Zootaxa 5353 (6): 533–550
https://www.mapress.com/zt/

Article

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

https://doi.org/10.11646/zootaxa.5353.6.2
http://zoobank.org/urn:lsid:zoobank.org:pub:DD342940-639F-4054-B153-932C318DF73E

Re-description of the genus Heterobiantes and its type species *H. geniculatus* (Opiliones: Laniatores: Epedanidae) with additional genital and external morphology data

DESMOND KAI TECK TAN[1,3], JONATHAN J. FONG[1,4] & CHAO ZHANG[2,5*]
[1]*Science Unit, Lingnan University, Hong Kong, China*
[2]*Key Laboratory of Zoological Systematics and Application of Hebei Province, Institute of Life Sciences and Green Development, College of Life Sciences, Hebei University, Baoding, China*
[3] *desmondtan@ln.hk; https://orcid.org/0009-0003-2388-7214*
[4] *jonfong@ln.edu.hk; https://orcid.org/0000-0002-3648-6730*
[5] *opiliones@163.com: https://orcid.org/0000-0003-1702-1206*
**Corresponding author.*

Abstract

The genus *Heterobiantes* Roewer, 1912 and its type species *Epedanus geniculatus* Pocock, 1903 are redescribed based on the type specimen currently housed within the British Museum of Natural History (BMNH), London, along with new specimens captured in Hong Kong, providing updated morphological data and male genital description. Closer inspections reveal how the species is different from other similar genera within Epedaninae and rationalizes its placement as a monotypic genus within the sub-family. Genetic data are also included.

Key words: Taxonomy, Arachnida, harvestmen, Epedaninae, Hong Kong

Introduction

Endemic to Asia, the harvestmen family Epedanidae Sørensen, 1886, currently contains 135 extant species in 61 genera (Kury 1993, 2003, Kury *et al*. 2022). Members of the family often possess a common ocularium with a prominent median spine (or a 'unicorn spine'), elongated pedipalps with robustly armed tibia, tarsus and chelicerae, which are clavate and adorned with numerous spines (Kury 2007, Lian *et al*. 2008). Four subfamilies are currently recognized: Acrobuninae Roewer, 1912; Sarasinicinae Roewer, 1923; Epedaninae Sørensen, 1886; and Dibuninae Roewer, 1912.

Classifying individuals and groups based solely on external morphology (*e.g*., tarsal process counts, tubercle/spine counts) is insufficient. Genital morphology, particularly in males, has been found to be valuable in clarifying taxonomy (Suzuki 1973, Ubick & Briggs 1989, Zhang & Zhang 2013). Characteristics of penis morphology described by Kury (1993, 2003, 2007) have become defining features for the inclusion of new members into the family of Epedanidae: setae arranged in a circular formation around the 'head' complex (*i.e*., glans), 'the presence of a well-developed immovable sac' (*i.e*., follis) and the absence of 'complex introverting structures in the penis' (Lian *et al*. 2008). With the identification of such features, species that have different external morphology can still be classified into the family Epedanidae (*e.g*., Dibuninae Loman, 1906).

With its unicorn spine, trapezoidal body and elongated pedipalps that are accompanied by two long claws, the species *Heterobiantes geniculatus* (Pocock, 1903) fits into the subfamily Epedaninae (Kury 1993, 2007). Originally classified under the genus *Epedanus* Thorell, 1876, this species was transferred to the then newly erected genus *Heterobiantes* Roewer, 1912 under the subfamily Acrobuninae. Roewer's rationale for this was due to it having scopulae on tarsi III and IV (Roewer 1912, 1923). After Roewer (1938) inspected two specimens claimed to have been studied by Pocock from the curator Arthur Stanley Hirst, he discarded the genus *Heterobiantes* because of its unreinforced pedipalpal patella, and placed the taxon in a newly-established genus *Epedanestus* Roewer, 1938. This new genus was then placed under the subfamily Epedaninae due to the absence scopulae on tarsi III–IV, as well

Accepted by A. Pérez-González: 15 Sept. 2023; published: 13 Oct. 2023

as its distitarsus I with only two tarsomeres, or in his words '2-membered narrow section on tarsus I'. Its strong resemblance to another genus *Epedanellus* Roewer, 1911 was also noted (Roewer 1911, 1938).

Unsurprisingly, this created confusion for future taxonomic work as it was difficult to differentiate between the genera *Epedanestus* and *Epedanellus* due to the insignificant difference of the latter's pedipalpal patella having one ventral-apical granule and the former with none (Roewer 1938). Kury *et al*. (2020) resolved the issue by concluding that *Epedanestus* is a junior synonym of *Heterobiantes* and placed the genus back under Epedaninae.

New techniques (*e.g*., scanning electron microscopy) have significantly enhanced the study of Opiliones. Such advancements enable the re-examination of previous taxonomic classifications, helping to resolve any confusion that may have arisen from outdated methods. There are many harvestman species in the world that are in need for treatment with new methods and technology, and one such example is the genus *Heterobiantes*. Described over a century ago, Pocock's original description was brief and lacked clarity. In addition, there have been no attempts to match historical specimens with modern specimens, despite this species being one of the most common harvestmen found in Hong Kong.

To resolve this issue, we collected new specimens of *H. geniculatus* to facilitate a comparison with previous descriptions. In late 2021, we collected specimens of *H. geniculatus* from its designated type locality in Hong Kong, as indicated by Pocock in 1903, and examined its morphology in more detail, including description, photographs and illustrations. We verify that modern specimens represent the same taxon by comparing our specimens to the holotype of *H. geniculatus* at the British Museum of Natural History (BMNH). From this work, we provide improved morphological data of one of the most common harvestman species in Hong Kong. Additionally, we gathered DNA sequence data to serve as valuable resource for future reference concerning this species.

Material and Methods

Specimens and other materials

Specimens were caught by hand, immediately euthanized with 70% ethanol and then stored at 4 °C. For this study we included 13 new specimens collected across four main sites in Hong Kong (Fig. 10): Aberdeen Country Park (LINGU-INV13), Pok Fu Lam (LINGU-INV04, LINGU-INV06, LINGU-INV07, LINGU-INV16), Discovery Bay (LINGU-INV01, LINGU-INV02, LINGU-INV03) and Tai Mo Shan (LINGU-INV05, LINGU-INV08, LINGU-INV09, LINGU-INV10, LINGU-INV14, LINGU-INV15). Note that Pok Fu Lam and Tai Mo Shan are the name of rather extensive areas, therefore on the map it is shown that there are two markings for each of these two areas, please refer to the detailed GPS location below and Figure 10 for more information. The code used for specimen tags is the abbreviation for the Lingnan University Natural History Invertebrate collection (LINGU-INV). In addition, pictures were taken by the BMNH of the specimens originally described by Pocock (1903) and designated *Epedanus geniculatus*. Both specimens are recorded under the collection record number 1643424. The following general morphological re-descriptions are based on LINGU-INV01, LINGU-INV05, LINGU-INV06 and LINGU-INV07, while genital morphology is based on six additional specimens (see Results section).

Morphological examination

Examination procedures follow Acosta *et al*. (2007) and Lian *et al*. (2011). Specimens were examined and measured with a stereomicroscope imaging system (Nikon Inc. SMZ800N) equipped with a P-IDT drawing tube and a 4K multi-output microscopic camera (ChineTek Scientific Limited).

We extracted male genitalia and cleaned them with drops of 70% ethanol. To prepare specimens for light microscopy, we followed the protocols of Acosta *et al*. (2007) and Schwendinger & Martens (2002). First, the genitalia were expanded by placing them in 50 °C lactic acid for 10–20 minutes, and then transferred to distilled water at room temperature to cool down for 5 minutes. Next, the genitalia were cleared by placing on a slide with a drop of glycerol for 5–10 minutes.

All illustrations were done with the GNU Image Manipulation Program (GIMP) (Montesanto 2015). All measurements and photographs were taken with the mounted 4K microscopic camera and ToupView camera control software (ToupTek Photonics Co., Ltd.).

For electron microscopy, the genitalia were further 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 placed in a graded ethanol series (30%, 45%, 65%, 80%, 90%) for at least 30 minutes at each concentration, then placed in acetone. 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 aluminium stubs with adhesive, fixed to show the ventral, dorsal, and lateral views. The genitalia were sputter-coated with gold for 50 s under 40mA current (BAL-TEC, SCD 005). Electron microscopy was performed with a scanning electron microscope (LEO 1530 FEG & Hitachi S-3400N).

DNA Sequencing

A total of six samples were selected for DNA sequencing (LINGU-INV06, LINGU-INV10, LINGU-INV13, LINGU-INV14, LINGU-INV15, LINGU-INV16). Legs I–IV were removed and DNA was extracted using a DNeasy® Blood and Tissue Kit (Qiagen) following the manufacturer's protocol. We follow Boyer *et al*. (2007), Pinto-da-Rocha *et al*. (2014) and Kumekawa *et al*. (2021) and target two loci: Cytochrome C oxidase subunit 1 (*COI*) and 16S ribosomal RNA (*16S*). *COI* was amplified using the primers LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Folmer *et al*. 1994), while *16S* was amplified using primers 16SA (5'-CGCCTGTTTATCAAAAACAT-3') and 16SB (5'-CTCCGGTTTGAACTCAGATC-3') (Xiong & Kocher 1991).

Polymerase chain reaction (PCR) was performed in a thermal cycler (Bio-Rad Laboratories, Inc. T-100TM) with the following condition: for *COI*, initial denaturing at 95 °C for 5 min; then 35 cycles of 95 °C for 30 s, annealing temperature at 42 °C for 30 s, and extension at 72 °C for 1 min; followed by a final extension at 72 °C for 10 min (Boyer *et al*. 2007). For *16S*, initial denaturing at 94 °C for 10 minutes, then 45 cycles of 94 °C for 1.5 min, 48 °C for 2 min and extension at 72 °C for 3 min; with a conclusion of final extension at 72 °C for 15 mins (Kumekawa *et al*. 2021). The size and quality of PCR products were checked using agarose gel electrophoresis (1% agarose), and purified using a QIAquick PCR Purification Kit (Qiagen). Final products were sequenced using the PCR primers on an ABI 3730xl System at Macrogen (Seoul, Korea).

Forward and reverse sequences for each individual were assembled in Geneious v.11.1 (Biomatters). Alignments of *COI* were checked by translating sequences to amino acids to ensure there were no erroneous stop codons. The final sequences were uploaded to GenBank (Table 3). Since the DNA sequence database is largely incomplete for the family Epedanidae and harvestmen in general, phylogenetic analyses were uninformative and not included in this study.

Taxonomy

Epedaninae Sørensen, 1886

Heterobiantes Roewer, 1912

Heterobiantes Roewer, 1912: 219; 1923: 191–192, f. 217; Kury *et al*. 2020: 32–33.
Epedanestus Roewer, 1938: 108. Type species by monotypy: *Epedanus geniculatus* Pocock, 1903. Synonymized by Kury *et al*. 2020: 32.

Type Species: *Epedanus geniculatus* Pocock, 1903, subsequent designation by Kury *et al*. 2020: 32.

Diagnosis: Large-sized epedanines (5.94–6 mm) with a long median spine on the ocularium. The body is trapezoidal in shape. Dorsal scutum distinctly segregated into four different areas (areas I–II fused). Two apparent yellow (sometimes pale green) spots are located on the posterior-lateral sides of prosoma. Areas I–II with a row of 8–10 granules, and often but not always with two that are positioned nearing the anterior margins of the area. Area V and all free tergites are lined with hair-tipped tubercles. Proximal segment of chelicerae strong and clavate, distally clustered with granules and hair-tipped tubercles. Pedipalps elongated, trochanter dorsally armed with one tubercle while femurs are slightly arcuate, armed with 3–5 small tubercles dorsally and 8–9 strong tubercles ventrally (Figs 3B-C). A disto-ental tubercle can also be found on the femur. Tibia and tarsus heavily armed with long spines on

both ventral sides, which form a 'basket claw' (Wolff *et al*. 2016) (Figs 3A–C). All distitarsi with three segments. Penis elongated and the shaft widens distally, armed with a lower transverse row of 7–10 strong, curved spines. The upper, subdistal section is protected by 10–15 similarly curved spines, along with three more pairs of ventral spines of glans. The positioning of the spines together resembles the shape of a crown, and is of resemblance to other Epedanidae members (e.g., K. insulanus). Total length of the penis is 2.4–2.6 mm.

Distribution: China (Hong Kong).

Heterobiantes geniculatus **(Pocock, 1903)**

Figs 1–6; 7B, E, G, N; 8L

Epedanus geniculatus Pocock, 1903: 446, plate XII, f. 1.
Pseudobiantes geniculatus Hirst, 1911: 633, 636.
Epedanestus geniculatus Roewer, 1938: 109, f. 27; Wang 1953: 504.
Heterobiantes geniculatus Roewer, 1912: 219; Roewer 1923: 191–192, f. 217; Li & Song 1993: 238.

Type Material Examined: Holotype (male) and syntype (sex unknown), both specimens collected under record number 1643424, both in 75% industrial methylated spirit (IMS). The former with the labels: '48.60, *Epedanus geniculatus*, Pocock. Hong Kong' and 'Roewer (Nr. 111.06) x. 1937 revid, sub: *Epedanestus* (n.g.) *geniculatus* (Pocock), Hong Kong, one specimen. (Typ.) verstümmelt vorgefunden [= found mutilated].' The latter also with two labels: '56.113, *Epedanus geniculatus*, Pocock. Hong Kong.' and 'Roewer (Nr. 11107) x. 1937 revid, snb: *Epedanestu*s (n.g.) *geniculatus*, (Pocock), Hong Kong, one specimen. (verstümmelt vorgefunden)' (Fig. 9).

New Material Examined: Males (LINGU-INV01, LINGU-INV05, LINGU-INV06) and female (LINGU-INV07), CHINA: Hong Kong, Lantau Island, Discovery Bay, 22.18916°N, 114.01322°E, 3 May 2022 (LINGU-INV01); CHINA: Hong Kong, New Territories, Tai Mo Shan, 22.40906°N, 114.12033°E (LINGU-INV05), 31 March 2022, CHINA: Hong Kong, Hong Kong Island, Lung Fu Shan, 22.27605°N, 114.132767°E, 6 May 2022 (LINGU-INV06); CHINA: Hong Kong, Hong Kong Island, Aberdeen Country Park, Lady Clementi's Ride, 22.25519°N, 114.18230°E, 24 May 2022 (LINGU-INV07). Six male genitalia (LINGU-INV02, LINGU-INV03, LINGU-INV04, LINGU-INV08, LINGU-INV09, LINGU-INV10), CHINA: Hong Kong, Lantau Island, Discovery Bay, 22.18946°N, 114.01294°E (LINGU-INV02); 22.316417°N, 114.021383°E (LINGU-INV03); CHINA: Hong Kong, New Territories, Tai Mo Shan, 22.409562°N, 114.118812°E (LINGU-INV09); 22.42820°N, 114.11852°E (LINGU-INV08); 22.408352°N, 114.118619°E (LINGU-INV10) CHINA: Hong Kong, Hong Kong Island, Pok Fu Lam (LINGU-INV04), 19 August 2021.

Etymology: Species name geniculatus is derived from the way the tibia is connected at an almost-right angle from the patella. Thus, the name is taken from the word 'geniculate', meaning 'bent at a sharp angle' (Pocock 1903).

Habitat: Roams on the forest ground or under leaf litter, also in small crevices within soil slopes besides walking trails. Mostly nocturnal but can be seen roaming during daytime.

Distribution: Throughout Hong Kong.

Dorsum (Figs 1A–B, 6B). Dorsal scutum trapezoidal in shape and divided into five scutal areas (areas I–II fused), largest in the fifth scutal area. Anterior margin of the scutum mostly unarmed, but with about three granules scattered on each side of the anterior margins. There are two yellow spots at both lateral sides of the lower prosoma. Lateral and posterior margins of the body lined with transverse granules. Ocularium well-defined with a long median spine between the two eyes. A total of 8–10 granules (varies among individuals) can be found transversely on areas I–II, often with two more granules found on both sides of the anterior margin of the area (oftentimes may not be obvious); 10 granules can be seen respectively on areas III and IV. Posterior border of area V and free tergites are lined with longitudinal rows of hair-tipped tubercles. The coxa IV extends out and backwards from the body.

Venter (Fig. 1C). Mostly unarmed; small granules scattered on coxae I–III, with a longitudinal row of granules situated in a small crevice between coxae II and III.

Chelicerae (Figs 2, 6A). Proximal segment strong, with 9–13 granules scattered around its ventral surface. Second segment with 12–14 dorsal hair-tipped tubercles, strong tubercles on both dorsal and ventral surface are clustered on the anterior margin of the segment. Fingers strong and bifid, movable finger with two dorsal tubercles located nearing the fingertip (Figs 2A–B). Numerous hairs are scattered throughout the second segment (Figs 2C–F).

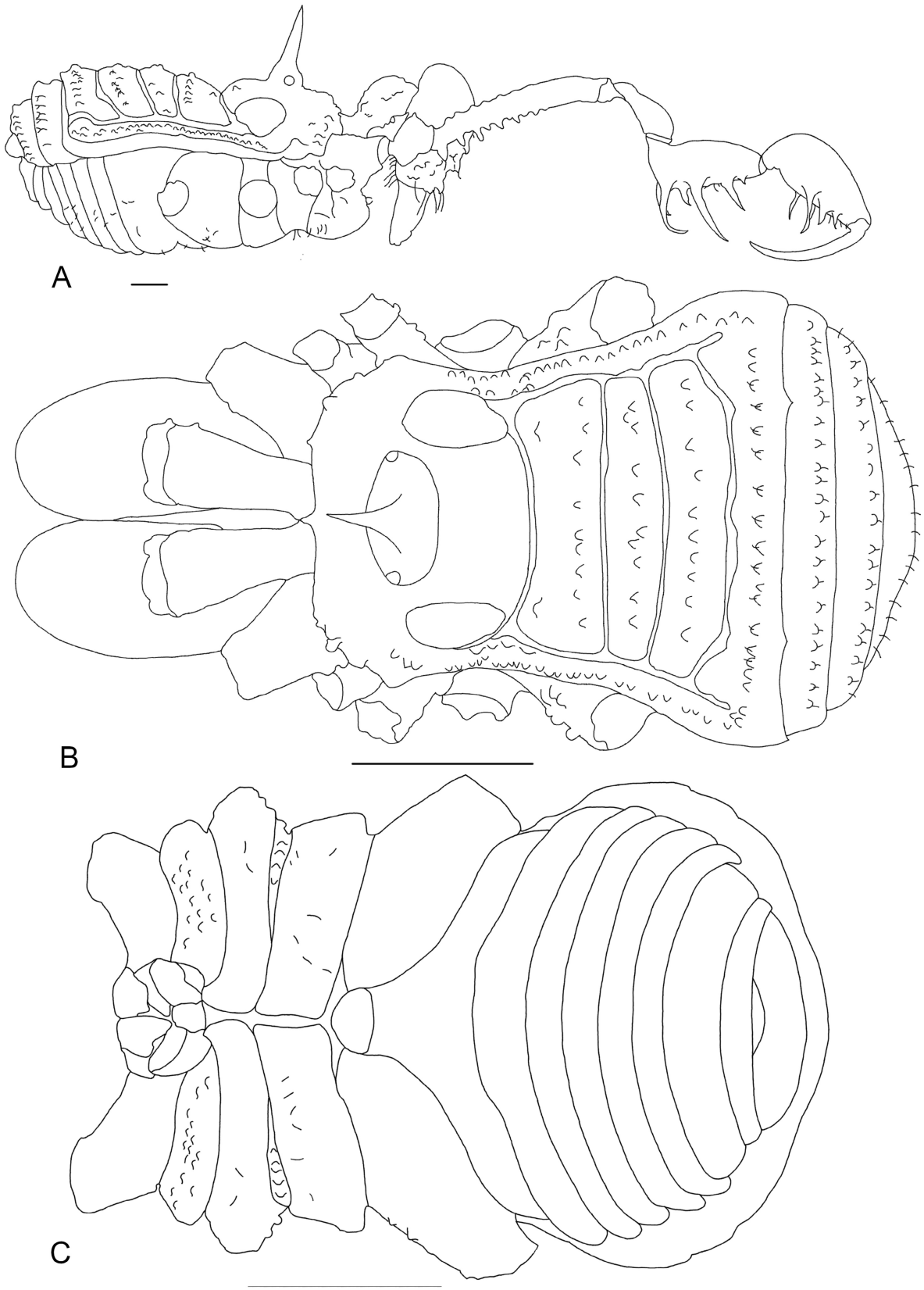

FIGURE 1. *Heterobiantes geniculatus* (Pocock, 1903), males, body. A lateral view (LINGU-INV02); B dorsal view (LINGU-INV06); C ventral view (LINGU-INV06). Scale bars: 1 mm.

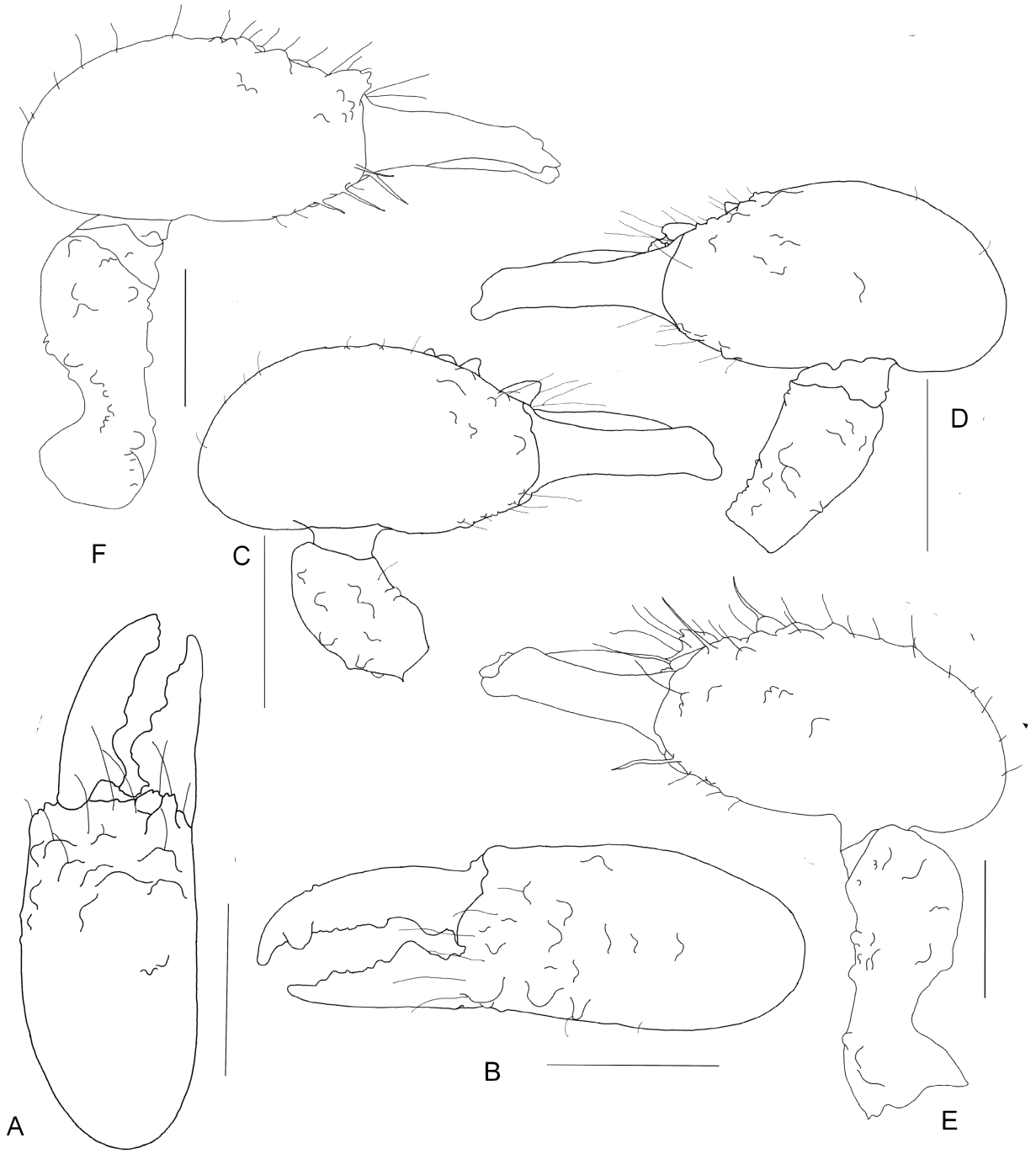

FIGURE 2. *Heterobiantes geniculatus* (Pocock, 1903), male (A–D, LINGU-INV06), male (E–F, LINGU-INV05), chelicera. A Distal segment of left chelicera, frontal view; B Distal segment of right chelicera, frontal view; C Left chelicera, lateral view; D Right chelicera, lateral view; E Full right chelicera, lateral view; F Full left chelicera, lateral view. Scale bars: 1mm.

Pedipalps (Figs 3A–C). Elongated and slender, pedipalpal coxae extend well beyond the body. Trochanter with one dorsal tubercle and two ventral hair-tipped tubercles. Femur slightly arcuate, armed with five tubercles dorsally and 8–9 hair-tipped tubercles ventrally; one disto-lateral tubercle can be found near the patella. Patella without apophysis and unarmed (Figs 3B–C). Both tibia and tarsus clavate, tibia extends in a straight angle from the patella. Ventral surface armed with three pairs of strong, curved, setiferous tubercles, and one pro-medial short tubercle; proximal tubercles being the longest while the distal pair being the shortest. Tarsus armed with three mesal- and four ectal-setiferous tubercles ventrally. Both tibia and tarsus are also armed with hairs and granules scattered ventrally. The claw is strong, long, and curved. The tubercles, along with the curved claw, which could be contracted inwards, form a 'basket claw' (Fig. 3A) (Wolff *et al*. 2016).

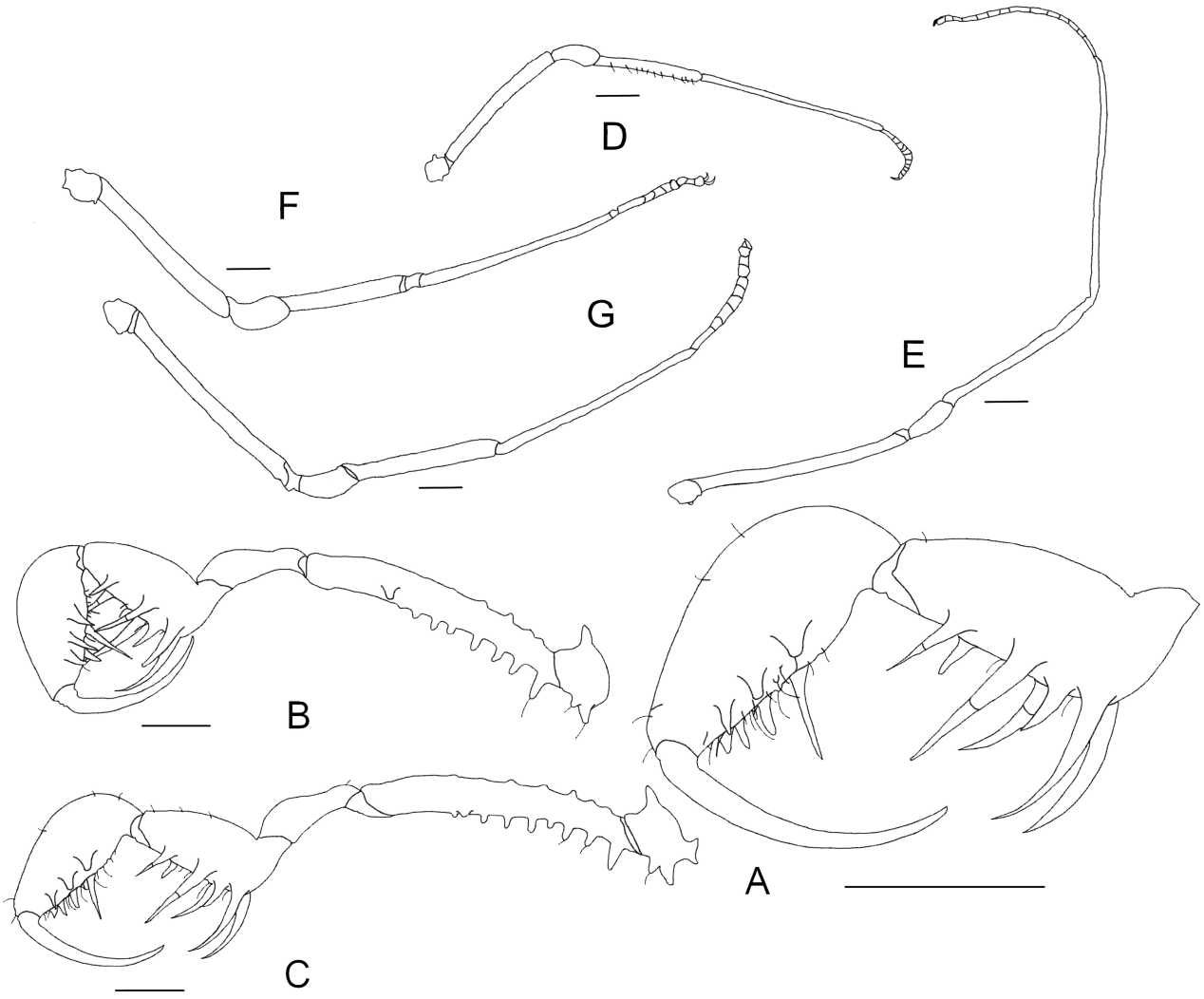

FIGURE 3. *Heterobiantes geniculatus* (Pocock, 1903), male (LINGU-INV06). A Close-up of pedipalpal tibia-tarsus-claw, lateral view; B Right pedipalp, lateral view; C Left pedipalp, lateral view; D Leg I, lateral view; E Leg II, lateral view; F Leg III, lateral view; G Leg IV, lateral view. Scale bars: 1 mm.

Legs (Figs 3D–G, 4A–C). Leg II is the longest, followed by IV, III, and finally I. All legs mostly unarmed, except for short hairs throughout the leg, especially on tarsus. Trochanter often, but not always, with one small dorsal tubercle. All femora elongated and arcuate. Tarsi I and II with single simple claw while III and IV with double simple claws. All distitarsi with three tarsomeres (Figs 4A–B). Tarsal formula: 11/24/9/9. All tarsi without scopulae (Fig. 4C).

Penis (Figs 4D–F; 5; 7B, E, G, N; 8L). Penis slender and elongated, with a complex, crown-like apical structure. There are 10 strong basal setae in a circular arrangement a little lower from the apical structure (Fig. 4F). The structure itself is divided into two visible components: the ventral plate and the glans. The ventral plate is narrowly-shaped like a knife, raising above and perpendicularly positioned to the glans (Fig. 5B). Though there is no reinforcement in the dorsal area of the structure, the lateral and ventral area is heavily armed with similarly strong setae. There are six ventral setae of the glans (three on each side), situated between the glans and the ventral plate. These are followed by 10–12 lateral setae (5–6 on each side) that surround both lateral sides of the lower ventral plate to the venter of the apical structure. The glans is comprised of the dorsal and ventral stylar lobe, which is kept hidden when unexpanded. When expanded, both lobes are unfolded outwards, like the petals of a blooming flower (Figs 4E–F). The glans also extends laterally and curved outwards. The straight and narrow stylus, located at the centre of the glans, protrudes out and upwards from the structure. The wall of the capsula interna is densely-lined with small soft spines, forming a 'prickly funnel' (Fig. 7E) (Stacheltrichter, Martens 1986). Basal sac is located within the shaft, around the area of the basal setae (Fig. 5).

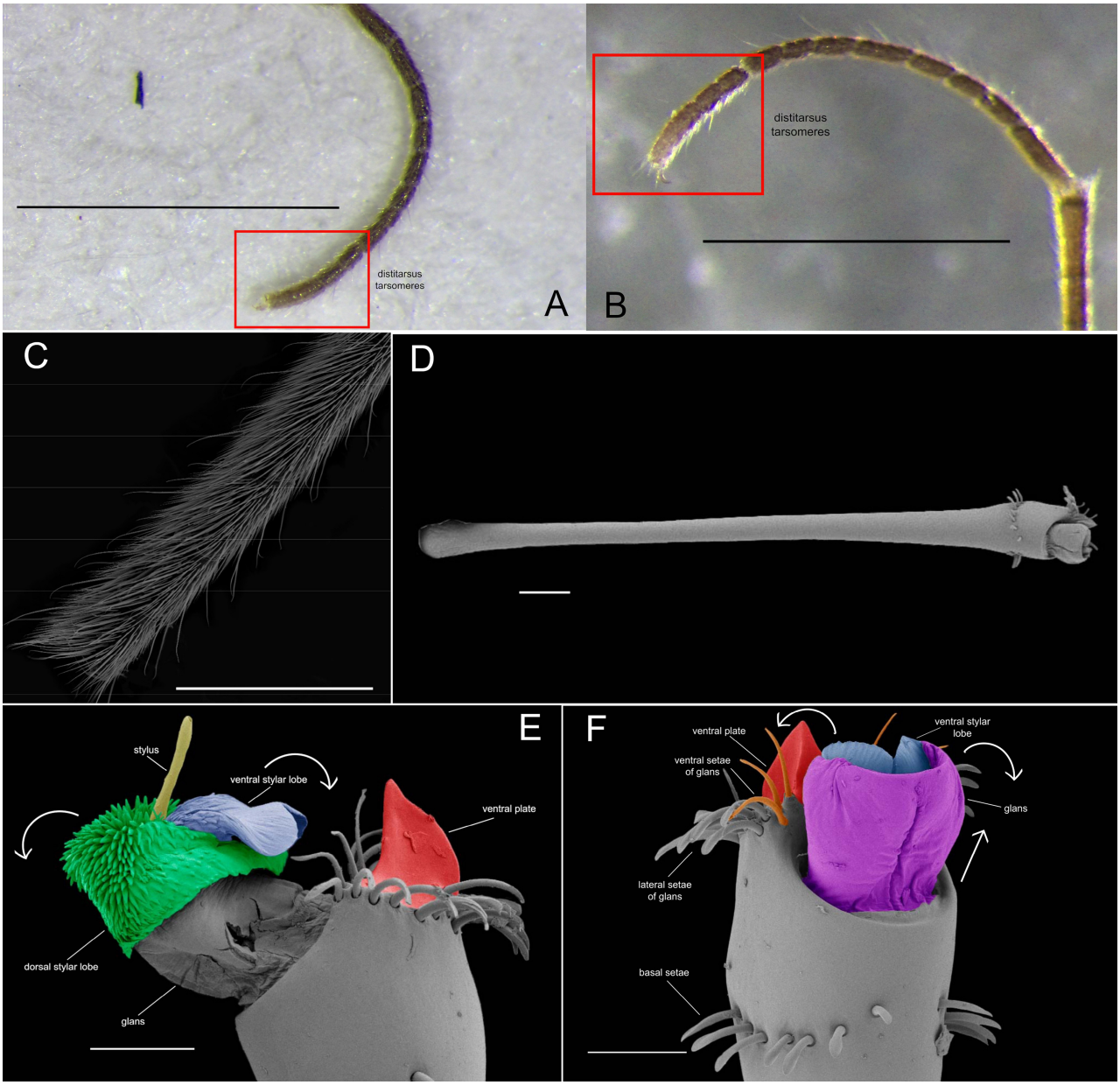

FIGURE 4. *Heterobiantes geniculatus* (Pocock, 1903). A photograph of the distitarsus I (LINGU-INV01); B Close-up of the distitarsus I (LINGU-INV06); C Scanning electron microscopic leg IV tarsus (LINGU-INV01), a part of the distitarsus is missing, but the lack of scopulae is still clearly shown; D Scanning electron microscopic full dorso-lateral view of male genitalia (LINGU-INV10); E Scanning electron microscopic lateral view of expanded male genitalia (LINGU-INV08), arrows indicate how the lobes unfold and expand; F Scanning electron microscopic dorsal view of unexpanded male genitalia (LINGU-INV10), arrows indicate how the lobes unfurl and the direction of penial expansion. Scale bar: 1 mm (A, B); 500 µm (C); 100 µm (D, E, F).

Female (Figs 6C–D). General appearance very similar to males, except with a slightly slenderer body shape, together with a shorter width at its widest portion (Fig. 6D). The most distinct difference is the size of the chelicerae, with the female chelicerae being significantly smaller (Fig. 6C). All distitarsi with three tarsalia. Tarsal formula: 12/25/9/9.

Measurements: Males LINGU-INV06 (LINGU-INV01): Body 6.7 (5.94) long, 5 (4.68) at the widest portion. Ocularium 0.82 (0.64) long, 1.45 (1.27) wide, median spine 2.47 (2.79) long. Penis: 2.44 (2.79) long. Pedipalpal claw 2.38 (2.36) long. The other measurements are in Table 1.

Female LINGU-INV07: Body 7.38 long, 5.06 wide at the widest portion. Ocularium 0.66 long, 1.23 wide, median spine 1.26 long. Pedipalpal claw 2.4 long. The other measurements are in Table 2.

FIGURE 5. *Heterobiantes geniculatus* (Pocock, 1903), penis. A apical structure (LINGU-INV10), ventral view; B apical structure (LINGU-INV17), lateral view; C full penis (LINGU-INV04), lateral view. Scale bars: 200 μm.

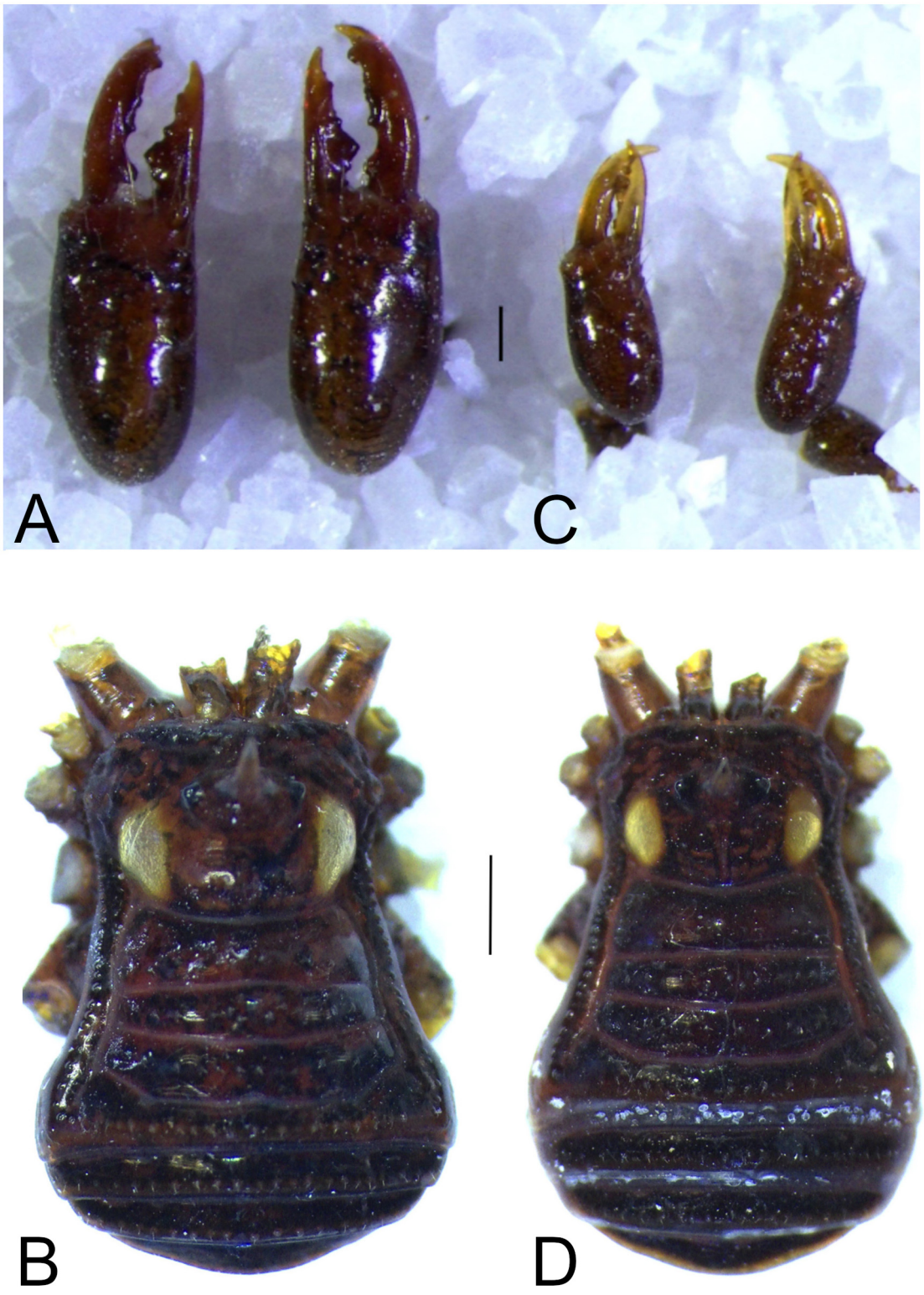

FIGURE 6. Photograph comparing chelicerae and the dorsal body of *Heterobiantes geniculatus* (Pocock, 1903) on sexual dimorphism. A Chelicerae of male (LINGU-INV06); B Dorsal body of male (LINGU-INV06); C Chelicerae of female (LINGU-INV07); D Dorsal body of female (LINGU-INV07). Scale bar: 1 mm.

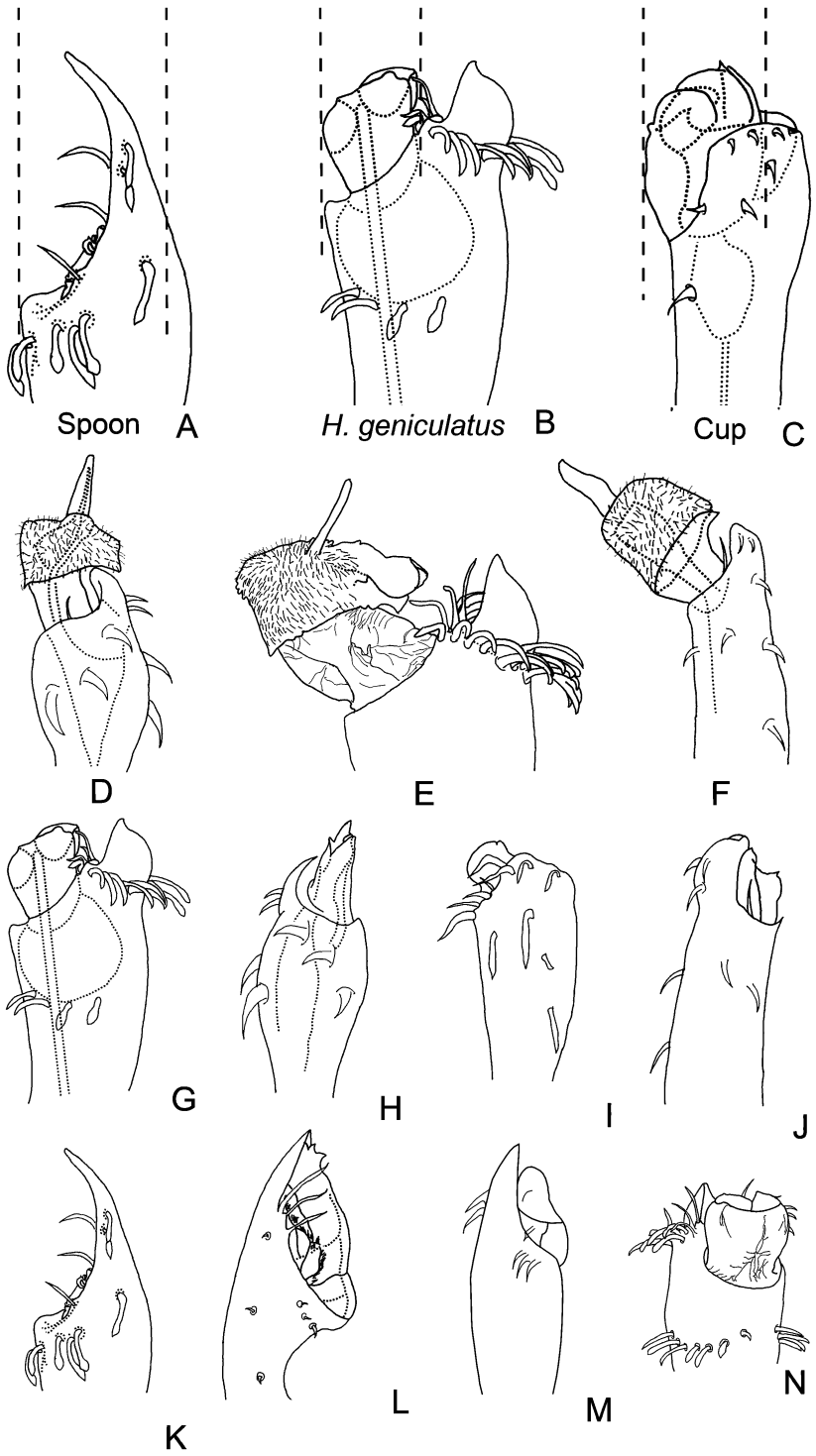

FIGURE 7. Comparisons of apical structures of male genitals. A – C Penis comparisons of 'spoon' and 'cup' form between *H. geniculatus* and other Epedanidae species; A *Pseudobiantes japonicus* Hirst, 1911, taken from Kury *et al*. 2019; B Heterobiantes geniculatus (Pocock, 1903); C *Parabeloniscus corneus* Zhang & Zhang, 2012; D – F Examples and comparisons of 'prickly funnels' in everted Epedanidae genitals, all genitals beside H. geniculatus are taken from Zhang & Martens 2020; D *Toccolus globitarsis* Suzuki, 1969; E *Heterobiantes geniculatus* (Pocock, 1903); F *Euepedanus dashdamirovi* Zhang & Martens, 2020; G – N Comparison of lateral genitals of male Epedanidae; G & N *Heterobiantes geniculatus* (Pocock, 1903); H *Toccolus globitarsis* Suzuki, 1969, taken from Zhang & Martens, 2020; I *Epedanus pictus* Thorell, 1876, taken from Kury *et al*. 2019; J *Euepedanus dashdamirovi* Zhang & Martens, 2020, taken from Zhang & Martens 2020; K *Pseudobiantes japonicus* Hirst, 1911, taken from Kury & Villarreal 2015; L *Kilungius bimaculatus* Roewer, 1915, taken from Suzuki 1973; M *Kilungius insulanus* (Hirst, 1911), taken from Suzuki 1973.

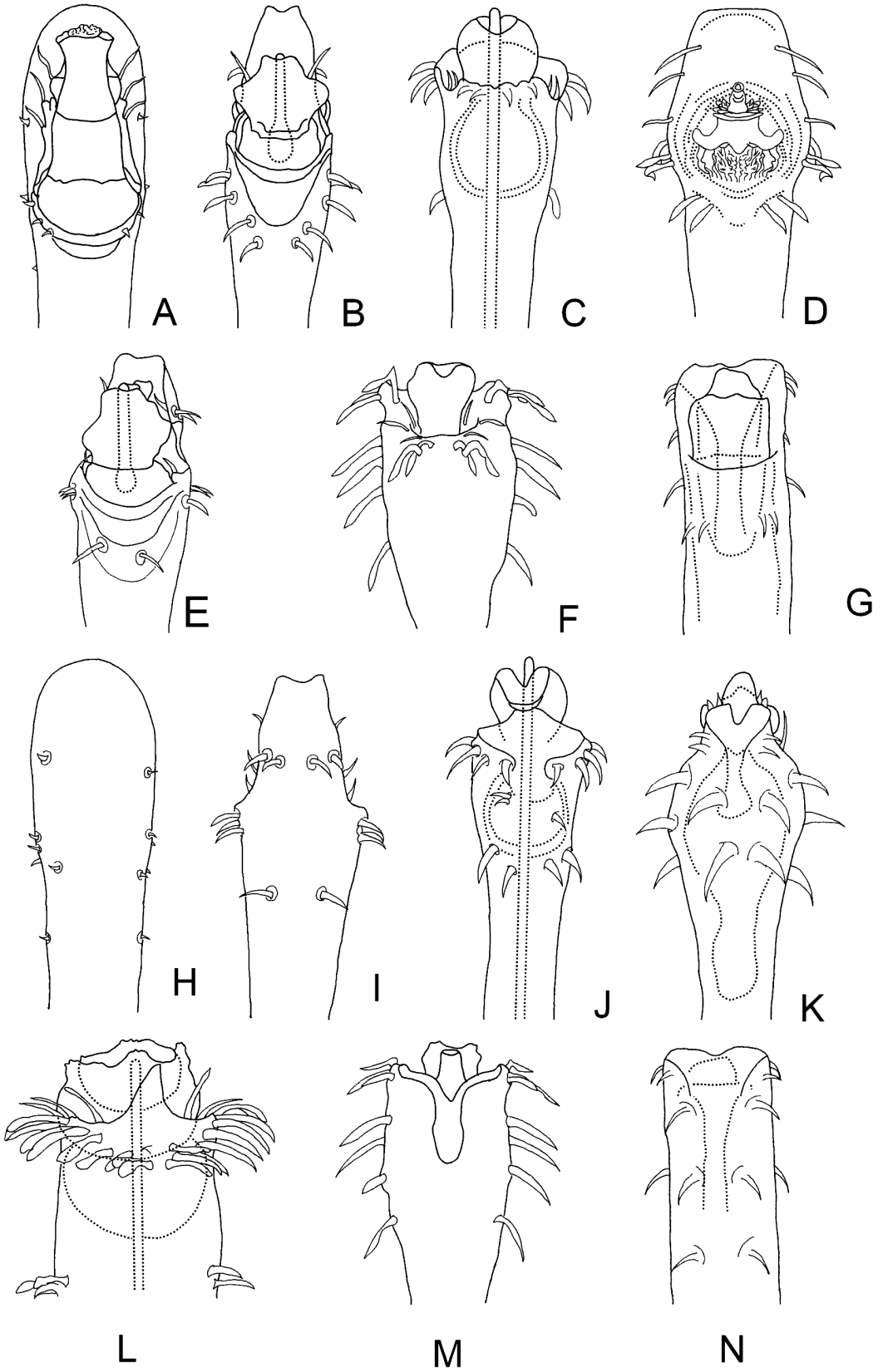

FIGURE 8. Comparison of dorsal and ventral genitals of male Epedanidae. A & H *Kilungius bimaculatus* Roewer, 1915, taken from Suzuki 1973; B, E & I *Kilungius insulanus* (Hirst, 1911), taken from Suzuki 1973; C & J *Plistobunus columnaris* Lian *et al*., 2011; D *Pseudobiantes japonicus* Hirst, 1911, taken from Kury & Villarreal 2015; F & M *Epedanus pictus* Thorell, 1876, taken from Kury *et al*. 2019; G & N *Euepedanus dashdamirovi* Zhang & Martens, 2020, taken from Zhang & Martens 2020; K *Toccolus globitarsis* Suzuki, 1969, taken from Zhang & Martens 2020; L *Heterobiantes geniculatus* (Pocock, 1903).

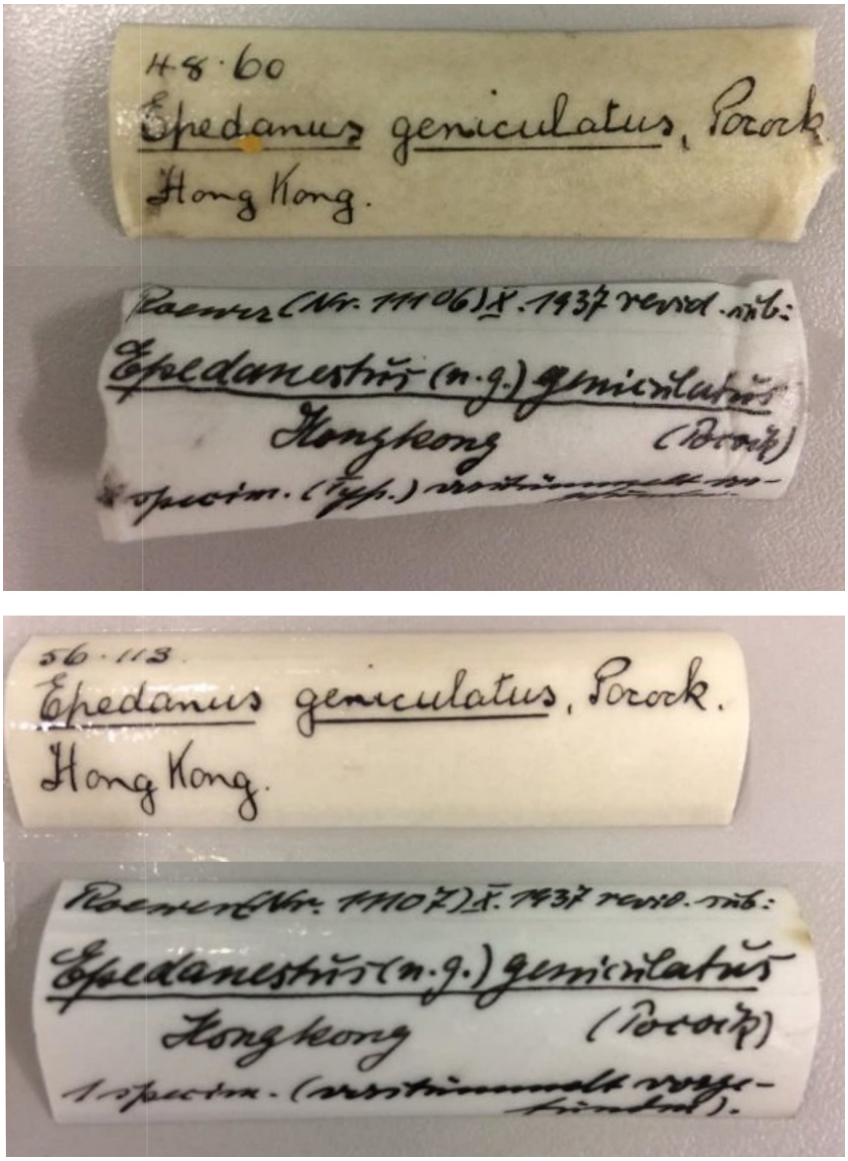

FIGURE 9. Type specimen tags found with the specimens studied by Roewer, photo taken by the British Museum of Natural History (BMNH).

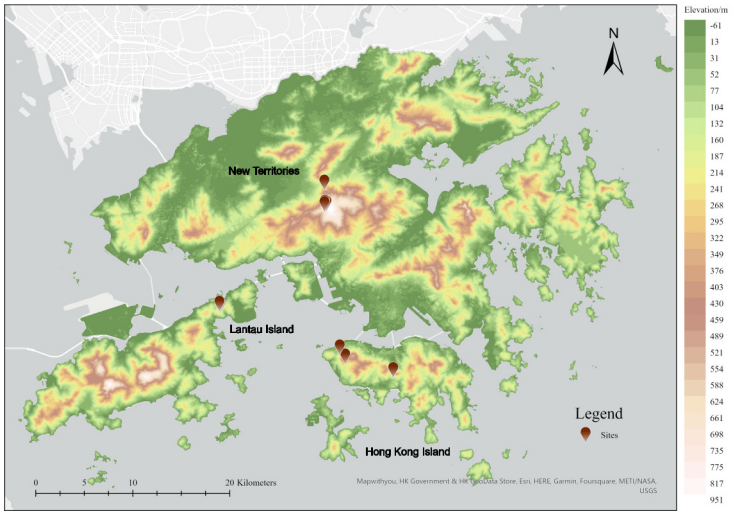

FIGURE 10. Altitude map of Hong Kong, China and the locations of the specimens used in this study. *Heterobiantes geniculatus* can be found throughout Hong Kong but tends to occur at higher altitudes (range 108–661 m).

TABLE 1. Morphological measurements for two male specimens LINGU-INV06 (LINGU-INV01). All measurements are in millimetres (mm).

	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
Leg I	0.7 (0.63)	3.54 (3.44)	1.06 (1.06)	2.48 (2.48)	4.18 (4.25)	1.91 (2.06)	13.87 (13.92)
Leg II	0.74 (0.66)	4.78 (4.8)	1.31 (1.24)	3.88 (3.88)	5.37 (5.38)	4.52 (4.46)	20.60 (20.42)
Leg III	0.98 (0.84)	3.96 (3.93)	1.16 (1.11)	2.78 (2.81)	4.65 (4.54)	2.44 (2.58)	15.97 (15.81)
Leg IV	0.85 (0.76)	5.04 (5.05)	1.43 (1.35)	3.28 (3.19)	5.95 (6.07)	2.71 (3.08)	19.26 (19.5)
Pedipalpus	0.76 (0.72)	4.24 (3.96)	1.39 (1.47)	2.11 (2.03)	- -	2.26 (2.13)	10.76 (10.04)

TABLE 2. Morphological measurements for female specimen LING-INV07. All measurements are in millimetres (mm).

	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
Leg I	0.73	3.41	0.94	2.56	4.20	1.96	13.80
Leg II	0.75	4.61	1.26	3.08	5.34	4.48	19.52
Leg III	0.81	3.77	1.46	2.81	4.55	2.57	15.97
Leg IV	0.79	5.12	1.24	3.32	5.95	3.13	19.55
Pedipalpus	0.81	3.62	1.33	2.08	-	2.36	10.20

TABLE 3. GenBank accession numbers for sample sequences.

Sample Label	COI	16S
LINGU-INV06	OP503573	OR045909
LINGU-INV10	OP503577	
LINGU-INV13	OP503574	OR045912
LINGU-INV14	OP503576	
LINGU-INV15	OP503575	OR045911
LINGU-INV16	OP503578	OR045910

Remarks: For this study, only one female specimen was captured and examined. Ovipositor was destroyed during the examination process. While researching the species, we have designated a vernacular name of 'Hong Kong Krabby Harvestman', derived from how it looks like Mr. Krabs from the hit children's TV show SpongeBob SquarePants when viewed dorsally and with its pedipalps extended. For the Chinese name, we designate '香港雙班盲蛛', inspired by the Chinese name of *Kilungius bimaculatus* Roewer (1915) '雙斑基隆盲蛛', which incorporated its distinctive yellow lateral spots on the posterior prosoma (Figs 1A–B & 6B–D).

Discussion

Putting aside the obvious first, it is reasonable for *Heterobiantes* to be classified under the subfamily Epedaninae using Roewer's classification basing on meristic morphological features: the absence of scopulae on tarsi III and IV, and the presence of only two tarsomeres on distitarsus I (Roewer 1912, 1938). We have re-examined the specimen's distitarsus I and found that it has three tarsomeres, which would result in a reassignment of the genus to Sarasinicinae (Roewer, 1923) as members of the subfamily is noted to possess three tarsomeres, along with the other similar features as Epedaninae (Kury 2003). However, many studies have shown that minute morphological features, such as tarsal spinal count, may be unreliable in taxonomic work since they can vary among individuals of the same species (Rambla 1978, Acosta 1999). Additional studies are needed to check the subfamily classification of *H. geniculatus*. But as of the moment, the following will attempt to distinguish *Heterobiantes* from other deceptively similar species.

Currently, there are only three available documents on the description of *H. geniculatus*: the original description (Pocock 1903) and two brief redescriptions by Roewer (1912, 1938). However, these descriptions are based only on sketchy external morphology. Pocock (1903) supported his separation of *Heterobiantes* from the genus *Epedanus* using the geniculation of the palpi tibia from patella. But this feature is shared among many other genera within Epedaninae and even in other subfamilies such as Sarasinicinae. Examples of these include *Epedanellus* Roewer, 1911; *Pseudobiantes* Hirst, 1911 and *Plistobunus* Pocock, 1903 (genus also found in Hong Kong). To begin with, *H. geniculatus* is distinct from *Epedanus* as the latter has a much heavily armed pedipalps, with the patella elongated and armed with 1–2 spines whereas *H. geniculatus* has no armed pedipalpal patella. This specimen is overall distinguished by its general larger size, with its body commonly measured at 6–7 mm long and 5 mm wide (see Measurements of *H. geniculatus* above). It also possesses more dorsal armament when compared with similar genera such as *Plistobunus*, with the dorsal areas lined transversely with tiny granules and hair-tipped tubercles whilst the latter has only a pair of tubercles on area II and similarly lined tubercles for area IV and free tergites. *Plistobunus* is also armed with 4–6 tubercles on each side of the frontal margin whereas *Heterobiantes* is not armed anteriorly (Lian *et al*. 2011).

To differentiate this species with *Epedanellus tuberculatus* Roewer, 1911, one can look at the elongated pedipalpal patella, where *E. tuberculatus* is armed with 1 small ventral spine. The pedipalpal femora of this species is also only proximally armed with ventral spines but not dorsally nor distally (Roewer 1927).

This genus is also easily mistaken for *Kilungius* Roewer, 1915, a genus found in Japan and Taiwan. It is diagnosed with generally unarmed dorsal scutum with no apparent spines, except for transverse alignments of small granules throughout areas I–IV and free tergites (*Kilungius bimaculatus Suzuki*, 1973). Area II of *Kilungius* sometimes also has a pair of long median spines (*Kilungius insulanus* (Hirst, 1911)). Despite also having the transversely-lined tubercles on its scutal areas and free tergites, this specimen also often has two smaller granules located at the frontal margin of area I and no additional long tubercles on the rest of the scutal areas. *Kilungius* is also smaller in size, with *K. bimaculatus'* total body length recorded at around 5 mm and 3.3 mm wide (Suzuki 1973).

Last but not least, when comparing to *Pseudobiantes japonicus* Hirst, 1911. It is a smaller species, around 3.5–4 mm in body length, the scutal areas (though it varies among individuals, as seen in Kumekawa *et al*. 2014) is generally unarmed and the patella is also armed with 1 minute apical ventral granule (Suzuki 1973).

Since external morphological features alone is deceptive, one may look into genital morphology to solidify *Heterobiantes* as a monotypic genus within Epedaninae. Firstly, *Heterobiantes* was classified under Epedanidae because of the presence of a sunken basal sac, a ventral plate that is not clearly defined from the rest of the truncus and the glans only consisting of stylus and stylar lobe (Kury 2003, Lian *et al*. 2011). Many attempts were made to organize the varying genital shapes of Epedanidae genitals. In their description of the Malaysian Opiliones family Beloniscidae and study of Epedanidae genitals, Kury *et al*. (2019) identified two common forms found within the family: the 'cup' form (Fig. 7C) and the 'spoon' form (Fig. 7A). For the first form, the ventral portion of the pars distalis forms a median depression, with soft, folding tissue that everts when expanded (pseudocalyx, Kury *et al*. 2019). An example of this is *Parabeloniscus nipponicus* Zhang & Zhang, 2012 (Fig. 7C). On the other hand, the 'spoon' form is recognized by a thin and curved ventral plate, usually extending much higher than the glans, the setae on the ventral plate and overall structure are also generally reduced in size, this is exemplified by *Pseudobiantes japonicus* Hirst, 1911 (Fig. 7A).

Interestingly, the genital of *H. geniculatus* is rather unique and falls into neither category. It is not of the 'cup' form since there is no apparent pseudocalyx, which was described to be 'thick setigerous folding lobes' (Kury *et al*. 2019). The glans of this specimen is not covered with additional skins and when it everts the base of the glans merely extracts outwards, and is not thick enough to be folded. Meanwhile, it is also not of the 'spoon' form as its ventral plate does not curve upwards and there is no presence of small spines. Instead of a flat thin plate, this ventral plate is sharp, formed perpendicular to the glans like a blade (Fig. 7B).

Further analysis of the ventral plate shows that the structure of *H. geniculatus* is rather unique. For one, despite having the similar 'ventral frame' that Zhang and Martens (2020) suggest is commonly found in epedanid species, the ventral plates of *Plistobunus columnaris* Lian *et al*., 2011; *Toccolus globitarsis* Suzuki, 1969 and *Euepedanus dashdamirovi* Zhang & Martens, 2020 are either flat, club-like, or curving inward, possibly providing ventral and upwards protection for the glans (Figs 7H–N, 8) whereas it is difficult to see the ventral plate of *H. geniculatus* providing any sort of protection for its large glans as it is thin and short, positioned perpendicular to the glans (Figs 8L, 7G & N).

In terms of setae distribution, *H. geniculatus* resembles most of other Epedanid members, such as *Plistobunus columnaris* and *Epedanus pictus* Thorell, 1876, whereby setae are more uniformly distributed and encircling the pars distalis, oftentimes symmetrical and forming a sort of crown (Figs 7 & 8). Though difficult, one may still distinguish *H. geniculatus* from other genitals based solely on setae arrangement. For instance, it is distinct from *Pseudobiantes* as the latter has more sparsely distributed spines over the lateral and ventral areas when compared to *Heterobiantes* (Kury & Villarreal 2015).

When the genitalia are expanded, *H. geniculatus* has an internal 'prickly funnel' (Stacheltrichter, Martens 1986), whereby the capsula interna is lined with 'a dense coat of fur-like microtrichia' (Zhang & Martens 2020). Though this character is not recorded to be universal amongst epedanid species, this feature is present in other epedanid species, such as *Toccolus globitarsis* Suzuki, 1969 and *Euepedanus dashdamirovi* Zhang & Martens, 2020. This structure is a common and defining feature amongst other Laniatorean families, such as the Assamiidae Sørensen, 1884; Stygnopsidae Sørensen, 1932 and Suthepiidae Martens, 2020. More studies are needed on the expanded penis to determine the classification value of this 'prickly funnel' feature in the family Epedanidae (Figs 7D–F).

On morphological characteristics alone, *H. geniculatus* may not stand out much from other similar looking Epedanidae gemera (*e.g*., *Kilungius* Roewer, 1915 or P*seudobiantes* Hirst, 1911). But when combined with its unique genital morphological structure, one can see how it is different from other members in the Epedanidae family since it does not fall under the main categories of shapes commonly seen. As shown in the above, although it is shown that *Heterobiantes geniculatus* is monotypic, more studies will need to be conducted to ascertain its taxonomic position within Epedaninae.

Finally, on the note of its preferred habitat. Based on the new specimens collected in this study, *H. geniculatus* seems to prefer forest areas with high altitudes (Fig. 10). They mostly occur in more humid, warm habitats. A spike in temperature in June–August 2022 resulted this species being much harder to find despite frequent field visits. These findings seem to corroborate those of Edgar (1971) regarding the relative humidity tolerance of harvestmen, where harvestmen were shown to lose water easily, thus requiring environments with higher humidity (Curtis & Machado 2007). However, additional studies are required to clarify the detailed environmental parameters of H. geniculatus.

Acknowledgements

This work is supported by grants from the American Arachnological Society and Science Unit, Lingnan University. Special thanks to Mr. Chan Man Ho, Henry; Mr. Lee Wing Him, Henry; Mr. Lam Pui Yin, Ivan; Mr. Yip Hon Tim, Tim; Mr. Liu Hua Bing, Alex; Ms. Yau Sze Man, Sandy (Science Unit, Lingnan University) for the help in fieldwork and collecting the specimens in Hong Kong. We would also like to give special thanks to Ms. Cai Wen Hui in her help with GIS analysis; Dr. Jan Beccaloni and Ms. Daniella Sherwood from the British Museum of Natural History for their help with the access and pictures of the type specimens. This study would also not be possible without the help from the Electron Microscope Unit, Hong Kong University. We would also like to thank this paper's reviewers: Dr. Jochen Martens and Dr. Adriano B. Kury, as well as our handler from Zootaxa, Dr. Abel Pérez González. This publication would not have been possible without their patience and guidance.

References

Acosta, L.E. (1999) The identity of *Pachyloides tucumanus* n. comb. (ex Bosqia), with a proposal of generic synonymy and the new name *Pachyloides yungarum* (Opiliones, Gonyleptidae, Pachylinae). The Journal of Arachnology, 27 (2), 458–464. [http://www.jstor.org/stable/3706043]

Acosta, L.E., Pérez-González, A. & Tourinho, A.L. (2007) Methods for taxonomic study. *In:* Pinto-da-Rocha, R., Machado, G. & Giribet, G. (Eds.), *Harvestmen: The Biology of Opiliones*. Harvard University Press, Cambridge, Massachusetts, pp. 494–510.

Bennett, M.K. & Townsend, V.R. Jr. (2013) Reproductive morphology of three species of neotropical harvestmen (Opiliones, Laniatores, Gonyleptoidea). *Journal of Morphology*, 274 (12), 1415–1424. https://doi.org/10.1002/jmor.20191

Boyer, S.L., Clouse, R.M., Benavides, L.R., Sharma, P., Schwendinger, P.J., Karunarathna, I. & Giribet, G. (2007) Biogeography of the world: a case study from cyphophthalmid Opiliones, a globally distributed group of arachnids. *Journal of Biogeography*,

2007 (34), 2070–2085.
https://doi.org/10.1111/j.1365-2699.2007.01755.x
Curtis, D.J. & Machado, G. (2007) Ecology. *In:* Pinto-da-Rocha, R., Machado, G. & Giribet, G. (Eds.), *Harvestmen: The Biology of Opiliones*. Harvard University Press, Cambridge, pp. 280–308.
https://doi.org/10.2307/j.ctv322v442.11
Edgar, A.L. (1971) Studies on the biology and ecology of Michigan Phalangida (Opiliones). Miscellaneous Publications, *Museum of Zoology*, University of Michigan, 144, 1–64. [https://api.semanticscholar.org/CorpusID:82181942]
Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R.C. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3 (5), 294–299. [https://www.mbari.org/wp-content/uploads/2016/01/Folmer_94MMBB.pdf]
Hirst, A.S. (1911) On some new Opiliones from Japan and the Loo-Choo Islands. *Annals and Magazine of Natural History*, Series 8, 8 (47), 625–636.
https://doi.org/10.1080/00222931108693070
Kumekawa, Y., Fujimoto, H., Miura, O., Arakawa, R., Yokoyama, J. & Fukuda, T. (2021) Morphological and molecular phylogenetic analyses of *Zepedanulus ishikawai* (Arachnida: Opiliones: Laniatores: Epedanidae) in the southern part of the Ryukyu Archipelago. *The Canadian Entomologist*, 153 (6), 800–827.
https://doi.org/10.4039/tce.2021.42
Kury, A.B. (1993) *Análise filogenética de Gonyleptoidea* (Arachnida, Opiliones, Laniatores). Unpublished Ph. D. Thesis, Instituto de Biociências, Universidade de São Paulo, São Paulo, 73 pp. [in Spanish]
Kury, A.B. (2003) Annotated catalogue of the Laniatores of the New World (Arachnida, Opiliones). *Revista Iberica de Aracnologìa*, 1, 1–337. [https://digitalcommons.usf.edu/kip_articles/259]
Kury, A.B. (2007) Taxonomy. *In:* Pinto-da-Rocha, R.; Machado, G. & Giribet, G. (Eds.), *Harvestmen: The Biology of Opiliones.* Harvard University Press, Cambridge, pp. 88–246.
https://doi.org/10.2307/j.ctv322v442.8
Kury, A.B., Pérez-González, A. & Proud, D. (2019) A new Indo-Malayan family of Grassatores (Arachnida, Opiliones, Laniatores). *Invertebrate Systematics*, 33 (6), 892–906.
https://doi.org/10.1071/IS19035
Kury, A.B. & Villarreal, M.O. (2015) The prickly blade mapped: establishing homologies and a chaetotaxy for macrosetae of penis ventral plate in Gonyleptoidea (Arachnida, Opiliones, Laniatores). *Zoological Journal of the Linnean Society*, 174 (1), 1–46.
https://doi.org/10.1111/zoj.12225
Kury, A.B., Mendes, A.C., Cardoso, L., Kury, M.S., Granado, A.de A. Giribet, G., Cruz-López J.A., Longhorn S.J., Medrano, M., Kury, I.S. & Souza-Kury, M.A. (2022) *World Catalogue of Opiliones*. WCO-Lite version 2.4.0. Available from: https://wcolite.com/ (accessed 15 July 2022)
Li, S.Q. & Song, D.X. (1993) A revision of Chinese Harvestmen, with a note on their geographical distribution. *Scientific Treatise on Systematic and Evolutionary Zoology*, 2, 237–245.
Lian, W.G., Zhang, C. & Zhang, F. (2011) Review of the genus *Plistobunus* Pocock, 1903, with description of a new species from Hainan Island, China (Opiliones, Laniatores, Epedanidae). *ZooKeys*, 112, 39–52.
https://doi,org/10.3897/zookeys.112.1110
Lian, W.G., Zhu, M.S. & Kury, A.B. (2008) A new species of the genus *Tithaeus* from China (Arachnida: Laniatores: Epedanidae). *Zootaxa*, 1841 (1), 53–60.
https://doi.org/10.11646/zootaxa.1841.1.4
Loman, J.C.C. (1906) Opilioniden aus Neu-Guinea. *Nova Guinea*, 5, 1–8. [in German]
Martens, J. (1986) Die Grossgliederung der Opiliones und die Evolution der Ordnung (Arachnida). *In:* Barrientos, J.A. (Eds.), *Actas del X Congreso Internacional de Aracnologia*. Editorial Juvenil, Barcelona, pp. 289–310. [in German]
Martens, J. (2020) A mysterious dwarf: Suthepiidae nov. fam., a new harvestman family from mountains of northern Thailand (Arachnida: Opiliones: Laniatores). *Revue suisse de Zoologiem*, 127, 381–391.
https://doi.org/10.35929/RSZ.0028
Montesanto, G. (2015) A Fast GNU method to draw accurate scientific illustrations for taxonomy. *ZooKeys*, 515, 191–206.
https://doi.org/10.3897/zookeys.515.9459
Pinto-da-Rocha, R., Bragagnolo, C., Marques, F.P.L. & Antunes Junior, M. (2014) Phylogeny of harvestmen family Gonyleptidae inferred from a multilocus approach (Arachnida: Opiliones). *Cladistics*, 30, 519–539.
https://doi.org/10.1111/cla.12065
Proud, D.N. & Townsend, V.R. (2019) Unusual penis morphology among cosmetid harvestmen (Arachnida: Opiliones) from Mesoamerica. *Zoomorphology*, 138 (2), 233–47.
https://doi.org/10.1007/s00435-019-00432-w
Pocock, R.I. (1903) Fifteen new species and two new genera of tropical southern Opiliones. *Annals and Magazine of Natural History*, Series 7, 11 (65), 433–450.
https://doi.org/10.1080/00222930308678797
Rambla, M. (1978) Systematics of laniatorid Opiliones. *Symposia of the Zoological Society of London*, 42, 303–307.
Roewer, C.F. (1911) Ost-asiatische Opiliones. *Zoologische Jahrbücher*, 31, 591–612. [in German]

Roewer, C.F. (1912) Die Familien der Assamiiden und Phalangodiden der Opiliones-Laniatores (Assamiden, Dampetriden, Phalangodiden, Epedaniden, Biantiden, Zalmoxiden, Samoiden, Palpipediden anderer Autoren). *Archiv für Naturgeschichte*, 78 (3), 1–242. [in German]
Roewer, C.F. (1915) 106 neue Opilioniden. *Archiv für Naturgeschichte*, 81, 1–152. [in German]
Roewer, C.F. (1923) Die Weberknechte der Erde. *Systematische Bearbeitung der bisher bekannten Opiliones*. Gustav Fischer, Jena, 1116 pp. [in German]
Roewer, C.F. (1927) Ostasiatische Opiliones, von Herrn Prof. F. Silvestri im Jahre 1925 erbeutet. *Bollettino del Laboratorio di Zoologia Generale e Agraria della Facoltà Agraria in Portici*, 20, 191–210. [in German]
Roewer, C.F. (1938) Über Acrobuninae, Epedaninae und Sarasinicinae. Weitere Weberknechte IX. (9. Ergänzung der "Weberknechte der Erde" 1923). *Veröffentlichungen aus dem Deutschen Kolonial- und Übersee-Museum in Bremen*, 2, 81–169. [in German]
Schwendinger, P.J. & Martens, J. (2002) A taxonomic revision of the family Oncopodidae III. Further new species of *Gnomulus* Thorell (Opiliones, Laniatores). *Revue Suisse De Zoologie*, 109 (1), 47–113.
https://doi.org/10.5962/bhl.part.79580
Sørensen, W.E. (1884) Opiliones Laniatores (Gonyleptides W. S. Olim) Musei Hauniensis. *Naturhistorisk Tidsskrift*, 14 (3), 555–646. [in German]
Sørensen, W.E. (1886) Opiliones. *In:* Koch, L.C.C. & Keyserling, E.von (Eds.), *Die Arachniden Australiens nach der Natur beschrieben und abgebildet*. Bauer & Raspe, Nürnberg, pp. 53–86.
Sørensen, W.E. (1932) Descriptiones Laniatorum (Arachnidorum Opilionum Subordinis). (Opus posthumum recognovit et edidit Kai L. Henriksen). Det Kongelige Danske Videnskabernes Selskabs skrifter, *Naturvidenskabelig og Mathematisk Afdeling*, 3, 197–422. [in German]
Suzuki, S. (1967) A remarkable new phalangodid, *Parabeloniscus nipponicus* (Phalangodidae, Opiliones, Arachnida) from Japan. *Annotationes Zoologicae Japonenses*, 40, 194–199.
Suzuki, S. (1969) Some phalangids from Thailand. *Journal of Science of the Hiroshima University*, 22 (3), 79–101.
Suzuki, S. (1969) On a collection of opilionids from Southeast Asia. *Journal of Science of the Hiroshima University*, 22 (2), 11–77.
Thorell, T.T.T. (1876) Descrizione di alcune specie di Opilioni dell' Arcipelago Malese appartenenti al Museo Civico di Genova. *Annali del Museo Civico di Storia Naturale di Genova*, 9, 111–138. [in German]
Ubick, D. & Briggs, T.S. (1989) The harvestmen family Phalangodidae. 1. The new genus *Calicina*, with notes on *Sitalcina* (Opiliones: Laniatores). *Proceedings of the California Academy of Sciences*, 46, 95–136. [https://biostor.org/reference/78259]
Wang, F.C. (1953) A list of Chinese spiders of the order Opiliones. *Acta Entomologica Sinica*, 3, 503–512.
Wolff, J.O., Schönhofer, A.L., Martens, J., Wijnhoven, H., Taylor, C.K. & Gorb, S.N. (2016) The evolution of pedipalps and glandular hairs as predatory devices in harvestmen (Arachnida, Opiliones). *Zoological Journal of the Linnean Society*, 177 (3), 558–601.
https://doi.org/10.1111/zoj.12375
Xiong, B. & Kocher, T.D. (1991) Comparison of mitochondrial DNA sequences of seven morphospecies of black flies (Diptera: Simuliidae). *Genome*, 34 (2), 306–311.
https://doi.org/10.1139/g91-050
Zhang, C., & Martens, J. (2020) A taxonomic study on Epedanidae from Thailand including functional aspects of male genital morphology (Opiliones, Laniatores). *ZooKeys*, 915, 25–58.
https://doi.org/10.3897/zookeys.915.47626
Zhang, C. & Zhang, F. (2012) A new species of *Parabeloniscus* (Opiliones: Laniatores: Epedanidae) from China. *Zootaxa*, 3565 (1), 55–64.
https://doi.org/10.11646/zootaxa.3565.1.5