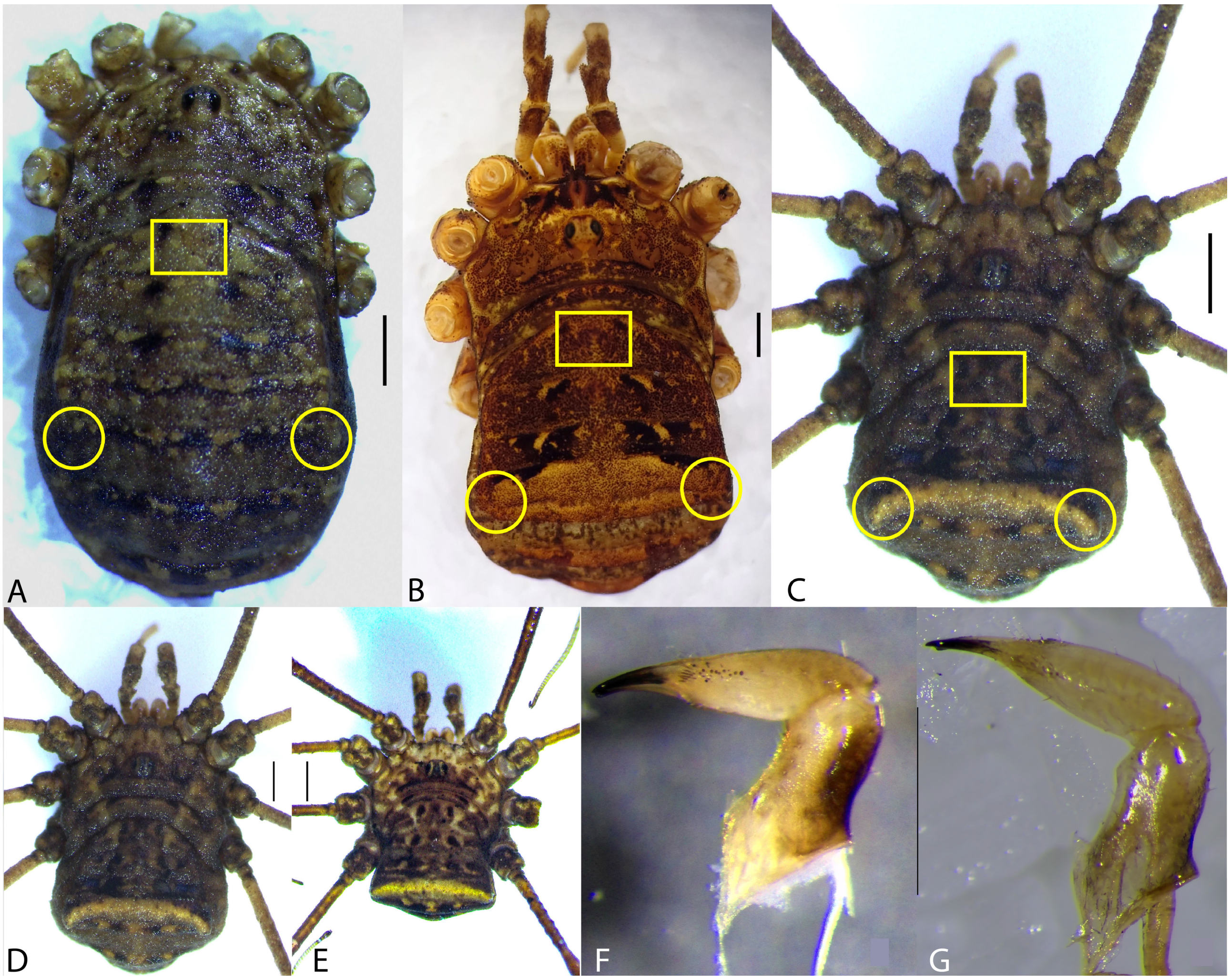

FIGURE 2. Comparisons between *Pseudoleiobunum* specimens. **A**–**C** Comparison of female dorsal bodies between three *Pseudoleiobunum* species, highlighting features of the genus, yellow rectangle highlighting the small central, dorsal hump on the dorsal scutum; yellow circles highlighting the elevated lateral-posterior edges of the dorsal scute, resembling a pair of tubercles. **D**–**E** Comparison of general body size between male and female. **F**–**G** Comparison of male and female cheliceral size. **A** *P. maximum distinctum*, female. **B** *P. japanense japonicus*, female. **C** *P. lutulentum* **sp. nov**, LINGU-INV117, female. **D** Dorsal view of the female body, LINGU-INV117. **E** Dorsal view of the male body, LINGU-INV118. **F** Full lateral view of male chelicera, LINGU-INV72. **G** Full lateral view of female chelicera, LINGU-INV146. Scale bars: 1 mm.

Distribution. Southeastern China, Hong Kong, Taiwan and southern Japan, including Ryukyu Islands (Figure 12).

Notes. The genus was established for *Pseudoleiobunum japanense* Müller, 1914 from Hakone, Kanagawa Prefecture, Japan. Suzuki & Ohrui (1972) amended the genus name *Pseudoliobunum* to *Pseudoleiobunum* to accommodate reinstatement of *Leiobunum* from *Liobunum* that was erroneously amended by Agassiz (1846) (Roewer 1957, Crawford 1992). The spelling was deemed unjustified following ICZN code (International Code of Zoological Nomenclature, Articles 33.1 & 33.2, Fowler 1984). The same rationale is applied to changing *Metaliobunum* to *Metaleiobunum* (Suzuki 1965).

The Suzuki (1976) revision showed that *Metaleiobunum* Suzuki, 1940 and *Pseudoleiobunum* are indistinguishable from other East Asian *Leiobunum* species. However, a monophyletic group was inferred in molecular phylogeny comprised of *L. japanense* (*maximum*-group), *L. rubrum* (*rubrum*-group) and all Japanese *Nelima* species (Hedin *et al.* 2012). Furthermore, the *maximum*-group can be distinguished from other species of *Leiobunum* by a combination of several characters (Table 1 in Tsurusaki 1985). The resurrection of *Pseudoleiobunum* accommodates all the above groups and resolves a part of the polyphyletic issue (*i.e.*, Asian clades) within the large genus of *Leiobunum*.

In the following we show the superspecies name in parentheses after the genus name following ICZN article 6.2 (International Code of Zoological Nomenclature 1999).

Pseudoleiobunum (superspecies *maximum*) *japanense japanense* Müller, 1914

Pseudoliobunum japanense Müller, 1914: 95; Roewer, 1923: 923–924.
Pseudoleiobunum japanense Suzuki, 1972: 47–48, Figure 3.
Leiobunum japanense japanense: Suzuki, 1976: 199–200; Tsurusaki & Sasaji, 1991: 11, Figures 5A–B; Kato *et al.*, 2023: 63.

Materials examined. (PREF. = Prefecture; Mt. = Mount; juv. = juvenile) JAPAN, SAITAMA PREF.: Chichibu City, Otaki-mura, Irikawa, Chichibu Experiment Forest of the University of Tokyo, 1♂ 26 July 1998, M. Imai.—JAPAN, CHIBA PREF.: Ichihara City, Umegase Gorge, 1♂, 26 March 2007, M. Watanabe.—JAPAN, JAPAN, KANAGAWA PREF.: Yokohama City, Kanazawa-ku, Kamariya-cho, E. valley of Mt. Daimaru, 1♂, 25 June 1994, Y. Goto. Sagamihara City, Shimomizo, 1♀, 25 May 1997, M. Imai.—JAPAN, FUKUI PREF.: Ohno City, Rokuroshi, 1♂, 4 August 1990, H. Sasaji.—JAPAN, NAGANO PREF.: Omachi City, Omachi Dam, 910 m, 1♀, 1 June 1994, W. Miyata; Kami-Ina-gun, Minami-Minowa-mura, Mt. Kyogadak, S. (Mt. Kitazawa), 1380 m, 2 juv., 14 May 1983, Y. Nishikawa.—JAPAN, SHIZUOKA PREF.: Fujinomiya City, Shiraito-no-taki Falls, 2♂, 11 July 1993, K. Ishii; Ito City, Lake Ippeki, 1♀, 27 May 1993, M. Ohrui; Izu-Amagi, Hacchoike, 1100 m, 3 juv., 8 October 1984, M. Ohrui; Amagi-toge Pass, Himuro, 750 m, 1 juv., 22 April 1985, M. Ohrui; Tabawa-gun, Amagi-Yugashima-cho, Himuro-enchi, 700m: 1♀, 8 July 1989, M. Ohrui; 1♀, 22 July 1992, M. Ohrui; 1♀, 27 July 1992, M. Ohrui.

Distribution. The central and eastern parts of Japan (Kanto and Chubu Districts) (Fig. 12).

Habitat. This species is univoltine and overwinters as juveniles. Adults can be found from March to early August. They can be found under logs, stones on wet forest ground and walls of wet cliffs along mountain streams.

Description. Ocularium low, supracheliceral lamellae well-developed and generally pointy, often armed with black-tipped granules (Suzuki 1973: figs 1, 120; Suzuki 1976: figs 128–132, 143, 156). Male labrum mushroom-shaped or slender (Suzuki 1976: figs 1–2, 4–5, 6, 9–13; Tsurusaki 1985: fig. 3A), without lateral denticles or armaments. Coxae I–IV armed with a marginal row of small tubercles anteriorly and posteriorly. Leg femora can be finely armed with minute, knob-like granules. Such granules may resemble pseudoarticulations, but they are smaller.

Pseudoleiobunum lutulentum Tan sp. nov.

Type material examined. Holotype ♂ (LINGU-INV154), CHINA: Hong Kong Special Administrative Region, New Territories, Tai Mo Shan [N22°24.5867' E114°7.9283'], 22 October 2024, Tan; paratype 1 (LINGU-INV72), CHINA: Hong Kong Special Administrative Region, Lantau Island, Tei Tong Zai [N22°15.1707' E113°56.3469'], 19 April 2023, Tan; paratype 2 (LINGU-INV59), CHINA: Hong Kong, New Territories, Tai Mo Shan [N22°24.49' E114°7.37'], 12 August 2021; Paratype 3 (LINGU-INV55), CHINA: Hong Kong Special Administrative Region, New Territories, Shing Mun Reservoir [N22°23.70', E114°8.83']; Paratype 4 (LINGU-INV60), same data as Paratype 3; Paratype 5 (LINGU-INV106), CHINA: Hong Kong Special Administrative Region, New Territories, Ma On Shan, Mui Tsz Lam [N22°22.803' E114°14.357'] and Paratype 6 (LINGU-INV107), same as Paratype 5; Paratype 7 (LINGU-INV118) and Paratype 8 (LINGU-INV115), CHINA: Hong Kong Special Administrative Region, New Territories, Ma On Shan [N22°24.012' E114°14.972']; Paratype 9 ♀ (LINGU-INV116), Paratype 10 ♀ (LINGU-INV117) and Paratype 11 ♀ (LINGU-INV119), all three same as Paratype 6 and 7; Paratype 12 ♂ (LINGU-INV132), Paratype 13 ♀ (LINGU-INV134), Paratype 14 ♀ (LINGU-INV145) and Paratype 15 ♀ (LINGU-INV146), CHINA: Hong Kong Special Administrative Region, New Territories, Shing Mun Reservoir [N22°23.9267', E114°9.164'].

Diagnosis. This species can be distinguished from other congeneric species by its smaller body size (male body 3 mm long, female body 5 mm long; meanwhile the body sizes of other species range from 6.3–9.8 mm in males and 9.2–13.7 mm in females). Additionally, the male genitalia of this species possess a fairly developed alate winging that is confined to the distal section of the shaft, similar to that found in Gagrellinae species (Figs 6A–C, 7) (Martens 1987) while other proposed *Pseudoleiobunum* species possess tapered alate sections (Suzuki 1976, Tsurusaki 1991).

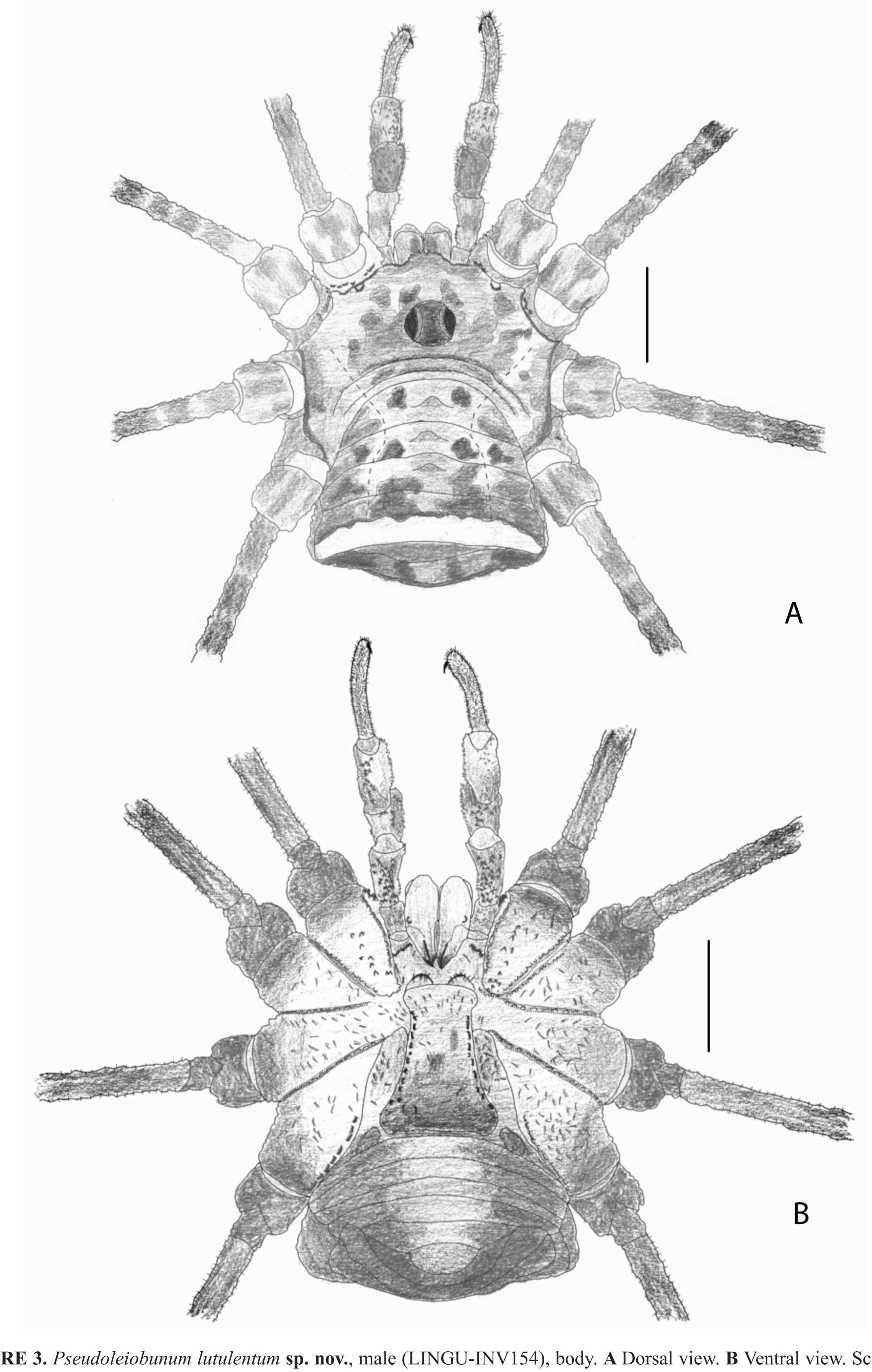

FIGURE 3. *Pseudoleiobunum lutulentum* **sp. nov.**, male (LINGU-INV154), body. **A** Dorsal view. **B** Ventral view. Scale bars: 1 mm.

Etymology. The species name "*lutulentum*" is derived from the Latin adjective for muddy and dirty, "*lutulentus*", referring to the overall mud-yellow colored and roughly granulated dorsal surface that is unique amongst Hong Kong harvestmen.

Distribution. Found throughout Hong Kong, although it occurs more commonly in areas with high humidity, lower temperature, high elevation and close to water sources, such as Tai Mo Shan and Mui Tsz Lam (Figs 1, 12).

Dorsum (Figs 2C–E, 3). Scutum parvum . Scutum widest at the prosoma; scutum weak and leathery, surface covered with tiny, coarse granules. The lateral margins of the scute elevated with two apparent lateral-posterior protuberances by the IV scutal area. Meanwhile the free tergites extend below the elevated scute, sometimes compressed and extending downwards from the angled dorsal scute (Figs 2C–E, 3). This is especially prominent in males or underfed individuals. Each scutal area with two small median protuberances, those on area I and II being the most apparent. Ocularium short and unarmed, shallowly canaliculate, its width longer than height. Supra-cheliceral lamina dorsally toothed with irregular and minute sub-quadratic tubercles (Figs 3A, 6G). Labrum smooth, short and unarmed, the terminal end curves downwards ventrally (Fig. 6D–F). Coxa I dorso-anteriorly and coxa IV dorso-posteriorly sometimes armed with visible small sub-quadratic tubercles.

Both scutal area and coxae dorsally muddy, yellowish brown, with small dark-brown and light-yellow spots scattered unevenly throughout; central figure borders slightly highlighted in light-yellow pattern. The IV area, including the two latero-posteriorly protuberances, is highlighted with a bright yellow or light brown horizontal band.

Ventral (Fig. 3B). Smooth and unarmed except for a scattering of short hairs; coxae scattered with tiny coarse granules similar to that of the dorsal. Lateral margins of both the genital operculum and coxae lined with sub-quadratic tubercles. Venter of trochanters unarmed.

Ventral surface light yellow. Coxae greyish brown. Free tergites brown. Posteriorly margins of free tergites and anal operculum dark brown.

Chelicera (Figs 2F–G, 4C–D). Short and slender, mostly unarmed. 1st segment armed with a ventral spur while 2nd segment scattered with dorsal hairs. Tiny granules are also found disto-laterally, more apparent in a small cluster behind the fingers. In some specimens a small dorso-lateral granule can be found, right behind the movable finger. Fingers toothed and curved.

The entire chelicerae are pale yellow with dark brown fingers and granules.

Pedipalpus (Fig. 4A–B) Slender and short; trochanters ventrally toothed. Femora also ventrally and retrolaterally armed with a row of sharp tubercles. A laterodistal apophysis can be found on both pedipalpal patella and a smaller (size varies among individuals) apophysis can be seen extending out of the sides of the tibia (Fig. 4). Both patella and tibia densely armed with dorsal and retrolateral, small, sharp tubercles. Tibiae and tarsi both armed with long hairs, with tarsi being the most densely armed. Pedipalps armed with a single terminal pectinate claw.

Trochanters, femora, patellae and tibiae brownish yellow, tarsi translucent yellow, similar to venter.

Legs (Fig. 5). All legs long and slender. Leg I femur generally longer than body. There are no pseudoarticulations on all legs. The surface of the leg filled with tiny granules that, at first glance, may resemble dirty soil particles stuck to it (Fig. 5C–D). Leg tarsi without scopulae and armed with a single simple claw.

Penis (Figs 6A–C, 7). Overall structure dorso-ventrally flattened. Truncus slender, long and unarmed. Glans short, with 1–2 lateral bristles (*Sinnesborst* from Martens 1987). Alate with larger ventral lamella and smaller dorsal mantle (*Lamelle* and *Ummantelung* from Martens 1987); the former curves dorsally at the edges and fuses with only the posterior section of the mantle, enveloping it. A large 'pocket' opening (*Tasche* from Marten 1987) is formed that extends to 2/3 of the lateral alate. The structure curves ventromedially, lamellae swollen. The mantle extends only slightly down 1/3 of the truncus. The ventral tendon (*Sehne* from Martens 1987) elongates and attaches to the posterior end of the truncus. Overall structure of the genital resembles a curved partisan spear with a pair of rounded lateral protrusions.

Female (Fig. 2C–D, F). Overall similar to its male counterpart but generally larger in overall size. Female abdominal free tergites longer than males', the latter shorter and compressed, slightly extending downward. Both pedipalps and chelicerae slightly larger in females than males (Fig. 2F).

Ovipositor Overall structure similarly flattened as penis. Shape of the seminal receptacle as shown in Fig. 6H.

Measurements (Tables 1–2). Male Holotype (Female paratype): body 3.61 (5.19) long, 2.67 (3.25) wide at the widest portion; ocularium 0.54 (0.56) wide, 0.46 (0.48) long; chelicera segment I 0.73 (1.82), segment II 1.10 (2.59). Measurements for the pedipalps and legs as in Table 1.

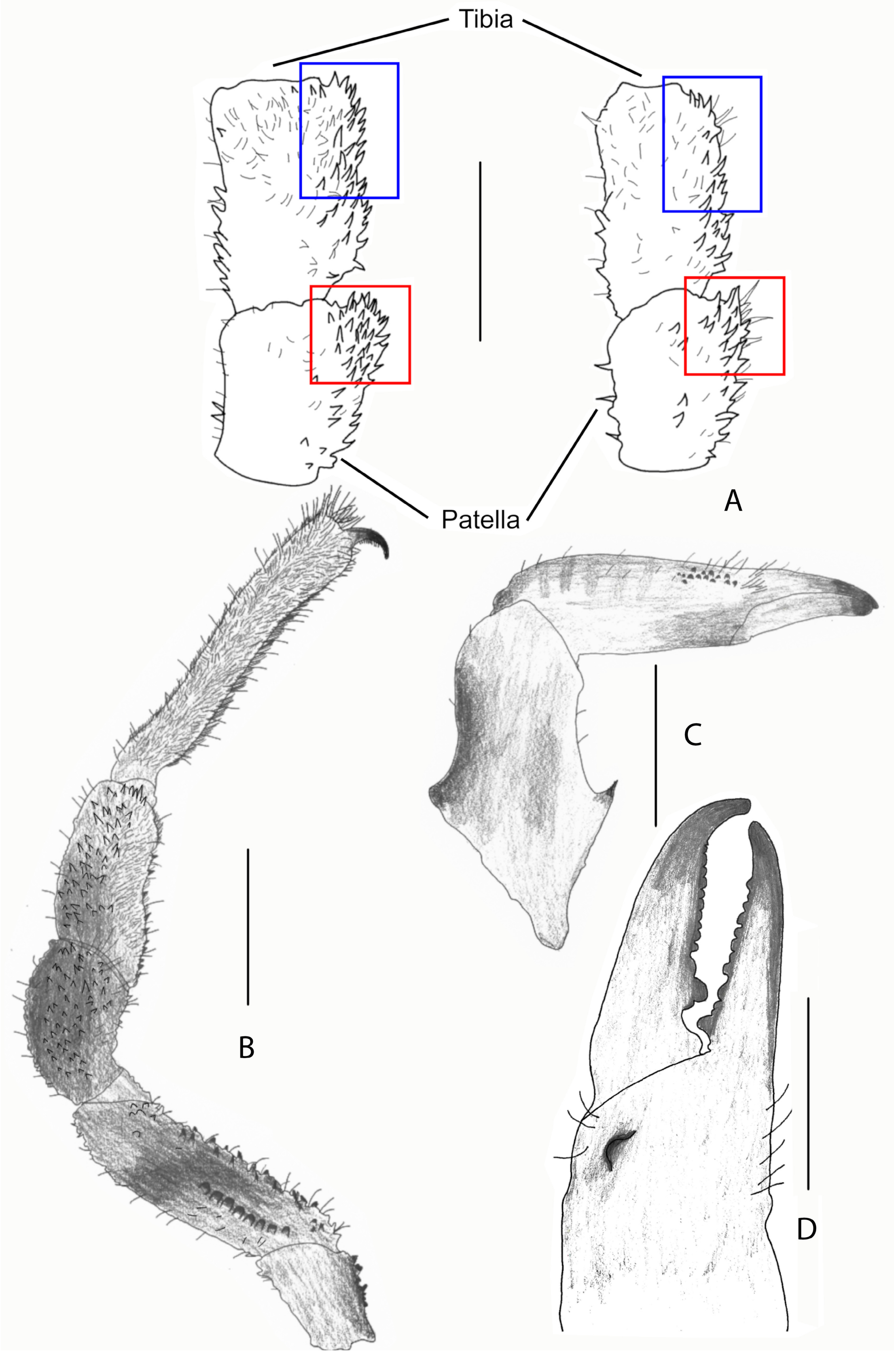

FIGURE 4. **A**–**B** *Pseudoleiobunum lutulentum* **sp. nov.**, close-ups of pedipalpal tibia and tarsus apophyses. **A (Left)** Close-up of male pedipalpal patella and tibia, LINGU-INV154. **A (Right)** Close-up of female pedipalpal patella and tibia, LINGU-INV146. Red rectangles for patella apophyses, blue rectangles for tibia apophyses. Scale bar: 2 mm. **B** Full lateral view of left pedipalp; **C**–**D** *Pseudoleiobunum lutulentum* **sp. nov. C** Full lateral view of left chelicera. **D** Close-up of left chelicerae distal structure. Scale bars: 0.5 mm.

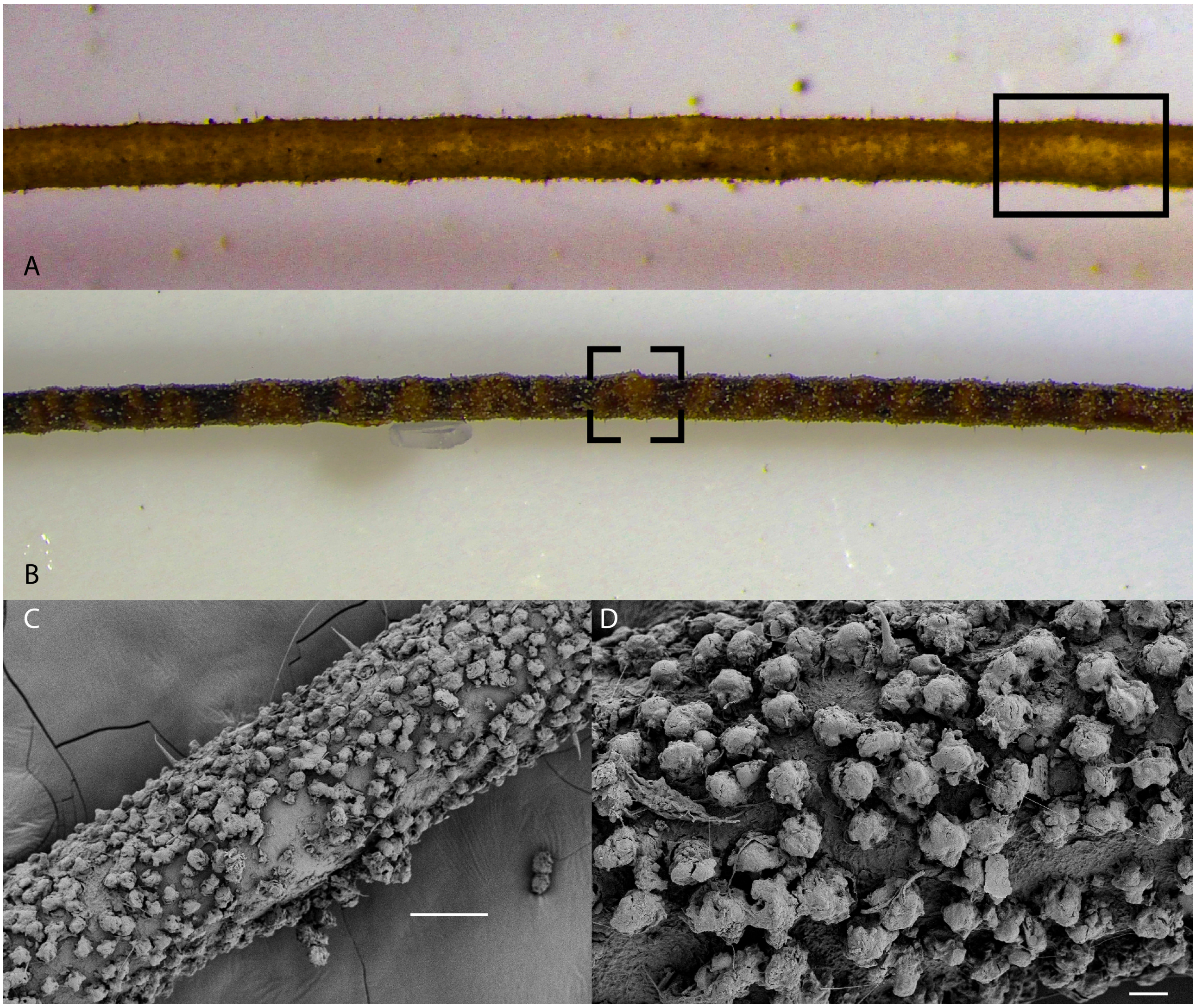

FIGURE 5. *Pseudoleiobunum lutulentum* **sp. nov.**, close-up comparisons of femora II under light microscope and scanning electron microscope of leg surface, revealing the granules that are present in the legs of *P. lutulentum* **sp. nov. A** Light microscopy of leg II femur, LINGU-INV72. **B** Light microscopy of leg II femur, LINGU-INV106. **C** Scanning electron microscopy of the surface of leg II femur, LINGU-INV115. **D** Close-up of the granules on leg surface, LINGU-INV116. Scale bars: 100 µm for C; 20 µm for D.

Variation. The shape of the dorsal scutum can vary between individuals from being overall oval to the abdominal scutum being triangular with the lateral-posterior edges being elevated, flat to a swollen, oval shape typical in Gagrellinae harvestmen (but still with an elevated, angled dorsal scutum). Overall coloring of individuals may vary from pale brown to overall dark, muddy yellow (See Fig. 11A–D). As mentioned in the Etymology section, all these colors are perfect to camouflage with their habitats along streams and muddy ground near water bodies (See Fig. 11E). When threatened, the harvestman flattens its body to the surface with all eight legs fully extended. Despite being a delimiting feature, the length of leg I femora is highly variable amongst individuals (See Table 1). For females, body is generally longer than femora while it is the opposite for most male individuals or even smaller female individuals (See Appendices 7–8).

TABLE 2. Morphological measurements of male body lengths (BL) and leg femora I lengths (FIL), body width at the widest portion together with a ratio of femora I length against body length (FIL/BL) for East Asian Leiobuninaes, including *Pseudoleiobunum lutulentum* **sp. nov.** All measurements in millimeters (mm).

Group	**Species**	**Locality**	**BL**	**BW**	**FIL**	**FIL/BL**
Pseudoleiobunum & *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	Lantau Island, Hong Kong	3.03	2.39	3.9	**1.29**
Pseudoleiobunum & *maximum*-group	*Pseudoleiobunum maximum distinctum*	Mt. Yuwan, Amami-oshima Island, Japan	9.8	6.8	9.7	**0.99**
Pseudoleiobunum & *maximum*-group	*Pseudoleiobunum maximum formosum*	Mt. Hsuehshan, Taiwan	5.81	4	9.3	**1.6**
Pseudoleiobunum & *maximum*-group	*Pseudoleiobunum maximum yushan*	Mt. Yushan, Taiwan	4.45	3.1	5.1	**1.15**
Pseudoleiobunum & *maximum*-group	*Pseudoleiobunum japanense japanense*	Nishitanzawa, Japan	6.3	4.2	7.5	**1.19**
Pseudoleiobunum & *maximum*-group	*Pseudoleiobunum japanense japoonicum*	Mt. Hikosan, Japan	7.6	4.5	5	**0.66**
					Mean	**1.60**
rubrum-group	*Leiobunum rubrum*	Yakushima Island, Japan	3.2	2.24	7.9	**2.47**
curvipalpe-group	*Leiobunum hikocola*	Mt. Hikosan, Japan	3.44	2.25	6.2	**1.8**
curvipalpe-group	*Leiobunum sadoense*	Mt. Myoken, Sado Island, Japan	3.3	2.2	6.3	**1.91**
curvipalpe-group	*Leiobunum montanum*	Mt. Tsubakuro, Japan	4.24	/	5.71	**1.35**
curvipalpe-group	*Leiobunum oharai*	Sihou, Taiwan	3.12	/	5.7	**1.83**
curvipalpe-group	*Leiobunum tohokuense*	Oirase, Japan	3.99	/	7.33	**1.84**
curvipalpe-group	*Leiobunum curvipalpi*	Kita-Karuizawa, Japan	5.8	3.4	5.7	**0.98**
curvipalpe-group	*Leiobunum manubriatum*	Nenokuchi, Japan	3.9	/	6.8	**1.74**
curvipalpe-group	*Leiobunum hiraiwai*	Kamikochi, Japan	5.0	2.9	6.2	**1.24**
curvipalpe-group	*Leiobunum globosum*	Nenokuchi, Japan	4.5	2.8	7.7	**1.71**
curvipalpe-group	*Leiobunum kohyai*	Mt. Koya, Japan	5.1	/	7.6	**1.49**
curvipalpe-group	*Leiobunum simplum*	Yokoo Hutte, Japan	3.1	1.1	7.0	**2.26**
curvipalpe-group	*Leiobunum hiasai*	Kitazawa Pass, Japan	4.2	/	5.4	**1.29**
					Mean	**1.51**
East Asian *Nelima*	*Nelima nigricoxa*	Mt. Hikosan, Japan	5.7	/	14.4	**2.53**
East Asian *Nelima*	*Nelima genufusca tuberculata*	Jeju Island, Korea	6	4.1	14.1	**2.35**
East Asian *Nelima*	*Nelima suzukii*	Nopporo, Japan	3.78	/	6.78	**1.79**
East Asian *Nelima*	*Nelima coreana*	Suyeo, Korea	3.8	2.6	7.2	**1.89**
East Asian *Nelima*	*Nelima parva*	Mt. Hikosan, Japan	2.2	1.8	6.1	**2.77**
East Asian *Nelima*	*Nelima similis*	Hakone, Japan	2.1	1.5	3.8	**1.81**
East Asian *Nelima*	*Nelima aokii*	Nippara, Japan	6.55	/	16.1	**2.46**
East Asian *Nelima*	*Nelima okinawaensis*	Nago Island, Okinawa, Japan	4.5	3.4	15.7	**3.49**
East Asian *Nelima*	*Nelima satoi*	Mt. Ishizuchi	5.73	/	9.37	**1.64**
East Asian *Nelima*	*Nelima taiwana*	Mt. Hsuehshan, Taiwan	3.1	/	10.9	**3.52**
					Mean	**2.43**

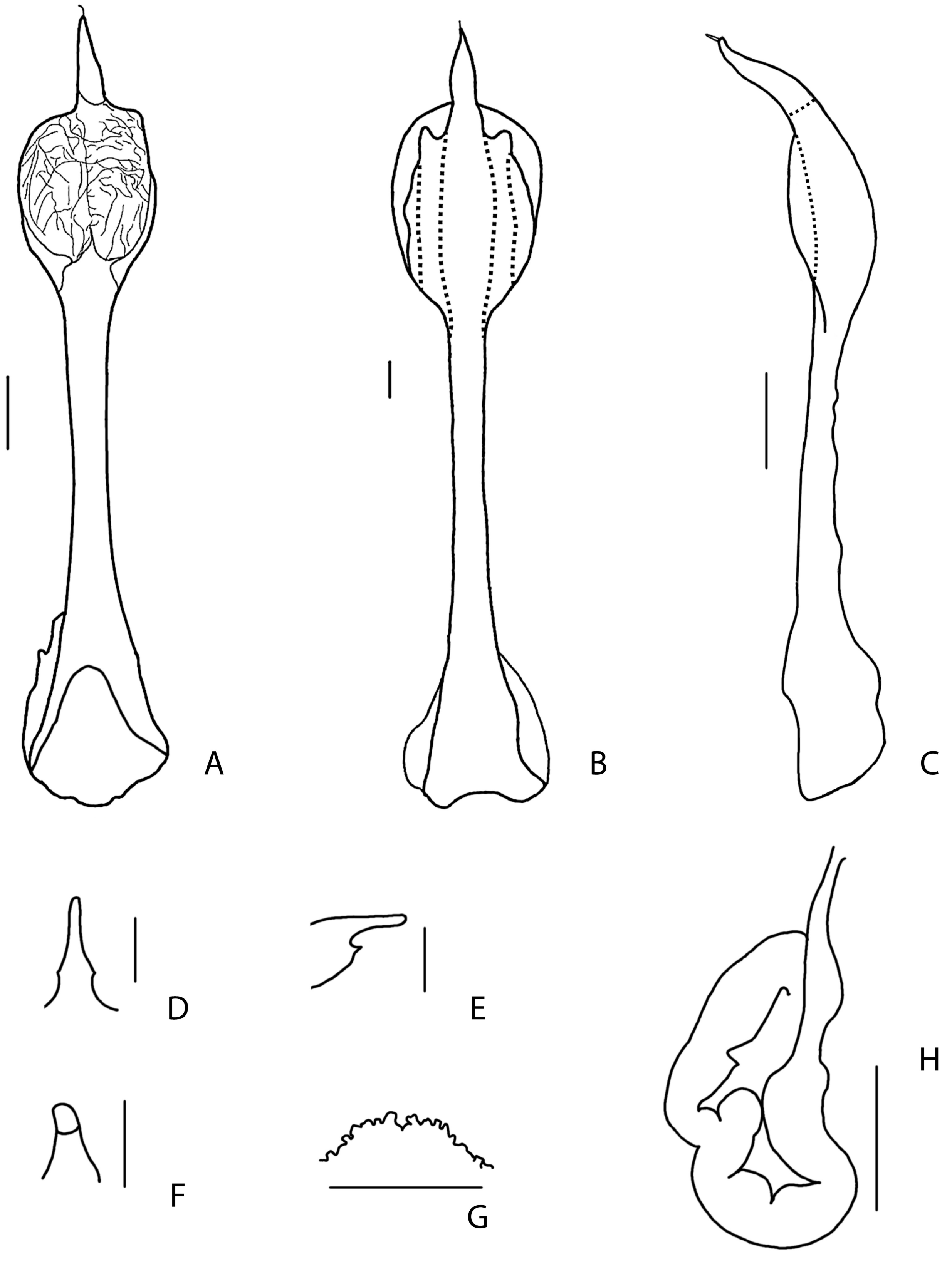

FIGURE 6. *Pseudoleiobunum lutulentum* **sp. nov.**, different views of male, female genitals, labrum, supracheliceral lamina and a close-up of the female seminal receptacle. **A** Ventral view of male genital, LINGU-INV47. **B** Dorsal view of male genital, LINGU-INV46. **C** Lateral view of male genital, LINGU-INV154. **D** Dorsal view of labrum, LINGU-INV154.. **E** Lateral view of labrum, LINGU-INV154. **F** Ventral view of labrum, LINGU-INV154. **G** Dorsal view of the supracheliceral lamina, LINGU-INV154. **H** Seminal receptacle, LINGU-INV145. Scale bars: 200 µm for A & B; 500 µm for C; 0.2 mm for D, E & F; 0.5 mm for G; 20 µm for H.

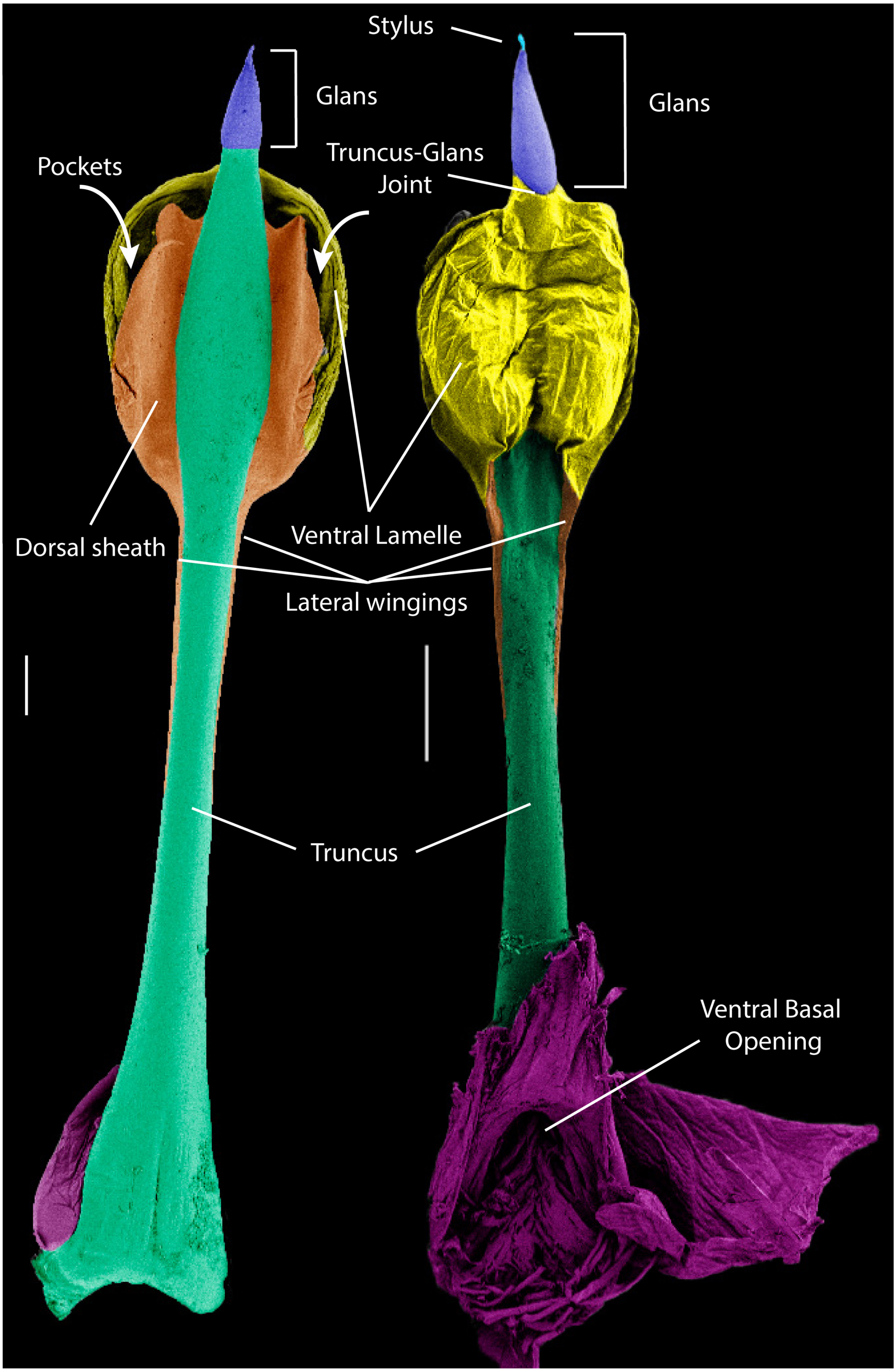

FIGURE 7. *Pseudoleiobunum lutulentum* **sp. nov.** Male genital under electron microscopy. **A** Dorsal view, LINGU-INV46. **B** Ventral view, LINGU-INV47. Scale bars: 100 µm for A; 200 µm for B.

Notes on other members of the superspecies *maximum*

***Pseudoleiobunum* (superspecies *maximum*) *maximum maximum* Roewer, 1910**

Liobunum maximum Roewer, 1910: 208–209 [Type: 1♂ & 1♀ from Fujian, Siemssen, China leg. in Museum, Hamburg; China: 1♀ from China Soo-Choo, N. A. Holst leg. 1892 in British Museum, London]; 1923: 894–895.
Leiobunum maximum Roewer, 1957: 343.
Leiobunum maximum maximum Suzuki, 1976: 195–196.

Notes. Four subspecies were described by Suzuki (1976). This species and *Pseudoleiobunum japanense* are allopatric and can be a pair of vicarious species that constitute a single superspecies.

Pseudoleiobunum* (superspecies *maximum*) *maximum formosum

Liobunum maximum (in part) Roewer, 1957: 343.
Leiobunum maximum formosum Suzuki, 1976: 196, Figures 1–3, 127–131, 287 (Type: Mt. Hsuehshan, Taipei, Taiwan); 1977: 149.

Diagnosis. General morphology similar to *Pseudoleiobunum maximum distinctum* Suzuki, 1973, but with less armament on the pedipalps and legs. Labrum unarmed, mushroom-shaped with an enlarged distal portion (Suzuki 1976: fig. 1–2). Female labrum thin, without the enlarged, mushroom-capped distal portion (Suzuki 1976: fig. 3). Supracheliceral lamina narrow and pointed (Suzuki 1976: fig. 128).

Distribution. Northern Taiwan (Figure 16).

***Pseudoleiobunum* (superspecies *maximum*) *maximum yushan* Suzuki, 1976**

Leiobunum maximum yushan Suzuki, 1976: 198, Figures 4–5, 132–138, 288–289 (♂ Holotype: Tongpoo Hütte, Mt. Yushan, Taiwan); Suzuki, 1977: 149.

Diagnosis. General morphology similar to *Pseudoleiobunum maximum formosum*, but the penis is shorter and the glans is stout with no developed distolateral portion, while for other *P. maximum* subspecies most possess a developed lateral alate winging (Martens 1987), generally folded dorsally (Suzuki 1976: figs 131, 138, 146, 160).

Distribution. Mt. Yushan, Eastern Taiwan. (Fig. 12).

***Pseudoleiobunum* (superspecies *maximum*) *maximum distinctum* Suzuki, 1973**

Leiobunum maximum distinctum Suzuki, 1973: 260–263, Figures 4–5, 132–138 (♂ Holotype: Mt. Yuwan-dake, Is. Amami-Oshima, Japan); 1976: 196, Figures 6–8, 95.

Materials examined. (Is. = Island) JAPAN, KAGOSHIMA PREF.: Is. Amami-Oshima, Amami City, Sumiyo-cho, Kawauchi, Kawauchi Dam, 22 May 1999, 1♀, H. Minato; Is. Amami-Oshima, Setouchi-cho, 2 juv., 22 February 2005; 1 juv., 27 February 2005; 2 juv., 28 February 2005, A. Tanikawa; Oshima-gun, Setouchi-cho, Is. Kakeroma, 2 juv., 26 February 2005, A. Tanikawa; Is. Uke-shima, 1 juv., 27 February 2005, A. Tanikawa; Kikai-cho, Is. Kikai-jima, Hyakunodai [N28°19.0506', E129°59.0491'], 190 m, 2 juv., 4 March 2005, M. Yago—JAPAN, OKINAWA PREF.: Is. Okinawa, Nago City, Mt. Kazu-u-dake, 1 juv., 13 February 1982, M. Shimojana; Kunikami-son, Hiji Campground, 12 March 1982, 2 juv. (subad.), H. Okada; Is. Iriomote, R. Aira-gawa, 1♀, 1 April 2009, K. Takenaka.

Diagnosis (Fig. 2B). General morphology similar to *P. maximum maximum*, except for having much stronger legs and chelicerae and pedipalps with more armaments (Suzuki 1976). Scutal surface densely but regularly granulated. Ocularium short, generally canaliculate but dorsally armed with a row of small, regularly spaced denticules. Supracheliceral lamina pointed, sparsely scattered with small but distinct sharp granules. Pedipalpal tarsal claws with general reduced teeth that is more significant compared to other subspecies of *P. maximum*, in some individuals the "teeth" are reduced to small, blunt granulations (Suzuki 1973). Legs unarmed except for scatterings of small sharp denticles. Penis glans long, similar to that of *P. maximum formosum*, with folded lateral alate wingings (Suzuki 1973, Martens 1987).

Distribution. The Ryukyu Islands (Is. Kikai-jima, Is. Amami-oshima, Is. Okinawa, Is. Iriomote) (Fig. 12).

Notes. This subspecies is univoltine and overwinters as juvenile. Adults appear from June to August.

***Pseudoleiobunum* (superspecies *maximum*) *japanense japonicum* Roewer, 1957**

Pseudoleiobunum japonicum Suzuki, 1940: 95.
Leiobunum suzukii Roewer, 1957: 343, Figures 12–13 in Tafel 26 (Type: 2♀ from Yokohama).
Leiobunum bifrons Roewer, 1957: 343, Figure 14 in Tafel 26 (Type 1♀ from Nagasaki).
Metaliobunum japonicum Suzuki, 1940: 276–279; 1960: 22; 1965: 353.
Leiobunum japanense japonicum Suzuki, 1976: 202–204, Figures 17–22, 96, 147–160; Tsurusaki & Sasaji, 1991: 11, Figure 5B; Suzuki, 1986:26, Figures 30–31; Kato *et al.*, 2023: 63.
Leiobunum japanense Tsurusaki, 2006: 163, Figure 8B.
Leiobunum japanense suzukii Crawford, 1992: 30.

Materials examined. (NT. = N. Tsurusaki). JAPAN, MIE PREF.: Owase City: Yanokawa, Mt. Takamine, 400 m, 2 juv., 25 March 1989, Y. Nishikawa; NE of Yanokawa Pass, 310–380 m, 3 juv., 26 March 1989, Y. Nishikawa—JAPAN, SHIGA PREF.: Otsu City, Katsuragawa-Sakashita-cho, 450 m, 1 juv., 3 October 2011, N. Nunomura; Koka City, Tsuchiyama-cho, Left Bank of Nosugawa Dam, 410 m, 1♀, 27 May, 2012, NT.; Maibara City, Kozuwara, Oku-Ibuki Skiing ground [N35°31.078', E136°22.5867'], 635 m, 1♂, 9 June 2017, NT.—JAPAN, KYOTO PREF.: Fukuchiyama City, Yakuno-cho, Oku-Mizusawa, 1♂2♀,13 July 2002, M. Sasakawa—JAPAN, OSAWA PREF.: Kishiwada City, Mt. Izumi-Katsuragi, 850 m, 2 juv., 28 March 1997, NT.; Ibaraki City, Shobo, Left Bank of R. Ai, 80 m, 10♂24♀, 2 June 1994, Y. Nishikawa; Mino-o City: Todoromi, 9 juv., 7 May 2010, H. Anaze *et al.*; Mino-o Park, Sasagare-no-komichi, ca. 370 m, 3 juv., 26 March 1977, Y. Nishikawa; Higashi-Osaka City, Yamate-cho, Hiraoka Shrine, 1♂1♀, 29 May 2005, H. Tanaka—JAPAN, HYOGO PREF.: Shiso City, Haga-cho, Hitsujigadaki-guchi, 1♀, 10 June 1990, K. Yamamoto; Shiso City, Oya-cho, Yokoiki-oku, 1♀, 2 August 1990, K. Yamamoto; 1 juv., 3 November 1990, K. Yamamoto—JAPAN, NARA PREF: Gojo City, Nishi-Yoshino-cho, Tentsuji Pass to Mt. Norikura [N34°14.051' E135°44.4341'], 850 m, 1 juv., 19 October 2015, NT.; Yoshino-gun, Totsukawa-mura, Mt. Shaka-ga-dake, Fudo-Kiyadani [N34°6.3368' E135°52.3868'], 1090 m, 3 juv., 20 October 2015, NT.; Kamikitayama-mura, Mt. Oda-ga-hara, 1 juv., 26 May 1973, H. Minato; Tanabe City: Mt. Jogamori, 1♂2 juv., 4 June 2018, I. Matoba; Ryujin-mura, Mt. Gomadan, 1♂, 15 July 2018, I. Matoba; Hongu-cho, Hatenashi Mountains, Higashinokawa-Oku, 1100 m, 1♀, 26 July 1978, H. Minato; Arida-gun, Aridagawa-cho, Mt. Higashidani, 1♂, 24 June 2017, I. Matoba; Mt. Toishi, 1♂, 4 July 2019, I. Matoba; Mt. Shirama, 1♂, 16 May 2019, I. Matoba; Kaiso-gun, Kimino-cho: Ta, 250 m, 4♀, 28 February 1994, K. Katsura; Machida, Seminar House, 270 m, 1♂1♀, 19 May 2012, R. Yuasa; Nishi-Muro-gun, Ohto-mura, Hyakken Gorge, 3 juv., 2 May 1999, H. Minato; Higashi-Muro-gun, Kozakawa-cho, Hirai, 1♀, 9 August 1980, H. Minato; Nachi-Katsu-ura-cho, Seigantoji Temple, 340 m, 1♀, 28 July 1983, NT.; Iwade City, Negoro, Genki-no-mori, [N34°17.7167', E135°19.8347'], 1♀, 23 May 2021, Y. Yamamoto—JAPAN, TOTTORI PREF.: Tottori City, Kokufu-cho, Amedaki Falls, 460 m, 1♀, 1 June 1989, NT.; M. Murakami, K. Shimokawa, 440 m, 1 juv., 15 November 2007, NT.; Tottori City, Kawahara-cho, Gobara, 1 juv., 29 October 2010, Yachiyo Enginering; Ochidani, 50 m, 1♀, 27 May 1988, NT.; Mitaki Gorge, 560 m, 1♂, 24 May 1992, M. Murakam; Kitamura, along Midori-shigen Forest Road [N35°23.4038', E134°5.216'], 440 m, 1 juv., 27 March 2017, NT.; Tottori City, Saji-cho, Sanno-daki, Falls, 430 m, 1♂2♀, 3 June 2001, NT.; T. Adachi & S. Okada; KItadani, 830–1200 m, 1♀, 1 June 2002, NT.; Tottori City, Shikano-cho, Mt. Jubo, Kochi to Azogoe, 370 m, 1♂, 14 June 1992, H. Kunimoto.; Tottori City, Shikano-cho, Mt. Jubo, Obata Forest Road, 230 m, 1 juv., 2 May 1992, NT.; 230 m, 1 juv., 18 May 1992, NT.; 230 m, 1♀, 16 June 1992, NT.; Iwami-gun, Iwami-cho, Nagatani, 200 m, 1♀, 18 May 2004, NT. *et al.*; Kugami, Higashihama, Kanro Shrine [N35°35.9478', E134°21.6338'], 10 m, 1 juv., 28 March 2017, NT.; Yazu-gun, Wakasa-cho, Mt. Hyonosen, Hibiki-no-mori, 850 m, 1♀, 3 August 2003, T. Okada; Yazu-gun, Chizu-cho, Ashizu-kei, Mitaki Dam [N35°16.54', E134°20.4293'], 820 m, 1♂, 3 June 2003, NT.; Ute Pass, 600 m, 1 juv., 9 August 2005, NT.; Mitaki Dam, 720–740 m, 1 juv., 26 November 1989, NT.—JAPAN, SHIMANE PREF.: Izumo City, Tachikue-kyo, 40 m, 1♀, 15 July 1988, NT.—JAPAN, OAKYAMA PREF.: Mimasaka City, Shiramizu, 225 m, 2♀, 22 June 2015, M. Yamada—JAPAN, HIROSHIMA PREF.: Shobara City, Takano-cho, Oka-Ouchi, 1♀, 22 June

2001, S. Okada; Saijo-cho, Misaka, 5 juv., 8 September 2005, S. Nakamura; Oi Pass, Oi Pass Shrine, 640 m, 1♂, 6 August 1990, NT.; Hiroshima City, Asa-kita-ku, Uga-kyo, 2♀, 30 May 1976, NT.; Kure City, Niko-kyo, 50m, 1♂, 17 July 1990, NT.; Hatsukaichi City, Mt. Gokurakuji, 1♀, 25 May 1975, NT.; Yamagata-gun, Aki-Ota-cho, Sandan-kyo Gorge, 1♂1♀, 3 July 1977, NT. & H. Komatsu—JAPAN, TOKUSHIMA PREF.: Tokushima City, Hachiman-cho, Bunka-no-mori, 1 juv., 25 November 1990, T. Tanabe; Myozai-gun, Kamiyama-cho, Mt. Kumosozan [N33°54.7095',E134°17.3679'], 1120–1140 m, 2♂, 1 August 1997, NT.; Oe-gun, Kamikawa-ho, Mt. Kotsuzan, 1080–1100 m, 1♂1♀1 juv., 18 May 1998, NT.; Miyoshi City, Ochiai Pass, 1320 m, 1 juv.,13 October 1994, T. Tanabe; Higashi-Iya, Sano, 1180m, 1♀, 13 July 1991, M. Kamata—JAPAN, KAGAWA PREF.: Zentsuji City, Oasa-cho, Mt. Oasa, ca. 450 m, 1 juv., 14 November 2006, S. Mitani; Kan-nonji City, Mt. Umpenji, 850 m, 1 juv., 16 May 2019, S. Mitani; Sanuki City, Okuboji Temple, 450 m, 1♀, 15 June 2007, NT. & M. Takeuchi; Takamatsu City, Shionoe-cho, Mt. Otaki, 1♂1♀, 27 July 2003, S. Mitani; Nakatado-gun, Kotonan-cho, Hirakawa, 1♀, 2 July 2001, S. Mitani; Kotoshira-cho, Mt. Kotohira, 1♂1♀, 15 September, 2002, S. Mitani; Chunan-cho, Mt. Onoseyama, 1♂, 14 July 2003, S. Mitani—JAPAN, EHIME PREF.: Matsuyama City, Mt. Takanawa, 1 juv., 5 May 1972, NT.; 1♂, 17 July 2010, R. Ogawa; 960 m, 1 juv., 3 May 1993, NT.; 920 m, 1 juv., 4 April 1994, NT.; Matsuyama City, Mt. Hikiji-yama, 900 m, 1♂, 11 August 2001, NT.; Mt. Sugitate, under Sugitate Bridge, 1 juv., 5 May 1970, NT.; Yuyama-Aonami, 2♂, 3 June 1973, H. Tsutsumi; Shuso-gun, Tambara-cho, Kurase, Iwane Shrine, 110 m, 1 juv., 23 April 2000, NT.; To-on City, Mt. Saragamine, Kambayashi, 1♂, 21 July 1972, NT. *et al.*; Kambayashi, Kambayashi Route, 1 juv., 3 May 1972, NT.; Kami-Ukena-gun, Kuma-kogen-cho, Mt. Saragamine, 1 juv., 23 April 1972, NT.; 3 juv., 29 April 1972, NT., Y. Yaeshima, A. Wake; 3 juv., 14 May 1972, NT & H. Yamashita; 1♂, 4 June 1972, NT. *et al.*; 950 m, 1 juv., 5 November 1974, NT.; 1♀, 21 May 1986, T. Tanabe; Kuma-kogen-cho, Teppoishigawa, 1♀, 13 August 2000, H. Ishikawa; Bansho-dani, 1♂, 20 August 2000, H. Ishikawa; Kuma-kogen-cho, Mt. Ishizuchi, Tchichigoya to Mt. Iwaguro, 1600 m, 1♂, 5 August 1982, NT.; Mt. Omogo, 1360–1500 m, 3♂2♀, 3 August 1982, Y. Sugino; Mt. Okawamine, 1250 m, 1 juv., 5 November 1993, NT.; 1400m, 1 juv., 5 November 1993, NT.; Kita-gun, Uchiko-cho, Oda-Miyama, 800 m, 3 juv., 6 October 1992, E. Yamamoto; 2 juv., 4 May 1994, E. Yamamoto; 800 m, 2 juv., 25 May 1993, E. Yamamoto; Koyayama, ca. 1200–1300 m, 3♂4♀, 12 June 1988, E. Yamamoto; Koyayama, 1♀, 2 August 1995, E. Yamamoto; Koyayama, 1♀, 5 August 1995, E. Yamamoto; Namakusa-dani, 8 juv., 1 May 1994, E. Yamamoto; Nakakusa-dani, 2♀, 25 June 1994, E. Yamamoto; Namakusa-dani, 1♀, 20 July 1994, E. Yamamoto; Nakmakusa-dani, 3 juv., 18 October 1994, E. Yamamoto; 1♂1♀, 10 June 1994, E. Yamamoto; Namakusa-dani, 1220 m , 4♀, 1 May 1994, NT. & C. Tsurusaki; Natural Forest, 800–900 m, 1 juv., 7 June 1988, E. Yamamoto; Shishigoe, 980 m, 1♀, 23 August 1994, E. Yamamoto; Namakusadani, 3♂8♀, 7 August 1995, E. Yamamoto; Namakusa-dani, 3♂1♀, 10 August 1995, E. Yamamoto; Masa-goya, 800m, 2 juv., 2 May 1994, NT.; 3♂4♀, 5 August 1991, E. Yamamoto; 1♂1♀, 11 August 1995, E. Yamamoto; Kita-gun, Uchiko-cho, Oda: Miyanotani, 400 m, 1 juv., 2 January 1995, E. Yamamoto; 1 juv., 1 April 1992, E. Yamamoto; 400 m, 1♂4♀, 10 August 1992, E. Yamamoto; Kita-gun, Hijikawa-cho, Yamatosaka, 1♂2♀, 22 June 2004, K. Uyeno; Kita-Uwa-gun, Kihoku-cho, Ogura, Odaru-Medaru Falls, 255 m, 2♂, 28 May 2013, NT.—JAPAN, KOCHI PREF.: Nagaoka-gun, Otoyo-cho, S. Ugi, Yasaka Shrine, 1 juv., 6 April 1994, Y. Murakami; Agawa-gun, Ino-cho, Nanokawagoe, 1♂, 22 June 2011, H. Ishikawa—JAPAN, FUKUOKA PREF.: Tagawa-gun, Soeda-cho, Mt. Hikosan [N33°29.1069', E130°55.8407'], 800 m, 2♂1♀, 17 June 2022, NT.; 1100–1199.5 m, 1♀, 30 July 1982, NT.; Asakura City, Mt. Koshozan [N33°29.0169', E130°43.5336'], 850 m, 1♂, 17 June 2022, NT.—JAPAN, NAGASAKI PREF.:: Iki-gun, Ishida-cho, Kuki, 2♀, 3 June 1990, M. Yamashita; Kuki, 1♂, 2 May 1991, M. Yamashita; Kuki, 3♂2♀, 25 May 1991, M. Yamashita; Kukishoku, 3 juv., 4 April 1994, M. Yamashita; Kukishoku, 3♂11♀, 18 May 1991, M. Yamashita; Kukishoku, 1♀, 8 May 1992, M. Yamashita; Kukishoku, 3♀, 10 May 1992, M. Yamashita; Unzen City, Unzen, Mt. Yadake, Hobaru, 730 m, 1 juv., 29 November 1993, NT. & C. Tusrusaki; Goto City, Is. Wakamatsu, Mt. Ryukan, 120 m, 1 juv., 7 February 2008, K. Okumura; Is. Fukue, Mt. Outou, 80 m, 1♂2♀, 9 May 2009, K. Okumura; Is. Fukue, Mt. Chichigadake, 150 m, 2 juv., 14 February 2009, K. Okumura; Is. Fukue, Mt. Chichigadake, 150 m, 5 juv., 2 March 2009, K. Okumura; Matsuura-gun, Shin-Kamigoto-cho, Is. Nakadori, Hifumi-daki Falls, 1 juv., 8 February 2009, K. Okumura—JAPAN, KUMAMOTO PREF: Kikuchi City, Kikuchi-keikoku, 1♂, 29 July 1970, M. Yoshikura—JAPAN, MIYAZAKI PREF.: Mito-gun, Nango-mura, Sasanotoge Pass, 1200 m, 1 juv., 15 November 2012, K. Nishi. Kobayashi City, Suki, along Ayaminami Forest Road, 400 m, 1 juv., 25 July 2012, K. Nishi; 1 juv., 25 December 2012, K. Nishi; Higashi-usuki-gun, Shiiba-son, Mt. Eboshi, 1470 m, 1♀, 16 June 2013, K. Nishi—JAPAN, KAGOSHIMA PREF.: Is. Yakushima, Arakawa, Collision trap, 1200 m, 1 juv., 30 October 2007, T. Yamauchi.

Diagnosis. (Fig. 2A) General morphology similar to type species *P. japanense japanense* but differs in the shape of leg trochanters, the former being unarmed and generally oval in appearance while the latter has two dorsolateral and anterior tubercles on the trochanters (Suzuki 1976: 202–204, figs 142, 152–155). This species also possesses relatively smaller pedipalpal patellar and tibial apophyses when compared to other species of the *Pseudoleiobunum* genus (Suzuki 1976).

Habitat. This subspecies is univoltine and overwinters as juveniles. Adults can be found from May to August. They can be found under logs or stones on well-moistened forest ground or on the wall of wet cliffs along mountain streams, rarely on tree trunks.

Distribution. Widespread in western Japan (Kyushu, Shikoku, Chugoku, Kinki District, West Chubu District) (Fig. 12).

Notes. *Pseudoleiobunum japonicum* was first described by Suzuki (1940) as *Metaliobunum japonicum* based on a male collected from Mt. Ishizuchi, Shikoku as the holotype. Suzuki considered this species and *P. japanense japanense* Müller, 1914 to be conspecific and redescribed the former as *Leiobunum japanense japonicum* (Suzuki 1976). Crawford (1992) considered the name *Leiobunum japanense japonicum* a junior homonym of *Leiobunum japonicum* Müller, 1914 and proposed the replacement name *Leiobunum japanense suzukii* Roewer, 1957.

However, upon phylogenetic analysis conducted by Hedin *et al.* (2012), *L. japonicum* was found to form a clade with *Pseudogagrella amamiana* Nakatsudi, 1942. Therefore, *L. japonicum* likely should be transferred to Gagrellinae in the future.

By transferring *L. japanense japonicum* to *Pseudoleiobunum*, the homonym problem is resolved. Thus, we use *P. japanense japonicum*, instead of Crawford (1972)'s replacement name *L. japanense suzukii*, for this subspecies.

Molecular Studies Result

All the sequence data for *P. lutulentum* **sp. nov.**, together with the three samples from Japan, have been deposited to GenBank (accession numbers in Appendix 6). Unlike Hedin *et al.* (2012), we employed a maximum likelihood method for the tree construction (See Methods). We highlight and discuss results from two datasets: *28S* and concatenated dataset, as they have the highest resolution amongst the datasets. Other trees constructed from other datasets are provided in Appendices 1–4.

***28S* Analysis (Fig. 8)**. The lengths of the sequences range from 310 to 1214 base pairs (bp). In the phylogeny, *Leiobunum* is separated into geographical clades (bootstrap values = 24–92). Leiobuninae from Mexico and United States are each separated into two distinct clades. The three *P. lutulentum* **sp. nov.** sequences are placed within the Asian Leiobuninae clade, along with other *Pseudoleiobunum* sp. and Japanese *Nelima* (bootstrap = 84). The bootstrap values for each of the smaller clades that are *Nelima*, *P. lutulentum* **sp. nov.** and the other *Pseudoleiobunum* are respectively

On the other hand, *Leiobunum japonicum*, was inferred to be in the same clade as Japanese Gagrellinae (*e.g.*, *Gagrellula ferruginea* and *Psathyropus tenuipes*), but is weakly supported (bootstrap = 32). This clade is the sister group to the larger combination of US & South American *Nelima* (See Fig. 8). Additionally, our analysis further reaffirms Hedin *et al.* (2012)'s result as the *curvipalpe*-group forms its own clade (bootstrap = 42).

Despite the low bootstrap values, the results support the polyphyly of *Leiobunum*, *Nelima* and Gagrellinae, separating into larger European, Asian, US and Mexican clades (Hedin *et al.* 2012). This result also supports our classification of grouping *P. lutulentum* **sp. nov.** and the *maximum*-superspecies (*P. maximum* distinctum, *P. japanense japonicum* and *Pseudoleiobunum japanense*, see Fig. 8) as they are separated from the rest of the Leiobuninae, forming a clade of their own (bootstrap = 84).

Concatenated Analysis (Figure 9). The concatenated analysis consists of 73 sequences with 3,709 bp, with the same three *P. lutulentum* **sp. nov.** individuals used in *28S* analysis and the rest taken from GenBank. The results are similar to the *28S* tree, but with generally higher support values; Leiobuninae species are divided into clades following their geographical occurrence.US Leiobuninae is split into two clades, with a respectively low bootstrap value of 17 and 25, while South American Leiobuninae is slightly more complex, splitting into three clades, with respective bootstrap values of 41, 81 and 54. The last clade is paraphyletic to the *Togwoteeus* clade (bootstrap = 22).

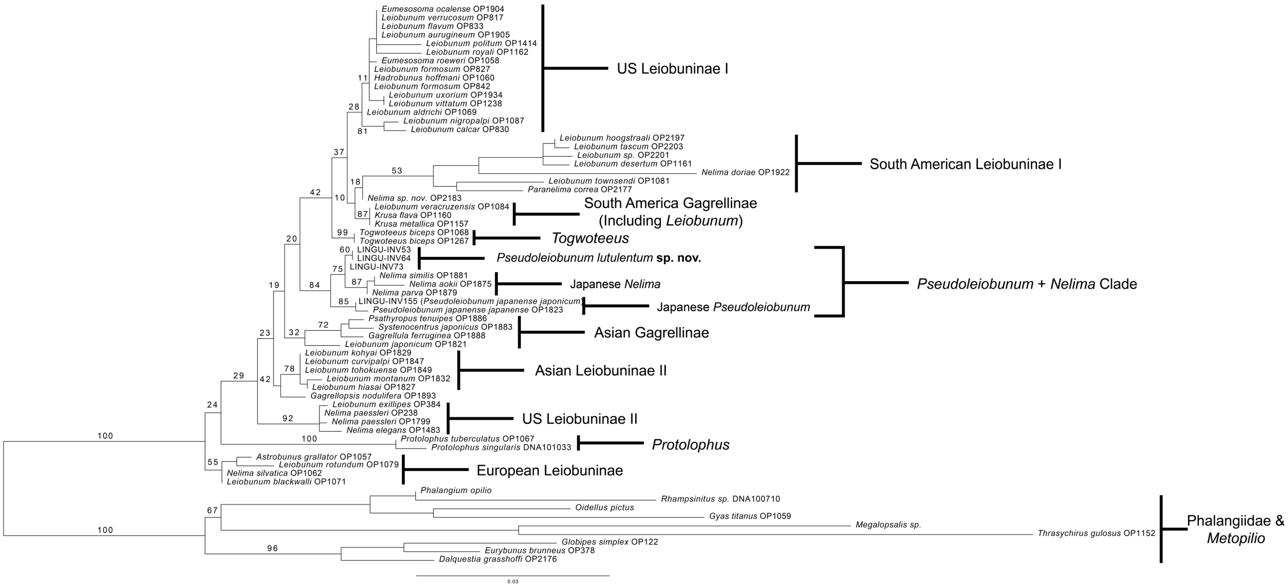

FIGURE 8. *28S* alignment maximum-likelihood phylogram. Tree rooted using *Odiellus pictus* OP1063 as outgroup shown.

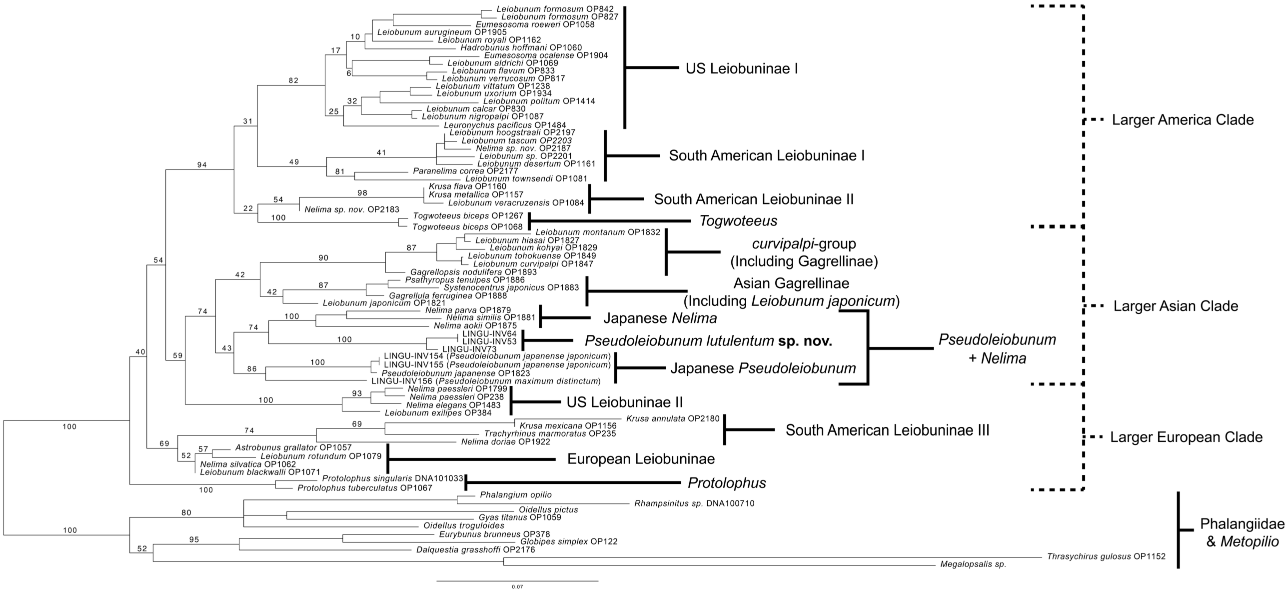

FIGURE 9. Concatenated sequence alignment maximum-likelihood phylogram. Tree rooted using *Odiellus pictus* as outgroup shown.

Pseudoleiobunum lutulentum **sp. nov.** is placed within the Asian Leiobuninae clade, alongside Japanese *Nelima* and other *Pseudoleiobunum* species (bootstrap = 43). *Pseudoleiobunum lutulentum* **sp. nov.** is sister to Japanese *Nelima* (bootstrap = 74).

Pseudoleiobunum japanense japonicum (LINGU-INV154, 155), *P. japanense* (OP1823) and *P. maximum distinctum* (LINGU-INV156) are found to be closer related to each other, forming a smaller clade within the *Pseudoleiobunum* clade (bootstrap = 86, Fig. 9). Reasons for this is explored in the following Discussion section.

The sister group to the *Pseudoleiobunum* clade is inferred to be the clade consisting of Japanese Gagrellinae, *curvipalpe*-group and *Leiobunum japonicum* (bootstrap = 42).

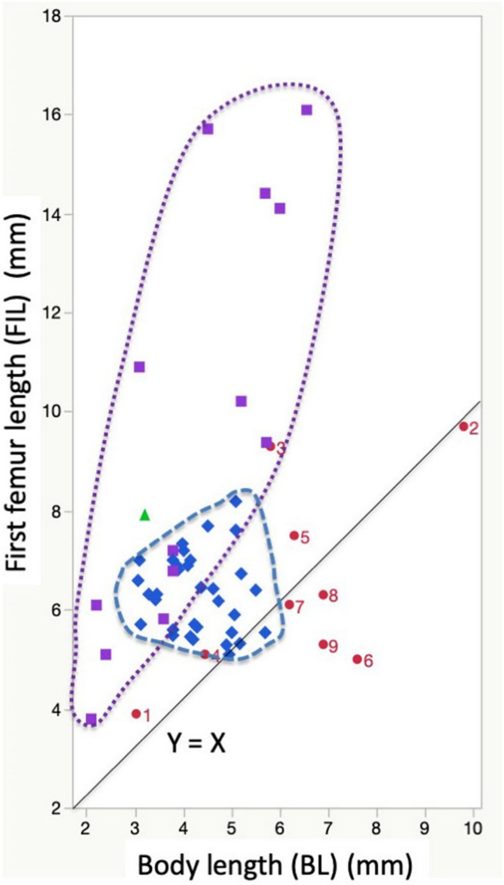

FIGURE 10. Relation of length of the first femur (FIL) to body length (BL) in East Asian Leiobuninae species based on data from Sato & Suzuki 1939; Suzuki 1940, 1953, 1957, 1966, 1973, 1974, 1976, 1977, 1983; Suzuki & Tsurusaki 1983, Tsurusaki 1982, 1985, 1990, 1991, 2006. Line meaning first femur length (FIL) is equal to body length (BL), anything below the line shows species with FIL shorter than BL. Red circles: *Pseudoleiobunum*. Blue diamonds: the *curvipalpe*-group; Green triangles are *Leiobunum rubrum*; Purple squares are East Asian species of *Nelima*. **1** *Pseudoleiobunum lutulentum* **sp. nov.**; **2** *P. maximum distinctum*; **3** *P. maximum formosum*; **4** *P. maximum yushan*; **5** *P. japanense japanense*; **6–9** *P. japanense japonicum* from various localities (**6** Mt. Hikosan; **7** Mt. Ishizuchi; **8** Hiroshima; **9** Mino-o, Osaka).

Discussion

Here we explain the rationale behind the resurrection of *Pseudoleiobunum* and why this new species *Pseudoleiobunum lutulentum* **sp. nov.** should be placed into this genus, along with the *maximum*-group. We provide a brief history of *Pseudoleiobunum* and another candidate genus (*Metaleiobunum*), followed by evidence from three different types of data: (1) general, external and genital morphology, (2) phylogenetic analysis and (3) ecological considerations.

Brief history of *Pseudoleiobunum*

Before discussing the rationale behind resurrecting *Pseudoleiobunum*, we must first address its history and why we choose it as opposed to *Metaleiobunum*.

Pseudoleiobunum is the oldest available generic name for the *maximum*-group (Suzuki 1976, Tsurusaki 1985). The genus, with its type species *P. japanense*, was separated from *Leiobunum* based on two morphological features: first femur shorter than the body and the pedipalpal patella and tibia armed with apophyses (Müller 1914, Suzuki 1976).

FIGURE 11. *Pseudoleiobunum lutulentum* **sp. nov.**, in-situ. **A** Resting on a leaf litter surface besides a stream, New Territories, Tai Mo Shan. **B** Resting on a rocky surface, New Territories, Tai Mo Shan. **C** Station besides water body in a rocky stream, Ma On Shan. **D** Full view of the individual on a rock. **E** Overview of the habitat, Ma On Shan.

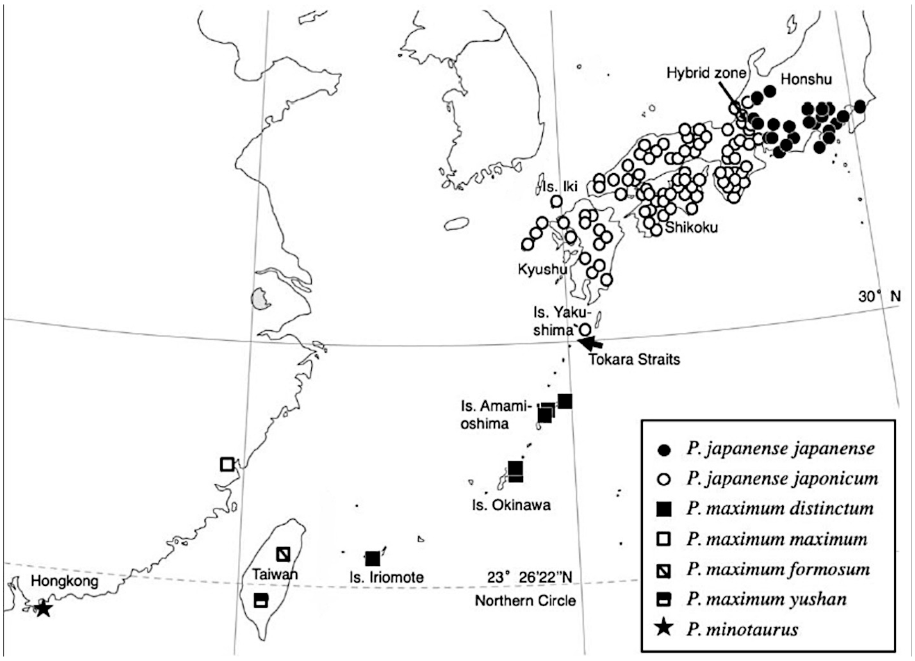

FIGURE 12. Distribution of all recorded *Pseudoleiobunum* species across East Asia.

Suzuki (1976) synonymized *Pseudoleiobunum* with *Leiobunum* because of 1) mensural characteristics, such as the femoral and body lengths, can vary even between individuals of the same species and 2) further inspection of other *Leiobunum* species in Japan uncovered similar pedipalpal patella and tibial apophyses (Suzuki 1976).

Another candidate, *Metaleiobunum* Suzuki, 1940, was considered for resurrection but was rejected. Its type species, *M. japonicum* Suzuki, 1940, was originally separated from *Leiobunum* due to differences in the number and arrangement of the dorsal coxal marginal tubercles from both *Pseudoleiobunum* and *Leiobunum* (Suzuki 1976). However, much like how pedipalpal apophyses are not unique to *Pseudoleiobunum*, the difference of tubercle numbers between *Metaleiobunum* and *Pseudoleiobunum* is also highly variable between individuals of the same species and therefore should not be relied on as species-defining features. In addition to *M. japonicum*'s overwhelming general resemblance with *P. japanense japonicum* (See Notes on *Pseudoleiobunum japanense japonicum*), they were synonymized with each other (Suzuki 1976). Furthermore, species connected to *Metaleiobunum* via previous established synonymies, such as *L. suzukii* Roewer, 1957 and *L. bifrons* Roewer, 1957, could all be synonymized with *P. japanense japonicum* due to similar geographical occurrences and type specimens being based on an immature female (Suzuki 1976).

General, external & genital morphology. The new species identification was narrowed down to the subfamily Leiobuninae because of the weakly sclerotized dorsal scutum, lack of apparent dorsal armament, unarmed ocularium and the lack of leg pseudoarticulations. The first morphological assessment would place it in Leiobuninae rather than Gagrellinae, as the latter is recognizable by its heavier sclerotized dorsal scutum and possessing at least one pseudoarticulation, particularly on leg II (Banks 1893, Pinto-da-Rocha & Giribet 2007).

The new species' coriaceous, unevenly granulated yet soft dorsal scutum narrowed the identification down to *Leiobunum* and *Nelima*. The classification of these two genera has been confusing, as both diagnoses have been revised numerous times since their establishment and *Leiobunum* has even been renamed on several occasions (Crawford 1992). Martens (1969) suggested that within *Nelima*, differences between species are so minute that it becomes impossible to delimitate them without direct comparison. To further complicate the issue, Hedin *et al.* (2012) showed that both genera are polyphyletic.

However, a rather unique combination of characters amongst *Leiobunum* is the coriaceous skin and flattened body with two angled posterior margins (sometimes) resembling two small pointy tubercles. Such features are shared by the *maximum*-group (Suzuki 1976, Tsurusaki 1990) (See Fig. 2). In addition, proposed reallocated species of *Pseudoleiobunum* possesses similar pedipalpal apophyses (*e.g.*, *Pseudoleiobunum maximum formosum*) (Suzuki 1976).

Such an apophysis is not confined to *Pseudoleiobunum* though, many *Leiobunum* and *Nelima* species possess such pedipalpal apophysis, such as *Leiobunum hiraiwai* Sato & Suzuki, 1939 and *Leiobunum oharai* Tsurusaki, 1991 (Suzuki 1976, Tsurusaki 1991).

Hence, one must consider other morphological features to help with the delimitation. Suzuki (1976) noted Leiobuninae species delimitation was facilitated by observing the labrum and the presence of distomesal and ventral armament on the pedipalpal tibiae. For instance, the *curvipalpe*-group possess labra armed with granules, while the labrum of *Leiobunum rubrum* Suzuki, 1966 is slim and unarmed (Suzuki 1976, figures 23–24, 36–94, Tsurusaki 1985). The labrum of *P. lutulentum* **sp. nov.** is slim, curved and unarmed. This feature is similar with the general labra that is found within the former *maximum*-group (Suzuki 1976, figures 1–22, 28–31).

Moving to the pedipalps, another feature that is mostly confined to *Pseudoleiobunum* is the possession of distomesal patellar and tibial apophyses. *Pseudoleiobunum lutulentum* **sp. nov.** also has both apophyses. Although the tibial apophysis is less distinct, it is important to note that both sexes of *P. lutulentum* **sp. nov.** possess two apophyses. Possession of both apophyses is uncommon in East Asian Leiobuninae (Suzuki 1976, Tsurusaki 1985, 1991); females of the *curvipalpe*-group also have well-developed patellar apophyses, but its males lack them (Suzuki 1976, Tsurusaki 1990). Meanwhile, the *rubrum*-group including *Leiobunum rubrum* Suzuki, 1966 and species of *Leiobunum* and *Nelima* (Suzuki 1976, Hedin *et al.* 2012), lack such distomesal apophyses on their palps. From the above two features, we see that this new species from Hong Kong is different from the described species within *Leiobunum* and is more similar to the *maximum*-group from *Leiobunum*.

It is important to note that even though the value of male genitalia is widely acknowledged for the study of harvestmen (Curtis 2007, Suzuki 1976), it is less useful in deducing the genus of a newly described species. Within *Leiobunum* alone, penis shape and size vary. Important features, such as the shape of the alate winging (Martens 1987) or the length of the glans, vary greatly amongst *Nelima* and *Leiobunum* individuals (Suzuki 1976, Tsurusaki 1990, 1991, Shultz 2018). Therefore, genital morphology is shown here because it can help distinguish individuals at the species level. Further study on the evolution of genital morphology in Leiobuninae determine the value of penis morphology in delimiting at the genus level.

Even though female seminal receptacles share a rough, general circular lobe, they can vary in size and minute structural details (Suzuki 1976: figs 95–126). *Pseudoleiobunum lutulentum* **sp. nov.** has a smaller receptacle compared to other *Pseudoleiobunum* species, in addition to being narrower and longer, with a wider channel where the aflagellate sperm is stored (Martens *et al.* 1981, Machado & Burns 2024). However, there is variation within the genus and often it is difficult to notice the small differences, much like with male genitalia. We include a description of the seminal receptacle (Fig. 6H), but further research is needed to determine its classification value at the genus level.

We also look at the mensural features for *Pseudoleiobunum*. This study compared specimens from three different groups: *Pseudoleiobunum*, *curvipalpe*-group and East Asian *Nelima*. Referring to Table 2, male *Pseudoleiobunum* and the *curvipalpe*-group have generally longer leg I femora than body length (with a respective average ratio of 1.6 times and 1.5 times longer femora I than body length). For other taxonomically similar groups such as East Asian *Nelima*, they possess significantly longer leg I femora (an average of 2.43 times longer femora I than body length) (Table 2).

On the other hand, female *Pseudoleiobunum* appears to have a shorter leg I femoral length than body length. Examining five female *Pseudoleiobunum* species, the ratio of femoral length to body length ranges from 0.51 to 0.94 (Appendix 3). In the *curviplapi*-group, there is no clear indication whether female femoral length is shorter than body length (ratio = 0.83–1.78). However, for other groups, such as East Asian *Nelima*, females have a longer femoral length than body lengths (ratio = 1.05–1.49).

Mensuration has long been a standard for harvestmen species delimitation (Curtis 2007). Particularly, Researchers have compared leg I femora against body length in Palpatores descriptions, most likely popularized by Roewer's descriptive papers (1910). However, Suzuki (1976) points out that such a feature is highly variable, not only between different localities, but even between individuals of the same species and males-females. The data gathered from this study and other related research into Leiobuninae (Suzuki 1940, 1953, 1957, 1966, 1973, 1976, 1977, 1982, 1985, Tsurusaki, 1990, 1991, 2006, Suzuki & Tsurusaki 1983, Sato & Suzuki 1939) shows that there is a trend of only male *Pseudoleiobunum* having longer leg I femora than body length while their female counterparts do not (Appendix 3), and that one can differentiate *curvipalpe*-group and *Pseudoleiobunum* from *Nelima* and *rubrum*-group based on leg I femora to body length ratio. However, despite their average ratio for males showing leg I femora longer than body (Table 2), there are species within the groups that have a shorter leg I femora than body (*e.g.*, *Pseudoleiobunum maximum distinctum* with a ratio of 0.99), there can be intraspecific variation (See *Pseudoleiobunum japanense japonicum* in Appendix 2, Fig. 10).

While we continue to record mensuration and ratio data for the description for the new species, more studies are needed to determine the taxonomic value of such data (especially within the subfamily of Leiobuninae) with larger sample sizes, species diversity and geographical coverage. In the meantime, one should pursue an integrative taxonomy approach combining morphological features and phylogenetic results to achieve more robust species delimitation.

In summary, we have placed the new Hong Kong species into the *maximum*-group because of morphological similarity, from the general external morphology, presence of two pedipalpal apophyses and labrum characteristics.

Phylogenetic Analysis. Hedin *et al.* (2012) established the groundwork for our study by performing a phylogenetic study of Leiobuninae, including species of Leiobuninae, Gagrellinae and Protolophidae from Europe, Americas and Asia. They highlight the need of taxonomic revision, since *Leiobunum* and *Nelima* are polyphyletic and species relatedness is strongly influenced by geographical occurrence (Hedin *et al.* 2012, figs 2–4; See Fig. 9 from this study).

Hedin *et al.* also showed that Asian/Japanese Leiobuninae species are separated into three major clades: (1) Japanese *Leiobunum curvipalpe* group, (2) Japanese *Leiobunum maximum* group, and (3) *Leiobunum rubrum* group and Japanese Gagrellines. However, Hedin only explored the phylogenetic relationship between these Leiobuninae species. In our study, we further examined the "Japanese *Leiobunum maximum* group" (also referred to as "*Leiobunum maximum* clade" or *maximum*-group in this study) and found morphological evidence that suggest species under this group stand out from the other Asian Leiobuninae clades and therefore deserves a redesignation to *Pseudoleiobunum*. The phylogenetic study from this study shows that*Pseudoleiobunum* also includes *P. japanense* and paraphyletic to several *Nelima* species that occur in neighboring regions (*N. parva* (OP 1879), *N. similis* (OP 1881) and *N. aokii* (OP 1875)) (Figure 8–9).

In our molecular analyses, we recover the *Pseudoleiobunum* + *Nelima* clade with varying support (28S: bootstrap = 84, Figure 8; concatenated: bootstrap = 43, Figure 9). The lower bootstrap support of the concatenated dataset, despite its increased amount of data, is likely due to the low resolution of the other genetic markers included in our study. Additional molecular analyses should be performed with different data types and more taxon sampling to evaluate our inference.

We provide two reasons why classify the present new species in *Pseudoleiobunum*, despite it being more closely related to Japanese *Nelima*, rendering *Pseudoleiobunum* a paraphyletic genus in the molecular phylogeny. First, *Nelima* is a problematic genus, as it is polyphyletic with several Leiobuninae genera (Hedin *et al.* 2012). The confusion is compounded by the fact that the type species of *Nelima* (*N. sylvatica* Simon, 1879) is found in Southern Europe, France and Algeria (Simon 1879). Confusing genera such as *Nelima* are often the result of classifying new species based solely on superficial morphological features. With further study, it is possible that the three *Nelima* species in question here will eventually be reallocated to *Pseudoleiobunum*, or that they share paedomorphic traits of *Pseudoleiobunum* (Hedin *et al.* 2012). In addition, the present molecular analysis does not include several (undescribed) species that are likely related to Japanese *Nelima* or *Pseudoleiobunum* from continental China. Without these taxa, the evolutionary history of this clade remains unclear. We expect there to be further revision of this group and believe it should wait until there is a proper dataset to address this issue.

Secondly, the new species seems similar and closely related to other species of *Pseudoleiobunum* based on the morphological features we studied. Defining features of *Pseudoleiobunum*, such as the elevation of lateral-posterior tips of the scutum and possession of distomesal patellar and tibial apophysis by both sexes, are consistent within the species of *Pseudoleiobunum* and distinct within Leiobuninae. In contrast, this new species is morphologically distinct from the three Japanese *Nelima* species included in the clade. Further investigation on the three *Nelima* species is warranted to confirm their placement within *Pseudoleiobunum*.

Furthermore, we do not believe that monophyly is a strict criterion for genera. Evolution is a complex process that is not always dichotomous (Hörandl 2006). Accepting paraphyly in classification acknowledges the diverse evolutionary paths taxa undertook (Hörandl 2006 & 2007). For example, speciation may take place at the peripheral range of a polytypic taxon, rendering the original taxon becomes paraphyletic as seen with the polar bear (*Ursus maritimus*) and brown bear (*U. arctos*) (Talbot & Shields 1996). Also, the buttercup plant *Ranunculus* Linnaeus forms numerous non-dichotomous branches (Hörandl 2006 & Rastipishe *et al.* 2011). These examples show that criteria other than monophyly should be considered to reflect the slow but ongoing evolutionary process (Hörandl 2006 & 2007). If we 'force' *Nelima* into *Pseudoleiobunum* to uphold the strict regulations of the monophyletic basis, we lose some of the complexity behind *Nelima* and *Pseudoleiobunum*'s evolutionary process. We therefore with an alternative classification method that is not rooted solely on monophyly and in which we proceed with the resurrection of *Pseudoleiobunum* while acknowledging its paraphyletic nature.

Based on our classification, *Pseudoleiobunum lutulentum* **sp. nov.** is relatively distantly related to other *Pseudoleiobunum* species, which may be due to geography. The three *Pseudoleiobunum* species included in our study (*P. maximum distinctum*, *P. japanense japonicum* and *P. japanense*) all occur in Japan, while *P. lutulentum* **sp. nov.** occurs, as of this study, strictly in Hong Kong. Hedin *et al.* (2012) has shown Leiobuninnae relationships reflect geography, so it is reasonable that the geographical distance between Japan and Hong Kong contributes to the divergence within the clade. *Pseudoleiobunum* species also occur in Taiwan (*e.g.*, *P. maximum formosum*) and China (*e.g.*, *P. maximum yushan*), and we expect them to be more closely related to *P. lutulentum* **sp. nov.** due to their geographic proximity.

Ecological Considerations. Although *P. lutulentum* **sp. nov.** is widespread in Hong Kong, it is rarely seen by the public (INaturalist 2024). This is likely because they are nocturnal and occur strictly near water bodies, such as streams or humid forest grounds at high attitudes (*e.g.*, Tai Mo Shan, Ma On Shan). In addition, extensive fieldwork conducted during this study suggests that this species is univoltine—they tend to be most prevalent in the autumn and early winter seasons (See description for *Pseudoleiobunum lutulentum* **sp. nov.**: Habitat). This is unusual for harvestmen in Hong Kong; our fieldwork has noted similar nocturnal eupnoan species, but none that are as restricted to their habitats as *P. lutulentum* **sp. nov.**

Our observations infer that this species hibernates over winter as juveniles, since a higher number of juveniles close to their adult counterparts can be found in the habitats in autumn and early winter seasons; adults emerge in the early autumn (late June–September). Tsurusaki (2003) identified four types of hibernation for Japanese Palpatores: 1) hibernation as eggs, 2) hibernation as adults, 3) hibernation as juveniles and eggs and 4) hibernation as juveniles. The last type was observed in only three species in his study, with *P. japanense* being one of them. Tsurusaki (2003) further postulates that such pattern may be related to more temperate climates in southern regions (Tsurusaki 2003). Further study conducted on *P. japanense japonicum* and *P. maximum distinctum* also showed that they share the same type of hibernation (Tsurusaki 2003).

Furthermore, *P. lutulentum* **sp. nov.** has rough, highly irregularly granulated and brownish-yellow colored dorsal scutum, as well as densely granulated legs. It is possible that this coloration and pattern serve as camouflage on the mossy rocks and wet, sandy substrate that are characteristic of freshwater stream environments. The presence of camouflage is unique for Eupnoan species found in Hong Kong thus far. Such muddy-brown/yellow coloration is also prominent within the *maximum*-group, which is another character linking the new species and the *maximum*-group.

Summary

Our study has shown that the *maximum*-group differs from the rest of the *Leiobunum*, from the coriaceous dorsal surface and posteriorly angled dorsal scutum, to the double pedipalpal apophyses. Our molecular work supports our hypothesis in separating this group from the rest of the Asian *Leiobunum*. Since *Pseudoleiobunum* is the oldest legitimate genus name for this group, we resurrect this genus name to highlight their difference from other *Leiobunum*, as well as resolve some of the confusing relationship amongst *Leiobunum* species.

The molecular and morphological analyses serve as strong justification for resurrecting *Pseudoleiobunum* since there is genetic and morphological difference between *Pseudoleiobunum* and other Asian Leiobuninae. However, we retain *Nelima* to refer to the Japanese *Nelima* included in this study Based on our classification, *Pseudoleiobunum* is paraphyletic in relation to Japanese *Nelima*. Due to the uncertainty regarding *Nelima* systematics, along with its morphological distinctness from *Pseudoleiobunum*, we think it is more appropriate to keep these three *Nelima* species, as opposed to reclassifying as *Pseudoleiobunum*, due to the morphological difference.

The discovery of *P. lutulentum* **sp. nov.** gave us an opportunity to reassess one of the groups within Asian *Leiobunum*, and we provide data supporting the resurrection of *Pseudoleiobnunum* and *P. lutulentum* **sp. nov.**'s placement in it. Our work highlights the knowledge gap of the complex evolutionary history of *Nelima*, *Pseudoleiobunum* and Leiobuninae. Future studies are needed with a larger dataset including Mainland Chinese and Japanese Leiobuninae to clarify Southeast Asian Leiobuninae's complicated taxonomic relationship.

Acknowledgement

Special thanks to Mr. Liu Hua Bing, Alex; Mr. Lee Wing Him, Henry; Mr. Lam Pui Yin, Ivan; Ms. Yuen Hiu Ching, Hilda; Mr. So, Halbert; Mr. Chan Man Ho, Henry; Ms. Fok Wing Lam, Amy (Science Unit, Lingnan University) and Mr. Moses Fu for the help in fieldwork and specimen collection, as well as all of the people who have collected and gifted *Pseudoleiobunum* specimens from various parts of Japan to Dr. Tsurusaki. We would also like to thank Dr. Jochen Martens and Mr. Panos Kontos (Senckenberg Natural History Museum) and Dr. Tobias Malm (Swedish Museum of Natural History for their help in the acquisition of type specimens and access to related papers. This study was made possible with the technical support of the Electron Microscope Unit, Hong Kong University, as well as the Science Unit, Lingnan University. This study is also supported by the Sir Edward Youde Memorial Fund, Sino-British Fellowship Trust Fund and the American Arachnological Society. Partial funding for Open Access was supported by Lingnan-Open Access Publishing Support Fund.

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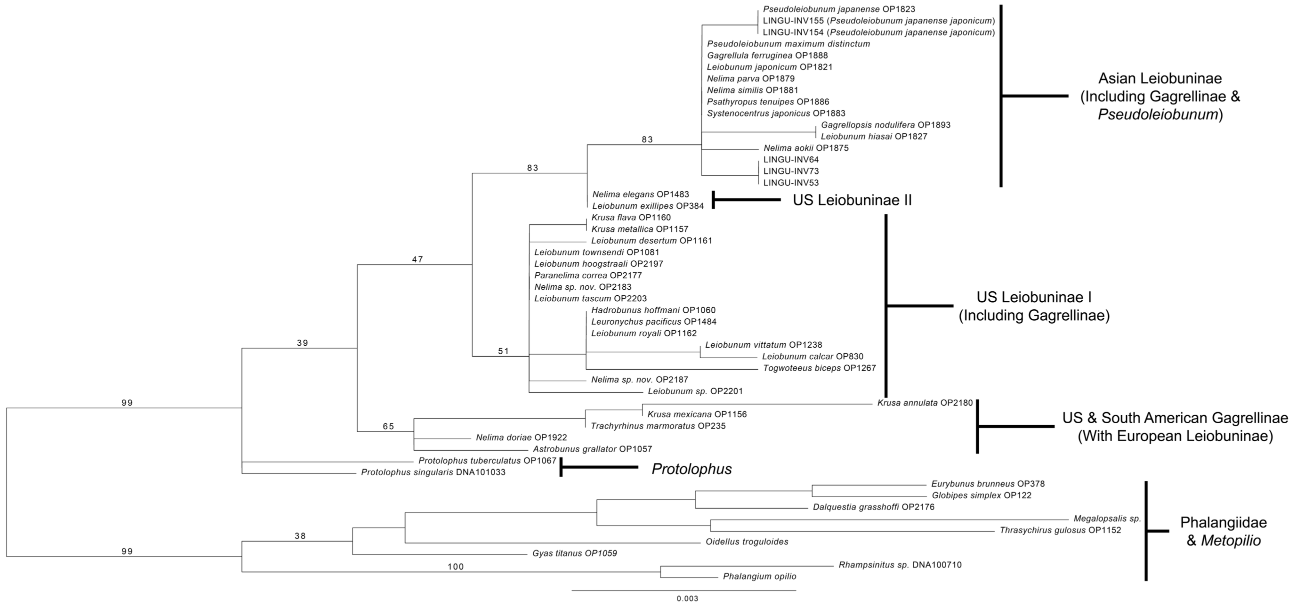
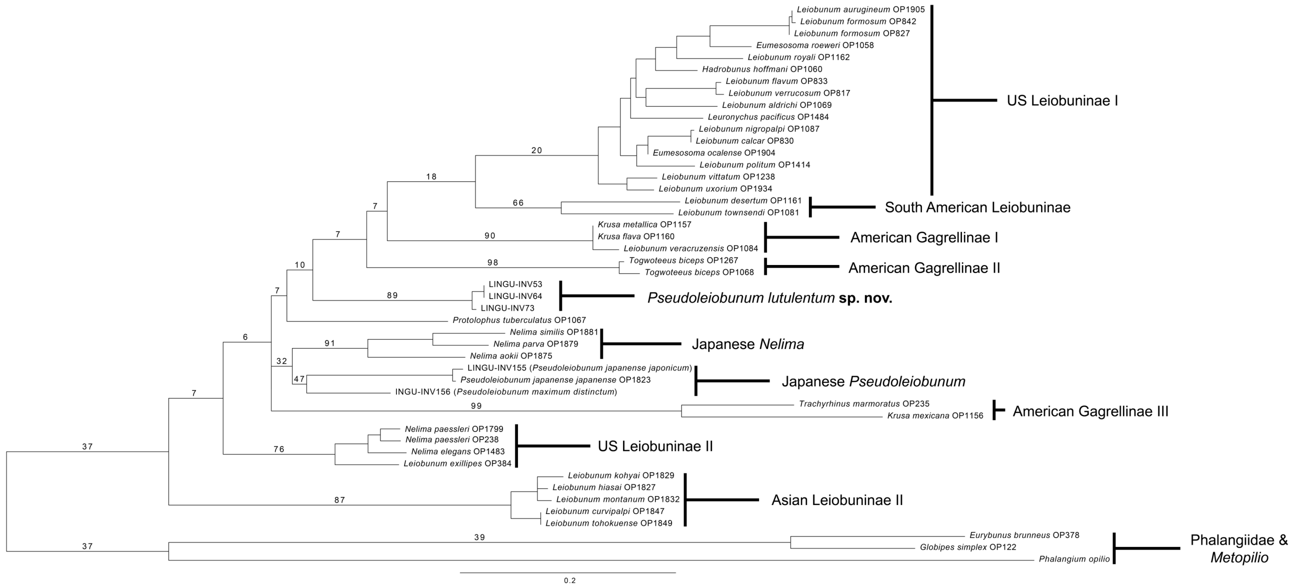
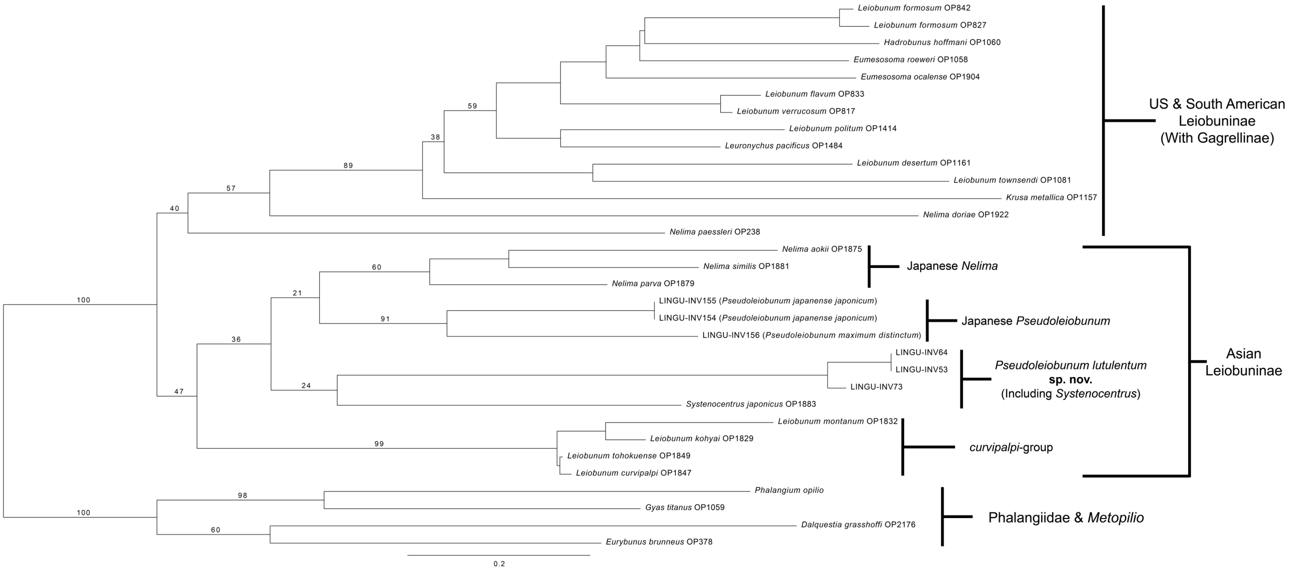


APPENDIX 1. *18S* alignment maximum-likelihood phylogram. Tree rooted using *Rhampsinitus sp.* DNA100710 and *Phalangium opilio* as outgroups shown.



APPENDIX 2. *16S* alignment maximum-likelihood phylogram. Tree rooted using *Phalangium opilio* as outgroup shown.



APPENDIX 3. *COI* alignment maximum-likelihood phylogram. Tree rooted using *Delquestia grasshoffi* OP2176 and *Eurybunus brunneus* OP378 as outgroups shown.

APPENDIX 4. PCR primers and respective conditions listed in the following: **A** Initial denaturation of 94°C for 3 min, then followed by 35 cycles of 94°C for 45 s, annealing temperature (AT) for 45 s, 72°C for 1.5 min and ending with elongation of 72°C for 5 min. **B** Initial denaturation of 94°C for 3 min, then 35 cycles of 94°C for 45 s, AT at 42 s with an increase of 0.2°C per cycle, 72°C for 1.5 min, completing with elongation at 72°C for 5 min. **C** Initial denaturation of 94°C for 5 min, 35 cycles of 95°C for 30 s, AT for 30 s, 72°C for 1 min and final extension of 72°C for 10 min. **D** Initial denaturation of 94°C 10 min, followed by 45 cycles of 94°C for 1.5 min, AT for 2 min, 72°C for 3 min and finishing with final extension of 72°C for 15 min.

Gene region	Primer Name	Primer Sequence (5' -3')	PCR Condition	Annealing Temperature (AT)	Reference
Elongation factor 1-alpha (EF1)	EF1-OP2 (forward)	GATTTCATCAARAACATGATYAC	**A**	45°C	Hedin *et al.* 2012 Hedin *et al.* 2010
	EF1-OP5LEIORC (reverse)	CTTTGTTCCAACATGTTATCTCC			
	EF1-OP4 (forward)	TACATYAAGAAGATTGGTTA			
	EF1-OPRC4LEIO (reverse)	GAACTTGCAAGCAATGTGAGC			
28S	ZX1 (forward)	ACCCGCTGAATTTAAGCATAT			Hedin *et al.* 2012
	ZR2 (reverse)	GCTATCCTGAGGGAAACTTCGG			

......continued on the next page

APPENDIX 4. (Continued)

Gene region	Primer Name	Primer Sequence (5' -3')	PCR Condition	Annealing Temperature (AT)	Reference
18S	18S1F (forward)	TACCTGGTTGATCCTGCCAGTAG	**A**	42°C	Hedin *et al.* 2012 Ba-Akdah *et al.* 2018
	18S5R (reverse)	CTTGGCAAATGCTTTCGC			
	18S3F (forward)	GTTCGATTCCGGAGAGGGA			
	18S9R (reverse)	GATCCTTCCGCAGGTTCACCTAC			
	18S4F (forward)	CCAGCAGCCGCGCTAATTC			
	18S7R (reverse)	GCATCACAGACCTGTTATTGC			
Histone 3 (H3)	H3aF (forward)	ATGGCTCGTACCAAGCAGACVGC	**A**	60°C	Hedin *et al.* 2012 Sharma & Giribet 2011
	H3aR (reverse)	ATATCCTTRGGCATRATRGTGAC			
mtDNA (COI/ COII)	C1-J-2350LEI (forward)	ACAGTAGGRATAGATGTAGA	**A**	48°C	Hedin *et al.* 2012
	C2-N-3389Phal (reverse)	TCATATGATCAGTATCATTGGTG			
	LCO1490 (forward)	GGTCAACAAATCATAAAGATATTGG	**C**	42°C	Tan *et al.* 2023 Folmer *et al.* 1994
	HCO2198 (reverse)	TAAACTTCAGGGTGACCAAAAAATCA			
mtDNA (16S/12S)	LR-J-13328LEI (forward)	TGATTATGCTACCTTWGCAC	**A**	45°C	Hedin *et al.* 2012
	SR-N-14214LEI (reverse)	ACAAATCGCCCGTCACTCTG			
	LR-J-12860LEI (forward)	TAGATAGAAACCAACCTGGC			
	LR-N-13396LEI (reverse)	CTGTTTATCAAAAACATTT			
	LR-J-12887LEI (forward)	CCGGTTTGAACTCAAATCACGT			
	SR-N-14588 (reverse)	AGGATTAGATACCCTATTAT			

APPENDIX 5. Taxon Sample and GenBank Accession Numbers, samples used in concatenated analysis are shown with an asterisk next to the voucher number.

Molecular Clade	Species	Voucher No.	Location	Collected By	28S	16S	18S	COI	References
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV46	CHINA: Hong Kong, New Territories, Shing Mun Reservoir	Tan Kai Teck Desmond	PP718891	PP718858	/	PP713117	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV50	CHINA: Hong Kong, New Territories, Tai Mo Shan	Tan Kai Teck Desmond	PP718892	PP718844	PP718877	PP713104	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV51	CHINA: Hong Kong, New Territories, Tai Mo Shan	Tan Kai Teck Desmond	PP718890	PP718856	PP718866	PP713110	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV52	CHINA: Hong Kong, New Territories, Tai Mo Shan	Tan Kai Teck Desmond	PP718893	/	PP718878	PP713105	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV53*	CHINA: Hong Kong, New Territories, Tai Mo Shan	Tan Kai Teck Desmond	PP718894	PP718843	PP718867	PP713118	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV57	CHINA: Hong Kong, New Territories, Tai Mo Shan	Tan Kai Teck Desmond	PP718895	PP718859	PP718862	PP713111	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV58	CHINA: Hong Kong, New Territories, Shing Mun Reservoir	Tan Kai Teck Desmond	PP718896	PP718846	PP718879	PP713108	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV59	CHINA: Hong Kong, New Territories, Tai Mo Shan	Tan Kai Teck Desmond	PP718897	PP718860	PP718871	PP713116	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV60	CHINA: Hong Kong, New Territories, Tai Mo Shan	Tan Kai Teck Desmond	PP718898	PP718855	PP718863	PP713109	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV61	CHINA: Hong Kong, Kowloon, Kowloon Peak	Tan Kai Teck Desmond	/	PP718837	PP718864	PP713119	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV62	CHINA: Hong Kong, New Territories, Fo Tan	Tan Kai Teck Desmond	PP718899	PP718853	PP718868	PP713112	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV63	CHINA: Hong Kong, New Territories, Fo Tan	Tan Kai Teck Desmond	PP718900	/	PP718881	PP713115	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV64*	CHINA: Hong Kong, New Territories, Fo Tan	Tan Kai Teck Desmond	PP718901	PP718857	PP718876	PP713114	This study

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APPENDIX 5. (Continued)

Molecular Clade	Species	Voucher No.	Location	Collected By	28S	16S	18S	COI	References
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV65	CHINA: Hong Kong, New Territories, Fo Tan	Tan Kai Teck Desmond	PP718910	PP718854	PP718880	PP713113	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV72	CHINA: Hong Kong, Lantau Island	Tan Kai Teck Desmond	PP718889	PP718840	PP718869	PP713101	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV73*	CHINA: Hong Kong, Lantau Island	Tan Kai Teck Desmond	PP718888	PP718838	PP718875	PP713102	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV74	CHINA: Hong Kong, Lantau Island	Tan Kai Teck Desmond	PP718886	PP718839	PP718882	PP713100	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV75	CHINA: Hong Kong, New Territories, Ma On Shan	Tan Kai Teck Desmond	PP718887	PP718841	PP718865	PP713103	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV106	CHINA: Hong Kong, New Territories, Ma On Shan, Mui Tsz Lam	Tan Kai Teck Desmond	PP718909	PP718842	PP718870	PP713106	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV107	CHINA: Hong Kong, New Territories, Ma On Shan, Mui Tsz Lam	Tan Kai Teck Desmond	PP718902	PP718852	PP718883	PP713107	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV122	CHINA: Hong Kong, New Territories, Tai Mo Shan	Tan Kai Teck Desmond	PP718908	PP718851	PP718874	/	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV123	CHINA: Hong Kong, New Territories, Tai Mo Shan	Tan Kai Teck Desmond	PP718903	PP718850	PP718873	/	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV125	CHINA: Hong Kong, New Territories, Tai Mo Shan	Tan Kai Teck Desmond	PP718904	PP718845	PP718884	/	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV142	CHINA: Hong Kong, New Territories, Shing Mun Reservoir	Tan Kai Teck Desmond	PP718905	PP718849	/	/	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV143	CHINA: Hong Kong, New Territories, Shing Mun Reservoir	Tan Kai Teck Desmond	PP718907	PP718861	PP718872	/	This study

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APPENDIX 5. (Continued)

Molecular Clade	Species	Voucher No.	Location	Collected By	28S	16S	18S	COI	References
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV144	CHINA: Hong Kong, New Territories, Shing Mun Reservoir	Tan Kai Teck Desmond	PP718885	PP718848	/	/	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum lutulentum* **sp. nov.**	LINGU-INV145	CHINA: Hong Kong, New Territories, Shing Mun Reservoir	Tan Kai Teck Desmond	PP718906	PP718847	/	/	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum japanense japonicum*	LINGU-INV154*	JAPAN: Amadaki Falls, Tottori City, Tottori Prefecture, Honshu	Nobuo Tsurusaki	/	PP962404	PP962405	PP963501	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum japanense japonicum*	LINGU-INV155*	JAPAN: Mt. Hyonosen, Hibiki-no-mori, Tottori Prefecture, Honshu	Nobuo Tsurusaki	/	/	PP962406	/	This study
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum maximum distinctum*	LINGU-INV156*	JAPAN: R. Aira Island, Inomote, Okinawa Prefecture	Nobuo Tsurusaki	/	PP962403	PP962407	PP963502	This study
Pseudoleiobunum/ *maximum*-group	*Nelima aokii*	OP1875*	JAPAN: Honshu, Yamanashi Pref., Kitamori City	Nobuo Tsurusaki	JQ437141	JQ439968	JQ437026	JQ437187	Hedin *et al.* (2012)
Pseudoleiobunum/ *maximum*-group	*Nelima parva*	OP1879*	JAPAN: Shikoku, Ehime Pref., Kuma-kôgen-cho, Mt. Godanjô	Nobuo Tsurusaki	JQ437143	JQ439970	JQ437027	JQ437188	Hedin *et al.* (2012)
Pseudoleiobunum/ *maximum*-group	*Nelima similis*	OP1881*	JAPAN: Honshu, Nagano Pref., Kowashimizu, Mt. Kirigamine	Nobuo Tsurusaki	JQ437144	JQ439971	JQ437028	JQ437189	Hedin *et al.* (2012)
Pseudoleiobunum/ *maximum*-group	*Pseudoleiobunum japanense japonicum*	OP1823*	JAPAN: Shikoku, Kagawa Pref., Sanuki City	Nobuo Tsurusaki	JQ437145	JQ439972	JQ437029	/	Hedin *et al.* (2012)

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APPENDIX 5. (Continued)

Molecular Clade	Species	Voucher No.	Location	Collected By	28S	16S	18S	COI	References
Pseudoleiobunum/ *maximum*-group	*Leiobunum japonicum*	OP1821*	JAPAN: Honshu, Ehime Pref., Mt. Saragamine, Kuma-kogen-cho	Nobuo Tsurusaki	JQ437147	/	JQ437030	/	Hedin *et al.* (2012)
Asian Gagrellinae	*Systenocentrus japonicus*	OP1883*	JAPAN: Honshu, Ehime Pref., Kuma-kogen-cho, Mt. Saragamine	Nobuo Tsurusaki	JQ437149	/	JQ437032	JQ437190	Hedin *et al.* (2012)
Asian Gagrellinae	*Gagrellula ferruginea*	OP1888*	JAPAN: Honshu, Nagano Pref., Suwa City, Tsuetsuki Pass	Nobuo Tsurusaki	JQ437150	/	JQ437033	/	Hedin *et al.* (2012)
Asian Gagrellinae	*Psathyropus tenuipes*	OP1886*	JAPAN: Honshu, Yamaguchi Pref., Nagato City, Ôura Beach	Nobuo Tsurusaki	JQ437151	/	JQ437034	/	Hedin *et al.* (2012)
curvipalpe-group	*Leiobunum montanum*	OP1832*	JAPAN: Shikoku, Ehime Pref., Ryûjin-daira, Mt. Saragamine, Kuma-kogen-cho	Nobuo Tsurusaki	JQ437156	JQ439976	/	JQ437191	Hedin *et al.* (2012)
curvipalpe-group	*Leiobunum hiasai*	OP1827*	JAPAN: Honshu, Nagano Pref., Lake Shirokoma, Mt. Yatsugatake, Koumi-Cho, Saku-gun	Nobuo Tsurusaki	JQ437157	JQ439977	JQ437036	/	Hedin *et al.* (2012)
curvipalpe-group	*Leiobunum kohyai*	OP1829*	JAPAN: Honshu, Wakayama Pref., Tanabe City, Mt. Ookamidawa, Nonaka	Nobuo Tsurusaki	JQ437158	JQ439978	/	JQ437192	Hedin *et al.* (2012)
curvipalpe-group	*Leiobunum curvipalpi*	OP1847*	JAPAN: Honshu, Nagano Pref., Sugadaira Highland, Sanada-machi, Chiisagata-gun	Nobuo Tsurusaki	JQ437160	JQ439979	/	JQ437193	Hedin *et al.* (2012)
curvipalpe-group	*Leiobunum tohokuense*	OP1849*	JAPAN: Honshu, Fukushima Pref., Alts Bandai Skiing Resort, Bandai-machi, Yama-gun	Nobuo Tsurusaki	JQ437161	JQ439980	/	JQ437194	Hedin *et al.* (2012)

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APPENDIX 5. (Continued)

Molecular Clade	Species	Voucher No.	Location	Collected By	28S	16S	18S	COI	References
curvipalpe-group	*Gagrellopsis nodulifera*	OP1893*	JAPAN: Honshu, Tottori Pref., Tottori City, Amedaki Falls, Kokufu-cho	Nobuo Tsurusaki	JQ437162	/	JQ437037	/	Hedin *et al.* (2012)
Togwoteeus group	*Togwoteeus biceps*	OP1068*	USA: Colorado	P. Paquin	JQ432313	JQ432371	/	/	Burns *et al.* (2012)
Togwoteeus group	*Togwoteeus biceps*	OP1267*	USA: New Mexico, Taos Co., Taos Ski Valley	Marshall Hedin	JQ437163	JQ439981	JQ437038	/	Hedin *et al.* (2012)
South American Leiobuninae	*Paranelima correa*	OP2177*	MEXICO: Jalisco, Tapalpa, Los Espinos	R. Macías-Ordóñez	JQ437165	/	JQ437039	/	Hedin *et al.* (2012)
South American Leiobuninae	*Leiobunum townsendi*	OP1081*	USA: Arizona, Portal	B. Tomberlin	JQ437164	JQ439982	JQ437040	JQ437195	Burns *et al.* (2012)
South American Leiobuninae	*Leiobunum hoogstraali*	OP2197*	MEXICO: Michoacan, Copandaro, Zirahuen Lake	R. Macías-Ordóñez	JQ437167	/	JQ437042	/	Hedin *et al.* (2012)
South American Leiobuninae	*Leiobunum tascum*	OP2203*	MEXICO: Jalisco, Tapalpa, Los Espinos	R. Macías-Ordóñez	JQ437168	/	JQ437043	/	Hedin *et al.* (2012)
South American Leiobuninae	*Leiobunum sp.*	OP2201*	MEXICO: Puebla, Teziutlán, Chignautla	Y. Perroni	JQ437171	/	JQ437044	/	Hedin *et al.* (2012)
South American Leiobuninae	*Leiobunum potosum*	OP1161*	MEXICO: Tlaxcala, Ixtacuixtla	R. Macías-Ordóñez	JQ437172	JQ439983	JQ437045	JQ437196	Hedin *et al.* (2012)
South American Leiobuninae	*Nelima* **sp. nov.**	OP2187*	MEXICO: Oaxaca, San Juan Yaguila, Ixtlan de Juarez	J. Camacho	/	/	JQ437046	/	Hedin *et al.* (2012)
South American Leiobuninae	*Leiobunum veracruzensis*	OP1084*	MEXICO: Veracruz, Xalapa, Javier Clavijero Botanical Garden	L. M. Cuenca	JQ437174	JQ439984	/	/	Hedin *et al.* (2012)
South American Gagrellinae	*Krusa flava*	OP1160*	MEXICO: Veracruz, Coatepec	G. Morales	JQ437175	JQ439985	JQ437047	/	Hedin *et al.* (2012)
South American Gagrellinae	*Krusa metallica*	OP1157*	MEXICO: Veracruz, Xalapa	R. Macías-Ordóñez	JQ437176	JQ439986	JQ437048	JQ437197	Hedin *et al.* (2012)
South American Gagrellinae	*Krusa mexicana*	OP1156*	MEXICO: Veracruz, Coatepec	G. Morales	JQ437121	JQ439962	JQ437019	/	Hedin *et al.* (2012)

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APPENDIX 5. (Continued)

Molecular Clade	Species	Voucher No.	Location	Collected By	28S	16S	18S	COI	References
South American Gagrellinae	*Krusa annulata*	OP2180*	MEXICO: Colima, Ixtlahuacán, Gruta San Gabriel	R. Macías-Ordóñez	JQ437122	/	JQ437020	/	Hedin *et al.* (2012)
South American Leiobuninae	*Nelima* **sp. nov.**	OP2183*	MEXICO: Oaxaca, San Juan Yaguila, Ixtlan de Juarez	J. Camacho	JQ437177	/	JQ437049	/	Hedin *et al.* (2012)
US Leiobuninae	*Leiobunum vittatum*	OP1238*	USA: Mississippi, Marshall Co., Wall Doxey SP	P. Miller; G. Stratton	JQ437178	JQ439987	JQ437050	/	Hedin *et al.* (2012)
US Leiobuninae	*Leiobunum uxorium*	OP1934*	USA: North Carolina, Guilford Co., Greensboro	P. B. Nunez	JQ432280	JQ432338	/	/	Hedin *et al.* (2012)
US Leiobuninae	*Leiobunum politum*	OP1414*	USA: Wisconsin, Dodge Co., Mayville	M. McCormack	JQ432268	JQ432326	/	JQ437198	Hedin *et al.* (2012)
US Leiobuninae	*Leiobunum nigropalpi*	OP1087*	USA: Ohio, Summit Co., Bath	J. W. Shultz	JQ432265	JQ432323	/	/	Burns *et al.* (2012)
US Leiobuninae	*Leiobunum calcar*	OP830; OP1091*	USA: Mississippi, Tishomingo Co., Tishomingo SP	M. Hedin *et al.*	JQ432261	JQ432319	JQ437051	/	Hedin *et al.* (2012)
US Leiobuninae	*Leiobunum aldrichi*	OP1069*	USA: Michigan, Calhoun Co., Marshall	J. W. Shultz	JQ432284	JQ432342	/	/	Hedin *et al.* (2010, 2012)
US Leiobuninae	*Leiobunum verrucosum*	OP817*	USA: North Carolina, Buncombe Co., Oteen	M. Hedin *et al.*	JQ432293	JQ432351	/	JQ437199	Burns *et al.* (2012)
US Leiobuninae	*Leiobunum flavum*	OP833*	USA: Arkansas, Garland Co., Hwy 7, Forest Hills Trail	M. Hedin *et al.*	JQ432295	JQ432353	/	JQ437200	Burns *et al.* (2012)
US Leiobuninae	*Leiobunum aurugineum*	OP1905*	USA: Florida, Highlands Co., Archbold Biological Station	J. Carrel	JQ437179	JQ439988	/	/	Hedin *et al.* (2012)
US Leiobuninae	*Leiobunum formosum*	OP827*	USA: Alabama, Jefferson Co., Oak Mountain SP	M. Hedin *et al.*	JQ432299	JQ432357	/	JQ437202	Hedin *et al.* (2012)
US Leiobuninae	*Leiobunum formosum*	OP842*	USA: Florida, Jackson Co., Florida Caverns SP	M. Hedin *et al.*	JQ432297	JQ432355	/	JQ437202	Hedin *et al.* (2012)
US Leiobuninae	*Hadrobunus hoffmani*	OP1060*	USA: Tennessee, Sevier Co., Great Smoky Mountains NP, Elkmontarea	M. Hedin; J. Cokendolpher	JQ432301	JQ432359	JQ437052	JQ437203	Hedin *et al.* (2012)

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APPENDIX 5. (Continued)

Molecular Clade	Species	Voucher No.	Location	Collected By	28S	16S	18S	COI	References
US Leiobuninae	*Leiobunum royali*	OP1162*	MEXICO: Veracruz, Coatepec	R. Macías-Ordóñez	JQ432309	JQ432367	JQ437053	/	Hedin *et al.* (2012)
US Leiobuninae	*Eumesosoma ocalense*	OP1904*	USA: Florida, Highlands Co., Archbold Biological Station	J. Carrel	JQ437180	JQ439989	/	JQ437204	Hedin *et al.* (2012)
US Leiobuninae	*Eumesosoma roeweri*	OP1058*	USA: Texas, Wichita Co. Burkburnett	J. Cokendolpher	JQ432307	JQ432365	/	JQ437205	Burns *et al.* (2012)
US Leiobuninae	*Leuronychus pacificus*	OP1484*	USA: California, San Diego Co., Palomar Mtn. SP	M. Hedin	/	JQ439990	JQ437055	JQ437206	Burns *et al.* (2012)
Neopilionidae	*Thrasychirus gulosus*	OP1152*	CHILE: Prov Chiloe, Isla Chiloe, near Puente Rio Pudeto	T. Cekalovic	JQ437101	/	JQ437009	/	Hedin *et al.* (2012)
Neopilionidae	*Megalopsalis sp.*	DNA100783*	/	/	EF108576	/	EF108573	/	Boyer *et al.* (2007)
Metopilio Group	*Eurybunus brunneus*	OP378*	USA: California, San Diego Co., Bow Willow CG	M. Hedin	JQ437102	JQ439946	JQ437010	JQ437181	Hedin *et al.* (2012)
Metopilio Group	*Globipes simplex*	OP122*	USA: California, Fresno Co., N Pinehurst	M. Hedin *et al.*	JQ437103	JQ439947	JQ437011	/	Hedin *et al.* (2012)
Metopilio Group	*Dalquestia grasshoffi*	OP2176*	MEXICO: Guanajuato, Atarjea, Mangoscuatos	P. Berea	JQ437105	/	JQ437013	JQ437182	Hedin *et al.* (2012)
Phalangiidae	*Oidellus pictus*	OP1063*	USA: Michigan, Calhoun Co. near Marshall	J. W. Shultz	JQ437107	/	X81441	/	Hedin *et al.* (2012), Shultz & Regier (2001), Giribet *et al.* (1996)
Phalangiidae	*Phalangium opilio*	OP1065*	USA: Maryland, Montgomery Co. Unity, Tusculum Farm	J. W. Shultz	JQ432314	EU523757	AF124937	EU523757	Hedin *et al.* (2012), Shultz & Regier (2001), Masta & Boore (2008), Giribet *et al.* (2009)

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APPENDIX 5. (Continued)

Molecular Clade	Species	Voucher No.	Location	Collected By	28S	16S	18S	COI	References
Phalangiidae	*Rhampsinitus sp.*	DNA100710*	/	/	GQ912757	/	GQ912708	/	Giribet *et al.* (2010)
Phalangiidae	*Gyas titanus*	OP1059*	SPAIN: location unknown	J. Cokendolpher	JQ437108	/	JQ437014	JQ437184	Hedin *et al.* (2012)
Protolophus	*Protolophus tuberculatus*	OP1067*	USA: California, Contra Costa Co., Mt. Diablo	S. Masta	JQ437109	JQ439948	JQ437015	/	Hedin *et al.* (2012)
Protolophus	*Protolophus singularis*	DNA101033*	/	/	EF028096	/	EF028095	/	Giribet *et al.* (2010)
European Leiobuninae	*Nelima doriae*	OP1922*	NETHERLANDS: Kessel	H. Wijnhoven	JQ437117		JQ437016	JQ437185	Hedin *et al.* (2012)
European Leiobuninae	*Astrobunus grallator*	OP1057*	SPAIN: location unknown	C. Ribera	JQ437119		AF124939		Hedin *et al.* (2012), Shultz & Reiger (2001), Giribet *et al.* (2009)
US Leiobuninae	*Trachyrhinus marmoratus*	OP235*	USA: Oklahoma, Harper Co., East of Buffalo	P. Paquin; N. Duperre	JQ437120	JQ439961	JQ437018	/	Hedin *et al.* (2012)
US Leiobuninae	*Leiobunum exilipes*	OP384*	USA: California, Siskiyou Co., Matthews Creek CG	M. Hedin	JQ437134	JQ439963	JQ437024		Hedin *et al.* (2012)
US Leiobuninae	*Nelima elegans*	OP1483*	USA: North Carolina, Alleghany Co., Doughton Park	M. Hedin	JQ437135	JQ439964	JQ437025	/	Hedin *et al.* (2012)
US Leiobuninae	*Nelima paessleri*	OP1799*	USA: Oregon, Coos Co., Golden & Silver Falls SNA	Richart, A. Fusek	JQ437136	JQ439965	/	/	Hedin *et al.* (2012)
US Leiobuninae	*Nelima paessleri*	OP238*	CANADA: Alberta, Waterton NP, Lake Cameron	P. Paquin; D. Wytrykush	JQ437137	JQ439966	/	JQ437186	Hedin *et al.* (2012)

APPENDIX 6. Morphological measurements, comparisons and ratio of interests for all male *Pseudoleiobunum* species and other male Asian Leiobuninae species for comparison. FIL: Leg Femur I Length; BL: Body length; BW: Body width at the widest portion; CL: Cephalothorax length; CW: Cephalothorax width; AL: Abdominal length; BLW: Ratio of body length to body width; ALW: Ratio of abdominal length to cephalothorax width; FIB: Ratio of leg I femoral length to body length.

Genus/Group	Species	Locality	FIL	BL	BW	CL	CW	AL	BLW	ALCW	FIB	Reference
Pseudoleiobunum/ *Maximum*-group	*P. lutulentum* **sp. nov.**	Lantau Island, Hong Kong	3.9	3.03	2.39	1.2	2.39	1.83	1.27	0.77	1.29	This study
Pseudoleiobunum/ *Maximum*-group	*P. maximum distinctum*	Mt. Yuwan, Amami-oshima Island, Japan	9.7	9.8	6.8	3.4	6.8	6.4	1.44	0.94	0.99	Suzuki, 1973
Pseudoleiobunum/ *Maximum*-group	*P. maximum formosum*	Mt. Hsueshan, Taiwan	9.3	5.81	4	1.81	4	3.9	1.45	0.98	1.60	Suzuki, 1976
Pseudoleiobunum/ *Maximum*-group	*P. maximum yushan*	Mt. Yushan, Taiwan	5.1	4.45	3.1	1.35	3.1	3.1	1.44	1	1.15	Suzuki, 1976
Pseudoleiobunum/ *Maximum*-group	*P. japanense japanense*	Nishitanzawa, Japan	7.5	6.3	4.2	2.4	4.2	3.9	1.5	0.93	1.19	Suzuki, 1976
Pseudoleiobunum/ *Maximum*-group	*P. japanense japonicum*	Mt. Hikosan, Japan	5	7.6	4.5	2.8	4.5	4.8	1.69	1.07	0.66	Suzuki, 1976
Pseudoleiobunum/ *Maximum*-group	*P. japanense japonicum*	Mt. Ishizuchi, Japan	6.1	6.2	4.2	2.3	3.2	3.9	1.48	0.93	0.98	Suzuki, 1976
Pseudoleiobunum/ *Maximum*-group	*P. japanense japonicum*	Hiroshima, Japan	6.3	6.9	4.2	2.6	4.2	4.3	1.64	1.02	0.91	Suzuki, 1976
Pseudoleiobunum/ *Maximum*-group	*P. japanense japonicum*	Mino-o, Japan	5.3	6.9	4.5	2.4	4.5	4.5	1.53	1.00	0.77	Suzuki, 1976
rubrum-group	*Leiobunum rubrum*	Yakushima Island, Japan	7.9	3.2	2.24	1.2	1.2	2.00	1.43	1.67	2.47	Suzuki, 1973
curvipalpe-group	*L. hikocola*	Mt. Hikosan, Japan	6.2	3.44	2.25	1.16	2.25	2.28	1.53	1.01	1.80	Suzuki, 1966
curvipalpe-group	*L. sadoense*	Mt. Myoken, Sado Island, Japan	6.3	3.3	2.2	1	2.2	2.3	1.5	1.05	1.91	Tsurusaki, 1982
curvipalpe-group	*L. montanum*	Mt. Tsubakuro, Japan	5.71	4.24	/	1.2	/	3.04	/	/	1.35	Tsurusaki, 1985
curvipalpe-group	*L. montanum*	Mt. Ontake, Japan	5.3	4.9	/	/	/	/	/	/	1.08	Tsurusaki, 1985
curvipalpe-group	*L. montanum*	Tatsumi Pass, Japan	8.2	5.1	/	/	/	/	/	/	1.61	Tsurusaki, 1985
curvipalpe-group	*L. montanum*	Mt. Daisen, Japan	6.32	3.45	/	/	/	/	/	/	1.83	Tsurusaki, 1985
curvipalpe-group	*L. montanum*	Mt. Tsurugi, Japan	5.6	3.78	/	/	/	/	/	/	1.48	Tsurusaki, 1985
curvipalpe-group	*L. montanum*	Mt. Ishizuchi, Japan	5.66	4.28	/	/	/	/	/	/	1.11	Tsurusaki, 1985
curvipalpe-group	*L. montanum*	Mt. Sobo, Japan	5.47	3.8	/	/	/	/	/	/	1.44	Tsurusaki, 1985

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APPENDIX 6. (Continued)

Genus/Group	Species	Locality	FIL	BL	BW	CL	CW	AL	BLW	ALCW	FIB	Reference
curvipalpe-group	*L. montanum*	Mt. Ishizuchi, Japan	4.9	4.4	/	/	/	/	/	/	1.1	Suzuki, 1953
curvipalpe-group	*L.oharai*	Sihou, Taiwan	5.7	3.12	/	/	/	/	/	/	1.83	Tsurusaki, 1991
curvipalpe-group	*L. tohokuense*	Oirase, Japan	7.33	3.99	/	/	/	/	/	/	1.84	Tsurusaki, 1990
curvipalpe-group	*L. tohokuense*	Ht. Haguro, Japan	7.19	4.01	/	/	/	/	/	/	1.79	Tsurusaki, 1990
curvipalpe-group	*L. tohokuense*	Asamushi-Hanchimangu, Japan	6.88	3.87	/	/	/	/	/	/	1.78	Tsurusaki, 1990
curvipalpe-group	*L. tohokuense*	Nasu-kogen, Japan	6.6	3.06	/	/	/	/	/	/	2.16	Tsurusaki, 1990
curvipalpe-group	*L. tohokuense*	Shiobara Spa, Japan	7	3.79	/	/	/	/	/	/	1.85	Tsurusaki, 1990
curvipalpe-group	*L. curvipalpe*	Tosho-gu Shrine, Japan	5.53	5.71	/	/	/	/	/	/	0.97	Tsurusaki, 1990
curvipalpe-group	*L. curvipalpe*	Ryuzu-no-taki Falls, Japan	6.42	4.61	/	/	/	/	/	/	1.39	Tsurusaki, 1990
curvipalpe-group	*L. curvipalpe*	Mt. Tanigawa, Japan	5.46	4.16	/	/	/	/	/	/	1.31	Tsurusaki, 1990
curvipalpe-group	*L. curvipalpe*	Mt. Akagi, Japan	5.1	4.96	/	/	/	/	/	/	1.03	Tsurusaki, 1990
curvipalpe-group	*L. curvipalpe*	Komagata, Kiryu, Japan	6.4	5.5	/	/	/	/	/	/	1.16	Tsurusaki, 1990
curvipalpe-group	*L. curvipalpe*	Minenochaya, Karuizawa, Japan	5.32	5.18	/	/	/	/	/	/	1.03	Tsurusaki, 1990
curvipalpe-group	*L. curvipalpe*	Kiyosato, Japan	5.9	5.05	/	/	/	/	/	/	1.17	Tsurusaki, 1990
curvipalpe-group	*L. curvipalpe*	Lake Higashi, Shirakaba, Japan	5.53	5.01	/	/	/	/	/	/	1.10	Tsurusaki, 1990
curvipalpe-group	*L. curvipalpe*	Kita-Karuizawa, Japan	5.7	5.8	3.4	/	3.4	/	1.71	/	0.98	Suzuki, 1953
curvipalpe-group	*L. hiraiwai*	Hiroshima Kenmin-no-mori, Japan	6.46	4.37	/	/	/	/	/	/	1.48	Tsurusaki, 2006
curvipalpe-group	*L. hiraiwai*	Notoro Pass, Japan	6.17	4.74	/	/	/	/	/	/	1.30	Tsurusaki, 2006
curvipalpe-group	*L. hiraiwai*	Yashajin Pass, Japan	6.9	4.1	/	/	/	/	/	/	1.68	Tsurusaki, 2006
curvipalpe-group	*L. hiraiwai*	Togakushi-chusha, Japan	6.73	5.19	/	/	/	/	/	/	1.30	Tsurusaki, 2006
curvipalpe-group	*L. hiraiwai*	Mt. Bushu-Mitake, Japan	7.01	4.16	/	/	/	/	/	/	1.69	Tsurusaki, 2006
curvipalpe-group	*L. hiraiwai*	Kamikochi, Japan	6.2	5	2.9	/	2.6	/	1.72	/	1.24	Suzuki, 1953
curvipalpe-group	*L. hiraiwai*	Mt. Fuji, Japan	5.9	5.9	3.2	/	2.85	/	1.84	/	1.00	Suzuki, 1953
curvipalpe-group	*L. hiraiwai*	Mt. Bushu-Mitake, Japan	6.7	5.8	3.3	/	/	/	1.76	/	1.16	Suzuki, 1957
curvipalpe-group	*L. manubriatum*	Nenokuchi, Japan	6.8	3.9	/	/	/	/	/	/	1.74	Suzuki, 1976
curvipalpe-group	*L. globosum*	Nenokuchi, Japan	7.7	4.5	2.8	1.2	2.8	3.3	1.61	1.18	1.71	Suzuki, 1976
curvipalpe-group	*L. kohyai*	Mt. Koya, Japan	7.6	5.1	/	/	/	/	/	/	1.49	Suzuki, 1953; 1976
curvipalpe-group	*L. simplum*	Yokoo Hutte, Japan	7	3.1	1.1	0.97	1.1	2.13	2.82	1.94	2.26	Suzuki, 1976

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APPENDIX 6. (Continued)

Genus/Group	Species	Locality	FIL	BL	BW	CL	CW	AL	BLW	ALCW	FIB	Reference
curvipalpe-group	*L. hiasai*	Kitazawa Pass, Japan	5.4	4.2	/	1.31	/	/	/	/	1.29	Suzuki, 1976
East Asian *Nelima*	*Nelima nigricoxa*	Mt. Hikosan, Japan	14.4	5.7	/	/	/	/	/	/	2.53	Sato & Suzuki, 1939
East Asian *Nelima*	*N. suzukii*	Nopporo, Japan	6.78	3.78	/	/	/	/	/	/	1.79	Suzuki & Tsurusaki, 1983
East Asian *Nelima*	*N. genufusca genufusca*	Nopporo, Japan	10.21	5.2	/	/	/	/	/	/	1.96	Suzuki & Tsurusaki, 1983
East Asian *Nelima*	*N. genufusca tuberculatus*	Jeju-do, Korea	14.1	6.0	4.1	/	4.1	/	1.46	/	2.35	Suzuki, 1983
East Asian *Nelima*	*N. coreana*	Suyeo, C., Korea	7.2	3.8	2.6	/	2.6	/	1.46	/	1.89	Suzuki, 1983
East Asian *Nelima*	*N. coreana*	Mt. Surii, Korea	5.8	3.6	2.2	/	2.2	/	1.64	/	1.61	Suzuki, 1983
East Asian *Nelima*	*N. parva*	Mt. Hikosan, Japan	6.1	2.2	1.8	/	1.8	/	1.22	/	2.77	Suzuki, 1974
East Asian *Nelima*	*N. parva*	Mt. Ishizuchi, Japan	5.1	2.4	1.2	/	2	/	1.2	/	2.13	Suzuki, 1974
East Asian *Nelima*	*N. similis*	Hakone, Japan	3.8	2.1	1.5	0.6	1.5	1.5	1.4	1	1.81	Suzuki, 1974
East Asian *Nelima*	*N. aokii*	Nippara, Japan	16.1	6.55	4.5	/	4.5	/	1.46	/	2.46	Suzuki, 1974
East Asian *Nelima*	*N. satoi*	Mt. Ishizuchi, Japan	9.37	5.73	/	/	/	/	/	/	1.64	Suzuki, 1940
East Asian *Nelima*	*N. okinawaensis*	Nago Island, Okinawa, Japan	15.7	4.5	3.4	1.5	3.4	3	1.32	0.88	3.49	Suzuki, 1964
East Asian *Nelima*	*N. taiwana*	Mt. Hsuehshan, Taiwan	10.9	3.1	/	/	/	/	/	/	3.52	Suzuki, 1977

APPENDIX 7. Morphological measurements, comparisons and ratio of interests for all female *Pseudoleiobunum* species and other female Asian *Leiobunum* species for comparison. FIL: Leg Femur I Length; BL: Body length; BW: Body width at the widest portion; CL: Cephalothorax length; CW: Cephalothorax width; AL: Abdominal length; BLW: Ratio of body length to body width; ALW: Ratio of abdominal length to cephalothorax width; FIB: Ratio of leg I femoral length to body length.

Genus/Group	**Species**	**Locality**	**FIL**	**BL**	**BW**	**CL**	**CW**	**AL**	**BLW**	**ALCW**	**FIB**	**Reference**
Pseudoleiobunum/ *maximum*-group	*P. lutulentum* **sp. nov.**	Lantau Island, Hong Kong	4.9	5.19	3.25	/	/	/	1.60	/	0.94	This study
Pseudoleiobunum/ *maximum*-group	*P. maximum distinctum*	Mt. Yuwan, Amami-oshima Island, Japan	9.8	13.7	/	4.2	6.8	9.5	/	1.40	0.72	Suzuki, 1973
Pseudoleiobunum/ *maximum*-group	*P. japanense japanense*	Nishitanzawa, Japan	7.8	9.2	/	3	5.2	6.2	/	1.19	0.85	Suzuki, 1976
Pseudoleiobunum/ *maximum*-group	*P. japanense japonicum*	Mt. Hikosan, Japan	5	9.9	/	3.1	5.1	6.7	/	1.31	0.51	Suzuki, 1976
Pseudoleiobunum/ *maximum*-group	*P. japanense japonicum*	Mt. Ishizuchi	5.9	9.3	/	3	5	6.3	/	1.26	0.57	Suzuki, 1976
rubrum-group	*Leiobunum rubrum*	Mt. Sogri	9.4	5.27	/	1.55	3.24	3.72	/	1.15	1.78	Suzuki, 1966
rubrum-group	*L. rubrum*	Yakushima Island, Japan	7.1	4.14	/	/	/	/	/	/	1.71	Suzuki, 1973
curvipalpe-group	*L. hikocola*	Mt. Hikosan, Japan	4.9	3.98	/	1.16	2.77	2.82	/	1.02	1.23	Suzuki, 1966
curvipalpe-group	*L. sadoense*	Mt. Myoken, Sado Island, Japan	5.3	5.3	/	1.4	2.4	3.3	/	1.38	1.00	Tsurusaki, 1982
curvipalpe-group	*L. curvipalpe*	Kita-Karuizawa, Japan	5.95	6.75	3.9	/	3.65	/	1.73	/	0.88	Suzuki, 1953
curvipalpe-group	*L. hiraiwai*	Kamikochi, Japan	5.3	6.5	3.7	/	2.8	/	1.76	/	0.82	Suzuki, 1953
curvipalpe-group	*L. kohyai*	Mt. Koya, Japan	5	5.3	/	/	/	/	/	/	0.94	Suzuki, 1953; 1976
curvipalpe-group	*L. simplum*	Yokoo Hutte, Japan	6.1	5	/	1.41	2.3	3.59	/	1.56	1.22	Suzuki, 1976
curvipalpe-group	*L. hiasai*	Kitazawa Pass, Japan	4.8	5.76	/	1.64	2.74	4.12	/	1.50	0.83	Suzuki, 1976

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APPENDIX 7. (Continued)

Genus/Group	Species	Locality	FIL	BL	BW	CL	CW	AL	BLW	ALCW	FIB	Reference
East Asian *Nelima*	*Nelima nigricoxa*	Mt. Hikosan, Japan	12.5	9	/	/	/	/	/	/	1.39	Sato & Suzuki, 1939
East Asian *Nelima*	*Nelima suzukii*	Nopporo, Japan	6.06	5.61	/	/	/	/	/	/	1.08	Suzuki & Tsurusaki, 1983
East Asian *Nelima*	*Nelima genufusca*	Nopporo, Japan	9.68	7.88	/	/	/	/	/	/	1.23	Suzuki & Tsurusaki, 1983
East Asian *Nelima*	*Nelima genufusca tuberculatus*	Jeju-do, Korea	8.4	6.9	/	/	4	/	/	/	1.22	Suzuki, 1983
East Asian *Nelima*	*Nelima coreana*	Mt. Surii, Korea	6.9	5.5	/	/	2.7	/	/	/	1.25	Suzuki, 1983
East Asian *Nelima*	*Nelima parva*	Mt. Hikosan, Japan	6.4	4.3	2.6	/	2	/	1.65	/	1.49	Suzuki, 1974
East Asian *Nelima*	*Nelima parva*	Mt. Ishizuchi, Japan	4.1	3.6	/	/	1.9	/	/	/	1.14	Suzuki, 1974
East Asian *Nelima*	*Nelima similis*	Hakone, Japan	4.1	3.9	2.5	0.8	2	3.1	1.56	1.55	1.05	Suzuki, 1974
East Asian *Nelima*	*Nelima aokii*	Nippara, Japan	15.2	9.65	5.9	/	/	/	1.64	/	1.58	Suzuki, 1974
East Asian *Nelima*	*Nelima satoi*	Mt. Ishizuchi, Japan	9.6	7.6	/	/	/	/	/	/	1.26	Suzuki, 1940
East Asian *Nelima*	*Nelima taiwana*	Mt. Hsuehshan, Taiwan	/	3.7	/	/	/	/	/	/	/	Suzuki, 1977