

A New Thai Millipede Species of the Genus *Coxobolellus* Pimvichai, Enghoff, Panha & Backeljau, 2020 (Diplopoda: Spirobolida: Pseudospirobolellidae)

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ABSTRACT.— A new millipede species of the genus *Coxobolellus* is described from Mae Hong Son Province, Thailand: *Coxobolellus sirindhornae* sp. nov. The new species is defined by its gonopod morphology and COI DNA barcodes. These latter place the new species within the well-supported *Coxobolellus* clade. The new species exhibits four gonopod synapomorphies that are diagnostic for the genus: (1) a protruding process on the coxae of the 3rd (and sometimes 4th) pair of male legs, (2) large, triangular coxae on the 4th and 5th pairs of legs, (3) a short process on the preanal ring extending to or slightly beyond the anal valves, and (4) the posterior gonopod telopodite divided into two parts, with a conspicuous pore opening at the mesal margin at the end of the coxal part. The new species is included in an updated morphological identification key for all currently recognized *Coxobolellus* species.

KEYWORDS: DNA barcoding, gonopod morphology, identification key, phylogeny

INTRODUCTION

Until recently, the millipede family Pseudospirobolellidae Brölemann, 1913 included only four species and two genera: *Pseudospirobolellus* Carl, 1912 (two species) and *Benoitolus* Mauriès, 1980 (two species) (Enghoff et al., 2015). However, fieldwork conducted in Thailand in recent years has led to the discovery of fifteen new pseudospirobolellid species and two new genera: *Coxobolellus* Pimvichai, Enghoff, Panha & Backeljau, 2020 (twelve species) and *Siliquobolellus* Pimvichai, Enghoff, Panha & Backeljau, 2022 (three species) (Pimvichai et al., 2020, 2022a, 2022b).

The genus *Coxobolellus* is characterized by four diagnostic synapomorphies: (1) a protruding process on the coxae of the 3rd (and sometimes 4th) pair of male legs, (2) large, triangular coxae on the 4th and 5th pair of legs, (3) a short process on the preanal ring extending to or slightly beyond the anal valves, and (4) the posterior gonopod telopodite divided into two parts with a conspicuous pore opening at the mesal margin at the end of the coxal part (Pimvichai et al., 2020). These four diagnostic synapomorphies were also observed in some specimens collected by two of us (PP and PP) during a field trip in Mae Hong Son Province, Thailand, in 2023. Yet, the specimens could not be assigned to any of the currently known *Coxobolellus* species. Therefore, the present contribution formally describes this material as a new species, viz. *Coxobolellus sirindhornae* sp. nov. by combining morphological characters and DNA barcoding.

MATERIALS AND METHODS

Four live specimens were hand-collected in October 2023. Two specimens (one ♂ and one ♀) were partly preserved in 70% ethanol for morphological study and partly kept in a freezer at –20 °C for DNA analysis. The two other specimens (♀♀) were entirely preserved in 70% ethanol.

This research was conducted under the approval of the Animal Care and Use regulations (numbers U1-07304-2560 and IACUC-MSU-037/2019) of the National Research Council of Thailand.

Morphology

Gonopods were photographed using a Nikon digital camera linked with the program Helicon Remote (ver. 3.1.1.w). The Zerene Stacker Pro software was used for image-stacking. For scanning electron microscopy (SEM: Hitachi TM4000Plus), the samples were air-dried directly from the alcohol and coated with gold for 60 seconds using a sputter coater (Hitachi: MC1000). SEM images were made at the Central Laboratory of Mahasarakham University. Drawings were created using a Leica MZ16 stereomicroscope and photographs. Voucher specimens have been deposited in the collection of Museum of Zoology, Chulalongkorn University, Bangkok, Thailand (CUMZ).

DNA extraction, amplification and sequencing

Total genomic DNA was extracted from legs of two specimens of *Coxobolellus sirindhornae* sp. nov. (CUMZ-D00156 and CUMZ-D00156-1) using the NuleoSpin Tissue kit (Macherey-Nagel, Düren, Ger-

TABLE 1. Specimens from which the COI gene fragment was used in this study. CUMZ, Museum of Zoology, Chulalongkorn University, Bangkok, Thailand; NHMD, Natural History Museum of Denmark; NHMW, Naturhistorisches Museum, Vienna, Austria; NHM, The Natural History Museum, London, United Kingdom. Abbreviations after species names refer to the isolate of each sequence. The COI column shows the GenBank accession numbers.

	Voucher code	Locality	COI
Ingroup			
Genus <i>Apeuthes</i>			
<i>A. maculatus</i> Amc	NHMW-Inv. No.2395	South Annam, VIETNAM	MF187404
<i>A. maculatus</i> Am26	NHMD-621697	Nha Trang, Bao Dai Villas Hotel, in garden, VIETNAM	MZ567159
<i>A. fimbriatus</i> BMP	CUMZ-D00144	Bach Ma Peak, Da Nang, VIETNAM	MZ567160
<i>A. longeligulatus</i> TPP	CUMZ-D00140	Tham Phet Po Thong, Klong Hard, Sa Kaeo, THAILAND	MZ567161
<i>A. pollex</i> SMR	CUMZ-D00141	Sra Morakot, Klongthom, Krabi, THAILAND	MZ567162
<i>A. pollex</i> SML	CUMZ-D00142	Koh 8, Similan islands, Phang Nga, THAILAND	MZ567163
<i>A. pollex</i> WTS	CUMZ-D00143	Tham Sue Temple, Muang, Krabi, THAILAND	MZ567164
? <i>A. spininavis</i> ABB	CUMZ-D00145	Air Banun, Perak, MALAYSIA	MZ567165
Genus <i>Atopochetus</i>			
<i>A. anaticeps</i> SVL	CUMZ- D00091	Srivilai temple, Chalermprakiet, Saraburi, THAILAND	MF187405
<i>A. dollfusii</i> DOL	NHM	Cochinchina, VIETNAM	MF187412
<i>A. helix</i> SPT	CUMZ- D00094	Suan Pa Thong Pha Phum, Kanchanaburi, THAILAND	MF187416
<i>A. mouleimensis</i> TAK	CUMZ- D00095	Km 87, Tha Song Yang, Tak, THAILAND	MF187417
<i>A. setiferus</i> HPT	CUMZ- D00097	Hub Pa Tard, Lan Sak, Uthaithani, THAILAND	MF187419
<i>A. spinimargo</i> Ton27	NHMD- 00047013	Koh Yo, Songkhla, THAILAND	MF187423
<i>A. truncatus</i> SML	CUMZ- D00101	Koh 8, Similan islands, Phang Nga, THAILAND	MF187424
<i>A. uncinatus</i> KMR	CUMZ- D00102	Khao Mar Rong, Bangsapan, Prachuap Khiri Khan, THAILAND	MF187425
<i>A. weseneri</i> Tos29	NHMD- 00047003	Supar Royal Beach Hotel, Khanom, Nakhon Sri Thammarat, THAILAND	MF187431
Genus <i>Aulacobolus</i>			
<i>A. uncopygus</i> Auc	NHMW-Inv. No.2375	Nilgiris, South India, INDIA	MF187433
Genus <i>Benoitolus</i>			
<i>B. birgita</i> BBG	NHMD 621687	Chiang Dao, Chiang Mai, THAILAND	MT328992
Genus <i>Coxobolellus</i>			
<i>C. albiceps</i> Stpw	CUMZ-D00121	Tham Pha Tub, Muang District, Nan Province, THAILAND (green individual)	MT328994
<i>C. albiceps</i> Stpl	CUMZ-D00122	Tham Pha Tub, Muang District, Nan Province, THAILAND (small, brown individual)	MT328993
<i>C. albiceps</i> TPB	CUMZ-D00123	Wat Tham Bampen Bun, Pan District, Chiang Rai Province, THAILAND	MT328996
<i>C. albiceps</i> Stvd	CUMZ-D00124	Tham Wang Daeng, Noen Maprang District, Phitsanulok Province, THAILAND	MT328995
<i>C. compactogonus</i> SKR	CUMZ-D00134	Sakaerat Environmental Research Station, Wang Nam Khiao District, Nakhon Ratchasima Province, THAILAND	MT328998
<i>C. compactogonus</i> KLC	CUMZ-D00135	Khao Look Chang, Pak Chong District, Nakhon Ratchasima Province, THAILAND	MT328997
<i>C. fuscus</i> HKK	CUMZ-D00133	Kroeng Krawia waterfall, Sangkhla Buri District, Kanchanaburi Province, THAILAND	MT328999
<i>C. nodosus</i> SPW	CUMZ-D00126	Chao Por Phawo Shrine, Mae Sot District, Tak Province, THAILAND	MT329000
<i>C. serratus</i> KKL	CUMZ-D00132	Khao Kalok, Pran Buri District, Prachuap Khiri Khan Province, THAILAND	MT329001
<i>C. simplex</i> TNP	CUMZ-D00136	Tham Pha Pha Ngam, Mae Prik District, Lampang Province, THAILAND	MT329002
<i>C. tenebris</i> KWP	CUMZ-D00119	Wat Khao Wong Phrohmmajan, Ban Rai District, Uthai Thani Province, THAILAND	MT329003
<i>C. tenebris</i> TPL	CUMZ-D00120	Wat Tham Phrom Lok Khao Yai, Sai Yok District, Kanchanaburi Province, THAILAND	MT329004
<i>C. tigris</i> TKP	CUMZ-D00130	Wat Tham Khao Plu, Pathio District, Chumphon Province, THAILAND	MT329005
<i>C. tigris</i> TYE	CUMZ-D00131	Tham Yai I, Pathio District, Chumphon Province, THAILAND	MT329006
<i>C. transversalis</i> Stpg	CUMZ-D00125	Tham Pha Tub, Muang District, Nan Province, THAILAND	MT329007
<i>C. valvatus</i> TCD	CUMZ-D00127	Wat Tham Chiang Dao, Chiang Dao District, Chiang Mai Province, THAILAND	MT329009

TABLE 1. Continued.

	Voucher code	Locality	COI
<i>C. valvatus</i> BRC	CUMZ-D00128	Tham Borichinda, Chom Thong District, Chiang Mai Province, THAILAND	MT329008
<i>C. valvatus</i> TST	CUMZ-D00129	Tham Sam Ta, Muang District, Mae Hong Son Province, THAILAND	MT329010
<i>C. saratani</i> PPLL2	CUMZ-D00153	Phu Pha Lom, Muang District, Loei Province, THAILAND	OP580097
<i>C. saratani</i> PPLL	CUMZ-D00153-1	Phu Pha Lom, Muang District, Loei Province, THAILAND	OP580098
<i>C. serratoligulatus</i> TCU	CUMZ-D00154	Tham Chan, Thong Saen Khan District, Uttaradit Province, THAILAND	OP580099
<i>C. serratoligulatus</i> TCU2	CUMZ-D00154-1	Tham Chan, Thong Saen Khan District, Uttaradit Province, THAILAND	OP580100
<i>C. sirindhornae</i> sp. nov. Wptw1	CUMZ-D00156	Wat Pa Tham Wua, Pang Mapha District, Mae Hong Son Province, THAILAND	PV612839
<i>C. sirindhornae</i> sp. nov. Wptw2	CUMZ-D00156-1	Wat Pa Tham Wua, Pang Mapha District, Mae Hong Son Province, THAILAND	PV612840
Genus <i>Leptogoniulus</i>			
<i>L. sorornus</i> BTN	CUMZ- D00109	Botanical Garden, Penang, MALAYSIA	MF187434
Genus <i>Litostrophus</i>			
<i>L. chamaeleon</i> PPT	CUMZ- D00111	Phu Pha terb, Mukdahan, THAILAND	MF187436
<i>L. saraburensis</i> PKS	CUMZ- D00113	Phukhae Botanical Garden, Saraburi, THAILAND	MF187438
<i>L. segregatus</i> Ls19	NHMD 621686	Koh Kut, Trad, THAILAND	MF187440
Genus <i>Macrurobolus</i>			
<i>M. macrurus</i> INT	CUMZ- D00147	Wat Tham Inthanin, Mae Sot District, Tak Province, THAILAND	MZ905519
Genus <i>Madabolus</i>			
<i>M. maximus</i> Mm4	NHMD-00047007	de Toliara Province, Parc National de Bermaraha, South Bank of Manambolo River, Near Tombeau Vazimba, MADAGASCAR	MF187441
Genus <i>Narceus</i>			
<i>N. annularis</i>		No locality data	NC 003343.1
Genus <i>Parabolus</i>			
<i>P. dimorphus</i> Pd34	NHMD-00047004	Dar es Salaam, TANZANIA	MF187442
Genus <i>Paraspirobolus</i>			
<i>P. lucifugus</i>		No locality data	AB608779.1
Genus <i>Pelmatojulus</i>			
<i>P. tigrinus</i> Pt2	NHMD-00047008	Southern part of the Comoé N.P., 30 km north of Kakpin, CÔTE d'IVOIRE	MF187443
<i>P. togoensis</i> Pto6	NHMD-00047006	Biakpa, GHANA	MF187444
Genus <i>Pseudospirobolellus</i>			
<i>Pseudospirobolellus</i> <i>avernus</i> GPG	CUMZ-D00117	Gua Pulau, Gua Musang, Kelantan, MALAYSIA	MT329011
<i>Pseudospirobolellus</i> sp. KCS	CUMZ-D00118	Koh Chuang, Sattahip, Chonburi, THAILAND	MT329012
Genus <i>Rhinocricus</i>			
<i>R. parvus</i> Rp49	NHMD-00047009	Puerto Rico, USA	MF187449
Genus <i>Siliquobolellus</i>			
<i>S. amicusdraconis</i> HPT2	CUMZ- D00149	Hub Pa Tard, Lan Sak, Uthaithani, THAILAND	OP174621
<i>S. constrictus</i> BYC	CUMZ- D00150	Ban Yang Chum, Kui Buri, Prachuap Khiri Khan, THAILAND	OP174622
<i>S. prasankokae</i> TPTG	CUMZ- D00148	Pha Thai, Ngao, Lampang, THAILAND	OP174623
Genus <i>Trachelomegalus</i>			
<i>T. sp.</i> Tr54	NHMD-00047012	Borneo Sabah, MALAYSIA	MF187445
Genus <i>Trigoniulus</i>			
<i>T. corallinus</i> Tco15	NHMD-00047010	Vientiane, LAOS	MF187446
Outgroup			
Genus <i>Anurostreptus</i>			
<i>A. barthelemyae</i> Tlb	CUMZ-D00003	Thale Ban N.P., Khuan Don, Satun, THAILAND	KC519469
Genus <i>Chonecambala</i>			
<i>C. crassicauda</i> Ttp	CUMZ-D00001	Ton Tong waterfall, Pua, Nan, THAILAND	KC519467
Genus <i>Thyropygus</i>			
<i>T. allevatus</i> Bb	CUMZ-D00013	BangBan, Ayutthaya, THAILAND	KC519479

many) following the manufacturer's instructions. PCR amplifications and sequencing of the standard mitochondrial COI DNA barcoding fragment were done as described by Pimvichai et al. (2020). The COI gene fragment was amplified with the primers LCO-1490 and HCO-2198 (Folmer et al., 1994). The new COI barcodes have been deposited in GenBank under accession numbers PV612839–PV612840. Sample data and voucher codes are provided in Table 1.

Alignment and phylogenetic analysis

The COI data set included 65 specimens, representing 19 genera and 48 species of ingroup taxa (Table 1). Three species of the order Spirostreptida, viz. *Anurostreptus barthelemyae* Demange, 1961 (Harpagophoridae), *Chonecambala crassicauda* Mauriès & Enghoff, 1990 (Pericambalidae) and *Thyropygus allevatus* (Karsch, 1881) (Harpagophoridae) were used as outgroup.

CodonCode Aligner (ver. 4.0.4, CodonCode Corporation) was used to assemble the forward and reverse sequences and to check for errors and ambiguities. All sequences were checked with the Basic Local Alignment Search Tool (BLAST) provided by NCBI and compared with reference sequences in GenBank. They were aligned using MUSCLE (ver. 3.6, see <http://www.drive5.com/muscle>; Edgar, 2004). The COI alignment consisted of 660 bp. The sequences were checked for ambiguous nucleotide sites, saturation and phylogenetic signal using DAMBE (ver. 5.2.65, see <http://www.dambe.bio.uottawa.ca/DAMBE/dambe.aspx>; Xia, 2018). MEGA (ver. X, see <http://www.mega-software.net>; Kumar et al., 2018) was used to (1) check for stop codons, (2) translate COI protein-coding sequences into amino acids, and (3) calculate uncorrected pairwise p-distances among sequences.

Phylogenetic trees were constructed using maximum likelihood (ML) and Bayesian inference (BI). The shape parameter of the gamma distribution, based on 16 rate categories, was estimated using maximum-likelihood analysis. ML trees were inferred with RAxML (ver. 8.2.12, see http://www.phylo.org/index.php/tools/raxmlhpc2_tgb.html; Stamatakis, 2014) through the CIPRES Science Gateway (Miller et al., 2010) using a GTR+G substitution model and 1000 bootstrap replicates to assess branch support. BI trees were constructed with MrBayes (ver. 3.2.7a, see http://www.phylo.org/index.php/tools/mrbayes_xsede.html; Huelsenbeck and Ronquist, 2001). Substitution models were inferred using jModeltest (ver. 2.1.10, see <https://www.github.com/ddarriba/jmodeltest2/releases>; Darriba et al., 2012) applying Akaike Information Criterion weights as selection criterion. This yielded GTR+I+G as best model.

BI trees were run for 4 million generations (heating parameter: 0.01), sampling every 1000 generations. Convergences were confirmed by verifying that the standard deviations of split frequencies were below 0.01. Then the first 1000 trees were discarded as burn-in, so that the final consensus tree was built from the last 6002 trees. Branch support was assessed by posterior probabilities.

For ML trees we consider branches with bootstrap values (BV) of $\geq 70\%$ to be well supported (Hillis and Bull, 1993) and $< 70\%$ as poorly supported. For BI trees, we consider branches with posterior probabilities (PP) of ≥ 0.95 to be well supported (San Mauro and Agorreta, 2010) and below as poorly supported.

RESULTS

Phylogeny

The uncorrected p-distance between the COI sequences (660 bp) ranged from 0.00 to 0.26 (see Appendix). The mean interspecific sequence divergence between *Coxobolellus sirindhornae* sp. nov. and the other *Coxobolellus* species was 0.13 (range: 0.12–0.15), while the mean interspecific sequence divergence among the other *Coxobolellus* species without *C. sirindhornae* sp. nov. was 0.12 (range: 0.06–0.15). The intraspecific sequence divergence of the new species (two sequences) was 0.003. The mean intergeneric sequence divergences between *Coxobolellus* (with *C. sirindhornae* sp. nov.) and other pseudospirobolellid genera were 0.21 (range: 0.20–0.23) for *Pseudospirobolellus*, 0.17 (range: 0.14–0.20) for *Siliquobolellus*, and 0.21 (range: 0.20–0.23) for *Benoitolus birgitae* (Hoffman, 1981).

The ML and BI trees constructed from the COI data were visually quite congruent with respect to well-supported branches (Fig. 1).

The genus *Coxobolellus* (Clade 1) showed up as a well-supported clade in which *C. sirindhornae* sp. nov. appeared as sister group to all other currently recognized *Coxobolellus* species. These latter involved five subclades (1A–E) and two species whose phylogenetic position remained unresolved (*C. fuscus* Pimvichai, Enghoff, Panha & Backeljau, 2020 and *C. simplex* Pimvichai, Enghoff, Panha & Backeljau, 2020) (Pimvichai et al. 2020, 2022a). As in previous studies, the monophyly of the Pseudospirobolellidae was well supported, but the sister group relationship of *Coxobolellus* was not. Finally, as observed before, *Benoitolus birgitae* showed up among *Litostrophus* species in the family Pachybolidae.

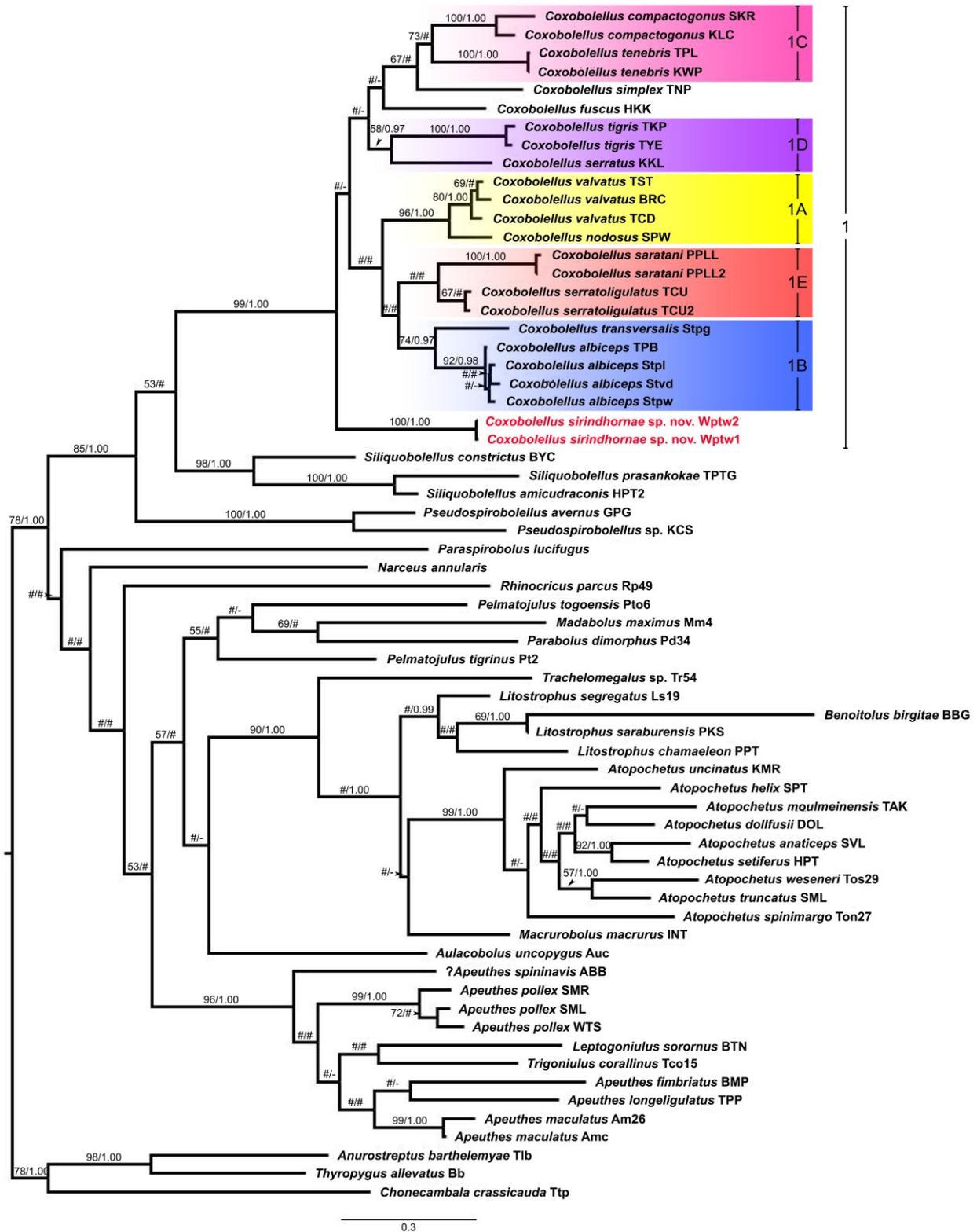


FIGURE 1. Phylogenetic position of *Coxobolellus sirindhornae* sp. nov. based on maximum likelihood analysis (ML) and Bayesian inference (BI) of the COI gene (660 bp). Numbers at nodes indicate branch support based on bootstrapping (ML) / posterior probabilities (BI). Scale bar = 0.3 substitutions/site. # indicates branches with < 50% ML bootstrap support and < 0.95 Bayesian posterior probability. - indicates non-supported branches. The coloured areas mark the subclades of *Coxobolellus* and are labelled as in Pimvichai et al. (2020, 2022a).

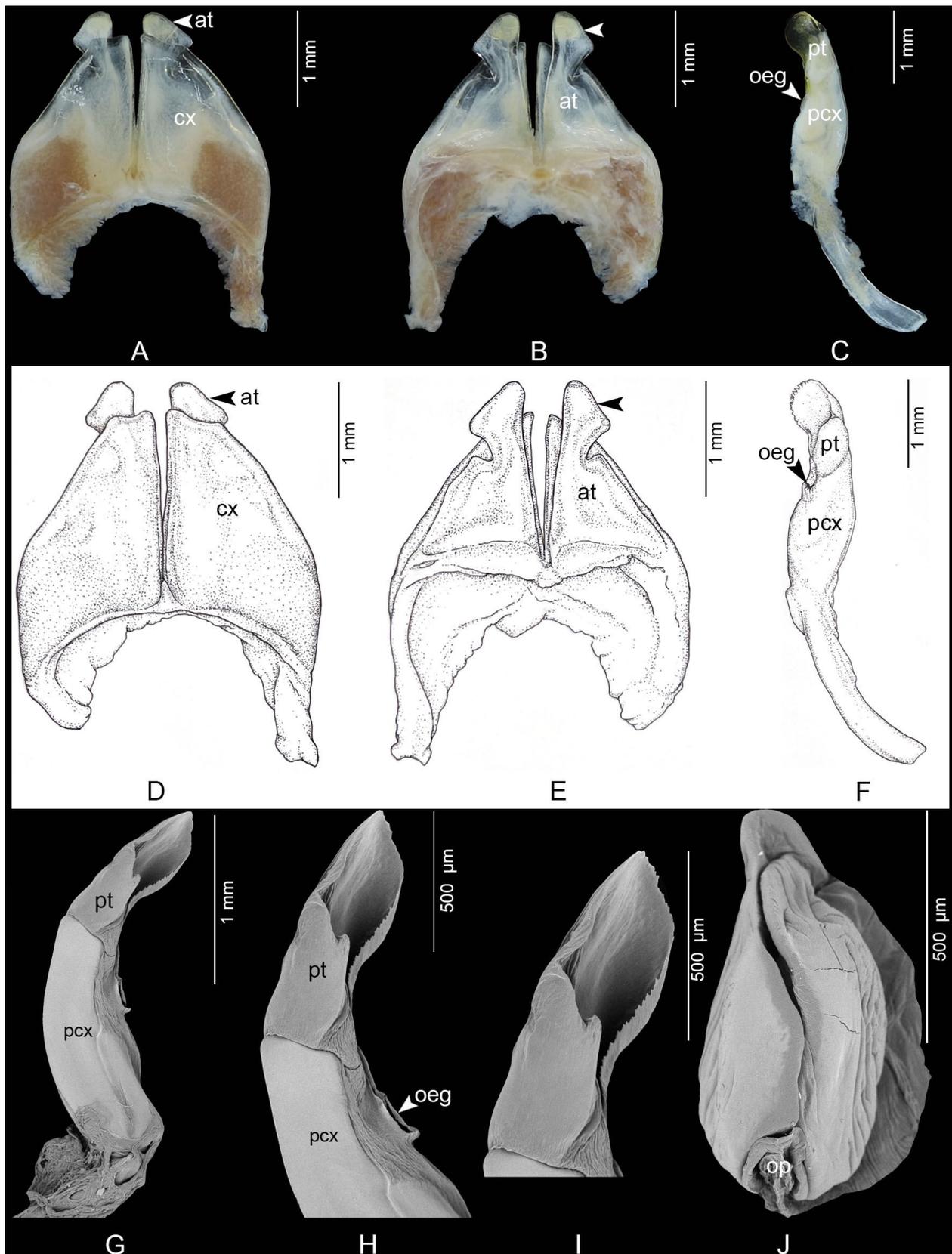


FIGURE 2. *Coxobolellus sirindhornae* sp. nov., holotype, gonopods (CUMZ-D00156) **A, D.** anterior gonopods, anterior view. **B, E.** anterior gonopods, posterior view, unlabelled arrows indicate a pigmented brown node. **C, F.** left posterior gonopod, lateral view. **G.** SEM, right posterior gonopod, posterior-mesal view. **H.** SEM, mesal part of posterior gonopod, posterior-mesal view. **I.** SEM, tip of posterior gonopod, posterior-lateral view. **J.** SEM, left vulva, posterior-mesal view. Abbreviations: at = anterior gonopod telopodite; cx = coxa; oeg = opening of efferent groove; op = operculum of vulva; pcx = coxal part of the posterior gonopod telopodite; pt = telopodital part of the posterior gonopod telopodite.

Taxonomy

Class Diplopoda de Blainville in Gervais, 1844
Order Spirobolida Bollman, 1893
Suborder Spirobolidea Bollman, 1893
Family Pseudospirobolellidae Brölemann, 1913

Genus *Coxobolellus* Pimvichai, Enghoff, Panha & Bäckeljau, 2020

Included species

Coxobolellus albiceps Pimvichai, Enghoff, Panha & Bäckeljau, 2020
Coxobolellus compactogonus Pimvichai, Enghoff, Panha & Bäckeljau, 2020
Coxobolellus fuscus Pimvichai, Enghoff, Panha & Bäckeljau, 2020
Coxobolellus nodosus Pimvichai, Enghoff, Panha & Bäckeljau, 2020
Coxobolellus serratus Pimvichai, Enghoff, Panha & Bäckeljau, 2020
Coxobolellus simplex Pimvichai, Enghoff, Panha & Bäckeljau, 2020
Coxobolellus tenebris Pimvichai, Enghoff, Panha & Bäckeljau, 2020
Coxobolellus tigris Pimvichai, Enghoff, Panha & Bäckeljau, 2020
Coxobolellus transversalis Pimvichai, Enghoff, Panha & Bäckeljau, 2020
Coxobolellus valvatus Pimvichai, Enghoff, Panha & Bäckeljau, 2020
Coxobolellus saratani Pimvichai, Enghoff, Panha & Bäckeljau, 2022
Coxobolellus serratoligulatus Pimvichai, Enghoff, Panha & Bäckeljau, 2022
Coxobolellus sirindhornae sp. nov.

Species description

A new species that shares the four diagnostic synapomorphies of the genus *Coxobolellus*, as described in the general description section in Pimvichai et al. (2020: 599–601) and listed in the introduction of the present contribution.

Coxobolellus sirindhornae sp. nov.

<https://zoobank.org/urn:lsid:zoobank.org:act:301FEC13-DFE4-4B04-9086-3554053E2F12>

(Figs 2–4)

Material examined.– **Holotype** ♂ (CUMZ-D00156), Thailand, Mae Hong Son Province, Pang Mapha District, Wat Pa Tham Wua; 19°31'39" N, 98°05'01" E; 437 m a.s.l.; 2 October 2023; P. Pimvichai and P. Prasankok leg. **Paratypes** 3 ♀♀; same data as holotype (CUMZ-D00156-1).

Etymology.– The species is named in honor of Her Royal Highness Princess Maha Chakri Sirindhorn to commemorate her 70th birthday. This species name recognizes her unwavering support for biodiversity research and conservation efforts in Thailand.

Diagnosis.– Differing from all other species of the genus *Coxobolellus* included in this paper by having the tip of the telopodital part (pt) forming a flattened, round lobe, with serrate mesal margin, without process or ridge protruding from mesal surface (Fig. 2C, F–I).

Description.– Adult male with 49 podous rings. Length ca 4 cm, diameter ca 4.0 mm. Adult females with 46–49 podous rings. Length ca 4–5 cm, diameter ca 3.8–4.1 mm.

Colour. Living animal reddish brown, except for metazona dark brown (Fig. 3).

Anterior gonopods (Fig. 2A, B, D, E) with high coxae, apically obliquely truncated, mesal margins straight, posterior surface with relatively high ridge laterally for accommodation of telopodite. Telopodite (at) projecting slightly over anterior gonopod coxa (cx), subdistally strongly constricted, distally forming a triangular process with pointed tip and a pigmented brown node (Fig. 2B, E, unlabelled arrow).

Posterior gonopods (Fig. 2C, F–I) simple, rounded, with long, smooth coxal part (pcx), with opening of efferent groove (oeg) at mesal margin at the end of coxal part (pcx); telopodital part (pt) basal part with lateral margin folds mesally, distally forming a flattened, rounded lobe, with serrate mesal margin, curving mesad (Fig. 2C, F–I).

Female vulvae (Fig. 2J): valves prominent, of equal size, operculum (op) small, rounded triangular.

DNA barcodes.– The GenBank accession numbers are PV612839 for the holotype (CUMZ-D00156; sequence isolate Wptw1) and PV612840 for the paratype (CUMZ-D00156-1; sequence isolate Wptw2).

Habitat.– Found under leaf litter on a limestone mountain.

Distribution.– Hitherto only known from the type locality in Mae Hong Son, Thailand (Fig. 4).

Key to species of the genus *Coxobolellus* (based on adult males, update of the key of Pimvichai et al. (2022a))

1. Tip of anterior gonopod coxa truncated 2
- Tip of anterior gonopod coxa concave/bilobed or forming a triangular process 6



FIGURE 3. Live *Coxobolellus sirindhornae* sp. nov., holotype, (CUMZ-D00156) from Mae Hong Son Province (Photos by P. Pimvichai).

2. Tip of anterior gonopod coxa transversely truncated; telopodital part (pt) of posterior gonopod long compared to coxal part (pcx) *C. transversalis*
– Tip of anterior gonopod coxa obliquely truncated ... 3
3. Telopodital part (pt) of posterior gonopod short compared to coxal part (pcx) *C. albiceps*
– Telopodital part (pt) of posterior gonopod fairly long compared to coxal part (pcx) 4
4. Telopodital part (pt) directed distad, pointed, with a sharp, pointed, folded process in the middle, with a small transverse ridge near tip, with serrate mesal margin *C. saratani*
– Telopodital part (pt) curving mesad, ending in a rounded lobe 5
5. Telopodital part (pt) forming a canopy, with a broad, flattened, serrate, tongue-like process protruding from mesal surface *C. serratoligulatus*
– Telopodital part (pt) without a process protruding from mesal surface, basal part of pt with lateral margin folds mesally, apically forming a flatten, rounded lobe, with serrate mesal margin, curving mesad (Fig. 2C, F–I) *C. sirindhornae* sp. nov.
6. Tip of anterior gonopod coxa concave/bilobed 7
– Tip of anterior gonopod coxa forming triangular process 8
7. Tip of anterior gonopod coxa bilobed, outer process broadly rounded, inner process triangular, protruding higher than outer process; telopodital part (pt) of posterior gonopod ending in a rounded margin with a sharp spine protruding from mesal surface near tip *C. valvatus*
– Tip of anterior gonopod coxa concave, forming equal outer and inner lobes; telopodital part of posterior gonopod (pt) ending in a long, sharp spine, with a flattened lamella protruding from mesal surface near tip *C. nodosus*
8. Tip of anterior gonopod coxa ending in an abruptly narrowed, pointed, triangular process 9
– Tip of anterior gonopod coxa ending in a simple triangular process 11
9. Tip of anterior gonopod telopodite (at) long, narrow, curving mesad; tip of telopodital part (pt) of posterior gonopod ending in coarsely serrate lamella with a sharp point *C. fuscus*
– Tip of anterior gonopod telopodite (at) forming a triangular process 10
10. Telopodital part (pt) of posterior gonopod with a sharp, curling lamella at base *C. tenebris*
– Telopodital part (pt) of posterior gonopod without a sharp, curling lamella at base *C. simplex*
11. Anterior gonopod telopodite (at) projecting slightly over anterior gonopod coxa (cx), with rounded tip *C. compactogonus*
– Anterior gonopod telopodite (at) far overreaching anterior gonopod coxa (cx), with narrowed tip ... 12
12. Anterior gonopod telopodite (at) directed distad; telopodital part (pt) of posterior gonopod ending in a rounded, serrate margin *C. tigris*
– Anterior gonopod telopodite (at) curving laterad; telopodital part (pt) of posterior gonopod laterally with serrate margin *C. serratus*

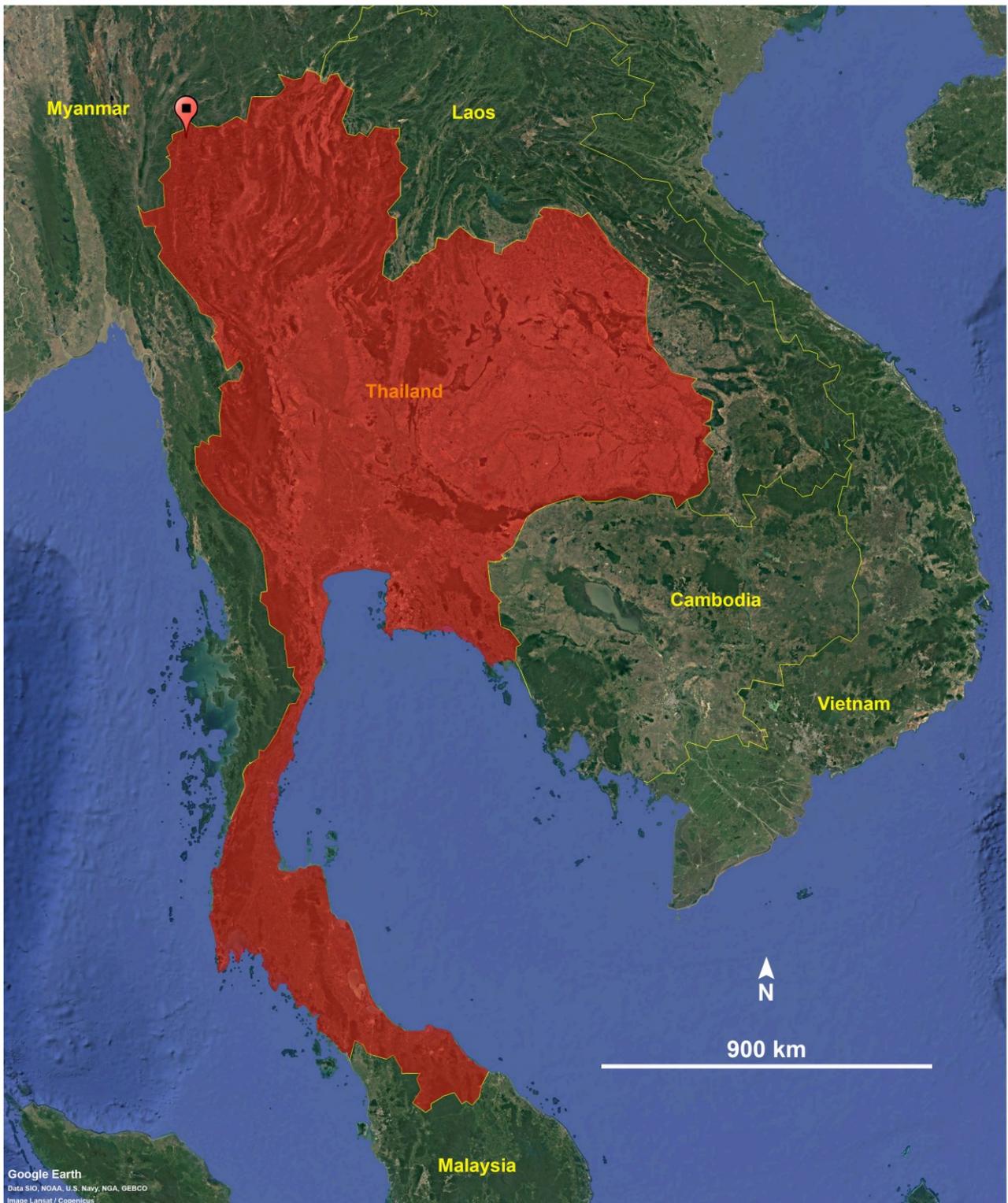


FIGURE 4. Known distribution of the *Coxobolellus* species (Pimvichai et al., 2020, 2022a) (red area) and geographic location of the type locality of *C. sirindhornae* sp. nov. Map generated using Google Earth Pro (Version 7.3.6.9796).

DISCUSSION

The new species described here undoubtedly belongs to the genus *Coxobolellus*, as it shares the diagnostic synapomorphies of this genus as described by Pimvi-

chai et al. (2020). Consistent with these morphological observations, the COI gene tree strongly support the placement of the new species within the well-supported *Coxobolellus* clade.

The mean COI sequence divergence between *C. sirindhornae* sp. nov. and the other *Coxobolellus* species (0.13; range: 0.12–0.15) not only aligns well with the mean interspecific COI sequence divergence in the genus *Coxobolellus* without *C. sirindhornae* sp. nov. (0.12; range: 0.06–0.15), but also with the mean interspecific COI sequence divergences in other genera such as *Silicobolellus* (0.12; range: 0.08–0.15) (Pimvichai et al., 2022b), *Litostrophus* Chamberlin, 1921 (0.11; range: 0.09–0.11) (Pimvichai et al., 2018), and *Atopochetus* Attems, 1953 (0.13; range: 0.09–0.16) (Pimvichai et al., 2018). These mean interspecific COI sequence divergences are in sharp contrast with the substantially lower intraspecific COI sequence divergence within *C. sirindhornae* sp. nov. (0.003) or within other *Coxobolellus* species such as *C. albiceps* (0.02), *C. compactogonus* (0.05), *C. serratoligulatus* (0.01), *C. tenebris* (0.003), *C. tigris* (0.02) or *C. valvatus* (0.03) (see Appendix). The consistency of these mean intra- and interspecific COI sequence divergences, as well as the obvious gap between them, suggest that the COI sequence divergence of *C. sirindhornae* sp. nov. reflects a species-level split. Taken together, the gonopod characteristics, phylogenetic positioning and amount of interspecific COI sequence divergence of *C. sirindhornae* sp. nov. underpin its interpretation under at least the biological, phylogenetic and lineage species concepts.

The inclusion of the new species in the phylogenetic analysis of the Pseudospirobolellidae did not change the observations made in previous studies (Pimvichai et al., 2020, 2022a, 2022b). However, despite their apparently robust character, the pseudospirobolellid phylogenetic data need to be expanded with additional nuclear and mtDNA gene fragments, as well as with new *Benoitolus* material, in order to determine to which family the latter genus belongs and to resolve the sister group relationships between the 3–4 pseudospirobolellid genera.

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APPENDIX

TABLE A1. Estimates of COI sequence divergences within and among *Coxobolellus* species and related taxa expressed as uncorrected p-distances (rounded to two decimals).

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1 <i>Apeuthes fimbriatus</i> BMP																	
2 <i>Apeuthes longeligulatus</i> TPP	0.15																
3 <i>Apeuthes maculatus</i> Am26	0.15	0.13															
4 <i>Apeuthes maculatus</i> Amc	0.14	0.11	0.03														
5 <i>Apeuthes pollex</i> SML	0.15	0.14	0.13	0.11													
6 <i>Apeuthes pollex</i> SMR	0.15	0.14	0.13	0.11	0.06												
7 <i>Apeuthes pollex</i> WTS	0.15	0.15	0.13	0.11	0.04	0.07											
8 <i>Apeuthes spininavis</i> ABB	0.16	0.14	0.14	0.12	0.15	0.14	0.15										
9 <i>Atopochetus anaticeps</i> SVL	0.23	0.20	0.20	0.19	0.18	0.18	0.19	0.19									
10 <i>Atopochetus dollfusii</i> DOL	0.22	0.19	0.21	0.20	0.19	0.19	0.20	0.20	0.11								
11 <i>Atopochetus helix</i> SPT	0.22	0.23	0.22	0.21	0.20	0.21	0.20	0.19	0.14	0.13							
12 <i>Atopochetus mouleimensis</i> TAK	0.23	0.22	0.23	0.22	0.22	0.23	0.23	0.22	0.14	0.12	0.15						
13 <i>Atopochetus setiferus</i> HPT	0.22	0.20	0.20	0.19	0.18	0.18	0.19	0.20	0.08	0.09	0.14	0.13					
14 <i>Atopochetus spinimargo</i> Ton27	0.22	0.22	0.22	0.22	0.21	0.20	0.20	0.22	0.15	0.14	0.14	0.16	0.14				
15 <i>Atopochetus truncatus</i> SML	0.22	0.20	0.21	0.19	0.20	0.19	0.21	0.20	0.13	0.10	0.12	0.14	0.12	0.14			
16 <i>Atopochetus uncinatus</i> KMR	0.21	0.21	0.22	0.20	0.19	0.20	0.20	0.20	0.13	0.14	0.14	0.15	0.13	0.15	0.13		
17 <i>Atopochetus weseneri</i> Tos29	0.21	0.21	0.21	0.20	0.21	0.20	0.22	0.20	0.14	0.12	0.14	0.13	0.12	0.16	0.10	0.13	
18 <i>Aulacobolus uncopygus</i> Auc	0.20	0.17	0.18	0.17	0.16	0.17	0.17	0.18	0.18	0.18	0.20	0.21	0.19	0.22	0.19	0.20	0.22
19 <i>Benoitolus birgatae</i> BBG	0.22	0.23	0.21	0.21	0.22	0.22	0.22	0.22	0.23	0.21	0.21	0.22	0.21	0.22	0.21	0.22	0.24
20 <i>Coxobolellus albiceps</i> Stpl	0.20	0.19	0.19	0.18	0.17	0.17	0.18	0.21	0.20	0.22	0.21	0.24	0.22	0.23	0.21	0.22	0.22
21 <i>Coxobolellus albiceps</i> Stpw	0.20	0.18	0.19	0.18	0.18	0.17	0.18	0.21	0.20	0.22	0.22	0.24	0.22	0.23	0.21	0.21	0.22
22 <i>Coxobolellus albiceps</i> Stvd	0.21	0.18	0.19	0.17	0.17	0.17	0.18	0.20	0.20	0.22	0.21	0.24	0.22	0.23	0.21	0.22	0.23
23 <i>Coxobolellus albiceps</i> TPB	0.20	0.18	0.19	0.18	0.17	0.17	0.18	0.21	0.20	0.22	0.21	0.24	0.22	0.23	0.21	0.22	0.22
24 <i>Coxobolellus compactogonus</i> KLC	0.20	0.17	0.20	0.19	0.17	0.16	0.17	0.19	0.20	0.21	0.23	0.24	0.21	0.22	0.22	0.22	0.22
25 <i>Coxobolellus compactogonus</i> SKR	0.21	0.18	0.21	0.19	0.19	0.18	0.19	0.19	0.21	0.21	0.22	0.24	0.21	0.23	0.21	0.21	0.22
26 <i>Coxobolellus fuscus</i> HKK	0.20	0.19	0.21	0.20	0.17	0.18	0.18	0.20	0.20	0.22	0.22	0.24	0.20	0.23	0.23	0.20	0.23
27 <i>Coxobolellus nodosus</i> SPW	0.22	0.18	0.20	0.20	0.18	0.19	0.19	0.20	0.21	0.20	0.21	0.24	0.21	0.23	0.22	0.22	0.23
28 <i>Coxobolellus serratus</i> KKL	0.20	0.18	0.20	0.18	0.18	0.18	0.18	0.20	0.20	0.21	0.22	0.23	0.20	0.23	0.21	0.22	0.22
29 <i>Coxobolellus simplex</i> TNP	0.20	0.18	0.20	0.19	0.18	0.18	0.18	0.18	0.21	0.21	0.23	0.22	0.23	0.23	0.23	0.23	0.22
30 <i>Coxobolellus tenebris</i> KWP	0.21	0.19	0.20	0.18	0.18	0.18	0.18	0.18	0.21	0.22	0.23	0.25	0.22	0.24	0.23	0.23	0.23
31 <i>Coxobolellus tenebris</i> TPL	0.21	0.19	0.20	0.18	0.18	0.18	0.18	0.18	0.21	0.22	0.23	0.25	0.22	0.24	0.23	0.23	0.23
32 <i>Coxobolellus tigris</i> TKP	0.22	0.20	0.20	0.20	0.20	0.20	0.20	0.21	0.19	0.22	0.22	0.24	0.21	0.24	0.21	0.21	0.21
33 <i>Coxobolellus tigris</i> TYE	0.22	0.19	0.20	0.20	0.20	0.20	0.20	0.21	0.19	0.22	0.22	0.25	0.21	0.24	0.22	0.22	0.22
34 <i>Coxobolellus transversalis</i> Stpg	0.21	0.18	0.19	0.18	0.18	0.18	0.19	0.20	0.20	0.20	0.20	0.23	0.21	0.21	0.20	0.22	0.22
35 <i>Coxobolellus valvatus</i> BRC	0.20	0.17	0.18	0.17	0.16	0.16	0.17	0.19	0.20	0.21	0.20	0.24	0.20	0.23	0.22	0.22	0.22
36 <i>Coxobolellus valvatus</i> TCD	0.21	0.17	0.18	0.17	0.16	0.17	0.17	0.19	0.20	0.20	0.20	0.23	0.20	0.22	0.22	0.22	0.23
37 <i>Coxobolellus valvatus</i> TST	0.19	0.17	0.17	0.17	0.16	0.16	0.17	0.19	0.19	0.20	0.21	0.23	0.20	0.22	0.21	0.22	0.22
38 <i>Coxobolellus saratani</i> PPLL	0.19	0.17	0.18	0.18	0.18	0.18	0.19	0.20	0.22	0.23	0.23	0.24	0.22	0.23	0.24	0.22	0.23
39 <i>Coxobolellus saratani</i> PPLL2	0.20	0.18	0.19	0.18	0.19	0.18	0.19	0.20	0.22	0.24	0.23	0.25	0.22	0.24	0.24	0.23	0.23
40 <i>Coxobolellus serratoligulatus</i> TCU	0.19	0.17	0.17	0.16	0.16	0.16	0.17	0.18	0.20	0.23	0.23	0.25	0.22	0.24	0.23	0.23	0.22
41 <i>Coxobolellus serratoligulatus</i> TCU2	0.19	0.17	0.17	0.16	0.16	0.16	0.16	0.18	0.20	0.22	0.23	0.25	0.21	0.24	0.22	0.23	0.22
42 <i>Coxobolellus sirindhornae</i> sp. nov. Wptw2	0.21	0.19	0.20	0.18	0.18	0.18	0.19	0.20	0.20	0.22	0.23	0.24	0.20	0.23	0.22	0.23	0.22
43 <i>Coxobolellus sirindhornae</i> sp. nov. Wptw1	0.21	0.19	0.20	0.18	0.17	0.18	0.19	0.20	0.21	0.22	0.23	0.24	0.20	0.23	0.23	0.23	0.22
44 <i>Leptogoniulus sorornus</i> BTN	0.16	0.16	0.14	0.13	0.14	0.14	0.15	0.14	0.18	0.18	0.19	0.21	0.19	0.20	0.19	0.22	0.22
45 <i>Litostrophus chamaeleon</i> PPT	0.20	0.20	0.19	0.18	0.18	0.18	0.20	0.19	0.17	0.16	0.15	0.18	0.16	0.18	0.15	0.17	0.17
46 <i>Litostrophus saraburensis</i> PKS	0.20	0.18	0.17	0.16	0.18	0.17	0.18	0.18	0.16	0.15	0.15	0.17	0.15	0.16	0.14	0.16	0.18
47 <i>Litostrophus segregatus</i> Ls19	0.20	0.19	0.20	0.18	0.18	0.18	0.19	0.19	0.13	0.13	0.15	0.16	0.13	0.15	0.14	0.14	0.17
48 <i>Macrurobolus macrurus</i> INT	0.21	0.18	0.18	0.17	0.18	0.18	0.18	0.18	0.16	0.14	0.15	0.17	0.14	0.17	0.15	0.16	0.16
49 <i>Madabolus maximus</i> Mm4	0.20	0.20	0.21	0.20	0.19	0.19	0.20	0.18	0.21	0.20	0.19	0.22	0.22	0.21	0.20	0.20	0.22
50 <i>Narceus annularis</i>	0.20	0.21	0.22	0.21	0.21	0.21	0.21	0.20	0.23	0.20	0.21	0.22	0.21	0.20	0.20	0.21	0.21
51 <i>Parabolus dimorphus</i> Pd34	0.22	0.21	0.21	0.20	0.19	0.19	0.19	0.21	0.18	0.20	0.19	0.22	0.18	0.20	0.21	0.19	0.21
52 <i>Paraspirobolus lucifugus</i>	0.23	0.25	0.23	0.22	0.22	0.22	0.22	0.22	0.23	0.23	0.23	0.23	0.23	0.23	0.23	0.23	0.24
53 <i>Pelmatojulus tigrinus</i> Pt2	0.19	0.18	0.18	0.17	0.18	0.17	0.19	0.18	0.22	0.22	0.20	0.23	0.22	0.23	0.22	0.22	0.22
54 <i>Pelmatojulus togoensis</i> Pto6	0.18	0.19	0.20	0.18	0.18	0.17	0.17	0.20	0.21	0.22	0.22	0.22	0.20	0.20	0.21	0.20	0.21
55 <i>Siliquobolellus amicusdraconis</i> HPT2	0.18	0.19	0.22	0.20	0.18	0.19	0.19	0.21	0.20	0.22	0.23	0.24	0.22	0.23	0.21	0.22	0.22
56 <i>Siliquobolellus prasankokae</i> TPTG	0.22	0.21	0.23	0.21	0.20	0.21	0.21	0.22	0.24	0.24	0.25	0.26	0.25	0.24	0.24	0.24	0.24
57 <i>Siliquobolellus constrictus</i> BYC	0.21	0.18	0.20	0.18	0.18	0.18	0.18	0.19	0.20	0.22	0.22	0.25	0.23	0.23	0.21	0.21	0.23
58 <i>Pseudospirobolellus avernus</i> GPG	0.23	0.21	0.22	0.20	0.19	0.20	0.20	0.19	0.21	0.22	0.22	0.23	0.21	0.23	0.22	0.23	0.23
59 <i>Pseudospirobolellus</i> sp. KCS	0.22	0.22	0.23	0.23	0.22	0.22	0.21	0.22	0.23	0.23	0.21	0.23	0.23	0.23	0.22	0.23	0.23
60 <i>Rhinocricus parvus</i> Rp49	0.23	0.24	0.24	0.23	0.23	0.23	0.22	0.23	0.24	0.21	0.22	0.22	0.24	0.21	0.23	0.22	0.23
61 <i>Trachelomegalus</i> sp. Tr54	0.20	0.20	0.22	0.20	0.19	0.19	0.20	0.19	0.19	0.18	0.17	0.20	0.19	0.18	0.18	0.18	0.18
62 <i>Trigoniulus corallinus</i> Tco15	0.13	0.15	0.12	0.12	0.13	0.13	0.14	0.14	0.18	0.19	0.20	0.23	0.19	0.20	0.20	0.21	0.21
63 <i>Aurostreptus barthelemyae</i> Tib	0.22	0.21	0.22	0.21	0.20	0.20	0.19	0.21	0.22	0.22	0.23	0.24	0.23	0.22	0.24	0.23	0.24
64 <i>Chonecambala crassicauda</i>	0.21	0.23	0.23	0.21	0.22	0.22	0.21	0.22	0.24	0.24	0.24	0.23	0.24	0.23	0.24	0.22	0.24
65 <i>Thyropygus allevatus</i> Bb	0.21	0.21	0.22	0.21	0.20	0.21	0.20	0.21	0.21	0.21	0.22	0.23	0.23	0.23	0.22	0.21	0.24

APPENDIX

TABLE A1. Continued.

Taxa	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
1 <i>Apeuthes fimbriatus</i> BMP																	
2 <i>Apeuthes longeligulatus</i> TPP																	
3 <i>Apeuthes maculatus</i> Am26																	
4 <i>Apeuthes maculatus</i> Amc																	
5 <i>Apeuthes pollex</i> SML																	
6 <i>Apeuthes pollex</i> SMR																	
7 <i>Apeuthes pollex</i> WTS																	
8 <i>Apeuthes spininavis</i> ABB																	
9 <i>Atopochetus anaticeps</i> SVL																	
10 <i>Atopochetus dollfusii</i> DOL																	
11 <i>Atopochetus helix</i> SPT																	
12 <i>Atopochetus moulmeinensis</i> TAK																	
13 <i>Atopochetus setiferus</i> HPT																	
14 <i>Atopochetus spinimargo</i> Ton27																	
15 <i>Atopochetus truncatus</i> SML																	
16 <i>Atopochetus uncinatus</i> KMR																	
17 <i>Atopochetus weseneri</i> Tos29																	
18 <i>Aulacobolus uncopygus</i> Auc																	
19 <i>Benoitolus birgitae</i> BBG	0.22																
20 <i>Coxobolellus albiceps</i> Stpl	0.18	0.22															
21 <i>Coxobolellus albiceps</i> Stpw	0.18	0.22	0.02														
22 <i>Coxobolellus albiceps</i> Stvd	0.18	0.21	0.02	0.02													
23 <i>Coxobolellus albiceps</i> TPB	0.18	0.21	0.02	0.02	0.02												
24 <i>Coxobolellus compactogonus</i> KLC	0.18	0.22	0.12	0.11	0.12	0.12											
25 <i>Coxobolellus compactogonus</i> SKR	0.19	0.23	0.14	0.14	0.14	0.14	0.05										
26 <i>Coxobolellus fuscus</i> HKK	0.19	0.22	0.12	0.12	0.12	0.13	0.11	0.13									
27 <i>Coxobolellus nodosus</i> SPW	0.18	0.21	0.11	0.11	0.10	0.11	0.11	0.13	0.11								
28 <i>Coxobolellus serratus</i> KKL	0.19	0.22	0.12	0.13	0.12	0.13	0.12	0.14	0.12	0.13							
29 <i>Coxobolellus simplex</i> TNP	0.20	0.23	0.13	0.13	0.13	0.13	0.11	0.12	0.12	0.12	0.11						
30 <i>Coxobolellus tenebris</i> KWP	0.19	0.22	0.13	0.13	0.12	0.13	0.09	0.10	0.11	0.12	0.14	0.11					
31 <i>Coxobolellus tenebris</i> TPL	0.19	0.22	0.13	0.13	0.13	0.13	0.09	0.10	0.12	0.12	0.14	0.11	0.00				
32 <i>Coxobolellus tigris</i> TKP	0.21	0.22	0.13	0.13	0.13	0.12	0.14	0.14	0.12	0.14	0.12	0.13	0.15	0.15			
33 <i>Coxobolellus tigris</i> TYE	0.21	0.22	0.13	0.13	0.13	0.12	0.13	0.14	0.12	0.13	0.12	0.13	0.14	0.15	0.02		
34 <i>Coxobolellus transversalis</i> Stpg	0.18	0.20	0.08	0.08	0.08	0.08	0.13	0.15	0.12	0.11	0.12	0.12	0.14	0.14	0.13	0.13	
35 <i>Coxobolellus valvatus</i> BRC	0.17	0.21	0.10	0.10	0.10	0.10	0.11	0.13	0.11	0.07	0.13	0.12	0.12	0.12	0.13	0.13	0.11
36 <i>Coxobolellus valvatus</i> TCD	0.16	0.21	0.11	0.11	0.11	0.11	0.11	0.13	0.11	0.06	0.13	0.11	0.11	0.12	0.13	0.12	0.10
37 <i>Coxobolellus valvatus</i> TST	0.17	0.21	0.11	0.11	0.11	0.11	0.11	0.13	0.12	0.06	0.13	0.11	0.12	0.12	0.13	0.12	0.10
38 <i>Coxobolellus saratani</i> PPLL	0.19	0.21	0.12	0.12	0.12	0.12	0.10	0.13	0.11	0.12	0.11	0.12	0.11	0.12	0.13	0.12	0.12
39 <i>Coxobolellus saratani</i> PPLL2	0.19	0.21	0.12	0.12	0.12	0.12	0.11	0.13	0.11	0.13	0.12	0.13	0.12	0.12	0.13	0.13	0.12
40 <i>Coxobolellus serratoligulatus</i> TCU	0.18	0.21	0.08	0.07	0.08	0.08	0.11	0.13	0.11	0.11	0.11	0.12	0.10	0.11	0.12	0.12	0.10
41 <i>Coxobolellus serratoligulatus</i> TCU2	0.18	0.20	0.07	0.06	0.07	0.07	0.11	0.13	0.11	0.11	0.11	0.12	0.11	0.11	0.12	0.12	0.10
42 <i>Coxobolellus sirindhornae</i> sp. nov. Wptw2	0.19	0.22	0.13	0.13	0.13	0.13	0.13	0.14	0.12	0.13	0.12	0.13	0.13	0.13	0.14	0.14	0.13
43 <i>Coxobolellus sirindhornae</i> sp. nov. Wptw1	0.18	0.22	0.13	0.13	0.13	0.13	0.13	0.15	0.13	0.13	0.12	0.13	0.13	0.13	0.14	0.15	0.13
44 <i>Leptogoniulus sorornus</i> BTN	0.17	0.22	0.20	0.21	0.20	0.20	0.18	0.20	0.20	0.19	0.19	0.18	0.20	0.20	0.20	0.20	0.19
45 <i>Litostrophus chamaeleon</i> PPT	0.19	0.18	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.21	0.21	0.21	0.21	0.20	0.21
46 <i>Litostrophus saraburensis</i> PKS	0.18	0.11	0.19	0.18	0.18	0.18	0.20	0.20	0.19	0.19	0.20	0.20	0.20	0.20	0.20	0.20	0.18
47 <i>Litostrophus segregatus</i> Ls19	0.18	0.17	0.21	0.21	0.20	0.21	0.22	0.21	0.21	0.21	0.20	0.22	0.21	0.21	0.21	0.21	0.20
48 <i>Macrurolus macrurus</i> INT	0.17	0.19	0.21	0.21	0.21	0.21	0.22	0.23	0.22	0.21	0.21	0.20	0.22	0.22	0.23	0.23	0.21
49 <i>Madabolus maximus</i> Mm4	0.18	0.21	0.21	0.20	0.21	0.20	0.22	0.23	0.22	0.21	0.22	0.22	0.24	0.24	0.22	0.22	0.21
50 <i>Narceus annularis</i>	0.20	0.24	0.22	0.22	0.22	0.22	0.23	0.23	0.21	0.23	0.22	0.22	0.23	0.23	0.22	0.22	0.22
51 <i>Parabolus dimorphus</i> Pd34	0.19	0.22	0.18	0.18	0.19	0.18	0.20	0.22	0.19	0.18	0.20	0.20	0.20	0.20	0.17	0.17	0.19
52 <i>Paraspirobolus lucifugus</i>	0.24	0.26	0.24	0.24	0.25	0.24	0.23	0.23	0.23	0.24	0.25	0.25	0.24	0.24	0.25	0.24	0.24
53 <i>Pelmatojulus tigrinus</i> Pt2	0.16	0.23	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.21	0.22	0.22	0.22	0.22	0.20	0.20	0.21
54 <i>Pelmatojulus togoensis</i> Pto6	0.17	0.22	0.19	0.19	0.19	0.19	0.19	0.20	0.19	0.19	0.19	0.21	0.20	0.20	0.20	0.20	0.20
55 <i>Siliquobolellus amicusdraconis</i> HPT2	0.21	0.23	0.18	0.18	0.18	0.18	0.17	0.19	0.18	0.17	0.19	0.18	0.18	0.18	0.18	0.17	0.17
56 <i>Siliquobolellus prasankokae</i> TPTG	0.22	0.24	0.18	0.18	0.18	0.18	0.18	0.20	0.19	0.17	0.20	0.20	0.19	0.19	0.19	0.19	0.18
57 <i>Siliquobolellus constrictus</i> BYC	0.19	0.22	0.15	0.15	0.14	0.14	0.16	0.17	0.16	0.15	0.17	0.15	0.17	0.17	0.17	0.17	0.15
58 <i>Pseudospirobolus avernus</i> GPG	0.20	0.23	0.21	0.20	0.21	0.20	0.21	0.21	0.20	0.21	0.20	0.21	0.21	0.21	0.21	0.20	0.20
59 <i>Pseudospirobolus</i> sp. KCS	0.22	0.23	0.22	0.22	0.22	0.22	0.22	0.22	0.21	0.21	0.22	0.22	0.23	0.23	0.23	0.22	0.22
60 <i>Rhinocricus parvus</i> Rp49	0.22	0.25	0.26	0.25	0.25	0.25	0.24	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.24	0.24	0.25
61 <i>Trachelomegalus</i> sp. Tr54	0.20	0.22	0.21	0.21	0.21	0.21	0.24	0.22	0.24	0.23	0.22	0.22	0.23	0.23	0.23	0.24	0.22
62 <i>Trigoniulus corallinus</i> Tco15	0.17	0.20	0.18	0.18	0.17	0.17	0.17	0.18	0.17	0.18	0.19	0.17	0.17	0.18	0.17	0.17	0.17
63 <i>Anurostreptus barthelemyae</i> Tib	0.20	0.25	0.20	0.19	0.19	0.20	0.20	0.21	0.19	0.19	0.20	0.19	0.20	0.20	0.20	0.19	0.19
64 <i>Chonecambala crassicauda</i>	0.22	0.26	0.23	0.23	0.23	0.23	0.22	0.23	0.22	0.23	0.22	0.22	0.23	0.23	0.22	0.22	0.22
65 <i>Thyropygus allevatus</i> Bb	0.20	0.23	0.20	0.20	0.20	0.20	0.19	0.19	0.20	0.20	0.19	0.19	0.20	0.20	0.19	0.19	0.20

APPENDIX

TABLE A1. Continued.

Taxa	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
1 <i>Apeuthes fimbriatus</i> BMP																	
2 <i>Apeuthes longeligulatus</i> TPP																	
3 <i>Apeuthes maculatus</i> Am26																	
4 <i>Apeuthes maculatus</i> Amc																	
5 <i>Apeuthes pollex</i> SML																	
6 <i>Apeuthes pollex</i> SMR																	
7 <i>Apeuthes pollex</i> WTS																	
8 <i>Apeuthes spininavis</i> ABB																	
9 <i>Atopochetus anaticeps</i> SVL																	
10 <i>Atopochetus dollfusii</i> DOL																	
11 <i>Atopochetus helix</i> SPT																	
12 <i>Atopochetus moulmeinensis</i> TAK																	
13 <i>Atopochetus setiferus</i> HPT																	
14 <i>Atopochetus spinimargo</i> Ton27																	
15 <i>Atopochetus truncatus</i> SML																	
16 <i>Atopochetus uncinatus</i> KMR																	
17 <i>Atopochetus weseneri</i> Tos29																	
18 <i>Aulacobolus uncopygus</i> Auc																	
19 <i>Benoitolus birgitae</i> BBG																	
20 <i>Coxobolellus albiceps</i> Stpl																	
21 <i>Coxobolellus albiceps</i> Stpw																	
22 <i>Coxobolellus albiceps</i> Stvd																	
23 <i>Coxobolellus albiceps</i> TPB																	
24 <i>Coxobolellus compactogonus</i> KLC																	
25 <i>Coxobolellus compactogonus</i> SKR																	
26 <i>Coxobolellus fuscus</i> HKK																	
27 <i>Coxobolellus nodosus</i> SPW																	
28 <i>Coxobolellus serratus</i> KKL																	
29 <i>Coxobolellus simplex</i> TNP																	
30 <i>Coxobolellus tenebris</i> KWP																	
31 <i>Coxobolellus tenebris</i> TPL																	
32 <i>Coxobolellus tigris</i> TKP																	
33 <i>Coxobolellus tigris</i> TYE																	
34 <i>Coxobolellus transversalis</i> Stpg																	
35 <i>Coxobolellus valvatus</i> BRC																	
36 <i>Coxobolellus valvatus</i> TCD	0.03																
37 <i>Coxobolellus valvatus</i> TST	0.02	0.03															
38 <i>Coxobolellus saratani</i> PPLL	0.10	0.11	0.11														
39 <i>Coxobolellus saratani</i> PPLL2	0.11	0.12	0.12	0.01													
40 <i>Coxobolellus serratoligulatus</i> TCU	0.10	0.10	0.10	0.07	0.08												
41 <i>Coxobolellus serratoligulatus</i> TCU2	0.10	0.10	0.10	0.08	0.08	0.01											
42 <i>Coxobolellus sirindhornae</i> sp. nov. Wptw2	0.12	0.12	0.12	0.13	0.13	0.12	0.12										
43 <i>Coxobolellus sirindhornae</i> sp. nov. Wptw1	0.12	0.12	0.12	0.13	0.14	0.12	0.12	0.00									
44 <i>Leptogoniulus sorornus</i> BTN	0.19	0.19	0.18	0.20	0.20	0.19	0.19	0.20	0.20								
45 <i>Litostrophus chamaeleon</i> PPT	0.20	0.21	0.20	0.21	0.21	0.21	0.20	0.22	0.22	0.18							
46 <i>Litostrophus saraburensis</i> PKS	0.19	0.18	0.18	0.19	0.20	0.20	0.19	0.20	0.20	0.18	0.11						
47 <i>Litostrophus segregatus</i> Ls19	0.20	0.20	0.19	0.22	0.22	0.21	0.21	0.20	0.21	0.18	0.11	0.09					
48 <i>Macrurobolus macrurus</i> INT	0.21	0.20	0.21	0.22	0.22	0.22	0.21	0.21	0.21	0.18	0.14	0.11	0.13				
49 <i>Madabolus maximus</i> Mm4	0.20	0.20	0.20	0.22	0.22	0.21	0.21	0.22	0.22	0.20	0.19	0.18	0.20	0.19			
50 <i>Narceus annularis</i>	0.22	0.21	0.21	0.21	0.21	0.23	0.22	0.21	0.21	0.21	0.20	0.20	0.21	0.20	0.20		
51 <i>Parabolus dimorphus</i> Pd34	0.18	0.18	0.18	0.19	0.19	0.19	0.19	0.21	0.21	0.21	0.19	0.18	0.20	0.20	0.17	0.20	
52 <i>Paraspirobolus lucifugus</i>	0.23	0.24	0.24	0.23	0.22	0.25	0.24	0.24	0.24	0.24	0.24	0.24	0.25	0.25	0.24	0.21	0.25
53 <i>Pelmatojulus tigrinus</i> Pt2	0.19	0.19	0.19	0.20	0.20	0.20	0.20	0.21	0.21	0.19	0.20	0.20	0.20	0.18	0.18	0.19	0.19
54 <i>Pelmatojulus togoensis</i> Pto6	0.18	0.18	0.18	0.19	0.19	0.18	0.18	0.19	0.19	0.18	0.18	0.18	0.19	0.21	0.19	0.20	0.18
55 <i>Siliquobolellus amicusdraconis</i> HPT2	0.16	0.17	0.16	0.16	0.17	0.18	0.18	0.19	0.19	0.20	0.20	0.20	0.20	0.21	0.19	0.22	0.20
56 <i>Siliquobolellus prasankokae</i> TPTG	0.17	0.16	0.16	0.18	0.18	0.19	0.18	0.20	0.20	0.20	0.22	0.21	0.21	0.22	0.22	0.24	0.21
57 <i>Siliquobolellus constrictus</i> BYC	0.15	0.15	0.15	0.16	0.16	0.15	0.14	0.17	0.17	0.17	0.21	0.18	0.21	0.19	0.20	0.21	0.18
58 <i>Pseudospirobolellus avernus</i> GPG	0.21	0.21	0.21	0.20	0.21	0.20	0.20	0.20	0.20	0.19	0.23	0.21	0.21	0.21	0.21	0.22	0.23
59 <i>Pseudospirobolellus</i> sp. KCS	0.22	0.22	0.22	0.21	0.22	0.23	0.22	0.21	0.21	0.21	0.23	0.22	0.22	0.23	0.24	0.22	0.21
60 <i>Rhinocricus parvus</i> Rp49	0.24	0.25	0.25	0.24	0.24	0.25	0.25	0.26	0.26	0.22	0.22	0.23	0.23	0.24	0.22	0.20	0.23
61 <i>Trachelomegalus</i> sp. Tr54	0.23	0.23	0.22	0.23	0.23	0.22	0.22	0.23	0.23	0.21	0.18	0.17	0.15	0.19	0.21	0.21	0.21
62 <i>Trigoniulus corallinus</i> Tco15	0.16	0.15	0.15	0.17	0.17	0.16	0.16	0.18	0.18	0.14	0.18	0.16	0.17	0.18	0.18	0.20	0.19
63 <i>Anurostreptus barthelemyae</i> Tlb	0.18	0.18	0.18	0.18	0.19	0.19	0.19	0.21	0.21	0.22	0.21	0.20	0.22	0.23	0.22	0.21	0.21
64 <i>Chonecambala crassicauda</i>	0.21	0.22	0.22	0.20	0.20	0.23	0.23	0.23	0.23	0.21	0.23	0.22	0.24	0.24	0.24	0.23	0.21
65 <i>Thyropygus allevatus</i> Bb	0.19	0.20	0.19	0.18	0.18	0.20	0.19	0.21	0.21	0.20	0.21	0.20	0.22	0.21	0.21	0.20	0.21

APPENDIX

TABLE A1. Continued.

Taxa	52	53	54	55	56	57	58	59	60	61	62	63	64	65
1 <i>Apeuthes fimbriatus</i> BMP														
2 <i>Apeuthes longeligulatus</i> TPP														
3 <i>Apeuthes maculatus</i> Am26														
4 <i>Apeuthes maculatus</i> Amc														
5 <i>Apeuthes pollex</i> SML														
6 <i>Apeuthes pollex</i> SMR														
7 <i>Apeuthes pollex</i> WTS														
8 <i>Apeuthes spininavis</i> ABB														
9 <i>Atopochetus anaticeps</i> SVL														
10 <i>Atopochetus dollfusii</i> DOL														
11 <i>Atopochetus helix</i> SPT														
12 <i>Atopochetus moulemeinensis</i> TAK														
13 <i>Atopochetus setiferus</i> HPT														
14 <i>Atopochetus spinimargo</i> Ton27														
15 <i>Atopochetus truncatus</i> SML														
16 <i>Atopochetus uncinatus</i> KMR														
17 <i>Atopochetus weseneri</i> Tos29														
18 <i>Aulacobolus uncopygus</i> Auc														
19 <i>Benoitolus birgatae</i> BBG														
20 <i>Coxobolellus albiceps</i> Stpl														
21 <i>Coxobolellus albiceps</i> Stpw														
22 <i>Coxobolellus albiceps</i> Stvd														
23 <i>Coxobolellus albiceps</i> TPB														
24 <i>Coxobolellus compactogonus</i> KLC														
25 <i>Coxobolellus compactogonus</i> SKR														
26 <i>Coxobolellus fuscus</i> HKK														
27 <i>Coxobolellus nodosus</i> SPW														
28 <i>Coxobolellus serratus</i> KKL														
29 <i>Coxobolellus simplex</i> TNP														
30 <i>Coxobolellus tenebris</i> KWP														
31 <i>Coxobolellus tenebris</i> TPL														
32 <i>Coxobolellus tigris</i> TKP														
33 <i>Coxobolellus tigris</i> TYE														
34 <i>Coxobolellus transversalis</i> Stpg														
35 <i>Coxobolellus valvatus</i> BRC														
36 <i>Coxobolellus valvatus</i> TCD														
37 <i>Coxobolellus valvatus</i> TST														
38 <i>Coxobolellus saratani</i> PPLL														
39 <i>Coxobolellus saratani</i> PPLL2														
40 <i>Coxobolellus serratoligulatus</i> TCU														
41 <i>Coxobolellus serratoligulatus</i> TCU2														
42 <i>Coxobolellus sirindhornae</i> sp. nov. Wptw2														
43 <i>Coxobolellus sirindhornae</i> sp. nov. Wptw1														
44 <i>Leptogoniulus sorornus</i> BTN														
45 <i>Litostrophus chamaeleon</i> PPT														
46 <i>Litostrophus saraburensis</i> PKS														
47 <i>Litostrophus segregatus</i> Ls19														
48 <i>Macruribolus macrurus</i> INT														
49 <i>Madabolus maximus</i> Mm4														
50 <i>Narceus annularis</i>														
51 <i>Parabolus dimorphus</i> Pd34														
52 <i>Paraspirobolus lucifugus</i>														
53 <i>Pelmatojulus tigrinus</i> Pt2	0.24													
54 <i>Pelmatojulus togoensis</i> Pto6	0.25	0.17												
55 <i>Siliquobolellus amicusdraconis</i> HPT2	0.23	0.21	0.19											
56 <i>Siliquobolellus prasankokae</i> TPTG	0.26	0.22	0.19	0.08										
57 <i>Siliquobolellus constrictus</i> BYC	0.24	0.19	0.19	0.13	0.15									
58 <i>Pseudospirobolus avernus</i> GPG	0.22	0.20	0.21	0.20	0.23	0.20								
59 <i>Pseudospirobolus</i> sp. KCS	0.22	0.22	0.22	0.20	0.22	0.21	0.14							
60 <i>Rhinocricus parvus</i> Rp49	0.22	0.21	0.22	0.25	0.25	0.26	0.22	0.21						
61 <i>Trachelomegalus</i> sp. Tr54	0.24	0.19	0.21	0.24	0.25	0.22	0.22	0.20	0.22					
62 <i>Trigoniulus corallinus</i> Tco15	0.23	0.18	0.17	0.17	0.20	0.17	0.23	0.22	0.23	0.20				
63 <i>Anurostreptus barthelemyae</i> Tib	0.23	0.21	0.20	0.20	0.21	0.20	0.22	0.21	0.23	0.23	0.19			
64 <i>Chonecambala crassicauda</i>	0.23	0.22	0.24	0.23	0.25	0.22	0.23	0.23	0.23	0.22	0.22	0.19		
65 <i>Thyropygus allevatus</i> Bb	0.22	0.23	0.21	0.20	0.21	0.21	0.22	0.22	0.21	0.24	0.20	0.15	0.20	