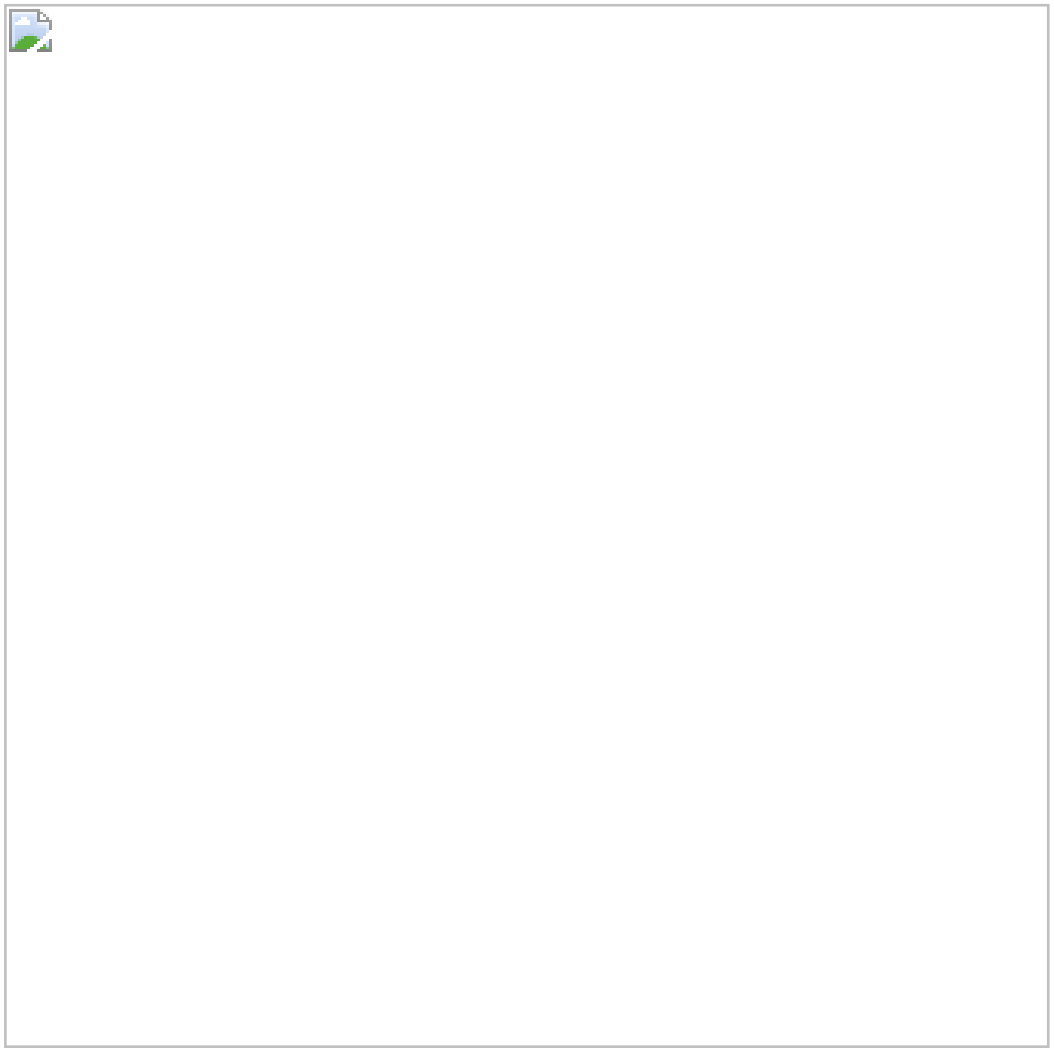

Integrative description of a new species of the genus Siphonorhinus Pocock, 1894 and first record of the family Siphonophoridae from India (Diplopoda: Siphonophorida)

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RESEARCH ARTICLE

Integrative description of a new species of the genus *Siphonorhinus* Pocock, 1894 and first record of the family Siphonophoridae from India (Diplopoda: Siphonophorida)

Pooja Avinipully Anilkumar[1,2], Thomas Wesener[2] & Leif Moritz[2]

Abstract

The Western Ghats of India are one of the world's major biodiversity hotspots. Approximately 60% of the millipede species (> 270) known from India were described from this region during the colonial period. Previously, only two orders and a total of six species of the subterclass Colobognatha were known from India: order Polyzoniida with three species of the family Siphonotidae Cook, 1895 from the Western Ghats (southern India), and order Siphonophorida with three species of the family Siphonorhinidae Cook, 1895 from the Himalayas (northern India). Based on morphological and molecular data, we describe a new Siphonorhinidae species (order Siphonophorida), *Siphonorhinus parambikulam* **sp. n.**, from the Parambikulam Tiger Reserve of the southern Western Ghats of Kerala, India, using scanning electron microscopy (SEM), micro-CT, light microscopy, and *COI* barcoding. The new species can be distinguished from the other eight species of the genus *Siphonophorus* by differences in the number of tergites, length and width of body, as well as overall body color, the number of anterior and posterior gonopod podomeres, and modifications of the apical podomeres of the anterior and posterior gonopods. Also, this is the first description of a male *Siphonorhinus* Pocock, 1894 from India. The available *COI* barcode dataset for the order Siphonophorida is expanded from three to 56 sequences, comprising new sequences of 33 specimens from southern India, 16 from Java (Indonesia), and four from New Zealand. This dataset was used to produce the most comprehensive molecular analysis of the order Siphonophorida to date. Furthermore, we provide the first records, including *COI* barcodes, of the family Siphonophoridae from India, which are suggestive of a huge undescribed diversity in the Indian Western Ghats. This study indicates that the Indian Western Ghats are undersampled for millipedes, and that this area could represent a biodiversity hotspot for the poorly studied Colobognatha.

Keywords: *COI* barcode, Colobognatha, diversity, Indian Western Ghats, micro-CT, SEM, Siphonorhinidae.

Zusammenfassung

Die Westghats Indiens sind weltweit einer der bedeutendsten Hotspots der Biodiversität. So wurden ungefähr 60% aller aus Indien bekannten Doppelfüßer (Diplopoda; > 270 Arten) während der Kolonialzeit aus dieser Region beschrieben. Bisher waren insgesamt lediglich sechs Arten aus zwei Ordnungen in der Subterklasse Colobognatha aus Indien bekannt: Die Ordnung Polyzoniida mit drei Arten in der Familie Siphonotidae Cook, 1895 aus den Westghats (Südindien) sowie die Ordnung Siphonophorida mit drei Arten in der Familie Siphonorhinidae Cook, 1895 aus dem Himalaya (Nordindien). Basierend auf Rastereletronenmikroskopie (REM), micro-CT, Lichtmikroskopie und *CO1*-Barcoding beschreiben wir mit morphologischen und molekularen Daten eine weitere Art, *Siphonorhinus parambikulam* **sp. n.** (Siphonophorida: Siphonorhinidae) aus dem Parambikulam Tiger Reservat der südlichen Westghats in Kerala (Indien). *Siphonorhinus parambikulam* **sp. n.** unterscheidet sich von den acht anderen Arten der Gattung durch Unterschiede in der Anzahl der Tergite, Körperlänge und -breite, Färbung, Anzahl der anterioren und posterioren Gonopodenglieder und in der Form der apikalen Podomere der anterioren und posterioren Gonopoden. Darüber hinaus beschreiben wir das erste Männchen der Gattung *Siphonorhinus* Pocock, 1894 aus Indien. Die verfügbare Anzahl an *CO1*-Sequenzen der Siphonophorida wurde von drei auf insgesamt 56 erweitert und beinhaltet nun neue Sequenzen von 33 Individuen aus Indien, 16 aus Java (Indonesien) und vier aus Neuseeland. Diese Daten lieferten die Grundlage für die bisher umfassendste molekulare Analyse der Ordnung Siphonophorida. Ebenso legen wir die ersten Nachweise sowie *CO1*-Sequenzen der Familie Siphonophoridae aus Indien vor, die auf eine hohe, bisher unbeschriebene Diversität in den indischen Westghats hindeuten. Diese Studie weist darauf hin, dass die Doppelfüßer der indischen Westghats nicht ausreichend besammelt sind und die Region ein Biodiversitätshotspot der nur unzureichend erforschten Colobognatha darstellen könnte.

Introduction

Millipedes (class Diplopoda) are slow-moving soil organisms with poor dispersal abilities, mostly found within the humid leaf litter of forest floors (Hopkin & Read 1992; Golovatch & Kime 2009). The Indian fauna consists of more than 270 known species of millipedes in 91 genera, 26 families, and 12 orders (Golovatch & Wesener 2016; Anilkumar et al. 2022). Over 60% of Indian millipedes have been described from southern India (Golovatch & Wesener 2016), especially from the Western Ghats region, a chain of tropical evergreen forests running 1,600 km along India's southwestern coast. This region is one of the world's 25 biodiversity hotspots (Myers et al. 2000). Indian millipedes, however, with ca. 270 species, are highly understudied compared to considerably smaller countries like Tanzania with 296 species (Enghoff et al. 2016), Madagascar with 266 species (Wesener & Enghoff 2022), and Italy with 473 species (Foddai et al. 1995). Globally, more than 12,000 millipede species have been described in 16 extant orders (Blanke & Wesener 2014; Enghoff et al. 2015). The subterclass Colobognatha comprises the four relictual millipede orders Platydesmida, Polyzoniida, Siphonophorida, and Siphonocryptida, which include approximately 260 described species worldwide (Enghoff et al. 2015), constituting 2% of all described Diplopoda species. Only two of these colobognathan orders are known from India: Polyzoniida (one genus, three species), recently reported from the Indian Western Ghats (southern India) (Anilkumar et al. 2022), and Siphonophorida (one genus, three species), from the Himalayan region of northern India (Golovatch & Wesener 2016). The order Siphonophorida comprises ~120 described species in 16 genera and two families: Siphonophoridae Newport, 1844 and Siphonorhinidae Cook, 1895 (Enghoff et al. 2015; Read & Enghoff 2018, 2019; Marek et al. 2023; Moritz & Parra-Gómez 2023a; Wesener 2023). The family Siphonophoridae consists of ten genera with ~104 described species, and is found in the Americas, Australia, Madagascar, New Zealand, northern Pakistan, and Southeast Asia (Enghoff et al. 2015). The family Siphonorhinidae has fossil species known from Cretaceous Myanmar amber (Wesener & Moritz 2018; Su et al. 2024) and currently includes 16 extant species classified in six genera: *Illacme* Cook & Loomis, 1928 (California), *Madagascarhinus* Wesener, 2023 (Madagascar), *Nematozonium* Verhoeff, 1939 (South Africa), *Notiorhinus* Moritz & Parra-Gómez, 2023a (Chile), *Siphonorhinus* (Southeast Asia and India), and *Kleruchus* Attems, 1938 (Vietnam). Among these, the genus *Siphonorhinus* is the most diverse, with eight species prior to this study, although its monophyly has not yet been demonstrated. Five of the *Siphonorhinus* species were described from Southeast Asia (Cambodia, Indonesia, Laos, Vietnam) and three from the Himalayan region of India (Attems 1936; Turk 1947; Jeekel 2001; Golovatch & Wesener 2016). The three Indian *Siphonorhinus* species, namely *Siphonorhinus cingulatus* (Attems, 1936), *S. coniceps* (Attems, 1936), and *S. larwoodi* (Turk, 1947), were described based on female specimens only. The taxonomy and identification of species in the genus *Siphonorhinus* are hindered by century-old descriptions lacking sufficient characters and illustrations, and by the absence of male characteristics like the species-specific gonopods, due to several species descriptions being exclusively based on females.

Carl (1941) mentioned the presence of *Siphonorhinus* specimens from southern India in his collection, but, to date, no Siphonophorida had been described from that part of the country, and a representative of the genus *Siphonorhinus* was last described from northern India 77 years ago (Turk 1947; Jeekel 2001). Here, we provide the first modern description of a *Siphonorhinus* species and the first description of a male *Siphonorhinus* from India, *Siphonorhinus parambikulam* **sp. n.** from the southern Western Ghats of Kerala, using light microscopy, scanning electron microscopy (SEM), micro-CT, and *COI* barcoding. This is also the first record of the family Siphonorhinidae from southern India, whereas the family Siphonophoridae is reported from India for the first time. Finally, we provide and analyse (p-distances, phylogeny) the largest *COI* barcode dataset for the order Siphonophorida, adding 53 new sequences from three countries (India, Indonesia, and New Zealand).

Material and methods

Abbreviations

LIPI = Lembaga Ilmu Pengetahuan Indonesia (Indonesian Institute of Sciences), Jakarta, Indonesia; MYR: Myriapoda; µCT: Micro-computed tomography; NP: National Park; SEM: scanning electron microscopy; SNP: Shola National Park; WG: Western Ghats; ZFMK: Zoological Research Museum Alexander Koenig, Leibniz Institute for the Analysis of Biodiversity Change, Bonn, Germany.

Material examined

The studied specimens were collected in November and December 2019 (at the onset of winter) from the southern Western Ghats of Kerala, India. The holotype male of *Siphonorhinus parambikulam* **sp. n.** (ZFMK-MYR 9076) was collected from the Muthuvarachal Range of the Parambikulam Tiger Reserve, a mid-elevation protected area in the northern region of the southern Western Ghats of Kerala (Fig. 2C). All 32 Siphonophoridae specimens were collected from three highland National Parks (Annamudi SNP, Eravikulam NP, Pambadum SNP) and from a mid- to high-elevation wildlife sanctuary, the Shendurney Wildlife Sanctuary. In each protected area, samples were collected for 3–5 days at 3–7 different sites. Specimens were collected by hand, sifting leaf litter, and by two overnight Winkler extractions. All specimens are preserved in 96% ethanol. The holotype and the voucher specimens of Indian Siphonophorida have been deposited at the Zoological Survey of India

(ZSI) in Calicut, Kerala, India. Details of collection and export permits can be found in the Acknowledgements section, below. All morphological data generated, including additional SEM images and μCT data, are deposited as Supplementary Material in Zenodo under the following link: https://doi.org/10.5281/zenodo.12598821.

DNA sequence extraction, editing, and alignment

Molecular genetic barcoding of the mitochondrial *cytochrome c oxidase subunit I* (*COI*) coding gene (Hebert et al. 2003) was performed for *Siphonorhinus parambikulam* **sp. n.** and the 32 Siphonophoridae specimens. The *COI* fragment was amplified using the degenerated primer pairs LCO1490-JJ [5'-CHACWAAYCATAAAGATATYGG-3'] and HCO2198-JJ [5'- AWACTTCVGGRTGVCCAAARAATCA-3'] (Astrin & Stüben 2008). Total genomic DNA was isolated from the muscle tissues of 3–5 mid-body rings using the DNeasy Blood and Tissue Kit and the BioSprint96 magnetic bead extractor from Qiagen (Hilden, Germany). DNA barcodes were generated according to the standard protocols of the German Barcode of Life (GBOL) project (Geiger et al. 2016). Unpurified PCR products were sent to the Beijing Genomic Institute (BGI), China for bidirectional Sanger sequencing. The *COI* dataset was edited for base-calling errors and aligned in Geneious R7 (v 7.1.19, Biomatters Ltd.).

The only three available Siphonophorida sequences on GenBank (at 12.2022) were added to the Indian dataset, as well as two Polyzoniida sequences which were utilized as far outgroup taxa. As so few Siphonophorida sequences are available on GenBank, we added a released dataset from the INDOBIOSYS project (Hilgert et al. 2019), containing barcodes of three Siphonorhinidae and 13 Siphonophoridae specimens collected in Indonesia, Java, Halimun-Salak National Park, close to Bogor, the type locality of *Siphonorhinus pallipes* Pocock, 1894, the type species of *Siphonorhinus*. In addition, we added four unpublished sequences belonging to Siphonophoridae specimens from New Zealand (see Appendix).

Our new sequences, and those of the Polyzoniida and Siphonophorida from GenBank were aligned by hand in BioEdit (Hall 1999). Our complete dataset included 58 sequences (53 previously unpublished) spanning 657 base pairs. The aligned *COI* dataset was translated into amino acids (mitochondrial DNA of invertebrates) in MEGA6 (Tamura et al. 2013) to detect pseudogenes and compared with the BLAST (Altschul et al. 1990) and BOLD databases (Ratnasingham & Hebert 2007) (at 04.2020) to confirm sequence identities and identify possible contaminants. All unpublished Siphonophorida sequences were uploaded to GenBank (Clark et al. 2016) (see Appendix for accession numbers).

Molecular analyses

The number of base differences per site (p-distances) between sequences was calculated (for p-distances, see Supplementary Table 1). The analysis involved 58 nucleotide sequences. Codon positions included were 1st+2nd+3rd+Noncoding. All ambiguous positions were removed for each sequence pair.

The best-fitting substitution model for a maximum likelihood analysis was calculated with Modeltest (Tamura & Nei 1993), as implemented in MEGA6. Models with the lowest BIC (Bayesian Information Criterion) scores are considered to best describe the substitution pattern (Nei & Kumar 2000). The best-fitting model was the Tamura-Nei Model (Tamura & Nei 1993), with gamma distribution and invariant sites (lnL = -7773.11, Invariant = 0.3915, Gamma = 0.817, R = 2.107; Freq A: 0.263, T: 0.346, C: 0.226, G: 0.165). Phylogenetic analysis were performed in MEGA6 based on the Tamura Nei Model (TN+G+I). A species tree was constructed using the maximum likelihood method with gamma distribution of 5 categories. The tree with the highest log likelihood (-7773.1195) is shown (Fig. 8). Initial tree(s) for the heuristic search were obtained automatically by applying the Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. A discrete gamma distribution was used to model evolutionary rate differences among sites (5 categories [+*G*, parameter = 0.8171]). The rate variation model allowed for some sites to be evolutionarily invariable ([+*I*], 39.1511% sites). The tree is drawn to scale, with branch lengths measured as the number of substitutions per site. Codon positions included were 1st+2nd+3rd+Noncoding. All positions with less than 5% site coverage were eliminated, meaning that fewer than 95% alignment gaps, missing data, and ambiguous bases were allowed at any position. There were 657 positions in the final dataset. The bootstrap consensus tree was calculated from 1,000 replicates (Felsenstein 1985) in MEGA6 (Tamura et al. 2013). The obtained tree was edited in Adobe Illustrator v.27.2.

Microscopy and photography

All specimens were examined and prepared with an Olympus SZX12 stereo microscope. Habitus images of the Indian specimens were taken with a Canon EOS 60D SLR digital camera equipped with a Canon EF-S 60mm 2.8 USM macro lens and Canon MP-E 65mm 2.8, 1–5x magnification lens. Stacked images were put together using the software Auto-Montage (Syncroscopy) at the ZFMK (see Hilgert et al. 2019).

Scanning electron microscopy (SEM)

After taking tissue samples for barcoding and obtaining μCT data, the holotype of *Siphonorhinus parambikulam* **sp. n.** was dissected and dried using a Leica EM CPD 300 critical point dryer for SEM. The samples were mounted with conductive tape on aluminum stubs and coated with gold (ca. 35 nm) in a Cressington 108 auto sputter coater for 240 seconds. SEM images were taken with a Zeiss Gemini Sigma 300 VP scanning electron microscope using the SmartSEM V05.00 software at ZFMK. Images were edited using Adobe Photoshop v.24.1.1 and later assembled into figure plates using INKSCAPE 1.2.2.

Micro-Computed Tomography (μCT)

μCT data for *Siphonorhinus parambikulam* **sp. n.** was obtained with a SKYSCAN 1272 (Bruker micro-CT, Kontich, Belgium) at the ZFMK. The specimen was scanned in 96% ethanol. Thermal-drift correction, ring artifact reduction, and digital section reconstruction were done in NRecon 1.7 (Bruker micro-CT, Kontich, Belgium). For scanning and reconstruction parameters, see Supplementary Material. Gray values and the orientation of the image stacks were adjusted in Fiji (ImageJ) version 1.53t (Schindelin et al. 2012). Volume rendering and measurements were done in Drishti Version 3.0 (Limaye 2012).

Distribution map

The map (Fig. 1) was created using the free software (Qgis.org 2023), with approximate coordinates obtained using Google Maps. The shapefiles for India were obtained from the GADM database, while the shapefiles for the Western Ghats, Kerala and its protected areas were prepared and obtained from Dr. C. J. Alex (Project Officer, International Council for Local Environmental Initiative South Asia, India).

Taxonomy

Class Diplopoda de Blainville in Gervais, 1844
Subterclass Colobognatha Brandt, 1834
Order Siphonophorida Newport, 1844
Family Siphonorhinidae Cook, 1895

Diagnostic remarks

The newly described species can be placed in the family Siphonorhinidae based on the following combination of characters: pear-shaped head, with mouthparts not extending into a beak (Figs. 2A, 3B), while it extends into a beak in Siphonophoridae (Fig. 2B) (see Read & Enghoff 2009); gnathochilarium divided into separate plates (Fig. 4D), while all plates are fused in extant Siphonophoridae (see Read & Enghoff 2019: 10, fig. 3E); antennomere 2 twice as long as antennomere 3 (Figs. 3B, 5A); antennae elbowed between antennomeres 3 and 5 (Figs. 3B, 5A), vs. straight in Siphonophoridae (Fig. 2B) (see Read & Enghoff 2009).

Genus *Siphonorhinus* Pocock, 1894

Type species: *Siphonorhinus pallipes* Pocock, 1894 (Indonesia: Java: Bogor).

Included species

Siphonorhinus angustus Pocock, 1894 (Indonesia: Java).
Siphonorhinus cingulatus (Attems, 1936) (India; Vietnam).
Siphonorhinus coniceps (Attems, 1936) (Cambodia; India).
Siphonorhinus larwoodi (Turk, 1947) (India).
Siphonorhinus latus Silvestri, 1895 (Indonesia: Sumatra).
Siphonorhinus pallipes Pocock, 1894 (Indonesia: Java).
Siphonorhinus pellitus (Attems, 1930) (Indonesia: Flores).
Siphonorhinus robustus (Attems, 1938) (Laos; Vietnam).
Siphonorhinus parambikulam Anilkumar et al., **sp. n.** (India).

Diagnostic remarks

The newly described species is assigned to the genus *Siphonorhinus* based on the following characters: head shape more acuminate (Fig. 4A) and less rounded than in *Illacme* (Marek et al. 2023: 273, fig. 1A) and *Notiorhinus* (Moritz & Parra-Gómez 2023a: 570, fig. 3A). It differs from *Notiorhinus* (Moritz & Parra-Gómez 2023a: 570, fig. 3C), *Illacme* (Marek et al. 2016: 9, fig. 3D), and *Madagascarhinus* (Wesener 2023: 170, fig. 4F), in which the salivary glands open in a single field above the labrum, and from the new species of *Siphonorhinus* by having its salivary gland openings arranged in two fields ventrally at the labral margin (Fig. 4F). Antero-lateral sides of gnathochilarial stipes with three macrosetae (Fig. 4C), while such setae are absent in the other five genera. However, the arrangement of the salivary gland openings and macrosetae have to be confirmed for the remaining *Siphonorhinus* species. Antennomere 6 strongly rounded and bulged (Fig. 5A, B), while it is cylindrical in *Illacme* (Marek et al. 2012: 90, fig. 8a), *Nematozonium* (Shelley & Hoffman 2004: 220, fig. 1), *Madagascarhinus* (Wesener 2023: 170, fig. 4D), and *Notiorhinus* (Moritz & Parra-Gómez 2023a: 570, fig. 3E), and weakly round/cylindrical and bulged in *Kleruchus* (Attems 1938: 296, fig. 194). Sensilla basiconica on antennomeres 5 and 6 in circular sensory pits (Fig. 5B), as reported for other *Siphonorhinus* (Attems 1930, 1938) and *Kleruchus* (Attems 1938), whereas these are not in a defined pit in *Illacme* (Marek et al. 2012: 90, fig. 8a) and *Madagascarhinus* (Wesener 2023: 170, fig. 4D), absent on antennomeres 5 and 6 in *Nematozonium* (Shelley & Hoffman 2004), and absent on antennomere 5 in *Notiorhinus* (Moritz & Parra-Gómez 2023a: 570, fig. 3E). Coxa and sternite of leg 1 fused (Fig. 6C) as in *Siphonorhinus robusta* (Attems, 1938) (Attems 1938: 302, fig. 213), *Notiorhinus*, in which the coxal portion is rectangular (Moritz & Parra-Gómez 2023a: 570, fig. 3G), and *Madagascarhinus*, in which it is triangular (Wesener 2023: 168, fig. 3A). The sternite and coxa of leg 1 are unfused in *Kleruchus* (Attems 1938: 296, fig. 193). Presence of paranota in *Siphonorhinus* (Figs. 3D, 5E, F) and *Kleruchus* (see Attems 1936, 1938), while they are absent in all other genera of the family: *Illacme* (Marek et al. 2012: 86, fig. 2), *Nematozonium* (Shelley & Hoffman 2004: 220, fig. 1), *Madagascarhinus* (Wesener 2023: 171, fig. 5A), and *Notiorhinus* (Moritz & Parra-Gómez 2023a: 571, fig. 4B). Last podomere of posterior gonopod extending in *Siphonorhinus* into a thin, long filament, dividing apically into two leaf-shaped styliform articles (Fig. 7F), whereas it bifurcates into three styliform articles in *Madagascarhinus andasibensis* Wesener, 2023 (Wesener 2023: 173, fig. 7B) and *Notiorhinus floresi* Moritz & Parra-Gómez, 2023a (Moritz & Parra-Gómez 2023a: 572, fig. 5F), and into 3–5 styliform articles in *Illacme* (Marek et al. 2023). In *Nematozonium*, the apical region of the extended podomere of the posterior gonopod is bifurcated into three spine-like processes, with a basal spine curving above the other two (Shelley & Hoffman 2004: 220, fig. 3), while in *Kleruchus* the last podomere of the posterior gonopod appears as three spine-like structures (Attems 1938: 298, fig. 203).

Siphonorhinus parambikulam sp. n.
(Figs. 2–7)

Diagnosis

As most *Siphonorhinus* species descriptions are 80–120 years old, incomplete, and based on female specimens, the following are some characters that could be unique for the species described below and should be checked for in other *Siphonorhinus* species: ventral side of labrum with two fields of salivary gland openings (Fig. 4F); collum laterally forming a triangular margin (Fig. 4B); legs 1–3 (Fig. 6C–E) and a few posterior body legs with a small accessory claw (Fig. 6A, B); base of posterior gonopod podomere 7 with a small spine (Fig. 7A, F).

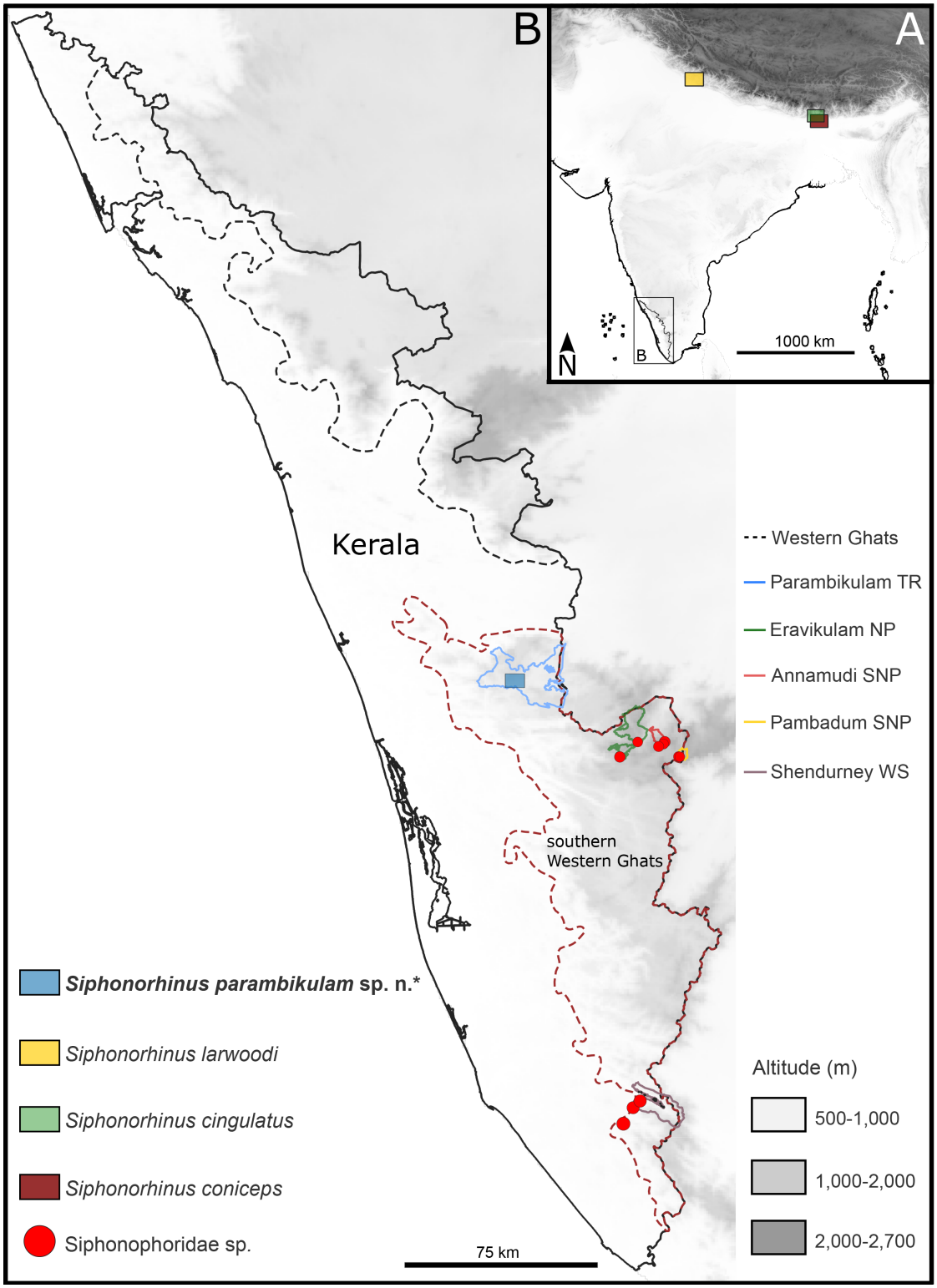

Fig. 1. Distribution of Indian Siphonophorida. **A**. Approximate locations of the three *Siphonorhinus* species previously described from northern India, based on Attems (1936) and Turk (1947). **B**. Locality of the newly-described species *Siphonorhinus parambikulam* **sp. n.** (blue rectangle) and records of Siphonophoridae (red dots) in the southern Western Ghats of Kerala, India. The asterisk (*) indicates the newly-described species. Abbreviations: NP = National Park; SNP = Shola National Park; TR = Tiger Reserve; WS = Wildlife Sanctuary.

Siphonorhinus parambikulam **sp. n.** is an elongate *Siphonorhinus* species with a flattened body and lateral paranota; with 58 tergites plus telson; ~13 mm long and ~1.15 mm wide, and orange-brown in color (Figs. 2A, 3C, F). The holotype of *Siphonorhinus parambikulam* **sp. n.** differs in tergite number from *S. angustus* (104 tergites), *S. cingulatus* (83), *S. coniceps* (68), *S. latus* (67), *S. pallipes* (74–94), and *S. robustus* (63), and in overall size, with these six species being much longer (length 23–43 mm) and wider (width 2.0–4.6 mm). *Siphonorhinus parambikulam* **sp. n.** also differs from the other seven *Siphonorhinus* species in its color: *S. larwoodi* is pale brownish-white, *S. cingulatus* brown with three dark stripes dorsally, *S. coniceps* and *S. pellitus* yellowish-brown, *S. latus* reddish-brown, *S. pallipes* grayish-black/dirty-white with a dark stripe dorsally, and *S. robustus* dark reddish-brown with a black-eel-striped pattern dorsally.

Siphonorhinus parambikulam **sp. n.** differs from the incompletely described *S. larwoodi* from the Himalayas in the higher segment number (58 vs. 40 in *S. larwoodi*), the longer antenna (shorter than the head in *S. larwoodi*), and the number of macrosetae (3 vs. 2 in *S. larwoodi*) on the lateral margin of the gnathochilarial stipes (Fig. 4C). *Siphonorhinus parambikulam* **sp. n.** differs in the number

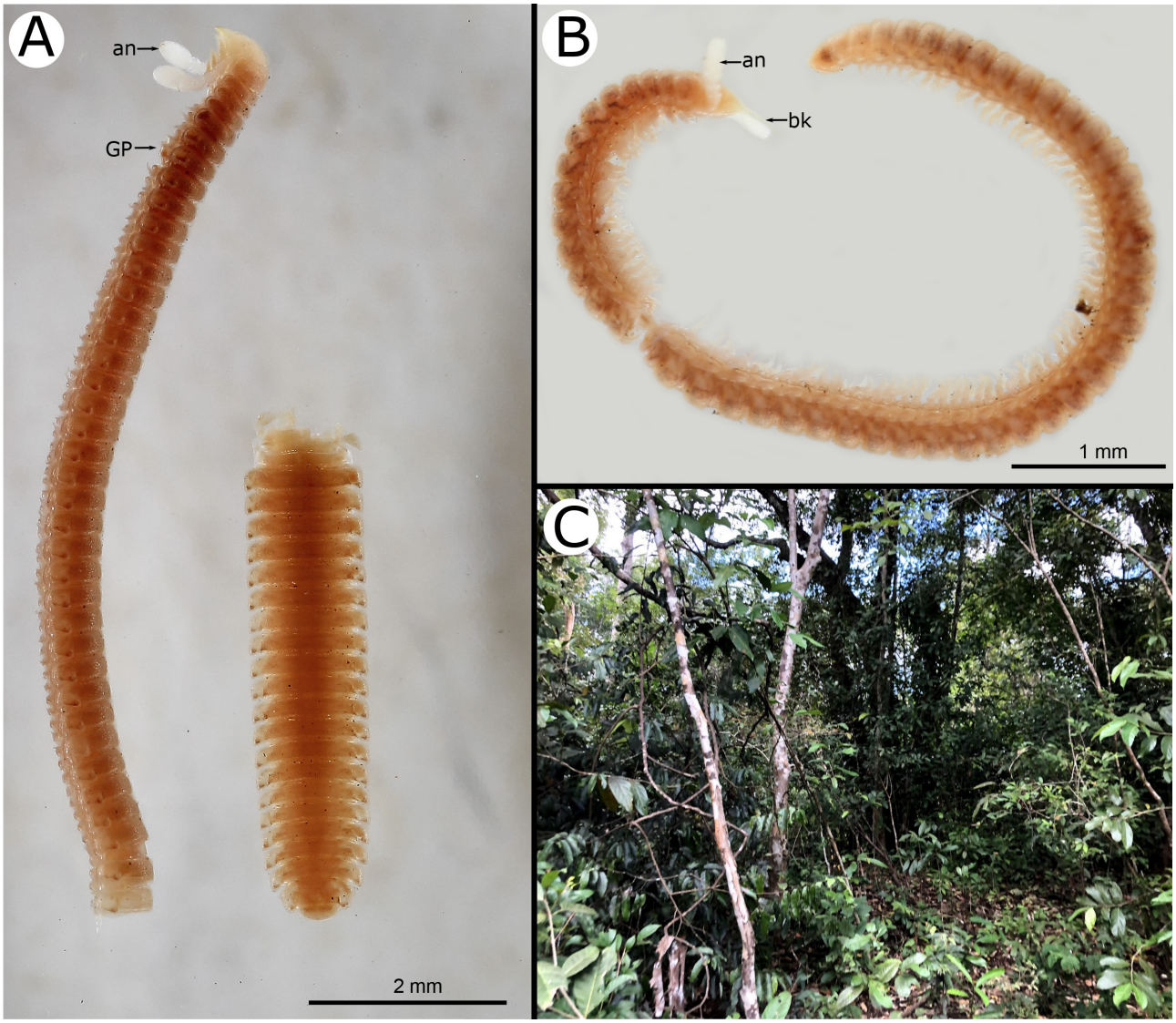

Fig. 2. Habitus and habitat of Indian Siphonophorida. **A, B.** Habitus. – **A**. *Siphonorhinus parambikulam* **sp. n.**, holotype ♂ (ZFMK-MYR 9076), dorsal and lateral views. **B**. Siphonophoridae sp., non-type (ZFMK-MYR 9048), lateral view. **C**. Habitat of *Siphonorhinus parambikulam* **sp. n.**, evergreen forest, Muthuvarachal, Parambikulam Tiger Reserve, Kerala, India. Abbreviations: an = antenna; bk = beak; GP = gonopod.

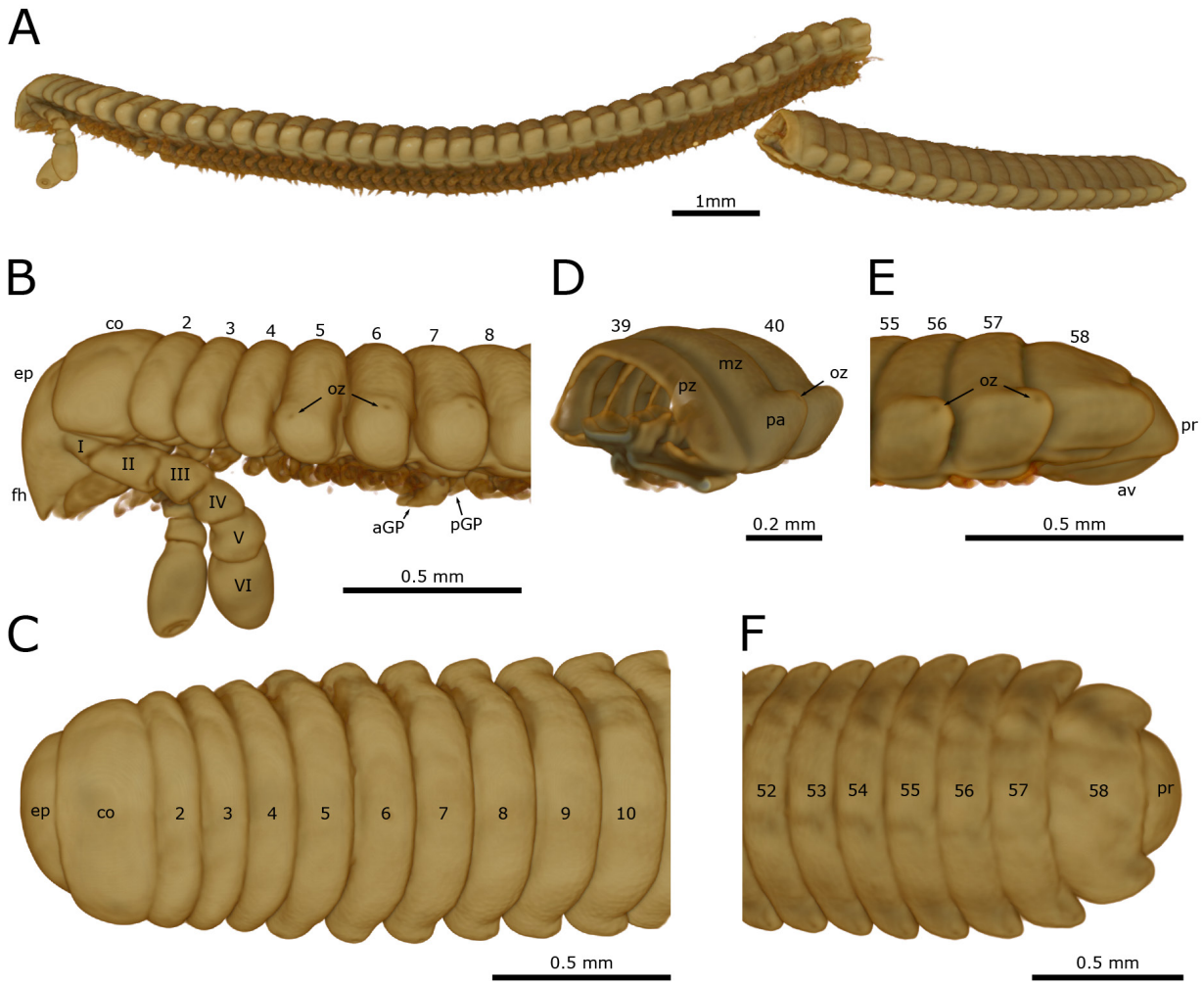

Fig. 3. *Siphonorhinus parambikulam* **sp. n.**, holotype ♂ (ZFMK-MYR 9076), volume rendering based on µCT-data. **A**. Habitus, lateral view. **B**. Head and anterior body, lateral view. **C.** Anterior body, dorsal view. **D**. Midbody rings, antero-lateral view. **E**. Telson and posterior body rings, lateral view. **F**. Posterior body, dorsal view. Abbreviations: aGP = anterior gonopod; av = anal valve (paraproct); co = collum; ep = epicranium; fh = forehead; mz = metazonite; oz = ozopore; pa = paranota; pGP = posterior gonopod; pr = preanal ring; pz = prozonite. I–VII indicates the number of antennomeres, 2–58 the number of tergites.

of tergites from the other two Indian species described from the Himalayas, *S. cingulatus* (58 vs. 83) and *S. coniceps* (58 vs. 68). *Siphonorhinus parambikulam* **sp. n.** differs from *S. pellitus* in the shape of the styliform articles on the posterior gonopod (leaf-shaped vs. claw-shaped in *S. pellitus*) and in the number of gonopod podomeres (anterior gonopod = six vs. five in *S. pellitus*; posterior gonopod = seven vs. six in *S. pellitus*) (see Attems 1930: 158, figs. 58–61). *Siphonorhinus parambikulam* **sp. n.** differs from *S. robusta* by the absence of elongated apical lamellae on podomere 6 of the anterior gonopod (Fig. 7A vs. Attems [1938, fig. 217]) and the bifurcation of the apical podomere of the posterior gonopod into a pair of leaf-shaped styliform articles (Fig. 7F) vs. a wart-like structure in *S. robusta* (see Attems 1938, fig. 218).

Etymology

The species epithet *parambikulam*, a noun in apposition, refers to the type locality of the species, Parambikulam Tiger Reserve, Kerala, India.

Type material

Holotype ♂ (Fig. 2A): ZFMK-MYR 9076, India, Province Kerala, Palakkad-Thrissur District, Parambikulam Tiger Reserve, evergreen forest, underside of a rotting log, hand collection, 10º23’42.3”N 76º39’07.2”E, 555 m, 2.XII.2019, leg. A. A. Pooja, P. P. Sudhin, R. S. Abhijith. Zoological Survey of India, Calicut, Kerala, India (ZSI).

Description

Male holotype. Measurements: after dissection, 58 tergites + telson, ~13 mm in length and ~1.15 mm in width.

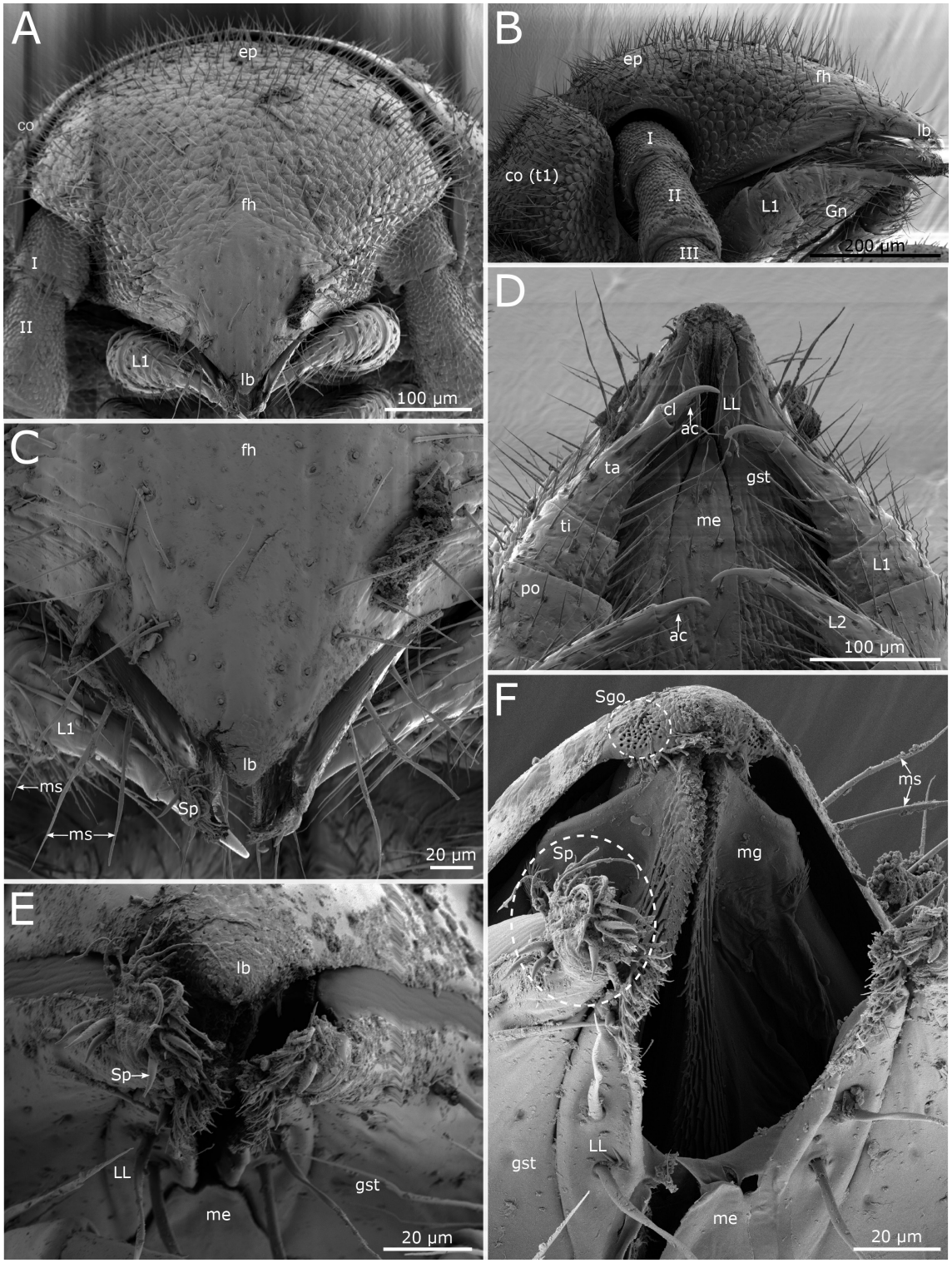

Fig. 4. *Siphonorhinus parambikulam* **sp. n.**, holotype ♂ (ZFMK-MYR 9076), SEM. **A**. Head, anterior view. **B**. Head, lateral view. **C**. Labrum and mouthparts, dorsal view. **D**. Mouthparts, ventral view. **E**. Mouthparts, anterior view. **F**. Labrum and mouthparts, ventral view. Abbreviations: ac = accessory claw; cl = claw; co = collum; ep = epicranium; fh = forehead; Gn = gnathochilarium; gst = gnathochilarial stipes; lb = labrum; LL = lamella lingualis; L = leg; me = mentum; mg = mandibular gnathal lobe; ms = macrosetae; po = postfemur; Sgo = salivary gland opening; Sp = sensory palp; ta = tarsus; t = tergite; ti = tibia. I–III indicates the number of antennomeres.

[A few body rings (+5) were dissected for barcoding prior to photographing the specimen.]

Coloration [after 4 months in ethanol]. Head light-orange, antennae white, tergites orange-brown, legs creamish-white (Fig. 2A).

Head. Pear-shaped, ~0.6 mm in length and ~0.5 mm in width; almost three times as long as collum. Epicranium slightly arching above antennal base (Figs. 3B, 4B). Densely setose except for forehead (Fig. 4A, C), laterally covered by tubercles (Fig. 4B). Salivary gland openings in fields of > 30 pores on both sides of the labrum, facing downwards (Fig. 4F). Gnathochilarium divided, with central mentum, paired flap-shaped lamellae lingualis anterior to the mentum, paired stipites lateral to the mentum anteriorly, and lamellae lingualis apically with sensory palps (Fig. 4D–F). Gnathochilarium anteriorly deeply divided between the lamellae lingualis, exposing preoral chamber. Anterior setae of mentum and lamellae lingualis apically flattened and spiraling (Fig. 4D–F). Three macrosetae on antero-lateral margin of gnathochilarial stipes (Fig. 4C). Mandibles internalized, not visible externally. Mandibular gnathal lobe elongated, mesal surface of each gnathal lobe covered by serrated structures (pectinate lamellae) facing each other, laterally with a tuft of spines (Fig. 4F). Antennae long, reaching tergite 5 (Fig. 3B), elbowed between antennomeres 3 and 5 (Figs. 3B, 5A). Seven antennomeres + apical disc (Fig. 5A). Relative length of antennomeres: 6>2>5>3=4>1>7. Antennomere 2 longer than wide, antennomeres 3–5 cup-shaped, antennomere 6 rounded, bulged, and widest of all, antennomere 7 retracted within antennomere 6 (Fig. 5B, D). Antennomeres 1–3 dorsally setose, antennomere 6 densely setose. All antennomeres with small tubercles, fewer on anterior margins (Fig. 5A). Ventro-lateral anterior margin of antennomeres 5 and 6 with circular, sunken-in sensory pit. Sensory pit on antennomere 6 more circular than on antennomere 5, with sensilla basiconica inside (Fig. 5B, C). Sensory pits on antennomere 5 with 41 (left antenna) and 31 (right antenna) sensilla basiconica. Sensory pit on antennomere 6 with 49 (left antenna) and 28 (right antenna) sensilla basiconica (Fig. 5B; for more SEMs, see Supplementary Material). Apical disc with 4 apical cones and 3 clusters of spiniform sensilla basiconica, lateral cluster with 15 sensilla basiconica, anterior cluster with 2 sensilla basiconica, and posterior cluster with 4 sensilla basiconica, projecting between apical cones (Fig. 5D).

Collum. Trapezoidal in dorsal view, slightly covering epicranium. Twice as long as following tergites (Fig. 3B, C). Triangular in lateral view. Densely setose and completely covered with tubercles (Fig. 4B).

Tergites. Free from pleurites and sternites (Fig. 6A, B). Tergites 2–4 ca. half as long as following tergites (Fig. 3B). Prozonites covered by preceding metazonite. Prozonites glabrous, anterior 3/4 covered with scales, posterior 1/4 with tubercles. Metazonites twice as long as prozonites (Fig. 5F). Metazonites arched, laterally extending into paranota, densely setose, and completely covered with tubercles (Fig. 5E, F). Paranota oriented posteriad and slightly arching posteriad from tergite 7. Paranota with ozopores from tergite 5 to tergite 57 (Fig. 3B, E). Ozopore of tergite 5 positioned close to lateral-anterior margin of paranota. Ozopore of following tergites positioned some distance from lateral-posterior margin of paranota (Figs. 3B, E, 5F). Ozopore opening facing dorsally, slightly elevated, encircled by a row of setae and surrounded by spine-like tubercles (Fig. 5F, G). Tergite 58 (last tergite) twice as long as and narrower than the preceding tergites (Fig. 3E); apodous, paranota triangular and extending posteriad (Figs. 3F, 6B).

Pleurites. Separated from tergites by a clear division (Fig. 6B). Pleurites almost rectangular, separated into prozonite and metazonite. Prozonite glabrous, covered with scales, like the tergal prozonite. Metazonite covered with tubercles and setae, like the tergal metazonite (Fig. 5H).

Sternites. Free, separated from pleurites. Triangular, posterior margin with two excavations to accommodate the associated legs. Covered with tubercles and a few setae laterally. Medial sternal ridge directed ventrally, with few setae anteriorly. Spiracles circular, open, slightly elevated, positioned lateral to legs (Fig. 6A).

Telson. Preanal ring narrower than body rings, forming complete ring. Completely covered with tubercles, densely setose. Paraprocts oval, tubercles absent in middle, with setae crossing over at opening. Hypoproct semi-hemispherical, small, 1/5 of length of paraproct (Fig. 6B).

Legs. Leg 1 slightly longer and thicker than following legs, coxa fused with sternite, with 5 free podomeres, prefemur triangular distally. Setae prominent mesally (Fig. 6C). Leg 2 with 6 podomeres (free coxa), setose mesally. Tibia and tarsus densely setose, with long setae mesally (Fig. 6D). Seven podomeres from leg 3 onwards, trochanter and coxal sac present (Fig. 6F). A few posterior legs devoid of coxal sac (Fig. 6B). Relative length of podomeres of midbody leg: femur>tarsus>prefemur>coxa >postfemur=tibia>trochanter (Fig. 6A). Claw of legs 1–4 and few posterior legs divided, with large dorsal part and short ventral part (accessory claw) (Fig. 6A, D, E). Accessory claw longer and thicker on midbody legs, reaching 2/3 of dorsal part in length (Fig. 6G).

Male sexual characters. Paired pseudopenes on coxae of leg 2, conical, carrying gonopores (Fig. 6D, F). Legs 9 and 10 modified into anterior and posterior gonopods (Figs. 3B, 7A). Anterior gonopod. Modified leg 9. Sternite rectangular, posterior margin excavated to hold gonopod anteriorly. Medial sternal ridge less prominent than on other legs, with 2 or 3 setae anteriorly. Tubercles confined to lateral and posterior margins. Spiracles circular, open,

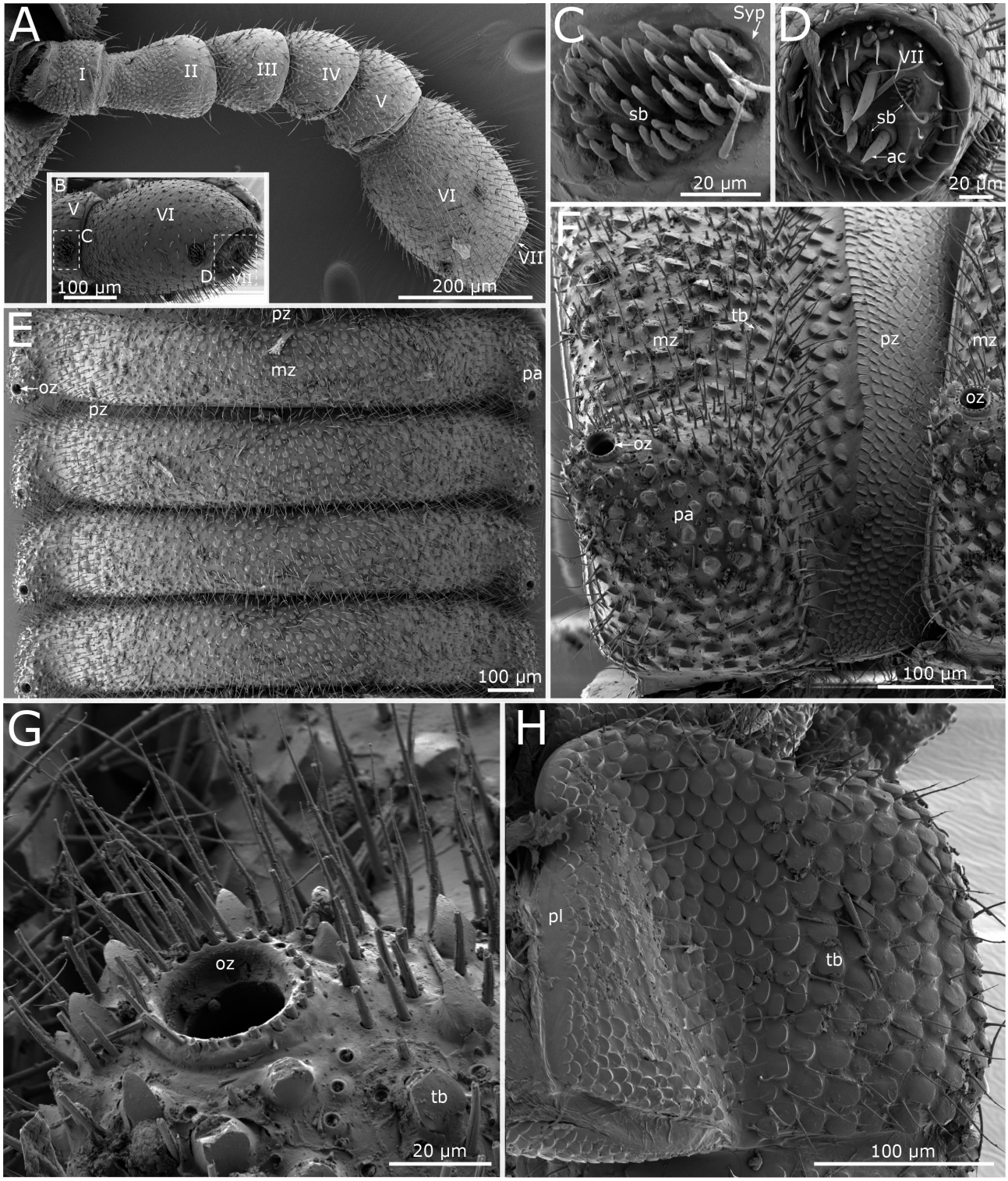

Fig. 5. *Siphonorhinus parambikulam* **sp. n.**, holotype ♂ (ZFMK-MYR 9076), SEM. **A**. Antenna, dorsal view. **B**. Antennomeres V and VI, ventral view. **C**. Sensory pit of antennomere V. **D**. Antennomere VII, apical disc with four sensory cones. **E**. Tergites, dorsal view. **F.** Tergites, lateral view. **G**. Ozopore, dorso-lateral view. **H**. Midbody pleurite, ventral view. Abbreviations: ac = apical cone; mz = metazonite; oz = ozopore; pa = paranota; pl = pleurite; pz = prozonite; sb = sensilla basiconica; Syp = sensory pit; tb = tubercles. I–VII indicates the number of antennomeres.

positioned laterally (Fig. 7B). With six podomeres; twice as thick as posterior gonopod. Podomeres 1 and 2 forming a rounded, stout base, tapering from podomere 3. Relative length of podomeres: a6>a4>a1>a3>a5>a2 (Fig. 7C). Podomeres 1–3 with a few setae. Podomeres 4 and 5 with a row of setae. Podomere 6 completely covered with setae, a few anterior setae apically serrated and twisted (Fig. 7A, C, E). Podomeres 3–6 extending mesad into a shovel-shaped structure. Setae at margin of shovel-shaped structure thicker than remaining setae. Apical region of podomere 6 tapering to a funnel-shaped structure, basally curving, forming a cup-like structure (Fig. 7A, B, E). Posterior gonopod. Modified leg 10. Sternite surface covered with scales. With seven podomeres. Relative length of podomeres: p7>p4>p1>p6>p5>p2=p3. Podomeres 1–3 stout and wide (Fig. 7C). Tapering from podomere 4. Podomere 6 cylindrical (Fig. 7D). Podomeres 4 and 5 mesally with few short setae (Fig. 7A). Base of podomere 7 with a small spine on a wart-like structure (Fig. 7A, F). Podomere 7 extending into a thin, long branch, apically divided into 2 styliform articles (upper and lower) with leaf-shaped tip (Fig. 7A, C, F).

Female unknown.

Family Siphonophoridae Newport, 1844

Material examined

[Assigned to Siphonophoridae based on the following features: head extending into beak; gnathochilarium not divided; antennae straight, not elbowed as in Siphonorhinidae; body slenderer than in Siphonorhinidae (Fig. 2A, B) (Enghoff et al. 2015).]

Barcoded specimens. India, Kerala Province: 1♂, Idukki District, Mannavan Shola, Annamudi Shola National Park, high altitude montane forest, hand collection (10º10′54.5″N, 77º11′25.8″E), 2140 m, 18.XI.2019, leg. A. A. Pooja, K. Ullas (ZFMK-MYR 09048). – 1♂ (ZFMK-MYR 09049). – 1♀ (ZFMK-MYR 09050). – 1♀ (ZFMK-MYR 09051). – 1♀ (ZFMK-MYR 09052). – 1♀ (ZFMK-MYR 09053). – 1♂, 19.XI.2019, leg. A. A. Pooja, K. S. Nafin, K. Ullas (ZFMK-MYR 09054). – 1♀ (ZFMK-MYR 09055). – 1♀, Idukki District, Idli motta Shola, Annamudi Shola National Park, high altitude montane forest, near grassland, hand collection (10º10′09.5″N, 77º10′58.1″E), 2345 m, 20.XI.2019, leg. A. A. Pooja, K. Ullas (ZFMK-MYR 09056). – 1♀, Idli motta Shola, Annamudi Shola National Park, high altitude montane forest (10º10′09.6″N, 77º10′22.2″E), 2471 m, (ZFMK-MYR 09057). – 1♂ (ZFMK-MYR 09058). – 1♂ (ZFMK-MYR 09059). – 1♂ (ZFMK-MYR 09060). – 1♂ (ZFMK-MYR 09061). – 1♀ (ZFMK-MYR 09062). – 1♀, Winkler extraction (ZFMK-MYR 09063). – 1♂, Idukki District, Pambadum Shola National Park, high altitude montane forest, hand collection (10º08′00.3″N, 77º15′13.6″E), 1818 m, 21.XI.2019, leg. A. A. Pooja, K. S. Nafin, K. Ullas (ZFMK-MYR 09064). – 1♀ (ZFMK-MYR 09065). – 1♂ (ZFMK-MYR 09066). – 1♂ (ZFMK-MYR 09067). – 1♂ (ZFMK-MYR 09068). – 1♂, Pambadum Shola National Park, high altitude montane forest, rain shadow (10º07′55.4″N, 77º15′44.1″E), 1970 m, 22.XI.2019, (ZFMK-MYR 09069). – 1♂ (ZFMK-MYR 09070). – 1♂, Idukki District, Kadalar Shola, Eravikulam National Park, high altitude montane forest, Winkler extraction (10º08′24.3″N, 77º02′39.3″E), 1703 m, 12.XII.2019, leg. A. A. Pooja, J. Jithin (ZFMK-MYR 09071). – 1♀ (ZFMK-MYR 09072). – 1♂ (ZFMK-MYR 09073), Eravikulam National Park, Erachilpara waterfalls, hand collection (10º10′28.0″N, 77º05′20.1″E), 1929 m, 13.XII.2019. – 1♀ (ZFMK-MYR 09074). – 1♀ (ZFMK-MYR 09075). – 1♂, Kollam District, Shendurney Wildlife Sanctuary, Sasthamnada Myristica Swamps, Winkler extraction (8º49′14.3″N, 77º02′50.6″E), 160 m, 19.XII.2019, leg. A. A. Pooja, P. P. Sudhin, R. S. Abhijith (ZFMK-MYR 09077). – 1♂ (ZFMK-MYR 09078). – 1♂, Shendurney Wildlife Sanctuary, Dharaphabhana chappath, mix of evergreen and deciduous forest, Winkler extraction (8°52′40.1″N, 77°04′55.9″E), 181 m, 20.XII.2019, leg. P. P. Sudhin, R.S. Abhijith (ZFMK-MYR 09079). – 1♂, Shendurney Wildlife Sanctuary, Onakathodu, Kadalar range, semi evergreen bordered with moist deciduous forest, Winkler extraction (8°54′06.1″N, 77°06′25.6″E), 174 m, 22.XII.2019, leg. A. A. Pooja, P. P. Sudhin, R. S. Abhijith (ZFMK-MYR 09080). – 1♀ (ZFMK-MYR 09081). – 1♂ (ZFMK-MYR 09082).

Non-barcoded specimens. India, Kerala Province: – 1♀, Idukki District, Mannavan Shola, Annamudi Shola National Park, high altitude montane forest, hand collection (10º10′54.5″N, 77º11′25.8″E), 2140 m, 18.XI.2019, leg. A. A. Pooja, K. Ullas (ZFMK-MYR 09503). – 1♂, 5♀, Idli motta Shola, Annamudi Shola National Park, high altitude montane forest, hand collection (10º10′09.6″N, 77º10′22.2″E), 2471 m, 20.XI.2019, leg. A. A. Pooja, K. Ullas (ZFMK-MYR 09540). – 1♀, Idukki District, Pambadum Shola National Park, high altitude montane forest, hand collection, (10º08′00.3″N, 77º15′13.6″E), 1818 m, 21.XI.2019, leg. A. A. Pooja, K. S. Nafin, K. Ullas (ZFMK-MYR 09566). – 1♀, Pambadum Shola National Park, rain shadow region (10º07′55.4″N, 77º15′44.1″E), 1970 m, 22.XI.2019, (ZFMK-MYR 09577). – 6♀, Idukki District, Erachilpara waterfalls, Eravikulam National Park, high altitude montane forest, hand collection (10º10′28.0″N, 77º05′20.1″E), 1929 m, 13.XII.2019, leg. A. A. Pooja, J. Jithin (ZFMK-MYR 09772). – 1 juvenile (sex undeterminable), Kollam District, Dharaphabhana chappath, Shendurney Wildlife Sanctuary, mix of evergreen and deciduous forest, Winkler extraction (8°52′40.1″N, 77°04′55.9″E), 181 m, 20.XII.2019, leg. P. P. Sudhin, R. S. Abhijith (ZFMK-MYR 09808).

COI barcoding

Family Siphonorhinidae

The phylogenetic analysis included just two of the six genera: *Illacme* (2 specimens) and *Siphonorhinus* (4 specimens). In the maximum likelihood analysis of the mitochondrial gene *COI*, the family Siphonorhinidae was not retrieved as monophyletic group. However, *Siphonorhinus* and *Illacme* form separate clades, with bootstrap support of 88% and 100%, respectively. Within the *Siphonorhinus* clade, the newly described Indian species *Siphonorhinus parambikulam* **sp. n.** is sister to the Indonesian clade, with bootstrap value of 88%. The p-distances between *Siphonorhinus parambikulam* **sp. n.** and the Indonesian *Siphonorhinus* are 23.0–23.3%. Within the Indonesian *Siphonorhinidae* clade, the p-distance between *Siphonorhinus* OQ708812 and OQ708813 is 0.2%, and that between these (OQ708812–13) and OQ708811 is 16.1%. The interspecific distance between the two species of

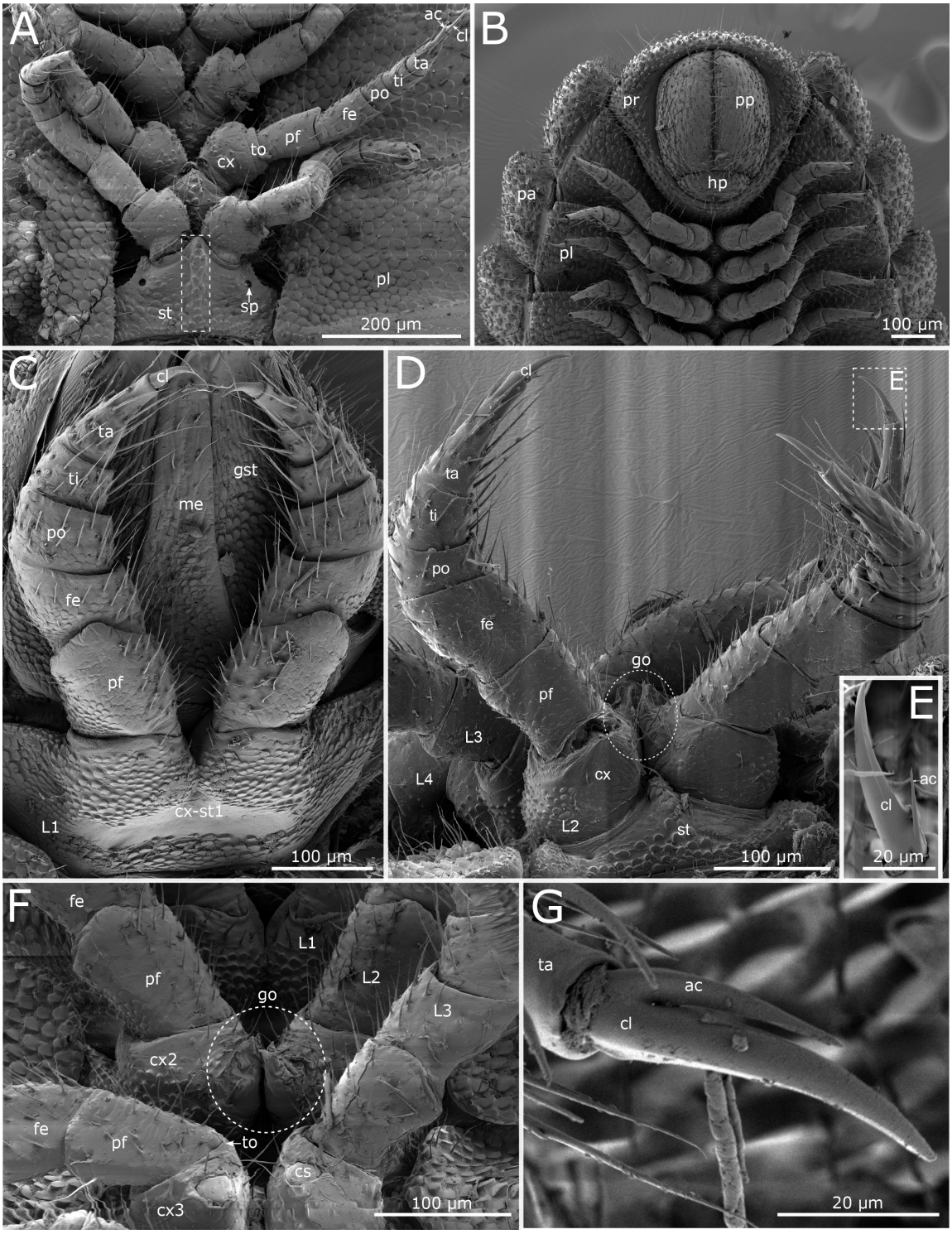

Fig. 6. *Siphonorhinus parambikulam* **sp. n.**, holotype ♂ (ZFMK-MYR 9076), SEM. **A**. Posterior body legs, antero-ventral view. **B**. Telson, ventral view. **C**. Leg 1, postero-ventral view; **D**. Leg 2 with gonopore, anterior view. **E**. Leg 3 claw, anterior view. **F**. Base of legs 2 and 3 with gonopore (circle) and coxal sac, posterior view. **G**. Midbody claw with accessory claw, lateral view. Abbreviations: ac = accessory claw; cl = claw; cs = coxal sac; cx = coxa; fe = femur; gst = gnathochilarial stipes; go = gonopore (pseudopenes); hp = hypoproct (anal scale); L = leg; me = mentum; pa = paranota; pf = prefemur; pl = pleurite; po = postfemur; pp = paraproct (anal valve); pr = preanal ring; sp = spiracle; st = sternite; ta = tarsus; ti = tibia; to = trochanter. The box in A indicates the medial sternal ridge; the circles in D and F indicate the pseudopenes.

Illacme is 19.9%. The p-distances between the *Siphonorhinus* species and *Illacme* are 28.4–30.9% (Fig. 8).

Family Siphonophoridae

The phylogenetic analysis includes a total of 50 sequences, of which 32 were from India, four from New Zealand, 13 from Indonesia, and one from the United States of America. Three clades of Indian Siphonophoridae could be identified in the analysis, each with bootstrap support > 96%. Clade I has bootstrap support of 99% and includes three putative lineages (lg. 1, lg. 2, lg. 3), each with bootstrap support of 100%. The p-distances within clade I are 0.0–2.1% for lg. 1, 0.0–0.8% for lg. 2, single haplotype for lg. 3, and the p-distances between these three lineages are above 7.6%. Clade II was also retrieved with three putative lineages (lg. 4, lg. 5, lg. 6), each with bootstrap support of 100%: lg. 4 has a p-distance of 1.2%, lg. 5 is a singleton, and lg. 6 is only represented by a single haplotype. The p-distances between these three lineages are 11.4–17.4%. In Clade III, three putative lineages (lg. 7, lg. 8, lg. 9) are present: lg. 7 is with a single haplotype, lg. 8 has a p-distance of 1.8%, and lg. 9 has a p-distance of 0.2–1.4%, while the p-distances between these three lineages are 10.0–18.9%. A monophyletic group containing the Siphonophoridae from New Zealand (NZ clade), with bootstrap support of 100%, was retrieved as sister to Clade I, with bootstrap support of 93%. The Indonesian specimens were retrieved as a monophyletic group (bootstrap support = 99%) and are the sister-group to the Clade I + NZ clade, with bootstrap support of 53% (Fig. 8).

Discussion

Characters of *Siphonorhinus* Pocock, 1894

The genus *Siphonorhinus* Pocock, 1894, which now contains nine extant species, is poorly defined, as most species have been described based on female somatic characters that are easily accessible, but might be of little taxonomic value. The previous species descriptions typically included information on the habitus, coloration, segment number, tergite shape, head shape, gnathochilarium, and antenna shape, but often lacked information on minute, taxonomically informative characters like the gonopods, sensilla, and setation on the antennae, etc. (see Pocock 1894; Silvestri 1895). This is especially true for the three previously-known Indian *Siphonorhinus* species, which were described and are so far known based only on female specimens (Attems 1936; Turk 1947). Here, we present the modern description of a new *Siphonorhinus* species based on SEM, µCT, and *COI* barcoding, documenting several characters for the first time. We recommend that the following characters should be checked in other *Siphonorhinus* species, as these were also suggested as being genus-specific in recent generic diagnoses for *Illacme* (Marek et al. 2012, 2016, 2023), *Notiorhinus* (Moritz & Parra-Gómez 2023a, 2023b), and *Madagascarhinus* (Wesener 2023): 1) gonopod shape, 2) number of gonopod podomeres, 3) modification of apical podomere of anterior and posterior gonopods, 4) arrangement of sensilla basiconica on the antenna, 5) shape and size of antennomeres, 6) arrangement of salivary gland openings, 7) presence and number of macrosetae at antero-lateral margin of stipes, 8) fusion of leg 1 coxa-sternite, 9) presence/absence of hypoproct on telson, and 10) length of the accessory claw on first few anterior and posterior legs. Thus, there is no clear indication as to whether the characteristics described here for *Siphonorhinus parambikulam* **sp. n.** are species- or genus-specific, nor if all previously described and synonymized *Siphonorhinus* species belong to the same genus. In order to gain a deeper understanding of this group's diversity and phylogenetic relationships, we recommend a genomic analysis, particularly by sequencing specimens from type series. A detailed examination of the external morphology using micro-CT, SEM, and light microscopy should also be conducted to determine if the characters addressed above are species- or genus-specific. Recently, two fossil "*Siphonorhinus*" species were described from Burmese amber (Su et al. 2024), but the characters presented are not consistent with this placement. *Siphonorhinus globosus* Su, Cai & Huang, 2024 is a representative of the family Siphonophoridae and not Siphonorhinidae, as evident from 1) the straight antenna with homogenous antennomeres (Su et al. 2024, figs. 1D, 2A, B, 4C, 5C, 6C), compared to the characteristic elbowed antenna with elongated 2nd antennomere of Siphonorhinidae (Figs. 3B, 5A), and 2) the head, which extends into a beak (Su et al. 2024, figs. 2B, 5C, 6E). *Siphonorhinus peculiaris* Su, Cai & Huang, 2024 is a member of Siphonorhinidae but might not be a representative of the genus *Siphonorhinus*, as it lacks the sunken-in sensory pits characteristic for the genus (Attems 1930, 1938).

COI barcoding

Besides the analyses of morphological characters using SEM and micro-CT, we provide a molecular analysis based on the largest *COI* dataset for the order Siphonophorida to date, as well as the first for Indian Siphonophorida.

Family Siphonorhinidae

Sequences were only available for two of the six genera of the family, *Siphonorhinus* and *Illacme*. The included representatives of Siphonorhinidae did not form a monophyletic group. However, this does not allow to assess the monophyly of the family Siphonorhinidae, as *COI* is not able to resolve deeper splits and our taxon sampling did not cover the full diversity of the family. *Siphonorhinus*

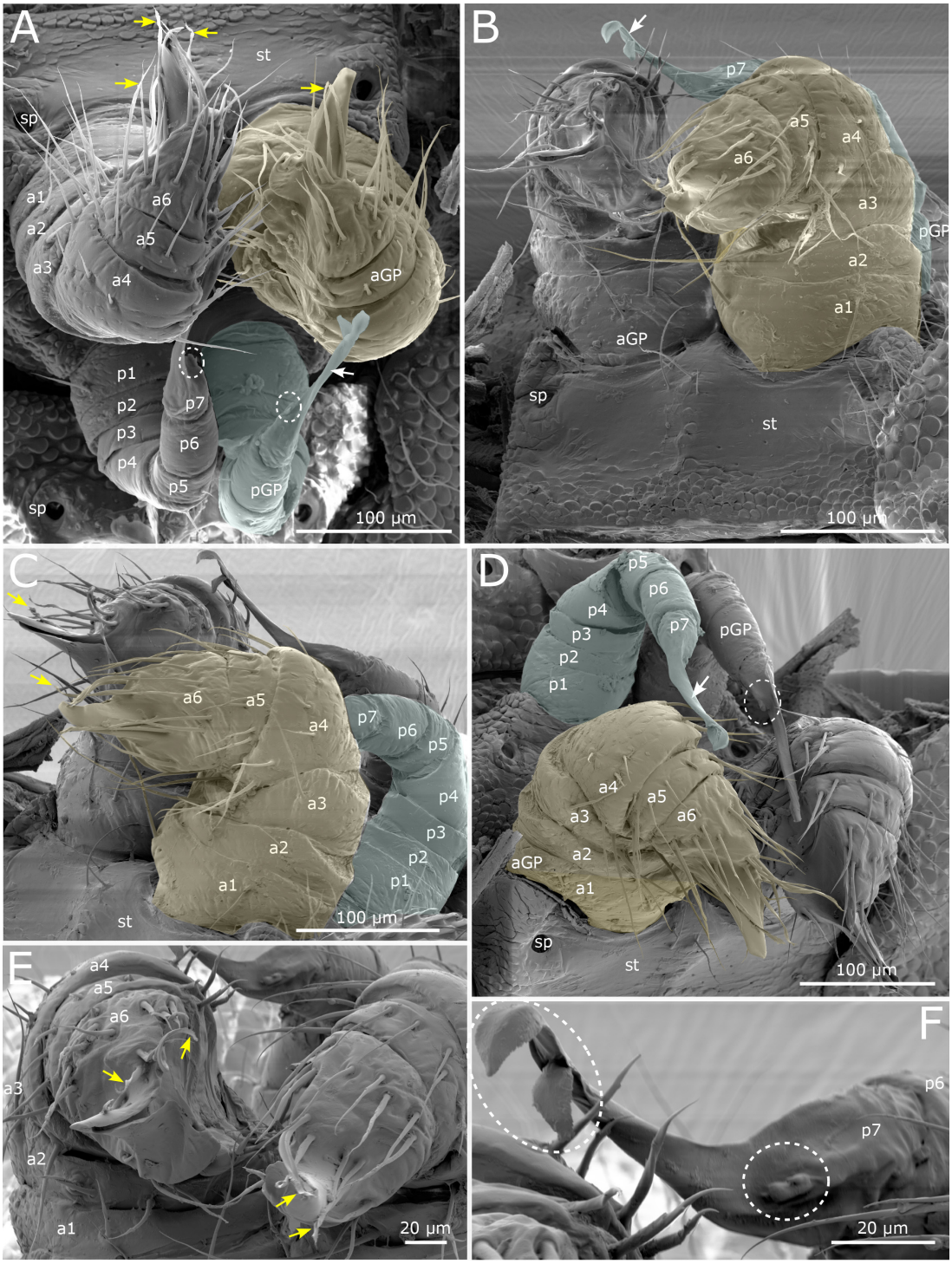

Fig. 7. *Siphonorhinus parambikulam* **sp. n.**, holotype ♂ (ZFMK-MYR 9076), SEM. **A**. Gonopods, dorsal view. **B**. Gonopods, anterior view. **C**. Gonopods, lateral view. **D**. Gonopods, antero-lateral view. **E**. Apical podomere of anterior gonopod, anterior view. **F**. Apical podomere of posterior gonopod, antero-lateral view. Abbreviations: a1–a6 = podomeres of the anterior gonopod; aGP = anterior gonopod; p1–p7 = podomeres of the posterior gonopod; pGP = posterior gonopod; sp = spiracle; st = sternite. The yellow-colored parts represent the anterior gonopod, while the blue-colored parts represent the posterior gonopod. The small circles in A, D, and F indicate the small spine at the base of podomere 7 of the posterior gonopod; the larger circle in F indicates the styliform article with leaf-shaped tips; the white arrows in A, B, and D indicate the thin, long filament-like extension of podomere 7 of the posterior gonopod; the yellow arrows in A, C, and E indicate the serrated-twisted setae on podomere 6 of the anterior gonopod.

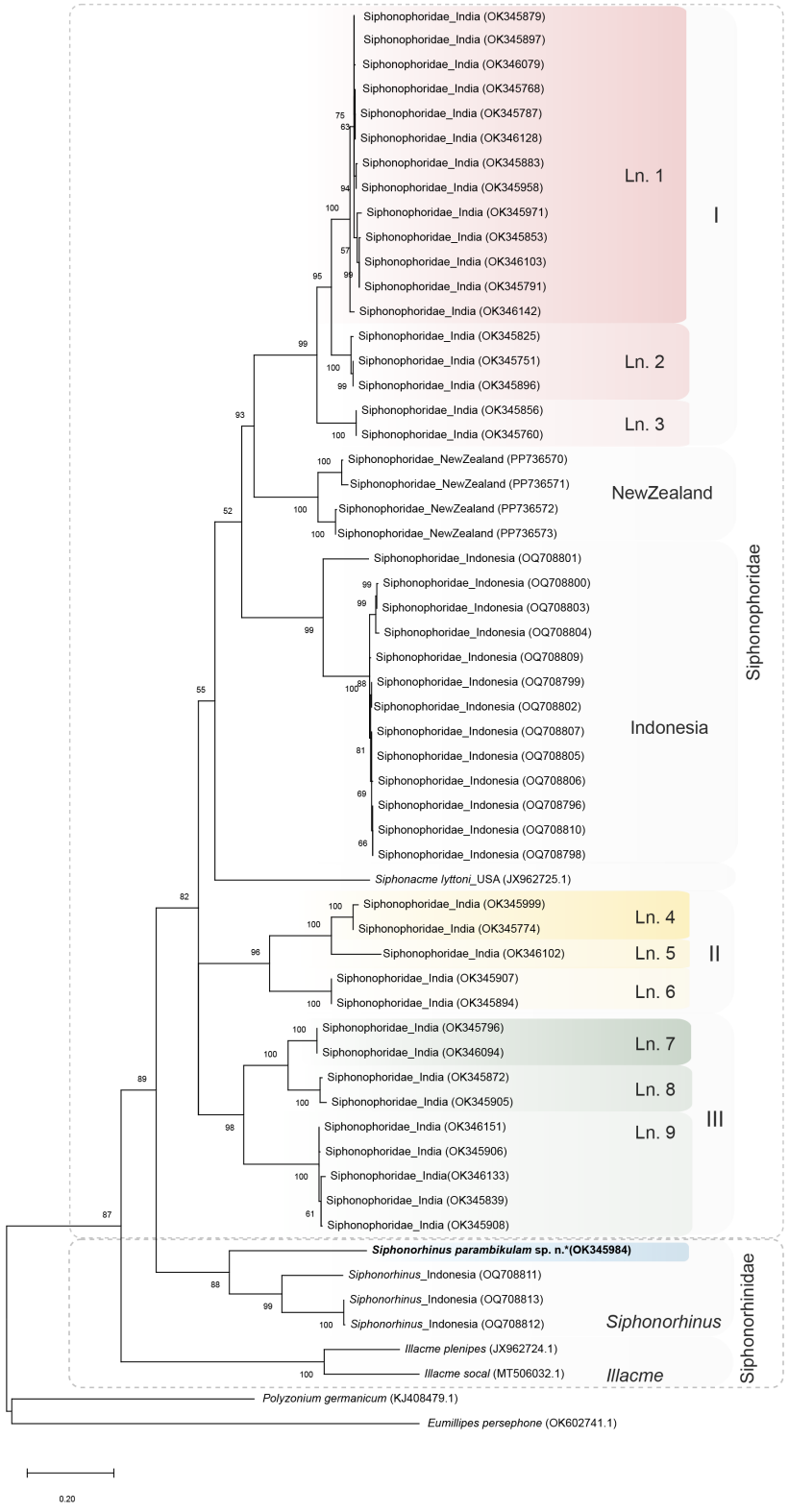

Fig. 8. Maximum likelihood tree inferred from the *COI* dataset with 1,000 bootstrap pseudo replicates implementing the TN+G+I model. The asterisk (*) indicates the newly-described species. Based on the tree, the Indian Siphonophoridae are divided into three clades (I, II, III). The colors within these clades correspond to the different putative lineages (Ln). Indicated in parentheses are GenBank numbers.

parambikulam **sp. n.**, described here, shows p-distances of 23.0–23.3% to the Indonesian *Siphonorhinus* species. These potential interspecific distances between the Indian and Indonesian *Siphonorhinus* species are slightly lower than in the Indian Polyzoniida genus *Theratta* Anilkumar, Wesener & Moritz, 2022 (20.9–25.3%) (Anilkumar et al. 2022), but higher than in the Polyzoniida genus *Siphonethus* Chamberlin, 1920 (13.9–14.3%) (Moritz et al. 2022), and the platydesmidan genera *Dolistenus* Fanzago, 1874 (16.6–20.7%), and *Brachycybe* Wood, 1864 (12.2–18.4%) (Recuero & Flores 2020). However, it should be noted that p-distances of the *COI* gene have not yet been studied in detail in Colobognatha.

Family Siphonophoridae new for India

While four species of the family Siphonorhinidae are known from India, to our knowledge, not a single specimen of the family Siphonophoridae had been recorded from India, although two were known from Sri Lanka (Jeekel 2001). This study presents the first Indian records of the family Siphonophoridae based on *COI* barcodes, with nine putative lineages. The p-distances between these lineages range from 7.6–8.9% and up to 2.1% within lineages. Furthermore, this study illustrates the importance of DNA barcoding in identifying these putative species lineages, which hopefully will facilitate the identification of potential new species as well as help us better understand the diversity and taxonomy of neglected taxa such as Siphonophorida.

Distribution and ecology of Indian Siphonophorida

This study presents the description of a new species, *Siphonorhinus parambikulam* **sp. n.** from the Indian Western Ghats (southern India), belonging to a genus that was previously known only from the Himalayas of India (northern India) and Southeast Asia. The distribution map of Indian Siphonophorida includes five protected sites (Fig. 1). *Siphonorhinus parambikulam* **sp. n.** was collected from under a rotting log in the Muthuvarachal Range of the Parambikulam Tiger Reserve in the southern Western Ghats of Kerala, at an altitude of 555 m. The specimens of Siphonophoridae were collected from soil and rotting barks from three highland Shola forests: Annamudi Shola National Park (SNP), Pambadum SNP, and Eravikulam NP, all located at altitudes above 1,500 m, and from a mid- to high-elevation forest, Shendurney Wildlife Sanctuary. All specimens were collected during the post-monsoon season (November–December). Based on the analyzed *COI* data, it can be assumed that there are several (up to nine) lineages/putative (undescribed) species of Siphonophoridae in our samples, from just four sites, in comparison to the ~104 Siphonophoridae species described worldwide (Enghoff et al. 2015). The p-distances between some specimens in our analysis were below 5.0%—a threshold for intraspecific distance observed in some millipede species (Reip & Wesener 2018)—and even as low as 0.0%. However, larger p-distances, reaching up to 24.8% (e.g., OK345760 vs. OK346102), were also commonly observed in our analysis. These high distances, as well as the newly described *Siphonorhinus parambikulam* **sp. n.** from the Indian Western Ghats, indicate that the millipedes of the Indian Western Ghats, especially the enigmatic Colobognatha, are greatly undersampled, with an underestimated diversity of Siphonophorida for this area. As these specimens were collected over a period of five weeks from just five different locations in a relatively small region of the Kerala province, it is reasonable to conclude that a great diversity of millipedes is awaiting discovery and description in India.

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Supplementary Table S1: Estimates of evolutionary divergence between the analyzed sequences. The number of base differences per site is shown. The analysis involved 58 nucleotide sequences. Codon positions included were 1st+2nd+3rd+Noncoding. All ambiguous positions were removed for each sequence pair. There were 657 positions in the final dataset. Evolutionary analyses were conducted in MEGA6.

Other supplementary material. SEM images (ZFMK-MYR09076_SEM) and µCT data (ZFMK-MYR09076_microCT).

Appendix. The molecular phylogenetic analysis includes a total of 58 sequences, comprising three barcodes from the order Siphonophorida, two barcodes from the order Polyzoniida as outgroups (both previously available on GenBank), and 53 newly-added Siphonophorida sequences. The specimen marked with an asterisk (*) is the species described in this study. Abbreviations: INCOL = specimens shared between ZFMK, Bonn and LIPI, Bogor, Indonesia; LIPI = Lembaga Ilmu Pengetahuan Indonesia (Indonesian Institute of Sciences), Jakarta, Indonesia; MYR = Myriapoda; NP = National Park; NZ = New Zealand; OG = outgroup taxon; SNP = Shola National Park; WS = Wildlife Sanctuary; ZFMK = Zoological Research Museum Alexander Koenig, Bonn, Germany.

Species	Voucher#	GenBank#	Locality
Eumillipes persephone Marek, 2021 (OG)	T147101-MPE5068	OK602741.1	Australia
Illacme plenipes Cook & Loomis, 1928	SPC001187	JX962724.1	United States of America
Illacme socal Marek & Shear, 2023	JCM-2020	MT506032.1	California, United States of America
Polyzonium germanicum Brandt, 1837 (OG)	ZFMK- MYR1351	KJ408479.1	Kent, United Kingdom
Siphonacme lyttoni Cook & Loomis, 1928	MIL0014	JX962725.1	United States
Siphonorhinus parambikulam **sp. n.***	ZFMK-MYR 09076	OK345984	Parambikulam Tiger Reserve, Kerala, India
Siphonorhinus sp.	INCOL1870-16	OQ708811	Indonesia, Java, Halimun-Salak National Park, Cikaniki
Siphonorhinus sp.	INCOL1848-16	OQ708813	Indonesia, Java, Halimun-Salak National Park, Cidahu
Siphonorhinus sp.	INCOL1859-16	OQ708812	Indonesia, Java, Halimun-Salak National Park, Cidahu
Siphonophoridae	ZFMK-MYR 09048	OK345971	Mannavan Shola, Annamudi SNP, Kerala, India
Siphonophoridae	ZFMK-MYR 09049	OK345879	Mannavan Shola, Annamudi SNP, Kerala, India
Siphonophoridae	ZFMK-MYR 09050	OK345883	Mannavan Shola, Annamudi SNP, Kerala, India
Siphonophoridae	ZFMK-MYR 09052	OK346079	Mannavan Shola, Annamudi SNP, Kerala, India
Siphonophoridae	ZFMK-MYR 09053	OK346142	Mannavan Shola, Annamudi SNP, Kerala, India
Siphonophoridae	ZFMK-MYR 09054	OK345897	Mannavan Shola, Annamudi SNP, Kerala, India
Siphonophoridae	ZFMK-MYR 09055	OK345958	Mannavan Shola, Annamudi SNP, Kerala, India
Siphonophoridae	ZFMK-MYR 09056	OK345768	Idli motta shola, Annamudi SNP, Kerala, India
Siphonophoridae	ZFMK-MYR 09059	OK345787	Idli motta shola, Annamudi SNP, Kerala, India

Species	Voucher#	GenBank#	Locality
Siphonophoridae	ZFMK-MYR 09060	OK346128	Idli motta shola, Annamudi SNP, Kerala, India
Siphonophoridae	ZFMK-MYR 09064	OK346103	Pambadum SNP, Kerala, India
Siphonophoridae	ZFMK-MYR 09065	OK345853	Pambadum SNP, Kerala, India
Siphonophoridae	ZFMK-MYR 09067	OK345791	Pambadum SNP, Kerala, India
Siphonophoridae	ZFMK-MYR 09061	OK345751	Idli motta shola, Annamudi SNP, Kerala, India
Siphonophoridae	ZFMK-MYR 09057	OK345825	Idli motta shola, Annamudi SNP, Kerala, India
Siphonophoridae	ZFMK-MYR 09058	OK345896	Idli motta shola, Annamudi SNP, Kerala, India
Siphonophoridae	ZFMK-MYR 09066	OK345856	Pambadum SNP, Kerala, India
Siphonophoridae	ZFMK-MYR 09068	OK345760	Pambadum SNP, Kerala, India
Siphonophoridae	ZFMK-MYR 09062	OK346102	Idli motta shola, Annamudi SNP, Kerala, India
Siphonophoridae	ZFMK-MYR 09069	OK345999	Pambadum SNP, Kerala, India
Siphonophoridae	ZFMK-MYR 09070	OK345774	Pambadum SNP, Kerala, India
Siphonophoridae	ZFMK-MYR 09071	OK346151	Kadalar Shola, Eravikulam NP, Kerala, India
Siphonophoridae	ZFMK-MYR 09073	OK346133	Erechipetta shola, Waterfalls, Eravikulam NP, Kerala, India
Siphonophoridae	ZFMK-MYR 09074	OK345839	Erechipetta shola, Waterfalls, Eravikulam NP, Kerala, India
Siphonophoridae	ZFMK-MYR 09072	OK345906	Kadalar Shola, Eravikulam NP, Kerala, India
Siphonophoridae	ZFMK-MYR 09075	OK345908	Erechipetta shola, Waterfalls, Eravikulam NP, Kerala, India
Siphonophoridae	ZFMK-MYR 09080	OK345907	Onakathodu, Kadalar range, Shendurney WS, Kerala, India
Siphonophoridae	ZFMK-MYR 09081	OK345894	Onakathodu, Kadalar range, Shendurney WS, Kerala, India
Siphonophoridae	ZFMK-MYR 09078	OK345796	Sasthamnada Myristica Swamps, Shendurney WS, Kerala, India
Siphonophoridae	ZFMK-MYR 09077	OK346094	Sasthamnada Myristica Swamps, Shendurney WS, Kerala, India
Siphonophoridae	ZFMK-MYR 09082	OK345872	Onakathodu, Kadalar range, Shendurney WS, Kerala, India
Siphonophoridae	ZFMK-MYR 09079	OK345905	Dharaphabhana chappath, Shendurney WS, Kerala, India
Siphonophoridae	INCOL1868-16	OQ708801	Indonesia, Java, Halimun-Salak NP, Cidahu
Siphonophoridae	INCOL1823-16	OQ708809	Indonesia, Java, Halimun-Salak NP, Cidahu
Siphonophoridae	INCOL1860-16	OQ708807	Indonesia, Java, Halimun-Salak NP, Cidahu
Siphonophoridae	INCOL1811-16	OQ708799	Indonesia, Java, Halimun-Salak NP, Cidahu

Species	Voucher#	GenBank#	Locality
Siphonophoridae	INCOL1847-16	OQ708802	Indonesia, Java, Halimun-Salak NP, Cidahu
Siphonophoridae	INCOL1912-16	OQ708800	Indonesia, Java, Halimun-Salak NP, Cidahu
Siphonophoridae	INCOL1916-16	OQ708803	Indonesia, Java, Halimun-Salak NP, Cidahu
Siphonophoridae	INCOL1948-16	OQ708806	Indonesia, Java, Halimun-Salak NP, Cidahu
Siphonophoridae	INCOL1940-16	OQ708796	Indonesia, Java, Halimun-Salak NP, Cidahu
Siphonophoridae	INCOL1952-16	OQ708810	Indonesia, Java, Halimun-Salak NP, Cidahu
Siphonophoridae	INCOL1964-16	OQ708805	Indonesia, Java, Halimun-Salak NP, Cidahu
Siphonophoridae	INCOL1924-16	OQ708804	Indonesia, Java, Halimun-Salak NP, Cidahu
Siphonophoridae	INCOL1960-16	OQ708798	Indonesia, Java, Halimun-Salak National Park, Cidahu
Siphonophoridae	ZFMK MYR13878	PP736570	New Zealand, South Island, Tasman, Takaka, Totaranui, Abel Tasman NP
Siphonophoridae	ZFMK-MYR11412	PP736571	New Zealand, South Island, Tasman, Takaka, Totaranui, Abel Tasman NP
Siphonophoridae	ZFMK-MYR11411	PP736572	New Zealand, South Island, Canterbury, Kaikoura, Puhi Puhi Scenic Reserve
Siphonophoridae	ZFMK-MYR11413	PP736573	New Zealand, South Island, Canterbury, Kaikoura, Puhi Puhi Scenic Reserve