RESEARCH ARTICLE



Revision of the Vietnamese millipede genus Annamina Attems, 1937, with descriptions of three new species (Diplopoda, Polydesmida, Paradoxosomatidae)

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Abstract

The hitherto monotypic diplopod genus *Annamina* contains now four species, including the revised typespecies *A. xanthoptera* Attems, 1937, as well as *A. attemsi* **sp. n.**, *A. irinae* **sp. n.** and *A. mikhaljovae* **sp. n.**, all from central or southern Vietnam. The genus is rediagnosed and a key to its constituent species given.

Keywords

Diplopoda, Paradoxosomatidae, Annamina, taxonomy, new species, Vietnam

Introduction

The monotypic millipede genus *Annamina* Attems, 1937, and its type species *A. xan-thoptera* Attems, 1937, were described twice nearly simultaneously from Vietnam, first in a global review of the family Paradoxosomatidae (= Strongylosomatidae) (Attems 1937) and the second time in a large paper on the Myriapoda of Indochina (Attems 1938). Although the designation of *Annamina xanthoptera* as a new genus and species appeared in 1938, the actual publication date was 1937.

The genus *Annamina* belongs to the tribe Sulciferini Attems, 1898 and differs from the other, mostly Asian genera by a remarkably short flagelliform solenomere and an even

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shorter, chitinous, tooth-shaped solenophore devoid of membranous elements (Jeekel 1968). *Annamina xanthoptera*, the only hitherto known species of the genus, was described from near Danang, central Vietnam (Attems 1937, 1938) and has never been recorded since.

Recently, three new *Annamina* species were discovered in southern and central Vietnam. One of these, *A. attemsi* sp. n., was incidentally found by NA when documenting the type material of *A. xanthoptera* in the Naturhistorisches Museum Wien (NHMW). In this work, we redescribe *A. xanthoptera*, based on the type material, and select a lectotype to stabilize the species' taxonomy. We also describe three new species: *A. attemsi* sp. n., *A. irinae* sp. n. and *A. mikhaljovae* sp. n., as well as refine the diagnosis of the genus and provide a key to all four species known to date.

Material and methods

New material that contained two new species of *Annamina* was taken in 2015 and 2016 during field trips of I. I. Semenyuk (Moscow, Russia) to southern Vietnam in the framework of the research activities of the Joint Russia-Vietnam Tropical Centre. The types of both are deposited in the Zoological Museum of the Moscow State University, Russia (ZMUM). The ZMUM types are preserved in 75% ethanol. Pictures were taken with a Canon EOS 5D digital camera and stacked using Zerene Stacker software.

The NHMW types are preserved in 75% alcohol. Measurements and photographs were taken with a Nikon DS-F2.5 camera mounted on a Nikon SMZ25 stereo microscope, using NIS-Elements Microscope Imaging Software with an Extended Depth of Focus (EDF) patch. All images were processed with Adobe Photoshop CS6 and assembled in Adobe InDesign. For taking SEM micrographs, the gonopods of *A. xanthoptera* and *A. attemsi* sp. n. were dehydrated in 96% ethanol and acetone, then air dried, mounted on aluminium stubs, coated with platinum and examined using a JEOL JSM 6610 scanning electron microscope.

Several paralectotypes of *A. xanthoptera*, preserved in 70% alcohol, are housed in the Muséum national d'Histoire naturelle, Paris (MNHN). They were only measured and checked for their species identity.

Results

Taxonomy

Polydesmida Leach, 1815 Paradoxosomatidae Daday, 1889

Genus Annamina Attems, 1937

Diagnosis. Medium-sized (ca 2–3 cm long) Sulciferini with 20 body segments, distinct, thin and mostly subhorizontal paraterga, evident transverse sulci on

metaterga 5–17(18), and a very high, tongue-shaped, setose, subtruncate lobe between $aa{\circ}$ coxae 4.

Gonopod mostly stout, prefemoral (= densely setose) region small, much shorter than femorite, the latter usually with evident, sometimes hyline, mesal and/or ventral lobes, clearly set off by sulci from both pre- and postfemoral parts; seminal groove mostly dorsal, not mesal, running onto a short flagelliform solenomere on mesal face near distal (= postfemoral) sulcus; acropodite consisting of a prominent central spine sometimes flanked by a mesal and/or a lateral process/outgrowth and carrying parabasally or near midway an inconspicuous, short, dentiform, ventral solenophore devoid of membranous elements and subtending the distal part of solenomere.

Type species. Annamina xanthoptera Attems, 1937

Other species included. A. attemsi sp. n., A. irinae sp. n. and A. mikhaljovae sp. n.

Annamina xanthoptera Attems, 1937

Figs 1-4

Type material. NHMW: Lectotype 3° , NHMW 8936, designated herein, Tourane (= Danang), Lien Chieu, Dawydoff C. leg., 09.1931, Dawydoff/Attems 1936 don., Attems det. Paralectotypes: 43° , 69° , 3 heads, 3 posterior sections, several midbody sections, NHMW 8937, two slide preparations, NHMW3477, same data as lectotype. MNHN JA 108: 23° , 39° , Touranne (C. Annam), 18.IX.31 Lien-Chiên.

Lectotype designation was necessary so that the species is based on a complete male that fully matches the original description of *A. xanthoptera* by Attems (1937). Gonopods were removed and newly examined using one of the NHMW paralectotypes.

Diagnosis. Differs from other members of the genus primarily by showing both the median lobe and the lateral process of the gonopod telopodite strongly microdenticulate-serrate. See also Key below.

Description. Measurements (mm): Males (both NHMW and MNHN): length 24.9–29, width of midbody prozonae 1.6–1.9, width of midbody metazonae 2.35–2.6. Females (both NHMW and MNHN): length 28–31, width of midbody pro- and metazonae 1.8–2.1 and 2.5–3.2, respectively.

General coloration after many years of preservation in alcohol apparently somewhat faded, rather uniformly light to castaneous brown, without a distinct pattern, sides lighter; telson, legs and ventral parts light brown to yellowish (Fig. 1). Clypeolabral region setose, setae becoming scattered between antennae; vertigial region with 2+2 setae; epicranial suture thin, superficial.

Antennae long, slender and moderately clavate, slightly extending back behind segment 3 ($\stackrel{\circ}{\bigcirc}$) (Fig. 1A, B) or 2 ($\stackrel{\circ}{\bigcirc}$) when stretched dorsally; in length, antennomere 2 = 3 = 4 = 5 = 6 > 1 = 7 (Fig. 1A, B). In width, collum = segment 3 = 4 < 2 < head = 5-16 ($\stackrel{\circ}{\bigcirc}$); thereafter body gradually tapering towards telson on segments 17–19. Tegument generally smooth, prozonae finely shagreened, rear halves of metaterga mostly striolate; surface below paraterga microgranulate. Collum regularly rounded laterally; dorsum strongly and regularly convex, but paraterga directed ventrolaterad.



Figure 1. *Annamina xanthoptera* Attems, 1937, ♂ paralectotype (NHMW). **A** habitus, lateral view **B** anterior part of body, lateral view **C** midbody segments, dorsolateral view.



Figure 2. Annamina xanthoptera Attems, 1937, \Im paralectotype (NHMW), right (**A**, **B**, **D**) and left (**C**) gonopods, **A** lateral **B** mesal **C** ventromesal and **D** subventral views, respectively (cx = coxite; fe = femorite; pf = prefemoral part; vl = ventral lobe; ml = mesal lobe; su = postfemoral sulcus; lp = lateral process; a = apical process; sl = solenomere; t = solenophore tooth).



Figure 3. Annamina xanthoptera Attems, 1937, δ paralectotype (NHMW), SEM micrographs of entire left gonopod (**A**, **B**), ventrolateral and subventral views, respectively, and of its distal parts (**C**, **D**), subventrolateral views (cx = coxite; fe = femorite, vl = ventral lobe; ml = mesal lobe; su = postfemoral sulcus; lp = lateral process; a = apical process; sl = solenomere; t = solenophore tooth).



Figure 4. Annamina xanthoptera Attems, 1937, \mathcal{S} paralectotype (NHMW), entire left (**A**, **B**) gonopod and distal part of right one (**C**), mesal, lateral and subventral views, respectively (cx = coxite; fe = femorite, vl = ventral lobe; ml = mesal lobe; su = postfemoral sulcus; lp = lateral process; a = apical process; sl = so-lenomere; t = solenophore tooth). After Attems (1937) (**A**) and Attems (1938) (**B**, **C**).

Postcollum paraterga well-developed, mostly set high (at about 1/5 metazonital height measured from dorsum), subhorizontal; paraterga 2 lower than others, drawn both forward and caudad into rounded lobes, with a distinct lateral tooth in fore 1/4; following paraterga broadly and regularly rounded anterolaterally, likewise with a small, but evident tooth in fore 1/4; caudal corner subrectangular until segment 5, increasingly dentiform and well drawn caudad, but evidently projecting behind caudal tergal margin only in segments 17-19, nearly always rounded, spiniform and almost pointed only in segment 19; calluses narrow, demarcated by a complete, distinct, deep sulcus only dorsally and by a faint and somewhat incomplete one ventrally, the latter sulcus reaching only until fore lateral tooth; poriferous calluses only a little thicker than poreless ones (Fig, 1). Ozopores lateral, placed inside an elongated ovoid groove located just behind a vague tubercle at about rear 1/4 callus. Transverse metatergal sulci thin, shallow, faintly sinuate medially and beaded at bottom, nearly reaching bases of paraterga, present on metaterga 5–18 (Fig. 1). Stricture dividing pro- and metazonae thin and deep, ribbed at bottom down to paraterga. Axial line very faint, traceable in places on metaterga. Pleurosternal carina a small ventral lobule on segment 2, thereafter very faint, subtransverse, granulated ridges traceable caudally until segment 7 (\mathcal{J}). Epiproct (Fig. 1A) long, clearly flattened dorsoventrally, conical, emarginate at apex, subapical lateral papillae small. Hypoproct subtriangular, with a rounded apex, caudal 1+1 setae well-separated, not borne on knobs (as in Fig. 11A).

Sterna flat, sparsely setose, cross-impressions faint, without modifications other than a prominent, very high, narrow, triangular, truncate lobe between 3° coxae 4 (as in Fig. 11B). Legs long, ca 2 times as long as midbody height, very slender in both sexes, with neither adenostyles nor ventral brushes; in length, femora > prefemora > tarsi > coxae = postfemora = tibiae (Fig. 1).

Gonopods (Figs 2–4) complex, telopodites stout. Coxite (**cx**) considerably shorter than telopodite, subcylindrical, densely setose distoventrally. Prefemoral (= densely setose) part (**pf**) short, set off from femorite (**fe**) by an oblique sulcus. Femorite (**fe**) voluminous, clearly flattened dorsoventrally, showing a prominent, spiculate-microdenticulate, mesal lobe (**ml**) and a smaller, rounded, hyaline, ventral lobe (**vl**); seminal groove running laterad along dorsal part of **fe**, distally detached near a subtransverse postfemoral sulcus (**su**) into a conspicuously short, flagelliform, coiled solenomere (**sl**). On ventral side, base of **sl** subtended by a small tooth (**t**) (= solenophore) devoid of membranous elements, **t** lying ventrally near base of **a** long, narrow, blade-shaped, apical process (**a**); the latter slightly curved laterad, with a rounded tip, much longer than a conspicuously serrate, slender, finger-shaped, lateral process (**lp**).

Comments. Attems (1937, 1938) failed to indicate the number of specimens in the type series of *A. xanthoptera* while the only measurements he gave in the descriptions (width of pro- and metazona 1.8 and 2.5 mm, respectively) may have misleadingly been taken as concerning a single specimen. However, the type series is quite large and presently divided between the MNHN and NHMW collections. Moreover, the NHMW type material actually houses two different species of *Annamina*, most of which truly represents *A. xanthoptera*. The minor admixture, however, is described below as still another new species, the types being deposited in the NHMW.

A complete catalogue of references to *A. xanthoptera* is available in Nguyen and Sierwald (2013).

Annamina attemsi sp. n.

http://zoobank.org/25C4DF37-7438-49B4-8764-EF365CA11F9F Figs 5–7

Type material. Holotype \Im , NHMW 8934, Tourane (= Danang), Lien Chieu, Dawydoff C. leg., 09.1931, Dawydoff/Attems 1936 don. Paratype: 1 \Im , NHMW 8935, with one gonopod dissected, same data as holotype.

Diagnosis. Differs from other species of the genus primarily by an unusually slender telopodite of the gonopod which is only supplied with an apical process. See also Key below.



Figure 5. *Annamina attemsi* sp. n., \circlearrowleft paratype (NHMW). **A** habitus, lateral view **B** anterior part of body, lateral view **C** midbody segments, dorsolateral view **D** caudal part of body, dorsolateral view.

Name. Honours the famous Austrian myriapodologist Carl Attems (1868–1952), one of the most prominent taxonomists of Diplopoda of his time.

Description. Measurements (mm): Body length ca 18.7 (holotype) or 21.6 (\Im paratype), width of midbody prozonae 1.2 (holotype) or 1.3 (\Im paratype), width of midbody metazonae 1.8 (holotype) or 2.0 (\Im paratype).

General coloration after many years of preservation in alcohol light, almost whitish to yellowish brown, sides, telson, legs and ventral parts pale whitish (Fig. 5). Clypeo-



Figure 6. Annamina attemsi sp. n., \bigcirc paratype (NHMW), right gonopod, **A** mesal **B** subventral and **C** submesal views, respectively (cx = coxite; fe = femorite, vl = ventral lobe; ml = mesal lobe; su = post-femoral sulcus; lp = lateral process; a = apical process; sl = solenomere; t = solenophore tooth).

labral region setose, setae becoming scattered between antennae (ca 3 pairs), vertigial region with 2+2 setae; epicranial suture thin, superficial.

All other characters (see Figs 5–7) as in A. xanthoptera, except as follows.

Caudal corner of paraterga dentiform and acute-angled starting with segment 4, drawn behind rear tergal margin starting with segment 11 (\mathcal{J}); a second lateral denticle on paraterga completely absent from segments 18 and 19. Transverse sulci fully developed on metaterga 5–17, deep, beaded at bottom and almost reaching the bases of paraterga, weaker on segment 18, absent from 19th.

Gonopods (Figs 6, 7) somewhat disjunct, especially intricate in structure; coxite (**cx**) moderately setose distoventrally; telopodite much more slender than in *A. xan-thoptera*; femorite (**fe**) much narrower, distally especially so, showing an inconspicuous and less strongly granulated mesal lobe (**ml**), as well as a hypertrophied, hyaline, irregularly rounded, ventral lobe (**vl**) folded mesad; seminal groove running laterad along dorsal part of **fe**, passing distally onto a short flagelliform solenomere (**sl**); the latter subtended distally by a small, apically bilobulate, ventral tooth (**t**) (= solenophore) arising from about midway of a long, pointed, spiniform, apical process (**a**), this being equipped with a minute, subapical, hyaline ridge (**r**); lateral process (**lp**) rudimentary, lying a little distal to postfemoral sulcus (**su**), with a minute spike on top, placed just at base of **a**; no mesal process whatsoever.



Figure 7. Annamina attensi sp. n., \Diamond paratype (NHMW), SEM micrographs. **A** entire right gonopod, ventral view **B–E** distal part of same gonopod **B** oral **C** subventral **D** ventral and **E** subventral views, respectively (cx = coxite; fe = femorite, vl = ventral lobe; ml = mesal lobe; r = subapical ridge; su = postfemoral sulcus; lp = lateral process; a = apical process; sl = solenomere; t = solenophore tooth).

Annamina irinae sp. n.

http://zoobank.org/44D470B6-EB4D-473F-8B15-E7626B4CB9F7 Figs 8, 9

Type material. Holotype 3° , ZMUM ρ 3548, Vietnam, Gia Lai Prov., Kon Ka Kinh National Park, N 14°12'43.4", E 108°18'57.1", 930 a.s.l., humid leaved tropical forest



Figure 8. Annamina irinae sp. n., \circlearrowleft paratype (ZMUM). **A** habitus, lateral view **B** anterior part of body, anteroventral view **C** midbody segments, dorsal view **D** caudal part of body, dorsal view **E** gonopods, ventral view. Pictures taken not to scale.



Figure 9. *Annamina irinae* sp. n., \circlearrowleft paratype (ZMUM), left gonopod, **A** dorsomesal, **B** ventral and **C** mesal views, respectively (cx = coxite; fe = femorite, vl = ventral lobe; ml = mesal lobe; su = postfemoral sulcus; lp = lateral process; mp = mesal process; a = apical process; sl = solenomere; t = solenophore tooth). Scale bar 0.5 mm.

in river valley, beaten from bush, V.2016, leg. I.I. Semenyuk. Paratypes: $2 \Im \Im$, ZMUM ρ 3549, same locality and habitat; $1 \Im$, ZMUM ρ 3550, same locality artificial *Pinus* cf. *kesia* plantation, V.2016, leg. I.I. Semenyuk.

Name. Honours Irina Semenyuk, the collector.

Diagnosis. Differs from other species of the genus primarily by the presence of a small ventral lobe and a large mesal lobe on the gonopod femorite, coupled with a small, simple, mesal process, a long, spiniform, lateral process and a prominent, simple, unciform, acuminate, apical process in the postfemoral portion of the gonopod. See also Key below.

Description. Measurements (mm): Body length of all types ca 24, width of midbody pro- and metazona 1.5 and 1.9, respectively.

General coloration in alcohol light brownish to brown, but with a characteristic pattern of a vague, lighter, subtriangular, central spot on each postcollum metatergum

flanked on each side by marbled brown patches fused into a complete transverse band in anterior 1/3; sides mostly brown to light brown, lighter closer to coxae; strictures between pro- and metazonae, paraterga both dorsally and ventrally, telson, legs and venter pale yellowish to whitish (Fig. 8). Antennae nearly pallid, only distal parts of antennomeres 2–5 slightly infuscate, light brown; entire antennomeres 6 and 7 brown; tip of antennae contrasting pallid.

All characters (see Figs 8, 9) as in A. xanthoptera, except as follows.

In width, segments 5–16 > head > 2 > collum = 3 = 4 (\mathcal{E}); body gradually tapering towards telson on segments 17–19 (Fig. 8B–D). Caudal corner of paraterga clearly drawn behind rear tergal margin on segments 16–19. Transverse sulci thin, slightly sinuate medially, finely beaded at bottom, fully developed on segments 5–17, weaker on segment 18, absent from 19th. Tergal setae ca 1/4 as long as metatergum, mostly abraded, often untraceable even as insertion points, pattern 2+2 in a transverse fore row. In length, midbody femora > tarsi > postfemora > coxae = prefemora = tibiae (Fig. 8B–D).

Gonopods (Figs 8E, 9) relatively complex; coxite (**cx**) moderately setose distoventrally; telopodite consisting of a short prefemoral (= densely setose) part set off from femorite (**fe**) by an oblique sulcus; femorite (**fe**) stout, distinctly flattened dorsoventrally, set off from acropodite by a subtransverse postfemoral sulcus (**su**), with a smaller, rounded, hyaline, ventral lobe (**vl**) and a much larger, parabasal, somewhat ear-shaped, mesal lobe (**ml**); seminal groove quickly moving laterad to mostly lie on dorsal side of **fe** before passing onto a short, free, flagelliform solenomere (**sl**) near **su**, with a small finger-shaped mesal process (**mp**) lying at base of **sl**; postfemoral part consisting of a large, spiniform, slightly curved, acuminate, apical process (**a**) flanked by a considerably shorter, likewise spiniform and slightly curved lateral process (**lp**) and a short, stout, ventral, trifid tooth (**t**) (= solenophore) subtending the basal half of **sl**.

Annamina mikhaljovae sp. n.

http://zoobank.org/C53AD3C4-4A6B-4F16-A8A0-BAC2ABB23F00 Figs 10, 11

Type material. Holotype 3° , ZMUM ρ 3551, Vietnam, Kon Tum Prov., Kon Plong Distr., N14°43.450', E108°18.882', 1000–1260 m a.s.l., tropical forest, on log, V.2015, leg. I.I. Semenyuk.

Name. Honours Elena Mikhaljova, a prominent specialist in the systematics of Asian Diplopoda.

Diagnosis. Differs from other species of the genus primarily by the presence of a small ventral lobule and a large mesal lobe on the gonopod femorite, coupled with, much like in *A. irinae* sp. n., a small, simple, mesal process, a similarly short, but spiniform, clearly serrate lateral process and a prominent, lobe-shaped, apical process in the postfemoral portion of the gonopod. See also Key below.

Description. Measurements (mm): Length ca 22 mm, width of midbody pro- and metazonae 1.8 and 2.7 mm, respectively. Coloration uniformly light brownish to yellow-



Figure 10. Annamina mikhaljovae sp. n., δ holotype (ZMUM). **A** habitus, lateral view **B** anterior part of body, ventral view **C** midbody segments, dorsal view **D** segments 5–7, ventral view **E** caudal part of body, dorsal view. Pictures taken not to scale.

brown, only antennomeres 6 and 7 contrasting dark brown; tegument largely thin and translucent (Fig. 10).

All characters (see Figs 10, 11) as in *A. xanthoptera*, except as follows.

In width, collum = 3 = 4 < segment 2 < head < 5-16 (\Im); thereafter body gradually tapering towards telson. Caudolateral corner of paraterga subrectangular until segment 8, thereafter increasingly well drawn caudad, but always remaining narrowly rounded, clearly projecting behind rear tergal margin only on segments 17–19 (Fig. 10).

Gonopods (Figs 10D, 11) much as in *A. irinae* sp. n.; femorite (**fe**) with a distinct, papillate, parabasal, mesal lobe (**ml**), a small, subtriangular, midway, hyaline, ventral lobe (**vl**); postfemoral part lying beyond a distinct sulcus (**su**) with a short flagelliform



Figure 11. Annamina mikhaljovae sp. n., \bigcirc holotype (ZMUM). **A** hypoproct, ventral view **B** sternal lobe between coxae 4 **C–E** right gonopod, **A** mesal, **B** subventral and **C** lateral views, respectively (cx = coxite; fe = femorite, vl = ventral lobe; ml = mesal lobe; su = postfemoral sulcus; lp = lateral process; mp = mesal process; a = apical process; sl = solenomere; t = solenophore tooth). Scale bar 0.5 mm.

solenomere (**sl**), a similarly short, slender, slightly curved, mesal process (**mp**), a short tooth (**t**) (= solenophore) subtending the basal portion of **sl**, a prominent, membranous, distally faintly serrate, lobe-shaped, laterad curved, acuminate, apical process (**a**), and a shorter, spiniform, slearly serrate, lateral process (**lp**).

Discussion

Even with such a considerable increase in species diversity as described above, *Annamina* remains a well-defined and quite homogeneous group within the paradoxosomatid tribe Sulciferini. The genus is remarkably uniform in most of the characters of its constituent species, both somatic and gonopodal, as well as in distribution which is confined to south-central and central Vietnam. *Annamina* is unique amongst the contribal genera in the high, well-developed, laterally mostly monodentate and caudally largely triangular (but never pointed) paraterga; the strongly ribbed strictures between pro- and metazonae; the microgranulate sides of metazonae; the inconspicuous, nearly missing pleurosternal carinae; the uniformly roundly subtriangular hypoproct; the unusually high, subtriangular, setose and apically truncate sternal lobe between δ coxae 4; the absence both of adenostyles and ventral brushes on remarkably long and slender legs; and, above all, the special conformation of the gonopodal telopodite.

It is the latter that provides most of the characters useful for a confident separation of species in Annamina (see Key below). The gonotelopodite always shows an enlarged basal part of the femorite which is clearly flattened dorsoventrally. The femorite is set off from the acropodite by a distinct subtransverse sulcus or cingulum (su) that marks a postfemoral region more distally, a trait that, together with the presence of a number of femoral and postfemoral outgrowths or processes, allows the placement of the genus in Sulciferini (cf. Jeekel 1968). In Annamina spp., the femorite (fe) shows no longitudinal mesal groove so characteristic of numerous Sulciferini (Oxidus Cook, 1911, Tylopus Jeekel, 1968, Sichotanus Attems, 1914, Cawjeekelia Golovatch, 1980, etc.), but instead it has two more or less distinct lobes: one hyaline, rounded and ventral in position (vl), often folded mesad and especially hypertrophied in *A. attemsi* sp. n., the other a mesal, typically papillate or microdenticulate bulge (ml) which is particularly prominent in A. xanthoptera and A. mikhaljovae sp. n. The seminal groove in Annamina, unlike that in the remaining sulciferines, runs along the femorite not so much mesally as dorsally, to follow onto a surprisingly short and flagelliform solenomere (sl) detached on the dorsomesal face about the level of the postfemoral sulcus. This condition seems to be apomorphic, as is the complete absence of significant membranous elements in the solenophore which is represented by a rather small and short tooth (t), sometimes subtruncate, bi- or trifid, that subtends the distal part of the solenomere, leaving only the latter's tip exposed beyond **t**. The solenophore tooth is located ventrally near the base (usually) or close to the midpoint (A. attemsi sp. n.) of a centro-apical process or spine (a), always hyaline, sometimes lobe-shaped, but more often acuminate, invariably the longest and largest of the postfemoral outgrowths. Process a can be flanked by two distinct, albeit shorter, processes: one lateral (lp), which is servate in A. xanthoptera and A. mikhaljovae sp. n., but simple in A. irinae sp. n., the other mesal (**mp**) which is long in A. mikhaljovae sp. n., very short in A. irinae sp. n. and absent from the other two congeners. Process lp can also be rudimentary: A. attemsi sp. n.

Based on gonopodal structure alone, this latter species seems to be the most disjunct among congeners (see its diagnosis above and Key below). Since it seems to co-occur with *A. xanthoptera* near Danang, this observation agrees well with the general wisdom that two sympatric or even syntopic congeners tend to differ more strongly than others.

The above outline of the diversity of and variations in gonopodal characters in *Annamina* spp. helps us not only to better redefine the genus against the other Sulciferini, but also to key all of its four presently known species. Because the millipede fauna of Vietnam is the richest in Indochina, but still quite poorly known, it seems very likely that further *Annamina* species will be found in the future.

Key to Annamina species (based on gonopodal characters)

1	Postfemoral region of gonopod with a distinct, slender, slightly curved, mesal
	process (mp); apical process (a) broad and lobe-shaped (Fig. 11C-E)
	A. mikbaljovae sp. n.
_	Mesal process either very short or absent

2	Mesal process (mp) very short, mesal lobe (ml) of femorite ear-shaped
	(Fig. 9)
_	Mesal process absent
3	Femorite slender, ventral lobe (vl) hypertrophied, postfemoral lateral process
	(lp) rudimentary (Figs 6, 7)
_	Femorite stout, ventral lobe (vl) small and inconspicuous, postfemoral lateral
	process (lp) very strong and serrate (Figs 2-4)

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RESEARCH ARTICLE



Two new species of the planthopper genus *Tenguna* Matsumura, 1910, with a key to all species (Hemiptera, Fulgoromorpha, Dictyopharidae)

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Abstract

Two new species of the genus *Tenguna* Matsumura, 1910, *Tenguna kuankuoshuiensis* **sp. n.**, *Tenguna plurijuga* **sp. n.**, collected from China, are described and illustrated, photographs of the new species are provided together. A key is given to identify all the known species of *Tenguna*.

Keywords

Dictyopharidae, distribution, new species, planthopper, taxonomy

Introduction

The planthopper genus *Tenguna* was established by Matsumura in 1910 based on a single species, *Tenguna watanabei* Matsumura, from Taiwan, China. Song and Liang (2007) reviewed this genus and added the second species, *T. medogensis*, from China. In this paper, two new species, *T. kuankuoshuiensis* sp. n., *T. plurijuga* sp. n., are described and illustrated. Photographs of the adults of the new species are presented.

Materials and methods

The morphological terminology and measurements used in this study follow Yang and Yeh (1994) and Song and Liang (2007). Material examined here is deposited in the Institute of Entomology, Guizhou University, Guiyang, China (**GUGC**). Dry specimens were used for the observations, descriptions, and illustrations. Genital segments of the examined specimens were macerated in boiling solution of 10% NaOH and drawn from preparations in glycerin jelly under a Leica MZ12.5 stereomicroscope. Color pictures for adult habitus were obtained by a KEYENCE VHX-1000 system. Illustrations were scanned with Canon Cano Scan LiDE 200 and imported into Adobe Photoshop CS6 for labeling and plate composition. Terminology of morphology, genital characters, and measurements follow Song and Liang (2013).

The following abbreviations are used in the text:

BL	body length (from apex of cephalic process to tip of fore wings);
HL	head length (from apex of cephalic process to base of eyes);
HW	head width (including eyes);
FWL	forewing length;
GUGC	Guizhou University, Guiyang, China.

Taxonomy

Tenguna Matsumura, 1910

Figs 1-37

Tenguna Matsumura, 1910: 104; Song and Liang 2007: 59.

Type species. Tenguna watanabei Matsumura, 1910 (original designation).

Diagnosis. Genus diagnostic characters: general color green or yellowish green (in death); vertex with median carina distinct and complete, lateral margins sub-parallel at base, slightly sinuate in front of eyes, then gradually narrowing to arrowhead at apex; pronotum with distinct median carina and two obscure lateral discal carinae, elevated only anteriorly; fore femur with one minute, short and blunt spine near apex; aedeagus with a pair of processes apically and phallobase with pairs of membranous lobes apically.

Distribution. Southern China (Guizhou, Hubei, Sichuan, Taiwan, Xizang).

Key to the species of the genus Tenguna based on males

Vertex narrow and long, ratio of length to width is greater than 2.42
Vertex broad and short, ratio of length to width is not greater than 2.43

Tenguna kuankuoshuiensis sp. n.

http://zoobank.org/55EFD65D-ADC5-4DBE-A001-51E98AD62C47 Figs 1–18

Measurements. ∂, BL: 13.1–14.1 mm; HL: 1.7–1.8 mm; HW: 1.5–1.6 mm; FWL: 9.9–10.3 mm. ♀, BL: 15.2–16.3 mm; HL: 1.8–1.9 mm; HW: 1.6–1.8 mm; FWL: 12.3–12.9 mm.

Diagnosis. This species is similar to *Tenguna medogensis*, but can be distinguished from phallobase. The former with three pairs of membranous lobes at apex, the latter with two pairs of membranous lobes at apex.

Description. General color green; carinae on cephalic process, frons, pronotum and mesonotum, and parts of veins on forewings, dark green; rostrum with extreme apex blackish; hind tibia with lateral and apex black-tipped spines.

Cephalic process (Figs 1–5) relatively short, a little upturned, ratio length to length of pronotum and mesonotum combined 0.6. Vertex (Figs 1–3, 5) with lateral margins carinate, sub-parallel at base, slightly sinuate in front of eyes, then gradually narrowing to arrowhead at apex, ratio of length to width between eyes 2.8. Frons (Fig. 4) elongate, median carina complete and elevated, length 2.6 times long than width. Pronotum (Figs 1–3) distinctly shorter than mesonotum medially in the middle line, median carina distinct, lateral carina obscure, ratio length to length approx. 0.2:1. Forewings (Figs 1, 6) with Sc+R, M and Cu all branched apically; stigma distinct, with 3–5 cells. Legs moderately long; fore femur not flattened and dilated, with one minute, short, blunt spine near apex; hind tibia with 6–7 lateral black-tipped spines and eight apical black-tipped teeth.

Male genitalia. Pygofer (Figs 8–10) wider ventrally than dorsally, posterior margin with a blunt process, ventral margin depressed to accommodate anal tube (Fig. 8). Parameres (Figs 8, 9) large, distinctly broadening towards apex in lateral view (Fig. 8),



Figures 1–13. *Tenguna kuankuoshuiensis* sp. n. 1 male, holotype 2 female 3 Head and thorax, dorsal view 4 Frons and clypeus, ventral view 5 Head and pronotum, lateral view 6 Forewing 7 Hind wing 8 Pygofer and anal tube, dorsal view 9 Pygofer and parameres, ventral view 10 Genitalia, lateral view 11 Aedeagus, lateral view 12 Aedeagus, ventral view 13 Aedeagus, dorsal view. Scale bars: 1–7 2 mm; 8–13 0.5 mm.



Figures 14–18. *Tenguna kuankuoshuiensis* sp. n. **14** Genitalia ventral view of female **15** Genitalia dorsal view of female **16** First valvulae (lateral view) **17** Second valvulae (ventral view) **18** Third valvulae (lateral view). Scale bars 0.5 mm.

posterior margin straight, upper margin with dorsally directed, black-tipped process near middle, with ventrally directed, hook-like process near sub-middle on outer upper edge. Anal tube (Figs 8, 10) oval in dorsal view, ratio length to width approx. 2.0:1. Aedeagus (Figs 11-13) with one pair of special long endosomal processes, processes with apex acute, sclerotized and pigmented. Phallobase sclerotized and pigmented at base, with three pairs of membranous lobes at apex: the dorsal lobe large and the ventral lobe with small lobe in lateral view (Fig. 11), two pairs of large lobes in dorsal view (Fig. 12), three pairs of lobes and numerous small spines on it in ventral view (Fig. 13).

Female genitalia. Anal tube (Fig. 15) round and large in dorsal view, ratio length to width at middle nearly 1.0. First valvula (Fig. 16) sclerotized with six different sized teeth in lateral view. Second valvulae (Fig. 17) triangular, symmetrical in ventral view, connected at base and separated from 1/5 base. Third valvula (Fig. 18) with two sclerotized lobes, lateral lobe with six long spines at apex.

Type material. Holotype 3, China, Guizhou, Kuankuoshui, Qing gang tang hui long county. 17.VIII. 2010, Lihu. Paratypes, 13299, same to Holotype; 933599, China, Guizhou, Fanjing mountain, 27.VII. 2001, Lizizhong.

Etymology. This new species is named for the holotype occurrence in "Kuanku-oshui", Guizhou province in southwestern China.

Tenguna plurijuga sp. n.

http://zoobank.org/F0E37768-11AC-4887-B16B-ADBED289B40B Figs 19–37

Measurements. ∂, BL: 14.9 mm; HL: 2.1 mm; HW: 1.6 mm; FWL: 11.4 mm. ♀, BL: 15.2–16.7 mm; HL: 2.2–2.5 mm; HW: 1.6–1.8 mm; FWL: 11.6–12.3 mm.

Diagnosis. This species can be distinguished from other species from aedeagus and phallobase. The aedeagus with pair of unequal long processes apically; phallobase with numerous membranous lobes at apex.

Description. General color and external characters as the *Tenguna kuankuoshuiensis* sp. n.

Cephalic process (Figs 19–24) relatively short, a little upturned, ratio length to length of pronotum and mesonotum combined 0.7. Vertex (Figs 19–22, 24) with lateral margins carinate, sub-parallel at base, slightly sinuate in front of eyes, then gradually narrowing to arrowhead at apex, ratio of length to width between eyes 2.3. Frons (Fig. 23) elongate, median carina complete and elevated, length 3.0 times long than width. Pronotum (Figs 21, 24) distinctly shorter than mesonotum medially in the middle line, median carina distinct, lateral carina obscure, ratio length to length approx. 0.2:1. Forewings (Figs 19, 20, 25) with Sc+R, M and Cu all branched apically; stigma distinct, with five cells. Legs narrow and moderately long; fore femur with one minute, short, blunt spine near apex; hind tibia with six lateral black-tipped spines and eight apical black-tipped teeth.

Male genitalia. Pygofer (Figs 27–29) wider ventrally than dorsally, posterior margin with a blunt process, ventral margin depressed to accommodate anal tube. Parameres (Figs 27, 28) large, distinctly broadening towards apex in lateral view (Fig. 27), posterior margin straight, upper margin with dorsally directed, black-tipped process near middle, with ventrally directed, hook-like process near sub-middle on outer upper edge. Anal tube (Figs 27, 29) oval in dorsal view, ratio length to width 2.0:1. Aedeagus (Figs 30–32) with one pair of unequal long processes apically, processes with apex acute, sclerotized and pigmented. Phallobase sclerotized and pigmented at base, with numerous membranous lobes at apex.

Female genitalia. Anal tube (Fig. 34) round and large in dorsal view, ratio of length to width at middle approx. 0.7. First valvula (Fig. 35) sclerotized with seven differently sized teeth in lateral view. Second valvulae (Fig. 36) triangular, symmetrical in ventral view, connected at base and separated from 1/5 base. Third valvula (Fig. 37) with 2 sclerotized lobes, lateral lobe with 4 long spines at apex.

Type material. Holotype \mathcal{J} , China, Guizhou, Institute of Entomology. XII. 2008, Light trap, Zhangyubo. Paratypes, $6\mathcal{Q}\mathcal{Q}$, data same as holotype.

Etymology. This new species is named for the Greek word "*plurijuga*" referring to aedeagus with numerous membranous lobes at apex.



Figures 19–32. *Tenguna plurijuga* sp. n. **19** male, holotype **20** Same, female **21** Head and pronotum, lateral view **22** Head and thorax, dorsal view **23** Frons and clypeus, ventral view **24** Head and pronotum, lateral view **25** Forewing **26** Hind wing **27** Pygofer and anal tube, dorsal view **28** Pygofer and parameres, ventral view **29** Genitalia, lateral view **30** Aedeagus, lateral view **31** Aedeagus, ventral view **32** Aedeagus, dorsal view. Scale bars **19–26** = 2 mm; **27–32** 0.5mm.



Figures 33–37. *Tenguna plurijuga* sp. n. **33** Genitalia ventral view of female **34** Genitalia dorsal view of female **35** First valvulae (lateral view) **36** Second valvulae (ventral view) **37** Third valvulae (lateral view). Scale bars 0.5 mm.

Discussion

The discovery of two new species broadens our knowledge of the morphology and biogeography of the genus. The two new species both occur in Guizhou, China. This may be due to the climate of Guizhou, warm and humid, subtropical humid monsoon, and minimal temperature changes. All described species are distributed in the Palearctic and Oriental regions.

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RESEARCH ARTICLE



Taxonomic revision of the endemic Bornean genera Anexodus Pascoe and Pantilema Aurivillius (Coleoptera, Cerambycidae, Lamiinae)

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Abstract

The genera *Anexodus* Pascoe, 1866 and *Pantilema* Aurivillius, 1911 (Cerambycidae: Lamiinae: Morimopsini), both endemic to Borneo, are revised. Four species of *Anexodus* are recognized: *A. aquilus* Pascoe, 1886 (Malaysia: Sabah), *A. sarawakensis* Sudre, 1997 (Malaysia: Sarawak), *A. syptakovae* **sp. n.** (Malaysia: Sarawak), and *A. tufi* **sp. n.** (Brunei). *Pantilema* is a monotypic genus containing *P. angustum* Aurivillius, 1911 (Malaysia: Sarawak) which is known only from the holotype. For the first time, genital structures are studied in these genera. An identification key for the species of *Anexodus* is provided and their intraspecific morphological variability and distributions are discussed.

Keywords

Brunei, diversity, endemism, hot-spots, longhorn beetles, Malaysia, Morimopsini

Introduction

Cerambycidae forms one of the largest and most well-known beetle lineages in the world (Švácha and Lawrence 2014, Nearns et al. 2017). However, some lineages, especially those from the tropical regions, are underinvestigated, with numerous new taxa described recently (e.g. Bezark et al. 2016, Bi and Lin 2016, Huang and Lin 2016, Ohbayashi et al. 2016, Santos-Silva et al. 2016, Toledo-Hernández et al. 2016). This is also currently the case with Morimopsini, an assemblage of about 50 lamiine genera known mainly from the Afrotropical and Oriental Regions (Sudre and Teocchi 2002, Vitali and Menufandu 2010, Weigel 2015, Gouverneur 2016). Several taxa now assigned to Morimopsini occur also in Borneo (Breuning 1950, Gabriš et al. 2016). Pascoe (1886) described the genus Anexodus Pascoe for A. aquilus Pascoe, 1886 from Sabah. Additionally, Aurivillius (1911) described *Dolichostyrax* and *Pantilema* for D. moultoni Aurivillius, 1911 and P. angustum Aurivillius, 1911 from Sarawak and later, he added D. longipes Aurivillius, 1913 from Sabah (Aurivillius 1913). Kriesche (1924) described Anexodus kuntzeni Kriesche, 1924 based on three specimens from Mt. Kinabalu. Breuning (1950) made a key to the World Morimopsini and synonymized A. kuntzeni with A. aquilus. Since then, nobody has published on the morimopsine fauna of Borneo until Sudre (1997) described Anexodus sarawakensis Sudre, 1997 based on three specimens from Sarawak. Recently, Gabriš et al. (2016) revised the Bornean species of *Dolichostyrax* and described four species from Sabah for which they established three new genera, i.e. Borneostyrax, Eurystyrax, and Microdolichostyrax. They also reported ovoviviparity for the first time in Cerambycidae, when they found large larvae within the females of Borneostyrax cristatus Gabriš, Kundrata & Trnka, 2016.

To finish a revision of the genera classified in Morimopsini in Borneo, we herein review the species of *Anexodus* and *Pantilema*. For the first time, male and female genitalia are investigated and an identification key is provided for the species of *Anexodus*.

Material and methods

In this study we examined mounted adults of both sexes. Genitalia were briefly submerged in hot 10% KOH, dissected and transferred to glycerol. Main diagnostics were photographed using a Zeiss Discovery.V12 with ZEN software. The line illustrations were derived from the photographs. All dissected parts were mounted on separate cardboards using Dimethyl Hydantoin Formaldehyde (DMHF) resin and pinned under the specimens. The measurements of taxonomically relevant morphological structures were taken with a measuring tool in ZEN software as follows: body length (BL) measured from the fore margin of head to the apex of elytra; body width (BW), pronotal width at the widest part; pronotal length at midline. Data from the locality labels are cited verbatim. A slash (/) is used to separate lines on the same label and a double slash (//) is used to separate different labels on the pin. The morphological terminology is used as in Gabriš et al. (2016), following those in Ślipiński and Escalona (2013) and Švácha and Lawrence (2014).

Depositories

BMNH	Natural History Museum, London, The United Kingdom (M. Barclay,
	M. Geiser)
MHNG	Muséum d'Histoire Naturelle, Geneva, Switzerland (G. Cuccodoro)
MNHUB	Museum für Naturkunde, Humboldt-Universtät Berlin (J. Willers)
NHRS	Swedish Museum of Natural History, Stockholm, Sweden (J. Bergsten)
PCDH	personal collection of Daniel J. Heffern, Houston, TX, USA
PCJC	personal collection of James S. Cope, San Jose, CA, USA
UBDC	Universiti Brunei Darussalam, Brunei
UPOL	Palacky University, Olomouc, Czech Republic

Taxonomy

Genus Anexodus Pascoe, 1886

Anexodus Pascoe, 1886: 242.

Type species. Anexodus aquilus Pascoe, 1886.

Differential diagnosis. This genus is easily recognizable among the Bornean Morimopsini by its antennae, which are always shorter than body (Figs 1–8), and with antennomere II distinctly longer than antennomere III (Figs 21–27).

Description. Body elongate to elongate-oval, small to medium-sized. Body densely clothed with very short pubescence; coloration either more or less uniformly brown or brown with yellowish stripes ranging from vertex through sides of pronotum to basal part of elytra, mouthparts lighter; in some cases antennae reddish brown or black (Figs 1–16).

Head about the same width as anterior margin of pronotum; genae sub-parallel at frontal view; frontoclypeus with distinct midline running from interantennal groove to labrum, sparsely covered with large, rounded, deep punctures; antennal tubercles prominent with deep narrow depression in between; antennal cavities opened dorsally; anterior margin of anteclypeus shallowly emarginate, with sparse long yellowish semi-erect setae. Labrum free, transverse, glabrous, either with one row of punctures bearing long setae (Figs 18–19) or with whole surface moderately sparsely, irregularly punctured (Figs 17, 20). Eyes small, reniform, vertically elongate, more or less emarginate at antennal articulations, lower parts distinctly narrower than genae. Antennae filiform, 11-segmented, shorter than body in both sexes; scape and pedicel covered with very short dense pubescence; the rest of antennomeres with much sparser pubescence; scape enlarged, swollen, slightly curved, longest, reaching at most center of pronotum, subparallel-sided, gradually slightly widened towards apex, thickest at apical part, apex either simple (Figs 23-27) or with distinct lateral hook-shaped projection (Figs 21–22), pedicel very long, apical antennomere simple, about two times as long as penultimate antennomere. Mandibles short and broad, apex unidentate (Fig. 17-20).

Maxillary palpi tetramerous, apical palpomere fusiform (Figs 17–20). Labial palpi trimerous, apical palpomere of same shape as maxillary one.

Prothorax subcylindrical, about as long as wide, widest before middle, then gradually narrowed towards posterior margin, laterally with one small more or less distinct tubercle; pronotal disc weakly convex, sparsely covered with deep punctures, with indistinct tubercles, anterior and posterior angles obtuse. Prosternum in front of coxae slightly shorter than diameter of coxal cavity, procoxal cavities circular, with lateral extension, narrowly separated. Scutellum transverse, widely rounded apically, about two times as wide as long. Elytra elongate, 1.6-1.8 times as long as wide at widest part, 1.7-2.1 times as long as pronotum in males and 2.0-2.3 times in females, basally slightly wider than posterior pronotal margin, widest near middle, from middle gradually tapered towards apex, fused along suture; each elytron with three rows of tubercles irregular in size, in some cases inner row forming a distinct ridge basally (Figs 3, 11), sparsely covered by large deep punctures arranged irregularly in rows; outer elytral margin curved at lateral view (Figs 9-16). Mesoventrite with anterior edge on different plane than metaventrite; mesocoxal cavities circular. Metaventrite transverse, more than two times as wide as long, posterior margin with more or less narrow, deep median groove. Metacoxal cavities separated as widely as mesocoxal ones, extending laterally to meet elytra. Hind wings absent. Legs long, slender; femora weakly swollen distally, tibial spurs 2-2-2, protibiae with pubescent groove (antennal cleaner) on inner face, mesotibiae with pubescent groove on outer face, metatibiae without groove; tarsal formula 4-4-4; last tarsomere with four long erected setae at ventral face, claws simple, empodium absent.

Abdomen with five ventrites (Figs 9–16), first ventrite (excluding intercoxal process) almost two times longer than second; intercoxal process broadly rounded apically. Fifth ventrite with apex rounded in males and truncate in females, margin with sparse semi-erect pubescence. Male genitalia with tegmen elongate, widest near middle, basally with more or less short strut; parameres elongate, setose apically (Figs 28–31). Penis subparallel-sided, apically truncate or subacute; dorsal struts diverged from about 1/2 of penis length. Internal sac long, with paired small medial sclerites and distinct flagellar sclerites. Female genitalia with ovipositor elongate, narrow, apically with short styli. Vagina narrow, with pair of vaginal plates. Spermatheca present, more or less sclerotized, slender, elongate, curved; sclerotized part of spermathecal duct simple or strongly coiled (Figs 32–34).

Anexodus aquilus Pascoe, 1886

Figs 1-3, 9-11, 17, 21, 22, 28, 32

Anexodus aquilus Pascoe, 1886: 242. Anexodus kuntzeni Kriesche, 1924: 291; synonymized by Breuning (1950): 258.

Type material examined (*A. aquilus*). Holotype, male, [Malaysia] "Type [circular label with red margin, printed] // N / Borneo [blue oval label, handwritten] // *Anexodus* /

aquilus / type Pasc. [handwritten] // *Anexodus* / *aquilus* / N. Borneo Pa [handwritten] // Pascoe / Coll. / 93-60" (BMNH).

Type material examined (A. kuntzeni). Holotype, female, [Malaysia] "N:Borneo / Kina-Balu-Geb. / Waterstradt S. [printed] // Anexodus / küntzeni Kriesche / Typ! [handwritten] // Anexodus / aquilus Pasc. / Breuning dét. // HOLOTYPUS / Anexodus / kuntzeni Kriesche 1924 / labelled by MNHUB 2014 [red label, printed]" (MN-HUB); male, "N:Borneo / Kina-Balu-Geb. / Waterstradt S. [printed] // Anexodus / küntzeni Kriesche / Paratyp! [handwritten] // PARATYPUS / Anexodus / kuntzeni Kriesche 1924 / labelled by MNHUB 2014 [red label, printed]" (MNHUB); female, "N. Borneo / Kinabalů [handwritten] // PARATYPUS / Anexodus / küntzeni Kriesche 1924 / labelled by MNHUB 2014 [red label, printed]" (MNHUB); female, "N. Borneo / Kinabalů [handwritten] // Anexodus / küntzeni [handwritten] // Anexodus / labelled by MNHUB 2014 [red label, printed]" (MNHUB); female, "N. Borneo / Kinabalů [handwritten] // Anexodus / küntzeni [handwritten] // Anexodus / labelled by MNHUB 2014 [red label, printed]" (MNHUB); female, "N. Borneo / Kinabalů [handwritten] // Anexodus / küntzeni [handwritten] // Anexodus / labelled by MNHUB 2014 [red label, printed]" (MNHUB); female, "N. Borneo / Kinabalů [handwritten] // Anexodus / küntzeni [handwritten] // Anexodus / labelled by MNHUB 2014" (MNHUB).

Other material examined. Female, "Malaysia, Sabah, / Crocker Range 20- / IV-2007 Cope / collection" (PCJC); female, "Malaysia, Sabah / Crocker Range / III-22-2009 / local coll" (PCDH); female, "Malaysia, Sabah / Sandakan / II-12-2007 / local coll // *Anexodus | aquilus* Pasc. / det. D. Heffern '07" (PCDH); female, "Malaysia, Sabah / Ranau 700 m / IV-23-2015 / local coll" (PCDH); female, "Malaysia, Sabah / Tenom / III-2-2008 / local coll" (PCDH); male, "Malaysia, Sabah / Tenom / III-2-2008 / local coll" (PCDH); male, "Malaysia, Sabah, Mt. / Trus Madi 26-IV-2010 / Cope Collection" (PCJC); male, "Malaysia, Sabah / Mt. Trus Madi 26-V-2012 / Cope Collection" (PCJC); male, "Malaysia, Sabah / Mt. Trus-Madi / IV-15-2005 / local coll // *Anexodus | aquilus | Pascoe | det. J. Sudre*" (PCDH).

Differential diagnosis. This species is similar to *A. tufi* sp. n. in general habitus, yellowish stripes on dorsal body surface and a labrum with the entire surface punctured but differs in having apex of scape with a distinct lateral hook-shaped projection (simple in *A. tufi* sp. n.; Figs 21, 22, 26, 27), relatively longer parameres (Fig. 28), and a widened second half of spermatheca (Fig. 32).

Description. Holotype (male). BL 11.5 mm, BW 3.8 mm. Body brown with yellowish stripes extending from vertex through sides of pronotum to basal part of elytra; mouthparts lighter; antennae reddish brown. Body densely clothed with very short brown pubescence. Head about as wide as anterior margin of pronotum. Labrum transverse, with whole surface moderately sparsely, irregularly punctured (Fig. 17). Eyes moderately emarginate at antennal articulations (Figs 9–11). Antennae 0.9 times as long as body; scape gradually slightly widened towards apex, thickest at apical part, apex with a distinct lateral hook-shaped projection (Fig. 21–22); the relative ratio of antennomere lengths 3.3 : 1.6 : 1.0 : 1.2 : 1.1 : 0.9 : 0.8 : 0.6 : 0.6 : 1.1.

Prothorax as long as wide, laterally with one distinct tubercle; pronotal disc with a pair of indistinct tubercles near middle and one median at second half; pronotal tubercles punctate. Prosternum in front of coxae 0.9 times shorter than diameter of coxal cavity. Scutellum transverse, two times as wide as long. Elytra elongate, 1.6 times as long as wide at widest part, 1.7 times as long as pronotum, widest near middle; each elytron with three rows of indistinct tubercles, inner row forming a distinct ridge basally; sparsely covered with large deep punctures arranged in slightly irregular rows. Legs long, slender; relative lengths of metatarsomeres 1.0 : 0.5 : 1.0 : 2.0.



Figures 1–4. Dorsal habitus of *Anexodus* spp.: **1** *Anexodus aquilus* Pascoe, holotype male **2** *Anexodus aquilus* Pascoe, female (= holotype of *Anexodus kuntzeni* Kriesche) **3** *Anexodus aquilus* Pascoe, large male from Trus Madi **4** *Anexodus syptakovae* sp. n., holotype male. Scale bar = 5 mm.

Male genitalia with tegmen elongate, widest near middle, basally with very short strut; parameres elongate, 3.5 times longer than wide, apically with long setae (Fig. 28). Penis subparallel-sided, apically truncate; dorsal struts diverged from about 1/3 of penis length. Internal sac long, with paired small medial sclerites and distinct flagellar sclerites.

Variability in males. BL 9.1–12.5 mm, BW 3.1–4.2 mm. Antennae are either reddish brown, brown or black. There is a gradual morphological variation in the pronotal and elytral tubercles, ranging from the less distinct tubercles in the holotype (Figs 1, 9) through the more distinct tubercles in most specimens to the strongly developed tubercles with inner elytral row forming a conspicuous ridge basally in the specimens from Trus Madi (Figs 3, 11).

Female. Most characters same as for males. BL 10.0–13.0 mm, BW 3.2–4.5 mm. Body more convex dorsally, with distinct tubercles on pronotum and elytra. Antennae shorter, 0.6–0.7 times as long as body. Elytra 1.7 times as long as wide, 2.0–2.1 times as long as pronotum. Spermatheca sclerotized, slender, elongate, curved, widened at second half, gradually tapered toward apex; sclerotized part of spermathecal duct simple (Fig. 32).

Distribution. Malaysia: Borneo (Sabah; Fig. 43).

Anexodus sarawakensis Sudre, 1997

Figs 5-6, 13-14, 18, 23-24, 29, 34

Anexodus sarawakensis Sudre, 1997: 253.

Type material examined. Holotype, male, "E. MALAYSIA: Sarawak / confl. Sun Oyan and / Mujong riv., E. Kapit / 50m, 18.V.1994, # 5 / Löbl & Burckhardt // Holotype // *Anexodus | sarawakensis* Nov sp. / J. Sudre det. 1996" (MHNG). Paratype, female, "E. MALAYSIA: Sarawak / confl. Sun Oyan and / Mujong riv., E. Kapit / 50m, 18.V.1994, # 5 / Löbl & Burckhardt // comparé zu type / d'*A. aquilus* per / J. Sudre 1996 // Paratype // *Anexodus* (\mathcal{Q}) / *sarawakensis* sp. n / J. Sudre det. 1996" (MHNG).

Differential diagnosis. Anexodus sarawakensis is similar to A. syptakovae sp. n. in having uniformly colored habitus and labrum with one row of distinct punctures with setae (Fig. 18). For more details see the differential diagnosis under the latter species.

Description. Holotype (male). BL 9.2 mm, BW 3.1 mm. Body uniformly brown, mouthparts lighter. Body densely clothed with very short brown pubescence. Head about as wide as anterior margin of pronotum. Labrum transverse, with one row of punctures bearing long setae (Fig. 18). Eyes less emarginate at antennal insertions (Figs 13–14). Antennae 0.8 times as long as body; scape gradually slightly widened towards apex, thickest at apical part, apex simple (Figs 23–24); the relative ratio of antennomere lengths 6.3 : 2.5 : 1.0 : 1.3 : 1.1 : 1.0 : 1.0 : 0.9 : 0.8 : 1.0 : 2.0.

Prothorax as long as wide, laterally with one moderately distinct tubercle; pronotal disc with a pair of distinct tubercles near middle and one median at second half; pronotal tubercles punctate. Prosternum in front of coxae 0.9 times shorter than diameter of coxal cavity. Scutellum transverse, two times as wide as long. Elytra elongate, 1.6



Figures 5–8. Dorsal habitus of *Anexodus* spp.: **5** *Anexodus sarawakensis* Sudre, holotype male **6** *Anexodus sarawakensis* Sudre, paratype female **7** *Anexodus tufi* sp. n., holotype male **8** *Anexodus tufi* sp. n., paratype female. Scale bar 5 mm.
times as long as wide at widest part, 1.8 times as long as pronotum, widest near middle; each elytron with three rows of distinct tubercles (Figs 5–6), sparsely covered with large deep punctures arranged in slightly irregular rows. Legs long, slender; relative lengths of metatarsomeres 1.0 : 0.7 : 1.1 : 2.0.

Male genitalia with tegmen elongate, widest near middle, basally with short strut; parameres elongate, 2.9 times longer than wide, apically with long setae (Fig. 29). Penis subparallel-sided, apically subacute; dorsal struts diverged from about one third of penis length. Internal sac long, with paired small medial sclerites and distinct flagellar sclerites.

Female. Most characters same as for males. BL 9.9 mm, BW 3.5 mm. Body more convex dorsally. Antennae slightly shorter than in male, 0.7 times as long as body; length ratio of antennomeres I–III: 6.5 : 2.7 : 1.0. Elytra 1.7 times as long as wide, 2.3 times as long as pronotum. Spermatheca only slightly sclerotized, slender, elongate; sclerotized part of spermathecal duct strongly coiled (Fig. 34).

Distribution. Malaysia: Borneo (Sarawak: Kapit; Fig. 43).

Anexodus syptakovae sp. n.

http://zoobank.org/DC100C9A-EB88-43D9-A812-CA8C4A20FEEE Figs 4, 12, 19, 25, 30

Type material. Holotype, male, [Malaysia] "SARAWAK: / 5th Division / Gn. Mulu NP // Camp 5 / Kerangas // Pitfall / trap // iv. 78, N. M. Collins / B.M.1978-11 // *Opsies* sp." (BMNH). Paratype, male, "SARAWAK: / 4th Division / Gn. Mulu NP // mixed / dipterocarp / forest // Site B / 130 m. // soil cores // N. M. Collins / B.M.1978-11" (BMNH).

Differential diagnosis. This species is similar to *A. sarawakensis* in having uniformly colored habitus and labrum with a row of distinct punctures with setae (Fig. 19). However, *A. syptakovae* sp. n. is smaller, with different ratio of antennomeres I–III (Figs 23–25), less distinct tubercles on pronotal disc and elytra (Fig. 4), and relatively shorter and wider parameres, with tufts of shorter setae apically (longer parameres with longer setae apically in *A. sarawakensis*; Figs 29–30).

Description. Holotype (male). BL 8.0 mm, BW 2.5 mm. Body uniformly brown, mouthparts lighter. Body densely clothed with very short brown pubescence. Head slightly wider than anterior margin of pronotum. Labrum transverse, with one row of punctures bearing long setae (Fig. 19). Eyes less emarginate at antennal insertions (Fig. 12). Antennae 0.9 times as long as body; scape gradually slightly widened towards apex, thickest at apical part, apex simple (Fig. 25); the relative ratio of antennomere lengths 4.4 : 1.7 : 1.0 : 1.1 : 1.0 : 0.9 : 0.9 : 0.8 : 0.7 : 0.9 : 1.4.

Prothorax as long as wide, laterally with one indistinct tubercle; pronotal disc with a pair of very indistinct tubercles near middle and one median at second half; pronotal tubercles punctate. Prosternum in front of coxae 0.9 times shorter than diameter of coxal cavity. Scutellum transverse, about two times as wide as long. Elytra elongate, 1.8 times as long as wide at widest part, 2.1 times as long as pronotum, widest near middle;



Figures 9–16. Lateral habitus of Anexodus spp.: 9 Anexodus aquilus Pascoe, holotype male 10 Anexodus aquilus Pascoe, female (= holotype of Anexodus kuntzeni Kriesche) 11 Anexodus aquilus Pascoe, large male from Trus Madi 12 Anexodus syptakovae sp. n., holotype male 13 Anexodus sarawakensis Sudre, holotype male 14 Anexodus sarawakensis Sudre, paratype female 15 Anexodus tufi sp. n., holotype male 16 Anexodus tufi sp. n., paratype female. Scale bar 5 mm.

each elytron with three rows of only slightly elevated tubercles (Fig. 12), sparsely covered with large deep punctures arranged in slightly irregular rows. Legs long, slender; relative lengths of metatarsomeres 1.0 : 0.7 : 1.1 : 1.9.

Male genitalia with tegmen elongate, widest near middle, basally with short strut; parameres elongate, 2.3 times longer than wide, apically with tufts of short setae (Fig. 30). Penis subparallel-sided, apically truncate; dorsal struts diverged from about half of penis length. Internal sac long, with paired small medial sclerites and distinct flagellar sclerites.

Intraspecific variability. Paratype is smaller (BL 7.00 mm, BW 2.3 mm), with reddish brown antennae.

Female unknown.

Distribution. Malaysia: Borneo (Sarawak: Gn. Mulu NP; Fig. 43).

Etymology. The specific name is a matronym in honor of Ms. Hana Gabriš Syptáková (Salisov, Czech Republic).

Anexodus tufi sp. n.

http://zoobank.org/85AFEBB7-502B-4303-8C86-B9DD45AD8F1F Figs 7–8, 15–16, 20, 26–27, 31, 33, 40

Type material. Holotype, male, "BRUNEI, Ulu Temburong NP / Kuala Belalong FSC / 4°32'47.6"N 115°09'27"E / I. H. Tuf leg. II.2013" (UBDC); paratype, female, same data as holotype (UPOL); 2 paratypes, females, "BRUNEI, Ulu Temburong NP / Kuala Belalong FSC / 4°32'47.6"N 115°09'27"E / Z. Mačát leg. I.2014" (BMNH); paratype, female, "BRUNEI, Ulu Temburong NP / Kuala Belalong FSC / 4°32'47.6"N 115°09'27"E / O. Machač leg. II.2015" (UPOL).

Differential dagnosis. This species is similar to *A. aquilus* in having yellowish stripes on the dorsal body surface and labrum with the whole surface punctured (Fig. 20), but it differs in shape of the scape (apex simple in *A. tufi* sp. n., apex with distinct lateral hook-shaped projection in *A. aquilus*; Figs 21–22, 26–27), length of the parameres (relatively longer in *A. aquilus*; Figs 28, 31), and shape of the spermatheca (simply elongated in *A. tufi* sp. n., widened at second half in *A. aquilus*; Figs 32–33).

Description. Holotype (male). BL 7.4 mm, BW 2.3 mm. Body brown with yellowish stripes ranging from vertex through sides of pronotum to basal part of elytra, densely clothed with very short brown pubescence. Head about as wide as anterior margin of pronotum. Labrum transverse, its surface with moderately sparse punctures (Fig. 20). Eyes moderately emarginate at antennal articulations (Figs 15–16). Antennae 0.9 times as long as body; scape gradually slightly widened towards apex, thickest at apical part, apex simple (Figs 26–27); the relative ratio of antennomere lengths 3.2 : 1.5 : 1.0 : 1.2 : 1.0 : 0.9 : 0.5 : 0.5 : 0.5 : 1.0.

Prothorax as long as wide, laterally with one distinct tubercle; pronotal disc with a pair of moderately distinct tubercles near middle and one median at second half and one indistinct median at anterior half; pronotal tubercles punctate. Prosternum in front of coxae 0.9 times shorter than diameter of coxal cavity. Scutellum transverse, two times as wide as long. Elytra elongate, 1.8 times as long as wide at widest part, 1.9 times as long as pronotum, widest near middle; each elytron with three rows of distinct, longitudinally elongate tubercles (Figs 7–8, 15–16), inner row forming a distinct ridge basally; sparsely covered with large deep punctures arranged in slightly irregular rows. Legs long, slender; relative lengths of metatarsomeres 1.0 : 0.6 : 1.0 : 2.1.

Male genitalia with tegmen elongate, widest before middle, basally with short strut; parameres elongate, 3.3 times longer than wide, apically with long setae (Fig. 31). Pe-



Figures 17–27. Anexodus spp.: 17–20 Head, frontal view: 17 Anexodus aquilus Pascoe, holotype male 18 Anexodus sarawakensis Sudre, holotype male 19 Anexodus syptakovae sp. n., holotype male 20 Anexodus tufi sp. n., holotype male 21–27 Antenna: 21 Anexodus aquilus Pascoe, male 22 Anexodus aquilus Pascoe, female 23 Anexodus sarawakensis Sudre, male 24 Anexodus sarawakensis Sudre, female 25 Anexodus syptakovae sp. n., male 26 Anexodus tufi sp. n., male 27 Anexodus tufi sp. n., female. Not to scale.

nis subparallel-sided, apically truncate; dorsal struts diverged from about 1/3 of penis length. Internal sac long, with paired small medial sclerites and distinct flagellar sclerites.

Intraspecific variability. The male paratype is larger (body length 9.4 mm, body width 2.8 mm).

Female. Most characters same as for males. BL 8.5–10.2 mm, BW 2.7–3.4. Antennae shorter, 0.7 times as long as body, with relatively longer scape and pedicel (length ratio of antennomeres I–III: 3.4–3.6 : 1.7–1.8 : 1.0). Elytra 2.2–2.3 times as long pronotum. Fifth ventrite with apex truncate. Spermatheca sclerotized, slender, elongate, curved, gradually tapered toward apex; sclerotized part of spermathecal duct simple (Fig. 33).

Distribution. Brunei (Fig. 43). All the specimens in the type series are from the vicinity of the Kuala Belalong Field Studies Centre (KBFSC) in the Ulu Temburong National Park (Fig. 41) which has been described in detail by Ševčík et al. (2014).

Etymology. This species is named after Mr. I. H. Tuf (UPOL, Czech Republic; Fig. 42), who collected a part of the type series.

Genus Pantilema Aurivillius, 1911

Pantilema Aurivillius, 1911: 196.

Type species. Pantilema angustum Aurivillius, 1911.

Differential diagnosis. *Pantilema* differs from the remaining Bornean Morimopsini by having a slender, narrow, parallel-sided body (body length/width ratio = 3.5), tibial spurs 1-1-2, truncate elytral apex, and tubercles only in the apical half of the elytra (Figs 35–36).

Description. Body slender, elongate, densely clothed with very short pubescence; coloration brown, with some parts paler, yellowish, antennae and legs reddish-brown (Figs 35–36).

Head about the same width as anterior margin of pronotum; genae convex at frontal view; frontoclypeus with distinct midline running from interantennal groove to labrum, sparsely punctured; antennal tubercles prominent with narrow, deep depression in between; antennal cavities opened dorsally; anterior margin of anteclypeus shallowly emarginate, with sparse long yellowish semi-erect setae. Labrum free, transverse, glabrous, with a row of distinct punctures and sparsely and irregularly distributed additional less distinct punctures, with sparse long semi-erect setae (Fig. 38). Eyes small, distinctly elongate vertically, narrow, about four times as long as wide, slightly emarginate at antennal insertions, lower parts distinctly narrower than genae (Fig. 36). Antennae filiform, 11-segmented, shorter than body; scape and first half of pedicel covered with very short dense light brown pubescence; the rest of antenna with much sparser pubescence; scape enlarged, swollen, reaching the first half of pronotum, subparallel-sided, apically slightly widened, pedicel short, apical antennomere simple, less than two times as long as penultimate antennomere (Fig. 37). Mandibles short





Figures 28–34. Anexodus species: 28–31 Aedeagus, ventral view: 28 Anexodus aquilus Pascoe, holotype 29 Anexodus sarawakensis Sudre, holotype 30 Anexodus syptakovae sp. n., holotype 31 Anexodus tufi sp. n., holotype 32–34 Spermatheca: 32 Anexodus aquilus Pascoe 33 Anexodus tufi sp. n. 34 Anexodus sarawakensis Sudre. Not to scale.

and broad, apex unidentate (Fig. 38). Maxillary palpi tetramerous, apical palpomere fusiform. Labial palpi trimerous, apical palpomere of same shape as maxillary one.

Prothorax about as long as wide, subparallel-sided at anterior half, widest slightly medially, then gradually narrowed towards posterior margin, laterally with one very weakly developed tubercle; pronotal disc weakly convex, sparsely covered with deep punctures, not smooth, without tubercles (Fig. 38), anterior and posterior angles obtuse. Prosternum in front of coxae slightly shorter than diameter of coxal cavity, procoxal cavities circular, with lateral extension, narrowly separated. Scutellum transverse, subtriangular, about three times as wide as long. Elytra elongate, twice as long as wide at widest part, basally as wide as posterior pronotal margin, without distinct humeral bulges, widest near middle, fused along the elytral suture, apically truncate; with tubercles present only at apical third of elytra; tubercles arranged in two rows, apical tubercles forming large transverse irregularly shaped bulge (Fig. 35), elytra sparsely covered with large deep punctures arranged in slightly irregular rows; outer elytral margin distinctly curved at lateral view (Fig. 36). Mesoventrite with anterior edge on different plane than metaventrite; mesocoxal cavities circular, separated slightly wider than in procoxal cavities. Metaventrite transverse, more than two times as wide as long. Metacoxal cavities extending laterally to meet elytra. Hind wings absent. Legs long, slender; femora weakly swollen distally, tibial spurs 1-1-2, protibiae with pubescent groove (antennal cleaner) on inner face, mesotibiae with pubescent groove on outer face, metatibiae without groove; tarsal formula 4-4-4, last tarsomere with four long erected setae at ventral face, claws simple, empodium absent.

Abdomen with five visible ventrites, first ventrite (excluding intercoxal process) almost 1.5 times longer than second; intercoxal process subparallel-sided basally, narrowed and broadly rounded apically. Fifth ventrite with apex truncate, margin with sparse semi-erect pubescence. Male genitalia with tegmen elongate, widest at apical third, basally with long strut; parameres moderately long, setose apically. Penis relatively long, with dorsal struts diverged from about two fifths of penis length (Fig. 39). Internal sac long, with paired medial sclerites and distinct complex of flagellar sclerites.

Pantilema angustum Aurivillius, 1911

Figs 35-39

Pantilema angustum Aurivillius, 1911: 196.

Type material examined. Holotype, male, "Samarahan / June 1906 [handwritten] // Type. // NHRS-JLKB / 000022859 // 5184 / E94 +" (NHRS).

Redescription. Holotype (male). BL 10.6 mm, BW 3.1 mm. Body brown, with antennae and legs reddish-brown, elytral apex and two median spots near anterior and posterior pronotal margins yellowish, mouthparts lighter (Figs 35–36). Body densely clothed with very short brown pubescence. Head about as wide as anterior margin of pronotum. Labrum with a row of distinct punctures and sparsely and irregularly distributed additional less distinct punctures, with sparse long semi-erect setae (Fig. 38). Eyes slightly emarginate at antennal insertions (Fig. 36); minimum interocular distance 1.9 times maximum eye diameter. Antennae (left present in whole length; right with antennomeres II–XI missing) 0.7 times as long as body; scape reaching the



Figures 35–39. *Pantilema angustum* Aurivillius, holotype male: 35 Dorsal habitus (scale bar 5 mm) 36 Lateral habitus (scale bar 5 mm) 37 Antenna 38 Head, frontal view 39 Aedeagus, ventral view. Scale bar 5 mm.

first half of pronotum, subparallel-sided, apically slightly widened, the relative ratio of antennomere lengths 2.9:0.7:1.0:1.1:0.9:0.8:0.7:0.7:0.6:0.7:1.3 (Fig. 37).

Prothorax 1.1 times as long as wide, laterally with one very weakly developed tubercle; pronotal disc without tubercles (Fig. 38). Prosternum in front of coxae 0.9 times as wide as diameter of coxal cavity. Scutellum transverse, about three times as



Figures 40–42. *Anexodus tufi* sp. n. in the Ulu Temburong National Park, Brunei: **40** Live specimen **41** Habitat near the Kuala Belalong Field Studies Centre **42** Ivan H. Tuf collecting invertebrates from the rainforest litter.

wide as long. Elytra 2.0 times as long as wide at widest part, 1.9 times as long as pronotum, without distinct humeral bulges, apically truncate; with tubercles present only at apical third of elytra; tubercles arranged in two rows, apical tubercles forming large transverse irregularly shaped bulge (Fig. 35), elytra sparsely covered with large deep punctures arranged in slightly irregular rows (Fig. 36). Legs long, slender, relative lengths of metatarsomeres 1.0 : 0.6 : 1.0 : 1.8.

Male genitalia with tegmen elongate, widest at apical third, basally with long strut; parameres moderately long. Penis long, apically broadly rounded; dorsal struts diverged from about two fifths of penis length (Fig. 39). Internal sac long, with paired small medial sclerites and distinct complex of flagellar sclerites formed by plates of sclerotized spines.

Distribution. Malaysia: Borneo (Sarawak: Samarahan; Fig. 43).

Identification key for the species of Anexodus Pascoe

1	Body uniformly brown (Figs 4–6); labrum with one row of distinct punctures
	with setae (Figs 18–19)2
_	Body brown with yellowish stripes dorsally (Figs 1-3, 7-8); labrum with
	whole surface with sparse punctures (Figs 17, 20)
2	Body length 7.0-8.0 mm; length ratio of antennomeres I-III 4.4-4.6 :
	1.7-1.9 : 1.0 (Fig. 25); less distinct tubercles on pronotal disc and elytra
	(Figs 4, 12); parameres wider, 2.3 times longer than wide, with tufts of short
	setae apically (Fig. 30); Malaysia: Sarawak (Fig. 43) A. syptakovae sp. n.
_	Body length 9.2–9.9 mm; length ratio of antennomeres I–III 6.3–6.5 : 2.5–
	2.7 : 1.0 (Figs 23-24); more distinct tubercles on pronotal disc and elytra
	(Figs 5-6, 13-14); parameres more elongated, 2.9 times longer than wide,
	with long setae apically (Fig. 29); Malaysia: Sarawak (Fig. 43)
	A. sarawakensis Sudre
3	Apex of the scape with distinct lateral hook-shaped projection (Figs 21-
	22); parameres relatively longer, 3.5 times longer than wide (Fig. 28); sper-
	matheca widened at second half (Fig. 32); Malaysia: Sabah (Fig. 43)
_	Apex of the scape simple (Figs 26–27); parameres relatively shorter, 3.3 times
	longer than wide (Fig. 31); spermatheca simple, elongated (Fig. 33); Brunei
	(Fig. 43)

Checklist of the Morimopsini in Borneo

Genus Anexodus Pascoe, 1886

A. aquilus Pascoe, 1886 (Malaysia: Sabah; Fig. 43) (type species, by monotypy)



Figure 43. The distribution of Morimopsini in Borneo. A *Anexodus* Pascoe, B *Borneostyrax* Gabriš, Kundrata & Trnka, D *Dolichostyrax* Aurivillius, E *Eurystyrax* Gabriš, Kundrata & Trnka, M *Microdolichostyrax* Gabriš, Kundrata & Trnka, P *Pantilema* Aurivillius.

- A. sarawakensis Sudre, 1997 (Malaysia: Sarawak; Fig. 43)
- A. syptakovae sp. n. (Malaysia: Sarawak; Fig. 43)
- A. tufi sp. n. (Brunei; Fig. 43)

Genus Borneostyrax Gabriš, Kundrata & Trnka, 2016

B. cristatus Gabriš, Kundrata & Trnka, 2016 (Malaysia: Sabah; Fig. 43) (type species, by original designation)

Genus Dolichostyrax Aurivillius, 1911

D. longipes Aurivillius, 1913 (Malaysia: Sabah; Fig. 43)

D. moultoni Aurivillius, 1911 (Malaysia: Sarawak; Fig. 43) (type species, by monotypy)

Genus Eurystyrax Gabriš, Kundrata & Trnka, 2016

E. nemethi Gabriš, Kundrata & Trnka, 2016 (Malaysia: Sabah; Fig. 43) (type species, by original designation)

Genus Microdolichostyrax Gabriš, Kundrata & Trnka, 2016

M. hefferni Gabriš, Kundrata & Trnka, 2016 (Malaysia: Sabah; Fig. 43) (type species, by original designation)

M. minutus Gabriš, Kundrata & Trnka, 2016 (Malaysia: Sabah; Fig. 43)

Genus Pantilema Aurivillius, 1911

P. angustum Aurivillius, 1911 (Malaysia: Sarawak; Fig. 43) (type species, by monotypy)

Discussion

In 2013, two Czech universities (Palacky University in Olomouc, University of Ostrava) and the Universiti Brunei Darussalam established a collaboration which resulted in the biodiversity survey of the Ulu Temburong National Park in Brunei (Dančák et al. 2013; Ševčík et al. 2014; Hroneš et al. 2015; Ježek et al. 2015; Kočárek et al. 2015; Hippa et al. 2016; Kuřavová et al. 2017a, b). The collection of several specimens of Anexodus during the sifting of forest litter (Figs 40–42) encouraged a taxonomical revision of this genus and its relatives in Borneo. In the first part (Gabriš et al. 2016), the genus Dolichostyrax was revised, including the material identified by various researchers as belonging to that genus, and here, the remaining genera Anexodus and Pantilema are revised. Altogether, the occurrence of eleven species in six genera currently classified in Morimopsini in Borneo is confirmed. All known species are distributed in the northern part of Borneo (Fig. 43), which is the presumed Pleistocene rainforest refugium with a very high biodiversity (e.g. Gathorne-Hardy et al. 2002). As demonstrated by Gabriš et al. (2016) and here, the diversity of the morimopsine genera in Borneo is much higher than ever expected. These beetles are also often overlooked in the field due to their cryptic life-style (Figs 40-41) and because entomologists interested in Cerambycidae only rarely use sifting (Fig. 42) or pitfall traps as the collecting methods in the tropical forests. However, sifting forest leaf litter is an effective method for collecting various flightless beetle groups (e.g. Anderson and Ashe 2000; Kodada et al. 2013; Grebennikov 2014, 2016; Gerstmeier 2015) and its use in the Bornean rainforest could result in discoveries of further morimopsine lineages.

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RESEARCH ARTICLE



A review of the cavernicolous genus Guiaphaenops Deuve, with the description of a new species (Coleoptera, Carabidae, Trechinae)

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Abstract

The subterranean ground beetle genus *Guiaphaenops* Deuve, 2002 is taxonomically reviewed. This poorly known genus is different from *Guizhaphaenops* Vigna Taglianti, 1997 in having convex propleura which is visible from above and elytral chaetotaxy especially the humeral group of the marginal umbilicate series, in which the 1st pore is transversely and backwardly shifted. The second species, *G. deuvei* Tian, Feng & Wei, **sp. n.**, is described from a limestone cave at Yangli Cun (Village), Lingyun Xian (County), Baise Shi (Prefecture), northwestern Guangxi Zhuang Autonomous Region, China. A key to the species and a distribution map of *Guiaphaenops* are also provided.

Keywords

China, Guangxi, ground beetle, new species, semi-aphaenopsian, subterranean

Introduction

Karstic landscapes are diverse in Guangxi Zhuang Autonomous Region, covering more than 42% of the total terrestrial area and having more than 60,000 caves (Zhang et al. 2011). Accordingly, the cave biodiversity is very rich in this region (Tian et al. 2011). For example, more than 30 cave-adapted trechine species belonging to 15 genera have been recorded, the majority of which are members of highly modified aphaenopsian genera, such as *Giraffaphaenops* Deuve, 2002, *Dongodytes* Deuve, 1993, *Pilosaphaenops* Deuve & Tian, 2008 (Tian 2010), *Sinaphaenops* Uéno & Wang, 1991 and *Uenotrechus* Deuve & Tian, 1999 (Tian et al. 2016).

Guiaphaenops Deuve, 2002 was established as a subgenus of *Guizhaphaenops* Vigna Taglianti, 1997 to arrange *Guiaphaenops lingyunensis* Deuve, 2002, a semi-aphaenopsian species (Deuve 2002). Uéno (2006) treated *Guiaphaenops* as an independent genus considering the peculiar characters of its prothorax and elytral chaetotaxy, and he added another locality cave for *G. lingyunensis*. Until today, *Guiaphaenops* is still a mono-specific genus, known only from two limestone caves in Lingyun Xian, northwestern Guangxi.

In recent years, more material of *Guiaphaenops* has been collected by SCAU team during the cave biological surveys carried out in Lingyun. The findings make it possible to contribute to the knowledge of this interesting genus by providing the new record for *G. lingyunensis* and the description of a new species.

Material and methods

The blind beetles for this study were collected visually using an aspirator and preserved in 50% ethanol before study. All specimens are deposited in the insect collection of South China Agricultural University, Guangzhou, China (**SCAU**).

Techniques, terminology and abbreviations used in the text follow Tian et al. (2016).

Taxonomic treatments

Genus Guiaphaenops Deuve, 2002

 Subgenus Guiaphaenops (of Guizhaphaenops Vigna Taglianti, 1997), Deuve, 2002: 516 (type species: Guizhaphaenops lingyunensis Deuve, 2002).
Genus Guiaphaenops, Uéno, 2006: 22

Main generic characteristics. Median sized and semi-aphaenopsian beetles, eyeless and depigmented; appendages rather long, antennae extending at (female) or over (male) elytral apices; dorsal surface glabrous though a few short hairs present on genae;

fore part including mandibles nearly as long as elytra. Head rather elongated, much longer than wide, sub-tubiform; genea slightly and gradually narrowed posteriorly, frontal furrows uncompleted, effaced posteriorly, presence of two pairs of frontal setiferous pores; mandibles thin and elongated, feebly curved apically, right mandibular teeth bidentate; mentum and submentum fused, mental tooth simple, base of mentum distinctly concave, submentum 8- to 10-setose. Prothorax evidently wider than head, propleura distinctly convex and evidently visible from above; pronotum sub-quadrate, slightly wider than head, evidently longer than wide, presence of two pairs of lateromarginal setae, side margins slightly or strongly sinuate before hind angles which are more or less broadly lobed. Elytra sub-ovate, much wider than prothorax, shoulders rounded, prehumeral borders arcuate or nearly oblique, lateral margins ciliate in basal half; striae lacking though somewhat traceable; presence of two dorsal pores and the preapical pore on each elytron. Chaetotaxy: the 1st pore in the humeral group of the marginal umbilicate series transversely and backwardly shifted, at level behind the 2nd pore; the 5th and 6th pores in the middle group close to each other. Protibia smooth, without longitudinal sulcus; only the 1st protarsomere modified in male. Abdominal ventrite VII bisetose in male, while quadrisetose in female. Male genitalia weakly sclerotized, very small, slightly curved ventrally in lateral view, with a quite large sagittal aileron; apical lobe broad in dorsal view; parameres moderately developed, each with 4 rather short apical setae.

Discussion. Though *Guiaphaenops* is more or less similar to the genus *Guizhaphaenops*, the peculiar characteristics such as propleura of prothorax convex and visible from above and the 1st pore of elytral marginal umbilicate series transversely and backwardly suggest that it has to be isolated from the latter genus (Uéno, 2006). *Guiaphaenops* is probably closer to *Zhijinaphaenops* Uéno & Ran, 2002 than to *Guizhaphaenops* in a strict sense because the above mentioned morphological features of *Guiaphaenops* are also shared by *Zhijinaphaenops*. However, *Guiaphaenops* is easily distinguished from the latter genus by its glabrous and smooth body (wholly pubescent in *Zhijinaphaenops*), roundly lobed hind angles (well-marked in *Zhijinaphaenops*), presence of anterior frontal pores on head and hind latero-marginal setae on pronotum (both absent in *Zhijinaphaenops*), and sub-ovate elytra (elongated ovate in *Zhijinaphaenops*).

Range. China (Guangxi). Known only by two species from four limestone caves in Lingyun Xian (Fig. 1).

Key to species of Guiaphaenops



Figure 1. Distribution of *Guiaphaenops* species. **a, b, d** *G. lingyunensis* Deuve **c** *G. deuvei* Tian, Feng & Wei, sp. n.

Guiaphaenops deuvei Tian, Feng & Wei, sp. n.

http://zoobank.org/623D0DFD-CA91-4AE0-9418-99D1F7B59C83 Figs 1c, 2, 3a, 4a, 5a, b, 6

Holotype. male, an anonymous cave near Yangli Cun, Jiayou Zhen, Lingyun Xian, Baise Shi, Guangxi, 24°28'39"N, 106°37'52"E, 643 m, VII-25-2012, Mingyi Tian, Weixin Liu, Feifei Sun & Haomin Yin leg., in South China Agricultural University, Guangzhou, China (SCAU).

Diagnosis. A larger species, latero-margins of pronotum strongly sinuate before hind angles which are distinctly lobed and reflexed (Fig. 3a); the 1st pore of the humeral set of umbilicate pores at level before anterior dorsal pore, while the 7th pore behind the level of the preapical pore (Fig. 4a); the median lobe of aedeagus a little slenderer, with apical lobe narrowly constricted towards apex in dorsal view (Fig. 5a, b).

Description. Length: 7.0 mm, width: 2.0 mm. Fore body (including mandibles) shorter than elytra. Habitus as in Fig. 2.

Yellowish brown, with pale appendages. Moderately shiny. Body smooth and glabrous, except genae, underside of head and prosternum each with several sparse setae, ventrites IV-VI with a few short setae between paramedian setae. Microsculptural engraved meshes finely transverse striated.

Head much longer than wide (HLm/HW = 2.45, HLl/HW = 1.75); genae fairly developed, slightly dilated laterally, slightly constricted posteriorly until the well-marked neck constriction; widest at about middle of head from labrum to base; frons and vertex



Figure 2. Habitus of Guiaphaenops deuvei Tian, Feng & Wei, sp. n., holotype, male.

convex, frontal furrows deep and well-marked, divergent at base and apex, ended a little behind the widest part; clypeus transverse, quadrisetose; labrum transverse, frontal margin more or less serrate, 6-setose; anterior and posterior frontal setiferous pores



Figure 3. Pronota of Guiaphaenops species. a G. deuvei Tian, Feng & Wei, sp. n. b G. lingyunensis Deuve.

located at about middle of head from labrum to neck constriction and 1/3 from base to labrum respectively; ligula well developed, bisetose at apex; submentum 8-setose. Antennae long, the 1st antennomere stouter than other, slightly shorter than the 2nd which is slightly shorter than the 11th; the 5th and 6th longest, each about twice as long as the 1st, then gradually shortened towards the 10th.

Prothorax (Fig. 3a) shorter than head (PrL/HLm = 0.55, PrL/HLl = 0.77), widest at about 1/3 from base, longer than wide (PrL/PrW = 1.08), wider than head (PrW/HW = 1.25), slightly wider than pronotum (PrW/PnW = 1.11), much narrower than elytra (PrW/EW = 0.46). Pronotum (Fig. 3a) longer than wide (PnL/PnW = 1.20), and wider than head (PnW/HW = 1.13), base wider than front (PbW/PfW = 1.29); lateral sides and finely bordered throughout, base and front unbordered; lateral margin slightly expanded medially, widest at a little behind middle, strongly sinuate before hind angles which are broadly lobed, fore angle obtuse; latero-marginal setae at about 1/4 of pronotum from front and a little before hind angles respectively. Scutellum small.

Elytra (Fig. 4a) longer than head plus prothorax (EL/(HL+PrL) = 1.21), longer than wide (EL/EW = 1.71); widest at about middle, prehumeral borders evidently



Figure 4. Left elytra of *Guiaphaenops* species, chaetotaxy shown by white points. **a** *G. deuvei* Tian, Feng & Wei, sp. n. **b** *G. lingyunensis* Deuve.

ciliate, and nearly oblique; disc moderately convex; striae present though superficial. Chaetotaxy: anterior and posterior dorsal pores at about 1/5 of elytra from base and middle of elytra, preapical pore at 1/6 of elytra from apex, much closer to suture than to apical margin; the 1st pore of the humeral set of umbilicate pores located before anterior dorsal pore, while the 7th pore behind the preapical.



Figure 5. Male genitalia of *Guiaphaenops* species, median lobe and parameres, lateral view (**a**, **c**) and apical lobe, dorsal view (**b**, **d**) (**a**, **b** *G. deuvei* Tian, Feng & Wei, sp. n. **c**, **d** *G. lingyunensis* Deuve).

Legs thin and rather long, the 1^{st} tarsomere as long as the $2^{nd}-4^{th}$ tarsomeres together in fore, but longer in middle and hind legs.

Male genitalia (Fig. 5a, b): Weakly sclerotized, small but stouter than in *G. ling-yunensis*, apical lobe narrower at apical part.

Etymology. Dedicated to Dr. Thierry Deuve of the National Museum of Natural History, Paris, a well-known carabidologist who has described many new ground beetles of China.

Distribution. China (Guangxi) (Fig. 1c). Known only from the limestone cave near Yangli, Jiayou, Lingyun Xian. This cave opens at bottom of a hill near Yangli Cun on the right side of the road from Lingyun to Leye. It is short cave and the large part inside was dry. The single type specimen was collected in a small wet area. Other cave animals observed in this cave were millipedes, crickets and bats.



Figure 6. The type locality cave of *Guiaphaenops deuvei* Tian, Feng & Wei, sp. n. **a** cave entrance **b** a millipede in cave.

Guiaphaenops lingyunensis Deuve, 2002

Figs 1, 3b, 4b, 5c, d

Guiaphaenops lingyunensis Deuve, 2002: 518 (type locality: Cave Shen Dong); Uéno, 2006: 24

Diagnosis. A smaller species, latero-margins of pronotum slightly sinuate before hind angles (Fig. 3b); elytra with prehumeral borders broadly arcuate, the 1st pore of the humeral set of umbilicate pores at level behind anterior dorsal pore, while the 7th pore before level of the preapical pore (Fig. 4b); the median lobe of aedeagus slenderer and more elongated than in *G. deuvei* sp. n., with apical lobe thinner in dorsal view (Fig. 5c, d).

Material studied. 1 male, X-14-2015, cave Mi Dong, Mawang Cun, Sicheng Zhen, Lingyun Xian, Baise, Guangxi, 24°24'20"N, 106°35'52"E, 410 m, XII-9-2015, Mingyi Tian & Jujian Chen leg., in SCAU; 1 female, ibid, VI-9-2015, Mingyi Tian, Weixin Liu, Xinhui Wang & Minruo Tang leg., in SCAU.

Distribution. China (Guangxi). Known from three caves (Shen Dong, Mi Dong and a cave near Dazai Tun) in Lingyun Xian (Deuve 2002; Uéno 2006) (Fig. 1a, b, d).

Mi Dong is located at about one kilometre from Mawang Cun, in a valley below the main road from Lingyun to Leye. It opens above a path from the village to Sha Dong, a deeper and larger cave nearby. It is short, after 20 m from the entrance there is a large and complete dark room of 30–50 m in diameter. Majority part of this room was muddy or wet. The two beetle specimens were found quickly running on the wet ground. Other cave animals observed in Mi Dong were two species of millipedes and a bat.

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RESEARCH ARTICLE



One new species and three new records of Chrysis Linnaeus from China (Hymenoptera, Chrysididae)

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Abstract

Four Chinese Chrysis species-groups, the antennata, capitalis, elegans, and maculicornis species-groups, are discussed. Chrysis lapislazulina Rosa & Xu, **sp. n.** is described in the elegans species-group; and three species, C. brachyceras Bischoff, 1910, C. subdistincta Linsenmaier, 1968 and C. yoshikawai Tsuneki, 1961, are reported for the first time from China in other species-groups. A new synonymy is proposed for C. ignifascia Mocsáry, 1893 = C. taiwana Tsuneki, 1970, **syn. n.** A short historical review of the elegans species-group is provided. C. goetheana Semenov, 1967 is transferred from the elegans species-group to the maculicornis species-group. C. mesochlora Mocsáry, 1893 is considered a nomen dubium.

Keywords

Chrysis, antennata species-group, *capitalis* species-group, *elegans* species-group, *maculicornis* species-group, new species, new records, China

Introduction

Kimsey and Bohart (1991) provided keys and detailed diagnoses for the identification of *Chrysis* species-groups from all zoogeographical regions. Their classification and characterization of species-groups is adopted here with few exceptions (Rosa et al. 2014). However, some species-groups are currently under investigation; in particular, the *antennata* species-

group which is more closely related to the genus *Praestochrysis* Linsenmaier, 1959 than to the genus *Chrysis*.

At present, there are 79 known species of Chinese *Chrysis* (Rosa et al. 2014, 2016a); but this genus needs to be more intensively investigated (Rosa et al. 2016a). Many Chinese chrysidid specimens have been collected over the last twenty years and some of the main findings have been published (Rosa et al. 2015a, 2015b, 2016a). In the present paper four *Chrysis* species-groups are discussed, namely the *antennata*, *capitalis*, *elegans*, and *maculicornis* species-groups. A new species is also described, *C. lapislazulina* sp. n. belonging to the *elegans* species-group, and three new records from China are reported: *C. brachyceras* Bischoff, 1910 in the *antennata* species-group, *C. yoshikawai* Tsuneki, 1961 in the *capitalis* species-group.

Materials and methods

All specimens were examined using a Leica MZ125 stereomicroscope. Photographs of specimens from South China Agricultural University (SCAU) were taken by a digital camera (CoolSNAP) mounted to a Zeiss Stemi 2000-CS stereomicroscope. All images were processed using Image-Pro Plus software. Photographs of the holotype of *C. taiwana* were taken with a Keyence microscope. Photographs of types from other museums were taken by a Nikon D-80 mounted on a Togal SCZ stereomicroscope and stacked through the software Combine ZP.

Terminology mostly follows Kimsey and Bohart (1991). Abbreviations used in the descriptions are as follows:

BOL	the shortest distance between mid-ocellus and transverse frontal carina
	(TFC);
F1, F2, F3,	etc. flagellomeres 1, 2, 3, etc.;
1/w	length/width ratio;
MOD	mid ocellus diameter;
MS	malar space, the shortest distance between base of mandible and lower margin of compound eye;
OOL	the shortest distance between posterior ocellus and compound eye;
Р	pedicel;
PD	puncture diameter;
POL	the shortest distance between posterior ocelli;
S2	metasomal sternite 2;
T1, T2, T3	metasomal tergites 1, 2, 3;
TFC	transverse frontal carina.

Types and other specimens have been examined from the following institutions:

HNHM Hungarian Natural History Museum, Budapest, Hungary;

MNHU	Museum of Natural History of the Humboldt-Universität, Berlin, Ger-
	many;
MSNG	Museum of Natural History "G. Doria", Genoa, Italy;
NMLS	Natur Museum Luzern, Switzerland;
OMNH	Osaka Museum of Natural History, Osaka, Japan;
SCAU	Hymenopteran Collection, South China Agricultural University, Guang-
	zhou, China;
SHEM	Shanghai Entomological Museum, Chinese Academy of Sciences, Shang-
	hai, China;
ZISP	Zoological Institute, St. Petersburg, Russia;
ZMUC	Zoological Museum, University of Copenhagen, Denmark.

Taxonomy

Chrysis antennata species-group

Chrysis antennata species-group: Kimsey and Bohart 1991: 328 (key), 323 (fig. 105d), 336 (fig. 109q), 337 (diagnosis), 350 (fig. 112d).

Diagnosis. The *antennata* species-group is characterised by broadened antennae, short and broad face, toothed metanotum, and similar habitus to *Praestochrysis* Linsenmaier except for four teeth on T3 (Kimsey and Bohart 1991).

Description. Male F1 l/w = 1.2; female F1 l/w = 1.5. Flagellomeres broadened, with F4 broader than long. TFC almost straight, slightly downcurved laterally, Mid ocellus lidded. Male MS = 1.5 MOD; female MS = 1.8-2.2 MOD. Metanotum with small, stout, postero-median tooth. T3 short, weakly saddled in female, with weak transversal prepit bulge; pit row deep; lateral margins simple; apex with four short apical teeth. Black spots on S2 round and well separated in *C. antennata*, triangular and almost fused in *C. brachyceras*.

Biology. Unknown.

Species included. Two species: *Chrysis antennata* Mocsáry, 1912 from Afrotropical Region (Mocsáry 1912a), and *C. brachyceras* Bischoff, 1910 from Oriental Region.

Distribution. Afrotropical and Oriental regions.

Chrysis brachyceras Bischoff, 1910

Fig. 1

Chrysis (*Tetrachrysis*) *brachyceras* Bischoff, 1910: 474. Holotype, ♀; Malaysia (MNHU) (examined).

Chrysis (Tetrachrysis) brachyceras: Bischoff 1913: 48 (Malaysia).

Chrysis brachyceras: Kimsey and Bohart 1991: 337 (Malaysia, Laos), 390 (Malaysia).

Type material. Holotype, \bigcirc , MALAYSIA, Malacca (MNHU). **Additional material:** 5 \bigcirc \bigcirc , CHINA, Guangxi, Maoershan National Nature Reserve, 3.VIII.2005, leg. Liu-sheng Chen, ANT001–ANT005 (SCAU); 2 \bigcirc \bigcirc , CHINA, Guizhou, Tianzhu, VIII.2009, leg. Yang-wen Wang, ANT006, ANT007 (SCAU).

Diagnosis. *Chrysis brachyceras* is a large species, with the following distinctive characteristics: flagellomeres broad and flat; metanotum with small and stout postero-median tooth; T3 with four short apical teeth.

Description. Female. Body length 10.0-11.0 mm.

Head. Scapal basin fully punctate. TFC medially straight, slightly downcurved at both ends and with two weak branches extending upwards (Fig. 1B). Relative length of P:F1:F2:F3 = 1.0:2.3:0.9:0.9. OOL = 1.5 MOD; BOL = 1.0 MOD; POL = 1.5 MOD; MS = 1.8 MOD; subantennal space 1.0 MOD. Anterior margin of clypeus emarginate. F3–F11 broadened and flattened. Genal carina sharp all over its length (Fig. 1D).

Mesosoma. Pronotal groove deep and almost reaching posterior margin; sublateral carina distinct and complete (Figs 1A, 1D); pronotal side with depression. Mesoscutum evenly punctate (Fig. 1C). Mesoscutellum simple, without anterior depression or fovea. Metanotum with a small, stout tooth pointing upwards (Figs 1A, 1C). Mesopleuron with broad episternal and scrobal sulci; the latter similar to elongate foveae (Fig. 1D).

Metasoma. Metasoma evenly punctate; the punctures as large as on mesoscutum. T2 and T3 without median ridge; T3 weakly saddled in female, with weak transversal prepit bulge over deep pit row; T3 with four apical teeth and simple lateral margins (Figs 1A, 1E). Black spots on S2 triangular, almost fused along the midline (Fig. 1F).

Colouration. Body blue, with dark blue to green metallic reflections, dark blue on ocellar area, mesoscutum medially, T1 medially, T2 and T3 antero-laterally.

Male. Not available for this study.

Distribution. China (new record). Malaysia and Laos (Bischoff 1913; Kimsey and Bohart 1991, not Indonesia).

Remarks. Kimsey and Bohart (1991) noticed some similarities between the species of the *antennata* species-group and those of the genus *Praestochrysis* Linsenmaier, 1959. The former ones are included in the genus *Chrysis* because of the four apical teeth on T3. Nevertheless, *C. brachyceras* shares with *Praestochrysis* the following characteristics: general habitus, shape of head distinctly broader than high, broadened flagellomeres, subantennal space 1.0 MOD and shorter than MS, TFC weakly indicated across strongly developed brow, scapal basin not microridged, pronotum with deep lateral depressions, metanotum with a short, stout tooth, scrobal and episternal sulci well developed and expanded ventrally, black spots on S2 small and almost fused along the midline. Several of above features (excluding broadened flagellomeres, weak TFC, metanotum with a small tooth) and pronotal sublateral carina distinct and complete are shared with the *T. lusca* species-group, which was considered belonging to the genus *Praestochrysis* by Kimsey and Bohart (1991) and *Trichrysis* lusca is considered as



Figure 1. *Chrysis brachyceras* Bischoff, 1910, \bigcirc from Guangxi. **A** Habitus, lateral view **B** head, frontal view **C** mesosoma, dorsal view **D** head, pronotum and mesopleuron, lateral view **E** apex of T3, dorsal view **F** black spots on S2, ventral view.

belonging to *Trichrysis* not only morphologically but also biologically. *Praestochrysis* are well known parasitoids of moth prepupae (Limacodidae) (Kimsey and Bohart 1991), whereas species in the *T. lusca* species-group are parasitoids of Sphecidae (Mocsáry 1889, 1912b; Tsuneki 1955; Linsenmaier 1959) or Eumeninae (Vespidae) (Kimsey and Bohart 1991). Unfortunately, the biology of *C. brachyceras* is unknown; therefore, we consider *C. brachyceras* as a member of the genus *Chrysis* until new biological or molecular evidence is available.

Chrysis capitalis species-group

Chrysis capitalis species-group: Kimsey and Bohart 1991: 325 (key), 329 (fig. 107p), 336 (fig. 110m), 339 (diagnosis), 350 (fig. 112j).

Diagnosis. The *capitalis* species-group is characterised by apex of T3 simple, TFC prominent and M-shaped, and mid ocellus lidded. Some species in the *capitalis* species-group are also easily recognised by female metasoma usually blue to green with golden stripes (e.g. *C. abuensis* Nurse, 1902, *C. bayadera* du Buysson, 1896, *C. ignifascia* Mocsáry, 1893, and *C. jalala* Nurse, 1902).

Description. Scapal basin microridged medially. Male F1 l/w = 1.5; female F1 l/w = 1.9–3.0. TFC usually well developed and M-shaped. Mid ocellus lidded. MS usually < 1.0 MOD. T2 with median ridge. T3 weakly saddled in female; pit row moderately impressed; apex of T3 convex or slightly concave medially, without apical teeth.

Biology. Unknown.

Species included. Fourteen species: seven Afrotropical, *Chrysis capitalis* Dahlbom, 1854, *C. dalmanni* Dahlbom, 1845, *C. infuscata* Brullé, 1846, *C. jugum* Dahlbom, 1850, *C. levioris* Edney, 1952, *C. rutilata* du Buysson, 1898b, and *C. sinuosa* Dahlbom, 1845 (Rosa and Vårdal 2015); six Oriental, *C. abuensis* Nurse, *C. bayadera* du Buysson, *C. ignifascia* Mocsáry, 1893 (= *C. taiwana* Tsuneki, 1970, syn. n.), *C. sumptuosa* Smith, 1858, *C. wroughtoni* du Buysson, 1896, and *C. yoshikawai* Tsuneki, 1961; and one Palaearctic species, *C. jalala* Nurse.

Distribution. Afrotropical, Oriental and Palaearctic regions.

Remarks. *Chrysis arabica* Mocsáry, 1911 was moved to the newly created *C. arabica* species-group by Linsenmaier (1994).

Key to Chinese species of the capitalis species-group

1	T2 with a broad transverse posterior reddish golden stripe, contrasting with
	the remaining body colouration (Figs 2E, 2F) <i>C. ignifascia</i> Mocsáry (Q)
_	T2 blue to green without reddish or golden stripe (Figs 3, 6)2
2	Female and male with sub-reniform and transverse black spots on S2 (Fig.
	7B) C. yoshikawai Tsuneki
_	Male with sub-triangular and longitudinal black spots on S2 (Fig. 7A)
	C. ignifascia Mocsáry (3)

Chrysis ignifascia Mocsáry, 1893

Figs 2, 3, 4, 5, 7A

- *Chrysis (Holochrysis) ignifascia* Mocsáry, 1893: 215. Holotype, ♀, Myanmar (MSNG) (examined). Rosa 2009: 233.
- *Chrysis (Holochrysis) birmanica* Mocsáry, 1893: 214. Holotype, ♂, Myanmar (MSNG) (examined). Rosa 2009: 221. (Synonymised by Kimsey and Bohart 1991: 420).
- Chrysis (Chrysura) taiwana Tsuneki, 1970: 7. Holotype, ♂, China (OMNH) (examined). Syn. n.

Type material. Holotype, \bigcirc , MYANMAR [Burma] Palon (Pegù), L. Fea VIII– IX.[18]87, *Chrysis ignifascia*, \bigcirc , Mocs. n. sp. <handwritten by Mocsáry>, Typus, *C. ignifascia*, Mocs., \bigcirc , typus! <handwritten by Mantero> (MSNG). Holotype, \bigcirc , MY-ANMAR [Burma] Bhamò, Birmania, Fea VIII 1885, *Chrysis birmanica*, \bigcirc , Mocs. n. sp. <handwritten by Mocsáry>, Typus, *C. birmanica*, Mocs., \bigcirc , typus! <handwritten by Mantero> (MSNG). Holotype, \bigcirc , [CHINA], Formosa [Taiwan], Pintung Hsien, Hengchun, 2.VIII.1966. leg. K. Tsuneki // *Chrysis (Chrysura) taiwana* Tsuneki Holotypus <handwritten> (OMNH). **Additional material:** 1 \bigcirc , CHINA, Guangdong, Fogang, Guanyinshan, 15–16.IX.2007, leg. Zai-fu Xu, CAP001 (SCAU); 1 \bigcirc , CHINA, Fujian, Jianning, 8.VI.1959, leg. Gen-tao Jin & Ming-yang Lin, 34022848 (SHEM); 1 \bigcirc , CHINA, Taiwan, Koshun, Apr. 1937, coll. K. Iwata (NMLS); 1 \bigcirc , MYANMAR, Lower Burma, Shwègyin 6.[18]98 Bingham, *Chrysis burmanica* [!] Mocs. det. Bingham, *Chrysis burmanica* [!] Mocs. det. Bingham, *Chrysis burmanica* [!] Mocs. det. Mocsáry (HNHM).

Diagnosis. *Chrysis ignifascia* Mocsáry female is easily recognised by the reddish golden stripe on T2 (Figs 2E, 2F). The male is green to blue, similar to *C. yoshikawai* Tsuneki, but can be separated by the longitudinal sub-triangular black spots on S2 (Fig. 7A) (transverse and sub-reniform in *C. yoshikawai* (Fig. 7B)).

Distribution. China (Fujian, Taiwan, Guangdong) (Rosa *et al* 2014), Myanmar (Mocsáry 1893; Kimsey and Bohart 1991).

Remarks. The colour dimorphism between male and female of *C. ignifascia* misled some authors including Mocsáry (1893), who described the female as *C. ignifascia* (Fig. 4) and the male as *C. birmanica* (Fig. 5). Tsuneki (1961, 1970) did not mention either *C. ignifascia* or *C. birmanica* in his publications and described the male as *C. taiwana* (Fig. 3), comparing its body colouration with that of *C. yoshikawai* Tsuneki, 1961. After types examination we propose the synonymy *C. ignifascia* Mocsáry, 1893 = *C. taiwana* Tsuneki, 1970, syn. n.



Figure 2. *Chrysis ignifascia* Mocsáry, 1893, ♀ from Fujian. **A** Habitus, lateral view **B** head, frontal view **C** mesosoma, dorsal view **D** head, pronotum and mesopleuron, lateral view **E** metasoma, dorsal view **F** T3, dorsal view.

Chrysis yoshikawai Tsuneki, 1961 Figs 6A–F, 7B

Chrysis yoshikawai Tsuneki, 1961: 371. Holotype, Q, Thailand (depository?). *Chrysis yoshikawai*: Kimsey and Bohart 1991: 479 (Thailand).

Additional material. 19, CHINA, Yunnan, Jingdong, Jingping, 28.IV.2005, leg. He-sheng Wang, CAP004 (SCAU); 19, CHINA, Yunnan, Dehong, Longchuan, 1–9.VIII.2011, leg. Ju-jian Chen, CAP005 (SCAU).


Figure 3. *Chrysis taiwana* Tsuneki, 1970, holotype, ♂. **A** Habitus, lateral view **B** head, frontal view **C** head and mesosoma, dorsal view **D** head, pronotum and mesopleuron, lateral view **E** metasoma, dorsal view **F** T3, dorsal view (photos by courtesy of Rikio Matsumoto, OMNH).

Diagnosis. *Chrysis yoshikawai* is similar to *C. ignifascia*, but can be separated by: female body entirely green to blue, without reddish or golden colouration (with reddish golden stripe posteriorly on T2 in *C. ignifascia*), male S2 with sub-reniform and transverse black spots (Fig. 7B) (sub-triangular and longitudinal in *C. ignifascia*, Fig. 7A), and T3 with darkened clover-shaped spot (Figs 6E, 6F).

Description. Female (Fig. 6A). Body length 7.5 mm.

Head. Scapal basin fully striate and with micropunctate ground sculpture. TFC double, sharply raised (Fig. 6B). Relative length of P:F1:F2:F3 = 1.0:1.3:1.0:0.7. OOL



Figure 4. *Chrysis ignifascia* Mocsáry, 1893, holotype, ♀. **A** Head, mesosoma and T1, dorsal view **B** head, frontal view **C** head and mesosoma, lateral view **D** metasoma, lateral view **E** metasoma, dorsal view **F** T2 and T3, dorso-lateral view.



Figure 5. *Chrysis birmanica* Mocsáry, 1893, holotype, \mathcal{J} (= *C. ignifascia* Mocsáry). **A** Head, mesosoma and T1, lateral view **B** head, frontal view **C** head, mesosoma and T1, dorsal view **D** metasoma, dorsal view **E** metasoma, lateral view **F** T2 and T3, dorsal view.



Figure 6. *Chrysis yoshikawai* Tsuneki, 1961, \bigcirc from Yunnan. **A** Habitus, lateral view **B** head, frontal view **C** mesosoma, dorsal view **D** head, pronotum and mesopleuron, lateral view **E** metasoma, dorsal view **F** T3, dorsal view.

= 2.0 MOD; BOL = 1.5 MOD; POL = 2.1 MOD; MS = 0.5 MOD; subantennal space 0.5 MOD. Genal carina well developed throughout its length (Fig. 6D).

Mesosoma. Pronotal groove shallow and reaching 2/3 of pronotum length. Mesoscutum and mesoscutellum evenly punctate; metanotum with coarse punctures (Fig. 6C). Mesopleuron with deep episternal and scrobal sulci, both sulci with large foveae (Fig. 6D).

Metasoma. Metasoma with large, even punctures; the punctures as large as on mesoscutum (Fig. 6E). T2 and T3 with median ridge; T3 weakly saddled with deep pit row; apex of T3 slightly concave in the middle (Fig. 6F). Black spots on S2 sub-reniform, transverse, separated by less than 1.0 MOD (Fig. 7B).



Figure 7. Black spots on S2 of females, ventral view. A *Chrysis ignifascia* Mocsáry, 1893 B *Chrysis yoshi-kawai* Tsuneki, 1961.

Colouration. Body metallic blue to green, with dark blue on vertex, mesoscutum medially, tegula, T1 anteriorly, T2 anteriorly and T3 anteriorly (a typical clover-shaped pattern) and posteriorly (from pit row to posterior margin).

Male. Similar to female.

Distribution. China (new record). Thailand (Tsuneki 1961; Kimsey and Bohart 1991).

Remarks. Tsuneki (1961) did not mention the repository of the holotype. Kimsey and Bohart (1991) reported it at OMNH, wherein it was not found (Dr. Rikio Matsumoto, pers. comm.).

Chrysis elegans species-group

Chrysis (Chrysis) elegans species-group: Linsenmaier 1959: 93 (key), 136 (diagnosis).
Chrysis elegans species-group: Kimsey and Bohart 1991: 325 (key), 345 (diagnosis), 329 (fig. 107d), 335 (fig. 109u), 341 (fig. 111a).

Diagnosis. The *elegans* species-group is characterised by having habitus cylindrical and elongate; TFC weak or indistinct; face slightly broadened below, with subparallel and short MS; head broadened behind compound eyes in dorsal view; apex of T3 without distinct teeth, at most undulate and laterally with blunt angles; posterior margin of T3 bending downwards in females; body pubescence short and whitish; forewing radial cell closed. Body length usually 7 to 11 mm; only the North-African *C. albitarsis* is smaller (5–6 mm). Most Palaearctic species have red to golden red metasoma; females and sometimes males have mesosoma partially red. Males of *C. elegans* from eastern Mediterranean countries and Middle East can be entirely emerald green to golden green.

Description. F1 l/w = 1.5-2.5. Scapal basin medially polished, especially in females. TFC weak or faint, weakly M-shaped. MS = 0.5-1.0 MOD. Pronotum longer than or as long as mesoscutellum; mesopleuron with deep scrobal sulcus. T3 pit row with small, separated pits; T3 without apical teeth, at most undulate. Black spots on S2

usually large, sometimes antero-medially fused. Male genitalia with apex of gonocoxae and cuspis considerably hirsute (Arens 2015).

Biology. Members of this species-group are parasitoids of Apidae Megachilinae (Linsenmaier 1959; Kimsey and Bohart 1991).

Species included. The *elegans* species-group currently includes eighteen species: *Chrysis albitarsis* Mocsáry, 1889; *C. angustifrons* Abeille de Perrin, 1878; *C. bovei* (du Buysson, 1898a); *C. castillana* (du Buysson in André, 1896); *C. deposita* Nurse, 1904; *C. dissimilis* Dahlbom, 1854; *C. eldari* (Radoszkowski, 1893); *C. elegans* Lepeletier, 1806; *C. hemera* Semenov, 1954; *C. io* Semenov, 1910; *C. joppensis* du Buysson, 1887; *C. lapislazulina* sp. n.; *C. lateralis* Dahlbom, 1845; *C. lepida* Mocsáry, 1889; *C. pushkiniana* Semenov, 1967; *C. pyrrha* Semenov, 1967; *C. rubricollis* du Buysson, 1900; *C. rueppelli* du Buysson, 1904.

Distribution. Palaearctic and Oriental regions.

Discussion. The *Chrysis elegans* species-group is primarily a West-Palaearctic group (Kimsey and Bohart 1991; Linsenmaier 1999; Rosa et al. 2015c), distributed from the Mediterranean basin to Middle East and central Asia, plus a new species herewith described. Only two species, *Chrysis dissimilis* Dahlbom, 1854, and *C. lapislazulina* sp. n. are known in the Oriental Region so far.

This species-group was established by Linsenmaier (1959), who originally included seven species: C. elegans Lepeletier, 1806; C. angustifrons Abeille de Perrin, 1878; C. joppensis du Buysson, 1887; C. castillana du Buysson in André, 1896; C. ignicollis Trautmann, 1926a; C. separata Trautmann, 1926a; and C. meyeri Linsenmaier, 1959. Later, Linsenmaier (1968) included also C. ashabadensis Radoszkowski, 1891 and synonymised C. meyeri with C. albitarsis Mocsáry. Kimsey and Bohart (1991) included twenty-one species, but their species-list has been partially modified in the last years: C. albitarsis Mocsáry which was placed into the cuprata species-group by Kimsey and Bohart (1991), was reintroduced into the *elegans* species-group by Linsenmaier (1999); C. kohli Mocsáry, 1889 was mistakenly placed into both genera Chrysis (elegans species-group) and Pseudospinolia Linsenmaier, 1951 (Kimsey and Bohart 1991: p. 428, sub C. kohlii, p. 547, as synonym of P. marqueti (du Buysson, 1887)), while it actually belongs to the genus Pseudospinolia; C. emarginatula Spinola, 1808 and C. tingitana Bischoff, 1935, both included by Kimsey and Bohart (1991) into the elegans species-group, are clearly separated by morphological (Linsenmaier 1959, 1999) and biological features, being parasitoids of Masarinae (Vespidae) (Linsenmaier 1968; Mauss 1996; http://www.chrysis.net/forum/) and not of Apoidea, the only known hosts of members in the *elegans* species-group (Linsenmaier 1959, 1999; Kimsey and Bohart 1991). Therefore, we follow Linsenmaier's interpretation (1959, 1999), including these two species into the *emarginatula* species-group.

More recently, after type examination, *C. ashabadensis* was transferred into the *succincta* species-group and *C. ignicollis* was considered as a junior synonym of *C. eldari* (Radoszkowski, 1893) (Rosa et al. 2015c); *C. separata* was considered as synonym of *C. lateralis* Dahlbom (Rosa and Vårdal 2015). Arens (2015) elevated the subspecies *C. ignicollis graeca* Arens, 2004 to species rank, but in our opinion *C. graeca* is to be regarded as synonym of *C. pushkiniana* Semenov (Rosa in Arens 2015). *C. goetheana* Semenov, 1967 (whose type material has been examined at ZISP) is here transferred into the *maculicornis* species-group because of the following characteristics: male with shortened F1 and F2, female with distinct straight TFC, scapal basin entirely microridged, and MS very short.

The synonymy proposed by Trautmann (1926b), *C. cupricollis* Trautmann, 1921 = *C. rubricollis* du Buysson, 1900 is to be verified. We propose to consider *C. mesochlora* Mocsáry a nomen dubium, since the holotype of *C. mesochlora* was destroyed in Hamburg during the World War II (Kimsey and Bohart 1991), and no specimen identified by Mocsáry can be traced in his collection in Budapest or in any other European collections. Moreover, this species has never been mentioned after Mocsáry's description, except in Kimsey and Bohart (1991).

Chrysis lapislazulina Rosa & Xu, sp. n.

http://zoobank.org/82BF0F09-535A-43C4-9AD8-FEE4F5C94D8E Figs 8, 9

Material examined. Holotype, ♀, CHINA, Yunnan, Yuxi (20°21'07"N 102°32'47"E), 20.VII.2003, leg. Qiang Li (SCAU).

Diagnosis. Chrysis lapislazulina sp. n. is recognised by the following characteristics: body blue with golden reflection (Figs 8, 9A); pronotum, mesoscutum and mesoscutellum medially with polished intervals among punctures (Fig. 9C); metasoma with fine and even punctures (Fig. 9E); apex of T3 without undulation or teeth (Fig. 9E). It can be distinguished from another Oriental species of the species-group, C. dissimilis by: almost uniform body colouration (mesosoma green with red scutellum and golden-red metanotum, and metasoma green with blue stripes antero-laterally on T2 and T3 in C. dissimilis (Fig. 10A)); apex of T3 without tooth or undulation (medially sinuous and with blunt lateral teeth in C. dissimilis, Figs 10C, 10E); black spots on S2 sub-rectangular (Fig. 9F) (sub-oval in C. dissimilis, Fig. 10F). The female of C. lapislazulina sp. n. can be separated from females of other Palaearctic species by: metasoma entirely blue (red to golden-red in other species); metasoma with even and fine punctures (large punctures, with or without intervals and usually decreasing in diameter posteriorly in other species); black spots on S2 sub-rectangular, basally separated by more than two MOD (vs. large and sub-oval, basally fused or narrowly separated in other species).

Description. Holotype: Female. Body length 8.0 mm.

Head. Scapal basin medially polished and laterally micropunctate (Fig. 9B). TFC M-shaped, with two weak branches extending to the level of mid ocellus. Anterior margin of clypeus medially not emarginate, laterally with thickened brownish rim. Vertex with coarse punctures. Genal carina weak, present from mid gena to mandible. Relative length of P:F1:F2:F3 = 1.0:1.3:0.8:0.7; OOL = 2.0 MOD; POL = 2.3 MOD; MS = 1.0 MOD; subantennal space 1.0 MOD.



Figure 8. Chrysis lapislazulina Rosa & Xu, sp. n., holotype, ♀, habitus, lateral view. Scale bar=1 mm.

Mesosoma. Pronotum slightly longer than mesoscutellum (Fig. 9C); pronotal groove broad and almost reaching 2/3 of pronotum length; pronotal side with depression in dorsal view; punctuation coarse along anterior and lateral margins, with smaller punctures on pronotal groove and along posterior margin; pronotal dorsum with two darker areas with minute scattered punctures and impunctate intervals. Median lobe of mesoscutum in anterior half with broad, darker median area, with larger punctures and broader polished intervals; posterior half with even larger, contiguous, irregular punctures; lateral lobes of mesoscutum with more or less close, partly confluent punctuation; parapsidal furrow well incised. Mesoscutellum darker medially, with large punctures and broader intervals, smooth towards anterior edge; laterally with smaller, dense punctures and micropunctate intervals, punctuation reaching posterior edge. Metanotum slightly convex, with somewhat uneven punctures becoming denser postero-medially; anterior margin of metanotum with row of narrow, antero-posteriorly elongate foveae. Mesopleuron with small, shallow and round punctures, and shallow scrobal and episternal sulci (Fig. 9D).

Metasoma. Finely and densely punctate; punctation unusually smaller than others species of this species-group; their diameter about 1/3 to 1/4 of largest punctures on mesoscutum. T1 elongate (Fig. 9E), half as long as T2. T2 with weak or faint median ridge. T3 weakly saddled, with row of shallow small pits; apex of T3 without tooth or undulate. Black spots on S2 sub-rectangular and connected to lateral margins, widely separated medially (Fig. 9F).



Figure 9. *Chrysis lapislazulina* Rosa & Xu, sp. n., holotype, \mathcal{Q} . **A** Habitus, dorsal view **B** head, frontal view **C** mesosoma, dorsal view **D** pronotum and mesopleuron, lateral view **E** metasoma, dorsal view **F** black spots on S2, ventral view. Scale bar 1 mm.

Colouration. Body blue, darker on vertex, pronotum dorso-laterally, median and lateral lobes of mesoscutum medially (Figs 8, 9A) and mesoscutellum medially, metallic green on face and metasomal sternites (Figs 9B, 9F), with golden reflection on clypeus, scape and pedicel. Flagellomeres black (Fig. 9B). Tegula blackish brown, almost without metallic reflections. Post-tegula bright metallic blue (Fig. 9C). Forewing infuscate, with darkened anterior margin.

Male. Unknown.



Figure 10. *Chrysis dissimilis* Dahlbom, 1854, holotype, \bigcirc . **A** Habitus, dorsal view **B** head, frontal view **C** habitus, lateral view **D** pronotum and mesopleuron, lateral view **E** metasoma, dorso-posterior view **F** black spots on S2, ventral view. Scale bar 1 mm (photos by courtesy of Lars Vilhelmsen, ZMUC).

Distribution. China (Yunnan).

Etymology. The specific epithet *lapislazulina* refers to the intense blue colouration with darkened areas and golden reflections; this peculiar colouration resembles the semi-precious stone lapis lazuli.

Chrysis maculicornis species-group

Chrysis (Cornuchrysis) maculicornis species-group: Linsenmaier 1959: 173 (*partim*). *Chrysis maculicornis* species-group: Kimsey and Bohart 1991: 353 (key), 341 (fig. 111m).

Diagnosis. The *maculicornis* species-group is characterised by having males with shortened F1 and F2, F1 slightly longer than F2, but shorter than F3; females with F1 l/w \approx 2.0; MS usually 0.2–1.3 MOD; face slightly wedge-shaped in frontal view.

Description. Male F1 l/w = 1.0-1.4; F1 slightly longer than F2, but shorter than F3. Female F1 l/w ≈ 2.0 . Scapal basin micropunctate or microridged medially. TFC well developed, biconvex. Mid ocellus sometimes lidded. MS usually 0.2-1.3 MOD. T3 in female sometimes with prepit bulge; pit row usually well developed. T3 with four sharp apical teeth. Black spots on S2 large and sub-oval, separated medially and sometimes connected to lateral margins.

Species included. Kimsey and Bohart (1991) in the species-group diagnosis included fifteen Palaearctic species, but in their checklist reported twenty-two Palaearctic species, one Oriental (*C. perfecta* Cameron, 1897) and one Afrotropical (*C. rhinata* Bohart, 1988). The list of Palaearctic species needs to be further verificated, because some species have been included in the *cerastes* species-group (e.g. *C. subdistincta* Linsenmaier).

Distribution. Palaearctic, Oriental and Afrotropical regions.

Remarks. Linsenmaier (1959, 1968) included in the *maculicornis* species-group only the species with shortened F1 and F2 and flagellomeres yellowish beneath in males (e.g. *C. maculicornis* Klug, 1845, *C. fulvicornis* Mocsáry, 1889, and *C. stigmaticornis* Linsenmaier, 1968). Kimsey and Bohart (1991) added the species close to *C. annulata* du Buysson, 1887 (e.g. *C. blanchardi* Lucas, 1849; *C. distincta* Mocsáry, 1887; *C. rectianalis* Linsenmaier, 1968, etc.) into the *maculicornis* species-group, whereas Linsenmaier (1959, 1968) included them in the *cerastes* species-group. In this paper we follow Kimsey and Bohart's (1991) interpretation of the *maculicornis* species-group.

Chrysis subdistincta Linsenmaier, 1968

Fig. 11

Chrysis (*Chrysis*) *subdistincta* Linsenmaier, 1968: 110. Holotype ♀; Turkmenistan (Transcaspia) (NMLS) (examined).

Chrysis subdistincta: Kimsey and Bohart 1991: 467 (cerastes species-group).

Type material. Holotype, \bigcirc , [TURKMENISTAN] Transcaspia Imam-baba W.Koshantschikoff // \bigcirc Type *Chrysis* L. *subdistincta* Lins. Linsenmaier det. 66 (NMLS). **Additional material:** 1 \bigcirc , CHINA, Gansu, Jiuquan, Huangnibao, 1700 m, 15.VII.2010, leg. Xu-feng Zhang & Feng-li Cui, No. 34020575 (SHEM); 1 \bigcirc , CHINA, Gansu, Jiuquan, Huangnibao, 1700 m, 16.VII.2010, leg. Xu-feng Zhang & Feng-li Cui, No. 34020062 (SHEM).

Diagnosis. *Chrysis subdistincta* belongs to the Palaearctic *C. annulata* sub-group and is the only known Chinese species of the *maculicornis* species-group. It can be recognised by apex of T3 with median pair of apical teeth longer than lateral pair (all the apical teeth are of similar length in other species), and pit row with large, fused pits (usually small, widely separated in other species).



Figure 11. Chrysis subdistincta Linsenmaier, 1968, \bigcirc from Gansu. **A** Habitus, lateral view **B** head, frontal view **C** mesoscutum, mesoscutellum and metanotum, dorsal view **D** head, pronotum and mesopleuron, lateral view **E** metasoma, dorsal view **F** T3, dorsal view.

Description. Female (Fig. 11A). Body length 6.5 mm.

Head. Scapal basin deep and micro-punctate (Fig. 11B), TFC well-developed, inverted U-shaped, with long branches in contact with eyes. Relative length of P:F1:F2:F3 = 1.0:1.2:1.0:1.0. OOL = 1.3 MOD; POL = 1.9 MOD; MS = 0.2 MOD; subantennal space 0.5 MOD. Anterior margin of clypeus broadly emarginate. Genal carina developed throughout its length.

Mesosoma. Pronotum medially narrowed, 0.8 times as long as mesoscutellum; pronotal groove faint. Pronotum, mesoscutum and mesoscutellum with large foveate

punctures; interspaces micropunctate. Notauli with large subquadrate foveae. Mesopleuron with deep and scrobiculate episternal and scrobal sulci (Fig. 11D).

Metasoma. Metasoma with deep, large round punctures (Fig. 11E). PD on T2 decreasing towards posterior margin. T2 and T3 with weak median ridge. T3 pit row slightly transversely bulging before pit row; pit row with large, laterally fused pits; apex of T3 with four pointed teeth, apically hyaline, with median pair of teeth longer than lateral pair (Fig. 11F).

Colouration. Head and mesosoma blue, with metallic green on TFC, vertex, pronotum and mesoscutum dorso-laterally, and mesoscutellum medially. Metasoma golden to metallic reddish, with metallic blue on T3 from pit row to apical teeth.

Male. Unknown.

Distribution. China (new record). Turkmenistan (Linsenmaier 1968).

Remarks. Kimsey and Bohart (1991) followed Linsenmaier (1968) and placed *Chrysis* subdistincta into the cerastes species-group. Nevertheless, this species is closely related to *C. annulata* du Buysson from which it is recognizable by the elongate teeth on T3. *C. annulata* and related species have been included in the *maculicornis* species-group by Kimsey and Bohart (1991). Therefore, we consequently include *C. subdistincta* in this species-group.

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RESEARCH ARTICLE



Revision of the phylogeny and chorology of the tribe Iphisini with the revalidation of Colobosaura kraepelini Werner, 1910 (Reptilia, Squamata, Gymnophthalmidae)

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Abstract

The family Gymnophthalmidae contains nearly 235 species with a distribution range from southern Mexico to central Argentina as well as in the Antilles. Among gymnophthalmids, the genus *Colobosaura* is a member of the tribe Iphisini, and currently is considered monotypic (*C. modesta*). The diversity of the tribe was studied recently, with the erection of several new genera. In this work genetic and morphological data of specimens of *Colobosaura* recently collected in Paraguay were analyzed. Genetic (16S barcode) data indicate that these samples are not conspecific with *C. modesta* and they are allocated to the nominal species *C. kraepelini*. Because the original primary type of the latter taxon is considered to be lost, a neotype (SMF 101370) is designated for this species and a redescription provided based on our material. *Colobosaura kraepelini* is distributed in the Humid Chaco, being the only member of the whole tribe in this ecoregion.

Keywords

16S barcodes, Humid Chaco, neotype, Paraguay, taxonomy

Introduction

Gymnophthalmids are among the least known Neotropical lizards given their secretive habits and small size, and some of them are known only from the original description (Castoe et al. 2004). Currently, 232 species of gymnophthalmid lizards are recognized (Goicochea et al. 2016) with a geographic distribution ranging from Argentina widely across South America to southern Mexico, including some Caribbean islands (Doan 2003, Vitt and Caldwell 2009), with several recently described taxa from the Caatinga and the Cerrado (Ribeiro Delfim et al. 2006). In fact, Cacciali (2010) pointed out the high diversity of gymnophthalmid lizards in the Paraguayan Cerrado with respect to other ecoregions in the country.

In the last decade, this family has been analyzed from a molecular perspective, leading to some changes in phylogenetic hypotheses (Castoe et al. 2004, Rodrigues et al. 2007, Peloso et al. 2011).

One of the genera that underwent taxonomic modifications is *Colobosaura*, which was established by Boulenger (1887) to include *Perodactylus modestus* Reinhardt & Lütken, 1862 described from Morro da Garça, Minas Gerais, Brazil. Somewhat later, Werner (1910) described *Perodactylus kraepelini* from Puerto Max, Concepción, Paraguay. Amaral (1933) considered *C. kraepelini* to be a synonym of *C. modesta* attributing the observed morphological variation to sexual dimorphism. In that contribution the author described *Colobosaura mentalis* which was later transferred to the genus *Acratosaura* by Rodrigues et al. (2009a). Burt and Burt (1933) recognized *C. kraepelini* as a valid species, a view followed by Peters and Donoso-Barros (1970) and Talbot (1979). Vanzolini and Ramos (1977) stated that the description of *C. kraepelini* is brief and not very informative so they suggested that the type specimen must be carefully analyzed to reach more solid taxonomic decisions. However, the type specimen of *C. kraepelini* (originally deposited in the Hamburg Zoological Museum) is considered to be lost (Rodrigues et al. 2007).

In this work, and in the framework of a DNA barcoding project of the Paraguayan herpetofauna, genetic and morphology data of recently collected specimens of *Colobosaura* tentatively assigned to *C. kraepelini* were analyzed, providing a redescription of its external morphology and information on its taxonomic status.

Materials and methods

Tissue samples for genetic analyses were extracted and stored as recommended by Gamble (2014). The protocol for DNA extraction follows Ivanova et al. (2006). Samples were washed in 50 μ l of diluted PBS buffer (1:9 of buffer and water respectively) for 14 h. A solution of vertebrate lysis buffer and proteinase K (60:6 μ l respectively), kept at 56°C for 14 h was used for digestion. After extraction, DNA samples were eluted in 50 μ L TE buffer. Amplification of mitochondrial 16S rRNA gene fragments was performed using the eurofins MWG Operon primers L2510 (forward: 5'–CGCCT-

GTTTATCAAAAACAT-3') and H3056 (reverse: 5'-CCGGTCTGAACTCAGAT-CACGT-3') in an Eppendorf Mastercycler pro. The PCR conditions were: denaturation 2 min (94°C) – denaturation 35 sec (94°C)×40 – hybridization 35 sec (48.5°C) – elongation 60 sec (72°C) – final elongation 10 min (72°C). The examination of DNA chromatograms and development of consensus sequences were performed with SeqTrace 0.9.0 (Stucky 2012).

The mtDNA 16S sample was compared with sequences available in GenBank for species of the most closely related clade (Iphisini: Gymnophthalminae, according to Colli et al. 2015), and a sample of *Cercosaura ocellata* (Cercosaurinae) as an outgroup. GenBank accession numbers and localities of genetic samples are provided in Appendix. It is important to note that currently the tribe Iphisini is composed of four monotypic genera (*Alexandresaurus, Colobosaura, Iphisa*, and *Stenolepis*) and two genera with two species (*Acratosaura* and *Rondonops*) (Colli et al. 2015), but we only had access to five of the eight species, missing *Acratosaura spinosa, Rondonops biscutatus*, and *R. xanthomystax*.

Sequences were aligned with Clustal W (Larkin et al. 2007) followed by a visual inspection and edition if necessary. Final sequence length was 512 bp. The best substitution model was chosen according to the corrected Akaike Information Criterion (AICc) (Burnham and Anderson 2002). We estimated the uncorrected genetic pairwise distances for our dataset, and performed a Maximum Likelihood (ML) analysis for a phylogenetic inference with 10,000 replicates. All these steps were executed in MEGA 6 (Tamura et al. 2013). We used FigTree v1.3.1 for tree editing (http://tree. bio.ed.ac.uk/software/figtree/).

Additionally, the external morphology of specimens of *Colobosaura* was examined (Appendix 2). We scored the following morphometric characters: snout–vent length (SVL) from the tip of the snout to the anterior edge of the cloaca; head length (HL) from the tip of the snout to the anterior edge of the ear opening; head width (HW) measured at the widest section of the head; eye diameter (ED); and ear opening (EO), both taken at the widest section. These measures (except SVL taken with a ruler) and other standard measurements were taken with digital calipers. Paired structures are presented in left/right orientation. In the color descriptions, the capitalized colors and the color codes (in parentheses) are those of Köhler (2012).

A distribution map was generated for the species of the tribe Iphisini to compare ecoregional affinities of the two species of *Colobosaura* and its closest relatives. Ecoregional information is based on Olson et al. (2001), downloaded from the web site of The Nature Conservancy (http://maps.tnc.org/gis_data.html). All coordinates are in decimal degrees and WGS 84 datum, and all the elevations are in meters above sea level. Geographic imagery produced using ArcMap 10.3. Minimum convex polygons were produced upon about 200 bibliographic records based on Brito et al. (2012) for *Acratosaura mentalis*; Rodrigues et al. (2009a) and Freitas et al. (2012) for *A. spinosa*; Freire et al. (2013) and Freitas (2014) for *Alexandresaurus camacan*; Nogueira (2001), Rodrigues et al. (2007), Cuoto-Ferreira et al. (2011), Cardozo Ribeiro et al. (2012), Freire et al. (2012), Cavalcanti et al. (2014), López Santos et al. (2014), da Silva et al.

(2015), Cacciali et al. (2016), and De Alcantara et al. (2016), for *Colobosaura modesta*; Avila-Pires (1995) and Castoe et al. (2004) for *Iphisa elegans*; Colli et al. (2015) for *Rondonops biscutatus* and *R. xanthomystax*; and Rodrigues et al. (2007) for *Stenolepis ridleyi*.

Acronyms of institutions used in the text are **SMF** (Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Frankfurt am Main, Germany), **LG** (Laboratorio de Citogenetica de Vertebrados, Universidade de São Paulo, Brazil), and **MNHNP** (Museo Nacional de Historia Natural del Paraguay, San Lorenzo, Paraguay).

Results

The best substitution model was GTR+G, and the phylogeny recovered is shown in Figure 1. Our genetic sample of *Colobosaura* (SMF 101370) is sister to, but deeply divergent from *C. modesta*. A similar arrangement is observed between *Acratosaura mentalis* and *Stenolepis ridleyi* which constitute the sister clade of *Colobosaura*. *Iphisa elegans* is recovered as a sister clade of the above mentioned groups, and *Alexandresaurus camacan* as the most basal representative of the tribe.

The pairwise distance shows a divergence of ~7.7% between *C. modesta* and SMF 101370, which is even higher than the divergence between SMF 101370 and *I. elegans* (~7.1%), SMF 101370 and *S. ridleyi* (~5.5%), *C. modesta* and *S. ridleyi* (~4.7%), or *A. mentalis* and *S. ridleyi* (~3.1%) (Table 1).

From the distribution it is possible to identify two groups within the tribe Iphisini: one strongly related to Amazonian ecoregions (*Iphisa* and *Rondonops*), and another linked to the Dry Diagonal (*Acratosaura, Alexandresaurus, Colobosaura, and Stenolepis*). Two monotypic genera (*Alexandresaurus* and *Stenolepis*) and *Acratosaura spinosa* are mainly associated to Caatinga environments, whereas *Acratosaura mentalis* have some records in Cerrado. *Colobosaura modesta* together with *Iphisa elegans* has the widest distribution, and it is strongly linked to Caatinga and Cerrado. The collecting site of SMF 101370 is in the Humid Chaco (Fig. 2).

The genetic data presented above demonstrate that our sample SMF 101370 is not conspecific with *C. modesta*. The only other available nominal species that SMF 101370 could be assigned to is *Colobosaura kraepelini* Werner, 1910. Unfortunately, the holotype and only known specimen of this taxon is considered to be lost (see above) and its original description is brief. Therefore, there is no morphological basis to support our claim that SMF 101370 is conspecific with *C. kraepelini* which leaves us with two options: The more conservative option is to assign SMF 101370 to *C. kraepelini* whereas the alternative would be to describe a new species based on our sample. Since we know of no diagnostic character that would differentiate between SMF 101370 and *C. kraepelini*, we think that the better option is to assign SMF 101370 to *C. kraepelini*. Thus, we herewith designate SMF 101370, a subadult male from 2.5 km E of Altos (25.2588°S, 57.2850°W, ca 280 masl), Cordillera Department, Paraguay, collected



Figure 1. Maximum Likelihood tree obtained from 16S mtDNA for the tribe Iphisini (Gymnophthalmidae). Numbers on the nodes represent the bootstrap values and numbers below branches (and scale bar at the bottom left corner) denote branch length (substitutions/site). Specimen highlighted in red indicates our sample. See Appendix 1 for details of specimens used in the analysis.

Table 1. Pairwise genetic distances (lower-left diagonal), and SD (upper-right diagonal) among speciesof Iphisini: Gymnophthalminae.

	A. mentalis	A. camacan	(SMF 101370)	C. modesta	I. elegans	S. ridleyi
Acratosaura mentalis		0.016	0.016	0.013	0.015	0.001
Alexandresaurus camacan	0.122		0.015	0.015	0.013	0.011
Colobosaura (SMF 101370)	0.122	0.101		0.013	0.012	0.011
Colobosaura modesta	0.079	0.103	0.077		0.013	0.010
Iphisa elegans	0.103	0.089	0.071	0.087		0.011
Stenolepis ridleyi	0.031	0.055	0.055	0.047	0.060	

on 27 February 2012 by Gunther Köhler, as the neotype of *C. kraepelini*. Thereby we clarify and stabilize this taxonomic situation and link the name *kraepelini* to a voucher specimen and a genetic sample which will help to avoid taxonomic uncertainties in the future. We provide a species account and description of the neotype as well as data on individual variation below.



Figure 2. Central and northern region of South America showing the distribution (ranges in color) of the members of the tribe Iphisini. LT indicate type localities. Note that type locality for *I. elegans* is not shown since is referred as the whole Brazilian State of Pará. Range for *A. spinosa* is not shown because records come from vicinities of type locality. *Colobosaura kraepelini* is known only from two areas: the locality mentioned in the original description (black dot) and the neotype locality (black star); the second specimen of *C. kraepelini* reported here is from near the neotype locality. Orange square represents locality of the genetic sample of *C. modesta* (Niquelândia, GO, Brazil). Data for ecoregions according to Olson et al. (2001).

Colobosaura kraepelini Werner, 1910

Colobosaura kraepelini Werner, 1910: 32 (neotype, SMF 101370 [by present designation] (Fig. 3); type locality: 2.5 km E of Altos (25.2588°S, 57.2850°W, ca 280 masl), Cordillera Department, Paraguay by neotype selection). Original type locality: Puerto Max, San Pedro Department, Paraguay.

Diagnosis. Colobosaura kraepelini differs from the other species of the family Gymnophthalmidae except for *C. modesta*, by a combination of the following characters: limbs short but well developed; Finger I vestigial, not clawed; dorsal and lateral body scales keeled; four longitudinal series of ventral scales; prefrontal present; occipital present; two pairs of chin shields. Colobosaura kraepelini differs from *C. modesta* by having two mid-central rows of immaculate scales (vs. four immaculate ventral rows in *C. modesta*); flanks completely dark (Fig. 3) (vs. clear mottling in that area in *C. modesta*, Fig. 4); and gular shields profusely suffused with dark reaching the midline (vs. dark mottling restricted to the external edge of the shields, Fig. 5).

Description of the neotype. Subadult male. Body elongated; neck not well differentiated; SVL 29 mm; tail (clipped) stump 14 mm; HL 6.55 mm; HW 4.52 mm; ED 1.42 mm; EO (oblique) 0.66 mm. Head with juxtaposed scales, except posterior edge of interparietal and parietals imbricate with occipital and first row of nuchal scales.

Rostral broad, wider (1.81 mm) than high (0.72 mm), contacting frontonasal, nasals, and first supralabials; frontonasal heptagonal, wider (1.81 mm) than long (1.30 mm), contacting rostral, nasals, loreals, and prefrontals; prefrontals wider (1.07 mm) than long (0.70 mm) with a 0.29 mm contact line between them, and contacting frontonasal, loreals, first and second supraocular, and frontal; frontal hexagonal, longer (1.67 mm) than wide (1.11), contacting prefrontals, second supraocular, and frontoparietals; frontoparietals regular pentagonal, with a 0.67 mm mid contact line between them, and contacting frontal, second (slightly) and third (broad contact) supraoculars, parietals, and interparietal; interparietal longer (2.15 mm) than wide (1.18 mm), contacting frontoparietals, parietals, first row of nuchals, and occipital; parietals broad, wider than interparietal, contacting the interparietal, frontoparietals, third supraocular, three rows of temporals, and the first row of nuchals; occipital pentagonal and small (0.57×0.83 mm) located between the interparietal and the first and second row of nuchals; nasal elongated (0.95×0.72 mm), with nares located in the mid-lower region, contacting the rostral, frontonasal, loreals, and first supralabial; loreal curved, higher (0.67 mm) than wide (0.41 mm), in contact with nasal, frontonasal, first supraocular, first superciliary, preocular (narrowly), frenocular, and first (slightly) and second superciliaries; of which the middle one is the shortest; three supraoculars, the first smaller than the other two; three elongated superciliars, being the middle scale shorter than the first and third; eleven upper palpebrals and ten lower palpebrals surrounding the orbit; semitransparent eyelid; four elongated suboculars, second and third longer than first and fourth; seven supralabials, first contacting rostral, nasal, and loreal narrowly; second contacting loreal, frenocular, and the first subocular; third and



Figure 3. Neotype of *Colobosaura kraepelini* (SMF 101370) from the vicinity of Altos, Cordillera Department, Paraguay.

fourth supralabials in contact with suboculars; fifth supralabial (largest) contacting third and fourth subocular, lower postocular, and lower first temporal, sixth contacting the lowermost scale of the second temporal row, and other scales in the temporal region, and seventh supralabial reaching the border of the ear opening; two postoculars, the upper (in contact with the two last upper palpebrals, third superciliary, third supraocular, and upper temporal) slightly larger than the lower (in contact with the last upper palpebral, fourth subocular, fifth supralabial, and the first row of temporals); two first temporals, the upper twice the size of the lower; three second temporals, the upper twice longer than the two lower.

Mental broad, wider (mm) than long (mm); postmental pentagonal, wider (mm) than long (mm), in contact with mental, first and second infralabials, and first pair of chin shields; two pairs of chin shields, the second larger than the first pair, and followed by elongated and oblique scales that separate the second pair of chin shields from the scales of the gular region; seven infralabials, the first the widest, and the fifth the longest.

Nuchal region with seven rows of paired imbricate scales; lateral sides of the neck with three to four irregular series of juxtaposed scales, and two imbricate located in the lowermost portion; seven paired rows of gular scales, first two rows irregular, and homogeneously arranged in pairs from the third to the seventh row.

Dorsal scales imbricate, 21 transversal rows between axilla and groin, wider at neck level, and narrower and homogeneously arranged in longitudinal rows on trunk; lateral scales similar to dorsals in the upper flanks, becoming wider towards the ventral



Figure 4. Specimen of *Colobosaura modesta* showing lateral coloration patter. Image given by Paul Smith (Fauna Paraguay). Additional photographs available at http://www.faunaparaguay.com/colobosauramodesta.html

region; sternal scale triangular, flanked by large rectangular scales in the clavicular region; four longitudinal rows of ventral scales; 26 scales around midbody; scales at insertion of limbs granular, except in the ventral region; all of tail with imbricate, elongated, hexagonal, and keeled scales.

Forelimbs covered with large, imbricate and smooth scales on the dorsal and lateral surfaces, being smaller on the ventral region of the limb; carpal region covered with large imbricate scales; palmar surface covered with granular juxtaposed scales; scales on fingers from I to V: 1/1-4/5-6/6-7/7-4/4; infradigital single lamellae under fingers from I to V: 2/2-8/8-10/10-11/12-6/5; fingers clawed except vestigial finger I.

Hind limbs medium-sized, imbricate, moderately keeled scales on the dorsal surface; anterior and posterior parts of the hind limbs with large, imbricate, and smooth scales; posterior part of hind limbs covered with granular juxtaposed scales on the thigh, and smooth medium-sized imbricate scales on the shank; tarsal region covered with large imbricate scales; plantar surface covered with granular juxtaposed scales; scales on toes from I to V: 3/3-4/4-8/8-10/10-6/(toe clipped as tissue sample); infradigital single lamellae under toes from I to V: 4/4-8/7-14/12-15/17-9/(toe clipped); toes clawed.

Coloration in life of the neotype. Dorsal surface of head Olive Clay Color (85) with Vandyke Brown (282) mottling on frontal and second supraocular and posteri-



Figure 5. Ventral view of the head showing the different coloration pattern between *Colobosaura modesta* (MNHNP 8521, left) and *C. kraepelini* (MNHNP 11726, right).

orly, and a diffuse Vandyke Brown (282) line edging anterior margin of frontal and second supraocular and anterior scales; lateral parts of the head homogeneous Vandyke Brown (282); supralabials with Medium Neutral Gray (298) bars in the center interleaved with Cyan White (155) in the sutures; background color of mandibular region Cyan White (155) with Medium Neutral Gray (298) blotches on infralabials (one per scale) and second pair of chin shields; iris Burnt Umber (48); dorsal scales Mikado Brown (42), anteriorly (before forelimbs level) with Vandyke Brown (282) suffusions more concentrated near the laterals, and posteriorly (after forelimbs level) with faint irregular suffusions of Warm Sepia (40), more regularly present on the scales margins; lateral sides of the neck and body Vandyke Brown (282) with irregular Mikado Brown (42) speckles and blotches after forelimbs level, grading into a reticulated Vandyke Brown (282) and Mikado Brown (42) pattern near the groin; background ventral color Cyan White (155) with intrusions of Vandyke Brown (282) on the throat, and a faint mottling of Vandyke Brown (282) on the lateral rows of ventral scales; forelimbs mostly Vandyke Brown (282), Cyan White (155) restricted to the anteroventral regions; hind limbs Mikado Brown (42) with suffusion of Vandyke Brown (282) on the scales margins, and Cyan White (155) on the ventral region of the limb; tail background color Plumbeous (295) with Brownish Olive (292) suffusions on the anterior third of the organ, and Pale Greenish White (97) paravertebral spots located every two scales; iridescent hue all along the body.

Coloration in preservative of the neotype. (After five years in 70% ethanol): The general pattern remains the same, and the background Mikado Brown (42) color also remains; the darker parts of the body (lateral sides of neck and body) turned to Sepia

(279); tail turned to Hair Color (277) on the dorsum, with the paravertebral spots faintly visible; ventral side of the head Smoky White (261); ventral side of the body Pale Buff (1).

Variations. MNHNP 11726 agrees well in most aspects of the scalation to those observed in the neotype, with the following differences: two superciliaries; 21 transversal rows between axilla and groin; 27 scales around midbody; 11 infradigital lamellae under IV finger; 16 infradigital lamellae under IV toe. Background color of MNHNP 11726 slightly clearer (Sayal Brown 41) than SMF 101370, and the dark (Fuscous 283) lateral suffusions are less dense. Ventrally Pale Buff (1). The coloration pattern is the same in both specimens with some differences: MNHNP 11726 has dark blotches also on the first pair of chinshields; posterior margin of dorsal scales strongly marked; caudal spots absent.

Distribution and habitat. The species is distributed in the Humid Chaco. The environment is basically a savanna composed of palms (*Copernicia alba*), native bunch grasses, and scattered islands of semideciduous temperate forest. The area is adapted to periodical floods from the Paraguay River. The locality of Puerto Max (former type locality of *C. kraepelini*) consists of a small village and cattle farm with intense anthropic pressure. The new specimens (SMF 101370 and MNHNP 11726) came from the vicinities of the capital city, about 280 km (airline) southwards from the original type locality, also in Humid Chaco.

Discussion

The tribe Iphisini was described recently by Rodrigues et al. (2009b) which was before merged within the tribe Heterodactylini. Nevertheless, Rodrigues et al. (2007) already discovered that the genera *Acratosaura, Alexandresaurus, Colobosaura, Iphisa,* and *Stenolepis* exhibit a strong sexual dimorphism, absent in other Heterodactylini. Our ML phylogenetic hypothesis of the tribe Iphisini based on the mtDNA 16S gene recovered *Acratosaura mentalis* and *Stenolepis ridleyi* as sister taxa which was also inferred by Rodrigues et al. (2007) and Colli et al. (2015). The position of *Iphisa* differs from the phylogeny presented by Colli et al. (2015), being the sister clade of *Acratosaura+Colobosaura+Stenolepis* in our analysis. It is important to note that sequences of *Rondonops biscutatus* used by Colli et al. (2015) were not available at GenBank. The placement of *Iphisa* as a basal clade in relation to *Acratosaura* and *Colobosaura* was also shown by Pellegrino et al. (2001) and Castoe et al. (2004). And *Alexandresaurus camacan* is shown as the most basal taxon in the group (Fig. 1) as also exposed by Pellegrino et al. (2007), and Colli et al. (2015).

From the genetic point of view there is no doubt that the neotype of *Colobosaura kraepelini* is different from *C. modesta*. The high genetic distance between these two species compared with the even lower genetic distance between some related genera (Table 1) could indicate that a new taxonomic arrangement should be proposed. Never-

theless, based on the little morphological differentiation in *Colobosaura* we keep a conservative approach. In our phylogeny, the divergence between *Colobosaura modesta* and *C. kraepelini* is as deep as the divergence between the genera *Acratosaura* and *Stenolepis*.

The only previously known reference to a specimen of *Colobosaura kraepelini* was in the original description based on an individual from Puerto Max, and the species was never found again. Given the brevity of the original description the species was considered as synonym of *C. modesta* (Vanzolini and Ramos 1977, Rodrigues et al. 2007). Vanzolini and Ramos (1977) additionally stated that maybe the specimen used for the description of *C. kraepelini* was not even a *Colobosaura* because in the description the author referred to some oblique folds on the tongue of the specimen, which is a character that does not occur in the group. Our specimen differs morphologically from *C. modesta* in some aspects of coloration, and it was found in the Humid Chaco (as is the original type locality of *C. kraepelini*) whereas *C. modesta* is restricted to Caatinga and Cerrado in areas adjacent to Atlantic Forest (Fig. 2). All three known localities for *C. kraepelini* are located in the drainage system of the Paraguay River sharing some topographical traits.

Biogeographically, Rodrigues et al. (2007) hypothesized that *Stenolepis* should have originally a wider distribution followed by a major constriction, resulting in its current restricted range associated with the Atlantic Forest. The basal location of *Alexandresaurus* in the tribe's phylogeny could suggest that it probably also had a wider distribution, although it is currently restricted to a small patch of Atlantic Forest on the coast of Bahia. In the remaining taxa it is possible to distinguish a major phylogenetic split of eastern (only *Iphisa* in our phylogeny) and western (*Acratosaura, Colobosaura,* and *Stenolepis*) clades, which was also noted by Colli et al. (2015). Whereas the western clade is strictly related to Amazonian forests, the eastern clade is present mainly in the Dry Diagonal, although *S. ridleyi* is also present in Atlantic Forest and Caatinga (Fig. 2). According to this biogeographical perspective and based on the distribution of the whole tribe, *C. kraepelini* could be the most derived member of the clade.

Rodrigues et al. (2007) highlighted the importance of analyzing the wide distribution ranges of *Colobosaura* and *Iphisa* and, in fact, more recently Nunes et al. (2012) revealed that *Iphisa* is actually composed of five different species, and Colli et al. (2015) suggest that a detailed analysis of *Colobosaura* could indicate a similar pattern. Here we provide evidence that at least the genus *Colobosaura* is composed of two species. The morphological traits proposed by Peters and Donoso-Barros (1970) to differentiate between *C. modesta* and *C. kraepelini* (shape of the interparietal) are useless. Instead, we show that coloration can differentiate between these two taxa. Following, we present a key for the identification of species in the tribe Iphisini.

Key to species of Iphisini

1	Two longitudinal rows of ventral scales	.2
_	Four or six longitudinal rows of ventral scales	.4

2	One pair of enlarged chin shields Iphisa elegans
_	Two pairs of enlarged chin shields (Rondonops) 3
3	Lateral neck scales smooth; 16–20 infradigital lamellae under toe IV
-	Lateral neck scales keeled; 20–26 infradigital lamellae under toe IV
4	Prefrontals absent
_	Prefrontals present
5	Occipitals absentAlexandresaurus camacan
-	Occipitals present
6	Three pairs of chin shields
_	Two pairs of chin shields
7	Lateral neck scales smooth and juxtaposed; dorsal scales slightly keeled (keel
	covers half of the scale) at midbody
-	Lateral neck scales keeled and imbricate; dorsal scales strongly keeled at mid-
	body
8	Ventrals immaculate; dark mottling on the external edge of gular shields
_	Two central rows of ventral scales immaculate, and dark mottling on the two
	external rows; gular shields profusely mottled with dark

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Appendix I

Species	Voucher	GBAN	Locality
Acratosaura mentalis	MRT 906448	AF420726	Morro do Chapéu, BA, Br
Alexandresaurus camacan	MD 1106	AF420739	Una, BA, Br
Colobosaura kraepelini	SMF 101370	KY782646	Altos, Cordillera, Pa
Colobosaura modesta	LG 1145	AY217953	Niquelândia, GO, Br
Iphisa elegans	MRT 977426	AF420714	Aripuanã, MT, Br
Stenolepis ridleyi	-?-	EF405619	-?-
Cercosaura ocellata OG	MRT 977406	AF420731	Aripuanã, MT, Br

Genetic samples

For each species the voucher specimen, GenBank accession number (GBAN), and the locality (Br = Brazil, Pa = Paraguay) are presented for samples used in the genetic analysis. Outgroup marked with OG. See Materials and methods section for indication of institutional acronyms. MRT and MD indicate Miguel Trefaut Rodrigues (Museu de Zoologia, Universidade de São Paulo, Brazil) and Marianna Dixo (Instituto de Biociências, Universidade de São Paulo, Brazil) voucher specimens, respectively. Data for the sample of *S. ridleyi* are missing in the original publication (Rodrigues et al. 2007).

Appendix 2

Examined specimens

Colobosaura kraepelini

PARAGUAY: Cordillera: San Bernardino, 50 metros del Lago Ypacarai (MNHNP 11726).

Colobosaura modesta

PARAGUAY: Amambay: Parque Nacional Cerro Corá (MNHNP 8454–56, 8521). San Pedro: Reserva Natural Laguna Blanca (MNHNP 11684, 11596, 11652).

RESEARCH ARTICLE



Simaonukia, a new genus of the leafhopper tribe Evacanthini (Hemiptera, Cicadellidae, Evacanthinae), with descriptions of a new species from China

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Abstract

Simaonukia, a new leafhopper genus of Evacanthini (Hemiptera, Cicadellidae, Evacanthinae), and a new species, *Simaonukia longispinus* **sp. n.**, from Yunnan, China are described.

Keywords

Homoptera, Auchenorrhyncha, morphology

Introduction

Evacanthini is a relatively small leafhopper tribe of the subfamily Evacanthinae (Cicadellidae) with most species (more than 220 species) present in China (see Li and Wang 1996). While sorting and identifying the evacanthine leafhopper material in Institute of Entomology of Guizhou University, we found a new genus and species which we describe here. The type specimen is deposited in the Institute of Entomology, Guizhou University, Guiyang, China (GUGC).

Taxonomy

Simaonukia Li & Li, gen. n. http://zoobank.org/F420F245-01D3-4474-A418-C6B52FFD9B5C

Type species. Simaonukia longispinus sp. n.

Description. Body medium-sized, usually black. Head (Figs 1, 4) in dorsal view narrower than pronotum; with five distinct carinae, a median carinae, two lateral carinae and two subocellar carinae converging to apex of vertex, area between median carina and submarginal carina with many fine longitudinal wrinkles; disc with a short transverse ridge basally, carinate. Front of head (Figs 1, 4) slightly conically produced; vertex about as long as or a little longer than pronotum and nearly two times longer and three times wider than eye. Ocelli (Figs 1, 2, 4, 5) placed just laterad of lateral carina, well in front of eye. Face (Fig. 3) including eyes shorter than wide; frontoclypeus (Figs 2, 3, 5) tumid, with median longitudinal carina strongly elevated; clypellus broad and swollen at base; lora nearly reaching middle of clypellus. Pronotum (Figs 1, 4) with sides strongly convergent cephalad. Scutellum (Fig. 1) with transverse depression distinct. Hind femur (Fig. 11) with apical macrosetal formula 2+1+1. Forewing (Figs 1–3) with R_{1a} present; with four apical cells and two closed subapical cells; appendix very narrow.

Male genitalia. Pygofer without ventral process, triangular in lateral view, with some small setae on ventral side near apex. Subgenital plate ligulate with many macrosetae and long fine setae ventrally. Aedeagal shaft short with pair of lamellae dorsally near base and pair of lateral processes subbasally. Style short, foot-like apically. Connective similar in length to style, arms very short.

Distribution. China (Yunnan).

Etymology. The genus name is formed from a combination of the collection locality and the similar evacanthine genus *Onukia* Matsumura.

Remarks. This genus can be distinguished by the moderately conically produced head with five distinct longitudinal carinae and dense striations and a transverse carinate ridge basally on disk. In the key to genera by Wang et al. (2015) the new genus runs to *Onukia* Ishihara but can be distinguished by: 1) Aedeagus (Figs 8–10, 13–15) with a pair of lateral processes subbasally; 2) Pygofer (Fig. 6) without processes.

Simaonukia longispinus Li & Li, sp. n.

http://zoobank.org/8FF80210-F181-4DDD-B902-0A329C574FF5 Figs 1–15

Measurements. body length (including forewing): 3: 4.9 mm.

Vertex, pronotum and scutellum black (Figs 1, 2, 4, 5). Frontoclypeus black, anteclypeus light yellow (Figs 2, 3, 5). Forewing black, with nearly pale white and subtranslucent plaque in middle of costal area and around R_{1a} , area along R_{1a} red (Figs 1–3).


Figures 1–5. *Simaonukia longispinus* sp. n. **1–3** Male, dorsal view, lateral view and ventral view **4–5** Head, dorsal view, lateral view.

Male pygofer (Fig. 6) without ventral process, with a hyaline lateral stripe near middle area. End of style foot-like (Figs 9, 11). Subgenital plate ligulate, blunt at base, with a uniseriate row of many macrosetae on ventral surface and many moderately long fine setae laterally (Fig. 7). Aedeagal shaft dorso-ventrally compressed, tapering



Figures 6–15. *Simaonukia longispinus* sp. n. 6 Male pygofer, lateral view 7 Subgenital plate 8 Aedeagus, ventral view 9 Aedeagus, style and connective, lateral view 10 Aedeagus, dorsal view 11 Style and connective, lateral view 12 Hind femur 13 Aedeagus, style and connective, ventral view 14 Aedeagus, style and connective, lateral view 15 Aedeagus, style and connective, dorsal view.

to digitate apex, the latter with a dorsal flange-like acute process (Figs 9, 14); with a pair of very long lateral subbasal processes (A in Figs 8–10), directed posteriorly then sharply turned dorsally near midlength with apex sinuate, with short sub-basal process (B in Figs 8–10).

Type material. Holotype: *(*), CHINA, **Yunnan**: Puer, Simao, Caiyanghe, 24 August 2014, coll. Guo Meina.

Etymology. The species name refers to the long lateral spine of the aedeagus.

Remarks. This species can be distinguished by the dorsum and upper part of face blackish brown and area along R_{1a} in the forewing red and in the male genitalia by the elongate lateral processes of the aedeagus bifurcate sub-basally.

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RESEARCH ARTICLE



Revision of the Neotropical water scavenger beetle genus Tobochares Short & García, 2007 (Coleoptera, Hydrophilidae, Acidocerinae)

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Abstract

The genus *Tobochares* Short & García, 2007 is revised. A combination of morphological and molecular data provide support for ten distinct species. Five new species are described: *T. canaliculatus* **sp. n.** (Venezuela), *T. emarginatus* **sp. n.** (Suriname), *T. kusad* **sp. n.** (Guyana), and *T. pallidus* **sp. n.** (Venezuela). All four preexisting species are redescribed. A tenth species, known from a single female from Venezuela, is left undescribed pending the collection of additional specimens. New collecting records are provided for *T. sulcatus* Short & García, 2007 and *T. kasikasima* Short, 2013. *Tobochares sipaliwini* Short & Kadosoe, 2011 is newly recorded from Guyana. All species are associated with seepage or wet rock habitats, although some species have also been found along the margins of streams that flow over rocky substrates. High-resolution images including scanning electron micrographs are provided, as well as a key to species and habitat photographs.

Keywords

South America, Guiana Shield, taxonomy, new species

Introduction

The genus *Tobochares* Short & García, 2007 was erected for a single unusual species found living under leaves on wet rock along a creek in southern Venezuela (Short and García 2007). In the decade that has elapsed since its description, additional fieldwork across the northern Guiana Shield has produced more than 400 additional specimens of the genus from Venezuela, Suriname, and Guyana. A few of these were described as they were identified (e.g. Short and Kadosoe 2011, Short 2013), and the genus has grown to contain a total of four species. A comprehensive morphological review of this material as well as DNA sequence data from the mitochondrial gene Cytochrome Oxidase I (COI) has uncovered six additional undescribed species, of which five are described herein. The sixth species is known only from a single partly disarticulated female, which we refrain from describing until additional material can be collected. The discovery of these new species has required a slight broadening of the concept of *Tobochares*, most notably that not all species have grooved elytra, and consequently the genus is here redescribed. We also provide detailed habitat information for all species, which appears to be narrowly restricted to rock seepages and associated habitats.

Materials and methods

Depositories of examined material.

CBDG	Center for Biological Diversity, University of Guyana, Georgetown			
MALUZ	Museo de Artrópodos de la Universidad del Zulia, Maracaibo, Venezuela			
	(J. Camacho, M. García)			
MIZA	Museo del Instituto de Zoología Agrícola, Maracay, Venezuela (L. Joly)			
NZCS	National Zoological Collection of Suriname, Paramaribo (P. Ouboter, V.			
	Kadosoe)			
SEMC	Snow Entomological Collection, University of Kansas, Lawrence, KS (A.			
	Short)			
USNM	U.S. National Museum of Natural History, Smithsonian Institution,			
	Washington, DC (C. Micheli).			

Morphological methods. Specimens were examined using an Olympus SZX16 microscope (to 110× magnification). Specimens for dissection were relaxed in warm water, and their genitalia were removed and placed in glycerin on a glass slide, which was then viewed and imaged using an Olympus BX51 to 200× magnification. Genitalia were mounted beneath the specimens in microvials with glycerin. Scanning electron micrographs were taken by mounting specimens on carbon tape and coated in gold. Habitus photographs were taken with a Visionary Digital imaging system. All final images were created by stacking multiple individual photographs from different focal planes using the software Zerene Stacker. Morphological terminology largely follows

Taxon	Extraction	Locality	Coordinates	GenBank Accession
T. emarginatus	SLE424	Suriname: Kasikasima	2.976883, -55.411385	KY679835
T. emarginatus	SLE482	Suriname: Kasikasima	2.976883, -55.411385	KY679836
T. emarginatus	SLE483	Suriname: Kasikasima	2.976883, -55.411385	KY679837
T. kasikasima	SLE1045	Suriname: Kappel Airstrip	3.791317, -56.149467	KY679850
T. kasikasima	SLE1046	Suriname: Kappel Airstrip	3.791317, -56.149467	KY679851
T. kasikasima	SLE1048	Suriname: Tafelberg Summit	3.926667, -56.188332	KY679849
T. kasikasima	SLE1049	Suriname: Tafelberg Summit	3.926667, -56.188332	KY679852
T. kasikasima	SLE1050	Suriname: Tafelberg Summit	3.926667, -56.188332	KY679848
T. kusad	SLE1021	Guyana: Kusad Mts.	2.80885, -59.865	KY679846
T. pallidus	SLE525	Venezuela: Tobogan de la Selva	5.386783, -67.615364	KY679853
T. sipaliwini	SLE422	Suriname: Kasikasima	2.976883, -55.411385	KY679838
T. sipaliwini	SLE478	Suriname: Kasikasima	2.976883, -55.411385	KY679839
T. sipaliwini	SLE497	Suriname: Kasikasima	2.976883, -55.411385	KY679840
T. sipaliwini	SLE1020	Guyana: Kusad Mts.	2.80885, -59.865	KY679841
T. sipaliwini	SLE1023	Suriname: Kwamala	2.182883, -56.787251	KY679842
T. striatus	SLE423	Suriname: Kasikasima	2.976883, -55.411385	KY679847
T. sulcatus	SLE0035	Venezuela: Tobogan de la Selva	5.386783, -67.615364	KC935327
T. sulcatus	SLE1027	Venezuela: Tobogan de la Selva	5.386783, -67.615364	KY679845
T. sulcatus	SLE1035	Venezuela: Tobogan de la Selva	5.386783, -67.615364	KY679843
T. sulcatus	SLE1037	Venezuela: Pijiguaos	6.593617, -66.820633	KY679844
<i>T.</i> sp. A	SLE526	Venezuela: Tobogan de la Selva	5.386783, -67.615364	KY679854

Table 1. List of specimens and GenBank accession numbers used in this study. All vouchers are deposited in SEMC.

Hansen (1991) except for the use of meso- and metaventrite instead of meso- and metasternum.

Molecular methods. Total genomic DNA was extracted from entire beetles using a DNeasy kit (Qiagen, Alameda, CA). All vouchers (Table 1) are deposited at the University of Kansas (Lawrence, USA). We selected specimens of each putative morphospecies from each locality for which we had specimens preserved in 100% ethanol; we did not have suitable material for two morphospecies (*T. canthus* and *T. canaliculatus*) which are thus not included in our molecular analyses. We used the COI primers and PCR protocols as given in Short and Fikáček (2013). Resulting DNA sequences were assembled and edited in Geneious R 8.0.5 (Biomatters, http://www.geneious.com/), which was also used to examine the raw pairwise distances between sequences. All new sequences are deposited in GenBank (see Table 1 for accession numbers). IQ-TREE 1.4.4 (Nguyen et al. 2015) was used to conduct a maximum likelihood analysis to infer phylogenetic relationships. The optimal model of substitution was selected using the Auto function in IQ-TREE 1.4.4; default settings were used for the analysis. In order to assess nodal support, we performed 1000 ultrafast bootstrap replicates (Minh et al. 2013). We included representatives of two related acidocerine genera (Short and Fikáček 2013) Chasmogenus ruidus Short, 2005 and Globulosis flavus Short, Garcia, & Giron, 2017 as outgroups to root the tree (GenBank accessions KC935240 and KY351811 respectively).

Results

The results of the maximum likelihood analysis (Fig. 1) of the COI sequence data supported the hypothesis that the morphologically differentiated species are also genetically distinct. For species for which we sequenced multiple representatives, the amount of raw intraspecific genetic divergence among individuals of *T. emarginatus*, *T. kasikasima*, and *T. sulcatus* was less than 1%. Within individuals of *T. sipaliwini*, the maximum raw genetic divergence found was 2.5%. The raw pairwise genetic distance between any two species in the tree was greater than 10% with the exception of *T. kusad* and *T. striatus*, in which it was 7.4%. Taken together with consistent morphological differences, we found support for ten distinct species among the material we examined.

List of species

1. Tobochares canaliculatus sp. n.	Venezuela (Amazonas)
2. Tobochares canthus sp. n.	Venezuela (Amazonas)
3. Tobochares emarginatus sp. n.	Suriname
4. Tobochares kasikasima Short, 2013	Suriname
5. <i>Tobochares kusad</i> sp. n.	Guyana
6. <i>Tobochares pallidus</i> sp. n.	Venezuela (Amazonas, Bolivar)
7. <i>Tobochares sipaliwini</i> Short & Kadosoe, 2011	Suriname, Guyana
8. Tobochares striatus Short, 2013	Suriname
9. Tobochares sulcatus Short & García, 2007	Venezuela (Amazonas, Bolivar)
10. Tobochares sp. A	Venezuela (Amazonas)

Characters of taxonomic importance

Species of *Tobochares*, in general, are morphologically well-defined and we found relatively little variation within species.

Dorsal coloration. The dorsal coloration of most species is medium to dark brown (Figs 2A–D, 3C–D), but may be extremely pale, almost appearing yellow (Fig. 3A–B) in a few species. This is not due to being teneral but is the true coloration of the adult beetle (care must be taken that teneral specimens of other, darker, species are not confused with non-teneral specimens). The coloration of the head is particularly helpful in diagnosing species, as some species may have an entirely black head while others have pale preocular patches of varying sizes (e.g. Fig. 6A–F).

Head. A lateral canthus of the frons emarginates the eye to some extent in all *To-bochares* species (e.g. Fig. 5D), while it nearly divides the eye in two in a few species (Fig. 6D); the degree of emargination is usually consistent within species. The coloration of the apex of the maxillary palps is helpful at separating some species. In some, the entire palpomere is pale (e.g. Fig. 8D), while in others the tip is darkened (e.g.



Figure 1. Maximum likelihood phylogeny of *Tobochares* spp. based on COI sequences, with map showing the localities of the sampled populations.

Fig. 8A–C). Like most coloration characters, there is some variation and it should not be alone used for definitive identification.

Thoracic venter. The condition of the mesoventrite slightly varies between species, but is not extremely useful for making identifications. In most species, it possesses a low transverse ridge which may vary in elevation (Fig. 9D–F). In a few species, the ridge is indistinct or absent, and instead represented by a bulge (Fig. 9A). The metaventrite has a distinct glabrous patch posteromedially (Fig. 10), and the size of this patch can vary between species.

Elytra. The condition of the elytra is extremely useful for separating species (Fig. 11). While all species have rows of serial punctures, how much these rows are impressed into striae varies from not at all (e.g. *T. emarginatus*) to deeply along their entire length (e.g. *T. sulcatus*, Fig. 11F). The form and strength of the ground punctation also varies between species.

Abdomen. The surface of the abdomen is densely pubescent in all species, but some species have cuticular projections mixed in amongst the setae (Fig. 13A), while others lack these projections (Fig. 13B). The aedeagus, particularly the shape of the parameres, is diagnostic for all species.

Genus Tobochares Short & García, 2007

Tobochares Short & García, 2007: 2.

Type species. Tobochares sulcatus Short & García, by original designation.

Differential diagnosis. Size small, 1.5–2.4 mm. Antennae with eight antennomeres, including three-segmented club. Elytra without sutural stria, but with serial punctures impressed into distinct grooves (serial punctures present but not impressed



Figure 2. Dorsal and lateral habitus of *Tobochares* spp. A *T. sulcatus* B *T. striatus* C *T. sipaliwini* D *T. kusad* sp. n.

into groves in *T. canthus*, *T. emarginatus*, and *T. pallidus*). Median elevation of mesoventrite low, forming a narrow transverse ridge or elevated bulge (Fig. 9). Metaventrite with distinct posteromedial ovoid glabrous patch (Fig. 10). Metafemora glabrous except for a few scattered setae (Fig. 12). Fifth abdominal ventrite evenly rounded, without apical emargination or coarse setae (Fig. 13). Aedeagus with basal piece very short (Fig. 14).

Description. Head. Antennae with eight antennomeres, including three-segmented pubescent club. Maxillary palps curved inward and moderately long, as long or longer than the width of head just anterior to eyes; inner face of palpomere 2 straight to slightly curved; apical palpomere slightly longer than penultimate. Labial palps short, distinctly shorter than mentum width. Mentum flat and set with a few scattered setae; strongly

emarginated anteromedially with a notch extending posteriorly about one-quarter to one-third of its length. Head with ground punctures. Frons with series of irregular systematic, setae-bearing punctures anterior to each eve. Systematic punctures also present on clypeus and labrum but blend with ground punctation. Eyes not bulging, continuous with outline of the head; slightly to strongly emarginated anteriorly by a small extension of the frons (Figs 4–6). Thorax. Pronotum with systematic punctation in lateral thirds, each puncture usually bearing a short seta. Prosternum narrow, not carinate medially; very slightly elevated in anterior third, and with a transverse crease. Mesoventrite with anapleural sutures distinctly concave. Mesoventrite with a low, transverse ridge medially (Fig. 9B-F) or rarely with only a weakly elevated bulge (Fig. 9A) without clear directionality (in T. canthus and T. emarginatus). Metaventrite with medium to large glabrous patch posteromedially (Fig. 10). Elytra without sutural stria; with ten rows of serial punctures which are depressed into grooves on at least the posterior half of the elytra (except T. canthus and T. emarginatus, which have weakly differentiated serial punctures that are not impressed into grooves); with irregular rows of small but distinct systematic punctures bearing short setae. Procoxae set with sparse setae, but without thickened spines. Hind femora glabrous, with only a few scattered setae (Fig. 12). All tarsi with five segments; with a few short setae on dorsal face but without long natatory setae. Ventral surface of tarsomeres 1-4 set with two rows of moderately long articulated spicules. Abdomen. With five densely pubescent ventrites, with setae slightly denser medially on each ventrite (Fig. 13); sometimes with small spicules interspersed amongst the setae. Fifth ventrite evenly rounded and without any thickened setae at apex. Aedeagus (Fig. 14) with short basal piece, less than one-third the length of the parameres. Median lobe moderately wide, as wide or wider than base of each paramere.

Larvae. The immature stages are unknown.

Distribution. Venezuela (Amazonas, Bolivar), Guyana, Suriname.

Biology. Nearly all collections of *Tobochares* are associated with hygropetric habitats, e.g. thin water films on rock. A handful of specimens have been collected from stream or forest pool margins that are fed by or adjacent to such habitats. Most seepages on which *Tobochares* tend to be found are littered with leaves and detritus (e.g. Figs 17A–B, 18A–B), though this is not always the case in some vertical seepage situations (e.g. Fig. 16E). The genus frequently co-occurs with other known seep specialists, including the hyrophilid genera *Oocyclus* Sharp, 1882 and *Radicitus* Short & García, 2014, the dytiscid genus *Fontidessus* Miller & Spangler, 2008, and several myxophagan groups.

Tobochares canaliculatus sp. n.

http://zoobank.org/177BBE60-D03B-4B44-A80A-5E28F1AA46CC Figs 3A, 4A–B, 8D, 9B, 10B, 11E, 12E, 14G, 15, 18A–B

Type material. Holotype (male): "VENEZULEA: Amazonas State/ 5°23.207'N, 67°36.922'W, 125m/ Tobogan de la Selva; 8.viii.2008/ leg. A. Short, M. García, L. Joly/ AS-08-080b; old "tobogancito"/ on seepage area w/ detritus", "[barcode]/



Figure 3. Dorsal and lateral habitus of *Tobochares* spp. A *T. canaliculatus* sp. n. B *T. pallidus* sp. n. C *T. kasikasima* D *T. canthus* sp. n.

SEMC0877724/ KUNHM-ENT" (MIZA). **Paratypes (23): VENEZUELA: Amazonas:** same data as type (10 exs., SEMC, MALUZ; includes 1 female mounted on SEM stub); same locality but 14.i.2009, leg. Short & Miller, "partly shaded wet rock w/ algae", VZ09-0114-01G (9 exs., SEMC); same locality but 14.i.2009, leg. Short, "clumps of wet leaves on rock", VZ09-0114-01D (3 exs., SEMC); same locality but 23.ii.1986, P.J. Spangler, sandy margin, Colln. #10 (1 ex., USNM).

Differential diagnosis. The combination of the pale dorsal coloration and deeply sulcate elytra along their entire length (Fig. 3A) will easily separate *Tobochares cana-liculatus* from its congeners. The genitalia is also distinctive in having very narrow parameres which are longer than the median lobe (Fig. 14G). Only *T. pallidus* is paler in coloration, but that species lacks deeply grooved elytra. Other species with deeply sulcate elytra (e.g. *T. sulcatus, T. striatus, T. kusad*) are all very dark brown in color, and also have the tips of their parameres distinctly expanded.



Figure 4. Front and lateral view of heads of *Tobochares* spp. **A–B** *T. canaliculatus* sp. n. **C–D** *T. sipaliwini* **E–F** *T. kasikasima*.

Description. *Size and form:* Body length 1.6–2.0 mm. Body elongate oval, moderately dorsoventrally compressed. *Color and punctation.* Dorsum of head brown to dark brown, anterolateral margins of clypeus with prominent pale preocular patches (Fig. 4A–B); maxillary palps distinctly pale. Pronotum light brown with the lateral margins slightly paler; elytra light brown to brown, slightly paler at lateral margins and posteriorly (Fig. 3A). Meso- and metathoracic ventrites dark brown, and abdominal ventrites very dark brown (nearly black), with prosternum slightly paler; epipleura, legs, labial palps, and antennae distinctly paler, with antennal club slightly darker than proximal antennal segments. Ground punctation on head, pronotum and elytra moderately fine. Head. Eyes measuring ~100µm anteroposteriorly, continuous with outline of head, emarginate at lateral margin, narrowing to half to slightly more than a third of the width. Thorax. Elytra with ten rows of serial punctures which are depressed into deep, smooth grooves running the full length of the elytra (Fig. 11E). Metafemora mostly glabrous on ventral face, with narrow band of pubescence along proximal third of anterior margin (Fig. 12E). Elevation of mesoventrite forming a low transverse carina, not quite elevated to the same plane as the ventral surface of the mesocoxae (Fig. 9B). Metaventrite with distinct median ovoid glabrous area that is more than half of the total metaventrite length, and about half as wide as it is long (Fig. 10B). Abdomen. Abdominal ventrites uniformly and very densely pubescent, with small spicules interspersed amongst the setae (e.g. Fig. 13A). Aedeagus (Fig. 14G) with parameres relatively narrow, nearly half as narrow as the median lobe; parallel sided in apical half and slightly convex in basal half; apex of parametes very slightly outwardly curved and about equal to the length of the median lobe; gonopore situated at the tip of the median lobe.

Etymology. Dimunuative of *canalis*, referring to the elytral grooves.

Distribution. Known only from the type locality in Venezuela (Fig. 15).

Biology. This species has been collected on several occasions on rock seepages along the margin of the Rio Coromoto (Fig. 18A).

Tobochares canthus sp. n.

http://zoobank.org/A2946B0F-ED87-4890-848E-7D2DF2CF41EA Figs 3D, 6C–D, 7D, 9A, 10A, 12D, 13B, 14H, 15, 18A–B

Type material. Holotype (male): "VENEZULEA: Amazonas State/ 5°23.207'N, 67°36.922'W, 125m/ Tobogan de la Selva; 8.viii.2008/ leg. A. Short, M. García, L. Joly/ AS-08-080b; old "tobogancito"/ on seepage area w/ detritus", "[barcode]/ SEMC0877726/ KUNHM-ENT" (MIZA). Paratypes (28): VENEZUELA: Amazonas: same data as type (28 exs., SEMC, MALUZ, MIZA; includes 1 male mounted on SEM stub).

Differential diagnosis. The lack of impressed striae on the elytra (Fig. 3D), strongly emarginated eye (Figs. 6C-D), lack of spicules on the surface of the abdominal ventrites, and extremely broad glabrous patch on the metaventrite (Fig. 10A) all serve to easily separate this species from other *Tobochares* with the exception of *T. emarginatus*. It may be separated from *T. emarginatus* by the paler dorsal coloration and the shape of the aedeagus (Fig. 14H).

Description. *Size and form:* Body length 1.7–2.0 mm. Body elongate oval, moderately dorsoventrally compressed. *Color and punctation.* Dorsum of head dark brown, frons darker (nearly black) laterally and around eyes, anterolateral margins

of clypeus with paler preocular patches (Fig. 6C–D); maxillary palps distinctly pale (Fig. 7D). Pronotum dark brown with the lateral margins paler; elytra dark brown, slightly paler at lateral margins and posteriorly. Meso- and metathoracic ventrites and abdominal ventrites very dark brown, with prosternum slightly paler; legs, labial palps, and antennae distinctly paler. Ground punctation on head, pronotum and elytra moderately fine. Head. Eyes measuring ~90µm anteroposteriorly, continuous with outline of head, emarginate at lateral margin, narrowing to about a fourth of the width (Fig. 6C-D). Thorax. Elytra with punctures loosely organized into rows. Metafemora mostly glabrous on ventral face (Fig. 12D). Elevation of mesoventrite forming a low transverse carina, not quite elevated to the same plane as the ventral surface of the mesocoxae (Fig. 9A). Metaventrite with distinct median ovoid glabrous area that is more than half of the total metaventrite length, and nearly as wide as it is long (Fig. 10A). Abdomen. Abdominal ventrites uniformly and densely pubescent (Fig. 13B). Aedeagus (Fig. 14H) with parametes narrow, slightly less than half as wide as the median lobe; generally straight and parallel sided along entire length; apex of parameres not expanded, slightly tapered to a blunt tip on the medial corner; apex of median lobe distinctly surpassing the apex of the parametes; gonopore situated just below the apex of the median lobe.

Etymology. Named after the condition of the eyes, in which a lateral canthus of the frons partially divides them into lower and upper surfaces.

Distribution. Known only from the type locality in Venezuela (Fig. 15).

Biology. This species was collected on a rock seepage along the margin of the Rio Coromoto (Fig. 18A–B). The seepage drains water from the surrounding area and is not fed directly by the creek itself. The rock surface had scattered leaves and detritus, as well as algae in some patches.

Tobochares emarginatus sp. n.

http://zoobank.org/A623B8AD-DEC7-4F2B-8DD4-9A49639AED02 Figs 6E–F, 14I, 15, 16C–D, F

Type material. Holotype (male): "SURINAME: Sipaliwini District/ N2°58.613', W55°24.683', 400m/ Camp 4 (high) Kasikasima/ leg. A. Short; main seepage area/ 24.iii.2012; SR12-0324-01C/ 2012 CI-RAP Survey", "[barcode]/ SEMC1088469/ KUNHM-ENT" (NZCS). **Paratypes (15): SURINAME: Sipaliwini:** Same data as type (11 exs., SEMC, NZCS; includes DNA vouchers SLE424, SLE482, and SLE483); Camp 1, Upper Palumeu, 11.iii.2012, leg. A. Short, around waterfall, SR12-0311-03A (1 ex., SEMC); Raleighvallen Nature Reserve, Voltzberg trail, 30.vii.2012, leg. Short & McIntosh, detrital pools along stream, SR12-0730-01B (2 exs., SEMC).

Differential diagnosis. The lack of impressed striae on the elytra, strongly emarginated eye (Fig. 6E–F), lack of spicules on the surface of the abdominal ventrites, and extremely broad glabrous patch on the metaventrite (e.g. Fig. 10A) all serve to easily separate this species from other *Tobochares* with the exception of *T. canthus*. It may be separated from *T. canthus* by the darker dorsal coloration and the shape of the aedeagus (Fig. 14I).

Description. Size and form: Body length 1.7-2.1 mm. Body elongate oval, moderately dorsoventrally compressed. Color and punctation. Dorsum of head brown, frons darker laterally and around eyes, anterolateral margins of clypeus with paler preocular patches (Fig. 6E–F); maxillary palps distinctly pale. Pronotum brown with the lateral margins paler; elytra brown, slightly paler at lateral margins and posteriorly. Meso- and metathoracic ventrites and abdominal ventrites brown to dark brown, with prosternum slightly paler; legs, labial palps, and antennae distinctly paler. Ground punctation on head, pronotum and elytra moderately fine. Head. Eyes measuring ~90µm anteroposteriorly, continuous with outline of head, emarginate at lateral margin, narrowing to about a fourth of the width (Fig. 6E-F). Thorax. Elytra with punctures loosely organized into rows. Metafemora mostly glabrous on ventral face. Elevation of mesoventrite forming a low transverse carina, not quite elevated to the same plane as the ventral surface of the mesocoxae. Metaventrite with distinct median ovoid glabrous area that is more than half of the total metaventrite length, and nearly as wide as it is long. *Abdomen.* Abdominal ventrites uniformly and densely pubescent. Aedeagus (Fig. 14I) with parameres moderately narrow, less than half as wide as the median lobe; straight and parallel sided in basal two-thirds, then bending inward and tapering on apical third; apex of parameres nearly flat, not expanded, tapered to a blunt tip on the medial corner; apex of median lobe slightly surpassing the apex of the parameres; gonopore situated just below the apex of the median lobe.

Etymology. Named after the condition of the eyes, in which a lateral canthus of the frons partially divides them into lower and upper surfaces.

Distribution. Known from several localities in central and southern Suriname (Fig. 15).

Biology. The majority of specimens were collected on a large granite seepage on Kasikasima (Fig. 16F), while one specimen was taken by floating clumps of leaves that were on wet rocks next to a large cascade (Fig. 16C–D) in a bucket of water. One specimen was taken from detrital pools along a stream.

Tobochares kasikasima Short, 2013

Figs 3C, 4E–F, 7B, 9D, 10D, 11B, 12A, 13A, 14E, 15, 16F, 17C–F

Tobochares kasikasima Short, 2013: 83.

Type material examined. Holotype (male): "SURINAME: Sipaliwini District/ N2°58.613', W55°24.683', 400m/ Camp 4 (high) Kasikasima/ leg. A. Short; main seepage area/ 24.iii.2012; SR12-0324-01C/ 2012 CI-RAP Survey", "[barcode]/ SEMC1088588/KUNHM-ENT" (NZCS). Additional material examined (59). SURINAME: Sipaliwini: Same data as type (1 ex., SEMC); Central Suriname Nature Reserve, near Kappel airstrip, leg. Short & Bloom, 24.viii.2013, seepage flowing into canal/ditch on S. side of airstrip, SR13-0824-02B (32 exs., SEMC, NZCS, includes DNA vouchers SLE1045, SLE1046); Same data but canal/ditch on S. side of airstrip, SR13-0824-02A (1 ex., SEMC); Central Suriname Nature Reserve, Tafelberg Summit, nr. Augustus Creek Camp, large seepage area, leg. Short & Bloom, 14.viii.2013, large seepage area, SR13-0814-03A (1 ex., SEMC); Central Suriname Nature Reserve, Tafelberg Summit, nr. Caiman Creek Camp, leg. Short & Bloom, 19.viii.2013, large seepage area, SR13-0819-01A (13 exs., SEMC, includes DNA vouchers SLE1048, SLE1049); same locality but leg. Short & Bloom, 20.viii.2013, washing seepage, SR13-0820-05A (11 exs., SEMC, including 2 specimens mounted on SEM stubs and DNA voucher SLE1050).

Differential diagnosis. The weakly impressed striae limited to the posterior third of the elytra (Fig. 11B), darkened apex of the maxillary palps (Fig. 7B), and overall darker body coloration serve to distinguish this species. The aedeagus of *T. kasikasima* (Fig. 14E) is also one of the most distinct within the genus, with its extremely long narrow parameres and broad, parallel sided basal median lobe. It is most similar to *T. sipaliwini* which has more extensive elytral grooves, pale maxillary palps, and an aedeagus of a much different form.

Description. Size and form. Body length 1.6-2.0 mm. Body elongate oval, moderately dorsoventrally compressed. Color and punctation. Dorsum of head very dark brown to black, anterolateral margins of clypeus with very faint paler preocular patches (Fig. 4E-F); maxillary palps distinctly pale, apex of maxillary palpomere 4 darkened (Fig. 7B). Pronotum very dark brown with the lateral margins paler; elytra very dark brown, slightly paler at lateral margins and posteriorly (Fig. 3C). Meso- and metathoracic ventrites and abdominal ventrites very dark brown (nearly black), with prosternum slightly paler; epipleura, legs, labial palps, and antennae distinctly paler, with antennal club slightly darker than proximal antennal segments. Ground punctation on head, pronotum and elytra moderately fine. Head. Eyes measuring ~100µm anteroposteriorly, continuous with outline of head, emarginate at lateral margin, narrowing to half the width (Fig. 4E-F). Thorax. Elytra with ten rows of serial punctures which are depressed into very shallow grooves in the posterior third, with depth of the grooves greatest near the elytral suture (Fig. 11B). Metafemora mostly glabrous on ventral face, with narrow band of pubescence along proximal half of anterior margin (Fig. 12A). Elevation of mesoventrite forming a transverse carina with a faint tooth, elevated to the same plane as the ventral surface of the mesocoxae (Fig. 9D). Metaventrite with distinct median ovoid glabrous area that is approximately half to slightly more than half of the total metaventrite length (Fig. 10D), and about half as wide as it is long. *Abdomen*. Abdominal ventrites uniformly and very densely pubescent, with small spicules interspersed amongst the setae. Aedeagus (Fig. 14E) with parametes thin and strap-like, about as wide as the median lobe in basal half, then gradually tapering in apical half, the apex less than half the width of the median lobe; apex of parameres blunt and rounded; apex of median lobe distinctly surpassing the apex of the parameres; median lobe with margins straight and parallel sided throughout, except at apex which is bluntly rounded; gonopore apparently absent (not observed in several examined specimens).

Distribution. The species was originally described from a single male from Mt. Kasikasima in south-central Suriname. It has subsequently been collected in longer series at several other localities in central and southern Suriname including from the summit of Tafelberg Tepui (Fig. 15).

Biology. The first specimen of this species was found in a seepage at the base of Kasikasima (Fig. 16F). This species has been collected in long series in seepages on the summit of Tafelberg Tepui, the only table mountain in Suriname (Fig. 17E–F); these records represent the highest known collecting event for any *Tobochares* species (c. 733 m). It was also collected on a seepage along the margin of Kappel Airstrip, which is near the base of Tafelberg (Fig. 17C–D). Both Tafelberg and Kappel Airstrip seepages were on sandstone and sedimentary rock and had an abundance of algal and moss growth.

Tobochares kusad sp. n.

http://zoobank.org/7A205A96-926F-4B27-9E4F-D0F45A3E52EF Figs 2D, 5A–B, 8A, 14A, 15, 17A–B

Type material. Holotype (male): "GUYANA: Region IX/ 2 48.531'N, 59 51.900'W, 170m/ Kusad Mts., Mokoro Creek/ main seepage area/ leg. Short, Isaacs, Salisbury/ 27.x.2013; GY13-1027-03B", "[barcode]/ SEMC1271353/ KUNHM-ENT" (CBDG). **Paratypes (29): GUYANA: Region IX:** Same data as type (4 exs., SEMC); same locality but leg. Short & Washington, 24.x.2013, GY13-1024-03C (13 exs., SEMC, CBDG, NZCS; includes DNA voucher SLE1021); same locality but "small rock pool with detritus", leg. Salisbury, 24.x.2013, GY13-1024-03A (12 exs., SEMC, CBDG).

Differential diagnosis. This species can be distinguished from most species by the impressed striae running the full length of the elytra and its overall dark brown coloration (Fig. 2D). It is most similar to *T. striatus* from which it can be separated by the apex of the last maxillary palpomere only slightly darkened (Fig. 8A) at the tip (more extensive darkening in *T. striatus*; Fig. 8B) and the eyes being slightly less emarginated laterally (compare Fig. 5B, D).

Description. *Size and form:* Body length 2.0–2.4 mm. Body elongate oval, moderately dorsoventrally compressed. *Color and punctation.* Dorsum of head very dark brown to black, anterolateral margins of clypeus with paler preocular patches (Fig. 5A–B); maxillary palps distinctly pale, with the apex of palpomere 4 slightly to significantly darker (Fig. 8A). Pronotum brown to dark brown with the lateral margins appearing slightly paler; elytra brown to very dark brown, slightly paler at lateral margins and posteriorly (Fig. 2D). Meso- and metathoracic ventrites and abdominal ventrites very dark brown (nearly black), with prosternum slightly paler; epipleura, legs, labial palps, and



Figure 5. Front and lateral view of heads of *Tobochares* spp. **A–B** *T. kusad* sp. n. **C–D** *T. striatus* **E–F** *T. sulcatus*.

antennae distinctly paler, with antennal club slightly darker than proximal antennal segments. Ground punctation on head, pronotum and elytra moderately fine. *Head.* Eyes measuring ~150 μ m anteroposteriorly, continuous with outline of head, emarginate at lateral margin, narrowing to roughly two thirds of the width (Fig. 5A–B). *Thorax.* Elytra with ten rows of serial punctures which are depressed into grooves



Figure 6. Front and lateral view of heads of *Tobochares* spp. A–B *T. pallidus* sp. n. C–D *T. canthus* sp. n. E–F *T. emarginatus* sp. n.

running the full length of the elytra. Metafemora mostly glabrous on ventral face, with narrow band of pubescence along proximal third of anterior margin. Elevation of mesoventrite forming a low transverse carina with a prominent "tooth," elevated to the same plane as the ventral surface of the mesocoxae. Metaventrite with distinct median ovoid glabrous area that is more than half of the total metaventrite length, and about



Figure 7. Ventral view of heads of *Tobochares* spp. A *T. sipaliwini* B *T. kasikasima* C *T. pallidus* sp. n. D *T. canthus* sp. n.

half as wide as it is long. *Abdomen.* Abdominal ventrites uniformly and very densely pubescent, with small spicules interspersed amongst the setae. Aedeagus (Fig. 14A) with parameres about as wide as median lobe basally, parallel sided in basal half, then gradually narrowing in apical third; apex of parameres weakly expanded and bluntly rounded. Median lobe gradually tapering to a bluntly rounded apex, which slightly extends beyond the apex of the parameres; gonopore situated distinctly below the apex of the median lobe.

Etymology. Named after Kusad Mountain in the South Rupununi region of Guyana, from where the species is known.

Distribution. Only known from the type locality in Guyana (Fig. 15).

Biology. The species was collected on a thin rock seepage flowing over granite that was associated with a small creek (Fig. 17A–B). The seepage was mostly covered with

dead leaves and detritus. Some specimens were also found in small pools in the rock that accumulated water from the seep as well as along the margins of the stream pool into which the seep flowed.

Tobochares pallidus sp. n.

http://zoobank.org/A4BC74D6-1D77-4EDE-82DF-E988FBA208F2 Figs 3B, 6A–B, 7C, 9C, 10C, 11D, 12C, 14F, 15, 18A–B, D–F

Type material. Holotype (male): "VENEZULEA: Amazonas State/ 5°23.207'N, 67°36.922'W, 125m/ Tobogan de la Selva; 8.viii.2008/ leg. A. Short, M. García, L. Joly/ AS-08-080b; old "tobogancito"/ on seepage area w/ detritus", "[barcode]/ SEMC0877702/ KUNHM-ENT" (MIZA). Paratypes (28): VENEZUELA: Amazonas: same data as type (10 exs., SEMC, MALUZ, MIZA); same locality but leg. M. Balke (1 ex., SEMC; DNA voucher SLE525); same locality but 23.ii.1986, leg. Spangler, sandy margin, Colln. #10 (1 ex., USNM); same locality but 18.i.1989, leg. Spangler, Faitoute, & Barr, upper seep (1 ex., USNM); nr. Hotel Nacamtur, 5°36'16.18"N, 67°34'56.24"W, 14.ix.2007, isolated rock seep w/ algae, leg. A. Short, AS-07-013x (1 ex., SEMC). Bolivar: Los Pijiguaos, 6°35.617'N, 66°49.238'W, 80 m, 16.ix.2007, leg. Short, García, & Joly, morichal/rock outcrop, AS-07-015 (5 exs., SEMC); same locality but 8.vii.2010, leg Short, Tellez, Arias, small stream on outcrop, VZ10-0708-01B (4 exs., SEMC; includes one ex. mounted on SEM stub); same locality but 9.vii.2010, leg. Short, Tellez, Arias, seeps and stream at night, VZ10-0709-03A (4 exs., SEMC); ca. 15 km NE Pijiguaos, 6°57.904'N, 66°36.392'W, 51 m, 9.vii.2010, leg. Short & Tellez, rock outcrop, detritus flotation, VZ10-0709-01B (1 ex., SEMC).

Differential diagnosis. This small species may be easily distinguished by the combination of its very pale dorsal coloration and lack of impressed elytral striae (Fig. 3B). The aedeagus is also unique among *Tobochares* for its outwardly bent parameres (Fig. 14F). Only *T. canaliculatus* is also nearly as pale, but the elytra of that species are deeply grooved. *Tobochares canthus* is not typically as pale as *T. pallidus*, and *T. canthus* can be further distinguished by its deeply emarginated eyes.

Description. *Size and form:* Body length 1.5–1.9 mm. Body elongate oval, moderately dorsoventrally compressed. *Color and punctation.* Dorsum of head very pale brown; maxillary palps pale (Fig. 7C). Pronotum very pale brown; elytra very pale brown and somewhat transparent. Meso- and metathoracic ventrites brown, and abdominal ventrites very dark brown (nearly black), with prosternum distinctly paler; epipleura, legs, labial palps, and antennae pale. Ground punctation on head, pronotum and elytra moderately fine. *Head.* Eyes measuring ~100µm anteroposteriorly, continuous with outline of head, emarginate at lateral margin, narrowing to roughly half the width (Fig. 6A–B). *Thorax.* Elytra with ten rows of serial punctures, not impressed into groves (Fig. 11D). Metafemora mostly glabrous on ventral face, with narrow band of pubescence along proximal third of anterior margin (Fig. 12C). Elevation of mesoventrite forming a low transverse carina, not quite elevated



Figure 8. Ventral view of heads of *Tobochares* spp. A *T. kusad* sp. n. B *T. striatus* C *T. sulcatus* D *T. canaliculatus* sp. n.

to the same plane as the ventral surface of the mesocoxae (Fig. 9C). Metaventrite with distinct median ovoid glabrous area that is half to slightly more than half of the total metaventrite length, and about half as wide as it is long (Fig. 10C). *Abdomen.* Abdominal ventrites uniformly and very densely pubescent, with small spicules interspersed amongst the setae (e.g. Fig. 13A). Aedeagus (Fig. 14F) with parameres relatively narrow, nearly half as narrow as the median lobe; parallel sided in a little more than basal half, then narrowing and bent outwards in apical third; apex of parameres bluntly rounded and about equal to the length of the median lobe; gonopore situated at the tip of the median lobe.

Etymology. Named for the species' relatively pale body coloration.

Distribution. Known from several localities along the northwestern shoulder of the Guiana Shield in Venezuela (Fig. 15).



Figure 9. Mesoventrite of *Tobochares* spp. A *T. canthus* sp. n. B *T. canaliculatus* sp. n. C *T. pallidus* sp. n. D *T. kasikasima* E *T. sipaliwini* F *T. striatus*.

Biology. All six collecting events of this species were from rock seepages. The type locality and longest series of specimens were collected on a rock seepage along the margin of the Rio Coromoto (Fig. 18A–B). The seepage drains water from the surrounding area and is not fed directly by the creek itself. The rock surface had scattered leaves and detritus, as well as algae in some patches. Other collections were on more isolated and seasonal seeps that are only flowing in the wet season (Fig. 18D).

Remarks. Because this species co-occurs with several other *Tobochares* in Venezuela, the extremely pale coloration makes specimens easily confused for teneral individuals of other species in the field until they can be examined under higher magnification.

Tobochares sipaliwini Short & Kadosoe, 2011 Figs. 2C, 4C–D, 7A, 9E, 10E, 11A, 12B, 14C, 15, 16A–B, E–F

Tobochares sipaliwini Short & Kadosoe, 2011: 85.

Type material examined. Holotype (male): "SURINAME: Sipaliwini District/ 2°10.973'N, 56°47.235'W, 210 m/ Camp 2, on Sipaliwini River/ leg. Short & Kadosoe; Inselberg/ 29–30. viii.2010; SR10-0829-01A/ 2010 CI-RAP Survey" (NZCS). **Paratypes (4): SURINAME: Sipaliwini District:** Same data as type (3 exs., SEMC,



Figure 10. Metaventrite of *Tobochares* spp. A *T. canthus* sp. n. B *T. canaliculatus* sp. n. C *T. pallidus* sp. n. D *T. kasikasima* E *T. sipaliwini* F *T. striatus.*

USNM, NZCS). Same camp but 31.viii.2010, sandy forest creek, SR10-0831-01B (1 ex., SEMC).

Additional material examined (120). SURINAME: Sipaliwini: Same data as type except 1.ix.2010, seep on inselberg, SR10-0901-01A (1 ex., SEMC; DNA voucher SLE1023); Raleighvallen Nature Reserve, plateau below Voltzberg, 28.vii.2012, leg. Short, Maier, & McIntosh, seep/wet rocks in shaded part of trail, SR12-0728-01J (1 ex., SEMC); same data but rock pool, SR12-0728-01F (1 ex., SEMC); Raleighvallen Nature Reserve, Voltzberg trail, 30.vii.2012, leg. Short & McIntosh, detrital pools along stream, SR12-0730-01B (6 exs., SEMC); same data but leg. Maier & Kadosoe, margin of stream, SR12-0730-01A (3 exs., SEMC; includes one specimen on SEM stub); Raleighvallen Nature Reserve, base of Voltzberg, 16.iii.2016, leg. A. Short, seepage on top of rock, SR16-0316-01C (38 exs., SEMC); same data but seepage spot on side of rock, SR16-0316-01A (45 exs., SEMC); same locality but 17.iii.2016, leg. Short & Girón, flotation of roots and debris from seepage, SR16-0317-01C (5 exs., SEMC); Camp 4 (high), Kasikasima, 24.iii.2012, leg. A. Short, main seepage area, SR12-0324-01C (9 exs., SEMC; includes DNA voucher SLE422); same data but "white rock seepage area on trail", SR12-0324-01B (2 exs., SEMC; DNA vouchers SLE478 and SLE497). GUYANA: Region IX: Kusad Mts., large seepage near basecamp, 24.x.2013, leg. Short & Washington, on wet rocks, GY13-1024-03C (6 exs., SEMC; includes DNA voucher SLE1020); Kusad Mts., nr. Basecamp, 24.x.2013, leg. Salisbury, small rock pool with detritus, GY13-1024-03A (3 exs., SEMC).



Figure 11. Elytra of *Tobochares* spp. A *T. sipaliwini* B *T. kasikasima* C *T. striatus* D *T. pallidus* sp. n. E *T. canaliculatus* sp. n. F *T. sulcatus*.

Differential diagnosis. This species can be distinguished from most other *Tobochares* by the elytral striae being impressed only on the posterior half (Fig. 11A), and its dark brown coloration (Fig. 2C). It is most similar to *T. kasikasima* from which it may be distinguished by the more extensive elytral striae (only in posterior third in *T. kasikasima*), the uniformly pale maxillary palps (Fig. 7A), and its differently shaped aedeagus (Fig. 14C).

Description. *Size and form:* Body length 1.7–2.1 mm. Body elongate oval, moderately dorsoventrally compressed. *Color and punctation.* Dorsum of head very dark brown to black, anterolateral margins of clypeus with paler preocular patches (Fig. 4C– D); maxillary palps distinctly pale (Fig. 7A). Pronotum very dark brown with the lateral margins paler; elytra very dark brown, slightly paler at lateral margins and posteriorly (Fig. 2C). Meso- and metathoracic ventrites and abdominal ventrites very dark brown



Figure 12. Metafemora (ventral view) of *Tobochares* spp. A *T. kasikasima* B *T. sipaliwini* C *T. pallidus* sp. n. D *T. canthus* sp. n. E *T. canaliculatus* sp. n. F *T. striatus*. Scale bars = 0.1 mm.

(nearly black), with prosternum slightly paler; epipleura, legs, labial palps, and antennae distinctly paler, with antennal club slightly darker than proximal antennal segments. Ground punctation on head, pronotum and elytra moderately fine. Head. Eyes measuring ~100µm anteroposteriorly, continuous with outline of head, emarginate at lateral margin, narrowing to about half to slightly greater than half the width. Thorax. Elytra with ten rows of serial punctures which are depressed into shallow grooves in the posterior half, with depth of the grooves greatest near the elytral suture (Fig. 11A). Metafemora mostly glabrous on ventral face, with narrow band of pubescence along proximal third of anterior margin (Fig. 12B). Elevation of mesoventrite forming a low transverse carina with an acute "tooth," elevated to the same plane as the ventral surface of the mesocoxae (Fig. 9E). Metaventrite with distinct median ovoid glabrous area that is more than half of the total metaventrite length, and about half as wide as it is long (Fig. 10E). Abdomen. Abdominal ventrites uniformly and very densely pubescent, with small spicules interspersed amongst the setae (e.g. Fig. 13A). Aedeagus (Fig. 14C) with parameres slightly wider than median lobe; parallel sided in basal half, then slightly narrowing in apical half to third; apex of parameres very slightly expanded and bluntly rounded. Median lobe



Figure 13. Abdominal ventrites of Tobochares spp. A T. kasikasima B T. canthus sp. n.

gradually tapering to a bluntly rounded apex, which slightly extends beyond the apex of the parameres; gonopore situated distinctly below the apex of the median lobe.

Distribution. Originally described from an inselberg on the Suriname-Guyana boarder, this species has now been found at other localities in both countries (Fig. 15).

Biology. The most frequently encountered species of the genus thus far in the eastern Guianas, *T. sipaliwini* has been found in a variety of seepage habitats, though most have been associated with more permanent flowing water (Fig. 16A–B, E–F). A few specimens have been taken along the margins of streams that were fed by or adjacent to rock seepages.

Tobochares striatus Short, 2013

Figs 2B, 5C–D, 8B, 9F, 10F, 11C, 12F, 14D, 15, 16F

Tobochares striatus Short, 2013: 83.

Type material examined. Holotype (male): "SURINAME: Sipaliwini District/ N2.24554°, W55.77000°, 800m/ Camp 2 Grensgebergte Rock/ leg. A. Short; rock



Figure 14. Aedeagi (ventral view) of *Tobochares* spp. A *T. kusad* sp. n. B *T. sulcatus* C *T. sipaliwini* D *T. striatus* E *T. kasikasima* F *T. pallidus* sp. n. G *T. canaliculatus* sp. n. H *T. canthus* sp. n. I *T. emarginatus* sp. n.

seepages/ 12.iii.2012; SR12-0312-01A/ 2012 CI-RAP Survey" (NZCS). **Paratypes** (11): SURINAME: Sipaliwini District: Same data as type (3 exs., SEMC, one mounted on SEM stub); Camp 1, Upper Palumeu, 10.iii.2012, leg. A. Short, small forest pool by boulders, SR12-0310-02A (1 ex.; SEMC); Camp 4 (Kasikasima), 24.iii.2012, leg. A. Short, main seepage area, SR12-0324-01C (7 exs., SEMC, NZCS).

Additional material examined (1). Camp 4 (Kasikasima), 24.iii.2012, leg. A. Short, main seepage area, SR12-0324-01C (1 ex., SEMC; DNA voucher SLE423).



Figure 15. Distribution of *Tobochares* spp.

Differential diagnosis. See differential diagnosis for T. kusad.

Description. Size and form: Body length 1.8-2.1 mm. Body elongate oval, moderately dorsoventrally compressed. Color and punctation. Dorsum of head very dark brown to black, anterolateral margins of clypeus with paler preocular patches (Fig. 5C–D); maxillary palps distinctly pale, with the distal half of palpomere 4 significantly darker. Pronotum brown to dark brown with the lateral margins appearing slightly paler (Fig. 8B); elytra brown to very dark brown, slightly paler at lateral margins and posteriorly (Fig. 2B). Meso- and metathoracic ventrites and abdominal ventrites very dark brown (nearly black), with prosternum slightly paler; epipleura, legs, labial palps, and antennae distinctly paler, with antennal club slightly darker than proximal antennal segments. Ground punctation on head, pronotum and elytra moderately fine. Head. Eyes measuring ~100µm anteroposteriorly, continuous with outline of head, emarginate at lateral margin, narrowing to half to slightly greater than half the width (Fig. 5C-D). Thorax. Elytra with ten rows of serial punctures which are depressed into grooves running the full length of the elytra (Fig. 11C). Metafemora mostly glabrous on ventral face, with narrow band of pubescence along proximal third of anterior margin (Fig. 12F). Elevation of mesoventrite forming a low transverse carina with an acute "tooth," elevated to the same plane as the ventral surface of the mesocoxae (Fig. 9F). Metaventrite with distinct median ovoid glabrous area that is more than half of the total metaventrite length, and about half as wide as it is long (Fig. 10F). Abdomen. Abdominal ventrites uniformly and very densely pubescent, with small spicules



Figure 16. Habitat of *Tobochares* spp. in Suriname. A–B Base of Voltzberg, collecting event SR16-0316-01C, habitat of *T. sipaliwini* C–D Waterfall in the upper Palumeu watershed, collecting event SR12-0311-03A, habitat of *T. emarginatus* sp. n. E Base of Voltzberg, collecting event SR16-0316-01A, habitat of *T. sipaliwini* F Kasikasima, collecting event SR16-0324-01C, habitat of *T. sipaliwini*, *T. kasikasima*, *T. striatus*, and *T. emarginatus* sp. n. Red arrows point to example microhabitats where specimens were collected

interspersed amongst the setae (e.g. Fig. 13A). Aedeagus (Fig. 14D) with parameres slightly wider than median lobe; weakly parallel sided in basal third, then bulging slightly in middle third before tapering in apical third; apex of parameres very slightly

expanded and bluntly rounded. Median lobe gradually tapering to a bluntly rounded apex, which slightly extends beyond the apex of the parameres; gonopore situated distinctly below the apex of the median lobe.

Distribution. Known only from two localities in south-central Suriname (Fig. 15).

Biology. Short (2013) noted that "most specimens were collected on a flowing seepage on granite (Fig. 16F). A single specimen was collected in a small forest pool near Camp 1 on the upper Palameu River, although this pool was situated directly beneath a group of large granite boulders.

Tobochares sulcatus Short & García, 2007

Figs 2A, 5E–F, 8C, 11F, 14B, 15, 18A–B

Tobochares sulcatus Short & García, 2007: 4.

Material examined (100). VENEZUELA: Amazonas: Tobogan de la Selva, 14.i.2009, leg. Short, García, Miller & Joly, wet rock covered with detritus, VZ09-0114-01F (50 exs., SEMC, MIZA, MALUZ; includes DNA vouchers SLE0035, SLE1027); same locality but 14.i.2009, leg. Short & Miller, partly shaded wet rock with algae, VZ09-0114-01G (2 exs., SEMC); same locality but 5.i.2006, leg. Short, wet rock with leaves, AS-06-011e (2 exs., SEMC includes DNA voucher SLE1037); same locality but 5.i.2006, leg. Short, pools in rock with sand, AS-06-011c (12 exs., SEMC); same locality but 16.xi.1987, leg. Spangler & Faitoute, Colln. #7 (1 ex., USNM); same locality but 26.i.1989, leg. Spangler, Faitoute, & Barr, seep at upper shelter (21, USNM); ca. 15 km S. Puerto Ayacucho, 13.ix.2007, leg. Short, AS-07-009a (3 exs., SEMC); nr. Iboruwa, "Tobogancito", 13.i.2009, leg. Short et al., VZ09-0113-02X (1 ex., SEMC); nr. Hotel Nacamtur, 14.ix.2007, leg. Short, isolated rock seep with algae, AS-07-013x (1 ex., SEMC). Bolivar: Los Pijiguaos, seeps and stream on outcrop at night, 9.vii.2010, leg. Short et al., VZ10-0709-03A (2 exs., SEMC; includes one specimen on SEM stub and DNA voucher SLE1035); ca. 15 km N. Los Pijiguaos, 17.ix.2007, leg. Short & García, outcrop seepage, AS-07-016 (4 exs., SEMC); ca. 25 km E El Burro, 13.i.2009, leg. Short et al., rocky morichal, VZ09-0113-01X (1 ex., SEMC).

Differential diagnosis. The dark brown coloration and deep elytral grooves, which are impressed along their entire length (Fig. 2A), separate this species from most other *Tobochares*, including *T. canaliculatus*, which also has deep grooves but is much paler and has a differently shaped aedeagus. Other congeners with impressed elytral grooves either have them only impressed on the posterior half of the elytra (e.g. *T. kasikasima*) or have very large serial punctures in those grooves (e.g. *T. striatus*, *T. kusad*), while the serial punctures themselves are minute to almost appearing absent in *T. sulcatus* (Fig. 11F).

Description. *Size and form*: Body length 1.8–2.2 mm. Body elongate oval, moderately dorsoventrally compressed. *Color and punctation*. Dorsum of head very dark brown to black, anterolateral margins of clypeus with paler preocular patches (Fig. 5E–F);



Figure 17. Habitat of *Tobochares* spp. in Guyana and Suriname. **A–B** Guyana, Kusad Mt., collecting event GY13-1027-03B, type locality for *T. kusad* sp. n. **C–D** Suriname, side of Kappel Airstrip, collecting event SR13-0824-02B, habitat of *T. kasikasima* **E–F** Suriname, summit of Tafelberg, Caiman Creek seepage, collecting event SR13-0819-01A, habitat of *T. kasikasima*. Red arrows point to example microhabitats where specimens were collected.

maxillary palps distinctly pale, with the apex of palpomere 4 darker (Fig. 8C). Pronotum brown to very dark brown with the lateral margins appearing slightly paler; elytra brown to very dark brown, slightly paler at lateral margins and posteriorly.



Figure 18. Habitat of *Tobochares* spp. in Venezuela. **A–B** Tobogan de la Selva, upstream, collecting event AS-08-080b, type locality for *T. canaliculatus* sp. n., *T. sulcatus, T. canthus* sp. n., and *T. pallidus* sp. n. **C** Tobogan de la Selva, collecting event VZ09-0114-01D **D** Outcrop near Pijiguaos, collecting event VZ10-0708-01B, habitat of *T. pallidus* sp. n. **E–F** Rock outcrop near Pijiguaos, collecting event VZ10-0709-01B, habitat of *T. pallidus* sp. n. Red arrows point to example microhabitats where specimens were collected.

Meso- and metathoracic ventrites and abdominal ventrites very dark brown (nearly black), with prosternum slightly paler; epipleura, legs, labial palps, and antennae distinctly paler, with antennal club slightly darker than proximal antennal segments. Ground punctation on head, pronotum and elytra moderately fine. Head. Eyes measuring $-100\mu m$ anteroposteriorly, continuous with outline of head, emarginate at lateral margin, narrowing to half to slightly more than half the width (Fig. 5E-F). Thorax. Elytra with ten rows of serial punctures which are depressed into deep, smooth grooves running the full length of the elytra. Metafemora mostly glabrous on ventral face, with narrow band of pubescence along proximal third of anterior margin. Elevation of mesoventrite forming a low transverse carina, not quite elevated to the same plane as the ventral surface of the mesocoxae. Metaventrite with distinct median ovoid glabrous area that is more than half of the total metaventrite length, and about half as wide as it is long. *Abdomen*. Abdominal ventrites uniformly and very densely pubescent, with small spicules interspersed amongst the setae (e.g. Fig. 13A). Aedeagus (Fig. 14B) with parametes about as wide as median lobe basally, parallel sided in basal half, then strongly narrowing in apical third; apex of parameres then broadly expanded and bluntly rounded. Median lobe gradually tapering to a bluntly rounded apex, which slightly extends beyond the apex of the parameres; gonopore situated distinctly below the apex of the median lobe.

Distribution. Known from a series of localities along the northwestern edge of the Guiana Shield in Venezuela (Fig. 15), though the vast majority of material has been collected at Tobogan de la Selva.

Biology. *Tobochares sulcatus* occurs on wet rocks with fallen leaves and other detritus along stream corridors (Fig. 18A–B). A handful of specimens have been collected from more isolated seepages, but these seem incidental compared to the long series—some in the hundreds—that have been found at the type locality Tobogan de la Selva. See Short and García (2007) for additional habitat details and images.

Tobochares sp. A

Material examined (1). VENEZUELA: Amazonas: Tobogan de la Selva, leg. M. Balke (1 female, SEMC; DNA voucher SLE526).

Differential diagnosis. This species is morphologically very similar to *T. pallidus*, and shares most diagnostic features of that species (in particular its very pale coloration). This species can be separated from *T. pallidus* by the faint but distinctly impressed striae in the posterior quarter of the elytra, and the slightly less emarginated eyes.

Remarks. This species is only known from a single specimen, which we also extracted for DNA. Molecular data also supports this taxon as sister to *T. pallidus*, to which it is also similar morphologically. We refrain from describing the species until additional specimens, including ideally a male, can be found.

Key to the species of *Tobochares* Short & García

1	Elytra with impressed grooves along their entire length (e.g. Figs 11C, E, F) 2
_	Elytra with impressed grooves in posterior half or less, or with grooves absent
	(e.g. Fig. 11A, B, D)5
2	Apical maxillary palpomere uniformly pale (Fig. 8D). Pronotum and elytra
	light brown to brown, head brown, clypeus with large, distinctly pale preocu-
	lar patches (Fig. 4A) (Venezuela)canaliculatus sp. n.
_	Apical maxillary palpomere darkened at least at apex, and sometimes on distal
	half or more (Fig. 8A-C). Pronotum and elytra brown to dark brown, head
	dark brown to black, clypeus with small, pale preocular patches
3	Punctures within elytral grooves small, grooves appearing fairly smooth
	(Fig. 11F). Elevation of mesoventrite forming transverse carina without
	tooth, not elevated to same plane as the ventral surface of the mesocoxae
	(Venezuela)
_	Punctures within elytral grooves strongly impressed and distinct (Fig. 11C).
	Elevation of mesoventrite forming transverse carina with tooth, elevated to
	same plane as the ventral surface of the mesocoxae
4	Apical maxillary palpomere with apex ranging from slightly to distinctly
	darkened (Fig. 8A). Eyes emarginate at lateral margin, narrowing to roughly
	two thirds the width (Fig. 5A–B) (Guyana)kusad sp. n.
_	Apical maxillary palpomere darkened in at least distal half (Fig. 8B). Eyes
	emarginate at lateral margin, narrowing to slightly greater than half the width
	(Fig. 5C–D) (Suriname)
5	Elytra with grooves on posterior third or posterior half, grooves most promi-
	nent near elytral suture (e.g. Fig. 11A, B). Dorsum of head very dark brown
	to black, clypeus with faintly pale preocular patches (Fig. 4C, E). Elevation
	of mesoventrite forming trasverse carina with tooth, elevated to same plane as
	the ventral surface of the mesocoxae (Fig. 9D–E)
_	Elvtra without grooves or with weak grooves on posterior quarter (e.g.
	Fig. 11D). Dorsum of head uniformly pale, or brown with distinctly pale
	preocular patches on clypeus (e.g. Fig. 6A, C, E). Elevation of mesoventrite
	forming low transverse carina without tooth, not elevated to same plane as
	the ventral surface of the mesocoxae (Fig. 9A, C)7
6	Elvtra with grooves on posterior half (Fig. 11A). Apical maxillary palpomere
	uniformly pale (Fig. 7A) (Guvana, Suriname) <i>sipaliwini</i> Short & Kadosoe
_	Elvtra with grooves on posterior third (Fig. 11B). Apical maxillary palpomere
	with apex darkened (Fig. 7B) (Suriname)kasikasima Short
7	Dorsum of head, pronotum, and elvtra uniformly pale (Fig. 3B); clypeus
	without pale preocular patches. Eves emarginate at lateral margin, narrowing
	to about half of the width or slightly less (Fig. 6A–B) (Venezuela)
_	Dorsum of head, pronotum, and elytra brown to dark brown (e.g. Fig. 2C):
	clypeus with pale preocular patches. Eves emarginate at lateral margin, nar-
	rowing to about a quarter of the width (Fig. 4C–F)9
8	Elytra without grooves (Fig. 11D). Eyes emarginate at lateral margin, nar-
---	--
	rowing to about half of the width (Fig. 6A–B) pallidus sp. n.
_	Elytra with weak grooves on posterior quarter. Eyes emarginate at lateral mar-
	gin, narrowing to slightly less than half of the width sp. A
9	Aedeagus (Fig. 14H) with outer margin of parameres straight. Dorsal colora-
	tion light brown (Venezuela)
	Aedeagus (Fig. 14I) with outer margin of parameres convex, tapering in an-
	terior third. Dorsal coloration medium to dark brown (Suriname)
	emarginatus sp. n.

Discussion

The water beetle seepage fauna of the Guiana Shield was essentially completely undescribed little more than 15 years ago. Since that time, numerous new lineages have been discovered in a variety of families, including Dytiscidae (e.g. *Fontidessus*), Noteridae (*Tonerus* Miller, 2009), and Hydroscaphidae (*Confossa* Short et al. 2015). In terms of Hydrophilidae, next to *Oocyclus*, species of *Tobochares* appear to be the dominant taxa in this habitat across the region.

Most sampled localities had only a single, or occasionally two species of *Tobochares* co-occurring in the same habitat. However, two particular sites had exceptional diversity with five and four species respectively: Tobogan de la Selva in Venezuela, and Mt. Kasikasima in Suriname. As there was no species composition overlap between them, a remarkable nine of the ten species covered in this revision could be collected by visiting just these two places.

Given how relatively little of the Guiana Shield has been surveyed, especially for hygropetric taxa, it is almost a certainty many more *Tobochares* species are left to be described.

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