Revision of the endemic Taiwanese millipede genus *Aponedyopus* Verhoeff, 1939, with descriptions of two new species (Diplopoda, Polydesmida, Paradoxosomatidae)

Chao-Chun Chen¹‡, Sergei I. Golovatch²‡, Hsueh-Wen Chang¹§

¹ Department of Biological Sciences, National Sun Yat-Sen University, 70 Lien-hai Rd. Kaohsiung, Taiwan 804, ROC. ² Institute for Problems of Ecology and Evolution, Russian Academy of Sciences, Leninsky pr. 33, Moscow 119071, Russia

† urn:lsid:zoobank.org:author:6C30BB40-2A48-4AC1-859C-3036FBC23019
‡ urn:lsid:zoobank.org:author:71532F45-BDD5-415D-BC54-86256E5D5D4A
§ urn:lsid:zoobank.org:author:B0F05141-340F-4B6C-8F43-6F64DAB5EBC2

Corresponding author: Hsueh-Wen Chang (hwchang@mail.nsysu.edu.tw)

Academic editor: Robert Mesibov

Received 19 November 2010 | Accepted 13 December 2010 | Published @@ December 2010

urn:lsid:zoobank.org:pub:002E6B8A-73DB-4FE3-A689-5E9BA7C24419

Citation: Chen C-C, Golovatch SI, Chang H-W(2010) Revision of the endemic Taiwanese millipede genus *Aponedyopus* Verhoeff, 1939, with descriptions of two new species (Diplopoda, Polydesmida, Paradoxosomatidae). Advances in the systematics of Diplopoda III. ZooKeys 72: 1–21. doi: 10.3897/zookeys.72.743

Abstract

The millipede genus *Aponedyopus* is endemic to Taiwan and contains three species. All previously described nominal species are considered to represent one species: *A. montanus* Verhoeff, 1939 (the type species), including *A. reesi* (Wang, 1957) and *A. maculatus* Takakuwa, 1942, syn. n. Two further species are described as new: *A. similis* sp. n. and *A. latilobatus* sp. n. The genus is re-diagnosed, all of its three species are keyed, and their distributions mapped.

Keywords

Millipede, *Aponedyopus*, taxonomy, new species, distribution, key, Taiwan
Introduction

The genus *Aponedyopus* Verhoeff, 1939 was first proposed to incorporate the single species *A. montanus* Verhoeff, 1939 said to be from the foot of Mt Fuji in Japan. The generic diagnosis was very poor, relying on a highly superficial resemblance in the gonopod conformation of *Aponedyopus* to the genus *Nedyopus* Attems, 1914 (Verhoeff 1939). Takakuwa (1942) was the first to add another species to this genus, *A. maculatus* Takakuwa, 1942 from Taiwan, and, later (1954), questioned the provenance of *A. montanus* from Honshu, suggesting it had also derived from Taiwan. Wang (1957a, 1957b) described two further species from Taiwan which he first placed in *Nedyopus*: *N. reesi* Wang, 1957 and *N. jeanae* Wang, 1957; then (1963a, 1963b) he transferred the latter species to *Aponedyopus* and referred to it as only a subspecies of *A. montanus*. Finally, in a checklist of the Taiwanese Diplopoda, Wang (1964) listed the following *Aponedyopus*: *A. montanus montanus*, *A. m. jeanae*, *A. reesi*, and *A. maculatus*, the former subspecies quoted as stemming from Japan and being common there, as opposed to the latter three taxa which were said to be endemic to Taiwan. Thus, Wang ignored the previous doubts expressed by Takakuwa (1954) concerning the origin of *A. montanus* in Japan. He also neglected Miyosi (1959) who had formally synonymized *A. jeanae* with *A. montanus* and who had also agreed with Takakuwa that *A. montanus* had to stem from Taiwan, not from Japan. Hoffman (1980) accepted that the genus occurred in both Taiwan and Japan. Murakami (1993) included *A. montanus* in the most recent checklist of the Japanese millipedes, but Shinohara and Tanabe (1999) emphasized that the original, type locality of *A. montanus*, i.e. Mt Fuji, might have been mislabeled. Yet, the genus *Aponedyopus* still remains on the generic list of Japanese Myriapoda (Tanabe 2001).

Jeekel (1968) was the first to properly, however succinctly, re-diagnose *Aponedyopus*, emphasizing it had nothing to do with the stem-name *Nedyopus*, because these genera show vastly different courses of their seminal grooves and several other important details of gonopod structure, and belong in different tribes. Yet Jeekel mistakenly listed *A. jeanae* as a valid species and erroneously believed he was the first to transfer both *A. jeanae* and *A. reesi* to *Aponedyopus*. In fact, Miyosi (1959) had done it before, followed also by Wang (1964).

Korsós (2004), in the latest catalogue of the Diplopoda of Taiwan, listed only two species in *Aponedyopus*: *A. montanus* and *A. maculatus*. Concerning the former species, he listed two junior synonyms claimed as new: *A. reesi* and *A. montanus jeanae*. However, he must have overlooked Miyosi (1959), who had already synonymized the latter taxon under *A. montanus*. He also erred in stating that *A. maculatus* had been described from Ikao, Japan, whereas it had actually been described from Piyanan (= Sih-uyanyakou (思源啞口), Datong Township(大同鄉), Yilan County (宜蘭縣)), Taiwan (Takakuwa 1942). In addition, not only all of the previous records of these species in Taiwan were summarized, but he also provided some new localities for *A. maculatus*.

The present study reviews the millipede genus *Aponedyopus*, based on abundant fresh material, including some near-topotypes of one of included species, covering
various parts of Taiwan. Thus, the previously described species could be re-assessed, two new species added, and a new synonym established.

**Material and methods**

New extensive collections of millipedes covering most parts of Taiwan were made between 1989 and 2009, using hand-sorting of the soil and litter. Specimens were preserved in 70% ethanol. External structures were examined and the drawings prepared with a LEICA MZ 16 stereomicroscope, as well as with a HITACHI S2400 scanning electron microscope. Coloration of the specimens is described from alcohol material. This material has been shared between the collections of Department of Life Science, National Chung Hsing University (NCHUL), Taiwan; Department of Biological Sciences, National Sun Yat-Sen University (NSYSUB), Taiwan; Department of Life Sciences, National Taiwan Normal University (NTNUL), Taiwan; National Museum of Natural Science (NMNS), Taiwan; Taiwan Forestry Research Institute (TFRI), Taiwan; and Zoological Museum of the State University of Moscow (ZMUM), Russia.

**Systematic Account**

**Genus Aponedyopus Verhoeff, 1939**

_Aponedyopus_ Verhoeff, 1939: 119; Takakuwa, 1954: 49; Jeekel, 1968: 75; Hoffman, 1980: 170; Shinohara and Tănabe, 1999: 681.

**Diagnosis.** Medium- to large-sized Paradoxosomatidae (15–55 mm long, 2.0–5.0 mm wide) with 20 segments. Pore formula normal. Paraterga poorly developed, evident only on segment 2. An evident sternal lobe between ♀ coxae 4; ♀ segment 7 with or without a pair of prominent sternal cones (= spiracles) flanking gonopod aperture. ♀ tarsal brushes present.

Gonopod coxae long, subcylindrical, setose distodorsally, cannula as usual. Telopodites rather long, their distal parts crossing medially _in situ_. Femorite long, moderately to evidently broadened parabasally on dorsal side, apically separated from postfemoral region by a clear oblique sulcus on lateral side; postfemoral part enlarged at base, tapering thereafter, demarcated from solenophore by a sulcus on mesal side; solenophore shorter than to as long as femorite, curved first ventrad and then dorsad on mesal face, distally holding subparallel to broadened part of femorite; base of solenophore with a small to obvious, apically deeply bifid lobe; seminal groove first running fully on mesal face of femorite, then turning dorsad near postfemoral part and continuing onto solenomere at base of solenophore on dorsal face; solenomere flagelliform, long, at most
only slightly longer than, and nearly completely supported/sheathed by, solenophore, with only tip of solenomere sometimes exposed.

Aponedyopus montanus Verhoeff, 1939
Figs 1–23, 40–43, 50–53

Aponedyopus montanus Verhoeff, 1939: 119–121, figs 5–7.
Aponedyopus montanus – Miyosi, 1959: 73; Jeekel, 1968, 75; Wang and Mauriès, 1996: 87; Korsós, 2004: 21.
Aponedyopus montanus montanus – Wang, 1964, 69.
Aponedyopus maculatus Takakuwa, 1942: 238, figs 3 & 4, syn. n.
Aponedyopus maculatus – Wang, 1958: 342; 1963a: 90; 1964: 69; Jeekel, 1968: 75; Wang and Mauriès, 1996: 87; Korsós, 2004: 20.
Nedyopus reesi Wang, 1957a: 104–106, fig. 2; first synonymized by Korsos, 2004.
Nedyopus reesi – Wang, 1958: 342.
Aponedyopus reesi – Miyosi, 1959: 73; Wang, 1964: 69; Jeekel, 1968: 75; Wang and Mauriès, 1996: 87.
Nedyopus jeanae Wang, 1957b: 113–115, fig. 8; first synonymized by Miyosi, 1959.
Nedyopus jeanae Wang, 1958: 342; Miyosi, 1959: 73.
Aponedyopus jeanae – Wang, 1963b: 288; Jeekel, 1968: 75; Wang and Mauriès, 1996: 87.
Aponedyopus montanus jeanae – Wang, 1963a: 90; 1964: 69.

Material examined: 1 ♀ (NSYSUB-DI 60), Taiwan, Taipei City, BeiTou area (北投區), 101 Jiia county road (101甲縣道), ca 860 m a.s.l., 4 May 2002, leg. S. Y. Wu. 1 ♂ (NCHUL), Taipei County (台北縣), Gongliao Township (貢寮鄉), upstream of Yuanwangkeng Stream (遠望坑溪上游), 6 June, 1998, leg. S. H. Wu. 1 ♂ (NSYSUB-DI 67), Taipei County (台北縣), ULai Township (烏來鄉), TaManShan (塔曼山), in decaying wood, 2,100 m a.s.l., 23 August 2002, same collector. 1 ♀ (NSYSUB-DI 59), same township, WuLai (烏來), 1,000–1,200 m a.s.l., March 2002, leg. C. C. Chen & C. S. Iang. 1 ♂, 2 ♀ (TFRI), same township, FuShan Botanical garden (福山植物園), ca 730 m a.s.l., 18–25 May 2001, leg. W. B. Huang. 1 ♂, 3 ♀ (NSYSUB-DI 61–64), Taiwan, Taoyuan County (桃園縣), FuSiing Township (復興鄉), HuaLeng Village (華陵村), Northern Cross-Island Highway (北部橫貫公路)/Provincial # 7 Highway (台七線), 53 km, ca 1,030 m a.s.l., 22 April 2003, same collector. 1 ♀ (NSYSUB-DI 73), same locality, 58 km, ca 1,110 m a.s.l., 29 May 2003, same collector. 1 ♀ (NSYSUB), same locality, 56 km, ca 1,030 m a.s.l., 23 June 2006, same collector. 3 ♂ (NSYSUB-DI 444–446), same township, Baling (巴陵), ca 600 m a.s.l., 3 April 2004, leg. H. D. Zhu. 1 ♀ (NTNUL-My 15), Hsinchu County (新竹縣), Wufeng Township (五峰鄉), GuanU (觀霧), ca 2,000 m a.s.l., 28 June 1993, leg. S. H. Chen. 1 ♂ 1 ♀ (NSYSUB), same township, ShihLu old path (石鹿古道), ca 1,600 m a.s.l., 22 September 2005, leg. H. D. Zhu. 1 ♀ (NSYSUB), same township, Syueba farm (雪壩農場), DaLu forest path (大鹿林道), ca 1,890
Revision of the endemic Taiwanese millipede genus *Aponedyopus* Verhoeff, 1939...

Figures 1–4. *Aponedyopus montanus* Verhoeff, 1939, showing different colour patterns, ♂♂ from Mt Taiping (太平山) 1 Zjhong (自忠) 2 Yima forest path (依麻林道) 3 NanSi forest path (楠溪林道) 4 dorsal view. Scale bars: 5.0 mm.

m a.s.l., 1 October 2006, leg. S. Y. Wu. 1 ♂, 1 ♀ (ZMUM), Yilan County (宜蘭縣), Yuanshan Township (員山鄉), Shuanglian Pond (雙連埤), ca 500 m a.s.l., 11 May 2007, same collector. 1 ♀ (NSYSUB), Datong Township (大同鄉), Cueifong Lake (翠峰湖), ca 1,900 m a.s.l., 29 July 2004, same collector. 1 ♂ (NSYSUB), same township, Northern Cross-Island Highway (北部橫貫公路)/Provincial # 7 Highway (台七線), MingChih (明池), ca 1,200 m a.s.l., 13 April 2006, same collector. 1 ♂ (NSYSUB), same township, Mt Taiping (太平山), ca 1,930 m a.s.l., 26 February 2007, 24°28’46”N, 119°31’03”E, leg. M. H. Hsu. 1 ♀ (NSYSUB), same township, forest path # 100 (100號林道), 21 km, ca 1,600 m a.s.l., 9 September 2009, leg. C. J. Jheng. 1 ♂ (NSYSUB-DI 65.), Taichung County (台中縣), HePing Township (和平鄉), AnMaShan forest amusement zone (鞍馬山森林遊樂園), ca 2,000 m a.s.l., 7 May 2003, leg. S. Y. Wu. 1 ♂ (NCHUL), Nantou County (南投縣), LuGu (鹿谷鄉), SiTou (溪頭), ca 1,140 m a.s.l., 31 October 1997, leg. S. H. Wu. 1 ♀ (NCHUL), same locality, ca 1,160–1,400 m a.s.l., 31 October 1997, leg. S. H. Chen. 1 ♀ (NSYSUB-DI 58), same locality, ShenMu walking path (神木步道), under stones, ca 1,200 m a.s.l., 15 November 2002, leg. J. D. Lee. 1 ♀ (JDLee20021114008, deposited at NSYSUB), same locality, TuDiGongLun walking path (土地公崙步道), ca 1,160–
1,400 m a.s.l., same date and collector. 2 juveniles (JDLee20021114004, deposited at NSYSUB), same locality, SiTou walking path (溪頭步道), same date and collector.

3 ♀ (NTNUL-My 6–9), same county, ShinYi Township (信義鄉), Zhong (自忠), ca 2,340 m a.s.l., 1 July 1989, leg. S. H. Chen. 3 ♂ (NTNUL-My 25–28), same locality, date and collector. 1 ♀ (NSYSUB), same county, Zhushan Township (竹山鎮), ShanLinSi amusement park (杉林溪遊樂園), ca 1,600 m a.s.l., 7 October 2004, leg. S. Y. Wu. 1 ♂ (NSYSUB), Taiwan, Hualien County (花蓮縣), Xiulin Township (秀林鄉), Mt. JiaLiWan (加裡宛山), ca 1,290 m a.s.l., 29 July 2005, leg. F. S. Jhou. 1 ♀ (NSYSUB), same township, Toroko (太魯閣), Lianhua Pond walking path (蓮花池步道), ca 1,060 m a.s.l., 24°13′10″N, 119°28′49″E, 28 February 2007, leg. M. H. Hsu. 1 ♀ (NSYSUB), same county, FengBin Township (豐濱鄉), Ruigang Highway (瑞港公路), ca 130 m a.s.l., 23°28′50″N, 119°27′31″E, 7 May 2009, leg. M. H. Hsu. 2 ♂ (NSYSUB-DI 69–70), same county, JhuoSii (卓溪鄉), WaLaMi (瓦拉米), YuShan National Park (玉山國家公園), ca 1,080 m a.s.l., 24 February 2003, leg. H. D. Zhu. 1 ♂, 3 juveniles (NTNUL-My 29–32), Chia-I County (嘉義縣), ALiShan Township (阿里山鄉), ALiShan (阿里山), ca 2,260 m a.s.l., 11 March 1989, leg. S. H. Chen. 1 ♂, 2 ♀ (NTNUL-My 49–51), 2,250 m a.s.l., 3 July 1989, 3 ♀ (NTNUL-My 49–51), 2,250 m a.s.l., 3 July 1989,
same locality and collector. 1 ♀ (NSYSUB-DI 74), same locality, ALiShan amusement park (阿里山遊樂園), under stones on soil, ca 2,280 m a.s.l., 24 June 2003, leg. Y. H. Lin. 1 ♀ (NSYSUB-DI 66), Kaohsiung County (高雄縣), TaoYuan (桃源鄉), TengJihh (藤枝), ShihShan forest path (石山林道), 6 km, ca 1,600 m a.s.l., 21 August 1998, collector unknown. 1 ♂ (NSYSUB-DI 66), same locality, 1 August 2001, leg. C. R. Wu. 1 ♀ (NSYSUB-DI 72), same locality, ca 1,450 m a.s.l., 14 April 2003, leg. S. Y. Wu. 1 ♂ (NSYSUB), same township, NanSi forest path (楠溪林道), ca 2,000 m a.s.l., 24 September 2002, leg. M. J. Hong & M. J. Wu. 1 ♀ (NSYSUB), same township, Southern Cross-Island Highway (南部橫貫公路), DaGuanShan (大關山), YaKou forest path (啞口林道), ca 2,720 m a.s.l., 13 May 2007, leg. Y. C. Chang. 1 ♀ (NSYSUB-DI 71), at boundary between MaoLin County (茂林鄉) of Kaohsiung and UTai County (霧臺鄉) of PingTung, YuGuTing (雨谷亭), under stone, ca 2,150 m a.s.l., 28 March 2003, leg. H. W. Chang. 1 ♂ (NSYSUB), Taitung County (台東縣), JinFeng Township (金峰鄉), Yima forest path (依麻林道), ca 1,110 m a.s.l., 2 July 2009, leg. M. H. Hsu. 1 ♀ (NSYSUB), PingTung County (屏東縣), ChunRih Township (春日鄉), DaHan forest path (大漢林道), 20 km, under stone, ca 250 m a.s.l., 9 July 2004, leg. W. J. Lee. 2 ♂ (NSYSUB), same county,
Diagnosis: Differs from the other *Aponedyopus* species in often containing specimens considerably more than 40 mm long, in the considerably longer ♂ legs (usually about twice as long as midbody height), a dentiform process b at the base of the gonopod prefemoral part and, above all, the slender terminal branches (x and y) of the solenophore (Figs 40, 42 & 43).

Description: Length 40–55 (♂, n=11) or 47–58 mm (♀, n = 13); width of midbody metazona 10 ca 3.5–5.0 (♂) or 5.0–6.0 mm (♀).

Coloration in alcohol entirely light yellow to dark brown (Figs 1–14). Antennae light yellow to dark brown, increasingly blackish distally, but tip pallid; head to anterior half of epiproct (epi) (Fig. 19), pleurosternal region (ple) (Fig. 18) light yellow to dark brown, prozona (pro) always darker than metazona (meta) (Fig. 18), anterior and hind edges of metazona evidently to slightly lighter brown; posterior half of epiproct, sterna and legs light yellow to orange-brown in ♂.

Head densely setose in clypeolabral region, vertex nearly bare, epicranial suture distinct. Postcollum constriction faint; in width, segments 2 = 3 = 4 < head =
Figures 15–23. *Aponedyopus montanus* Verhoeff, 1939, ♂ from Mt JiaLiWan (加禮宛山). 15 Entire body, lateral view 16 Anterior body portion, lateral view. 17, 18 Midbody segments, dorsal and lateral views, respectively 19–20 Epiproct (*epi*), dorsal and lateral views, respectively 21 Hypoproct (*hyp*), ventral view 22, 23 Sternal lobe between ♂ coxae 4, subventral views. Scale bars: 1.0 mm for 15–21, 0.5 mm for 22, 23. *al*: axial line; *cal*: calluses; *col*: collum; *meta*: metazona; *o*: ozopore; *pap*: pre-apical papillae; *par*: paraterga; *ple*: pleurosternal region; *pro*: prozona; *rug*: rugulose; *str*: stricture; *sul*: transverse sulcus; *tar*: tarsal brushes.
segment 5 = 6 < collum (col) (Fig. 16) = segments 7–17 in ♂, or segments 2 = 3 = 4 < head < collum = segments 5–16 in ♀; thereafter body gradually and gently tapering both in width and height towards telson. Antennae medium-sized to long, stout, reaching behind middle of metatergite 3 to middle of metatergite 4 dorsally (♂) (Fig. 16), or midway to end of segment 3 (♀). Surface generally shining and rather smooth, only metaterga rugulose (rug) (Fig. 16) (post-sulcus halves (Fig. 17) usually slightly more so); surface below paraterga (par) (Fig. 18) visibly and densely granular on anterior segments, increasingly sparsely granular towards telson in both sexes, sometimes densely granular until segment 19 in ♀. Paraterga (par) (Fig. 18) poorly developed, especially evident as low ridges drawn considerably forward into a rounded lobe on segment 2 in both sexes, nearly to totally wanting on segments 16–19 (sometimes only a dorsal sulcus above ozopore (o) (Fig. 18) still present); calluses (cal) (Fig. 17) always delimited by a sulcus dorsally, calluses thinner on poreless segments, broader on pore-bearing ones, but a ventral sulcus mostly observed in caudal 1/3 only until segment 15; paraterga even more strongly reduced in ♀. Axial line (al) usually absent to traceable in places on collum and following metaterga, sometimes evident on metaterga in both sexes (Fig. 17). A medially sinuate transverse sulcus (sul) (Fig. 17) evident on segments 5–17, traceable on segments 4 and 18(19) in both sexes, narrow, shallow, very faintly beaded to smooth at bottom, not reaching bases of paraterga. Limbus (= region between two arrows, Fig. 16) thin, caudal margin entire. Stricture (str) (Fig. 17) between pro- and metazona shallow, narrow, faintly ribbed at bottom in both sexes. Pleurosternal carinae (arrow) (Fig. 16) nearly wanting, present as slight flaps only on segment 2, barely traceable on segment 3 (Fig. 16). Tergal setae almost fully abraded, pattern traceable mostly as 1+1 or 2+2 insertion points at anterior edge of collum in both sexes, as well as 2+2 in anterior (pre-sulcus) and 2+2 in posterior (post-sulcus) row on following metaterga. Ozopores (o) (Fig. 18) lateral, lying on callus ca 1/3 metatergal length in front of caudal edge (Figs 17 & 18). Epiproct (epi) (Figs 19 & 20) moderately long, conical, only slightly curved in lateral view, ratio of epiproct length to pre-epiproct length of telson 1.3:1 in ♂, tip emarginated in both sexes in dorsal view (Fig. 19); pre-apical papillae (pap) (Fig. 19) evident, close to apex. Hydropoc (hyp) (Fig. 21) usually subtrapeziform (♂, ♀), more rarely subtriangular to semi-circular (♀), 1+1 setae at caudal corners situated on well-separated knobs, sides straight (♂) or slightly convex (♀).

Sterna sparsely setose, each cross-impression with neither a transverse sulcus nor an axial groove; a slightly to very slightly notched, setose, ventrally bulging lamina only between ♂ coxae 4 (Figs 22 & 23). Ridges/cones (= spiracles) flanking gonopod aperture present or absent. Legs long, ca twice as long as midbody height, shorter and slenderer in ♀; legs 1 to posterior legs of segment 15 with obvious tarsal brushes (tar) (Fig. 18) only in ♂, ♀ without tarsal brushes; ♂ coxa 2 with a small apical process carrying a gonopore.

Gonopods (Figs 40–43, 50–53) simple. Coxite (cx) (Fig. 41) elongate, subcylindrical, setose distodorsally; cannula normal. Telopodites (T) (Fig. 40) curved distally,
longer than coxite. Prefemoral part (pf) (Fig. 41) short and stout, almost 1/3 femur length, as usual densely setose. Femorite (fe) (Fig. 41) evidently broadened near base on dorsal side, with a clear demarcation sulcus (su) (Fig. 41) on lateral side separating a postfemoral part (pst) (Fig. 41); the latter showing an obvious, spiniform, (nearly) pointed branch (b) (Figs 42 & 43) parabasally on lateral side; solenophore (sph) (Fig. 41) with another demarcation sulcus separating it from pst on medial side, long, only slightly shorter than to as long as femorite, twisted and curved first ventrad and then dorsad on medial side in ventral view, distally holding subparallel to broadened part of femorite; base of sph with an obvious, subspiniform lobe (l) (Fig. 40), either well separated from or holding quite adjacent to sph base; terminal part of sph divided into two slender, separated branches: one wide, flattened dorsoventrally, with a rounded membranous end (y), the other spiniform (x) (Fig. 40). Seminal groove (sg) (Fig. 50) first running fully on mesal face of fe, then turning dorsad near pst to continue onto solenomere (sl) (Fig. 41) at base of sph on dorsal face; sl flagelliform, long, only slightly longer than sph and nearly completely supported/sheathed by sph, only tip of sl exposed.

**Distribution:** Type material has not been revised, presumably in the collection of the Zoologische Staatssammlung in Munich, Germany.

This species is highly variable in size and coloration, and is the most widespread amongst Aponedyopus species in Taiwan. Its distribution covers much of the island and vertically ranges from 175 to over 2,720 m a.s.l. (Map).

* Aponedyopus similis* sp. n.

urn:lsid:zoobank.org:act:80CFF96F-2331-45EB-B4B5-DF5814A57660
Figs 24–31, 44, 45, 54 & 55

**Material examined:** Holotype ♂ (TFRI), Taiwan (R. O. C.), Taichung County (台中縣), HePing (和平鄉), Shengguang (勝光), ca 2,200 m a.s.l., 26 March – 25 April, 2003, leg. W. C. Yeh.

Paratype ♂ (NSYSUB-DI 75), Taiwan (R. O. C.), Hsinchu County (新竹縣), Wufeng Township (五峰鄉), GuanU (觀霧), 24.5 km from entrance to national park, ca 2,000 m a.s.l., 13 August 2002, leg. C. C. Chen, Y. H. Lin & J. N. Huang.

**Name:** To emphasize the close resemblance to the next new species.

**Diagnosis:** Being apparently the most similar to *A. latilobatus* sp. n., based both on several peripheral characters (shorter legs, mostly a smaller body size etc.) and gonopod conformation, it is distinguished by the gonopod lobe b being membranous and lobiform, the terminal branches of the solenophore differing in length and crossing each other, with branch x carrying an inconspicuous lobe (see also Key below).

**Description:** Length ca 22 mm (♂, n=2); width of pro- and metazona 10 ca 1.8 and 2.0 mm, respectively.

General coloration in alcohol brown to dark brown (Figs 24–27), with a clear pattern of a lighter brown to yellow brown axial stripe consisting of narrower subtriangu-
lar spots on proterga and twice as wide central spots on metaterga, these spots growing slightly infuscate, to blackish both towards stricture and posterior half of metaterga; prozona slightly darker than metazona, thus providing a vague cingulate pattern as well; paraterga, legs and venter slightly lighter than background, light grey-brown; head marbled brown, especially well so in vertigial region, genae contrasting yellowish, a square median spot above antennal sockets contrastingly brown; antennae increasingly infuscate, up to blackish distad, distinctly darker at margins, marbled and lighter centrally, only tip contrastingly pallid; both collum and segment 2 with a very

Figures 24–31. *Aponedypus similis* sp. n., ♂ holotype (24) ♂ paratype (25–31). 24 Entire body, dorsal view 25 Anterior body portion, lateral view 26–27 Midbody segments, dorsal and lateral views, respectively 28–29 Epiproct, dorsal and lateral views, respectively 30 Hypoproct, ventral view 31 Sternal cones near gonopod aperture. Scale bars: 1.0 mm for 24–29, 0.5 mm for 30, 31. cal: calluses; pap: pre-apical papillae.
faint, yellow-brown, axial line; epiproct uniformly light brown, only very slightly infuscate near base.

Postcollum constriction evident; in width, segment 2 = 3 < 4 < collum < head = segments 5–15; thereafter body gradually and gently tapering towards telson both in width and height. Antennae (Fig. 25) medium-sized, slender, reaching behind stricture of tergite 3. Paraterga (Figs 26 & 27) very poorly developed, very evident and low only on segment 2, calluses (cal) (nearly) completely delimited by a sulcus dorsally, in caudal 1/3 also ventrally only on pore-bearing segments. Transverse sulcus (Figs 26, 27) developed on segments 5–17, traceable on segment 18, wanting on 19th, narrow, shallow, neither beaded at bottom nor reaching bases of paraterga. Surface smooth throughout, slightly granulated only below paraterga 2–4. Limbus thin, caudal margin entire. Stricture dividing pro- and metazona shallow, narrow, not beaded at bottom (Figs 26 & 27). Pleurosternal carinae present only on segments 2 and 3 (Fig. 25). Ter-gal setae almost fully abraded, 2+1 retained only at anterior edge of collum; pattern untraceable. Ozopores lateral, lying on calluses ca 1/2 metatergal length in front of caudal edge (Figs 26 & 27). Epiproct long (Figs 28 & 29), flattened dorsoventrally, straight, not curved caudoventrad in lateral view, ratio of epiproct length to pre-epiproct length of telson 1: 1.3, tip of epiproct slightly concave; pre-apical papillae (pap) evident, close to apex. Hypoproct (Fig. 30) rounded, subtrapeziform, 1+1 setae at caudal corners situated on well-separated knobs, sides slightly concave.

Sterna sparsely setose; lamina between coxae 4 setose and emarginate (Fig. 31); segment 7 with a pair of prominent sternal cones (= spiracles) flanking gonopod aperture; each cross-impression with a transverse sulcus, but without axial groove. Legs (Fig. 27) moderately long and slender, legs 1 to anterior legs of segment 17 with tarsal brushes, thereafter legs broken off in both available ♂♂, each midbody leg ca 1.2 times as long as body height, coxa 2 with a small apical process supporting a gonopore.

Gonopods (Figs 44, 45, 54 & 55) with process b at base of postfemoral part lobe-shaped, membranous, not like a distinct process; l at base of solenophore rather vague; distal part of gonopod deeply bifid, divided into a longer solenomere (sl), more complex at end and bearing a low terminal lobe, and a slightly shorter, simple, nearly pointed solenophore branch (sph); ends of both branches crossing.

Distribution: This species seems to be local, occurring only rather high (2,000–2,200 m a.s.l.) in the mountains of northern Taiwan (Map).

Aponedyopus latilobatus sp. n.
urn:lsid:zoobank.org:act:9365404E-6E43-4CBA-ABA9-4C0466D27E42
Figs 32–39, 46–49, 56–58

Material examined: Holotype ♂ (NSYSUB-DI 76), Taiwan (R. O. C.), Taichung County (台中縣), HePing (和平鄉), Sihyuanyakou (思源啞口), forest path no. 710, 1.5 km from entrance to path, ca 2,050–2,100 m a.s.l., 21 August 2002, leg. C. C. Chen & Y. H. Lin.
Paratypes: 3 ♀ (NSYSUB-DI 77–79), same locality, date, and collectors, together with holotype.

Diagnosis: Apparently being the most similar to A. similis sp. n., it differs in the texture of the tegument (mostly rugulose in A. latilobatus sp. n.) and, especially, in certain details of gonopod structure: lobe I is neither so wide nor membranous, the terminal branches are subequal in length, and the solenomere is supplied with a far more evident terminal lobe (see also Key below).

Description: Length 15 mm (♂, n=1) and 18 mm (♀, n =3); width of pro- and metazona 10 ca. 1.8 and 2.0 (♂) or 1.9–2.0 and 2.0–2.2 mm (♀), respectively.

Coloration in alcohol entirely light brown to brown (Figs 32–35); antennae light brown, growing increasingly blackish distally, but tip pallid; pattern much clearer in ♀, much like in A. similis sp. n.: a light brown, wide, axial stripe from anterior edge
of collum to end of epiproct; paraterga and sternites contrastingly lighter brown; legs pallid to yellow; axial line wanting.

Postcollum constriction clear (♂) or faint (♀), segment 4 < 3 < 2 < collum = segments 5–16 < head (♂), or collum = segments 2–4 < head = segments 5–18 (♀), thereafter body gradually and gently tapering both in width and height towards telson. Antennae (Fig. 33) medium-sized (♂) to short (♀), slender, reaching behind stricture of tergite 3 dorsally (♂), or end of collum to posterior edge of segment 2 (♀). Paraterga (Figs 34 & 35) as in A. similis sp. n., but sometimes not or nearly not delimited by a ventral sulcus (♀). Surface transversely rugulose on metaterga 2 close to paraterga, sparsely longitudinally rugulose in places on post-sulcus halves of metaterga. Pleurosternal carinae (Fig. 33) present only on segments 2 and 3. Tergal setae almost fully abraded, 3+3 retained only at anteriorter edge of collum; pattern untraceable. Epiproct (Figs 36 & 37) same as in A. similis sp. n., but tip either slightly concave or subtruncate.

Sterna sparsely setose; lamina (Fig. 39) between ♂ coxae 4 evidently emarginate and setose; ♂ segment 7 with a pair of prominent, ventral, sternal cones (= spiracles)
Figures 44, 45. Aponedyopus similis sp. n., ♂ paratype, left gonopod 44, 45, submesal and sublateral views, respectively. Scale bar = 0.5 mm.

Figures 46–49. Aponedyopus latilobatus sp. n., ♂ holotype, left gonopod 46, 47, submesal and dorsal views, respectively 48, 49 telopodite tip, submesal and lateral views, respectively. Scale bar = 0.5 mm for 46, 47, 0.25 mm for 48, 49.
Revision of the endemic Taiwanese millipede genus *Aponedyopus* Verhoeff, 1939...

Figures 50–53. *Aponedyopus montanus* Verhoeff, 1939, ♂♂. 50, 51 right gonopod, mesal and lateral view, respectively. 52–53 left gonopod, mesal and lateral view respectively. Scale bar = 1 mm. \textit{sg}: seminal groove.

Figures 54–58. *Aponedyopus similis* sp. n., ♂ paratype, right gonopod, lateral and mesal views, respectively 54, 55. *A. latilobatus* sp. n., ♂ holotype, right gonopod and telopodite tip, mesal view, respectively 56, 57, right gonopod, lateral view 58. Scale bar = 0.5 mm.
flanking gonopod aperture. Legs short and slender, shorter than to almost as long as midbody height; tarsal brushes present from legpair 1 to anterior legs of segment 10; coxa 2 with a small apical process supporting a gonopore.

Gonopod (Figs 46–49, 56 & 57) with more like in A. montanus, but especially indistinct, and distal part of solenophore (sph), albeit also deeply bifid, having both terminal branches of subequal length, as well as a far more evident terminal lobe on solenomere (sl) not crossing a simple end of sph.

**Distribution:** This seems to be a very local high-montane species in central Taiwan (Map).

**Key to Aponedyopus species (based on adult males):**

1. **Midbody legs about twice as long as body height. Gonopod with terminal part of solenophore divided into two slender branches (x and y, Figs 40–43, 50–53)................................................................. A. montanus**
   – **Midbody legs only up to 1.2 times as long as body height. Gonopod with terminal part of solenophore divided into wide branches .................2**

2. **Terminal branches of solenophore differing in length and crossing each other, branch y with a rather inconspicuous terminal lobe (Figs 44, 45, 54 & 55) ................................................................. A. similis sp. n.**
   – **Terminal branches of solenophore subequal in length and not crossing each other, branch y with a highly inconspicuous terminal lobe (Figs 46–49, 56–58) ................................................................. A. latilobatus sp. n.**

**Discussion**

*Aponedyopus* seems to be a small genus endemic to Taiwan. Based on available information, among its three constituent species two are pretty local in distribution, *A. latilobatus* sp. n. and *A. similis* sp. n., each restricted to the northern or central, mostly montane parts of the island, respectively (Map). In contrast, *A. montanus* appears to be extremely widespread, living at various elevations in all parts of Taiwan, including the small islet of Lanyu off the southeastern coast of Taiwan. Whether this species could have been introduced to, and originally described from, Japan, remains open to question. There is only a single example of a basically Taiwanese paradoxosomatid to have become successfully established at least in southern Japan: *Chamberlinius hualienensis* Wang, 1956 in Kyushu Island and the Ryukyus (Higa and Kishimoto 1986, 1989; Yamaguchi et al. 2000; Nijima and Arimura 2002).
Map. Distribution of Aponedyopus species in Taiwan. *A. montanus* Verhoeff, 1939: filled black squares; *A. similis* sp. n.: filled red circles; *A. latilobatus* sp. n.: filled green triangle.
The distribution of *Aponedyopus* species in Taiwan shows allopatry. Syntopic occurrences are nearly missing, a feature already reported, e.g., for the paradoxosomatid genus *Anoplodesmus* (Chen et al. 2010), but contrasting with several other adequately known diplopod groups in Taiwan, in which 2–3 congeners are often capable of sharing the same habitat (Chen et al. 2006; Golovatch et al. 2010; Mikhaljova et al. 2010).

Concerning the tribal position of *Aponedyopus*, it has long been placed in the tribe Tonkinosomatini (Jeekel 1968; Hoffman 1980). However, we rather think that the few basically East to Southeast Asian paradoxosomatid genera forming the tribe Chamberlininini are actually the closest to *Aponedyopus*. Yet, no formal transfer is advanced here prior to a revision of the type genus *Chamberlinius* Wang, 1956 (Chen et al., in preparation).

**References**

Chen CC, Golovatch SI, Chang HW (2006) The millipede tribe Nedyopodini, with special reference to the fauna of Taiwan (Diplopoda: Polydesmida: Paradoxosomatidae). Journal of Natural History 39(47): 3997–4030.

Chen CC, Golovatch SI, Mikhaljova EV, Chang HW (2010) The millipede genus *Anoplodesmus* Pocock, 1895, recorded in Taiwan for the first time, with descriptions of two new species (Diplopoda: Polydesmida: Paradoxosomatidae: Sulciferini). Zootaxa 2399: 20–30.

Golovatch SI, Mikhaljova EV, Chang HW (2010) Pill-millipedes (Glomerida, Diplopoda) in Taiwan. Zootaxa 2477: 1–20.

Higa Y, Kishimoto T (1986) Unusual outbreak and control of millipedes, *Chamberlinius haulienensis* Wang in Okinawa. Annual Report of Okinawa Prefectural Institute of Public Health 20: 62–72. (In Japanese)

Higa Y, Kishimoto T (1989) Expansion of distribution area of millipede, *Chamberlinius haulienensis* Wang, in Okinawa. Annual Report of Okinawa Prefectural Institute of Public Health 23: 72–76. (In Japanese)

Hoffman RL (1980) Classification of the Diplopoda. Muséum d’histoire naturelle, Genève: 237 pp. [for 1979]

Jeekel CAW (1968) On the classification and geographical distribution of the family Paradoxosomatidae (Diplopoda, Polydesmida). Academisch Proefschrift, Rotterdam: 162 pp.

Korsós Z (2004) Checklist and bibliography of millipedes (Diplopoda) of Taiwan. Collection and Research 17: 11–32.

Mikhaljova EV, Golovatch SI, Chang HW (2010) The millipede family Diplomaragnidae in Taiwan, with descriptions of nine new species (Diplopoda, Chordeumatida). Zootaxa 2615: 23–46.

Miyosi Y (1959) Über japanische Diplopoden. Arachnological Society of East Asia, Osaka: 223 pp, plates 1–19. (In Japanese)
Revision of the endemic Taiwanese millipede genus Aponedyopus Verhoeff, 1939...

Murakami Y (1993) Diplopoda, Pauropoda, Symphyla. A list of Japanese species. Invertebrates 1. Shizen-Kankyô-Kenkyû Center. Environmental Agency Japan, Tokyo: 95–106. (In Japanese)

Nijima K, Arimura T (2002) Obstruction of trains by the outbreaks a millipede Chamberlinius hualienensis Wang (Diplopoda: Polydesmida). Edaphologia 69: 47–49. (In Japanese)

Shinohara K, Tanabe T (1999) Diplopoda. In: Aoki J (Ed) Pictorial Keys to Soil Animals of Japan. Tokai University Press, Tokyo, 647–683. (In Japanese).

Takakuwa Y (1942) Einige neue Arten von Diplopoda aus Nippon. Zoological Magazine, 54: 237–239.

Takakuwa Y (1954) Diplopoden aus Japan und ihr angrenzenden Gebieten. Japan Society for Promotion of Science, Tokyo, 241 pp. (In Japanese)

Tanabe T (2001) The biology of centipedes and millipedes. Tokai University Press, Tokyo, i-xi + 178 pp.

Verhoeff KW (1939) Zur Kenntnis ostasiatischer Diplopoden. III. Zoologischer Anzeiger 127: 115–125.

Wang D, Mauriès JP (1996) Review and perspective of study on myriapodology of China. In: Geoffroy JJ, Mauriès JP, Nguyen Duy-Jacquemin M (Eds) Acta Myriapodologica. Mémoires du Muséum National d’Histoire Naturelle 169: 81–99.

Wang YHM (1957a) Serica 1g: Records of Myriapods on Taiwan Islands (4) Six new polydesmids. Quarterly Journal of the Taiwan Museum 10: 103–111.

Wang YHM (1957b) Serica 1h: Records of myriapods on Taiwan Islands (5) with description of three new species. Quarterly Journal of the Taiwan Museum 10: 113–116.

Wang YHM (1958) Serica 1i, On Diplopoda from Taiwan with a new strongylosomids. Quarterly Journal of the Taiwan Museum 11: 340–344.

Wang YHM (1963a) Serica 1Q: Millipedes and centipedes of Quemoy, Fukien Province and Taiwan Island, Botel Tobago (Lan Yu), Taiwan Province and of Singapore. Quarterly Journal of the Taiwan Museum 16: 89–96.

Wang YHM (1963b) On millipedes and centipedes from Taiwan, China. Proceedings of the XVIth International Congress of Zoology, Washington D.C., 1963 1: 285, 288–291.

Wang YHM (1964) Serica 1 op: Wallacea and insular fauna of millipedes. Quarterly Journal of Taiwan Museum 17: 67–76.

Yamaguchi T, Izumi S, Takemura K, Torigoe H, Matunaga T., Nagata K (2000) Annual occurrence of Chamberlinius hualienensis Wang on Amami-Oshima Island and possible chemicals for controlling it. Proceedings of the Association for Plant Protection of Kyushu 46: 118–122. (In Japanese)
Review of the genus *Tylopus* Jeekel, 1968, with descriptions of five new species from Thailand (Diplopoda, Polydesmida, Paradoxosomatidae)

Natdanai Likhitrakarn¹†, Sergei I. Golovatch²‡, Rujiporn Prateepasen³§, Somsak Panha¹|

¹ Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok, 10330, Thailand. ² Institute for Problems of Ecology and Evolution, Russian Academy of Sciences, Leninsky pr. 33, Moscow 119071, Russia. ³ The Scientific and Technological Research Equipment Center, Chulalongkorn University, Bangkok, 10330, Thailand.

† urn:lsid:zoobank.org:author:46C52EE1-A383-4C86-BF97-39E07C195075 ‡ urn:lsid:zoobank.org:author:71532F45-BDD5-415D-BC54-86256E5D5D4A § urn:lsid:zoobank.org:author:B003CBAC-C965-4BD1-A0D8-579AF9F8CCF4 |

Corresponding authors: Sergei I. Golovatch (sgolovatch@yandex.ru), Somsak Panha (somsakp@sc.chula.ac.th)

Academic editor: Robert Mesibov  |  Received 19 November 2010 | Accepted 11 December 2010 | Published 17 December 2010

Citation: Likhitrakarn N, Golovatch SI, Prateepasen R, Panha S (2010) Review of the genus *Tylopus* Jeekel, 1968, with descriptions of five new species from Thailand (Diplopoda, Polydesmida, Paradoxosomatidae). Advances in the systematics of Diplopoda III. ZooKeys 72: 23–68. doi: 10.3897/zookeys.72.744

**Abstract**

The genus *Tylopus* currently contains 41 species, all keyed and mapped, including five new from northern Thailand: *T. bispinosus* sp. n., *T. grandis* sp. n., *T. extremus* sp. n., *T. veliger* sp. n. and *T. parajeekeli* sp. n. Species of *Tylopus* are predominantly forest-dwellers, especially in montane habitats where up to 9–10 species can coexist per faunule. We expect many more congeners to be discovered in future, in particular from poorly or relatively poorly prospected regions such as Laos (only two species recorded), Cambodia (no species yet), Vietnam (a few species), Myanmar (a few species) and southern China (one species only). Because the genus is so species-rich and as yet so poorly sampled, a phylogenetic analysis of *Tylopus* would be premature.

**Keywords**

millipede, *Tylopus*, taxonomy, new species, key, Thailand
**Introduction**

*Tylopus* Jeekel, 1968, is one of the largest and most common genera in the millipede family Paradoxosomatidae in Southeast Asia and adjacent parts of southern China. When last reviewed (Golovatch and Enghoff 1993), it comprised 35 species. Only one more has since been added (Golovatch 1995), thus bringing the number of known species to 36.

The present paper provides a new review of *Tylopus*, based on numerous recently collected samples which also include five new species from northern Thailand. These new species are described herein, another seven are redescribed based on additional samples, and a new key is provided to incorporate all 41 species currently known to comprise *Tylopus*. We are confident that many more species in this genus will be found in future, given that several large areas in Laos, Myanmar, Cambodia and Vietnam, as well as in southern China, are as yet poorly sampled for millipedes. At present, perhaps only Thailand can be regarded as relatively well prospected, and has already yielded 26 *Tylopus* species.

**Material and methods**

New material derives from several provinces of northern Thailand taken between 2006 and 2010. All holotypes, as well as most of the paratypes and non-types, are in the collection of the Museum of Zoology, Chulalongkorn University, Bangkok, Thailand (CUMZ), some duplicates also being donated to the collections of the Natural History Museum of Denmark, University of Copenhagen, Denmark (ZMUC), and of the Zoological Museum, State University of Moscow, Russia (ZMUM), as indicated in the text.

Coloration was photographed in the laboratory (both live and alcohol material) for all of the encountered species. Material was then fixed, preserved in 75% ethanol and studied in the lab using a standard Olympus stereomicroscope. Scanning electron micrographs (SEM) were taken using a JEOL, JSM-5410 LV microscope. After SEM examination of the gonopods, they were returned to alcohol.

**Taxonomic part**

**Checklist**

The following species of *Tylopus* have heretofore been described, all arranged in alphabetic order and supplied with geographic details:

*T. affinis* Golovatch & Enghoff, 1993 – Thailand, Chiang Mai Province, Doi Suthep National Park, Doi Pui summit, 1650 m; Doi Inthanon National Park, Mae Chaem road, 1700 m; same locality, main road, 1900 m.
Review of the genus *Tylopus* Jeekel, 1968, with descriptions of five new species from Thailand

25

*T. allorugosus* Golovatch & Enghoff, 1993 – Thailand, Chiang Mai Province, Doi Inthanon National Park, Siriphum Waterfall, 1300–1400 m; same locality, ca 1600 m; same locality, Mae Chaem road, 1700 m; same locality, main road, 1900 m; same locality, main road, 2200 m; same locality, 2200–2500 m; Doi Suthep National Park, Doi Pui summit, 1650 m.

*T. amicus* Golovatch & Enghoff, 1993 – Thailand, Chiang Mai Province, Doi Pha Hom Pok National Park, northwest of Fang, 1550–1750 m.

*T. asper* Golovatch & Enghoff, 1993 – Thailand, Chiang Mai Province, Doi Inthanon National Park, 1500 m.

*T. baenzigeri* Golovatch & Enghoff, 1993 – Thailand, Chiang Mai Province, Doi Suthep National Park, Doi Pui-Chang Khian, 1400 m; same locality, 1400–1500 m; Doi Suthep National Park, near stream, 1100 m.

*T. coriaceus* Golovatch & Enghoff, 1993 – Thailand, Chaiyaphum Province, Khon San District, Phu Kheio, 16°22′N, 101°34′E, 1000 m.

*T. crassipes* Golovatch, 1984 – Vietnam, Lao cai Province, O quy ho, near Sa pa, 1900 m; same locality, near stream, 1950 m.

*T. degerboelae* Golovatch & Enghoff, 1993 – Thailand, Chiang Mai Province, Doi Suthep National Park, forest near stream, 1000 m; same locality, Doi Pui road, 1000 m; same locality, 1100 m; same locality, evergreen forest, 1300 m; same locality, evergreen forest, 1400 m; same locality, 1450 m; same locality, 1500 m; Doi Inthanon National Park, 1500 m; same locality, main road, 1600 m; Doi Chiang Dao, limestone area.

*T. doriae* (Pocock, 1895) – east-central Myanmar, Yado, 1000–1400 m, Bia-po, 1000–1200 m, Meteleo, 900–1200 m; Puepoli, 900–1200 m; Thailand, Chiang Mai Province, Doi Suthep National Park, 1400–1500 m.

*T. granulatus* Golovatch, 1984 – Vietnam, Ninh binh Province, Cuc Phuong Nature Reserve, forest.

*T. haplorugosus* Golovatch & Enghoff, 1993 – Thailand, Chiang Mai Province, Doi Inthanon National Park, main road, 1900 m.

*T. hilaris* (Attems, 1937) – Vietnam, Bana, 1500 m.

*T. hilaroides* Golovatch, 1984 – Vietnam, Ninh binh Province, Cuc Phuong Nature Reserve, forest.

*T. hoffmani* Golovatch & Enghoff, 1993 – Thailand, Chiang Mai Province, Doi Suthep, summit, 1600 m.

*T. jeekeli* Golovatch & Enghoff, 1993 – Thailand, Chiang Mai Province, Doi Inthanon National Park, Siriphum Waterfall, 1200–1300 m.

*T. maculatus* Golovatch, 1984 – Vietnam, Lao cai Province, O quy ho, near Sa pa, 1950 m.

*T. magicus* Golovatch, 1984 – Vietnam, Lao cai Province, O quy ho, near Sa pa, 1950 m.

*T. mutilatus* (Attems, 1953) – Laos, Luang Prabang; Xieng Kuang; Vietnam, Lam Dong Province, Peak Langbian.

*T. nodulipes* (Attems, 1953) – Laos, Luang Prabang; Vietnam, Lao cai Province, Mt Fan-Si-Pan.
T. pallidus Golovatch & Enghoff, 1993 – Thailand, Chiang Mai Province, Doi Pha Hom Pok, northwest of Fang, 1550–1750 m.

T. perarmatus Hoffman, 1973 – Thailand, Chiang Mai Province, Doi Suthep National Park, east slope, 1100–1275 m; same locality, 1000 m, same locality, 1100 m; same locality, Mahidol Waterfall, 1250 m; same locality, 1400–1500 m; ca 10 miles west of Chiang Mai; Doi Inthanon National Park, Siriphum Waterfall, 1300–1400 m; same locality, Vajirathan Waterfall, 750 m; Doi Chiang Dao, ca 500 m; same locality, limestone cave; Lampang Province, Thoen District, ca 8 km east of Ban Huai Kaeo, sandy bank of stream, 900 m.

T. perplexus Golovatch & Enghoff, 1993 – Thailand, Chiang Mai Province, Doi Pha Hom Pok, northwest of Fang, 1550–1750 m.

T. poolpermorum Golovatch & Enghoff, 1993 – Thailand, Chiang Mai Province, Doi Pha Hom Pok, northwest of Fang, 1550–1750 m.

T. procurvus Golovatch, 1984 – Vietnam, Lao cai Province, O quy ho, pass between Lao cai and Lai chau provinces, 2160 m; same locality, O quy ho, near Sa pa, near stream, 1950 m.

T. prosperus Golovatch & Enghoff, 1993 – Thailand, Chiang Mai Province, Doi Inthanon National Park, main road, 2200 m; same locality, summit, 2500 m.

T. pulvinipes Golovatch & Enghoff, 1993 – Thailand, Chaiyaphum Province, Phu Kheio, 16°22'N, 101°34'E, Tong Kamang Noi, forest, 1000 m.

T. rugosus Golovatch & Enghoff, 1993 – Thailand, Chiang Mai Province, Chiang Dao, 1800 m.

T. semirugosus Golovatch & Enghoff, 1993 – Thailand, Tak Province, Mae Sot District, Ban Mussoe.

T. sigma (Attems, 1953) – Vietnam, Lao cai Province, Sa pa.

T. silvestris (Pocock, 1895) – Myanmar, village of Thao (Carin Ghecu), 1200–1400 m.

T. similirugosus Golovatch & Enghoff, 1993 – Thailand, Chiang Mai Province, Doi Suthep National Park, 1000 m; same locality, 1400–1500 m.

T. sinensis Golovatch, 1995 – China, Yunnan Province, Mengzi County, Pot Hole No. 2 (Ha Fa Tiao Dong).

T. strongylosomoides (Korsós & Golovatch, 1989) – Vietnam, Vinh phu Province, Tam Dao, north of the village.

T. subcoriaceus Golovatch & Enghoff, 1993 – Thailand, Chiang Mai Province, Doi Suthep National Park, near stream, 1000 m; same locality, evergreen forest, 1100 m.

T. tamdaoensis Korsós & Golovatch, 1989 – Vietnam, Vinh phu Province, Tam Dao, north of the village; same locality, subtropical rain forest, ca 800–1200 m.

T. topali Golovatch, 1984 – Vietnam, Ninh binh Province, Cuc Phuong Nature Reserve.

Gonopod structure

*Tylopus* is known to be defined, among other characters, by its relatively elaborate gonopod conformation, sometimes perhaps amongst the most complex not only in the tribe
Review of the genus Tylopus Jeekel, 1968, with descriptions of five new species from Thailand

Sulciferini it belongs to, but also in the Paradoxosomatidae as a whole. Even though a thorough, still fully valid review of gonopod structure is available (Golovatch and Enghoff 1993), we feel tempted to reiterate here the main morphological terms before describing new species and providing some descriptive notes concerning already known congeners.

The gonopod telopodite in Tylopus usually shows a distinct transverse ring, or cingulum, demarcating the postfemoral region which starts at the base of a free, flagelliform solenomere. The solenomere is largely sheathed by a slender and sigmoid solenophore usually bearing a number of outgrowths at its base. The cingulum is only rarely incomplete due to a somewhat reduced sulcus at the base of lobe I, like the one observed in T. grandis sp. n. (Figs 5 and 6). Usually lobe I is simple, but sometimes it can be crowned with a larger (e.g. T. extremus sp. n., Figs 8 and 9, or T. veliger sp. n., Figs 11 and 12) or smaller outgrowth (e.g. T. degerboelae, Figs 20 and 21, or T. nodulipes). In addition to lobe I, the postfemoral region is nearly always supplied with a more or less evident process h lying mesally of the lobe. However, h is absent from T. strongylosomoides. All other disto- and/or postfemoral outgrowths, based on their positions, appear to be even more optional. Thus, process z is mostly discernible, yet occasionally very small (e.g. T. parajeekeli, Figs 14 and 15, T. jeekeli, Figs 26 and 27, or T. hoffmani) to fully missing (e.g. T. degerboelae, Figs 20 and 21, T. haplorogus, Figs 23 and 24, or T. prosperus, Figs 29 and 30). Only a few species appear to show particularly complex gonopods. Then not only does the postfemoral region bear a long, spiniform process z, e.g. T. perarmatus (Figs 34 and 35), but also the femorite can be supplied with a small, inconspicuous, lobiform (e.g. T. tamdaoensis) to very long, knife- to spine-shaped, distodorsal outgrowth m (T. extremus sp. n., Figs 8 and 9, or T. perplexus). Besides this, even a few more structures can be added to the postfemoral region, as is observed in T. perplexus. It is the sizes and shapes of these various outgrowths that provide several further important species-specific characters in addition to a good number of peripheral ones (Golovatch and Enghoff 1993).

Description of new species

Tylopus bispinosus sp. n.
urn:lsid:zoobank.org:act:D501889C-39AB-427B-A47D-0903412C651C
Figs 1–3

Holotype ♀ (CUMZ), Thailand, Tak Province, Umphang District, near Umphang City, ca 490 m, 16°2′20″N, 98°52′E, 6.07.2009, leg. S. Panha, J. Sutcharit & N. Likhitrakarn.

Paratypes: 1 ♂, 1 ♀, 2 juv. (CUMZ), same locality, together with holotype. 6 ♂, 4 ♀ (CUMZ), 3 ♂ (ZMUC), 3 ♂ (ZMUM), Tak Province, Umphang District, Doi Hua Mod, 900 m, 16°3′14″N, 98°49′16″E, 5.06.2009, leg. S. Panha, J. Sutcharit & N. Likhitrakarn. 6 ♂, 1 ♀ (CUMZ), same Province, same District, Cave Ta Ko Bi, ca 530 m, 16°03′14″N, 98°49′14″E, 5.07.2009, leg. S. Panha, J. Sutcharit & N. Likhitrakarn.
Name: To emphasize the spiniform processes $h$ and $z$ of the gonopod.

Diagnosis: Differs from congeners in both processes $h$ and $z$ of the gonopod being spiniform.

Description: Length 26 mm (holotype), 25–29 mm ($\delta$), 33–38 mm ($\varphi$), width of midbody pro- and metazona 2.0 and 2.9 mm (holotype), 1.8–2.4 and 3.1–3.2 mm ($\delta$), 2.4–2.7 and 3.3–3.8 mm ($\varphi$), respectively. Coloration of live animals black-
Review of the genus *Tylopus* Jeekel, 1968, with descriptions of five new species from Thailand

Figure 2. *Tylopus bispinosus* sp. n., ♂ paratype from Doi Hua Mod. A, B right gonopod, mesal and lateral views, respectively. C–F distal part of right gonopod, mesal, lateral, subcaudal and suboral views, respectively. Scale bar: 0.2 mm.

Figure 3. *Tylopus bispinosus* sp. n., ♂ paratype from Doi Hua Mod. A, B right gonopod, lateral and mesal views, respectively. Scale bar: 0.5 mm.
brown (Fig. 1A); calluses of paraterga, venter and legs only slightly lighter, dark brown, but turning light brown in alcohol (Fig. 1A–K).

Clypeolabral region of head very densely, vertigial region sparsely setose. Epicranial suture distinct. Antennae long and slender, reaching behind segment 4 (♂) or 3 (♀) dorsally. In width, head < collum < segments 3–4 < 2 < 5–16 (♂), or head = segment 3 < 4 < collum < segments 5–16 (♀); thereafter body gradually and gently tapering towards telson (Fig. 1B).

Tegument generally rather smooth and shining, but prozona very finely rugulose, metaterga often rugose (Fig. 1B–G); surface below paraterga finely microgranular (Fig. 1E, F). Collum with three transverse rows of setae: 5+5 in anterior, 2+2 in middle, and 4+4 in posterior row; paraterga evident, rounded, flap-shaped (Fig. 1B, C). Metaterga with two transverse rows of rather long setae: 2+2 in anterior and 2(3)+2(3) in posterior row, the latter often abraded, but then readily traceable as insertion points. Axial line at most barely visible only on metaterga. Paraterga strongly developed (Fig. 1A–G), lying high (at 1/3–1/4 midbody height), only slightly inclined laterally, pointed caudally and acutangular already from segment 2, especially strongly so on caudal segments; calluses very thin on poreless segments, slightly thicker on pore-bearing ones; anterior 1/3 of poreless calluses with two evident (anterior larger, posterior smaller), lateral, setigerous incisions, but with only a single strong one (anterior) on pore-bearing calluses (Fig. 1B–G); paraterga more strongly developed in ♂. Ozopores entirely lateral, lying in an ovoid groove about 1/3 in front of caudal corner, the latter always surpassing rear tergal contour (Fig. 1B–H). Transverse sulcus evident on metaterga 4–18, reaching base of paraterga, evident and rather deep, faintly rugulose at bottom. Stricture between pro- and metazona very clearly ribbed (Fig. 1D). Epiproct tip faintly concave to subtruncate, pre-apical papillae evident (Fig. 1G). Hypoproct roundly subtrapeziform, caudal setae strongly separated (Fig. 1H). Pleurosternal carinae well-developed on segments 2–17 (♂) or 2–7 (♀), mostly as low bulges anteriorly and a distinct spine posteriorly (Fig. 1C, E, F).

Sternal moderately setose, without modifications; a deeply notched sternal lobe between ♂ coxae 4 (Fig. 1I, J). Legs long and slender (Fig. 1B, C, H), especially so in ♂ compared to ♀ (1.3–1.5 versus 0.9–1.1 times as long as midbody height); prefemora distinctly bulged laterally (Fig. 1K), acropodites with particularly dense, nearly adpressed setae, including tarsal brushes.

Gonopods (Figs 2, 3) with lobe l well-demarcated; spine h very small; spine z considerably more prominent.

Tylopus grandis sp. n.
urn:lsid:zoobank.org:act:148C0F96-F560-437A-92FC-6FA159B96699
Figs 4–6

Holotype ♂ (CUMZ), Thailand, Mae Hong Son Province, Pangmapha District, near Cave Pha Mon, 19.07.2008, leg. S. Panha, J. Sutcharit & N. Likhitrakarn.
Paratypes: 1 ♂, 2 ♀ (CUMZ), same locality, together with holotype. 1 ♂ (CUMZ), same District, Mae Lana crossroads, 19.07.2008, leg. S. Panha, J. Sutcharit & N. Likhittrakarn.

Name: To emphasize the large size of this species

Diagnosis: Differs from congeners in the large size, coupled with a short spiniform process h, a basally only poorly delimited lobe l, and a small lobiform process z of the gonopod.

Description: Length 41 mm (holotype), 40–42 mm (♂), 38–39 mm (♀), width of midbody pro- and metazona 3.0 and 4.5 mm (holotype), 2.8–3.0 and 4.3–4.5 mm (♂), 3.6–3.8 and 4.7–5.0 mm (♀), respectively. Coloration in alcohol dark
Figure 5. *Tylopus grandis* sp. n., ♀ paratype from Mae Lana. **A, B** right gonopod, mesal and lateral views, respectively. **C–E** distal part of right gonopod, mesal, lateral and suboral views, respectively. Scale bar: 0.2 mm.

Figure 6. *Tylopus grandis* sp. n., ♂ paratype from Mae Lana. **A, B** right gonopod, lateral and mesal views, respectively. Scale bar: 0.5 mm.
brown to black-brown (Fig. 4A–G): calluses, venter and antennomeres 1–5 slightly to considerably lighter, brown to light yellow-brown (Fig. 1A–G), antennomeres 6 and 7 dark brown.

All characters as in *T. bispinosus* sp. n., except as follows.

Antennae short and slender (Fig. 4B), reaching behind segment 3 (♂) or 2 (♀) dorsally. In width, head < collum = segments 3–4 < 2 = 5–16 (♂), or head < segments 3–4 < collum < segment 2 < 5–16 (♀); thereafter body gradually and gently tapering towards telson (Fig. 4A–F).

Tegument generally rather smooth and either dull (only in places modestly shining) or shining (Fig. 4A–G). Paraterga strongly developed (Fig. 4A–G), lying high (at 1/4–1/5 midbody height), subhorizontal to slightly upturned laterally (Fig. 4A–F). Transverse sulcus either absent or poorly developed, then not reaching bases of paraterga 4, always evident and reaching bases of paraterga 5–18, rather faintly rugulose at bottom. Stricture between pro- and metazona rather faintly beaded to striolate (Fig. 4A–C). Epiproct tip evidently emarginate, pre-apical papillae very distinct (Fig. 4F, G). Hypoproct semi-circular, caudal setae strongly separated (Fig. 4G). Pleurosternal carinae visible on segments 2–15(16) (♂) or segments 2–6 (♀), mostly as low bulges anteriorly and a more or less distinct denticle posteriorly (Fig. 4B, D).

Sternae moderately setose, without modifications; a slightly notched sternal lobe between ♂ coxae 4 (Fig. 4H, I). Legs long and slender (Fig. 1B, C, H), especially so in ♂ compared to ♀ (1.7–1.8 versus 1.5–1.6 times as long as midbody height); ♂ prefemora distinctly bulged laterally (Fig. 4J), acropodites with particularly dense, nearly adpressed setae, but tarsal brushes missing.

Gonopods (Figs 5, 6) with lobe *l* poorly demarcated at base; spine *h* very small; process *z* not spiniform, but like a short lobe.

**Tylopus extremus** sp. n.
urn:lsid:zoobank.org:act:188F2E10-CAC7-406A-B176-6818DF526D0B
Figs 7–9

**Holotype** ♂ (CUMZ), Thailand, Chiang Mai Province, Fang District, Doi Phahom Pok National Park, 6.07.2009, leg. A. Pansook.

**Paratypes:** 1 ♂, 1 ♀ (CUMZ), 1 ♂ (ZMUC), 1 ♂ (ZMUM), same locality, together with holotype.

**Name:** To emphasize the extremely long spines *h* and *m* of the gonopod.

**Diagnosis:** Differs from congeners in process *h* being subflagelliform while process *m* extremely long and prominent.

**Description:** Length ca 30 mm (holotype), 27–30 mm (♂), 32.5 mm (♀), width of midbody pro- and metazona 2.0 and 2.9 mm (holotype), 1.9–2.4 and 2.8–3.3 mm (♂), 2.5 and 3.0 mm (♀), respectively. Coloration of live animals, as well as of alcohol material black-brown (Fig. 7A–G): calluses of paraterga and antennae only slightly
lighter, light brown to brown, venter and legs contrastingly light, yellow (Fig. 7A–G), tip of antennae pallid.

All characters as in *T. bispinosus* sp. n., except as follows.

Antennae rather short and slender, reaching behind to end of segment 3 (♂) dorsally. Collum with paraterga like rudimentary flaps, especially poorly developed in ♀. In width, head < collum = segments 3–4 < 2 < 5–16 (♂) (Fig. 7B), or head < collum < segment 3 < 2 and 4 < 5–16(♀); thereafter body gradually and gently tapering towards telson.

**Figure 7.** *Tylopus extremus* sp. n., ♂ paratype (A–K). A habitus, live coloration B, C anterior part of body, dorsal and lateral views, respectively D, E segments 10 and 11, dorsal and lateral views, respectively F, G, H posterior part of body, lateral, dorsal and ventral views, respectively I, J sternal cones between coxae 4, subcaudal and sublateral views, respectively K midbody leg.
Review of the genus *Tylopus* Jeekel, 1968, with descriptions of five new species from Thailand

Figure 8. *Tylopus extremus* sp. n., ♂ paratype. A, B right gonopod, mesal and lateral views, respectively. C–F distal part of right gonopod, mesal, lateral, subcaudal and suboral views, respectively. Scale bar: 0.2 mm.

Figure 9. *Tylopus extremus* sp. n., ♂ paratype. A, B right gonopod, lateral and mesal views, respectively. Scale bar: 0.5 mm.
Metaterga with two transverse rows of rather long setae: 2+2 in anterior and 2(3)+2(3) in posterior row, the latter often abraded, but then readily traceable as insertion points on low longitudinal ridges or tubercles (Fig. 7B–G). Axial line thin, visible on both halves of metaterga. Paraterga strongly developed (Fig. 7A–G), lying rather low (at 1/2–1/3 midbody height), slightly inclined laterally, pointed caudally and acutangular already from segment 2, especially strongly so on caudal segments, very clearly surpassing rear contour only on segments 16–19; anterior 1/3 of poreless calluses with two barely visible, lateral, setigerous incisions, but with only a single, likewise poorly developed incision anteriorly on pore-bearing calluses (Fig. 7B–F); paraterga slightly less strongly developed in ♀. Transverse sulcus evident on metaterga 5–18, reaching bases of paraterga, evident and rather deep, faintly rugulose at bottom. Stricture between pro- and metazona weakly striolate (Fig. 7B–G). Epiproct emarginate at tip, pre-apical papillae evident (Fig. 7G). Hypoproct subtrapeziform, caudal setae widely separated (Fig. 7H). Pleurosternal carinae as compete ridges with a caudal tooth on segments 2–4 (♂) or 2 and 3 (♀), like separated anterior bulges and increasingly poorly developed caudal denticles until segment 16 (Fig. 7C, E, F).

Sternae moderately setose, without modifications; an entire, linguiform, sternal lobe between ♀ coxae 4 (Fig. 71. J). Legs long, in ♀ very distinctly incrassate, 1.7–2.0 or ca 1.3 times as long as midbody height in ♀ and ♀, respectively (Fig. 7B, C, H), ♀ prefemora very distinctly bulged laterally and clothed with dense and adpressed pilosity ventrally (Fig. 7K), acropodites also with similarly dense and ventrally adpressed pilosity, including tarsal brushes. All ♀ postfemora and tibiae except for a few posteriormost ones with a small, but evident adenostyle (= tubercle) at midway on ventral side (Fig. 7K).

Gonopods (Figs 8, 9) with lobe l well-demarcated, but unusually prominent, high and elongated; spine h long, extremely slender and subflagelliform; spine z rather short and simple; spine m very prominent, straight and long.

**Tylopus veliger** sp. n.
urn:lsid:zoobank.org:act:54694D7D-8C76-4705-B81F-0949DFE0D787
Figs 10–12

**Holotype** ♀ (CUMZ), Thailand, Nan Province, Pua District, Ton Tong Waterfall, ca 1130 m, 19°10’52”N, 101°5’45”E, 10.10.2009, leg. S. Panha, J. Sutcharit & N. Likhitrakarn.

**Name**: To emphasize the velum-shaped end of gonopod lobe l.

**Diagnosis**: Differs from congeners except *T. perplexus* Golovatch & Enghoff, 1993 in the distal part of gonopod lobe l being velum-shaped and supplied with two denticles, from *T. perplexus* in the gonopod lacking spines m and q, as well as in a much shorter and knife-shaped spine z, and a rudimentary spine h.

**Description**: Length ca 28 mm, width of midbody pro- and metazona 2.0 and 2.6 mm, respectively. Coloration of live animal and alcohol material rather uniformly
dark brown to blackish (Fig. 1A); calluses of paraterga only slightly flavous, brown; antennomeres 1–6 and genae light brown; venter and legs contrastingly yellowish to light brown (Fig. 10A–G).

All characters as in *T. bispinosus* sp. n., except as follows.

Clypeolabral region of head very densely setose, but vertigial region bare. Antennae short and barely reaching behind segment 2 dorsally. In width, head = segments 3 and 4 < collum < segment 2 < 5–16; thereafter body gradually and gently tapering.
Figure 11. *Tylopus veliger* sp. n., ♂ holotype. A, B right gonopod, mesal and lateral views, respectively C–F distal part of right gonopod, mesal, lateral, subcaudal and suboral views, respectively. Scale bar: 0.2 mm.

Figure 12. *Tylopus veliger* sp. n., ♂ holotype. A, B right gonopod, lateral and mesal views, respectively. Scale bar: 0.5 mm.
Review of the genus Tylopus Jeekel, 1968, with descriptions of five new species from Thailand

...towards telson (Fig. 10A–G). Collum with small, narrowly delimited, rounded, strip-shaped paraterga (Fig 10B, C).

Metaterga with two transverse rows of long setae: 2+2 in anterior and 2(3)+2(3) in posterior row, the latter often abraded, but then readily traceable as insertion points. Axial line thin, in places incomplete, but readily visible on both halves of metaterga. Paraterga strongly developed (Fig. 10A–G), lying relatively low (at 1/2–1/3 midbody height), evidently inclined ventrolaterally, pointed caudally and acutangular already from segment 2, especially strongly so and surpassing rear tergal contour on segments 16–19; calluses slightly thinner on poreless segments than on pore-bearing ones; poreless calluses with two lateral setigerous incisions, but with only a single, more evident one (anterior) on pore-bearing calluses (Fig. 10B–G). Transverse sulcus evident on metaterga 5–18, reaching bases of paraterga, evident and rather deep, finely, densely and clearly ribbed at bottom. Stricture between pro- and metazona very clearly ribbed (Fig. 10B–G). Epiproct tip clearly emarginate, pre-apical papillae evident (Fig. 10F–H). Hypoproct semi-circular, caudal setae strongly separated (Fig. 10H). Pleurosternal carinae as complete ridges on segments 2–4, thereafter broken into an anterior bulge and a caudal tooth, both growing increasingly reduced until segment 16 (Fig. 10C, E, F).

Sternae rather densely setose, without modifications except for a subquadrate, setose, sternal lobe between coxae 4 (Fig. 10I, J). Legs relatively short, ca 1.2–1.3 times as long as midbody height, evidently incrassate (Fig. 10C, F, K); prefemora distinctly bulged laterally and clothed with mostly adpressed setae ventrally (Fig. 10K), acropodites likewise with very dense, mostly adpressed setae ventrally; postfemora and tibiae slightly bulged ventrally; tarsal brushes missing.

Gonopods (Figs 11, 12) with lobe \( l \) well-demarcated, high and prominent, apically with a pointed fan-shaped structure (= velum) and two denticles; spine \( h \) very small, dentiform; spine \( z \) prominent, knife-shaped, lying above \( l \) on lateral side.

**Tylopus parajeekeli** sp. n.

urn:lsid:zoobank.org:act:703DB743-0898-4B3A-8D37-A4DD31FE7CD1

Figs 13–15

**Holotype** ♂ (CUMZ), Thailand, Chiang Mai Province, Chom Thong District, Doi Inthanon National Park, summit, 2520 m, 18°34'29"N, 98°28'48"E, 12.10.2009, leg. S. Panha, J. Sutcharit & N. Likhitrakarn.

**Paratype:** 1 ♂ (CUMZ), same locality, together with holotype.

**Name:** To emphasize the close resemblance to *T. jeekeli* Golovatch & Enghoff, 1993.

**Diagnosis:** Very similar to *T. jeekeli*, especially as regards its gonopod conformation, but differs in the paraterga lying much lower (at ca 1/3 versus 1/4–1/5 midbody height), in the caudal corners of the paraterga protruding behind the rear tergal contour already from segment 16 (versus segment 2), and also in gonopod spine \( z \) being much smaller and placed closer to the base of spine \( h \).
Description: Length 31 mm (holotype) or 31.5 mm (♂), width of midbody pro- and metazona 2.4 and 3.2 mm (holotype) or 2.3 and 3.4 mm (♂), respectively. Coloration of live animals and alcohol material uniformly blackish-brown (Fig. 13A–G); calluses of paraterga a little lighter, brown; antennomeres 1–5 light brown to yellowish, legs and venter light brown to grey-yellowish (Fig. 13A–G).

All characters as in *T. bispinosus* sp. n., except as follows.

Figure 13. *Tylopus parajeekeli* sp. n., ♂ holotype (A) and ♂ paratype (B–K). A habitus, live coloration B, C anterior part of body, dorsal and lateral views, respectively D, E segments 10 and 11, dorsal and lateral views, respectively F, G, H posterior part of body, lateral, dorsal and ventral views, respectively I, J sternal cones between coxae 4, subcaudal and sublateral views, respectively K midbody leg.
Figure 14. Tylopus parajeekeli sp. n., ♀ paratype. A, B right gonopod, mesal and lateral views, respectively. C–F distal part of right gonopod, submesal, sublateral, subcaudal and suboral views, respectively. Scale bar: 0.2 mm.

Figure 15. Tylopus parajeekeli sp. n., ♂ paratype. A, B right gonopod, lateral and mesal views, respectively. Scale bar: 0.5 mm.
Antennae rather short and slender, reaching behind segment 3 dorsally. In width, head = segment 3 < collum < segments 2 and 4 < 5–16; thereafter body gradually and gently tapering towards telson (Fig. 1B).

Paraterga on collum like large rounded flaps (Fig. 13B, C). Following paraterga lying at about 1/3 midbody height, evidently declined ventrolaterally, subhorizontal only on a few posteriormost segments, mostly pointed caudally, subrectangular until segment 15, thereafter increasingly well protruding behind rear tergal contour (Fig. 13A–G). Metaterga with 2(3)+2(3) and 3–5+3–5 long setae arranged in two transverse rows. Axial line present on both halves of metaterga. Transverse sulcus present on segments 5–18, very finely beaded at bottom (Fig. 13B, F, G). Stricture between pro- and metazona finely striolate (Fig. 13B, D). Epiproct tip broad and emarginate (Fig. 13G, H). Hypoproct semi-circular, both caudal setae widely separated (Fig. 13H). Pleurosternal carinae as complete ridges on segments 2–4, thereafter retained until segment 17 mostly as a small caudal tooth (Fig. 13C–F).

A low, only slightly divided, setose lobe between coxae 4 (Fig. 13I, J). Legs relatively short, ca 1.6–1.7 times as long as midbody height (Fig. 13K). Femora evidently bulged laterally (Fig. 13K); all postgonopodal legs except two last pairs with an evident adenostyle in parabasal 1/3 of each postfemur and tibia; tarsal brushes missing; all telopoditomeres except tarsi with dense adpressed pilosity (Fig. 13K).

Gonopods (Figs 14, 15) with lobe l well-demarcated; spine h small, but elongate, not bifid; spine z very small, dentiform, placed at base of spine h.

New faunistic records

The following seven species have been illustrated in additional detail to confirm their identities, as well as to provide further information concerning both their variation and distribution.

**Tylopus allorugosus** Golovatch & Enghoff, 1993
Figs 16–18

*Tylopus allorugosus* Golovatch & Enghoff, 1993: 100. *Tylopus allorugosus*: Enghoff, 2005: 98.

**Material:** 2 ♂ (CUMZ), Thailand, Chiang Mai Province, Chom Thong District, Doi Inthanon National Park, Siriphum Waterfall, ca 1320 m, 18°32'49"N, 98°30'57"E, 13.10.2009, leg. S. Panha, J. Sutcharit & N. Likhitrakarn; 2 ♂ (CUMZ), same locality, main road, 10 km before summit, ca 1700 m, 18°31'15"N, 98°30'1"E, 13.10.2009, leg. S. Panha, J. Sutcharit & N. Likhitrakarn.

**Remarks.** This strictly topotypic material fully agrees with the original description (Golovatch and Enghoff 1993), showing no evident variation in peripheral and gonopod structure (Figs 16–18).
Review of the genus Tylopus Jeekel, 1968, with descriptions of five new species from Thailand

*Tylopus degerboelae* Golovatch & Enghoff, 1993

*Tylopus degerboelae* Golovatch & Enghoff, 1993: 111.

*Tylopus degerboelae* Enghoff, 2005: 99.

**Figure 16.** *Tylopus allorogosus* Golovatch & Enghoff, 1993. ♂ from 10 km before Doi Inthanon summit (A–K). A habitus, live coloration B, C anterior part of body, dorsal and lateral views, respectively D, E segments 10 and 11, dorsal and lateral views, respectively F, G, H posterior part of body, lateral, dorsal and ventral views, respectively I, J sternal cones between coxae 4, subcaudal and sublateral views, respectively K midbody leg.

*Tylopus degerboelae* Golovatch & Enghoff, 1993

Figs 19–21

*Tylopus degerboelae* Golovatch & Enghoff, 1993: 111.
*Tylopus degerboelae*: Enghoff, 2005: 99.
Figure 17. *Tylopus allorugosus* Golovatch & Enghoff, 1993, ♂ from 10 km before Doi Inthanon summit. 
A, B right gonopod, mesal and lateral views, respectively C–F distal part of right gonopod, submesal, sublateral, subcaudal and suboral views, respectively. Scale bar: 0.2 mm.

Figure 18. *Tylopus allorugosus* Golovatch & Enghoff, 1993, ♀ from 10 km before Doi Inthanon summit. 
A, B right gonopod, lateral and mesal views, respectively. Scale bar: 0.5 mm.
Review of the genus Tylopus Jeekel, 1968, with descriptions of five new species from Thailand

Material: 3 ♂ (CUMZ), Thailand, Chiang Mai Province, Mueang Chiang Mai District, Doi Suthep National Park, ca 1300 m, 18°48'9"N, 98°54'11"E, 20.04.2009, leg. S. Panha, J. Sutcharit & N. Likhitrakarn; 4 ♂, 3 ♀, 2 juv. (CUMZ), same Province, WiangKaen District, Doi Phatang, 6.07.2009, leg. S. Panha & J. Sutcharit.

Remarks. This partly topotypic material fully agrees with the original description (Golovatch and Enghoff 1993), showing only slight variation in general coloration (ranging from pale castaneous to piceous), in ♂ prefemora often being considerably bulged laterally, and in the tip of lobe I of the gonopod often devoid of apical denticles (Figs 19–21).

Tylopus haplorugosus Golovatch & Enghoff, 1993
Figs 22–24

Tylopus haplorugosus Golovatch & Enghoff, 1993: 99.
Tylopus haplorugosus: Enghoff, 2005: 99.

Material: 1 ♂ (CUMZ), Thailand, Chiang Mai Province, Chom Thong District, Doi Inthanon National Park, main road, 10 km before summit, ca 1700 m, 18°31'15"N, 98°30'1"E, 13.10.2009, leg. S. Panha, J. Sutcharit & N. Likhitrakarn.

Remarks. This strictly topotypic material fully agrees with the original description (Golovatch and Enghoff 1993), showing no evident variation in peripheral and gonopod structure (Figs 22–24).

Tylopus jeekeli Golovatch & Enghoff, 1993
Figs 25–27

Tylopus jeekeli Golovatch & Enghoff, 1993: 108.
Tylopus jeekeli: Enghoff, 2005: 99.

Material: 4 ♂, 7 ♀, 1 juv. (CUMZ), Thailand, Chiang Mai Province, Mueang Chiang Mai District, Doi Suthep National Park, ca 1300 m, 18°48'9"N, 98°54'11"E, 22.10.2009, leg. S. Panha, J. Sutcharit & N. Likhitrakarn.

Remarks. This represents a second record of this species, the type locality being Doi Inthanon National Park in the same province. Our material almost fully agrees with the original description (Golovatch and Enghoff 1993), showing slight variation only in spine h of the gonopod being non-bifid, but simple and entire (Figs 25–27).
Figure 19. *Tylopus degerboelae* Golovatch & Enghoff, 1993, ♂ from Doi Suthep National Park (A–K). A habitus, live coloration B, C anterior part of body, dorsal and lateral views, respectively D, E segments 10 and 11, dorsal and lateral views, respectively F, G, H posterior part of body, lateral, dorsal and ventral views, respectively I, J sternal cones between coxae 4, subcaudal and sublateral views, respectively K midbody leg.

*Tylopus prosperus* Golovatch & Enghoff, 1993

Figs 28–30

*Tylopus prosperus* Golovatch & Enghoff, 1993: 93.  
*Tylopus prosperus*: Enghoff, 2005: 99.
Review of the genus Tylopus Jeekel, 1968, with descriptions of five new species from Thailand

Figure 20. Tylopus degerboelae Golovatch & Enghoff, 1993, ♂ from Doi Suthep National Park. A, B right gonopod, mesal and lateral views, respectively C–F distal part of right gonopod, mesal, lateral, subcaudal and suboral views, respectively. Scale bar: 0.2 mm.

Figure 21. Tylopus degerboelae Golovatch & Enghoff, 1993, ♂ from Doi Suthep National Park. A, B right gonopod, lateral and mesal views, respectively. Scale bar: 0.5 mm.
Material: 2 ♂ (CUMZ), Thailand, Chiang Mai Province, Chom Thong District, Doi Inthanon National Park, summit, 2520 m, 18°34'29"N, 98°28'48"E, 12.10.2009, leg. S. Panha, J. Sutcharit & N. Likhitrakarn.

Remarks. This strictly topotypic material fully agrees with the original description (Golovatch and Enghoff 1993), showing no evident variation in peripheral and gonopod structure (Figs 28–30).

Figure 22. *Tylopus haplorugosus* Golovatch & Enghoff, 1993, ♂ (A–K). A habitus, live coloration B, C anterior part of body, dorsal and lateral views, respectively D, E segments 10 and 11, dorsal and lateral views, respectively F, G, H posterior part of body, lateral, dorsal and ventral views, respectively I, J sternal cones between coxae 4, subcaudal and sublateral views, respectively K midbody leg.
Review of the genus *Tylopus* Jeekel, 1968, with descriptions of five new species from Thailand

Figure 23. *Tylopus haplorugosus* Golovatch & Enghoff, 1993, ♂. **A, B** right gonopod, mesal and lateral views, respectively. **C–F** distal part of right gonopod, mesal, lateral, subcaudal and suboral views, respectively. Scale bar: 0.2 mm.

Figure 24. *Tylopus haplorugosus* Golovatch & Enghoff, 1993, ♂. **A, B** right gonopod, lateral and mesal views, respectively. Scale bar: 0.5 mm.
**Tylopus rugosus** Golovatch & Enghoff, 1993

Figs 31–33

*Tylopus rugosus* Golovatch & Enghoff, 1993: 95.

*Tylopus rugosus*: Enghoff, 2005: 99.

**Material:** 4 ♂ (CUMZ), Thailand, Chiang Mai Province, Phrao District, Bua-thong Waterfall forest park, 510 m, 19°4′10"N, 99°4′46"E, 29.09.2009, leg. N. Likhitratkarn.
Review of the genus *Tylopus* Jeekel, 1968, with descriptions of five new species from Thailand

Figure 26. *Tylopus jeekeli* Golovatch & Enghoff, 1993, ♂. A, B right gonopod, mesal and lateral views, respectively. C–F distal part of right gonopod, mesal, lateral, suboral and subcaudal views, respectively. Scale bar: 0.2 mm.

Figure 27. *Tylopus jeekeli* Golovatch & Enghoff, 1993, ♂. A, B right gonopod, lateral and mesal views, respectively. Scale bar: 0.5 mm.
Remarks. This near-topotypic material fully agrees with the original description (Golovatch and Enghoff 1993), showing no evident variation in peripheral and gonopod structure (Figs 31–33).

Figure 28. *Tylopus prosperus* Golovatch & Enghoff, 1993, ♂ (A–K). A habitus, live coloration B, C anterior part of body, dorsal and lateral views, respectively D, E segments 10 and 11, dorsal and lateral views, respectively F, G, H posterior part of body, lateral, dorsal and ventral views, respectively I, J sternal cones between coxae 4, subcaudal and sublateral views, respectively K midbody leg.
Figure 29. *Tylopus prosperus* Golovatch & Enghoff, 1993, ♂. A, B right gonopod, mesal and lateral views, respectively C–F distal part of right gonopod, sublateral, mesal, suboral and subcaudal views, respectively. Scale bar: 0.2 mm.

Figure 30. *Tylopus prosperus* Golovatch & Enghoff, 1993, ♂. A, B right gonopod, lateral and mesal views, respectively. Scale bar: 0.5 mm.
Figure 31. *Tylopus rugosus* Golovatch & Enghoff, 1993, ♂ (A–K). A habitus, live coloration B, C anterior part of body, dorsal and lateral views, respectively D, E segments 10 and 11, dorsal and lateral views, respectively F, G, H posterior part of body, lateral, dorsal and ventral views, respectively I, J sternal cones between coxae 4, subcaudal and sublateral views, respectively K midbody leg.

*Tylopus perarmatus* Hoffman, 1973

Figs 34–38

*Tylopus perarmatus* Hoffman, 1973: 372.  
*Tylopus perarmatus*: Golovatch & Enghoff, 1993: 106.  
*Tylopus perarmatus*: Enghoff, 2005: 99.
Review of the genus *Tylopus* Jeekel, 1968, with descriptions of five new species from Thailand

Figure 32. *Tylopus rugosus* Golovatch & Enghoff, 1993, ♂. A, B right gonopod, mesal and lateral views, respectively. C–F distal part of right gonopod, mesal, lateral, suboral and subcaudal views, respectively. Scale bar: 0.2 mm.

Figure 33. *Tylopus rugosus* Golovatch & Enghoff, 1993, ♂. A, B right gonopod, lateral and mesal views, respectively. Scale bar: 0.5 mm.
Material: 5 ♂, 3 ♀, 1 juv. (CUMZ), Thailand, Chiang Mai Province, Chom Thong District, Doi Inthanon National Park, Siriphum Waterfall, ca 1320 m, 18°32'49"N, 98°30'57"E, 13.10.2009, leg. S. Panha, J. Sutcharit & N. Likhitrakarn; 2 ♂, 2 ♀ (CUMZ), same province, Wiang Kaen District, Doi Phatang, 25.10.2008, leg. S. Panha & J. Sutcharit; 5 ♂, 2 ♀ (CUMZ), Lampang Province, Ngao District, Thum Pha Thai, 23.10.2008, leg. S. Panha, J. Sutcharit & N. Likhitrakarn; 1 ♂,

Figure 34. *Tylopus perarmatus* Hoffman, 1973, ♂ from Ton Tong Waterfall (A–K). A habitus, live coloration B, C anterior part of body, dorsal and lateral views, respectively D, E segments 10 and 11, dorsal and lateral views, respectively F, G, H posterior part of body, lateral, dorsal and ventral views, respectively I, J sternal cones between coxae 4, subcaudal and sublateral views, respectively K midbody leg.
Review of the genus *Tylopus* Jeekel, 1968, with descriptions of five new species from Thailand

Figure 35. *Tylopus perarmatus* Hoffman, 1973, ♂ from Ton Tong Waterfall. **A, B** right gonopod, mesal and lateral views, respectively. **C–F** distal part of right gonopod, mesal, lateral, suboral and subcaudal views, respectively. Scale bar: 0.2 mm.

Figure 36. *Tylopus perarmatus* Hoffman, 1973, ♂ from Ton Tong Waterfall. **A, B** right gonopod, lateral and mesal views, respectively. Scale bar: 0.5 mm.
Figure 37. *Tylopus perarmatus* Hoffman, 1973, ♂ from Ban Pang Rim Kon (A, B), ♂ from Ton Tong Waterfall (C, D), ♂ from Phucheeah (E, F), and ♂ from Ton Tong Waterfall (G, H). A–H distal part of right gonopod, lateral, mesal, lateral, mesal, lateral, mesal, lateral, and mesal views, respectively. Scale bar: 0.2 mm.

1 ♀ (CUMZ), Chiang Rai Province, Mueang Chiang Rai District, Ban Pang Rim Kon, 10.07.2006, leg. S. Panha; 1 ♂ (CUMZ), same province, Thoeng District, Phucheeah, 10.07.2006, leg. S. Panha & J. Sutcharit; 2 ♂, 1 ♀ (CUMZ), same province, Wiang Kaen District, Doi Pha Tang, 10.07.2006; 1 ♂, 2 ♀ (CUMZ), Phayao Province, Chiang Kham District, Nam Min Waterfall, 23.10.2008, leg. S. Panha & J. Sutcharit; 2 ♂, 2 ♀ (CUMZ), Phrae Province, Rong Kwang District, Tham Pha Nang Khoi, ca 280 m, 18°22’10”N, 100°21’12”E, 9.10.2009, leg. S. Panha, J. Sutcharit, & N. Likhitrakarn; 2 ♂, 2 ♀ (CUMZ), same locality, 29.09.2010, leg. J. Sutcharit & P. Pimvichai; 9 ♂, 6 ♀, 2 juv. (CUMZ), Nan Province, Pua District, Ton Tong Waterfall, ca 1130 m, 19°12’36”N, 101°4’14”E, 10.10.2009, leg. S. Panha, J. Sutcharit & N. Likhitrakarn.

Remarks. This species has long been known as perhaps the most widespread and common congener in northern Thailand, also showing considerable variation both in body texture and gonopod structure (Golovatch and Enghoff 1993). The new samples add to this variation in the gonopods often with spine h rather narrow and spiniform to broadly denti- or lobiform, and spine z nearly straight to strongly unciform (Figs 34–38).
A key to species of Tylopus (based chiefly on ♂)

1  Most ♂ prefemora evidently swollen laterally (Figs 1K, 4J, 7K, 10K, 13K, 16K, 19K, 22K, 25K, 28K, 31K, 34K) .........................................................

2  – All ♂ prefemora normal, not bulged laterally .....................................

25  Surface of metaterga virtually smooth, at best extremely faintly rugulose in certain places and/or with a few barely traceable (setiferous) tubercles near caudal margin (setae mostly broken off) .........................................................

3  – Surface of metaterga mostly rugulose to coarsely rugose/tuberculate ........

6  Paraterga moderately developed (Fig. 28A–G), ratio of ♂ midbody prozonite to metazonite width ca 1:1.15. Transverse sulcus on metaterga starting from segment 5, but fully developed and reaching base of paraterga only from segment 6. Calluses without incisions (Fig. 28A–G). Gonopod solenophore particularly slender (Figs 29, 30) ......................................................... T. prosperus

4  – Paraterga relatively well-developed, ratio of ♂ midbody prozonite to metazonite width over 1:1.2. Transverse sulcus on metaterga starting from segment 4 or 5, always fully developed and reaching base of paraterga on segment 5  ....
4 Calluses without incisions. Gonopod postfemoral lobe I much broader than long; area basal to I delimited by a distinct cingulum .......................... *T. magicus*
  – Calluses mostly with 1–2 incisions. Gonopod postfemoral lobe I either as long as broad or longer; no cingulum basal to I................................. 5

5 Metatergal surface entirely smooth, polished, without tubercles. Midline wanting. Pleurosternal carinae relatively weak, as small teeth only on a few anterior-most segments; ♀ legs without adenostyles (= tubercles). Gonopods with three rather small, spiniform processes near base of lobe I.................. *T. mutilatus*
  – Metaterga at best only very faintly rugulose near waist, near sulcus and/or at base of paraterga, with 2–3 weak, oblong tubercles near rear margin. Midline mostly traceable at least on anterior halves of metaterga. Pleurosternal carinae more strongly developed; most ♀ postfemora and tibiae tuberculiferous. Gonopods with only two larger outgrowths near base of lobe I........... *T. similirugosus*  

6 Metaterga without evident setiferous tubercles, only sometimes with very small, rudimentary wrinkles or knobs .......................................................... 7
  – Metaterga with evident setiferous tubercles ...................................................................................................................... 11

7 Body larger: 38–42 mm long, 2.8–3.8 and 4.3–5.0 mm wide on pro- and metaterga, respectively. Gonopod with a short spiniform process h, a basally only poorly delimited lobe I, and a small lobiform process z (Figs 5, 6)........
  .......................................................... *T. grandis* sp. n.
  – Body smaller. Gonopod otherwise ................................................................. 8

8 Both processes h and z of the gonopod spiniform (Figs 2–3) .........................
  .......................................................... *T. bispinosus* sp. n.
  – Gonopod otherwise .................................................................................. 9

9 Gonopod process h subflagelliform, process m extremely long and prominent (Figs 8, 9) ........................................................................ *T. extremus* sp. n.
  – Gonopod otherwise .................................................................................. 10

10 ♀ legs shorter, ca 1.2–1.3 times as long as midbody height (Fig. 10K). Gonopod lobe I velum-shaped and supplied with two denticles; spine z short and knife-shaped while spine h rudimentary (Figs 11, 12).......... *T. veliger* sp. n
  – ♀ legs longer, ca 1.6–1.7 times as long as midbody height (Fig. 13K). Gonopod spine z small, placed closer to base of spine h (Figs 14, 15)..........................
  .......................................................... *T. parajeekeli* sp. n.

11 Most metaterga with a pattern of 2+2 and 2+2 setiferous tubercles in two rows, rear row somewhat less strongly developed than fore one...... *T. doriae* 
  – Most metaterga with rear row of setiferous tubercles or wrinkles more strongly developed than fore row, the latter (next to) wanting .................. 12

12 Transverse sulcus on metaterga starting from segment 4, either fully or almost fully developed there, always fully developed from segment 5 .................. 13
  – Transverse sulcus on metaterga starting only from segment 5 ................. 16

13 Transverse sulcus fully developed and reaching base of paraterga already from segment 4. Gonopod tooth z at base of lobe I coarsely serrate along proximal margin ........................................ *T. hilaris*
Transverse sulcus fully developed only from segment 5. Gonopod tooth \( z \) either devoid of serration or serrate along distal margin .................\( T. \).affinis

Paraterga 2 caudolaterally rather broadly rounded. Gonopod relatively simple, process \( h \) poorly developed, no additional outgrowths near base..............................

........................................................................................................

\( T. \). affinis

Paraterga 2 caudally pointed. Gonopods more complex............................

Coloration dark brown, without cingulate pattern. Sternal lamina between \( \delta \) coxae 4 low and distinctly bimodal (Fig. 31I, J). Gonopods (Figs 32, 33) with tooth \( z \) prominent and serrate along distal margin.......................\( T. \).rugosus

Coloration pale, with a cingulate pattern. Sternal lamina between \( \delta \) coxae 4 high, subquadrate. Gonopod tooth \( z \) smaller and spiniform ....\( T. \).semirugosus

Paratergal corner protruding caudad beyond rear contour only from segment 15, being obtusangular or subrectangular and lying more or less within the contour until segment 14.................................\( T. \).bilaroides

Paratergal corner protruding caudad before segment 14, mostly pointed ....

Pattern of tergal setation on segments 18 and/or 19: 2+2 and 5+5 in two rows.................................................................\( T. \).poolpermorum

Pattern of tergal setation 2+2 and 5+5 on both segments 18 and 19. Paraterga 2 caudally pointed. Epiproct with pre-apical incisions very close to apical knobs. Sternal lamina between \( \delta \) coxae 4 an unusually low, even ridge. Adenostyles on midbody \( \delta \) postfemora and, to a lesser extent, tibiae exceptionally prominent............................

\( T. \).poolpermorum

Pattern of tergal setation 2+2 and 5+5 on segment 19. Paraterga 2 more or less narrowly rounded. Pre-apical incisions on epiproct better removed from tip. Sternal lamina between \( \delta \) coxae 4 concave medially. Ventral adenostyles on \( \delta \) legs less prominent.................................................................\( T. \).haplorugosus

Body smaller: width ca 2.0 mm. Sternal lamina between \( \delta \) coxae 4 as a pair of separate, setiferous tubercles (Fig. 22I, J). Ventral adenostyles on \( \delta \) legs almost missing (Fig. 22K). Gonopods without any outgrowth near base of process \( h \) (Figs 23, 24) ..................................................\( T. \).haplorugosus

Body larger: width over 3.0 mm. Sternal lamina between \( \delta \) coxae 4 single. Ventral adenostyles on \( \delta \) legs more prominent. Gonopod with a spine near base of process \( h \) ..............................................................................\( T. \).allorugosus

Sternal lamina between \( \delta \) coxae 4 high, emarginate (Fig. 16I, J). Adenostyles on \( \delta \) postfemora and tibiae well-developed (Fig. 16K). Gonopods rather simple, spine \( z \) inconspicuous (Figs 17, 18).................................\( T. \).allorugosus

Sternal lamina between \( \delta \) coxae lower, slightly concave. Adenostyles on \( \delta \) postfemora and tibiae less strongly developed. Gonopods more complex, spine \( z \) long and large (Figs 35–38)..............................\( T. \).perarmatus

Paraterga 2 pointed caudally. Sternal lamina between \( \delta \) coxae 4 exceptionally densely setose, low, concave ventrally (Fig. 25I, J). Gonopods with a medi-
um-sized process \( h \), and a smaller lobular \( z \) at base of \( h \) (Figs 26, 27). .................. \( T. jeekeli \)

- Paraterga 2 more or less narrowly rounded caudally. Sternal lamina between \( \delta \) coxae 4 higher and less strongly setose. Gonopod outgrowths \( h \) and \( z \) either almost wanting or very large ................................................................. \( T. jeekeli \)

22 Sternal lamina between \( \delta \) coxae 4 with a straight ventral margin. Pleurosternal carinae poorly developed, in \( \delta \) slightly projecting caudal beyond rear margin only until segments 8–10 .................................................................

- Sternal lamina between \( \delta \) coxae 4 slightly concave ventrally. Pleurosternal carinae better developed, in \( \delta \) slightly projecting caudal beyond rear margin at least till segment 15 .................................................................

23 Body smaller: width up to 3.1–3.2 mm. Mid-dorsal line very clear on both halves of metaterga. Gonopods relatively simple, with both \( h \) and \( z \) almost wanting.................................................. \( T. hoffmani \)

- Body larger: width 4.0–5.3 mm. Mid-dorsal line not so well-developed at least on rear halves of metaterga. Gonopods more complex, with both \( h \) and \( z \) very conspicuous .................................. \( T. baenzigeri \)

24 Metatergum 19 slightly rugulose posteriorly. Calluses on segment 2 with three, on following paraterga with two, incisions. Gonopods extremely complex, with numerous spiniform outgrowths ........................................ \( T. perplexus \)

- Metatergum 19 entirely smooth. Calluses with two and three incisions on poreless and poriferous paraterga, respectively. Gonopod less strongly differentiated .................................................. \( T. amicus \)

25 Either most of \( \delta \) sterna with oblique tubercles or spines, or only anterior sterna with small cones near coxae .................................................................

- Neither spines nor tubercles on \( \delta \) sterna .................................................................

26 Only rear sternum on most of \( \delta \) segments with a pair of small spines. Metaterga mostly with 2+2 and 3+3 setiferous tubercles in two transverse rows. Gonopod process \( h \) and lobe \( l \) relatively well-developed........................ \( T. silvestris \)

- Fore and rear sterna of most of \( \delta \) segments with a pair of tubercles and spines, respectively. Fore row of tergal setae not borne on tubercles, rear row on 2+2 tubercles .................................................................

27 Transverse sulcus starting from metatergum 4, fully developed from metatergum 5. \( \delta \) tarsal brushes missing. Northern Vietnam ........................................ \( T. maculatus \)

- Transverse sulcus starting from metatergum 3, still underdeveloped on metatergum 4, fully developed from metatergum 5. \( \delta \) tarsal brushes present only on a few anteriormost legs. Yunnan, China ......................... \( T. sinensis \)

28 Metaterga entirely smooth and polished, devoid of evident tubercles, at best extremely faintly rugulose near transverse sulcus ........................................

- Metaterga rather clearly rugose/tuberculate/granulate, posterior row of setae at least partly borne on tubercles .................................................................

29 Transverse sulcus on metaterga starting from segment 4, but fully developed and reaching base of paraterga only from segment 5. Ventral adenostyles on
Review of the genus Tylopus Jeekel, 1968, with descriptions of five new species from Thailand

♂ legs: a distal knob on femur, a distomedial knob on postfemur, and a parabasal knob on both tibia and tarsus

- Transverse sulcus on metaterga starting only from segment 5. Pattern of ♂ leg adenostyles otherwise

Head a little wider than collum and subequal in width to segment 3. Paraterga caudally considerably acutangular and beak-shaped only from segment 14. Gonopod process h at about midlength with a strong ventral outgrowth.

- T. procurvus

Head a little narrower than collum and subequal in width to segment 2. Paraterga caudally beak-shaped already from segment 7, especially strongly so from segment 12. Gonopod process h without outgrowth

Larger species: body width 3.1 mm. Pattern of tergal setation: 2+2 and 3+3 to 6+6 in two rows, rear row easily traceable due to insertion points. Metaterga very finely rugulose only near transverse sulcus. Epiproct unusually broad. Pads instead of adenostyles on ♂ femora, postfemora, tibiae (all distally) and tarsi (almost entirely)

- T. crassipes

- T. pulvinipes

- T. sigma

Metaternal surface polished and smooth except for conspicuous tubercles in two rows

- Metaterga at least partly rugulose/rugose to granular; at most one row of tubercles

Paraterga very poorly developed, rounded, low, projecting slightly caudad beyond rear contour like small knobs only on segments 18 and 19. Calluses virtually devoid of incisions. Transverse sulcus on metaterga poorly developed, starting already from segment 2, although fully developed only from segment 5. A paramedian pair of denticles between ♂ coxae 5 behind a prominent, subquadrate lamina between ♂ coxae 4. Gonopod process h entirely missing, lobe l normal

- T. strongylosomoides

Paraterga better developed, protruding caudad beyond rear contour at least from segment 5. Calluses always at least with one lateral incision. Transverse sulcus starting only from segments 3–5. Dentiform tubercles between ♂ coxae 5 missing. Gonopod process h invariably present, lobe l with a spine apically

- T. granulatus

Paraterga acutangular caudally and pointed beak-like already from collum. Tergal setiferous tubercles: 3+3 and 5+5 on segments 16–19. Adenostyle pattern on ♂ legs: a distal knob on femora and a parabasal knob on most of postfemora, tibiae, and tarsi. Gonopod process h large, lamellar, sigmoid

- T. pulvinipes

Paraterga acutangular caudally and pointed beak-like only from segment 4. 2+2 and 4+4 tergal setiferous tubercles on segments 16–19. Adenostyle pattern on ♂ legs: a proximal finger-shaped tubercle crowned with a bunch of
setae only on femora 6, 8, and 9. Gonopod process h smaller, spiniform ........

........................................................................................................... T. topali

35 Transverse sulcus on metaterga starting and fully developed from segment 5. Ventral adenostyles present on all ♀ podomerases except coxa .................36

– Transverse sulcus on metaterga starting from segment 4, but fully developed only from segment 5. Ventral tubercles only on some of ♀ telopoditomerases ...

........................................................................................................... T. tamdaoensis

36 Metaterga rugulose also in front of transverse sulcus, at rear margin with several oblong tubercles. Sternal lamina between ♀ coxae 4 like a pair of setiferous knobs. Neither gonopod lobe m nor lobe l spinigerous...

– Metaterga rugose only behind transverse sulcus, without evident tubercles at rear margin. Sternal lamina between ♀ coxae 4 single. Both gonopod lobe m and lobe l crowned with a spine......................... T. nodulipes

37 Metaterga modestly rugulose only near transverse sulcus, posteriorly neither granular nor microtuberculate. Calluses broad. Gonopod process h simple, high, never particularly coiled; lobe l very modestly serrate at apex ...........

– Metaterga distinctly rugose-granular/microtuberculate even on fore halves. Calluses narrow. Gonopod process h better developed and more strongly coiled; lobe l apically either bare or with a digitiform outgrowth................ T. degerboelae

38 Caudal corner of paraterga pointed from segment 3. Pleurosternal carinae particularly well-developed, surpassing rear contour until segment 16 or 17. Adenostyles often present on ♀ prefemora, pattern as in Fig. 19K. Gonopods as in Figs 20, 21 ...................................................................... T. degerboelae

– Caudal corners of paraterga mainly narrowly rounded, pointed only from segment 15. Pleurosternal carinae less strongly developed ........ T. pallidus

39 Coloration dark, brown. Sternal lamina between ♀ coxae 4 like a pair of separate, setiferous tubercles preceded by another pair of very small tubercles between coxae 3. Gonopod with lobe l devoid of an apical process ......

– Coloration uniformly pale. Sternal lamina between ♀ coxae 4 single, not accompanied by additional tubercles in front or behind. Gonopod lobe l with a strong, apical, finger-shaped process ........................................... T. asper

40 Mostly 3+3 tubercles at rear margin of metaterga. Sternal lamina between ♀ coxae 4 distinctly emarginate. Larger adenostyles close to midlength on ♀ postfemora and tibiae, femora with a distal knob. Gonopod process h slenderer and shorter, apex of lobule m not developed into a spine ........ T. subcoriaceus

– Mostly 4+4 tubercles at rear margin of metaterga. Sternal lamina between ♀ coxae trapeziform. Larger adenostyles on both postfemora and tibiae more distal, femoral knob missing. Gonopod process h unusually prominent, with a hook at base, apex of lobule m spiniform .................................. T. coriaceus
Conclusion

Tylopus appears to be one of the largest millipede genera in Southeast Asia. The genus is best known from Thailand, which has 26 (>63%) of the described species. With further progress in our knowledge of the millipede faunas of other, still poorly prospected, mostly neighbouring countries such as Laos, Myanmar, Cambodia and Vietnam, as well as southern China, the total of 41 Tylopus species can readily be expected at least to double. More congeners are likely to be found in Thailand as well. Golovatch and Enghoff (1993) attempted a preliminary phylogenetic analysis of Tylopus based on the 35 species then known, but given the incomplete state of our knowledge of Tylopus, we believe that a new phylogenetic analysis would be premature.

In Thailand, all Tylopus are confined to the northern, mountainous parts of the country (Map). Finding congeners south of Tak Province seems unlikely, but, since Tylopus are known also from all over Vietnam, including the southern parts of the country, this genus is likely to occur at least in the adjacent parts of Cambodia, from where no species have hitherto been recorded. At present the northern range limit of Tylopus lies in Yunnan Province, China, but it seems plausible that many more regions in southern China, even some north of Yunnan, might also prove to support Tylopus species. Since only a few species have been reported from Laos and Myanmar, another considerable increase in the number of congeners is more than likely after further collecting in those countries as well.

Almost all Tylopus species are confined to forest habitats, especially montane ones. Most are local to highly local in distribution. There are only very few relatively widespread congeners, e.g. *T. doriae*, *T. perarmatus* or *T. degerboelae*. At one locality, as many as nine congeners can co-occur, e.g. in Doi Inthanon and Doi Suthep mountains. This remarkable result indicates that many other high- to mid-montane forested areas in Indochina and southern China could support similarly rich faunules of Tylopus.

Within Tylopus sympatric groups, only *T. degerboelae* appears to show a highly extended, almost annual pattern of seasonal activity, judging from the occurrence of adults of both sexes at Doi Inthanon and, especially, Doi Suthep. Adults of the bulk of congeners living at either (four species each) or both (five species) of these mountain ranges tend to be autumnal, their collection being confined to September to November. This probably means that these species represent a single, autumnal phenofauna. The sole, possibly noteworthy exception is *T. asper* which has heretofore been found only at Doi Inthanon and only in May. Whether this species represents a different phenofauna or not, remains open to question. Special observations are required to reveal the phenology and breeding seasons of Tylopus at least in northern, mostly montane Thailand.
Map  Distribution of *Tylopus* species: 2 species (Myanmar), 26 species (Thailand), 2 species (Laos), 1 species (China), 13 species (Vietnam): 1 Yado: *T. doriae* (Pocock, 1895). 2 Village of Thao: *T. silvestris* (Pocock, 1895). 3 Pha Mon Cave: *T. grandis* sp. n. 4 Doi Inthanon: *T. affinis* Golovatch & Enghoff, 1993, *T. allorugosus* Golovatch & Enghoff, 1993, *T. asper* Golovatch & Enghoff, 1993, *T. degereboelae* Golovatch & Enghoff, 1993, *T. haplorugosus* Golovatch & Enghoff, 1993, *T. jeekeli* Golovatch & Enghoff, 1993, *T. perarmatus* Hoffman, 1973, *T. prosperus* Golovatch & Enghoff, 1993, *T. parajeekeli* sp. n. 5 Ban Mussoe: *T. semirugosus* Golovatch & Enghoff, 1993. 6 Doi Suthep: *T. affinis* Golovatch & Enghoff, 1993, *T. allorugosus* Golovatch & Enghoff, 1993, *T. baenzigeri* Golovatch & Enghoff, 1993, *T. degereboelae* Golovatch & Enghoff, 1993, *T. doriae* (Pocock, 1895), *T. hoffmani* Golovatch & Enghoff, 1993, *T. jeekeli* Golovatch & Enghoff, 1993, *T. perarmatus* Hoffman, 1973, *T. similirugosus* Golovatch & Enghoff, 1993, *T. subcoriaceus* Golovatch & Enghoff, 1993. 7 Doi Chiang Dao: *T. degereboelae* Golovatch & Enghoff, 1993, *T. perarmatus* Hoffman, 1973, *T. rugosus* Golovatch & Enghoff, 1993. 8 Umphang District: *T. bispinosus* sp. n. 9 Doi Pha Hom Pok: *T. amicus* Golovatch & Enghoff, 1993, *T. pallidus* Golovatch & Enghoff, 1993, *T. perplexus* Golovatch & Enghoff, 1993, *T. poolpermorrum* Golovatch & Enghoff, 1993, *T. extremus* sp. n. 10 Buathong Waterfall: *T. rugosus* Golovatch & Enghoff, 1993. 11 Doi Phatang: *T. degereboelae* Golovatch & Enghoff, 1993, *T. perarmatus* Hoffman, 1973. 12 Ban Pang Rim Kon: *T. perarmatus* Hoffman, 1973. 13 Thum Pha Thai: *T. perarmatus* Hoffman, 1973. 14 Phucheefah: *T. perarmatus* Hoffman, 1973. 15 Nam Min Waterfall: *T. perarmatus* Hoffman, 1973. 16 Tham Pha Nang Khoi: *T. perarmatus* Hoffman, 1973. 17 Ton Tong Waterfall: *T. veliger* sp. n. 18 Phu Kheio: *T. coriaceus* Golovatch & Enghoff, 1993, *T. pulvinipes* Golovatch & Enghoff, 1993. 19 Luang Prabang: *T. nodulipes* (Attems, 1953), *T. mutilatus* (Attems, 1953). 20 XiengKuang: *T. mutilatus* (Attems, 1953). 21 Mengzi County: *T. sinensis* Golovatch, 1995. 22 Mt Fan-Si-Pan: *T. nodulipes* (Attems, 1953). 23 O quy ho: *T. crassipes* Golovatch, 1984, *T. maculatus* Golovatch, 1984, *T. magicus* Golovatch, 1984, *T. procurvus* Golovatch, 1984. 24 Tam Dao: *T. strongylomooides* (Korsós & Golovatch, 1989), *T. tamdaensis* Korsós & Golovatch, 1989. 25 Cuc Phuong Nature Reserve: *T. granulatus* Golovatch, 1984, *T. hilaroides* Golovatch, 1984, *T. topali* Golovatch, 1984. 26 Bana: *T. hilaris* (Attems, 1937). 27 Peak Langbiang: *T. mutilatus* (Attems, 1953).
Acknowledgements

We would like to extend our deep gratitude to all of the collectors involved, mainly staff of the Animal Systematics Research Unit of Chulalongkorn University, Bangkok. The first author is deeply obliged to the programme Strategic Scholarships for Frontier Research Network for the Joint Ph.D. Program Thai Doctoral degree from the Office of the Higher Education Commission, CHE–RG under the Limestone Biodiversity Project and the BRT Programme (TRF/BIOTECH Thailand Biodiversity Research and Training Program) for their financial support.

References

Attems C (1937) Myriopoda 3. Polydesmoidea I. Fam. Strongylosomidae. Das Tierreich 68: 1–300.
Attems C (1953) Myriopoden von Indochina. Expedition von Dr. C. Dawydoff (1938–1939). Mémoires du Muséum national d’Histoire naturelle, N.S., 5A: 133–230.
Enghoff H (2005) The millipedes of Thailand (Diplopoda). Steenstrupia 29(1): 87–103.
Golovatch SI (1984) Contributions to the millipede fauna of Vietnam (Diplopoda) II. Acta Zoologica Hungarica 30: 53–77.
Golovatch SI (1995) On several new or poorly-known Oriental Paradoxosomatidae (Diplopoda, Polydesmida, Paradoxosomatidae). Steenstrupia 19: 85–125.
Hoffman RL (1973) Descriptions and allocations of new or poorly known genera and species of Paradoxosomatidae from south-eastern Asia (Diplopoda: Polydesmida). Journal of Natural History 7: 361–389.
Korsós Z, Golovatch SI (1989) Addenda to the millipede fauna of Vietnam (Diplopoda). Acta Zoologica Hungarica 35: 211–220.
Pocock RI (1895) The Myriapoda of Burma, Pt. IV. Report upon the Polydesmoidea collected by Sig. L. Fea, Mr. E. W. Oates and others. Annali del Museo Civico di Storia Naturale di Genova, Ser. 2 14: 787–834.