

Morphological and DNA Sequence Data of Two New Millipede Species of the *Thyropygus induratus* Subgroup (Diplopoda: Spirostreptida: Harpagophoridae)

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ABSTRACT.– The common cylindrical millipede genus *Thyropygus* (family Harpagophoridae) comprises four informal species groups, one of which is the *T. allevatus* group. This group is characterized by two synapomorphic gonopodal characters: (1) gonopods with tibial and femoral spines and (2) the tibial spine is very long and recurved proximad towards the femoral spine. The *T. allevatus* group is further divided into four subgroups: (1) *T. allevatus* subgroup, (2) *T. opinatus* subgroup, (3) *T. induratus* subgroup, and (4) *T. cuisinieri* subgroup. Based on gonopodal characters and COI barcoding, two new species of the *T. induratus* subgroup are described from Loei Province, Thailand, viz. *T. panhai* **sp. nov.** and *T. somsaki* **sp. nov.** The small uncate subterminal lobe (a hook-like process) at the basal part of the palette of the telopodite is the synapomorphy that assigns these two new species to the *T. induratus* subgroup. The two species are morphologically also well-differentiated from each other. In contrast, the COI data neither provide strong support for their placement in the *T. induratus* subgroup, nor provide strong support for their species level differentiation, since their interspecific COI divergence of 7% is at the borderline between the intraspecific divergences in *T. induratus*, *T. uncinatus* and *T. resimus* (5–6%, but with values of up to 12%) and the mean interspecific divergence within the *T. induratus* subgroup (12%; range: 7–15%). Hence, the taxonomic interpretation of *T. panhai* **sp. nov.** and *T. somsaki* **sp. nov.** as separate species within the *T. induratus* subgroup is, for the time being, almost entirely based on morphology.

KEYWORDS: COI, gonopod, Thailand

INTRODUCTION

The common giant cylindrical millipede genus *Thyropygus* Pocock, 1894 currently comprises 65 nominal species of which 44 occur in Thailand (Eng-hoff, 2005; Jeekel, 2006; Pimvichai et al., 2016). Based on telopodite morphology, the shape of the femoral spines, and geographic distribution patterns, Hoffman (1975) divided the genus into four informal species groups, viz. the *T. allevatus* group, the *T. aterrimus* group, the *T. luxuriosus* group and the *T. erythro-pleurus* group. Subsequent taxonomic revisions by Pimvichai et al. (2009a, b, 2011a, b) focused on the *T. allevatus* group and culminated in a phylogenetic mtDNA analysis suggesting that the *T. allevatus* group could be further subdivided into four well-supported monophyletic subgroups (clades) (Pimvichai et al., 2014): (1) the *T. opinatus* subgroup (Pimvichai et al., 2009a; Pimvichai et al., 2016), (2) the *T. induratus* subgroup (Pimvichai et al., 2011a), (3) the *T. cuisinieri* subgroup (Pimvichai et al., 2011b), and (4) the *T. allevatus* subgroup. Besides their DNA-based delineation, these four subgroups are also morphologically well-defined by gonopodal characters (Pimvichai et al., 2014).

The present paper uses gonopod morphology and COI sequence data to describe two new species, viz.

Thyropygus panhai **sp. nov.** and *T. somsaki* **sp. nov.**, of the *T. induratus* subgroup that were discovered during recent fieldwork in northeastern Thailand.

MATERIALS AND METHODS

Live specimens were hand-collected during the rainy season and were partly preserved in 70% ethanol for morphological study and partly placed in a freezer at –20 °C for DNA analysis.

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 Thai government.

Morphology

Gonopods were photographed with a digital camera and drawings were made using a stereomicroscope and photographs. Voucher specimens were deposited in the collections of the Museum of Zoology, Chulalongkorn University, Bangkok, Thailand (CUMZ).

Pimvichai et al. (2011a: 48) defined a number of terms for gonopods of the *T. induratus* subgroup and most of these are used in the following descriptions, viz. (terms in bold are not mentioned by Pimvichai et al. (2011a)):

TABLE 1. Specimens from which the COI gene fragment was sequenced. CUMZ, Museum of Zoology, Chulalongkorn University, Bangkok, Thailand; NHMW, Naturhistorisches Museum, Vienna, Austria. Names of provinces are in capitals. Abbreviations after species names refer to the isolate of each sequence. GenBank accession numbers are indicated for each species.

	Voucher code	Locality
Family Harpagophoridae, subfam. Rhynchoproctinae		
<i>Anurostreptus barthelemyae</i> Demange, 1961 (Tlb)	CUMZ-D00003	Thale-Ban, Khuan-Don, SATUN, Thailand
<i>A. sculptus</i> Demange, 1961 (Pl)	CUMZ-D00004	Phu-Lan-Kha, Nong-Bua-Deang, CHAIYAPHUM, Thailand
<i>Thyropygus allevatus</i> group, <i>allevatus</i> subgroup:		
<i>T. allevatus</i> (Karsch, 1881)		
<i>T. allevatus</i> Bb	CUMZ-D00013	Bang Ban, AYUTTHAYA, Thailand
<i>T. allevatus</i> Bk	CUMZ-D00014	Bang Kruey, NONTABURI, Thailand
<i>T. allevatus</i> group, <i>cuisinieri</i> subgroup		
<i>T. foliaceus</i> (Demange, 1961) (Kj)	CUMZ-D00050	Pha Tam, Khong-Chiam, UBONRATCHATHANI, Thailand
<i>T. jarukchusri</i> Pimvichai, Enghoff & Panha, 2011 (Np)	CUMZ-D00053	Ban Nong-Pue, Chaturaphakphiman, ROI-ET, Thailand
<i>T. allevatus</i> group, <i>induratus</i> subgroup:		
<i>T. induratus</i> Attems, 1936		
<i>T. induratus</i> Ldn	CUMZ-D00022	Kang Lamduan, Nam-Yeun, UBONRATCHATHANI, Thailand
<i>T. induratus</i> Nru	CUMZ-D00023	Nang-Rin waterfall, Non-Sa-Ard, UDONTHANI, Thailand
<i>T. induratus</i> Ps	CUMZ-D00024	Phanomsawai, SURIN, Thailand
<i>T. induratus</i> Pw	CUMZ-D00025	Phu-Wiang, KHON KAEN, Thailand
<i>T. induratus</i> Ssk	CUMZ-D00026	Kantarakuk, SRISAKET, Thailand
<i>T. induratus</i> Tt	CUMZ-D00027	Ban Ta Toom, Muang, MAHASARAKHAM, Thailand
<i>T. laterolobatus</i> Pimvichai, Enghoff & Panha, 2011	CUMZ-D00048	Koh Sa-Med, Muang, RA-YONG, Thailand
<i>T. macrosiamensis</i> Pimvichai, Enghoff & Panha, 2011	CUMZ-D00049	Pha Tam, Khong-Chiam, UBONRATCHATHANI, Thailand
<i>T. panhai</i> sp. nov. (PRL)	CUMZ-D00151	Phu Ruea, Phu Ruea, LOEI, Thailand
<i>T. quietus</i> Attems, 1938	CUMZ-D00029	Con Dao N.P., BA RIA-VUNG TAU, Vietnam
<i>T. resimus</i> Attems, 1938		
<i>T. resimus</i> Kc	CUMZ-D00030	Kang Ched Khaew, Wat Bod, PHITSANULOK, Thailand
<i>T. resimus</i> Ksp	CUMZ-D00032	Kang So-Pa, Nakhonchai, PHITSANULOK, Thailand
<i>T. resimus</i> Ntp	CUMZ-D00033	Poi waterfall, Wang-Thong, PHITSANULOK, Thailand
<i>T. resimus</i> Pk	CUMZ-D00034	Phu Kum-Khao, Sahussakhan, KALASIN, Thailand
<i>T. resimus</i> Pnk	CUMZ-D00035	Phu-No, Ta-Khan-Tho, KALASIN, Thailand
<i>T. resimus</i> Pp	CUMZ-D00036	Sae-Ri-Thai cave, Phu-Pan, SAKONNAKHON, Thailand
<i>T. resimus</i> Wnt	CUMZ-D00037	Wana-Thara resort, Wang-Thong, PHITSANULOK, Thailand
<i>T. siamensis</i> Verhoeff, 1938	CUMZ-D00047	Chulalongkorn University area, Kang-Khoi, SARABURI, Thailand
<i>T. somsaki</i> sp. nov. (PPLT)	CUMZ-D00152	Phu Pha Lom, Muang, LOEI, Thailand
<i>T. uncinatus</i> (Demange, 1961)		
<i>T. uncinatus</i> Kdb	CUMZ-D00038	Khao Kra-Dong, Muang, BURIRUM, Thailand
<i>T. uncinatus</i> Pj	CUMZ-D00039	Parchantakham, PRACHINBURI, Thailand
<i>T. uncinatus</i> Pks	CUMZ-D00040	Phu-Khae, Chalermpraiat, SARABURI, Thailand
<i>T. uncinatus</i> Pn	CUMZ-D00041	Rice field, Ban Nong-Pue, Chaturaphakphiman, ROI-ET, Thailand
<i>T. uncinatus</i> Ps	CUMZ-D00042	Phanomsawai, SURIN, Thailand
<i>T. uncinatus</i> Rcb	CUMZ-D00043	Rajabhat Burirum, BURIRUM, Thailand
<i>T. uncinatus</i> Sc	CUMZ-D00044	Koh Si-Chang, Koh Si-Chang, CHONBURI, Thailand
<i>T. uncinatus</i> Sm	CUMZ-D00045	Srimathani Hotel, Muang, NAKHONRATCHASIMA, Thailand
<i>T. uncinatus</i> Sn	CUMZ-D00046	Surasammanakhan, Muang, NAKHONRATCHASIMA, Thailand

TABLE 1. Continued.

	Voucher code	Locality
<i>T. allevatus</i> group, <i>opinatus</i> subgroup		
<i>T. opinatus</i> (Karsch, 1881) (Arw)	CUMZ-D00054	Aerawan waterfall, Srisawad, KANCHANABURI, Thailand
<i>T. inflexus</i> (Demange, 1989) (Kk)	CUMZ-D00056	Srinakharin Dam, Srisawad, KANCHANABURI, Thailand
<i>T. bearti</i> Pimvichai, Enghoff & Panha, 2009 (Ks)	CUMZ-D00057	Khao Sai, Si Chon, NAKHONSRI THAMMARAT, Thailand
<i>T. bispinus</i> Pimvichai, Enghoff & Panha, 2009 (Tm)	CUMZ-D00058	Thep Muang Thong temple, Lansak, UTHAITHANI, Thailand
<i>T. bispinispatala</i> Pimvichai, Enghoff & Panha, 2009 (Kb)	CUMZ-D00059	Tam Khao Krieb temple, Lang Suan, CHUMPORN, Thailand
<i>T. brachyacanthus</i> Pimvichai, Enghoff & Panha, 2009 (Sk)	CUMZ-D00060	Sathitkhirirom temple, Khiriratnikhom, SURATTHANI, Thailand
<i>T. cimi</i> Pimvichai, Enghoff, Panha & Backeljau, 2016 (Nws1)	CUMZ-D00086	Namwang Srithammasokarach, Lanska, NAKHONSRI THAMMARAT, Thailand
<i>T. cristagalli</i> Pimvichai, Enghoff & Panha, 2009 (Yn)	CUMZ-D00064	Koh Yao Noi, Koh Yao, PHANG-NGA, Thailand
<i>T. culter</i> Pimvichai, Enghoff, Panha & Backeljau, 2016 (Nr)	CUMZ-D00078	Rorn waterfall, Khlong Thom, KRABI, Thailand
<i>T. demangei</i> Pimvichai, Enghoff & Panha, 2009 (Cm)	CUMZ-D00066	Ban Chang Lang, Hat Chao Mai, Si kao, TRANG, Thailand
<i>T. enghoffi</i> (Demange, 1989) (Kl)	CUMZ-D00067	Khao Lak Lam Ru, Takuepa, PHANG-NGA, Thailand
<i>T. forceps</i> Pimvichai, Enghoff, Panha & Backeljau, 2016 (Nws2)	CUMZ-D00073	Namwang Srithammasokarach, Lanska, NAKHONSRI THAMMARAT, Thailand
<i>T. loxia</i> Pimvichai, Enghoff & Panha, 2009 (Ty)	CUMZ-D00065	Tam Yai temple, Tha Cha Na, SURATTHANI, Thailand
<i>T. mesocristatus</i> Pimvichai, Enghoff, Panha & Backeljau, 2016 (Pb2)	CUMZ-D00077	Srikasorn, Rattaphum, SONGKHLA, Thailand
<i>T. navychula</i> Pimvichai, Enghoff, Panha & Backeljau, 2016 (KSR)	CUMZ-D00089	Surin Islands, Khuraburi, PHANG-NGA, Thailand
<i>T. peninsularis</i> Hoffman, 1982 (Wm)	CUMZ-D00011	Wang-Matcha, Kapoe, RANONG, Thailand
<i>T. planispina</i> Pimvichai, Enghoff, Panha & Backeljau, 2016 (Tsk2)	CUMZ-D00088	Tham Sua temple, Muang, KRABI, Thailand
<i>T. quadricuspis</i> Pimvichai, Enghoff & Panha, 2009 (Hy)	CUMZ-D00069	Khao Pina temple, Hui Yod, TRANG, Thailand
<i>T. richardhoffmani</i> Pimvichai, Enghoff & Panha, 2009 (TCH)	CUMZ-D00085	Tham Chang Hai, Hui Yod, TRANG, Thailand
<i>T. sutchariti</i> Pimvichai, Enghoff, Panha & Backeljau, 2016 (KCP)	CUMZ-D00090	Kaeng Krachan, Kaeng Krachan, PHETCHABURI, Thailand
<i>T. undulatus</i> Pimvichai, Enghoff, Panha & Backeljau, 2016 (Pb2)	CUMZ-D00087	Khao Pha Nom Bencha, Muang, KRABI, Thailand
<i>T. ursus</i> Pimvichai, Enghoff, Panha & Backeljau, 2016 (LTK)	NH MW-Inv.7855	Lanta Islands, Koh Lanta, KRABI, Thailand

- Anterior coxal fold (*ac*): The main part of gonopod in anterior view. Confusingly called posterior coxal fold by Demange (1961) and Hoffman (1975).
- Blepharochaete (pl. -ae) (*bp*): The normal form of apical setae, long, slender, stiff, and usually pigmented, somewhat reminiscent of the mammalian eyelash (Hoffman, 1975).
- Femoral spine (*fe*): A usually long, curved spine on the telopodite, originating slightly distal to the point where the telopodite emerges from the coxa.
- Lamellar lobe (*ll*): A small, slightly folded lobe at the basis of the apical part of the telopodite.
- Telopodite lobe (*lo*): A protruding lobe on the telopodite, distal to *fe*.

- Palette (*pa*): The distalmost lobe of the apical part, carrying the row of blepharochaetae.
- Posterior coxal fold (*pc*): The main part of gonopod in posterior view, usually shorter than *ac*.
- Mesal process of posterior coxal fold (*pmp*): The mesal part of the posterior coxal fold.
- Paracoxite (*px*): The basal, lateral part of the posterior coxal fold.
- Shelf (*sh*): The distal surface of the posterior coxal fold.
- Sternum (*st*): A small, usually triangular sclerite between the basal parts of the anterior coxal folds.
- Tibial spine (*ti*): A usually long spine on the telopodite, originating distal to the femoral spine, at the basis of the apical part of the telopodite,

usually curved in the opposite direction of the femoral spine, the two together forming a circle.

- **Small spine on tibial spine (tss):** an additional small spine originating from the middle part of the tibial spine.
- Uncate subterminal lobe on the telopodite (*usl*): a hook-like process at the basal part of the palette (*pa*).
- Apical part: The part of the telopodite distal to the tibial spine.

DNA extraction, amplification and sequencing

Total genomic DNA was extracted from legs of a single specimen (the holotype) of both species using the NucleoSpin Tissue kit following the manufacturer's instructions. PCR amplifications and sequencing of the standard mitochondrial COI DNA barcoding fragment (Hebert et al., 2003) were done as described by Pimvichai et al. (2020). The COI fragment was amplified with the primers LCO-1490 and HCO-2198 (Folmer et al., 1994). The new COI nucleotide sequences have been deposited in GenBank under accession numbers OP549748–OP549749. Sample data and voucher codes are provided in Table 1.

Alignment and phylogenetic analysis

The COI data included 56 specimens, representing 34 nominal species of the genus *Thyropygus* (Table 1). Two species of the subfamily Rhynchoproctinae, viz. *Anurostreptus barthelemyae* Demange, 1961 and *A. sculptus* Demange, 1961 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. Sequence alignment (660 bp) was done with MUSCLE (ver. 3.6, see <http://www.drive5.com/muscle>; Edgar, 2004). 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). MEGA11 (ver. 11.0.10, see <http://www.megasoftware.net>; Tamura et al., 2021) was used to (1) check for stop codons, (2) translate 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](http://www.phylo.org/index.php/tools/raxmlhpc2_tgb.html);

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 the Akaike Information Criterion weights as selection criterion. This yielded TIM1+I+G (–lnL = 7767.9511, gamma shape = 0.9470) as best model.

BI trees were run for 10 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 15002 trees. Support for nodes was assessed by posterior probabilities.

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

RESULTS

DNA data

The uncorrected p-distances between the sequences of *Thyropygus* species for which COI sequences are available ranged from 0.00 to 0.21 (Table A1). The mean interspecific sequence divergence within the *Thyropygus allevatus* group (all subgroups included) was 0.14 ± 0.02 (range: 0.02–0.18). The mean interspecific sequence divergences within subgroups were: 0.12 ± 0.03 (range: 0.02–0.17) for the *T. opinatus* subgroup; 0.12 ± 0.02 (range: 0.07–0.15) for the *T. induratus* subgroup; and 0.11 ± 0.00 for the *T. cuisinieri* subgroup. There are no interspecific divergence data for the *T. allevatus* subgroup as this subgroup comprises only one species (*T. allevatus*). In contrast, mean intraspecific divergences within the *T. induratus* subgroup appeared to be lower, viz. 0.05 ± 0.02 (range: 0.02–0.07) in *T. induratus*, 0.06 ± 0.04 (range: 0.00–0.10) in *T. resimus*, and 0.06 ± 0.03 (range: 0.00–0.12) in *T. uncinatus*. In comparison with these intra- and interspecific divergences the COI sequence divergence between *T. panhai* sp. nov. and *T. somsaki* sp. nov. had the somewhat ambiguous value of 0.07.

The mean interspecific sequence divergences among the two *Anurostreptus* species was 0.15 ± 0.00

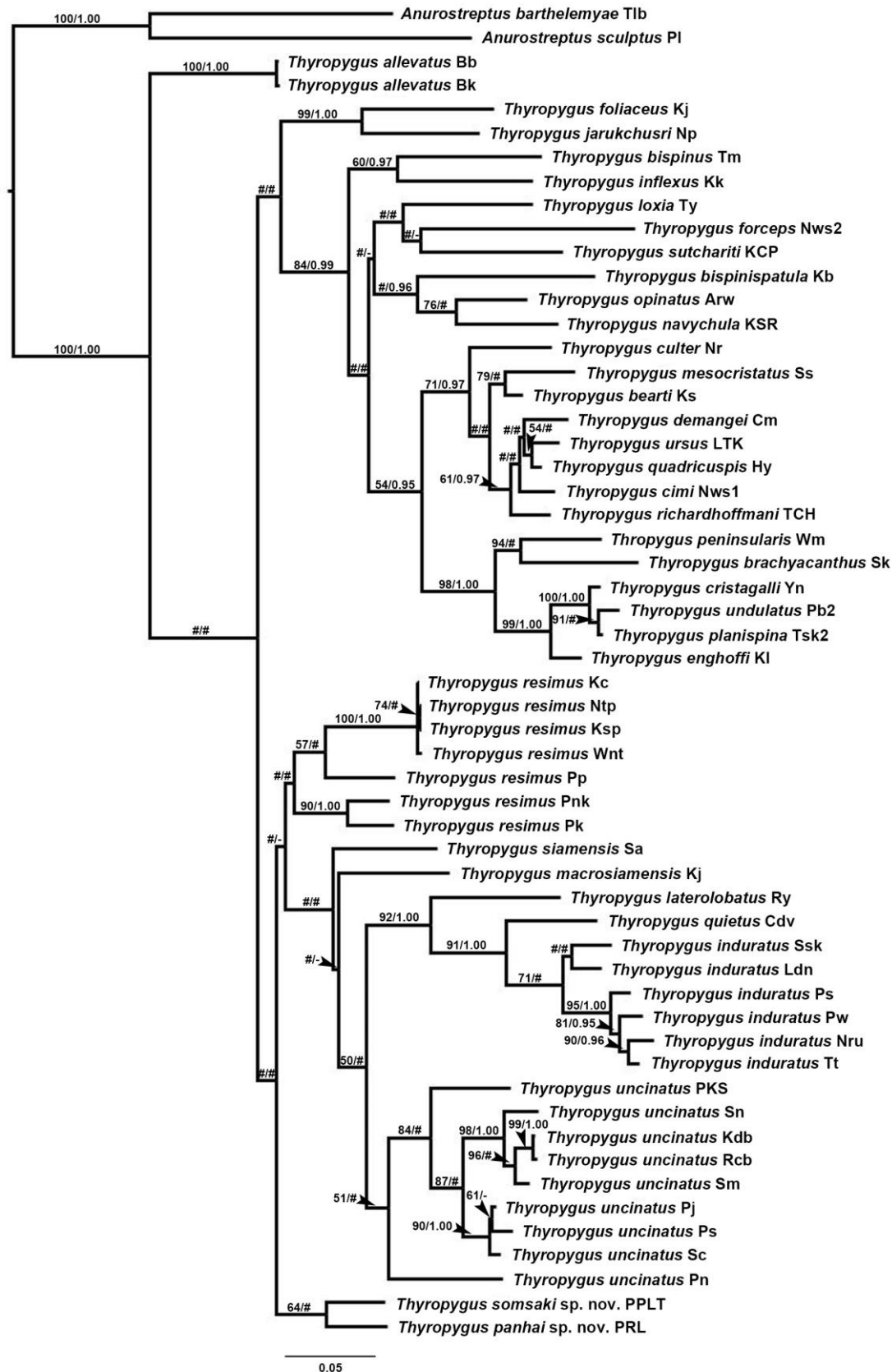


FIGURE 1. Phylogenetic relationships of *Thyropygus* species based on maximum likelihood analysis (ML) and Bayesian inference (BI) of a 660 bp COI gene fragment. Numbers at nodes indicate branch support based on bootstrapping (ML) / posterior probabilities (BI). Scale bar = 0.05 substitutions/site. # indicates branches with < 50% ML bootstrap support or < 0.95 posterior probability, - indicates non-supported branches.

(range: 0.15–0.16). The mean intergeneric sequence divergences between *Thyropygus* and the two *Anurostreptus* species was 0.18 ± 0.01 (range: 0.15–0.21).

The BI and ML COI trees (Fig. 1) placed the two new species as putative sister taxa in the clade of the *T. induratus* subgroup (as sister group to all other species of this subgroup), though with poor BV and PP support both for their sister group relationship and their assignment to the *T. induratus* subgroup. Moreover, the monophyly of this subgroup was not supported by the present analyses, irrespective of whether or not the two new species were included. In contrast, the monophyly of the *T. opinatus* subgroup was well supported (BV = 84, PP = 0.99), as was that of the *T. cuisinieri* subgroup (BV = 99, PP = 1.00, but this involves only two singleton species, viz. *T. foliaceus* (Demange, 1961) and *T. jarukchusri* Pimvichai, Enghoff & Panha, 2011). The *T. allevatus* subgroup only comprises its nominal species. Finally, there was (nearly) no support for the monophyly of each of the species represented by more than one unique sequence in the *T. induratus* subgroup, viz. *T. induratus* Attems, 1936, *T. resimus* Attems, 1938 and *T. uncinatus* (Demange, 1961).

Systematics

Class Diplopoda de Blainville in Gervais, 1844

Order Spirostreptida Brandt, 1833

Suborder Spirostreptidea Brandt, 1833

Family Harpagophoridae Attems, 1909

Genus *Thyropygus* Pocock, 1894

Informal taxon *Thyropygus allevatus* group

Diagnosis.— The *T. allevatus* group is characterized by (1) the gonopod telopodite having both tibial and femoral spines, and (2) tibial spine very long and recurved toward the femoral one (Hoffman, 1975).

Informal taxon *Thyropygus induratus* subgroup

Diagnosis.— A subgroup of the *T. allevatus* group. Differing from the *T. opinatus*, *T. cuisinieri* and *T. allevatus* subgroups by having (1) an uncate subterminal lobe on the telopodite (while the *T. allevatus* subgroup has a flattened process on the telopodite), (2) no additional projection on the anterior coxal fold (present in the *T. opinatus* subgroup), (3) a single femoral spine, (4) no spatulate lobe on the telopodite (present in the *T. opinatus* subgroup), and (5) no slender lamellar lobe on the telopodite (present in the *T. cuisinieri* subgroup). This makes the *T. induratus* subgroup morphologically well-defined.

The two new species share the typical characters of the *T. induratus* subgroup, as described in the general description section in Pimvichai et al. (2011a: 49) except for:

Gonopods: Posterior coxal (*pc*) fold much lower than anterior coxal fold (*ac*) (slightly lower than *ac* in other species); femoral spine (*fe*) relatively long, ca. half-length of tibial spine (*ti*) (much shorter than *ti* in other species); apically with a row of 10–12 brownish blepharochaetae (*bp*) (with a row of 4–8 *bp* in other species).

Included species

Thyropygus induratus Attems, 1936

Thyropygus quietus Attems, 1938

Thyropygus resimus Attems, 1938

Thyropygus siamensis Verhoeff, 1938

Thyropygus uncinatus (Demange, 1961)

Thyropygus dormiens Pimvichai, Enghoff & Panha, 2011

Thyropygus laterolobatus Pimvichai, Enghoff & Panha, 2011

Thyropygus macrosiamensis Pimvichai, Enghoff & Panha, 2011

Thyropygus panhai sp. nov.

Thyropygus somsaki sp. nov.

Species descriptions

Thyropygus panhai sp. nov.

<http://zoobank.org/urn:lsid:zoobank.org:act:7CF67863-9E3C-4722-A9FA-193536223D1F>

(Figs 2, 4, 5)

Material examined.— Holotype male (CUMZ-D00151), THAILAND, Loei Province, Phu Ruea District, Phu Ruea, 671 m a.s.l., 17°27'44"N, 101°21'20"E, 25/09/2021, leg. P. Pimvichai, P. Prasankok and S. Saratan. Paratypes 5 males (CUMZ-D00151-1), same data as holotype.

Etymology.— The species is named after Prof. Dr. Somsak Panha, former mentor of P. Pimvichai and an outstanding biologist who initiated modern millipede research in Thailand, by starting with the study of the genus *Thyropygus* and by establishing many long lasting, productive and highly appreciated international collaborations for which the authors are grateful.

Diagnosis.— A species of the *T. induratus* subgroup in the *T. allevatus* group. Differs from all other species of the *T. induratus* subgroup by having (1) the anterior coxal fold (*ac*) apically ending in a single rounded lobe, distomesally protruding into a pointed, triangular process, forming a canopy and (2) an extremely long

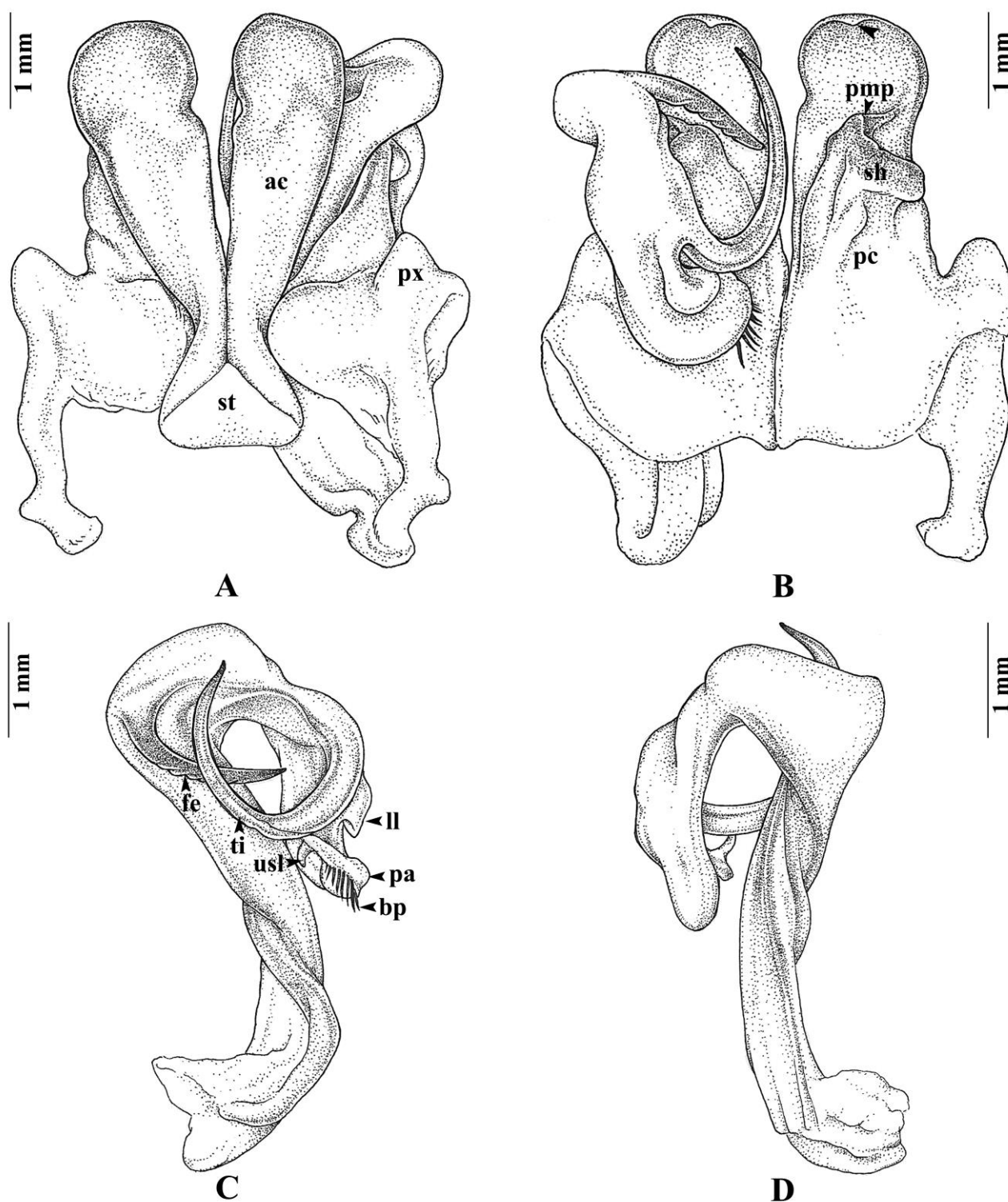


FIGURE 2. *Thyropygus panhai* sp. nov., holotype, gonopods (CUMZ-D00151). **A.** anterior view, left telopodite removed. **B.** posterior view, left telopodite removed. **C.** left telopodite, posterior-mesal view. **D.** left telopodite, anterior-lateral view.

femoral spine (*fe*). The species differs from *T. somsaki* sp. nov. by the overall reddish brown color of the living animal.

Description.— Adult males with 62–64 podous rings, no apodous rings. Length ca. 16–17 cm, width ca. 10.7–12.2 mm. Overall color of living animal (Fig. 4A) reddish brown, legs pinkish brown, epiproct, paraprocts and hypoproct yellowish brown.

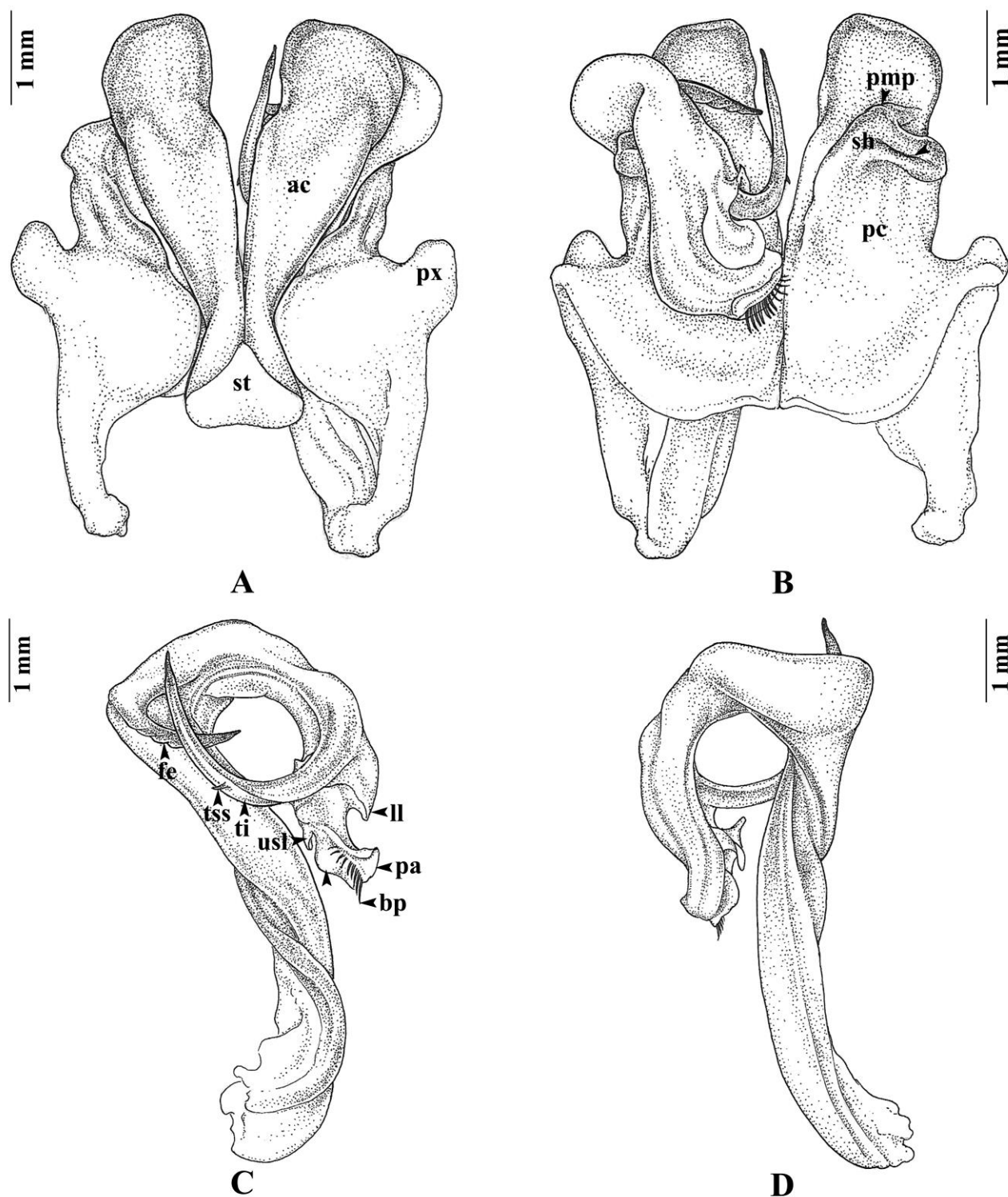


FIGURE 3. *Thyropygus somsaki* sp. nov., holotype, gonopods (CUMZ-D00152). **A.** anterior view, left telopodite removed. **B.** posterior view, left telopodite removed. **C.** left telopodite, posterior-mesal view. **D.** left telopodite, anterior-lateral view.

Gonopods (Figs 2A–D).— Anterior coxal fold (*ac*) (Fig. 2A) basally narrow, gradually widening towards tip, apically ending in a single rounded lobe, distomesally protruding into a pointed, triangular process, forming a canopy (Fig. 2B, unlabeled arrow). Posterior coxal fold (*pc*) (Fig. 2B) basally with moderately high

lateral paracoxites (*px*); mesal process of posterior coxal fold (*pmp*) much lower than *ac*, rounded, forming a shelf (*sh*) for accommodation of telopodite, curved distolaterad. Telopodite (Figs 2C–D) leaving coxite over shelf of posterior coxal fold; femoral spine (*fe*) extremely long, curving in a horizontal plane, very

distinctly crenulated along outer curvature, *in situ* resting against mid of tibial spine; tibial spine (*ti*) very long, slender, curving in an oblique-sagittal plane, *in situ* resting between the two *ac*, its tip close to mesal margin of *ac*; apical part: lamellar lobe (*ll*) broad, rounded, transparent; palette (*pa*) simple, basally with a small uncate subterminal lobe ventrally (*usl*); distally with ca. ten brownish blepharochaetae (*bp*).

DNA barcode.— The GenBank accession number of the COI barcode of the holotype is OP549748 (voucher code CUMZ-D00151).

Ecology.— Crawling around during the rainy season and found under leaf litter.

Distribution.— Known only from the type locality in Loei Province, Thailand (Fig. 5).

***Thyropygus somsaki* sp. nov.**

<http://zoobank.org/urn:lsid:zoobank.org:act:30D7162B-536B-440A-8097-517530694BE1>

(Figs 3, 4, 5)

Material examined.— Holotype male (CUMZ-D00152), THAILAND, Loei Province, Muang District, Phu Pha Lom, 400 m a.s.l., 17°33'16"N, 101°52'03"E, 25/09/2021, leg. P. Pimvichai, P. Prasankok and S. Saratan. Paratypes 1 male (CUMZ-D00152-1), same data as holotype.

Etymology.— The species is named after Prof. Dr. Somsak Panha, former mentor of P. Pimvichai and an outstanding biologist who initiated modern millipede research in Thailand and who continuously provided great support to P. Pimvichai.

Diagnosis.— A species of the *T. induratus* subgroup in the *T. allevatus* group. Differs from all other species of the *T. induratus* subgroup by having (1) the tibial spine (*ti*) with a small, slender, pointed spine (*tss*) mesally, and (2) a swollen lobe at mesal part of the palette (*pa*). The species differs from *T. panhai* sp. nov. by having a yellowish brown prozona that contrasts with the dark brown metazona.

Description.— Adult male with 66–70 podous rings, no apodous rings. Length ca. 20–21 cm, width ca. 10.6–11.4 mm. Overall color of living animal (Fig. 4B) dark brown, legs pinkish brown, metazona dark brown, prozona, epiproct, paraprocts and hypoproct yellowish brown.

Gonopods (Figs 3A–D).— Anterior coxal fold (*ac*) (Fig. 3A) basally narrow, gradually widening towards

tip, in posterior view disolateral margins slightly folded caudad, apically ending in a single rounded lobe, with truncated distomesal margin. Posterior coxal fold (*pc*) (Fig. 3B) basally with high lateral paracoxites (*px*); mesal process of posterior coxal fold (*pmp*) much lower than *ac*, forming a shelf (*sh*) for accommodation of telopodite, shelf basally with a deep horizontal groove (Fig. 3B, unlabeled arrow). Telopodite (Figs 3C–D) leaving coxite over shelf of posterior coxal fold; femoral spine (*fe*) very long (shorter than in *T. panhai* sp. nov. but longer than in all other species in the *T. induratus* subgroup), curving in a horizontal plane, very distinctly crenulated along outer curvature, *in situ* resting near the tip of tibial spine; tibial spine (*ti*) very long, slender, with a small, slender, pointed spine mesally (*tss*), curving in an oblique-sagittal plane, *in situ* resting between the two *ac*; apical part: lamellar lobe (*ll*) broad, rounded, transparent; palette (*pa*) simple, basally with a small uncate subterminal lobe ventrally (*usl*); mesally with a swollen lobe ventrally; distally with ca. twelve brownish blepharochaetae (*bp*).

DNA barcode.— The GenBank accession number of the COI barcode of the holotype is OP549749 (voucher code CUMZ-D00152).

Ecology.— Crawling around during the rainy season and found on a log.

Distribution.— Known only from the type locality in Loei Province, Thailand (Fig. 5).

Key to species of the *T. induratus* subgroup (based on adult males; update of the key of Pimvichai et al., 2011a)

- 1 Mesal process of posterior coxal fold (*pmp*) much lower than anterior coxal fold (*ac*).....2
 - Mesal process of posterior coxal fold (*pmp*) extremely high or slightly lower than anterior coxal fold (*ac*).....3
- 2 Anterior coxal fold (*ac*) ending in a simple, rounded lobe, with a pointed, triangular process distomesally, forming a canopy (Fig. 2B, arrow); mesal process of posterior coxal fold (*pmp*) rounded; femoral spine (*fe*) extremely long; tibial spine (*ti*) without a small spine mesally.....
 -*Thyropygus panhai* sp. nov.
 - Anterior coxal fold (*ac*) with truncated distomesal margins, with slightly folded caudad disolateral margins; mesal process of posterior coxal fold (*pmp*) basally with a deep groove mesally (Fig. 3B, arrow); femoral spine (*fe*) shorter; tibial spine (*ti*) with a small, slender, pointed spine mesally (*tss*)



FIGURE 4. Live *Thyropygus* species from Thailand. A: *Thyropygus panhai* sp. nov. (from Phu Ruea), male (paratype, CUMZ-D00151-1). B: *Thyropygus somsaki* sp. nov. (from Phu Pha Lom), male (holotype, CUMZ-D00152).

- (Fig. 3C); palette (*pa*) with a swollen lobe mesally*Thyropygus somsaki* sp. nov.
- 3 Anterior coxal fold (*ac*) distally with one process (Pimvichai et al., 2011a: figs 3a, 4a, 7a, 8a).....4
- Anterior coxal fold (*ac*) distally with two distinct processes (Pimvichai et al., 2011a: figs 1a, 2a, 5a, 6a).....7
- 4 Anterior coxal fold (*ac*) apically bent abruptly mesad, with an acute narrowed, slender tip (Pimvichai et al., 2011a: fig. 3a).....*Thyropygus resimus* Attems, 1938
- Anterior coxal fold terminating in a relatively broad, rounded process.....5
- 5 Telopodite distally to femoral spine (*fe*) with a relatively large, broad, rounded lobe (*lo*); *ac* distola

- terally rounded, distomesally produced in distad rounded lobe (Pimvichai et al., 2011a: figs 7a, c)....
.....*Thyropygus laterolobatus* Pimvichai et al., 2011
- Telopodite distally to *fe* without a relatively large, broad, round lobe (*lo*).....6
- 6 Femoral spine (*fe*) relatively long, originating from mesal part of the telopodite ‘knee’, curving rearwards and closely appressed to telopodite shaft; tip of *ac* a broadly rounded lobe pointing distomesad (Pimvichai et al., 2011a: fig. 4c).....
.....*Thyropygus siamensis* Verhoeff, 1938
- Femoral spine (*fe*) short, slender, curving almost in a horizontal plane, at right angles to the telopodite shaft; distal, disto-mesad lobe of *ac* relatively narrow (Pimvichai et al., 2011a: fig. 8c).....
.....*Thyropygus macrosiamensis* Pimvichai et al., 2011
- 7 Telopodite distally to *fe* with a relatively large, broad, round lobe (*lo*); anterior coxal fold (*ac*) rounded distolaterally, mesally produced into distad, pointed process with a smaller accessory process on its lateral side (Pimvichai et al., 2011a: fig. 6a, c).....
.....*Thyropygus dormiens* Pimvichai et al., 2011
- Telopodite distally to *fe* without a large, broad, round lobe (*lo*).....8
- 8 Anterior coxal fold (*ac*) distally with two acuminate processes, the outer shorter and smaller than the inner one; femoral spine (*fe*) relatively long, very distinctly crenulated along outer curvature (in Pimvichai et al., 2011a: figs 5a–c, e).....
.....*Thyropygus uncinatus* (Demange, 1961)
- Anterior coxal fold (*ac*) distally with two processes, the outer forming a slender, sharp spine, curving mesad, the inner broadly rounded, flattened, transparent, flexible; *ac* laterally very thick in posterior view.....9
- 9 Paracoxites (*px*) extremely high; male body diameter 10.2–14.3 mm (Pimvichai et al., 2011a: fig. 1a).....
.....*Thyropygus induratus* Attems, 1936
- Paracoxites (*px*) high (but not extremely high); male body diameter 5.6–6.5 mm (Pimvichai et al., 2011a: fig. 2a).....*Thyropygus quietus* Attems, 1938

DISCUSSION

The two new species are morphologically best placed in the *T. induratus* subgroup because they share the uncate subterminal lobe on the ventral part of telopodite palette (*pa*), which is the primary synapomorphy defining this subgroup. Moreover, the two new species also comply well with the four other synapomorphies of the subgroup: (1) no additional projection

on the anterior coxal fold, (2) with a single femoral spine, (3) no spatulate lobe on the telopodite, and (4) no slender lamellar lobe on the telopodite.

In contrast to the convincing morphological assignment of *T. panhai* sp. nov. and *T. somsaki* sp. nov. to the *T. induratus* subgroup, the COI data are far less decisive on this issue and on the putative sister group relationship of the two new species. These two observations are in line with the overall lack of support for the monophyly of the *T. induratus* subgroup and the lack of support for the species level monophyly of *T. induratus*, *T. resimus* and *T. uncinatus*. While this lack of support for species level monophyly was already reported by Pimvichai et al. (2014), the lack of support for the *T. induratus* subgroup is here reported for the first time. It is expected that increased taxon and DNA sampling will be needed to resolve all these issues. In await of such data, the two new species are provisionally kept in the *T. induratus* subgroup, which for the time being is considered as a morphology-based informal taxon with 10 nominal species.

The interspecific COI divergence of 7% between *T. panhai* sp. nov. and *T. somsaki* sp. nov. is at the borderline between the mean intraspecific divergences within the *T. induratus*, *T. resimus* and *T. uncinatus* (5–6%, with values up to 12%), and the mean interspecific divergence in the *T. induratus* subgroup (12%; range 7–15%). However, the two new species showed consistent and convincing differences in three gonopodal characters, viz. (1) the tip of anterior coxal fold (*ac*), (2) the length of the femoral spine (*fe*), and (3) the small spine on the tibial spine (*tss*). Moreover, *T. somsaki* sp. nov. is substantially longer and more slender, than *T. panhai* sp. nov. Therefore, these two taxa are regarded as separate species. As such, this study illustrates that morphological characters still have their value, both in assessing putative phylogenetic relationships and in deciding about species level differentiation.

The recent discovery of two further giant species of *Thyropygus*, a genus which has been subject of rather intense studies for more than a decade, underlines the immense richness of the Thai millipede fauna. It is expected that further new *Thyropygus* species still remain to be discovered in Thailand, and that the study of these, as well as the inclusion of more genes in the DNA dataset, will lead to a better understanding of the evolution of these remarkable millipedes.

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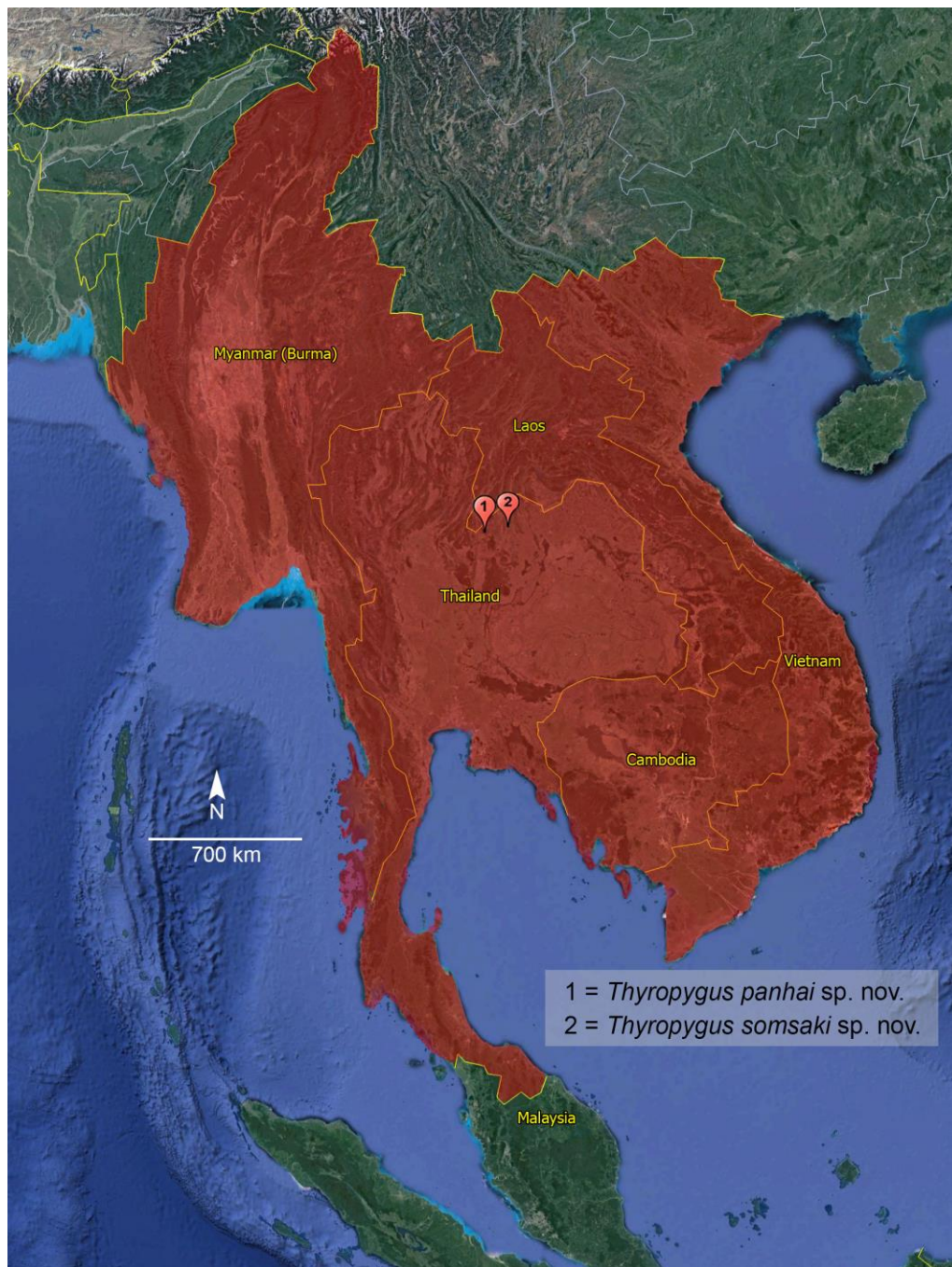


FIGURE 5. Known distribution of the *Thyropygus induratus* subgroup (Pimvichai et al., 2011a) on country level (brown area) and geographic location of the type localities of *T. panhai* sp. nov. and *T. somsaki* sp. nov.

Technology) and Sathit Saratan (Sirindhorn Museum) are greatly acknowledged for their assistance in collecting material. We are indebted to Thita Krutchuen (College of Fine Arts, Bunditpatanasilpa Institute) for the excellent drawings.

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APPENDIX

TABLE A1. Estimates of COI sequence divergences within and among all *Thyropygus* species for which COI sequences are available and the outgroup taxa, expressed as uncorrected p-distances (rounded off to two decimals).

No.	Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	<i>Anurostreptus barthelemyae</i> Tlb																				
2	<i>Anurostreptus sculptus</i> Pl	0.15																			
3	<i>Thyropygus allevatus</i> Bb	0.15	0.17																		
4	<i>Thyropygus allevatus</i> Bk	0.16	0.17	0.00																	
5	<i>Thyropygus bearti</i> Ks	0.19	0.20	0.16	0.17																
6	<i>Thyropygus bispinispatula</i> Kb	0.19	0.19	0.15	0.15	0.13															
7	<i>Thyropygus bispinus</i> Tm	0.18	0.17	0.16	0.16	0.14	0.14														
8	<i>Thyropygus brachyacanthus</i> Sk	0.20	0.19	0.17	0.17	0.12	0.14	0.16													
9	<i>Thyropygus cimi</i> Nws1	0.20	0.19	0.17	0.18	0.05	0.14	0.13	0.13												
10	<i>Thyropygus cristagalli</i> Yn	0.18	0.20	0.14	0.14	0.13	0.14	0.17	0.10	0.13											
11	<i>Thyropygus culter</i> Nr	0.18	0.20	0.16	0.16	0.07	0.13	0.13	0.12	0.08	0.13										
12	<i>Thyropygus demangei</i> Cm	0.20	0.21	0.17	0.17	0.06	0.13	0.13	0.13	0.05	0.13	0.08									
13	<i>Thyropygus enghoffi</i> Kl	0.17	0.18	0.13	0.13	0.11	0.13	0.14	0.10	0.12	0.05	0.12	0.13								
14	<i>Thyropygus foliaceus</i> Kj	0.20	0.18	0.15	0.15	0.14	0.15	0.15	0.17	0.14	0.17	0.15	0.14	0.15							
15	<i>Thyropygus forceps</i> Nws2	0.19	0.19	0.17	0.17	0.13	0.13	0.13	0.16	0.12	0.15	0.13	0.13	0.14	0.16						
16	<i>Thyropygus induratus</i> Ldn	0.16	0.19	0.13	0.14	0.14	0.14	0.15	0.16	0.13	0.16	0.13	0.14	0.15	0.16	0.16					
17	<i>Thyropygus induratus</i> Nru	0.17	0.20	0.14	0.15	0.15	0.15	0.16	0.17	0.14	0.18	0.13	0.14	0.16	0.17	0.16	0.06				
18	<i>Thyropygus induratus</i> Ps	0.17	0.20	0.14	0.14	0.14	0.14	0.16	0.16	0.14	0.17	0.13	0.14	0.15	0.17	0.16	0.06	0.04			
19	<i>Thyropygus induratus</i> Pw	0.17	0.20	0.14	0.14	0.15	0.15	0.16	0.17	0.14	0.18	0.14	0.15	0.15	0.17	0.16	0.06	0.03	0.03		
20	<i>Thyropygus induratus</i> Ssk	0.17	0.19	0.13	0.14	0.14	0.13	0.15	0.15	0.14	0.15	0.13	0.14	0.13	0.16	0.15	0.04	0.07	0.06	0.07	
21	<i>Thyropygus induratus</i> Tt	0.17	0.19	0.14	0.14	0.15	0.14	0.16	0.16	0.14	0.17	0.13	0.14	0.15	0.17	0.16	0.06	0.02	0.03	0.03	0.06
22	<i>Thyropygus inflexus</i> Kk	0.18	0.17	0.16	0.16	0.13	0.13	0.12	0.14	0.14	0.16	0.12	0.13	0.15	0.15	0.13	0.15	0.16	0.15	0.16	0.15
23	<i>Thyropygus jarukchusi</i> Np	0.19	0.18	0.14	0.14	0.15	0.15	0.15	0.16	0.15	0.16	0.15	0.15	0.13	0.11	0.16	0.14	0.14	0.14	0.14	0.13
24	<i>Thyropygus laterolobatus</i> Ry	0.18	0.18	0.15	0.15	0.15	0.15	0.14	0.17	0.14	0.17	0.13	0.15	0.14	0.15	0.16	0.11	0.12	0.12	0.13	0.12
25	<i>Thyropygus loxia</i> Ty	0.18	0.17	0.15	0.15	0.11	0.12	0.11	0.15	0.11	0.14	0.12	0.11	0.12	0.15	0.14	0.15	0.15	0.15	0.16	0.15
26	<i>Thyropygus macrosiamensis</i> Kj	0.17	0.18	0.14	0.14	0.13	0.14	0.13	0.14	0.12	0.15	0.13	0.12	0.13	0.14	0.15	0.12	0.13	0.12	0.13	0.12
27	<i>Thyropygus mesocristatus</i> Ss	0.18	0.19	0.17	0.17	0.05	0.13	0.14	0.13	0.07	0.13	0.08	0.08	0.12	0.15	0.13	0.14	0.15	0.14	0.15	0.14
28	<i>Thyropygus navychula</i> KSR	0.20	0.17	0.16	0.16	0.12	0.13	0.13	0.13	0.12	0.14	0.12	0.11	0.13	0.14	0.14	0.16	0.16	0.16	0.17	0.16
29	<i>Thyropygus opinatus</i> Arw	0.18	0.18	0.15	0.15	0.11	0.12	0.14	0.13	0.12	0.12	0.12	0.12	0.11	0.15	0.13	0.14	0.15	0.15	0.16	0.14
30	<i>Thyropygus panhai</i> sp. nov. PRL2	0.18	0.18	0.14	0.14	0.15	0.15	0.14	0.16	0.15	0.17	0.15	0.15	0.16	0.13	0.16	0.13	0.14	0.14	0.14	0.14
31	<i>Thyropygus peninsularis</i> Wm	0.20	0.20	0.16	0.16	0.12	0.16	0.15	0.10	0.11	0.10	0.11	0.12	0.09	0.16	0.15	0.15	0.16	0.15	0.16	0.15
32	<i>Thyropygus planispinus</i> Tsk2	0.18	0.19	0.14	0.15	0.13	0.14	0.16	0.10	0.13	0.02	0.13	0.13	0.05	0.17	0.16	0.16	0.18	0.17	0.18	0.15
33	<i>Thyropygus quadricuspis</i> Hy	0.20	0.19	0.17	0.17	0.05	0.13	0.13	0.12	0.03	0.13	0.07	0.03	0.12	0.14	0.12	0.14	0.14	0.14	0.15	0.14
34	<i>Thyropygus quietus</i> Cdv	0.17	0.20	0.15	0.15	0.14	0.15	0.14	0.15	0.14	0.15	0.14	0.14	0.15	0.16	0.16	0.09	0.09	0.09	0.10	0.09
35	<i>Thyropygus resimus</i> Kc	0.18	0.17	0.15	0.15	0.14	0.13	0.13	0.16	0.13	0.16	0.13	0.13	0.14	0.13	0.14	0.12	0.12	0.12	0.13	0.12
36	<i>Thyropygus resimus</i> Ksp	0.19	0.17	0.15	0.15	0.14	0.14	0.13	0.16	0.13	0.16	0.13	0.13	0.14	0.13	0.14	0.12	0.12	0.12	0.13	0.12
37	<i>Thyropygus resimus</i> Ntp	0.19	0.17	0.15	0.15	0.14	0.14	0.13	0.16	0.13	0.16	0.13	0.13	0.14	0.13	0.14	0.12	0.12	0.12	0.13	0.12
38	<i>Thyropygus resimus</i> Pk	0.18	0.17	0.14	0.14	0.14	0.14	0.12	0.15	0.14	0.16	0.14	0.13	0.14	0.14	0.15	0.12	0.14	0.14	0.14	0.12
39	<i>Thyropygus resimus</i> Pnk	0.17	0.17	0.13	0.13	0.12	0.13	0.12	0.15	0.12	0.16	0.14	0.12	0.14	0.12	0.14	0.12	0.14	0.14	0.13	0.12
40	<i>Thyropygus resimus</i> Pp	0.18	0.17	0.13	0.14	0.15	0.13	0.12	0.14	0.15	0.14	0.13	0.15	0.13	0.14	0.13	0.12	0.14	0.13	0.14	0.12
41	<i>Thyropygus resimus</i> Wnt	0.18	0.17	0.15	0.15	0.14	0.13	0.13	0.16	0.13	0.16	0.13	0.14	0.14	0.14	0.14	0.12	0.12	0.12	0.12	0.12
42	<i>Thyropygus richardhoffmani</i> TCH	0.20	0.19	0.16	0.16	0.05	0.14	0.13	0.13	0.05	0.14	0.08	0.05	0.12	0.14	0.13	0.14	0.14	0.14	0.15	0.14
43	<i>Thyropygus siamensis</i> Sa	0.18	0.17	0.13	0.13	0.14	0.14	0.13	0.15	0.15	0.14	0.14	0.15	0.13	0.14	0.15	0.12	0.13	0.13	0.13	0.13
44	<i>Thyropygus somsaki</i> sp. nov. PPLT	0.17	0.17	0.11	0.11	0.16	0.14	0.13	0.16	0.16	0.17	0.16	0.16	0.15	0.14	0.16	0.13	0.13	0.13	0.13	0.13
45	<i>Thyropygus sutchariti</i> KCP	0.19	0.18	0.15	0.15	0.14	0.14	0.12	0.15	0.13	0.15	0.13	0.13	0.13	0.16	0.13	0.16	0.17	0.17	0.17	0.15
46	<i>Thyropygus uncinatus</i> Kdb	0.17	0.16	0.13	0.13	0.14	0.14	0.14	0.16	0.15	0.17	0.15	0.16	0.14	0.15	0.17	0.12	0.14	0.13	0.13	0.12
47	<i>Thyropygus uncinatus</i> Pj	0.17	0.17	0.14	0.14	0.13	0.13	0.13	0.15	0.14	0.15	0.13	0.14	0.12	0.14	0.15	0.13	0.13	0.13	0.13	0.13
48	<i>Thyropygus uncinatus</i> Pks	0.17	0.18	0.14	0.15	0.14	0.15	0.15	0.16	0.14	0.16	0.14	0.14	0.14	0.15	0.15	0.14	0.14	0.13	0.14	0.14
49	<i>Thyropygus uncinatus</i> Pn	0.17	0.18	0.14	0.14	0.13	0.14	0.15	0.15	0.13	0.15	0.14	0.13	0.13	0.14	0.15	0.12	0.13	0.13	0.14	0.12
50	<i>Thyropygus uncinatus</i> Ps	0.17	0.18	0.14	0.15	0.14	0.14	0.13	0.16	0.14	0.16	0.14	0.14	0.13	0.14	0.16	0.13	0.14	0.13	0.14	0.13
51	<i>Thyropygus uncinatus</i> Rcb	0.16	0.16	0.13	0.13	0.14	0.13	0.14	0.16	0.15	0.16	0.15	0.15	0.14	0.15	0.16	0.12	0.13	0.13	0.13	0.12
52	<i>Thyropygus uncinatus</i> Sc	0.17	0.17	0.14	0.14	0.14	0.14	0.13	0.15	0.14	0.15	0.13	0.14	0.12	0.14	0.15	0.13	0.13	0.13	0.13	0.13
53	<i>Thyropygus uncinatus</i> Sm	0.17	0.17	0.13	0.13	0.15	0.13	0.13	0.16	0.15	0.15	0.15	0.15	0.13	0.16	0.16	0.11	0.13	0.12	0.12	0.12
54	<i>Thyropygus uncinatus</i> Sn	0.17	0.18	0.13	0.13	0.15	0.14	0.13	0.16	0.16	0.15	0.14	0.15	0.13	0.16	0.16	0.13	0.14	0.13	0.13	0.13
55	<i>Thyropygus undulatus</i> Pb2	0.18	0.20	0.15	0.15	0.12	0.15	0.17	0.11	0.13	0.03	0.13	0.13	0.05	0.17	0.17	0.16	0.17	0.17	0.17	0.15
56	<i>Thyropygus ursus</i> LTK	0.20	0.19	0.16	0.16	0.05	0.13	0.13	0.11	0.05	0.12	0.08	0.04	0.11	0.15	0.13	0.13	0.14	0.13	0.15	0.14

APPENDIX

TABLE A1. Continued.

No.	Taxa	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
1	<i>Anurostreptus barthelemyae</i> Tlb																				
2	<i>Anurostreptus sculptus</i> Pl																				
3	<i>Thyropygus allevatus</i> Bb																				
4	<i>Thyropygus allevatus</i> Bk																				
5	<i>Thyropygus bearti</i> Ks																				
6	<i>Thyropygus bispinispatula</i> Kb																				
7	<i>Thyropygus bispinus</i> Tm																				
8	<i>Thyropygus brachyacanthus</i> Sk																				
9	<i>Thyropygus cimi</i> Nws1																				
10	<i>Thyropygus cristagalli</i> Yn																				
11	<i>Thyropygus culter</i> Nr																				
12	<i>Thyropygus demangei</i> Cm																				
13	<i>Thyropygus engghoffi</i> Kl																				
14	<i>Thyropygus foliaceus</i> Kj																				
15	<i>Thyropygus forceps</i> Nws2																				
16	<i>Thyropygus induratus</i> Ldn																				
17	<i>Thyropygus induratus</i> Nru																				
18	<i>Thyropygus induratus</i> Ps																				
19	<i>Thyropygus induratus</i> Pw																				
20	<i>Thyropygus induratus</i> Ssk																				
21	<i>Thyropygus induratus</i> Tt																				
22	<i>Thyropygus inflexus</i> Kk	0.15																			
23	<i>Thyropygus jarukchusri</i> Np	0.13	0.16																		
24	<i>Thyropygus laterolobatus</i> Ry	0.12	0.15	0.14																	
25	<i>Thyropygus loxia</i> Ty	0.15	0.13	0.14	0.14																
26	<i>Thyropygus macrosiamensis</i> Kj	0.12	0.14	0.13	0.13	0.14															
27	<i>Thyropygus mesocristatus</i> Ss	0.15	0.13	0.16	0.16	0.13	0.15														
28	<i>Thyropygus navychula</i> KSR	0.16	0.12	0.13	0.15	0.12	0.14	0.13													
29	<i>Thyropygus opinatus</i> Arw	0.14	0.13	0.14	0.14	0.11	0.13	0.11	0.08												
30	<i>Thyropygus panhai</i> sp. nov. PRL2	0.14	0.15	0.13	0.13	0.14	0.12	0.16	0.13	0.15											
31	<i>Thyropygus peninsularis</i> Wm	0.16	0.15	0.15	0.15	0.14	0.13	0.13	0.14	0.13	0.17										
32	<i>Thyropygus planispinus</i> Tsk2	0.17	0.16	0.16	0.17	0.14	0.15	0.13	0.14	0.12	0.17	0.10									
33	<i>Thyropygus quadricuspis</i> Hy	0.14	0.13	0.15	0.15	0.11	0.12	0.07	0.11	0.12	0.14	0.11	0.13								
34	<i>Thyropygus quietus</i> Cdv	0.09	0.16	0.15	0.11	0.14	0.12	0.16	0.16	0.15	0.15	0.14	0.15	0.14							
35	<i>Thyropygus resimus</i> Kc	0.12	0.13	0.12	0.11	0.12	0.13	0.14	0.12	0.13	0.10	0.14	0.16	0.13	0.12						
36	<i>Thyropygus resimus</i> Ksp	0.12	0.13	0.13	0.11	0.12	0.13	0.14	0.12	0.13	0.10	0.14	0.16	0.13	0.12	0.00					
37	<i>Thyropygus resimus</i> Ntp	0.12	0.13	0.13	0.11	0.12	0.13	0.14	0.12	0.13	0.10	0.14	0.16	0.13	0.12	0.00	0.00				
38	<i>Thyropygus resimus</i> Pk	0.13	0.13	0.14	0.13	0.12	0.11	0.14	0.12	0.13	0.10	0.15	0.16	0.13	0.14	0.08	0.09	0.09			
39	<i>Thyropygus resimus</i> Pnk	0.13	0.12	0.13	0.13	0.12	0.10	0.13	0.13	0.13	0.10	0.15	0.15	0.12	0.14	0.10	0.10	0.10	0.05		
40	<i>Thyropygus resimus</i> Pp	0.14	0.14	0.13	0.12	0.13	0.11	0.15	0.12	0.12	0.10	0.16	0.14	0.14	0.14	0.08	0.08	0.08	0.09	0.09	
41	<i>Thyropygus resimus</i> Wnt	0.12	0.13	0.12	0.11	0.12	0.12	0.14	0.12	0.13	0.09	0.15	0.16	0.13	0.12	0.00	0.00	0.00	0.09	0.10	0.08
42	<i>Thyropygus richardhoffmani</i> TCH	0.15	0.13	0.15	0.14	0.11	0.13	0.07	0.12	0.13	0.15	0.12	0.13	0.04	0.14	0.14	0.14	0.14	0.13	0.15	
43	<i>Thyropygus siamensis</i> Sa	0.13	0.15	0.13	0.12	0.15	0.10	0.15	0.14	0.14	0.11	0.14	0.14	0.14	0.13	0.10	0.10	0.10	0.11	0.10	0.10
44	<i>Thyropygus somsaki</i> sp. nov. PPLT	0.13	0.15	0.12	0.13	0.14	0.11	0.16	0.14	0.15	0.07	0.16	0.17	0.15	0.15	0.11	0.11	0.11	0.10	0.10	0.09
45	<i>Thyropygus sutchariti</i> KCP	0.16	0.12	0.15	0.17	0.12	0.13	0.15	0.13	0.13	0.14	0.13	0.15	0.13	0.16	0.14	0.14	0.14	0.13	0.12	0.14
46	<i>Thyropygus uncinatus</i> Kdb	0.13	0.15	0.15	0.13	0.13	0.11	0.16	0.15	0.15	0.14	0.14	0.16	0.15	0.12	0.12	0.12	0.12	0.12	0.12	0.11
47	<i>Thyropygus uncinatus</i> Pj	0.13	0.13	0.15	0.12	0.13	0.11	0.15	0.15	0.13	0.14	0.14	0.15	0.14	0.11	0.11	0.11	0.11	0.12	0.12	0.11
48	<i>Thyropygus uncinatus</i> Pks	0.14	0.15	0.15	0.12	0.14	0.10	0.17	0.15	0.14	0.13	0.16	0.17	0.14	0.12	0.12	0.12	0.12	0.13	0.12	0.12
49	<i>Thyropygus uncinatus</i> Pn	0.13	0.14	0.16	0.12	0.13	0.11	0.15	0.14	0.13	0.13	0.15	0.15	0.13	0.11	0.13	0.13	0.13	0.13	0.13	0.12
50	<i>Thyropygus uncinatus</i> Ps	0.14	0.14	0.15	0.13	0.13	0.11	0.16	0.15	0.13	0.14	0.15	0.16	0.14	0.11	0.12	0.12	0.12	0.12	0.12	0.12
51	<i>Thyropygus uncinatus</i> Rcb	0.13	0.15	0.15	0.13	0.13	0.11	0.16	0.15	0.15	0.14	0.14	0.16	0.15	0.11	0.12	0.13	0.13	0.12	0.13	0.11
52	<i>Thyropygus uncinatus</i> Sc	0.12	0.13	0.15	0.12	0.12	0.11	0.15	0.15	0.13	0.13	0.14	0.15	0.14	0.11	0.11	0.11	0.11	0.12	0.12	0.11
53	<i>Thyropygus uncinatus</i> Sm	0.12	0.15	0.16	0.13	0.13	0.12	0.16	0.16	0.16	0.14	0.15	0.15	0.15	0.12	0.12	0.12	0.12	0.12	0.12	0.10
54	<i>Thyropygus uncinatus</i> Sn	0.13	0.15	0.15	0.12	0.14	0.12	0.17	0.15	0.16	0.14	0.14	0.14	0.15	0.11	0.12	0.12	0.12	0.12	0.13	0.11
55	<i>Thyropygus undulatus</i> Pb2	0.17	0.16	0.16	0.17	0.14	0.15	0.13	0.15	0.12	0.17	0.10	0.02	0.12	0.15	0.17	0.17	0.17	0.16	0.15	0.15
56	<i>Thyropygus ursus</i> LTK	0.14	0.12	0.15	0.15	0.11	0.12	0.07	0.11	0.12	0.15	0.11	0.12	0.02	0.14	0.14	0.14	0.14	0.13	0.13	0.14

APPENDIX

TABLE A1. Continued.

No.	Taxa	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56
1	<i>Anurostreptus barthelemyae</i> Tlb																
2	<i>Anurostreptus sculptus</i> Pl																
3	<i>Thyropygus allevatus</i> Bb																
4	<i>Thyropygus allevatus</i> Bk																
5	<i>Thyropygus bearti</i> Ks																
6	<i>Thyropygus bispinispatula</i> Kb																
7	<i>Thyropygus bispinus</i> Tm																
8	<i>Thyropygus brachyacanthus</i> Sk																
9	<i>Thyropygus cimi</i> Nws1																
10	<i>Thyropygus cristagalli</i> Yn																
11	<i>Thyropygus culter</i> Nr																
12	<i>Thyropygus demangei</i> Cm																
13	<i>Thyropygus enghoffi</i> Kl																
14	<i>Thyropygus foliaceus</i> Kj																
15	<i>Thyropygus forceps</i> Nws2																
16	<i>Thyropygus induratus</i> Ldn																
17	<i>Thyropygus induratus</i> Nru																
18	<i>Thyropygus induratus</i> Ps																
19	<i>Thyropygus induratus</i> Pw																
20	<i>Thyropygus induratus</i> Ssk																
21	<i>Thyropygus induratus</i> Tt																
22	<i>Thyropygus inflexus</i> Kk																
23	<i>Thyropygus jarukchusri</i> Np																
24	<i>Thyropygus laterolobatus</i> Ry																
25	<i>Thyropygus loxia</i> Ty																
26	<i>Thyropygus macrosiamensis</i> Kj																
27	<i>Thyropygus mesocristatus</i> Ss																
28	<i>Thyropygus navychula</i> KSR																
29	<i>Thyropygus opinatus</i> Arw																
30	<i>Thyropygus panhai</i> sp. nov. PRL2																
31	<i>Thyropygus peninsularis</i> Wm																
32	<i>Thyropygus planispinus</i> Tsk2																
33	<i>Thyropygus quadricuspis</i> Hy																
34	<i>Thyropygus quietus</i> Cdv																
35	<i>Thyropygus resimus</i> Kc																
36	<i>Thyropygus resimus</i> Ksp																
37	<i>Thyropygus resimus</i> Ntp																
38	<i>Thyropygus resimus</i> Pk																
39	<i>Thyropygus resimus</i> Pnk																
40	<i>Thyropygus resimus</i> Pp																
41	<i>Thyropygus resimus</i> Wnt																
42	<i>Thyropygus richardhoffmani</i> TCH	0.14															
43	<i>Thyropygus siamensis</i> Sa	0.10	0.15														
44	<i>Thyropygus somsaki</i> sp. nov. PPLT	0.11	0.15	0.11													
45	<i>Thyropygus sutchariti</i> KCP	0.14	0.13	0.13	0.14												
46	<i>Thyropygus uncinatus</i> Kdb	0.12	0.15	0.11	0.12	0.15											
47	<i>Thyropygus uncinatus</i> Pj	0.11	0.14	0.10	0.13	0.15	0.05										
48	<i>Thyropygus uncinatus</i> Pks	0.12	0.15	0.10	0.12	0.15	0.09	0.07									
49	<i>Thyropygus uncinatus</i> Pn	0.13	0.13	0.12	0.12	0.16	0.10	0.10	0.10								
50	<i>Thyropygus uncinatus</i> Ps	0.12	0.14	0.10	0.13	0.15	0.06	0.02	0.08	0.10							
51	<i>Thyropygus uncinatus</i> Rcb	0.12	0.15	0.11	0.12	0.15	0.00	0.05	0.10	0.10	0.06						
52	<i>Thyropygus uncinatus</i> Sc	0.11	0.14	0.10	0.13	0.15	0.06	0.01	0.07	0.10	0.02	0.06					
53	<i>Thyropygus uncinatus</i> Sm	0.12	0.15	0.10	0.12	0.15	0.02	0.06	0.09	0.11	0.06	0.02	0.06				
54	<i>Thyropygus uncinatus</i> Sn	0.12	0.15	0.10	0.13	0.16	0.04	0.06	0.09	0.12	0.07	0.04	0.06	0.03			
55	<i>Thyropygus undulatus</i> Pb2	0.17	0.13	0.14	0.17	0.16	0.16	0.16	0.17	0.15	0.16	0.16	0.15	0.15	0.15		
56	<i>Thyropygus ursus</i> LTK	0.14	0.05	0.15	0.16	0.14	0.15	0.13	0.14	0.13	0.14	0.15	0.13	0.15	0.15	0.12	