

The melectine bee genera *Brachymelecta* and *Sinomelecta* (Hymenoptera, Apidae)

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Abstract

The enigmatic, cleptoparasitic bee genera *Brachymelecta* Linsley and *Sinomelecta* Baker (Apinae: Melectini) are redescribed, each represented by a single species which has not been reencountered since capture of the type series ca. 1878 and 1900, respectively. Both genera are the only melectines to possess two submarginal cells in the forewing but are otherwise wholly dissimilar. *Brachymelecta mucida* (Cresson), a species known only from the male holotype collected in “Nevada”, is newly described and figured, including the first account of the hidden sterna and genitalia. *Sinomelecta oreina* Baker is similarly described and figured based on the holotype male and paratype female, apparently collected from the eastern Tibetan Plateau. Both genera are valid and from the available data do not appear to represent merely autapomorphic forms of *Melecta* Latreille. Indeed, the terminalia of *S. oreina* are in some respects more similar to those of species of *Thyreus* Panzer.

Keywords

Apoidea, Anthophila, Apinae, Melectini, Nevada, China, taxonomy, morphology

Introduction

The objective of this paper is to fully describe two genera of the anthophorine tribe Melectini. Each is known from only one or two specimens collected over a century ago and preserved without adequate locality data. One or both may now be extinct.

The two genera do not appear to be close relatives, although they share a striking common character: both have only two submarginal cells in the forewing although all other Melectini have three. The genera involved are *Brachymelecta* Linsley and *Sinomelecta* Baker; each is discussed and described below. Since each genus contains only a single species, the descriptions combine specific characters with probable generic characters, i.e., characters that differentiate other genera of Melectini. A very unusual feature of *Sinomelecta* is that the male, like the female, has 12 antennomeres. In nearly all bees males have 13 antennomeres. There is no reason to believe that *Brachymelecta* shares this character but since the antennae of the sole specimen of that genus are broken, new material will be necessary if the antennomeres of that taxon are to be counted.

Given the rarity of this material, the few references to them in the literature, and thereby their general unfamiliarity to many, it is worthwhile to summarize the historical details for each genus. The only known specimen of *Brachymelecta* is preserved in the Academy of Natural Sciences of Philadelphia. Described in 1879 as “*Melecta? mucida*”, its source was given as “Nevada (Morrison)” (Cresson 1879a) although the label on the specimen is merely “Nev.” (Fig. 1). The label (“Nev.”) on the specimen is exactly like labels on other Hymenoptera described by Cresson that do occur in Nevada and adjacent states. Of course an error in labeling is possible but there is no evidence of such an error. Cresson described various Hymenoptera collected by Morrison, sometimes given as H.K. Morrison [Herbert Knowles Morrison (1854–1885)], mostly from the western United States but some from the southeast (Georgia). In spite of extensive collecting in the western United States by persons interested in bees, no other specimens have been obtained. *Brachymelecta* might be extinct, or may exist in or near Nevada, less likely elsewhere. If not extinct, it is presumably exceedingly rare. Like other Melectini, it would be a cleptoparasite in nests of other bees. The only equally small North American melectine is *Zacosmia* Ashmead which also occurs in the western United States and is a cleptoparasite of *Anthophora* (*Heliophila*).

The two known specimens of *Sinomelecta*, one of each sex, were in the collection of Donald B. Baker (1922–2004) for many years and are today preserved in the Division of Entomology of the University of Kansas Natural History Museum. They were described by Baker as *Sinomelecta oreina* in 1997 (Baker 1997). These specimens were found by Baker in a mixed batch of “dealer material” probably collected near the “turn of the century”, i.e., about 1900. With other insects of various orders, they stood above a penciled label “Sungpan” or “Songpan”. After discussing the probable meaning of this label and noting that there is no certainty that all the insects came from the same locality, Baker (1997) summarized by indicating the probability “that the *Sinomelecta* came from a montane locality on the eastern fringe of the Tibetan plateau. The general locality would approximate to the Ta-hsueh Shan and Chiunghsia Shan of the *Times Atlas*.” That additional specimens have not been taken, so far as we know, may merely reflect the scarcity of bee collectors in this region.

Material and methods

The material discussed herein consists of the unique type material for *B. mucida*, housed in the Department of Entomology, Academy of Natural Sciences, Philadelphia (ANSP), while the holotype male and paratype female of *S. oreina* are in the Division of Entomology, University of Kansas Natural History Museum, Lawrence (SEMC). Through the kindness of Jason Weitraub (ANSP) we were permitted to dissect the metasomal apex of the *B. mucida* holotype and to clean the genitalia for imaging. Despite being over 134 years old (by comparison to the merely 112+ year old genitalia of *S. oreina*), the genital capsule and hidden sterna were easily removed from between TVII and SVI and after a gentle bath in a weak potassium hydroxide solution, most of the surrounding connective tissue proved no challenge to detach from the sclerites. The terminalia of *S. oreina* had been dissected and partially cleaned by the late Donald B. Baker at some point prior to his published account of the species (Baker 1997). Given the uniqueness of the material we did not subject it to further preparation and cleaning. Photomicrography was undertaken with a Nikon D1x digital camera attached to an Infinity K-2 long-distance microscope lens. Measurements were made with an ocular micrometer on an Olympus SZX-12 stereomicroscope. The following abbreviations are used in the descriptions: F, flagellomere; S, metasomal sternum; T, metasomal tergum. Morphological terminology generally follows that of Engel (2001) and Michener (2007). Given that each genus is monobasic we have composed generic diagnoses from those characters which elsewhere serve to differentiate genera in the tribe.

Systematics

Genus *Brachymelecta* Linsley

<http://species-id.net/wiki/Brachymelecta>

Brachymelecta Linsley, 1939: 458. Type species: *Melecta mucida* Cresson, 1879a, by original designation. Michener 1944: 287; Michener 2000: 748, 750; Michener 2007: 771, 773.

Diagnosis (male). Antenna with F1 over 1.5 times as long as F2. Mesoscutellum with subhorizontal dorsal surface about twice as long as vertical surface; dorsal and posterior surfaces divided by longitudinal depression resulting in bilobed form, posterior dorsal part of each lobe forming narrowly rounded, obtuse angle projecting posteriorly. Arolia present. Forewing with two submarginal cells (i.e., 1rs-m absent). Metasomal T1 to T4 densely covered with pale brown, appressed, plumose setae; T1 with midlength of horizontal surface subequal to that of vertical (anterior) surface and considerably shorter than midlength of exposed part of T2.

***Brachymelecta mucida* (Cresson)**

http://species-id.net/wiki/Brachymelecta_mucida

Figs 1–10

Melecta? *mucida* Cresson, 1879a: 205 [♂]. Cresson 1887: 298 [checklist]; Fox 1893:

143 [♂, key]; Cresson 1916: 125 [type catalog, note on broken antennae].

[*Melecta?*] *mucida* Cresson; Cresson 1879b: 218 [checklist].

Melecta mucida Cresson; Dalla Torre 1896: 317 [checklist].

Brachymelecta mucida (Cresson); Linsley 1939: 459 [♂].

Brachymelecta mucida (Cresson); Hurd 1953: 37 [♂, note].

Holotype. ♂ (Fig. 1), labeled “Nev. [presumed abbreviation for Nevada, USA]” // “*Melecta? mucida*, 2 sub cells, Cr” // “Holotype 2294 [red label]” (Fig. 1); deposited in the Department of Entomology, Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.

Diagnosis. As for the genus (*vide supra*).

Description. *Male (holotype):* Body length 9 mm, forewing length 8 mm. Head width 2.7 mm; head length (lower margin of clypeus to vertex in facial view) 2.1 mm. Intertegular distance 2.0 mm; distance between outer margins of tegulae 3.0 mm.

Clypeus strongly protuberant, in lateral view extending anteriorly about compound eye width in front of lower compound eye margin; lower margin straight, middle third slightly depressed. Mandible with distal half almost parallel sided, less than half as wide as base; apex bidentate, upper tooth slightly smaller and shorter than lower tooth; basal tooth not evident but mandibles closed and not fully exposed. Malar space very short, base of mandible closely approaching compound eye. Labrum not fully exposed but apparently about as long as broad. Inner orbits converging below (Fig. 3); vertex rather strongly and uniformly convex (Fig. 3). Gena broadest at upper third, not as broad as compound eye; preoccipital ridge sharply angulate; median ocellus with transverse diameter (= ocellar diameter) greater than that of lateral ocellus, ocellular distance approximately equal to interocellar distance, ocelloccipital distance less than twice ocellar diameter, distance between lateral and median ocelli equal to diameter of lateral ocellus. Antenna with scape scarcely over twice as long as maximum width which is scarcely greater than width of flagellum (based on first four flagellomeres only); pedicel exposed as narrow ring about four times as broad as long; F1 over 1.5 times as long as F2; F2, 3, and 4 subequal, each broader than long, F2 and F3 together longer than F1 (Fig. 3) (antennae broken so that F5 and beyond cannot be described; breakage occurred long ago as indicated by Cresson 1916: 125). Mesoscutellum with subhorizontal dorsal surface about twice as long as vertical surface; dorsal and posterior surfaces divided by longitudinal depression resulting in bilobed form, posterior dorsal part of each lobe forming narrowly rounded, obtuse angle projecting posteriorly; angle between posterior and dorsal surfaces approximately orthogonal but not formed by carina; posterior surface not overhanging metanotum; lower margin of mesoscutellum above metanotum marked by strong transverse carina. Metatibia

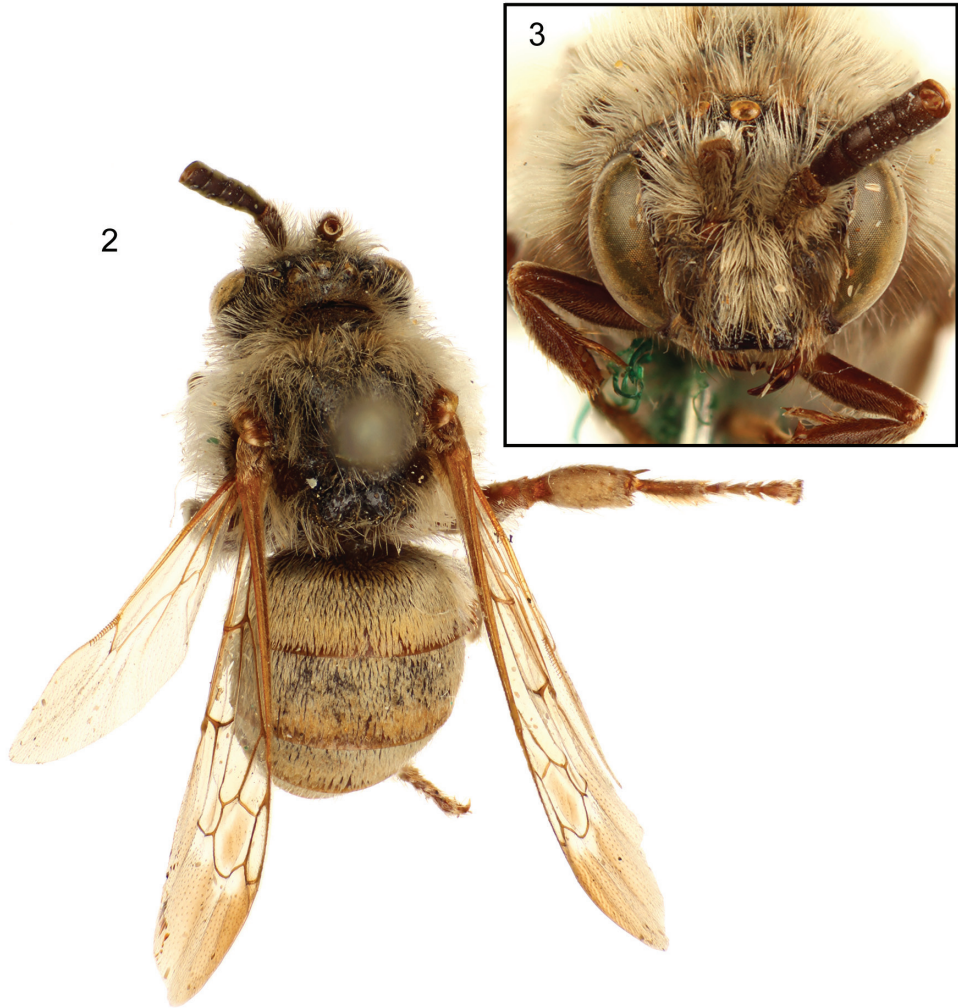


*Brachymelecta
mucida* (Cresson)

Figure 1. Lateral habitus of male holotype of *Brachymelecta mucida* (Cresson) (ANSP Type No. 2294); inset depicts the three original labels associated with the specimen.

with outer surface coarsely nodulose; outer apical margins of tibiae protuberant but without conspicuous spines; mesotibial spur and outer metatibial spur about as long as tibial diameter; inner metatibial spur longer than tibial diameter; arolia well developed; pretarsal claws cleft, outer ramus slender, sharply pointed, inner ramus flattened, expanded, much shorter than outer ramus, apex approximately right angular [much as in *Xeromelecta* (*Melectomorpha*) *californica* (Cresson): *vide* Michener 2007: fig 117d]. Forewing with surface beyond venation strongly papillate (Fig. 4); basal vein strongly basad cu-a; submarginal cells two because of loss of 1rs-m; other aspects of wing venation shown in figures 4 and 5. Metasomal T1 with midlength of horizontal surface subequal to that of vertical (anterior) surface and considerably shorter than midlength of exposed part of T2; posterior margins of sterna straight, transverse, to gently concave on more posterior sterna to S5; S1 with midbasal tubercle, not carinate; S7, S8, and genitalia illustrated in Figures 6–10.

Because of rather dense vestiture, surface in some areas seen only locally; following might change considerably if setae removed from certain areas: Clypeus coarsely and



Figures 2–3. Dorsal (2) and facial (3) views of male holotype of *Brachymelecta mucida* (Cresson) (ANSP Type No. 2294).

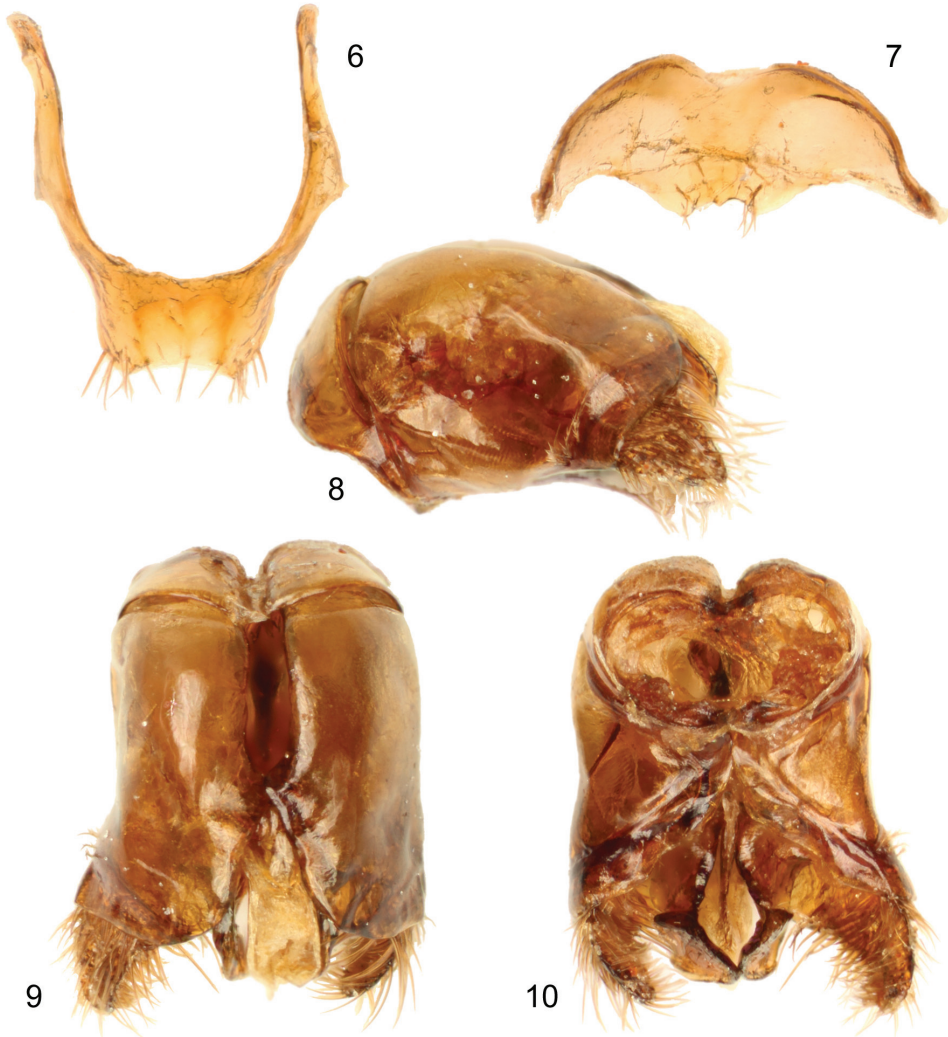
closely punctate medially, anterior margin with even larger and irregular punctures; most of remainder of head with dense coarse punctures with irregular smooth shiny areas between some punctures; lower half of frons, adjacent parts of paraocular area, and supra-clypeal area dull with dense small punctures. Mesosoma largely coarsely punctate with punctures similar to those of center of clypeus but with more shiny ground between punctures which often separated by one-half puncture width although close in other areas; median part of mesoscutellum and especially mesoscutellar lobes with punctures even larger, leaving only a network of ridges; metanotum and propodeal triangle with punctures smaller, as close as they can be, on lateral part of triangle forming series of transverse (vertical) irregular striae. Metasomal punctures minute, mostly separated by several punc-



Figures 4–5. Forewing (4) and hind wing (5) of male holotype of *Brachymelecta mucida* (Cresson) (ANSP Type No. 2294).

ture diameters, surface between punctures largely lineolate, especially on sterna where large areas lack punctures almost completely; posterior margins of terga smooth.

Setae of head and mesosoma rather abundant, mostly two to three ocellar diameters in length, grayish white (cinereous) with brownish tints on lower parts of gena, blackish on axilla, largely white on sides of mesosoma and center of face; antennal scape and coxae with similar grayish white setae, mostly one ocellar diameter in length. Antennal pedicel with dense very short setae; flagellum asetose; legs beyond coxae largely with short, yellowish white setae, dense and yellow on under sides of tarsi; profemur with strong fringe of white setae two or more ocellar diameters in length on posterior surface; similar fringe of much shorter and less conspicuous white setae on mesofemur; outer surface of mesotibia except near base densely covered with white setae that obscure surface; protibia with similar white setae, less dense, and absent on both base and apex. Metasomal T1 to T4 densely covered with pale brown, appressed, plumose setae, except posterior margins smooth and bare, these margins narrow on T1 to T3, broader especially medially on T4; T5 and T6 with exposed parts like margins of more anterior terga but T6 with some pale brown plumose setae basally; T1 to T4 with a few long simple setae laterally, very few on T1, number increasing and more dorsal from T2 to T4; S1 to S3 with few long pale setae, large median areas on S2 and S3 asetose; S4 and S5 with fringes of long pale brown setae.



Figures 6–10. Male terminalia of holotype of *Brachymelecta mucida* (Cresson) (ANSP Type No. 2294). **6** Seventh metasomal sternum **7** Eighth metasomal sternum **8** Genital capsule, lateral view **9** Genital capsule, dorsal view **10** Genital capsule, ventral view.

Integumental coloration black, legs and middle third of mandible dark reddish brown except tibial spurs black; metasomal sterna and posterior margins of terga dark brown; under side of antenna brownish black; tegula translucent brownish black. Wings transparent, shaded with dusky brown beyond venation of forewing, darkest near costal margin distal to marginal cell (Fig. 1), weakly darkened within distal cells; veins dusky brown, pterostigma light brown.

Female: Unknown.

Comments. Cresson (1879a) records the specimen as from “Nevada, (Morrison)” (p. 205) even though the preserved label provides only “Nev.” (Fig. 1), presumably

an abbreviation for Nevada. The specific epithet also appears in a checklist of North American Apidae as, “? *mucida* Cress. *ibid.* 205, ♂. Nevada.” (Cresson 1879b). As noted above, Cresson described various Hymenoptera collected by H.K. Morrison in Colorado, Georgia, Nevada, and elsewhere. Many of these are well known North American species. According to Mann (1885) Morrison is known to have collected in Nevada in 1878 and sold his collections back east.

Genus *Sinomelecta* Baker

<http://species-id.net/wiki/Sinomelecta>

Sinomelecta Baker, 1997: 245. Type species: *Sinomelecta oreina* Baker, 1997, by original designation. Michener 2000: 748, 751; Rightmyer and Engel 2003: 3, 6; Michener 2007: 771, 774.

Diagnosis. Antenna with 12 antennomeres in both sexes; F1 nearly twice as long as apical width and about twice as long as F2. Body without patches of appressed, white setae. Mesoscutellum with subhorizontal dorsal surface about twice as long as subvertical surface, both surfaces divided by weak longitudinal median depression so that mesoscutellum is weakly biconvex, each convexity emphasized by small posteriorly directed sublateral projection that almost overhangs metanotum. Arolia present but small. Forewing with two submarginal cells (i.e., 1rs-m absent). Metasomal T1 with long cinereous setae laterally; T2 to T5 with similar setae, some of them brownish, at extreme sides; T2 to T4 with subapical bands of white setae (broken medially on T2); T1 with midlength of horizontal surface about half as long as declivitous anterior surface and about half as long as midlength of exposed part of T2.

Sinomelecta oreina Baker

http://species-id.net/wiki/Sinomelecta_oreina

Figs 11–23

Sinomelecta oreina Baker, 1997: 246 [♂♀].

Holotype. ♂ (Figs 11–12), labeled “China: Szechuan, Ta-hsuëh Shan or Chiunghsia Shan” // “Holotype ♂, *Sinomelecta oreina*, D.B. Baker 1993 [actual publication date was 1997] [red label]”; deposited in the Division of Entomology, University of Kansas Natural History Museum, Lawrence, Kansas, USA.

Paratype. 1♀ (Figs 22–23), with same labels as holotype except second label blue and reading “Paratype ♀, *Sinomelecta oreina*, D.B. Baker 1993 [actual publication date was 1997] [blue label]”; deposited in the Division of Entomology, University of Kansas Natural History Museum, Lawrence, Kansas, USA.

Diagnosis. As for the genus (*vide supra*).



Figures 11–12. Lateral (**11**) and dorsal (**12**) habitus images of holotype male of *Sinomelecta oreina* Baker (SEMC Type No. 9280).

Description. *Male (holotype):* Body length 11.5 mm (apex of metasoma damaged, as noted by Baker 1997, and dissected, so that body length measurement is not exact), forewing length 10 mm. Head narrower than thorax, head width 3.15 mm, head length (lower margin of clypeus to vertex in facial view) 2.75 mm. Intertegular distance 3.0 mm, distance between outer margins of tegulae 4.0 mm.

Clypeus strongly protuberant, in lateral view extending anteriorly more than compound eye width on front of compound eye margin; lower margin of clypeus straight, mandibles closed and difficult to see, but distal half narrow, tapering to narrowly rounded apex, no teeth visible. Malar space very short, base of mandible separated



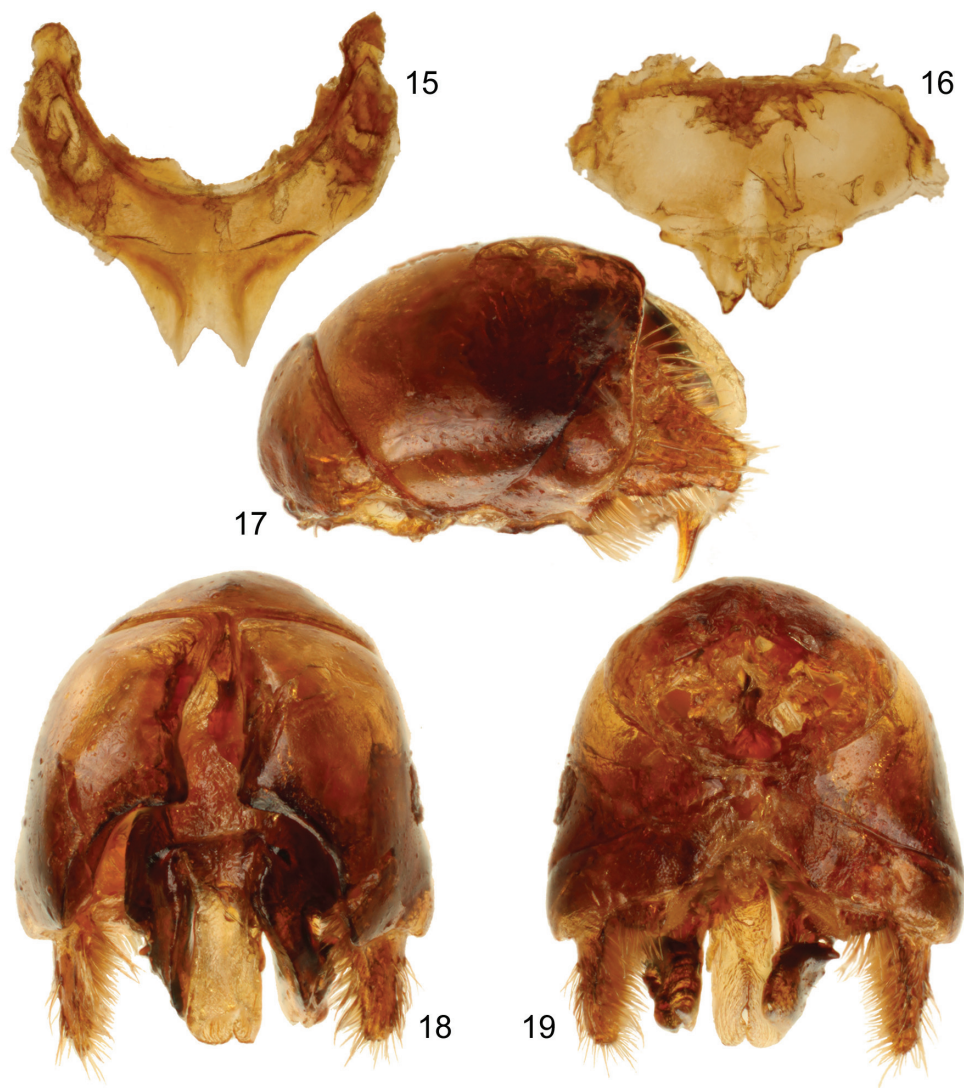
Figures 13–14. Forewing (13) and hind wing (14) of holotype male of *Sinomelecta oreina* Baker (SEMC Type No. 9280).

from compound eye by about one-fourth of distal diameter of F1. Labrum broader than long. Inner orbits weakly concave, slightly converging below (Fig. 20), vertex strongly convex as seen in facial view (Fig. 20); gena broadest near lower end, broader than compound eye in lateral view; preoccipital ridge rounded; ocelli about equal in diameter; ocellocular distance more than twice interocellar distance which is less than ocellar diameter; ocellocapital distance about three ocellar diameters but indefinite because of rounding onto occiput. Distance between lateral and middle ocelli about two-thirds of ocellar diameter. Antenna with 12 antennomeres; scape (without basal bulb) nearly three times as long as its maximum width which is slightly less than apical width of F1; pedicel small, exposed part about three times as wide as long; F1 nearly twice as long as apical width and about twice as long as F2; F2 to F9 broader than long, F10 scarcely longer than F9, scarcely longer than broad, apex broadly rounded; flagellum on left hand side and as shown by Baker (1997: fig. 14) tapering slightly from F2 to F10 so that F2 maximum width is about 1.24 times F10 width, but on right hand side tapering less evident. Mesoscutellum with subhorizontal dorsal surface about twice as long as subvertical surface, both surfaces divided by weak longitudinal median depression so that mesoscutellum is weakly biconvex, each convexity emphasized by small posteriorly directed sublateral projection that almost overhangs metanotum. Metatibia

with outer surface nodulose posteriorly; apex of protibia with two sharp spines, one anterior, the other posterior; other tibiae without evident apical spines although apical outer margin, especially of metatibia, protuberant; spurs of meso- and metatibiae about as long as tibial diameters, those of metatibia subequal in length; arolia small, much less than half as long as pretarsal claws; pretarsal claws cleft, inner ramus shaped more or less like outer ramus but somewhat shorter than outer ramus. Metasomal T1 with midlength of horizontal surface about half as long as declivitous anterior surface and about half as long as midlength of exposed part of T2, but since dorsal surface of T1 curves gradually onto anterior surface, these measurements are arbitrary; apical terga fragmented but apparent apex of T7 slightly less produced medially than S7 but notched like S7; surface of S7 with longitudinal median depression; posterior margins of S2 to S5 straight, transverse; S6 somewhat produced medially so that posterior margin is strongly convex; S7, S8, and genitalia shown in figures 15–19.

Setae mostly sparse enough that details of surface sculpturing visible (unlike in *B. mucida*). Head including labrum coarsely and closely punctate, upper part of head somewhat more coarsely so than lower part; area in front of ocelli, extending down medially as frontal carina, smooth and impunctate; area around base of mandible, including malar space, smooth and shining; scape and basal half of mandible more finely punctate except for anterior apical smooth shining swelling of scape and smooth mandibular area near articulation. Mesosoma mostly coarsely and closely punctate, punctation similar to that of clypeus except somewhat coarser (like upper frons and vertex) in much of mesoscutum; median part of mesoscutum, except anteriorly, with many punctures separated from one another by smooth ground often one-third as wide as nearby punctures; lateral margin of mesoscutum (about as wide as nearby tegula), lateral extremity of mesoscutellum, and axilla much more finely punctate, these punctures as dense as they can be, variable but most about one-third as wide as those on disc of mesoscutum; posterior propodeal areas with sculpturing grading toward granular. Metasomal terga and sterna with coarse, dense, shallow punctures about size of punctures of frons; posterior margins of T1 to T3 narrowly impunctate, T4 more broadly impunctate, T5 with impunctate zone much broader than exposed punctate zone; S1 to S5 with narrow apical smooth margins.

Setae of head and mesosoma mostly four to five ocellar diameters in length, those of clypeus shorter than elsewhere; setae largely absent on posterior three-fourths of mesoscutum, mostly not branched, dull whitish or cinereous but dusky brownish on genal and hypostomal areas, grading to brownish cinereous on labrum and clypeus (although whitish on upper margin of clypeus medially) and black on lateral margin of clypeus, on lower paraocular area below level of antennal base, and on posterior lateral angle of mesoscutum, on upper part of axilla, and perhaps on extreme basolateral margin of mesoscutellum. Setae of antennal scape and basal parts of legs including upper surfaces of femora similar to cinereous setae of mesosoma but shorter; posterior margins of pro- and mesofemora with fringes of long, pale setae, slightly darkened apically on mesofemur; setae of flagellum and pedicel extremely short; under surfaces of femora with areas of brownish dusky setae, grading to dusky on outer surfaces of



Figures 15–19. Male terminalia of holotype of *Sinomelecta oreina* Baker (SEMC Type No. 9280). **15** Seventh metasomal sternum **16** Eighth metasomal sternum **17** Genital capsule, lateral view **18** Genital capsule, dorsal view **19** Genital capsule, ventral view.

meso- and metatibiae; posterior outer surface of metatibia with large area of extremely dense, appressed setae that hide surface, these setae brown medially and whitish marginally; under surfaces of tarsi with short, yellowish brown setae. Metasomal T1 with long cinereous setae similar to those of mesosoma; T2 to T5 with similar setae, some of them brownish, at extreme sides; T2 to T4 with subapical bands of white setae (broken medially on T2); anterior to these bands setae inconspicuous, short (about one ocellar diameter in length), dusky; T5 largely hidden by T4, thus setal characters not clear but



Figures 20–21. Male holotype (20) and female paratype (21) facial views of *Sinomelecta oreina* Baker (SEMC Type No. 9280).

band of pale setae absent; S2 to S6 with long whitish setae, up to five ocellar diameters in length, sparse on S2 and S3, denser and forming preapical bands on S4 and S5.

Integumental coloration black throughout. Wings transparent, with brownish dusky stain in distal halves, darker distal to marginal cell, clear near and for short distance distal to 1rs-m and 2m-cu and along anterior margins of both submarginal cells; veins and pterostigma black.

Female (paratype): As described for holotype male except as follows: Apex of metasoma intact. Forewing length 9.5 mm. Head width 3.3 mm; head length 2.8 mm; distance between outer margins of tegulae 4.25 mm.

Malar space a depressed groove, base of mandible separated from compound eye by about one-third of distal diameter of F1. Labrum broader than long, apical margin concave. Inner orbits more distinctly converging below than in male; ocellocular distance about 1.5 times interocellar distance, nearly three ocellar diameters; distance between lateral and median ocellus nearly one ocellar diameter. Apical width of F1 approximately equal to apical width of scape; pedicel fully exposed, broader than long; F1 about 2.5 times as long as its apical width, F2 about as long as broad, subsequent flagellomeres similar but progressively very slightly longer so that F7 is slightly longer than broad, F10 only slightly longer than F9 with apex broadly rounded; flagellum not tapering so that F1 and F10 approximately equal in width. Distitarsi broken off and lost except for one front leg that is difficult to see, although pretarsal claws smaller than in male; apical tibial spines represented by outer apical anterior and posterior protuberances except posterior spine of protibial apex present and that of mesotibia a large, long, blunt process; thickened spinelike setae also present on meso- and metatibial apices and on outer surface of metatibia; tibial spurs



Figures 22–23. Lateral (22) and dorsal (23) habitus images of paratype female of *Sinomelecta oreina* Baker (SEMC Type No. 9280).

slightly longer than maximum tibial diameters. Metasomal T6 with well-defined pygidial plate, pointed at apex; T6 apparently produced as slender apical process above comparable slender apical process of S6 which has strongly notched apex exceeding tergal apex.

Area in front of ocelli not entirely smooth, with somewhat irregular punctures; scape without smooth, shining apical swelling. Metasomal terga and sterna with punctures slightly better spaced than in male, middorsally separated by shining ground one-third puncture width to full puncture width; apical impunctate margins of T1 to T3 slightly wider than in male, not contrasting with that of T4.

Most setae of legs from coxae to upper surfaces of tarsi whitish; area of dense setae on outer surface of mesotibia absent. Discal area of mesoscutum, upper inner extremity of axilla, and anterior margin of mesoscutellum with setae blackish (setae largely absent from discal area of mesoscutum in male). Metasomal T2 to T4 with discal setae largely palid and longer than in male so that subapical white setal bands contrast with their background less than in male; T5 and T6 without subapical bands of white setae; S2 to S5 with abundant long whitish setae, those of S2 and S3 not contrastingly sparse, as in male.

Comments. Although peculiar, the 12 antennomeres in the male of *S. oreina* is not unheard of among bees and this condition is found in various genera. For example, this same reduced antennomere count is well known and fixed across species in the augochlorine genus *Chlerogas* Vachal (Brooks and Engel 1999; Engel 2000), the ammobatine genus *Chiasmognathus* Engel (Engel 2006, 2009), the biastine genus *Neopasites* Ashmead (Linsley 1943), and the ammobatoidine genus *Holcopasites* Ashmead (Hurd and Linsley 1972; Michener 2007). Accordingly we do not consider this to merely represent an isolated teratology.

Note that the mention of “*Melecta oreina* Baker” in the key to Eastern Hemisphere genera of Melectini by Rightmyer and Engel (2003) should have read “*Melecta emodi* Baker” (*oreina* is, of course, the type species of *Sinomelecta* which they recognized as a valid genus).

Discussion

Brachymelecta mucida is wholly unique in the North American fauna. Not only is it completely dissimilar from the other known melectine fauna for the continent, superficially more similar to some Asiatic forms, but also the type specimen is the only known individual to have ever been collected, despite considerable effort in Nevada and neighboring states. It is even possible that the species is today extinct, although not too much can be made from decades of absence data as putatively lost species can still turn up [e.g., *Epeoloides pilosula* (Cresson) which was not seen for 42 years before being recaptured in Nova Scotia and Connecticut (Sheffield et al. 2004; Wagner and Ascher 2008)]. Nonetheless, the prospects of recovering new material, as well as the unknown female, certainly dwindle with each passing year. Naturally, this complete absence of additional or new material leads one to speculate whether *B. mucida* is even native to North America, its association with Morrison’s material being erroneous, potentially leaving the specimen mistakenly labeled as coming from “Nev.” The currently available historical evidence certainly does not support such a conjecture as no clearly foreign samples of Hymenoptera appear to have been received and processed in Philadelphia at about the same time as the material from Morrison’s 1878 field work in Nevada (Mann 1885). Although Morrison did sell material to other institutions and collectors (e.g., Horn et al. 1990; Rasmussen 2012), all specimens were collected in the USA and therefore unlikely to have been mixed with material from foreign sources (at least not mixed by Morrison!). Thus, in the absence of clear, or even mildly suggestive, historical

documents to imply otherwise, we consider *B. mucida* native to the western United States, presumably to an undisclosed region in Nevada. It is, without a doubt, the most rare of North American bee species, assuming it is still living.

In regard to *Sinomelecta*, it may be tantalizing to suspect that *S. oreina*, with its various external features reminiscent of Palearctic *Melecta* [e.g., *Melecta* (*Melecta*) *emodi* Baker], is merely an autapomorphic species of that genus with its two submarginal cells and reduced flagellar count in males. This might seem particularly likely given that 1-rm is lost easily in apoids, thereby resulting in the two submarginal cell condition. From Baker's (1997) account and figures there was no reason to readily exclude a placement within *Melecta*, perhaps considering the taxon as a subgenus. Indeed, the genital capsule is somewhat reminiscent of *Pseudomelecta* Radoszkowski in its broad, squat form with a broad gonostylus that is densely setose throughout, and with a broad ventral setose lobe (*vide* Lieftinck 1972). The hidden sterna, however, are quite unlike those of *Pseudomelecta*. Indeed, the seventh sternum is rather different from that of *Melecta*, more closely resembling the form found in *Thyreus* [e.g., *Thyreus ramosus* (Lepeletier de Saint Fargeau): *vide* Lieftinck 1968: figs 31–33]. In addition, the long first flagellomere and narrowly triangular pygidial plate of the female are unlike *Melecta* and the form of the mesoscutellum, pubescence, and presence of arolia readily exclude *S. oreina* from *Thyreus*. Naturally, cladistic work is needed throughout the Melectini, particularly to determine whether *Melecta* as constituted is monophyletic, and it is hoped that this fuller account of two rare genera might encourage and bolster such work.

Acknowledgements

We are immensely grateful to Jason Weintraub, Academy of Natural Sciences of Philadelphia, for permitting us to borrow and dissect the holotype and only known specimen for *B. mucida*; to the late Donald B. Baker for donating his type material of *S. oreina*; and to three anonymous reviewers and Michael Ohl for comments on the manuscript. Partial support was provided by U.S. National Science Foundation grants EF-0341724 and DBI-1057366 (both to MSE). This is a contribution of the Division of Entomology, University of Kansas Natural History Museum.

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Description of three new *Triaenodes* species from Fiji (Trichoptera, Leptoceridae)

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| [urn:lsid:zoobank.org:author:26467FCB-F05C-425E-88C4-2C58180640CC](https://doi.org/urn:lsid:zoobank.org:author:26467FCB-F05C-425E-88C4-2C58180640CC)

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Abstract

The following three new species are illustrated and described from Fiji: *Triaenodes rebellus* Eriksson & Johanson, **sp. n.**, *Triaenodes oscitus* Müller & Johanson, **sp. n.**, and *Triaenodes forcipatus* Puranen Li & Johanson, **sp. n.** All species are endemic to Viti Levu. A key to the male *Triaenodes* species of Fiji is provided. With this report, the number of *Triaenodes* species known from Fiji is doubled.

Keywords

Caddisflies, Terrestrial Arthropod Survey of Fiji, new species, taxonomy

Introduction

In number of species, Trichoptera (caddisflies) constitute the second largest monophyletic group of aquatic animals (Malm et al. submitted). About 13.500 species are described so far, of which about 15% are classified in the family Leptoceridae Leach, 1815, which globally is ranked as the 2nd largest family in the order (Morse 2012). With 276 described species (Morse 2012) the leptocerids is the family in the Austral-

ian Region comprising the highest species diversity. The species of the family are characteristic in having adults with very long antennae, two rows of setae dorsally on the mesonotum, and narrow forewings. The sistergroup to the Leptoceridae is presently not identified, but based on phylogenetic analyses derived from molecular data the family is hypothesized related to Calamoceratidae, Atriplectidae, Odontoceridae and Philorheithridae (Malm et al. submitted). In the Australian Region, the Leptoceridae are easily distinguished from these families in the absence of preapical tibial spurs on the mid legs, from Philorheithridae by the long antennae, from Philorheithridae and Odontoceridae by having separate R1 and R2 at the forewing margin, and from Calamoceratidae and Philorheithridae by the narrower forewings (Neboiss 1986). The family comprises two subfamilies Leptocerinae Leach, 1815 and Triplectidinae Ulmer, 1906. Triaenodini is one of 11 tribes within Leptocerinae, and comprises the three genera *Adicella* McLachlan, 1877, *Erotesis* McLachlan, 1877 and *Triaenodes* McLachlan, 1865 (Malm and Johanson 2011). *Triaenodes* is known from all major faunal biogeographic regions and about 240 extant species have been described so far (Morse 2012, Johanson et al. 2011), and the extinct *Triaenodes fossilis* Wichard & Barnard, 2005 dated to Eocene, described from Baltic amber, represents the only fossil species in the genus. With 78 previously recorded species, the diversity is higher in the Australian Region compared to other regions. More than half of these (44 species) were described by Neboiss and Wells (1998) as endemic to Australia. So far two species are known from Vanuatu (Johanson et al. 2011), four from Solomon Islands (Kimmins 1957), 21 from New Guinea (Morse 2012), and three from Fiji. The first record of of the genus from Fiji was given by Mosely (1934) who described *T. dubius* Mosely, 1934 from Wainganiu. Banks (1936) described a second species, *T. manni* Banks, 1936, from Wainganiu. The third species *T. fijianus* Mosely, 1941 was described from Viti Levu. This paper adds three more species of the genus from Fiji.

Material and methods

The study is based on five males collected in the Terrestrial Arthropod Survey of Fiji project (Evenhuis and Bickel 2005) funded by the US National Science Foundation and the Schlinger Foundation. In this project Trichoptera were collected in Malaise traps situated at 47 localities (Johanson and Oláh 2012) on the four major islands Viti Levu, Vanua Levu, Taveuni Island and Kadavu Island between September 21 2002 and January 5 2005. The *Triaenodes* specimens covered in this report were collected from four different localities at Viti Levu Island. The material is stored in 80% alcohol. Right wing pairs of the holotype of all new species and non-types of previously described species were removed, mounted on slides in glycerol and photographed using the Lumenera InfinityX digital camera mounted on an Olympus SZX12 stereomicroscope. The Extended Focus Option in the DeltaPix Insight software was used to create high-resolution photos with high focus depth. The abdomens were cleared in hot 8% KOH for about one hour. The abdomens were dehydrated in absolute alcohol and temporarily mounted

in Euparal on a microscope slide before examination and drawing. All drawings were produced using a pencil on plain white A4 paper sheets using a drawing tube mounted on a Leitz Ortholux II. After the drawings were completed the abdomens were returned to the alcohol vial with the rest of the animal. Each pencil illustration was digitalized in a scanner at low resolution and thereafter used as a background layer in Adobe® Photoshop® 8.0. The illustrations were completed after being re-drawn on a new layer using a Wacom drawing pad before the background layer was deleted.

The nomenclature applied to the genitalic morphology follows that of Malm and Johanson (2011). Specimens in this study are deposited in the following repositories:

FNIC Fiji National Insect Collection, Suva, Fiji (currently held at BPBM)
NHRS Swedish Museum of Natural History, Stockholm, Sweden

The geographical setting of the localities are presented in Johanson and Oláh (2012).

Descriptions

Triaenodes rebellus Eriksson & Johanson, sp. n.

urn:lsid:zoobank.org:act:CC66BD00-165A-446E-BF77-EC1CAEEECAD9

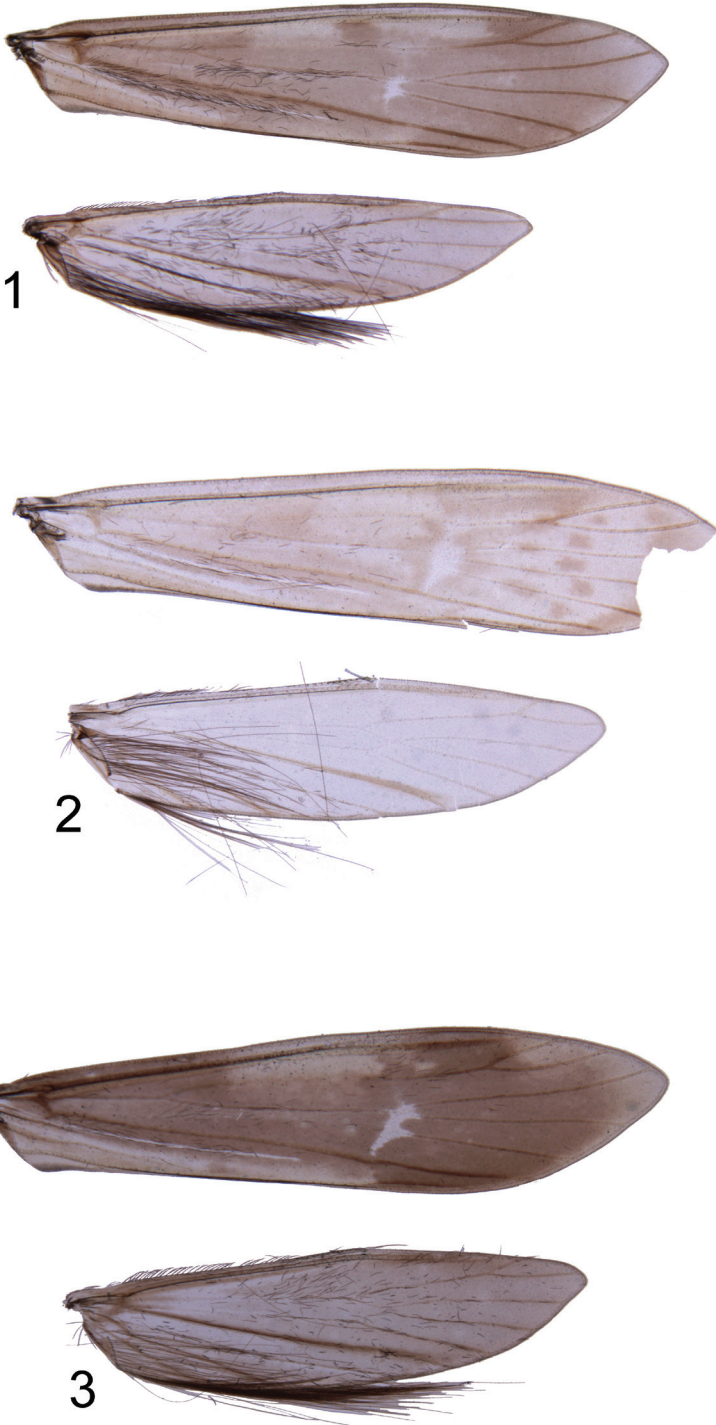
http://species-id.net/wiki/Triaenodes_rebellus

Figs 1, 4–8

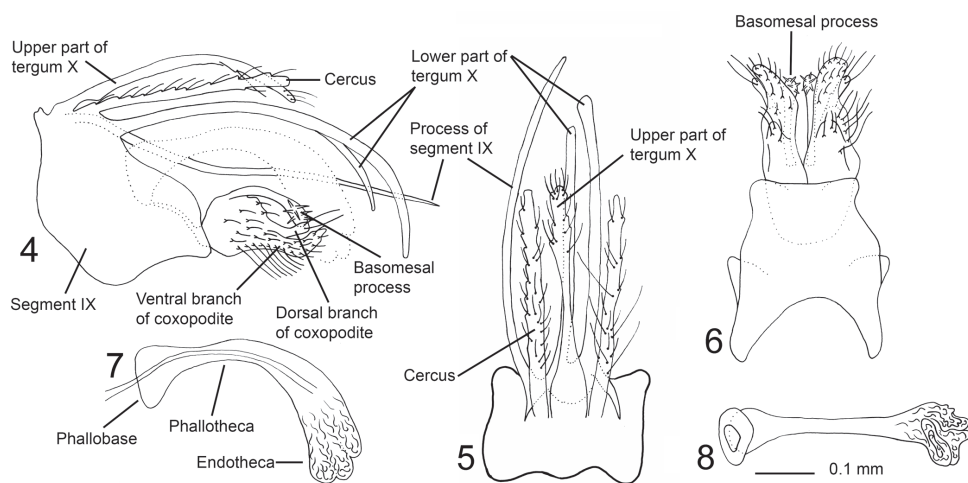
Diagnosis. *Triaenodes rebellus* resembles the New Guinean species *T. mondoanus* Kimmins, 1962 by having the dorsal right posterior margin of segment IX strongly produced posteriorly into a needle-shaped process. The new species is easily separated from *mondoanus* by the upper part of tergum X being about as long as the cerci, not much longer than cerci as in *T. mondoanus*; and the basomesal process and dorsal branch of each coxopodite is present, while absent in *mondoanus*.

Description, male. Wings (Fig 1). Forewing 5.2 mm, hind wing 4.3 mm (N=1). Forewing: stem of M absent; forks I and V present; wing membrane with pale area along apical margin, mid-anterior margin, and basal two-thirds of posterior margin. Hyaline area present at anastomosis. Hind wing: uniformly gray without apparent patterns.

Genitalia (Figs 4–8). Segment IX wide, asymmetric; in lateral view with ventral part produced posteriorly, anterior margin slightly convex, ventral margin concave; in dorsal view almost rectangular, anterior margin with central part slightly produced anterad; in ventral view broad anterior half and slightly narrower posterior half separated by narrow incision, anterior margin of segment IX deeply concave, lateral margins slightly concave, posterior margin straight. Dorsal right posterior margin of segment IX strongly produced posterad, forming almost straight, needle-shaped process exceeding processes of tergum X (visible in dorsal view and right lateral view), bow-shaped, gently curved mesally. Cerci straight, thin, elongate; covered with long, robust, and short, weak se-



Figures 1–3. Right wings of holotypes. **1** *Triaenodes rebellus* sp. n. **2** *Triaenodes oscitus* sp. n. **3** *Triaenodes forcipatus* sp. n.



Figures 4–8. *Triaenodes rebellus* sp. n., holotype. **4** genitalia lateral view **5** genitalia dorsal view **6** genitalia ventral view **7** phallus lateral view **8** phallus ventral view.

tae. Tergum X with well-developed upper and lower part, upper part about as long as cerci; forming central, slender, elongate, slightly dorsoventrally flattened process, setose at apical one-third; in lateral view with basal half almost straight, curving ventrally from mid-length (Fig. 4); in dorsal view slender, hourglass-shaped, with irregular lateral margins at distal one-third. Lower part of tergum X bilobed from base, each lobe thin, strongly elongate, significantly longer than cerci, right lobe slightly shorter than left lobe and tuboid at apex, left lobe slightly club-shaped at apex; in lateral view each lobe curved ventrally; in dorsal view almost parallel. Coxopodites in lateral view, with basal half almost circular, each divided at mid-length into dorsal and ventral branch, posterior margin above dorsal branch undulating. Each dorsal branch about one-third as long as total length of each coxopodite, originating from mid-height of basal part, tube-shaped, with two long apical setae; weakly bent dorsally at mid-length in lateral view; diverging apically in ventral view. Ventral branch of each coxopodite abundantly setose, more densely posteriorly; in lateral view bent dorsad at mid-length, apical part thin; in ventral view widest at base, lateral margin undulating, mesal margin sigmoid, apically diverging. Each basomesal process slender, apically club-shaped with abundant thick spines; in lateral view curved ventrally, reaching as far out as apex of dorsal branch; in ventral view straight or weakly curving mesally. Phallic organ about as long as dorsal part of tergum X; strongly curved ventrally immediately before mid-length, phallobase subtriangular, phallotheca slender immediately after phallobase, uniformly widening apically; endotheca apparently trilobed, membranous, without spines.

Material examined. Holotype male: Fiji: Viti Levu Island, Naitasiri Province, Nakobalevu Mt., rainforest, 18°03'S, 178°25'E, 340 m, Malaise trap, 22.ix–9.x.2002, leg. M. Irwin, E. Schlinger & M. Tokoka'a. [FNIC, alcohol]

Etymology. *Rebellus*, from Latin *rebellis*, insurgent in English, referring to genitalia being armed by many pointed processes.

***Triaenodes oscitus* Müller & Johanson, sp. n.**

urn:lsid:zoobank.org:act:72DEDCDE-DE32-4177-B248-28AA3F894EE0

http://species-id.net/wiki/Triaenodes_oscitus

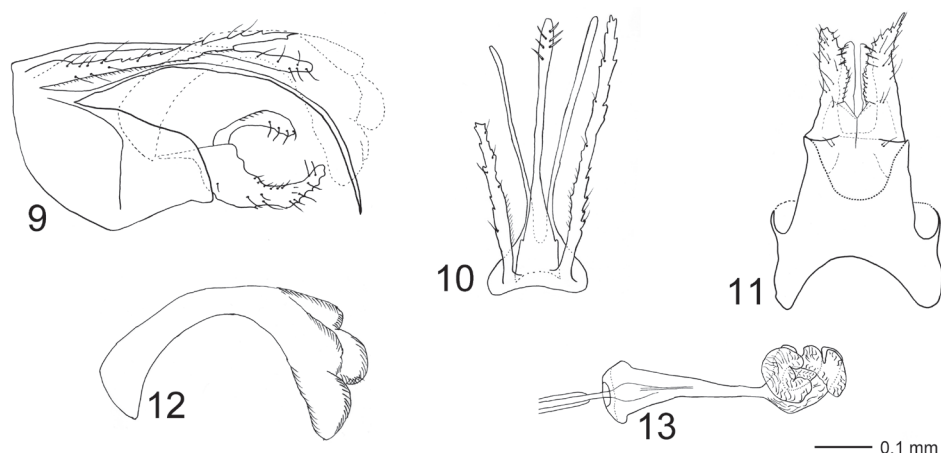
Figs 2, 9–13

Diagnosis. The species resembles *T. rebellus* sp. n. in the shape of the ventral branch of the coxopodites and basomesal processes, but dorsal branch of each coxopodite is absent. The dorsal appendages of *oscitus* resemble those of *T. grifo* Malicky, 2005, but the upper part of tergum X of *oscitus* is longer.

Description, male. Wings (Fig. 2). Forewing damaged, hind wing 4.1 mm (N=1).

Forewing: stem of M absent; forks I and V present; apex missing in holotype; membrane pale, except in distal one-third with two almost vertical series of dark spots, and a larger dark patch above vertical series. Hyaline area at anastomosis. Basal two-thirds with irregular pale fields. Hind wing: uniformly gray, with faint spots at apical half.

Genitalia (Figs 9–13). Segment IX in lateral view with slightly convex anterior margin, dorsal margin short, continuous with dorsal margin of tergum X; ventral two-thirds strongly produced into posterior lobe; posterior lobe with weakly undulating dorsal margin and nearly straight ventral margin except bending ventrally at apex, posterior margin almost truncate. Large triangular, vertical, posteriorly oriented plate located laterally and at mid-length of segment IX, forming narrow, posteriorly orienting processes. In ventral view anterior margin deeply concave; widest before lateral plates, with slightly concave lateral margins; uniformly narrowing after lateral plates. Posterior margins distinct laterally, mesally apparently fusing with gonopods. Cerci elongate, straight, serrated along their lengths, scattered setose, with row of minute setae along anterior three-quarters of ventral margin; in lateral view oriented almost horizontally, basal one-fifth about two times thicker than distal part; in dorsal view slightly diverging, equally wide along their lengths. Tergum X divided into well-developed upper and lower part. Upper part of tergum X slender, about as long as each cercus; slightly curvilinear ventrally along its length in lateral view; basally wide, slender after one-third its length in dorsal view, apex club-shaped, with short, stout setae. Width of base and apex subequal in lateral view. Lower part of tergum X branching at base into two long, needle-shaped processes, clearly longer than upper part of tergum X, curved ventrally along their lengths, reaching further posteriorly than apex of dorsal part of tergum X; in dorsal view slightly diverging. Gonopods each divided into one-branched coxopodite and basomesal process; about two-fifths as long as each cercus. Coxopodites with scattered setae; each with row of smaller setae along central part of dorsal margin; wide at base in lateral view, stepwise narrowing from about one-third, almost sickle-shaped; apex produced dorsally, nearly tangential with phallus. In ventral view, basal one-quarter of coxopodites separated by longitudinal suture, well-separated from one-quarter, each coxopodite forming dorsoventrally flattened, spoon-shaped plate, with serrated mesal margin; apices of coxopodites diverging. Left coxopodite shorter than right coxopodite, apically blunt. Basomesal processes about two-thirds as long as coxopodites; sickle-shaped in lateral view, each process oriented dorsally at base,



Figures 9–13. *Triaenodes oscitus* sp. n., holotype. **9** genitalia lateral view **10** genitalia dorsal view **11** genitalia ventral view **12** phallus lateral view **13** phallus ventral view.

curving posterad and slightly broadening towards apex, bearing strong, lateroventrally and slightly anteriorly directed spines. In ventral view processes running parallel along their lengths; each process with slightly narrowing apex, mesal margin almost straight, lateral margins with small indentations. Phallic organ widest at base and endotheca, narrowest immediately before endotheca; in lateral view with nearly triangular phallobase; phallotheca slender, widening distally and strongly curving ventrally at about mid-length. In dorsal view endotheca forming irregular lobes.

Remarks. The right cercus is broken at mid-length in the holotype.

Material examined. Holotype male: Fiji: Sigatoka Province, Sigatoka Sand Dunes National Park, coastal forest, 18°10'S, 177°30'E, 10 m, Malaise trap, 22.ix–8.x.2002, leg. M. Irwin, E. Schlinger & M. Tokoka'a. [FNIC, alcohol]

Etymology. *Oscitus*, from Latin *oscito*, gape or open mouth in English, in reference to the shape of the male gonopods in lateral view.

***Triaenodes forcipatus* Puranen Li & Johanson, sp. n.**

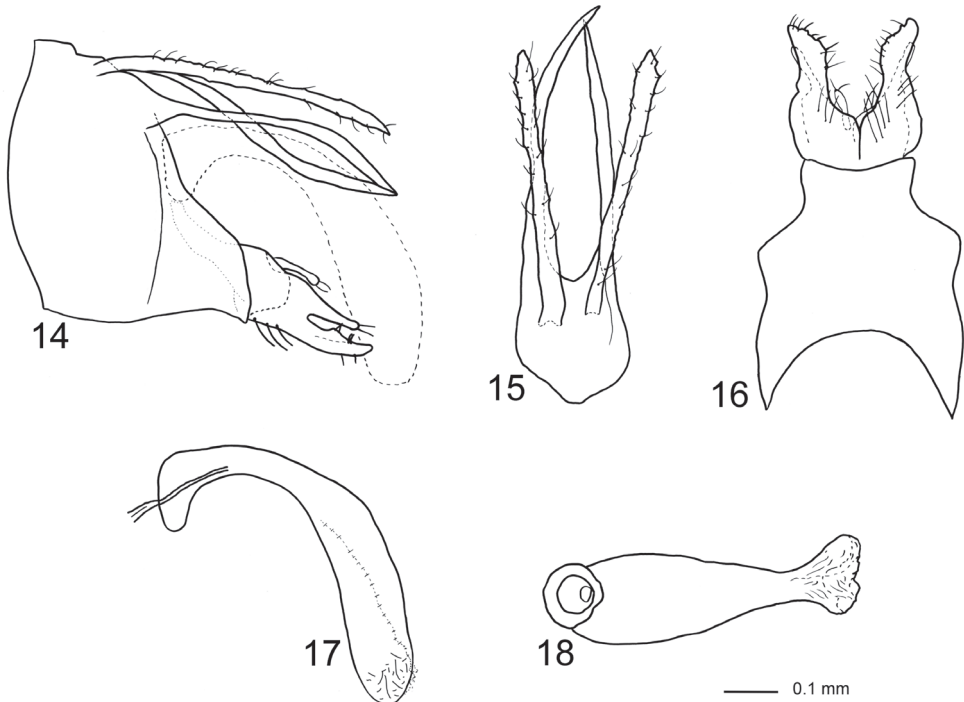
urn:lsid:zoobank.org:act:FECEF693-62B6-4747-B626-531F63F49B43

http://species-id.net/wiki/Triaenodes_forcipatus

Figs 3, 14–18

Diagnosis. The species is most similar to *T. kalydon* (Malicky, 2005) from Sumatra, particularly in the male genitalia which comprise two-branched coxopodites and absence of the upper part of tergum X. *Triaenodes forcipatus* is easily distinguished from *kalydon* by having much smaller basomesal processes, downward curving gonopods and longer cerci.

Description, male. Wings (Fig 3). Forewing 5.2–5.9 mm (N=3), hind wing 4.0–4.6 (N=3). Forewing: stem of M absent; forks I and V present; wing membrane with pale area at apex and basal one-third of posterior margin, two rectangular pale fields



Figures 14–18. *Triaenodes forcipatus* sp. n., holotype. **14** genitalia lateral view **15** genitalia dorsal view **16** genitalia ventral view **17** phallus lateral view **18** phallus ventral view.

at anterior margin, well separated by dark area. Hyaline area present at anastomosis. Hind wing: uniformly gray, without apparent patterns.

Genitalia (Figs 14–18). Segment IX almost triangular in lateral view, ventrally produced posterad before gonopods; ventral margin two times longer than dorsal margin; in dorsal view slightly longer than wide, central part of anterior margin produced anteriorly into rounded lobe; in ventral view anterior margin deeply concave, posterior margin shallowly concave, anterior two-thirds almost two times wider than posterior one-third, slightly pointed laterad at mid-length. Cerci originating from posterodorsal margin of segment IX, uniformly broad along their lengths, with irregular lateral and mesal margins; setose; apex unevenly narrowing; in lateral view posteriorly slightly exceeding gonopods. Tergum X consisting of lower part, upper part vestigial and not evident; lower part separated from near base into lateral branches slightly longer than cerci, forming a pair of posteriorly elongate processes originating immediately below cerci; basally wide in lateral view, strongly narrowing from basal one-sixth, uniformly slender along posterior five-sixths, apex pointed, proximal two-thirds of left branch nearly straight, distal one-third slightly curving ventrally; right branch sigmoid, with posteriorly orienting distal one-third; connected ventrally by concave plate. Gonopods in lateral view as high as posteriormost part of segment IX,

each divided at mid-length into dorsal and ventral branch, dorsal branch about half width of ventral branch, slightly shorter than ventral branch, dorsal branch bearing marginal setae, ventral branch with scattered setae. In ventral view, anterior half of gonopods forming broad plates being completely fused anteriorly, distal half about half as wide as anterior half, slightly curving laterally, two times longer than wide; each with mesal margin sigmoid, apex almost pointed. Basomesal processes as long and wide as ventral branches, originating from anterior one-quarter of gonopods; apex club-shaped with few setae. Phallic organ strongly curving ventrally; in lateral view phallobase slightly elliptic, phallicata widening immediately after phallobase; endotheca rounded; in ventral view distal end of phalotheca about half as wide as proximal end; endotheca rounded, almost triangular, membranous.

Material examined. Holotype male: Fiji: Viti Levu Island, Pabitra, 17.5833°S, 178.0833°E, 1034 m, Malaise trap, 17–20.xi.2003, leg. Delena Veikovi, Wabu Baseline Survey [FNIC, alcohol].

Paratypes: 5 males: Fiji: Viti Levu Island, Vuda Province, Koroyanitu Natural History Park, Savuione Trail, 17°40'S, 177°33'E, 450 m, Malaise trap, 12–19.x.2002, leg. M. Irwin, E. Schlinger & M. Tokoka'a [NHRS, alcohol].

Etymologi. *Forcipatus*, from Latin *forceps*, claw in English, referring to the claw-shaped gonopods in lateral view.

Key to the Fijian species of *Triaenodes*, based on characters on male genitalia

- 1 Cerci in dorsal view about three times longer than wide..... *T. dubia* Mosely, 1934
- Cerci in dorsal view more than four times longer than wide (Figs 4, 9, 14)2
- 2 Each coxopodite with one branch (Fig. 9)3
- Each coxopodite with two branches (Figs 4, 14)5
- 3 Uppermost part of tergum X less than five times longer than wide *T. fijianus* Mosely, 1941
- Uppermost part of tergum X more than six times longer than wide (Figs 9, 10).....4
- 4 In lateral view, ventral branch of coxopodite about as thick as basomesal process (Fig. 9)..... *T. oscitus* Müller & Johansson, sp. n.
- In lateral view, ventral branch of coxopodite about two times thicker than basomesal process *T. manni* Banks, 1936
- 5 Basomesal process curving ventrad in lateral view; dorsal and ventral branches of coxopodite curving dorsad in lateral view (Fig. 4) *T. rebellus* Eriksson & Johanson, sp. n.
- Basomesal process nearly straight and almost parallel with dorsal and ventral branches of coxopodite in lateral view (Fig. 14) *T. fuscipatus* Puranen Li & Johanson, sp. n.

Acknowledgements

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A new species of *Nitocra* Boeck, 1865 (Harpacticoida, Ameiridae, Ameirinae) from South Africa, with notes on its ecology and remarks on the status of *Nitocra sewelli husmanni* Kunz, 1976

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Abstract

A new species of the genus *Nitocra* Boeck, 1865, *Nitocra taylori* **sp. n.** is described from the St Lucia Estuary, Africa's largest estuarine lake. It is also suggested that *Nitocra sewelli husmanni* Kunz, 1976 and *N. reducta fluviatilis* Galhano, 1968 are granted full species rank as *N. husmanni* **stat. n.** Kunz, 1976 and *N. fluviatilis* **stat. n.** Galhano, 1968. *Nitocra taylori* **sp. n.** appears to be closely related to *N. husmanni*. Unfortunately, the original description of the micro-characters of the species lacks the detail needed to make reliable comparisons between species of the genus *Nitocra*. The main differences observed are the number of spinules along the posterior margin of the anal operculum, length ratio of the exopod and endopod of the first swimming leg, shape of the outer spine on the male third endopodal segment of the third swimming leg, number of segments of the male antennule, relative length of the setae on the male baseoendopod of the fifth leg, shape of the male exopod of the fifth leg, relative length of the two setae of the male sixth leg, and shape of the female baseoendopod of the fifth leg. The current distribution of *N. taylori* **sp. n.** is limited to the lake part of the estuary, an area which is most severely affected by the current freshwater deprivation crisis. During closed mouth conditions, these regions (South/North Lake

and False Bay) are characterized by low water levels, high salinities and high turbidity levels. This suggests that *N. taylori* sp. n. may favor these environmental conditions and the significant correlations found between the abundance of *N. taylori* sp. n. and salinity and turbidity confirm this to a degree. *Nitocra taylori* sp. n. individuals are also able to withstand a wide range of fluctuations. They were recorded at turbidities ranging from 2 to 102 NTU, temperatures from 20.9 to 34.8 °C and salinity levels ranging from 9.81 to 53.7 psu. However, in the current state of the system, salinity and temperature levels in the northern regions frequently exceed this value. Continued freshwater deprivation may, therefore, further limit the distribution range of this species.

Keywords

Nitocra, taxonomy, ecology, St Lucia Estuary, South Africa

Introduction

During the course of routine quarterly monitoring surveys undertaken during the last six years in the St Lucia Estuary, South Africa, several specimens of an unidentified harpacticoid copepod were retrieved from zooplankton samples. The St Lucia Estuary is the largest estuarine lake in Africa and has high priority for conservation as it forms part of South Africa's first World Heritage Site - iSimangaliso (formerly Greater St Lucia) Wetland Park (Fielding et al. 1991, Cyrus and Vivier 2006) and is a Ramsar Wetland of International Importance (Begg 1978).

St Lucia characteristically experiences cyclical wet and dry phases, each lasting between four and ten years (Begg 1978). The below average rainfall which the area has received since 2002, coupled with a range of anthropogenic interventions undertaken during the last century, have resulted in the current drought cycle being one of the most severe the estuary has ever experienced (Whitfield and Taylor 2009). Low freshwater input and high evaporation rates have led to the persistence of a reversed salinity gradient, with hypersaline conditions in the upper reaches, i.e. False Bay and North/South lakes (Figure 1). The northern lakes are also extremely susceptible to desiccation. At the peak of the drought in 2005–2006, up to 70% of the lake bed was dry (Whitfield and Taylor 2009) and water temperatures in the shallow regions at times reached 50°C.

In light of the current crisis, research efforts have been directed at clarifying the biodiversity structure of the ecosystem and the effects of this stress on its functioning. A number of new and potentially endemic taxa have been identified recently from samples collected during routine monitoring surveys in the St Lucia Estuary (Daly et al. 2012, Todaro et al. 2011). High densities of an unidentified harpacticoid of the genus *Nitocra*, here described as *N. taylori* sp. n., were collected from South Lake and False Bay. The genus *Nitocra* belongs to the large and heterogenous family Ameiridae. Ameirids inhabit a wide range of sediment types and occur in virtually all salinity regimes (Boxshall and Halsey 2004). The first record of *N. taylori* sp. n. in the St Lucia Estuary dates back to 2006, when low densities were collected from Charters Creek, which is situated on the western shore of South Lake. It is possible that this species was present in earlier assessments conducted by Grindley (1976), however, in these assessments, harpacticoid copepods were not identi-

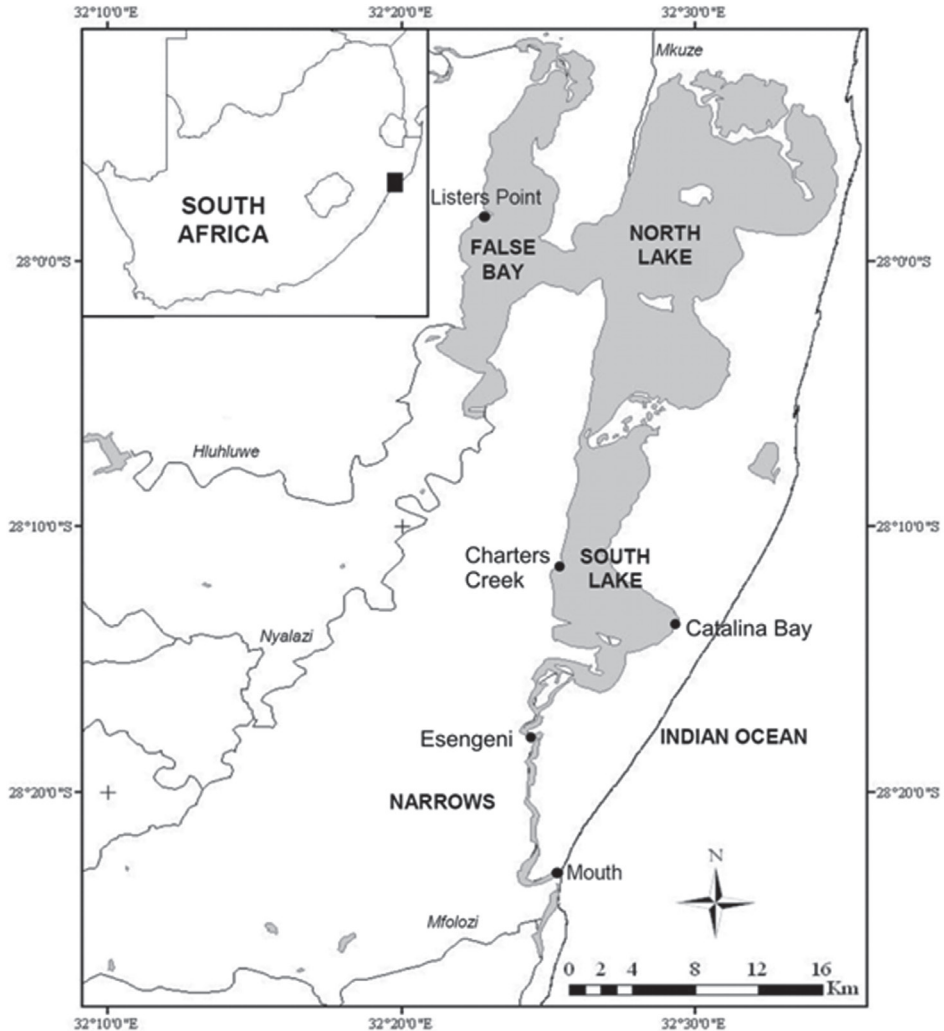


Figure 1. St Lucia Estuary showing the sampling stations and geographic location within South Africa.

fied to species level. This study, therefore, aims to describe this species as well as document the basic characteristics of the habitat in which it occurs, in order to provide management with knowledge for the adequate protection of this potentially endemic species.

Material and methods

Quarterly surveys were undertaken at five representative stations within the St Lucia Estuary, from February 2006 through to May 2011. These stations included the Mouth, Esengeni, Catalina Bay, Charters Creek and Listers Point (Figure 1). The study period covered three different hydrological phases, viz. a closed-mouth phase (Febru-

ary 2006 to February 2007), an open-mouth phase (March 2007 to August 2007), and a re-closed period (November 2007 to May 2011). Zooplankton together with physico-chemical data, were collected at each site on each sampling occasion.

Physico-chemical variables

Physico-chemical measurements were taken with a YSI 6920 water quality logger, fitted with temperature (°C), depth (m), conductivity (mS/cm), dissolved oxygen (mg.L⁻¹), pH and turbidity (Nephelometric Turbidity Units or NTUs) probes.

Zooplankton sampling

Single daytime mesozooplankton samples were collected using an epibenthic sled (100 µm mesh). The sled was towed in the shallow waters near-shore at all stations, except at Esengeni, where a boat was used. The mouth of the net was semi-circular in shape (radius = 18.5 cm) and was mounted on a sled that was towed just above the sediment surface. Sampling with this sled, therefore, allowed the suitable collection of epibenthic harpacticoids. In regions where water depth was too shallow, or when zooplankton was too dense for the sled to be used, 30 L of water was passed through a 100 µm sieve. Samples were emptied into 500 mL bottles containing 4% phloxine-stained formaldehyde.

In the laboratory, samples were suspended in 0.5 to 5 L solutions, depending on the density of organisms. The main sample was then stirred vigorously so that all the organisms remained in a homogenous suspension. A 20 mL plastic vial attached to a metal rod was then used to withdraw three subsamples from mid-depth (Perissinotto and Wooldridge 1989, Carrasco et al. 2010). Individuals of *N. taylori* sp. n. within the samples were identified and counted with a Kyowa 129 SDZ dissecting microscope (400 x) and density was then calculated as ind.m⁻³.

Statistical analyses

Univariate statistical analyses were conducted with SPSS version 19 for Windows, where a Pearson correlation was used to test for relationships between environmental variables and species abundance. This analysis was performed on log-transformed abundance data for all non-zero records.

Species description

A number of adult males and females were fixed in 4% formalin and preserved in 70% ethanol for taxonomic analyses and description. Observations and drawings were done

at a magnification of 1000 x from whole and dissected specimens mounted in lactophenol with a Leica compound microscope equipped with phase contrast and a drawing tube. The type material was deposited in the collection of the Instituto de Ciencias del Mar y Limnología, Unidad Académica Mazatlán (Mexico) (EMUCOP) and in the collection of the Iziko South African Museum, Cape Town (South Africa) (SAM). The terminology proposed by Huys and Boxshall (1991) for the general description was adopted. The relative length of the setae of the male and female P5 was calculated dividing the length of each seta by the total length of the longest element. Abbreviations used in the text and tables are: P1-P6, first to sixth swimming legs; EXP, exopod; ENP, endopod; P1(P2-P4)EXP(ENP)1(2, 3) denotes the proximal (middle, distal) exopodal (endopodal) segment of P1, P2, P3 or P4; BENP, baseoendopod; ae, aesthetasc.

Taxonomic account

Family Ameiridae Monard, 1927

Subfamily Ameirinae Lang, 1944

Genus *Nitocra* Boeck, 1865

***Nitocra taylori* sp. n.**

urn:lsid:zoobank.org:act:AF4F4062-2DF8-41B5-9089-B62EECAB56B1

http://species-id.net/wiki/Nitocra_taylori

Figures 2–9

Type material. One female holotype (EMUCOP-080311-03) and one male allotype (EMUCOP-080311-06) preserved in alcohol, one female (EMUCOP-080311-04) and one male (EMUCOP-080311-05) dissected paratypes, and 15 adult females, 11 adult males, one CIII, three CIV and three CV paratypes preserved in alcohol (EMUCOP-080311-07) were deposited in the Copepoda collection of the Instituto de Ciencias del Mar y Limnología, Mazatlan Marine Biological Station; 26 additional paratypes (SAM-A45750) were deposited in the collection of the Iziko South African Museum; collected from Listers Point, St Lucia Estuary, South Africa; 8 March 2011; leg. N. K. Carrasco.

Type locality. Listers Point, False Bay, St Lucia Estuary, South Africa (27°58'09.4"S, 32°22'48.11"E).

Etymology. The species is named after Dr Ricky H. Taylor, former Regional Ecologist at Ezemvelo KZN Wildlife, St Lucia Estuary, for his invaluable help provided to research and his lifetime efforts towards the conservation of the St Lucia Estuary. The specific epithet is a noun in the genitive singular.

Female. Habitus (Figure 2A) tapering posteriorly; total body length measured from tip of rostrum to posterior margin of caudal rami ranging from 460 to 685 µm (mean, 537 µm; n= 11; holotype, 525 µm). Rostrum (Figure 2A, B) defined at base, elongate, small, barely reaching distal margin of first antennular segment, with pair of

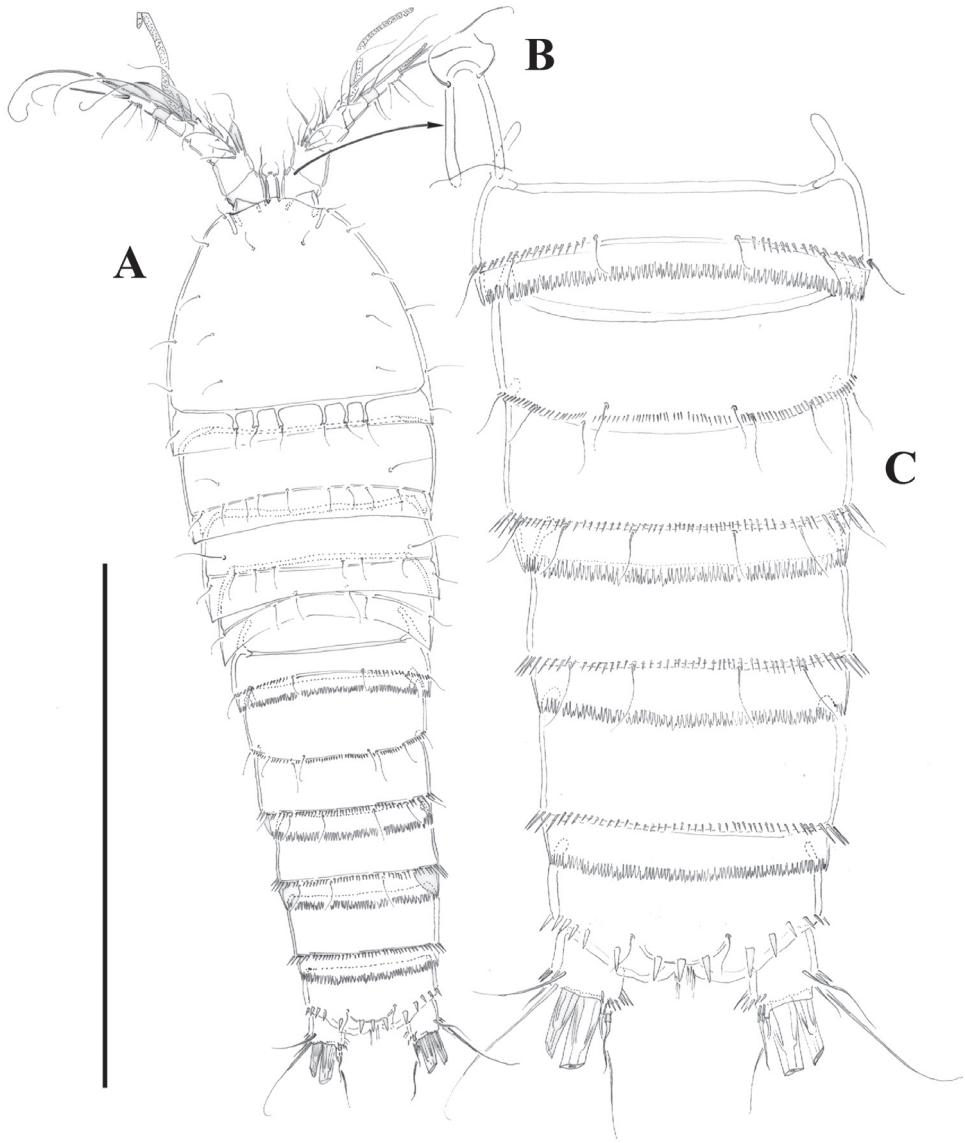


Figure 2. *Nitocra taylora* sp. n. Female. **A** habitus **B** rostrum, dorsal **C** urosome, dorsal. Scale bar: A=300 μ m; B=75 μ m; C=150 μ m.

sensilla subapically. Dorsal surface of cephalic shield and free prosomites without spinular ornamentation, with plain caudal frill (Figure 2A). P5-bearing somite with medially interrupted row of minute spinules close to posterior margin dorsolaterally, with deeply serrate caudal frill (Figure 2A, C). Subcuticular rib of genital double-somite with dorsolateral row of small spinules indicating former division between second and third urosomites (Figure 2A, C), but completely fused ventrally (Figs 3B, 10F); third urosomite with comparatively stronger spinules close to posterior margin dorsally and

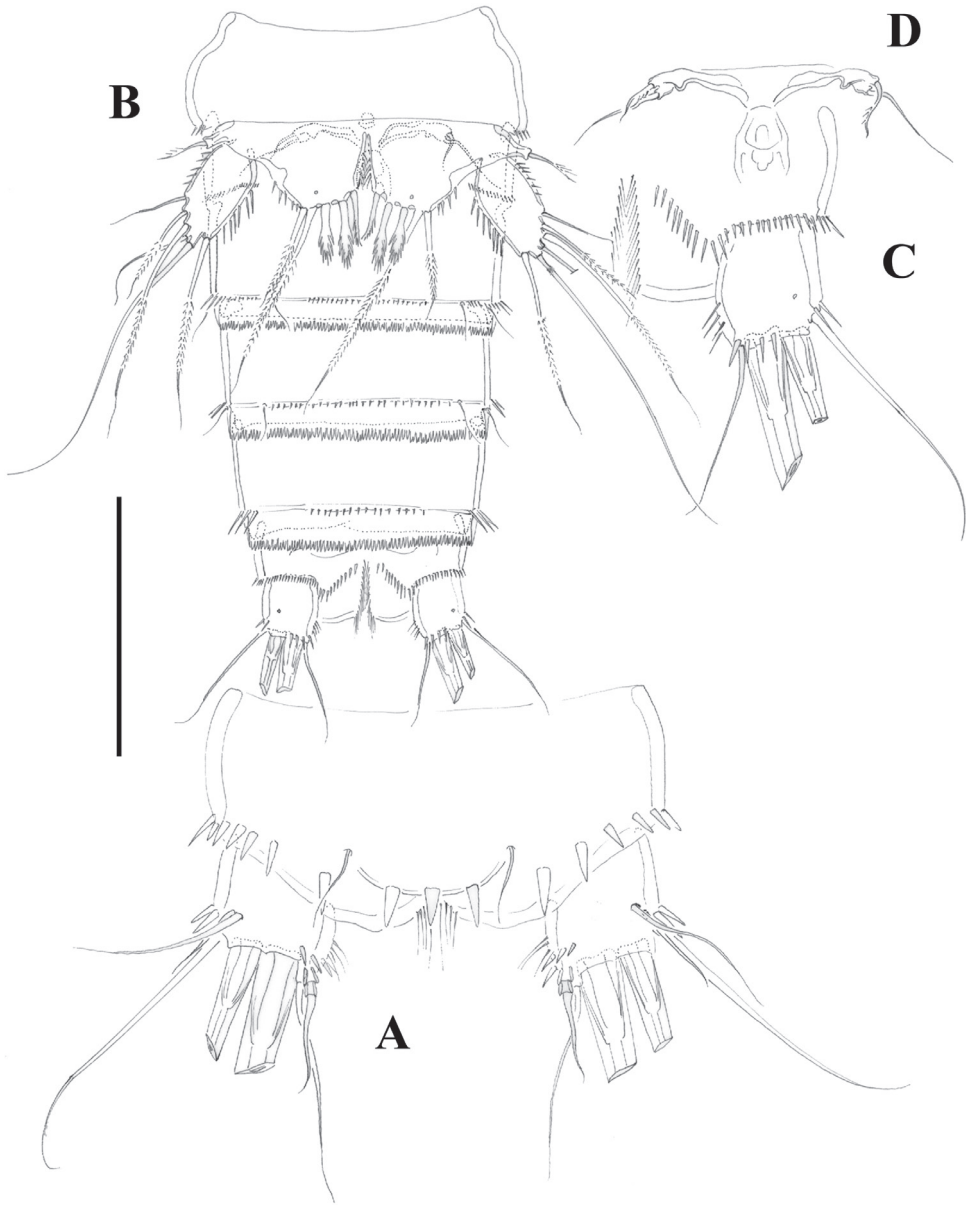


Figure 3. *Nitocra taylori* sp. n. Female. **A** anal somite and caudal rami, dorsal **B** urosome, ventral, showing P5 **C** left caudal ramus, ventral **D** P6 and genital complex. Scale bar: **A**=44 μ m; **B**=100 μ m; **C**=50 μ m; **D**=71 μ m.

laterally, with median row of minute spinules ventrally, with deeply serrate caudal frill. Fourth and fifth urosomites as previous somite dorsally and ventrally, except for less and lack of sensilla in fourth and fifth urosomites, respectively. Anal somite somewhat shorter than previous somite, with strong spinules dorsally and laterally close to joint

with caudal rami (Figs 2A, C, 3A), with comparatively smaller spinules ventrally (Figs 3B, C, 10F); rounded anal operculum with three strong spinules close to posterior margin, and flanked by pair of sensilla (Figs 2C, 3A). Caudal rami nearly as long as wide from dorsal view, but slightly longer than wide ventrally (Figs 2C, 3A, B, C, 10B), with seven setae as follows: seta I small, nearly as long as caudal ramus; seta II dorsal to seta I, about twice as long as the latter; seta III about twice as long as seta II, arising close to outer distal corner; setae IV and V well developed, the latter longest; seta VI arising from inner distal corner, slightly shorter than seta III; seta VII biarticulated, rather short, arising close to base of seta VI at inner distal corner.

Antennule (Figure 5A) eight-segmented, surface of segments smooth except for spinular row on first segment. Armature formula as follows: 1-(1), 2-(9), 3-(8), 4-(3 + [1+ae]), 5-(2), 6-(3); 7-(4); 8-(5+acrothek). Fourth segment with one outer spinule. Acrothek consisting of two setae and one aesthetasc fused at their base.

Antenna (Figure 4A) with small coxa. Allobasis without abexopodal setae, and ornamented with one long spinule and a short row of minute spinules proximally. Free endopodal segment with inner spinules proximally and subdistally, with two lateral inner spines and one slender seta, and four single geniculate setae and one geniculate element fused basally to pinnate seta. Exopod one-segmented; with few spinules, and three setae (two pinnate spine like elements and one bipinnate seta).

Mandible (Figure 4B) robust; gnathobase with bi- and multicuspidate teeth, and one lateral seta. Mandibular palp two-segmented; first segment (basis) with some spinules and one seta; second segment (endopod) with one lateral and four apical setae.

Maxillule (Figure 4C). Arthrite of praecoxa with few spinules, with two surface setae, and three bare spines and two serrate/multicuspidate elements. Coxa with two elements. Basis seemingly with four setae; exopod vestigial represented by one seta; endopod two-segmented, first segment without any setae, second segment with two setae.

Maxilla (Figure 6A). Syncoxa with minute outer spinules; with one endite bearing three setae. Allobasis drawn into strong claw with one accompanying strong element. Endopod one-segmented, with two setae.

Maxilliped (Figure 6B) subchelate. Syncoxa with spinular rows and with one seta on inner distal corner. Basis unarmed, with longitudinal row of spinules, with some outer spinules distally. Endopod drawn into long and slender claw with one accompanying small seta.

P1 (Figure 4D, E). Intercoxal sclerite without spinular ornamentation; distal margin convex. Basis with inner and outer flagellate spine; with strong spinules at base of inner spine, between rami and at base of exopod. Exopod and endopod three-segmented; EXP1 without inner seta, EXP2 with plumose inner seta; EXP3 with one outer proximal bipinnate spine, two outer naked spines and two geniculate elements. Endopod three-segmented; slightly beyond EXP; first segment slightly shorter than second and third segments combined, reaching insertion level of inner seta of EXP2; first segment with inner seta ornamented medially with setules and with spinules along outer margin distally; second segment with plumose inner seta; third segment with one inner plumose seta apically, one median geniculate element, and one apical outer spine. Armature formula as below.

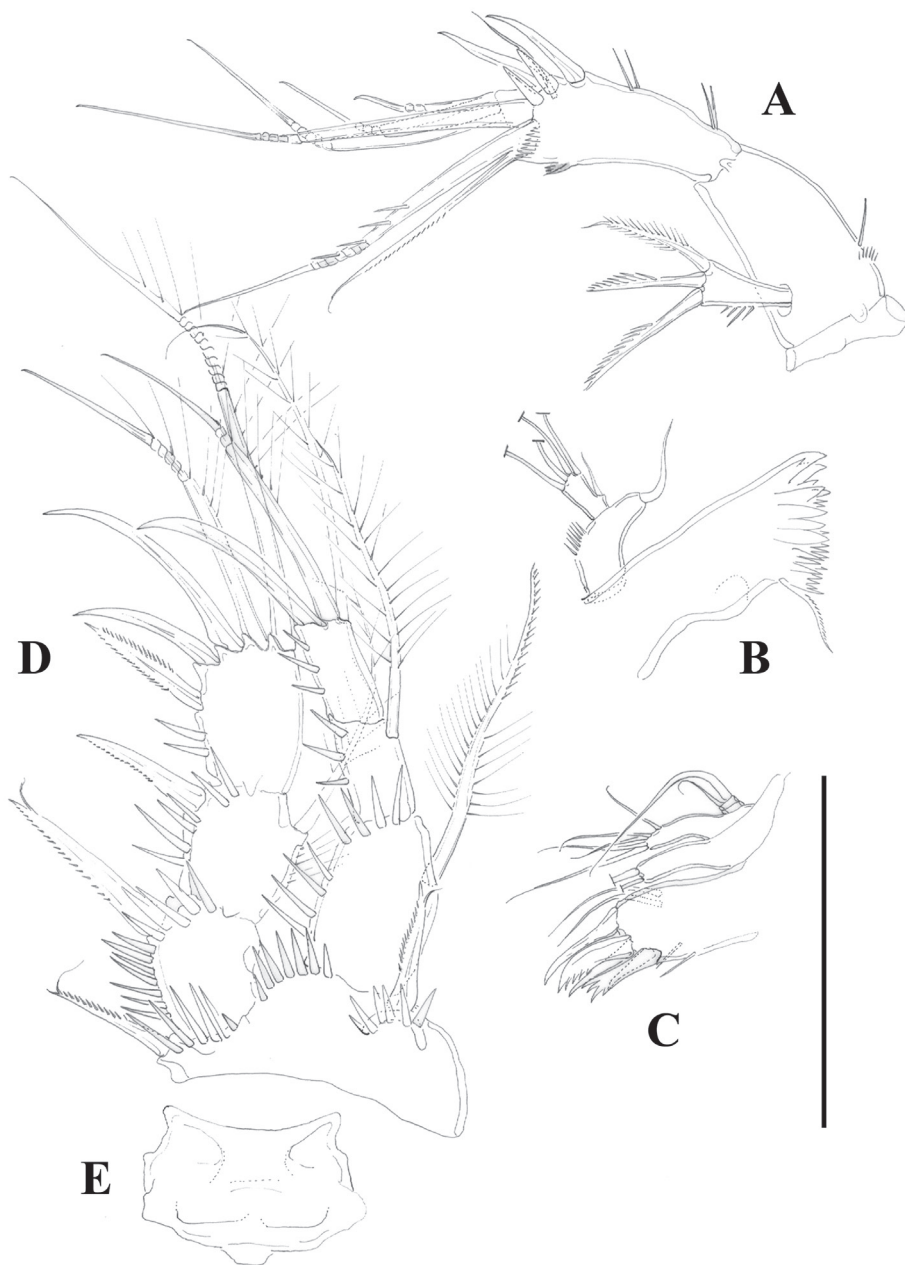


Figure 4. *Nitocra taylora* sp. n. Female. **A** antenna **B** mandible **C** maxillule **D** P1, anterior **E** intercoxal sclerite of P1, anterior. Scale bar: **A–E**=50 μm.

P2 (Figure 5B). Intercoxal sclerite with transverse spinular row distally on both lobes. Praecoxa with spinules close to joint with coxa. The latter with long outer setules and minute spinules close to outer and inner distal corner, respectively. Basis

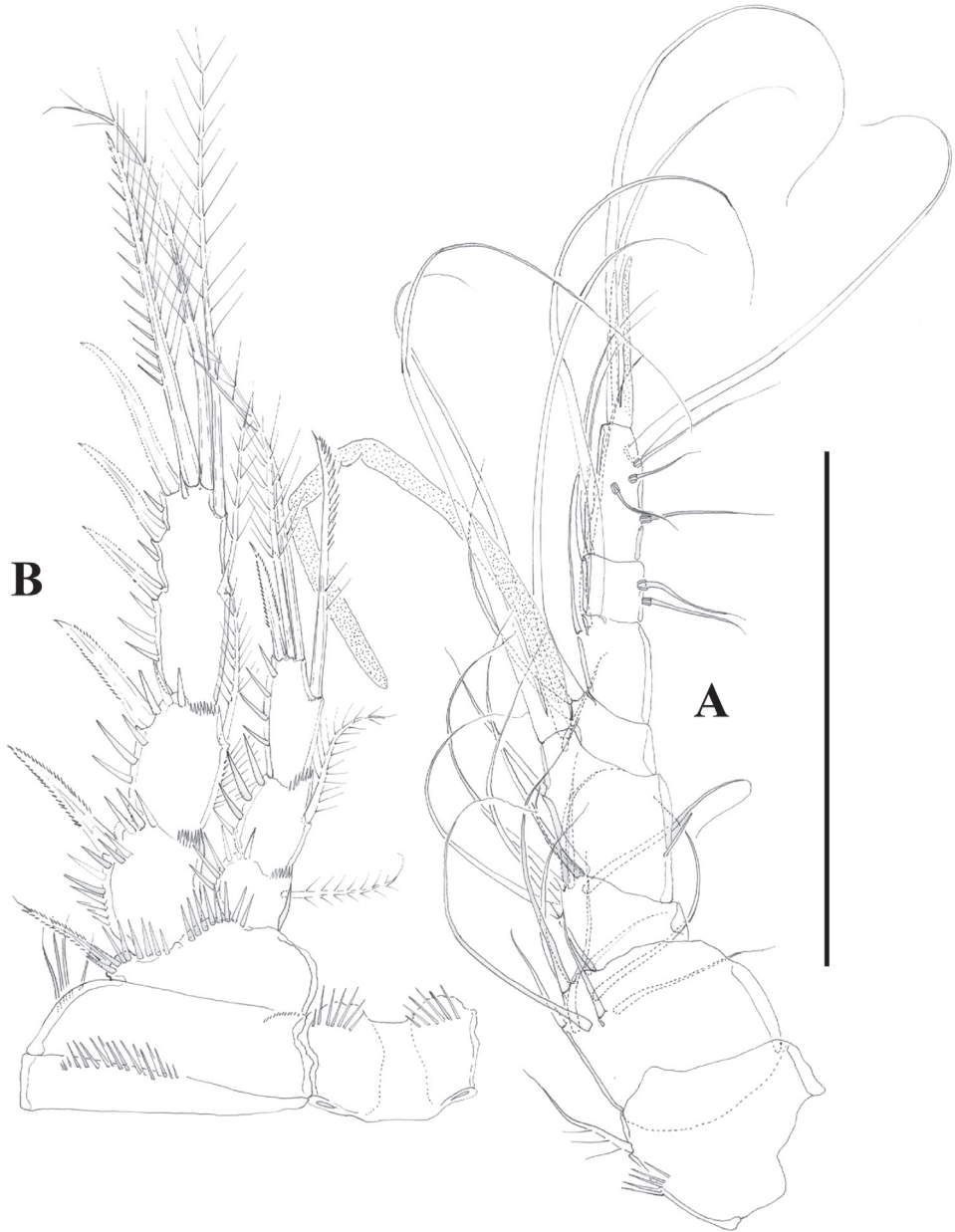


Figure 5. *Nitocra taylora* sp. n. Female. **A** antennule **B** P2, anterior. Scale bar: **A**=70 μ m; **B**=100 μ m.

with outer spine; with strong spinules between rami and at base of EXP. Exopod three-segmented; first segment without setae, second segment with plumose inner seta; third segment with three outer bipinnate spines, one outer apical seta ornamented with strong spinules and setules along outer and inner margin, respectively, one inner apical plumose seta and one inner plumose seta. Endopod three-segmented, reaching

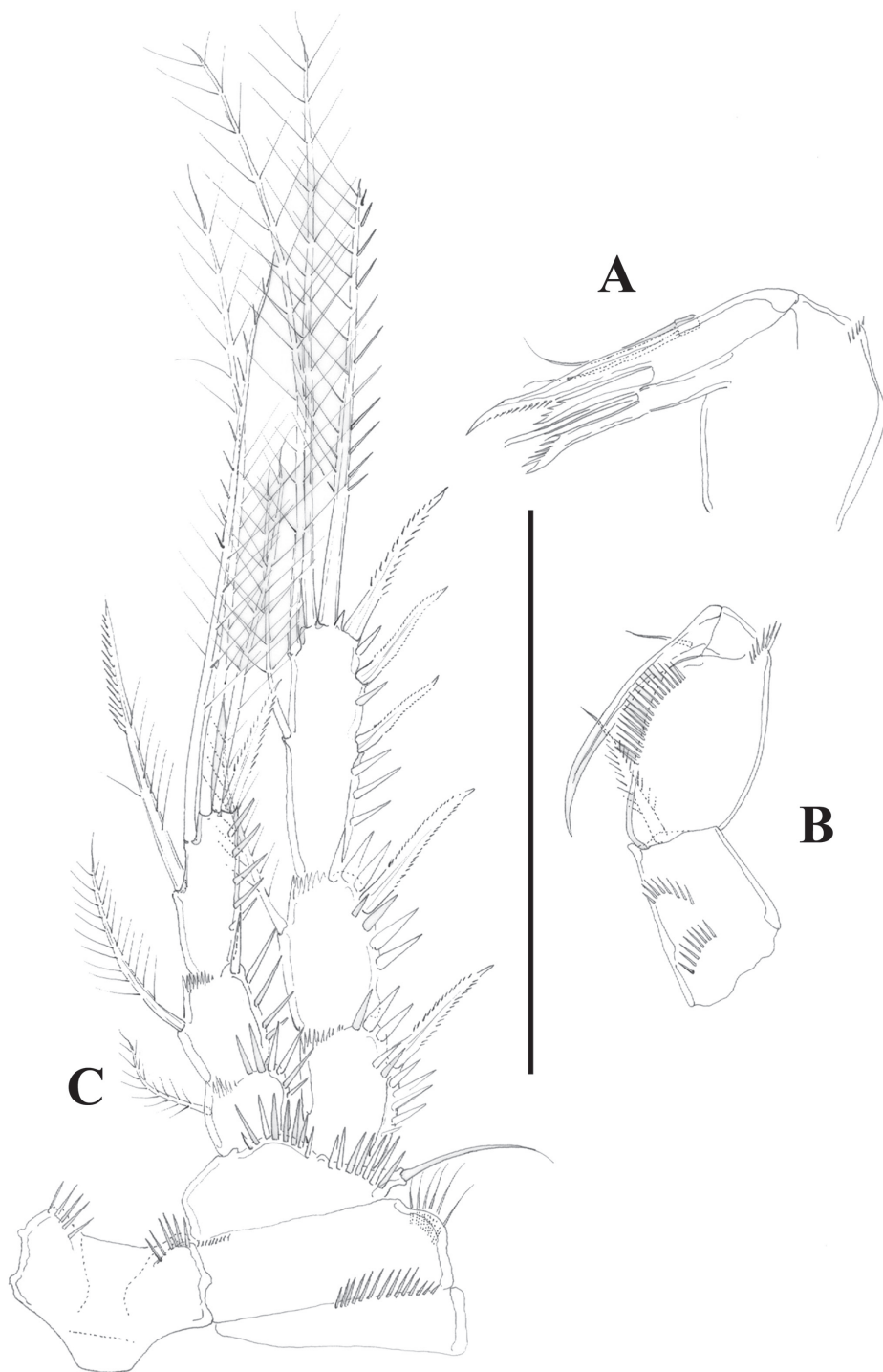


Figure 6. *Nitocra taylori* sp. n. Female. **A** maxilla **B** maxilliped **C** P3, anterior. Scale bar: **A**, **B**=70 µm; **C**=100 µm.

proximal fourth of EXP3; first and second segments with inner plumose and short seta; third segment with one strong inner seta ornamented with few setules medially and with spinules along outer margin distally, two apical plumose setae and one outer bipinnate spine. Armature formula as below.

P3 (Figure 6C). Intercoxal sclerite, praecoxa and coxa as in P2. Basis as in P2 except for outer seta-like element in P3. Exopod as in P2. Endopod as in P2 except for additional inner element in P3ENP3 ornamented with setules proximally and with spinules along outer margin distally; reaching proximal third of EXP3.

P4 (Figure 7A). Intercoxal sclerite without spinules. Praecoxa (not shown), coxa and basis as in P3. Exopod as in P3 except for comparatively stronger inner distal seta of P4EXP3 ornamented with outer and inner spinules, and for outer apical seta ornamented with inner setules and outer spinules. Endopod as in P3, except for bipinnate inner proximal seta on P4ENP3; slightly beyond EXP2.

P5 (Figure 7B). Both legs separated. Exopod and baseoendopod not fused. Exopod ovate; with inner and outer spinules; with six elements; relative length of the setae from inner to outer element as follows: 0.73, 1, 0.38, 0.69, 0.38, 0.25. Endopodal lobe with five setae/spines; relative length of the setae from inner to outer element as follows: 0.30, 0.31; 0.30, 1, 0.52; with inner and outer spinules.

Armature formula of female P1-P5 as follows:

	P1	P2	P3	P4	P5
EXP	I-0;I-1;III,2,0	I-0;I-1;III,2,2	I-0;I-1;III,2,2	I-0;I-1;III,2,2	6
ENP	0-1;0-1;I,2,0	0-1;0-1;I,2,1	0-1;0-1;I,2,2	0-1;0-1;I,2,2	5

P6 (Figure 3D) represented by median plate in anterior half of second urosomite (first genital somite); each vestigial leg represented by one outer short and one inner long seta.

Male. Habitus (not shown) as in female, except for distinct second and third urosomites; total body length measured from tip of rostrum to posterior margin of caudal rami ranging from 385 to 520 μm (mean, 437 μm ; $n = 7$; allotype, 490 μm). Ventral spinular ornamentation of third-sixth urosomites coarser and stronger than in female (Figs 8, 10D). Caudal rami (Figs 8, 10D) as in female.

Sexual dimorphism expressed in the antennule, P1Basis, P3ENP, P5 and P6.

Antennule (Figure 9A) haplocer, nine-segmented; armature formula difficult to define, but most probably as follows: 1-(1), 2-(11), 3-(8), 4-(1), 5-(14+[1+ae]), 6-(1), 7-(2); 8-(1); 9-(9+acrothek); fifth, sixth and seventh (Figure 9B) and eight (Figure 9C) segments with modified setae and blunt spines/processes. Acrothek consisting of two setae and one aesthetasc basally fused.

Antenna (Figure 10E), mandible, maxillule, maxilla and maxilliped (not shown) as in female.

P1-P4 as in female, except for sexually dimorphic male P1 Basis (Figs 9D, 10A) and P3ENP (Figure 9E). The former with modified inner spine. The latter three-segmented; first and second segment as in female; third segment with outer longitudinal row of small spinules and armed with five setae/spines.



Figure 7. *Nitocra taylora* sp. n. Female. **A** P4, anterior **B** P5, anterior. Scale bar: **A**, **B**=100 μ m.

P5 (Figs 9F, 10C). Both legs fused medially. Exopod and baseoendopod separated. The former ovate, with six setae, relative length of elements from inner to outer margin as follows: 0.47, 0.35, 1.0, 0.44, 0.17, 0.39. Baseoendopodal lobe poorly developed, with three elements; relative length of elements from inner to outer margin as follows: 1.0, 0.79, 0.67.

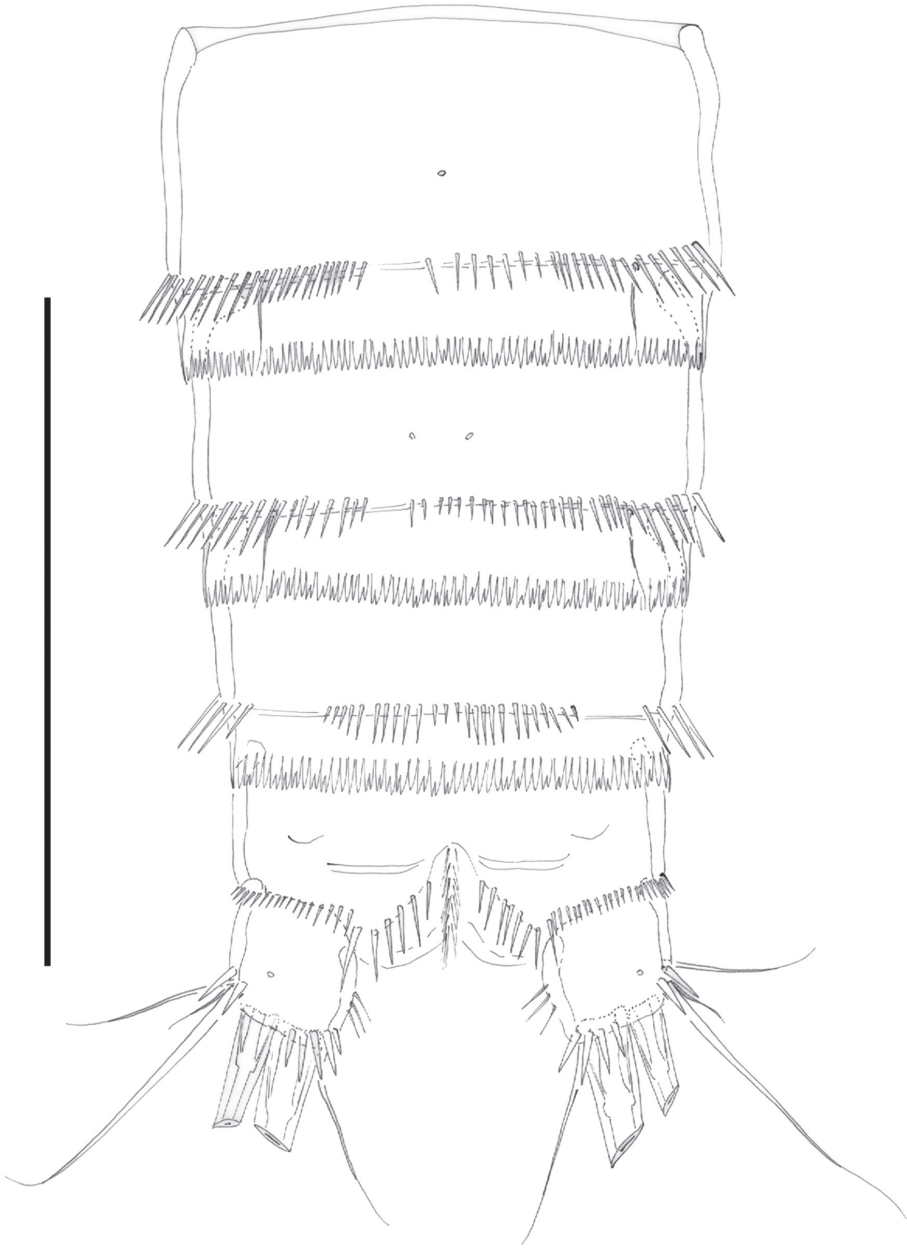


Figure 8. *Nitocra taylori* sp. n. Male. Urosome, ventral (P5- and P6-bearing somites omitted). Scale bar: 100 μ m.

P6 (Figs 9G, 10C) represented by two setae situated rather laterally, outer seta smaller than inner element.

Ecology. Habitat characteristics. During closed-mouth conditions, the St Lucia Estuary was characterised by a reversed salinity gradient, with salinities ranging from

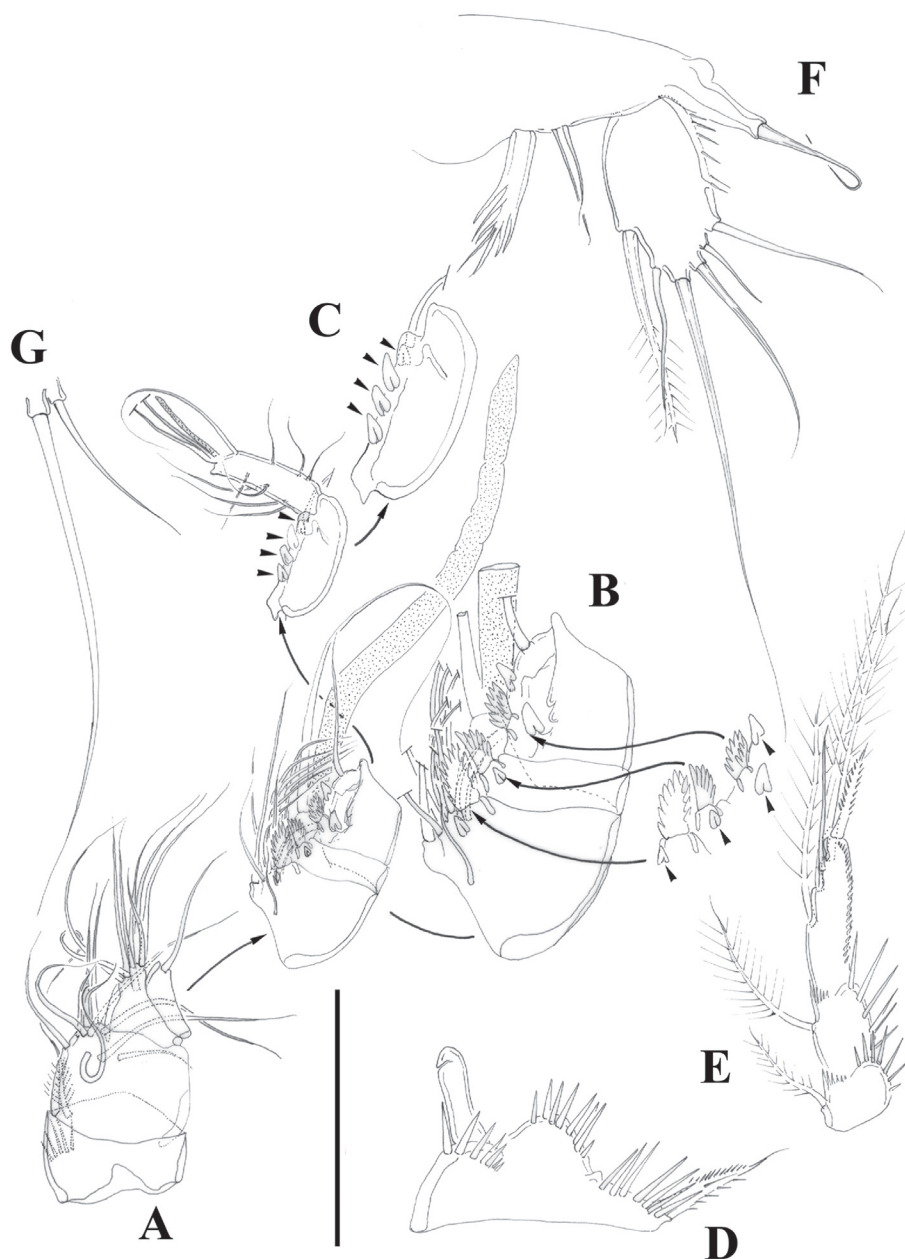


Figure 9. *Nitocra taylori* sp. n. Male. **A** antennule **B** fifth, sixth and seventh segments of the antennule, showing modified setae and blunt processes **C** eighth segment of the antennule **D** P1 basis, anterior **E** P3ENP **F** P5, anterior **G** P6, anterior. Scale bar: **A**, **E**=50 μm ; **B**, **C**=67 μm ; **D**, **F**, **G**=35 μm .

near freshwater conditions at the Mouth and Narrows, to up to 200 psu at times in the northern regions of the lake (Table 1). Salinity levels were also more variable in the lakes than in the Mouth and Narrows region. Throughout the study period, salinity

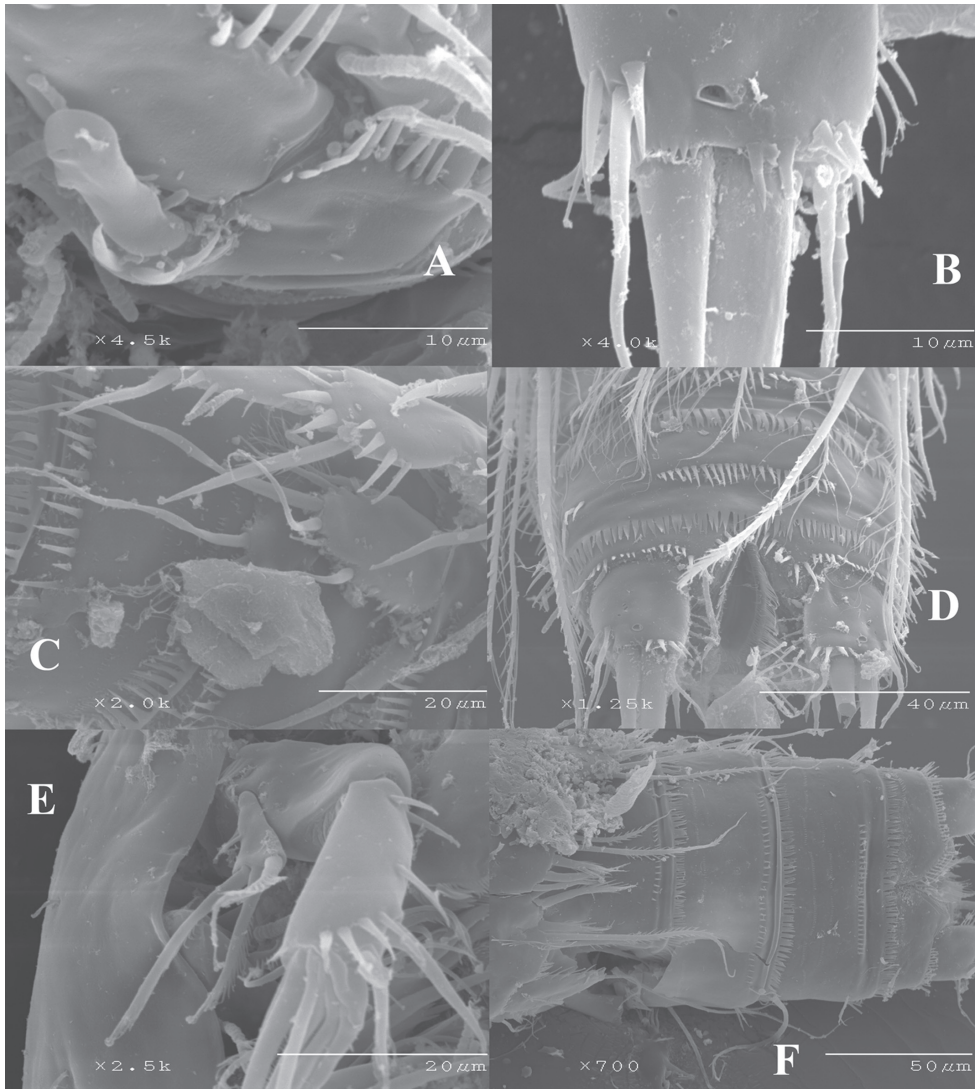


Figure 10. *Nitocra taylori* sp. n. SEM photographs **A** male P1 showing inner modified spine of basis **B** female caudal rami **C** male P5 exopod and P6 **D** posterior part of male urosome including caudal rami **E** male antenna **F** anterior part of female urosome.

levels at the Mouth ranged from 3.2 to 37.6 psu, while at Listers Point they ranged from 18.3 to 216 psu. During closed-mouth conditions, water depth was also generally highest at the Mouth and Esengeni and shallower (~0.2 m) in the lakes (Table 1). High wind action, coupled with the fine sandy substratum in the lakes, also resulted in higher turbidity levels experienced here relative to the Mouth and Narrows. Listers Point and Charters Creek generally experienced the highest turbidities, while levels at the Mouth were usually at least one order of magnitude lower (Table 1). During open-mouth conditions, there was little disparity between sites in terms of the physico-

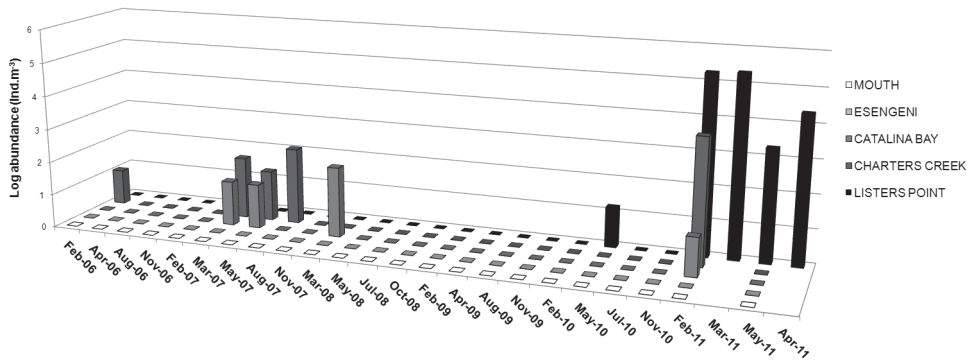


Figure 11. Abundance of *Nitocra taylori* sp. n. (ind.m⁻³) in the St Lucia Estuary from February 2006–April 2011.

Table 1. Physicochemical variables measured at each station during the different mouth phases (mean \pm SE). NTU: Nephelometric Turbidity Units; DO: dissolved oxygen.

Mouth state	Station	Depth (m)	DO (mg.L ⁻¹)	pH	Salinity (psu)	Temperature (°C)	Turbidity (NTU)
Closed	Mouth	2.05 \pm 0.52	7.9 \pm 0.52	8.02 \pm 0.37	12.8 \pm 1.67	26.5 \pm 2.32	9.36 \pm 5.82
	Esengeni	1.38 \pm 0.12	7.75 \pm 1.13	8.37 \pm 0.17	6.45 \pm 1.52	24.5 \pm 1.98	28.7 \pm 3.76
	Catalina Bay	0.15 \pm 0.04	9.06 \pm 0.91	8.52 \pm 0.14	14.5 \pm 3.24	24.8 \pm 2.58	42.8 \pm 20.5
	Charters Creek	0.11 \pm 0.02	8.38 \pm 1.04	8.79 \pm 0.22	24 \pm 4.48	29.2 \pm 2.5	33.2 \pm 11.0
	Listers Point	0.07 \pm 0.02	4.96 \pm 1.52	8.17 \pm 0.14	43.9 \pm 21.58	29.8 \pm 1.44	49.6 \pm 12.7
Open	Mouth	0.75 \pm 0.35	7.57 \pm 0.63	8.08 \pm 0.14	34.6 \pm 1.05	23.1 \pm 1.6	24.4 \pm 15.8
	Esengeni	1.51 \pm 0.21	5.23 \pm 1.48	8.25 \pm 0.07	37.4 \pm 9.38	20.3 \pm 2.98	45.6 \pm 13.5
	Catalina Bay	0.33 \pm 0.18	7.5 \pm 1.26	7.99 \pm 0.38	29.1 \pm 3.26	23.7 \pm 3.4	8.37 \pm 4.18
	Charters Creek	0.53 \pm 0.22	7.82 \pm 1.52	8.11 \pm 0.21	29.6 \pm 3.1	24.5 \pm 3.63	13.4 \pm 5.96
	Listers Point	0.43 \pm 0.28	6.91 \pm 0.91	7.01 \pm 1.01	35.1 \pm 4.25	23.8 \pm 2.73	32.8 \pm 17.7
Re-closed	Mouth	1.4 \pm 0.23	6.85 \pm 1.02	8.72 \pm 0.26	15.3 \pm 2.44	23.0 \pm 0.87	20.0 \pm 3.68
	Esengeni	1.35 \pm 0.13	7.51 \pm 0.58	8.36 \pm 0.17	9.39 \pm 2.19	23.3 \pm 0.81	60.3 \pm 12.6
	Catalina Bay	0.21 \pm 0.04	7.01 \pm 1.18	8.61 \pm 0.26	37.5 \pm 5.25	24.8 \pm 1.23	50.6 \pm 10.5
	Charters Creek	0.2 \pm 0.04	7.51 \pm 0.39	8.65 \pm 0.19	45.3 \pm 5.3	26.3 \pm 1.06	197 \pm 61.2
	Listers Point	0.31 \pm 0.05	7.53 \pm 0.58	8.53 \pm 0.19	87.4 \pm 12.8	25.6 \pm 1.73	155 \pm 41.1

chemical parameters measured. Salinity was generally within the range of sea water (~ 35 psu) across the estuarine lake and water levels in the lakes rose to approach the levels recorded at the Mouth and Narrows (Table 1).

***Nitocra taylori* sp. n. abundance and distribution.** Occurrence of *Nitocra taylori* sp. n. through the study years has been irregular and the distribution has been limited to Catalina Bay and Charters Creek in South Lake and Listers Point in False Bay (Figs 1, 11). *Nitocra taylori* sp. n. was first recorded at Charters Creek in February 2006 in low densities (10.4 ind.m⁻³), while maximum densities (2.2×10^5 ind.m⁻³) were recorded at Listers Point in March 2011. These high densities followed heavy dilution of hypersaline waters after high rainfall in early 2011. Densities remained high in this

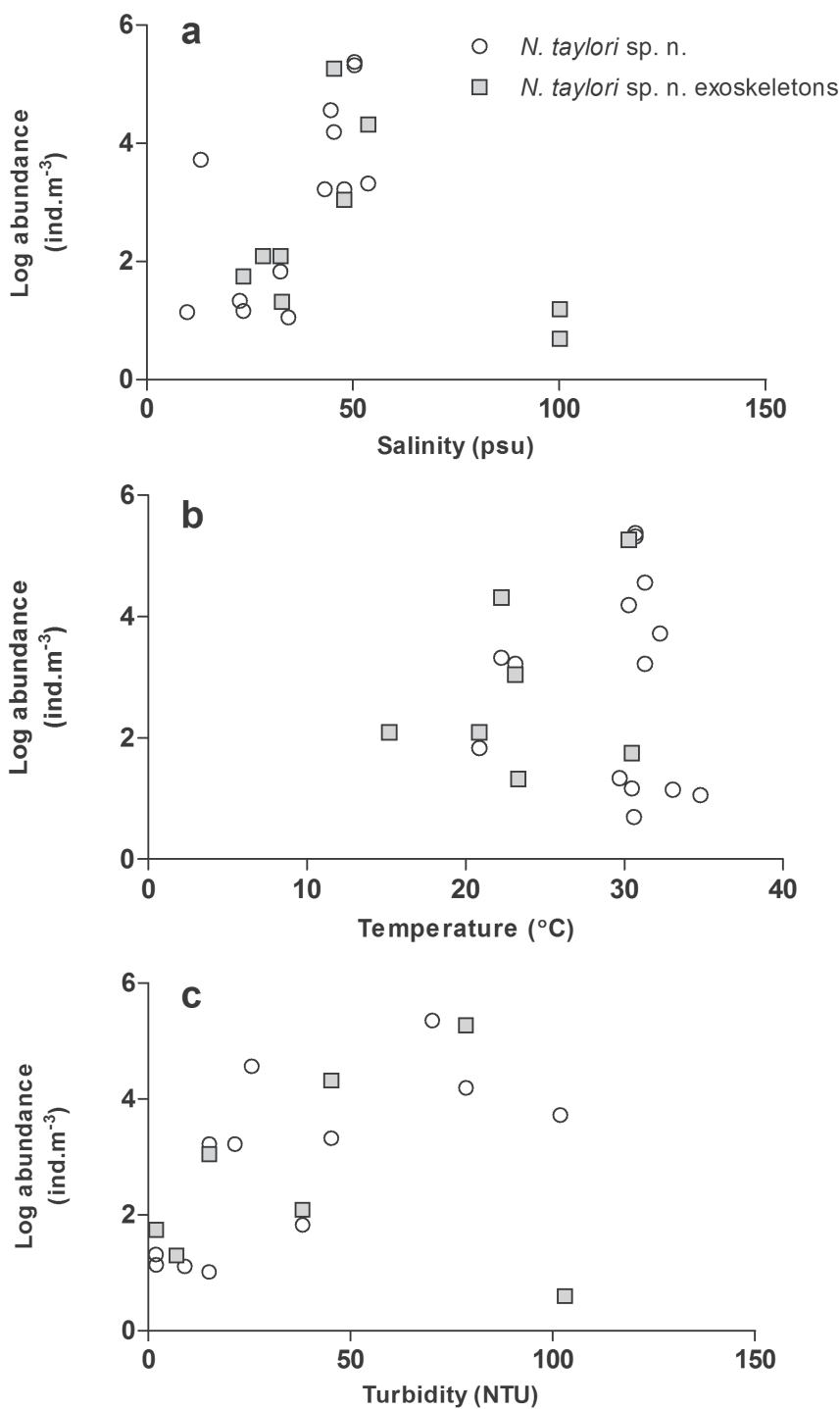


Figure 12. Abundance of *Nitocra taylori* sp. n. (alive and discarded exoskeletons) at different **a** salinity **b** temperature and **c** turbidity levels recorded in the St Lucia Estuary.

region up until May 2011, after which salinities rose again above 53.7 psu and *N. taylori* sp. n. virtually disappeared. Correlation analysis found significant positive correlations between the abundance of *N. taylori* sp. n. and salinity ($R = 0.621$, $p < 0.05$, $df = 12$) and turbidity ($R = 0.681$, $p < 0.05$, $df = 12$). *Nitocra taylori* sp. n. individuals were able to withstand a wide range of fluctuations. They were found at salinity levels ranging from 9.81 to 53.7 psu, turbidities ranging from 2 to 102 NTU and temperatures from 20.9 to 34.8 °C (Figure 12). In many instances specimens preserved in phloxine-stained formaldehyde did not take up the stain, but were rather completely transparent, resembling discarded exoskeletons. While these individuals were perfectly intact, it is unlikely that they were alive at the time of collection.

Discussion

Taxonomic remarks

The phylogenetic relationships of the species within the genus *Nitocra* are still obscure. At first glance, three species groups can be recognized based on the combination of the armature formula of the P1EXP2-3. The less speciose group, composed only by *N. sewelli* Gurney, 1927 and *N. platypus bakeri* Chappuis, 1930, exhibits one inner seta and four elements on the P1EXP2 and EXP3 respectively. This two-species group is followed by that lacking inner armature on the P1EXP2, but with five setae on P1EXP3 (*N. reducta* s. str. (Schäfer 1936), *N. delaruei* Soyer, 1974, and *N. blochi* Soyer, 1974). The rest of the species/subspecies belongs to the most diverse and seemingly primitive group characterized by the presence of one inner, and five elements on the P1EXP2 and EXP3, respectively.

The creation of species and subspecies of Harpacticoida might appear, sometimes, based on questionable grounds. This holds true, as evidenced by Wells and Rao (1987), for *N. spinipes* s. str. Boeck, 1865, *N. spinipes orientalis* Sewell, 1924 and *N. spinipes armata* Lang, 1965. The same applies at least for the subspecies of *N. reducta* and *N. sewelli*. As evidenced upon a brief analysis, the subspecific relationship of *N. reducta* s. str. and *N. reducta fluviatilis* Galhano, 1968 is questioned given the lack of inner armature in the former and the presence of an inner element in the latter. In our opinion, such difference is not evidence of the presence of a subspecies of *N. reducta*, but of a different species. Galhano (1968) herself noted also a remarkable difference in the armature formula of the female P5 baseoendopod (with four setae in Schäfer's *N. reducta*, but with five elements in Galhano's material). In the view of this evidence it is suggested to grant *N. reducta fluviatilis* Galhano, 1968 full species rank as *N. fluviatilis* stat. n. Galhano, 1968, until the variability of these two species is properly assessed.

A similar case was observed for *N. sewelli*. Sewell (1924) described a new variety of the European *Nitocra typica* Boeck, 1865, *Nitocra typica lacustris* Sewell, 1924. However, the name *lacustris* was already occupied by *Nitocra lacustris* (Schmankevitch

1875) and Gurney (1927) renamed and gave full species rank to *Nitocra typica lacustris* as *Nitocra sewelli*. He also presented a key to species of the genus in which he recognized 11 members as valid (*N. pusilla* Sars, 1911, *N. inuber* (Schmankevitch, 1875), *N. affinis*, *N. typica*, *N. dubia* Sars, 1927, *N. lacustris*, *N. fragilis* Sars, 1905, *N. wolterecki* Brehm, 1909, *N. spinipes*, *N. sewelli* and *N. platypus* Daday, 1906. Lang (1948) recognized 16 valid species and 7 subspecies, and relegated *N. inuber* (= *Dactylopus inuber* Schmankevitsch, 1875), *N. gracilimana* Giesbrecht, 1902, *N. wolterecki*, *N. phlegraea* Brehm 1909, and *N. chelifera* Wilson, 1932, as *incertae sedis* within the genus. Kunz (1976) described a new subspecies of *N. sewelli*, *N. sewelli husmanni* Kunz, 1976 from Bremen (Germany). In his analysis, Kunz (1976) noted that *N. sewelli husmanni* showed the same armature formula as in *N. spinipes* s. str., *N. spinipes orientalis*, *N. spinipes armata* (not *armatus* as in Kunz (1976); note that these subspecies were rejected by Wells and Rao 1987, and were not considered in Wells (2007)), *N. elegans* (T. Scott, 1905), *N. fragilis*, *N. bdellurae* (Liddell, 1912), *N. sewelli* and *N. medusae* Humes, 1953 (which was considered synonym of *N. spinipes* by Lang (1965)). However, as shown by Sewell (1924), the P1EXP3 of *N. sewelli* is armed with four setae/spines instead of five elements as in the rest of the above species. Kunz (1976) observed some other differences between his material and Sewell's (1924) description of *N. sewelli*, such as the number of setae on the male P5BENP, relative length of the setae of the male and female P5EXP and shape of the outer dimorphic spine on the male P3ENP3. Sewell (1924) found two males and one female and nothing is said about the intraspecific variability of the species, which for other species seems to be important in subspecies acceptance or rejection (i.e. Wells and Rao 1987). On the other hand, Kunz (1976) found some variability mainly expressed in the armature formula of the female P2ENP2 and P3EXP3, and in the relative length of the setae on the male P5BENP, but the armature formula of the P1EXP remains constant. It seems, therefore, unlikely that the armature formula of P1EXP3 observed by Sewell (1924) in the Indian material is due to intraspecific variability, which, by the way, was not observed by Kunz (1976) in the German specimens. In our opinion, Kunz (1976) erected his new subspecies based more on the differences with some other species, than on the similarities with *N. sewelli* (to which it is implicitly assumed to be more closely related), being the different armature formula of P1EXP and the differences observed by Kunz (1976: 33) enough to separate *N. sewelli* from *N. sewelli husmanni*. It is, therefore, suggested that the latter be granted full species rank as *N. husmanni* stat. n. Kunz 1976.

At present and taking into account the rejection of all the described subspecies of *N. spinipes* by Wells and Rao (1987), as well as the amendments above, 45 species within the genus are considered as valid. Of these, eight species (*N. affinis*, *N. divaricata* Chappuis, 1923, *N. fallaciosa* Klie, 1937, *N. hibernica* (Brady, 1880), *N. lacustris*, *N. mediterranea* Brian, 1928, *N. minor* Willey, 1930, *N. platypus*) contain 22 subspecies (Wells 2007). Also, the same species as in Lang (1948) (except for *N. phlegraea* which does not appear in Wells' (2007) list of species) plus *N. hyperidis* Jakobi, 1956, are regarded as *incertae sedis* within the genus (Lang 1965, Wells 2007).

Within the most speciose group (see above), *N. australis* Soyer, 1974, *N. fragilis*, *N. spinipes*, *N. intermedia* Pesce, 1983, and *N. husmanni* are unique in the combination of the number of setae/spines of the P2-P4Enp3 and P2-P4EXP3 (4,5,5 and 7,7,7, respectively) and number of inner setae on the P2-P4Enp1 (1,1,1). Note that Scott (1905) and Monard (1935) described the P4EXP3 with 7 setae/spines. In his description of the male and amendments to the description of the female of *N. elegans*, Gee (2009) showed that the P4EXP3 possesses in fact eight setae/spines (three inner setae, two apical elements and three outer spines), being the distalmost inner seta very slender and relatively short, implicitly suggesting that this seta might have been overlooked in previous descriptions, being *N. elegans* probably more related to the *N. affinis* complex of subspecies and to *N. hamata* Bodin, 1970.

The South African material herein described agrees well with the description of *N. husmanni* by Kunz (1976), to which it seems to be closely related. Unfortunately, Kunz (1976) description lacks the detail needed to make reliable comparisons between species of the genus *Nitocra*. On the other hand, due to some restrictions regarding the import/export permits of biological material, we were unable to check the specimens of *N. husmanni* deposited by Kunz (1976) in the collection of the Zoologisches Museum Hamburg under catalogue numbers K-30399 and K-30400. The main differences observed between the South African material and *N. husmanni* as described by Kunz (1976), are the number of spinules along the posterior margin of the anal operculum, which is variable in *N. spinipes* (Wells & Rao, 1987) (about seven spines in *N. husmanni*, but three in *N. taylori* sp. n.) ; P1EXP:ENP length ratio (exopod shorter than endopod in *N. husmanni*, but exopod nearly as long as endopod in *N. taylori* sp. n.), shape of the outer spine on the male P3ENP3 (curved in *N. husmanni*, but straight in *N. taylori* sp. n.), number of segments of the male antennule (10 segments in *N. husmanni*, but only nine in *N. taylori* sp. n.), relative length of the setae on the male P5BENP (innermost element visibly shorter than the two adjacent outer setae in *N. husmanni*, but innermost element longer in *N. taylori* sp. n.), shape of the male P5EXP (comparatively more elongate in *N. taylori* sp. n.), relative length of the two setae of the male P6, shape of the female P5BENP (broader, less developed and barely reaching the proximal third of the exopod in *N. taylori* sp. n., but well developed, more elongate and reaching far beyond the middle of the exopod in *N. husmanni*).

Ecological remarks

The nature of freshwater deprivation in the St Lucia Estuary has resulted in a northward gradient of drought effects. While regions in the south have recently been relatively protected from the drought, due to freshwater input from the Mpate and Mfolozi Rivers through the link canal (Whitfield and Taylor 2009), hypersalinity and low water levels have become increasingly more severe towards the north. This profile has fractionated the system into a variety of different habitats in relatively close proximity.

The first record of *N. taylori* sp. n. in the St Lucia Estuary dates back to 2006, when low densities were collected from Charters Creek, which is situated on the western shore of South Lake. It is possible that this species was present in earlier assessments conducted by Grindley (1976), however, in these assessments, harpacticoid copepods were not identified to species level. The distribution of *N. taylori* sp. n. within the St Lucia Estuary appears to be limited to Catalina Bay and Charters Creek in South Lake and Listers Point in False Bay. No specimens have been recorded from the Mouth or Narrows regions. During closed mouth conditions, False Bay and South Lake are generally characterised by low water levels, high salinities and high turbidities, particularly at Charters Creek and Listers Point. The Mouth and Narrows, on the other hand, are relatively deeper stations with higher water levels and lower salinities.

During this study, *N. taylori* sp. n. individuals were recorded at salinity levels ranging from 9 to 53.7 psu. Many species of *Nitocra* exhibit wide salinity tolerance, since they occur in a variety of different habitats (rock pools, lagoons and sandy beaches), which naturally experience wide salinity fluctuations (Matias-Peralta et al. 2005). In a study by Matias-Peralta et al. (2005), *N. affinis* was capable of tolerating salinity levels of 10 to 35 psu. Although this species was capable of surviving a broad range of salinities, reproductive capacity was hindered at the lower part of the salinity range, while levels of 30 to 35 psu were found to provide the best conditions for development. *Nitocra spinipes* has a slightly wider salinity tolerance, surviving salinity levels ranging from 0.5 to 30 psu (Wulff 1972). In the St Lucia Estuary, *N. taylori* sp. n. was not found at salinity levels lower than 9 psu. It is, therefore possible that the low salinities prevailing in the lower reaches of the estuary are restricting *N. taylori* sp. n. populations to the lakes region. While a large number of individuals were collected at salinities around 100 psu, these individuals were completely transparent, (having not taken up the stain) and resembled discarded exoskeletons. It is most likely, therefore, that they were not alive at the time of collection. Those individuals that did take up the phloxine stain were only recorded at salinity levels up to 53.7 psu.

Matias-Peralta et al. (2005) also found that low light intensities were more favorable for the overall reproduction, population growth and development of *N. affinis*. The high turbidity levels experienced in the lakes of the St Lucia Estuary may, therefore, be favorable to the development of *N. taylori* sp. n. to a certain extent and may also play a role in its distribution within the system. Lastly, water levels in the Mouth and Narrows are deeper than those found in the lakes, which, during closed-mouth conditions, are usually only ~20 cm deep. It is, therefore, possible that shallow water depths are favoured/ required for the survival of this species.

Species belonging to the genus *Nitocra* are also known to inhabit a wide range of sediment types (Boxshall and Halsey 2004). Pillay and Perissinotto (2008) classified the sediment of the St Lucia Estuary in 2005. Average values (\pm SE) of sediment particle size (ϕ) indicate that sediment was generally medium to very fine sand at the mouth (3.1 ± 0.5), but was finer at Esengeni (4.08 ± 0.89) where it was classed as very fine sand to coarse silt. Sediments in the South Lake were classed as fine to very fine sand (Charters Creek: 2.48 ± 0.44 , Catalina Bay: 2.38 ± 0.48). The finest sediments were recorded at Listers Point in False Bay (6.63 ± 0.86), where they were classed as

fine silt. This station, therefore, exhibited the highest silt content of 73.38 ± 6.55 % (Pillay and Perissinotto 2008). Within the St Lucia estuarine lake, *N. taylori* sp. n. individuals were found in both the South Lake and False Bay which have a variable sediment composition ranging from fine silt to fine sands. Similar sediment is found in other areas of the estuarine lake (i.e. Mouth and Narrows), however, no *N. taylori* sp. n. individuals were recorded here. It is, therefore, more likely that a parameter other than sediment size is restricting their distribution.

Whether the main controlling factor is salinity, turbidity, water level, sediment composition, or a combination of all of them, the distribution of this new potentially endemic species is clearly limited to the lake part of the estuary, an area which is most severely affected by the current freshwater deprivation crisis. It appears that this species cannot tolerate salinity levels above 53.7 psu, however, in the current state of the estuary; salinity levels at Charters Creek and Listers Point often exceed this value. Continued freshwater deprivation would, therefore, further limit the distribution range of this species, but may also threaten its survival within the system. Up until now, research within the St Lucia Estuary has been focused at 5 representative stations, however, further investigations are needed in order to document the full extent of the distribution of *N. taylori* sp. n. within the lakes. Additionally experimental studies on the salinity and temperature tolerance limits of this species would aid in the understanding of the physiological factors which affect its survival.

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A new species of *Coccus* (Hemiptera, Coccoidea, Coccidae) from China

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Abstract

A new species of soft scale, *Coccus multisetus* Wang & Feng, **sp. n.** is described and illustrated from Yunnan, China. A key to adult females of all *Coccus* known from China is provided.

Keywords

Hemiptera, Coccoidea, soft scale, new species, China

Introduction

The Coccidae or soft scales (Hemiptera: Sternorrhyncha: Coccoidea) is the third largest family of the Coccoidea after the Diaspididae (armored scales) and the Pseudococcidae (mealybugs) (Ben-Dov et al. 2012). Soft scales are widespread throughout the world and many of them are important pests on agricultural and horticultural crops and ornamental plantings (Henderson and Hodgson 2005), such as *Ceroplastes rubens* Maskell, *C. japonicus* Green and *Didesmococcus koreanus* Borchsenius. Nonetheless,

some species are very beneficial to man, such as *Ericerus pela* (Chavannes), whose wax provides an important raw material for many industries (Tang 1991).

Coccus is the oldest genus within the Coccidae (Avasthi and Shafee 1991). The genus was proposed by Linnaeus in 1758, with *Coccus hesperidum* Linnaeus as its type species, and belongs to the tribe Coccini, subfamily Coccinae (Hodgson 1994). *Coccus* is a very large genus present in all zoogeographical regions (Hodgson 1994) but is in urgent need of revision. Hitherto, coccidologists have listed about 94 species in this genus (Williams and Ben-Dov 2009, Martin and Lau 2011, Ben-Dov et al. 2012), of which 10 have been recorded from China (Takahashi 1932, Tao et al. 1983, Tang 1991, Martin and Lau 2011). Moreover, some *Coccus* species are pests of horticultural and ornamental plants in China (Yang 1982).

In this paper, we describe and illustrate the adult female of a new species, *Coccus multisetus* Wang & Feng, sp. n. This new species shares certain characteristics with *C. formicarii* (Green), which has previously been placed in *Taiwansaissetia* Tao et al., 1983, but that genus has now been synonymised with *Coccus* (Lin et al. in press). A key is provided for separation of the 11 species of *Coccus* currently known from China.

Materials and methods

The specimens were all immersed in 75% ethanol, and then prepared and mounted mainly according to the method of Hodgson and Henderson (2000). The terminology used in the description is mainly that of Hodgson (1994). Characters were examined under a Nikon compound microscope. An Olympus BH-2 stereoscopic microscope was used for drawing. The illustrations show adult female specimens, with the dorsum depicted on the left side and the venter on the right side, with enlargements of important characters shown around the main illustration. All measurements were made using the software NIT-Elements D and were given in micrometers (μm) or millimeters (mm).

All specimens are deposited in the Entomological Museum of Northwest A&F University, Yangling, Shaanxi, China (NWAUFU).

Taxonomy

Genus *Coccus* Linnaeus, 1758

<http://species-id.net/wiki/Coccus>

Coccus Linnaeus, 1758: 455–457. Type species: *Coccus hesperidum* Linnaeus, 1758.

Generic diagnosis. Adult female. Body oval, elongate or pyriform; usually flat, moderately convex, or nearly hemispherical. **Dorsum.** Derm membranous; gradually in-

creasing in thickness during ageing. Dorsal setae setose, spinose, clavate or cylindrical. Dorsal tubular ducts and dorsal submarginal tubercles present or absent. Preopercular pores present or absent, varying in number and shape. Anal plates together quadrate. Anal ring with 6 or 8 setae. **Margin.** Marginal setae simple to branched; stigmatic clefts deep or shallow, each with 2–8 stigmatic spines. **Venter.** Antennae 2–8 segmented. Legs well developed or reduced; with or without a tibio-tarsal articulatory sclerosis. Spiracular disc-pores with 5 loculi. Pregenital disc-pores mainly with 10 loculi, present around anal opening, or extending anteriorly, even as far as head. Ventral tubular ducts present or absent; when present located medially, or forming a sparse or dense submarginal band.

Key to adult female *Coccus* known from China

- 1 Body elongate, tapering at both anterior and posterior ends; antennae 6 segmented; with a dense submarginal band of ventral tubular ducts *C. takanoi* Takahashi
- Characters not in the above combination..... 2
- 2 Dorsal submarginal tubercles present..... 3
- Dorsal submarginal tubercles absent 9
- 3 Antennae 2 segmented; interantennal setae absent.... *C. cambodiensis* Takahashi
- Antennae 6–8 segmented; interantennal setae present..... 4
- 4 With only 1 pair of pregenital setae *C. capparidis* (Green)
- With 3 pairs of pregenital setae..... 5
- 5 Ano-genital fold with 4 pairs of setae along anterior margin *C. longulus* (Douglas)
- Ano-genital fold with 2 pairs of setae along anterior margin 6
- 6 Dorsal tubular ducts present; the outer ductules of dorsal tubular ducts very wider than those on venter..... *C. moestus* De Lotto
- Dorsal tubular ducts present or absent; if present, the outer ductules of dorsal tubular ducts narrower than those on venter..... 7
- 7 Marginal setae mostly fine and not branched *C. hesperidum* L.
- Marginal setae mostly branched 8
- 8 Body elongate oval; ventral tubular ducts present medially between the middle and hind legs..... *C. viridis* (Green)
- Body broadly oval; ventral tubular ducts sparsely scattered over venter, and not restricted to the median area..... *C. discrepans* (Green)
- 9 Dorsal setae spinose *C. pseudomagnoliarum* (Kuwana)
- Dorsal setae setose 10
- 10 With 3 pairs of pregenital setae; without a submarginal band of ventral tubular ducts..... *C. formicarii* (Green)
- With 2 pairs of pregenital setae; with a sparse submarginal band of ventral tubular ducts..... *C. multisetus* sp. n.

***Coccus multisetus* Wang & Feng, sp. n.**

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http://species-id.net/wiki/Coccus_multisetus

Figure 1

Material examined. Holotype: adult female. CHINA, Yunnan Prov., Natural reserve of Mengyang. 17.v.2012, on *Mangifera indica* (Anacardiaceae), Fang Wang (NWAFU).

Paratypes: 3 adult females, the data same as holotype.

Adult female. Unmounted material. Convex, sometimes nearly hemispherical; dark brown with a pale brown marginal band. Dried materials hard, bearing many ridges from median longitudinal ridge.

Mounted material. Body broadly oval, 2.6–3.6 mm long, 2.0–2.8 mm wide. Anal cleft about 1/7th of body length. Stigmatic clefts distinct.

Dorsum. Derm membranous, with cell-like clear areas. Dorsal setae setose, slender, each 16–30 µm long, with well-developed basal sockets, sparsely distributed over dorsum but absent from median area. Dorsal pores circular, each with a dark rim and about 1–2 µm in diameter, sparsely distributed on dorsum. Dorsal microducts, each with a very short outer ductule and a normal inner filamentous ductule, present in each cell-like area. Dorsal tubular ducts and dorsal submarginal tubercles absent. Preopercular pores, each 3–4 µm in diameter, present in an elongate group anterior to anal plates. Anal plates each broadly triangular, 152–169 µm long, 90–98 µm wide; anterior and posterior margins subequal in length, outer angle nearly a right-angle; each plate with 6 or 7 apical or subapical setae, each 9–16 µm long. Ano-genital fold with 2 pairs of long setae, each 45–60 µm long, present along anterior margin plus 3 pairs of setae, each 28–40 µm long, along each lateral margin. Anal ring subcircular, with 2 or 3 rows of translucent pores and 6 anal ring setae.

Margin. Marginal setae, each 18–29 µm long, setose, fine, straight or curved, all with well-developed basal sockets; with 40–57 setae between anterior clefts, 14–18 setae between each anterior cleft and posterior cleft, and 32–43 setae between each posterior cleft and anal cleft. Stigmatic clefts shallow, each with 3–8 stigmatic spines: with 3 median spines, each 22–38 µm long, blunt, stout, larger than more lateral spines and broadly based; lateral spines, each 8–19 µm long, blunt, smaller and with pointed apices. Eyespots not found.

Venter. Derm entirely membranous. Antennae 8 segmented, each 260–284 µm long; third segment longest; with 2 pairs of interantennal setae, each 20–38 µm long. Clypeolabral shield 206–217 µm long, 166–190 µm wide; labium 102–115 µm long, 96–109 µm wide, with 4 setae (24–28 µm) on each side. Legs rather slender; each trochanter with a pair of sensory pores on each side and a single long seta on its ventral surface; each leg with a weak articulation between tibia and tarsus, but with no articulatory sclerosis; tarsal digitules both slender, knobbed and longer than claw digitules, claw digitules both with knobbed apices, but one smaller than the other; claws without a denticle; dimensions of metathoracic leg: coxa 60–75 µm, trochanter+femur 132–160 µm, tibia 80–98 µm and tarsus 68–87 µm. With 2 pairs of long pregenital setae

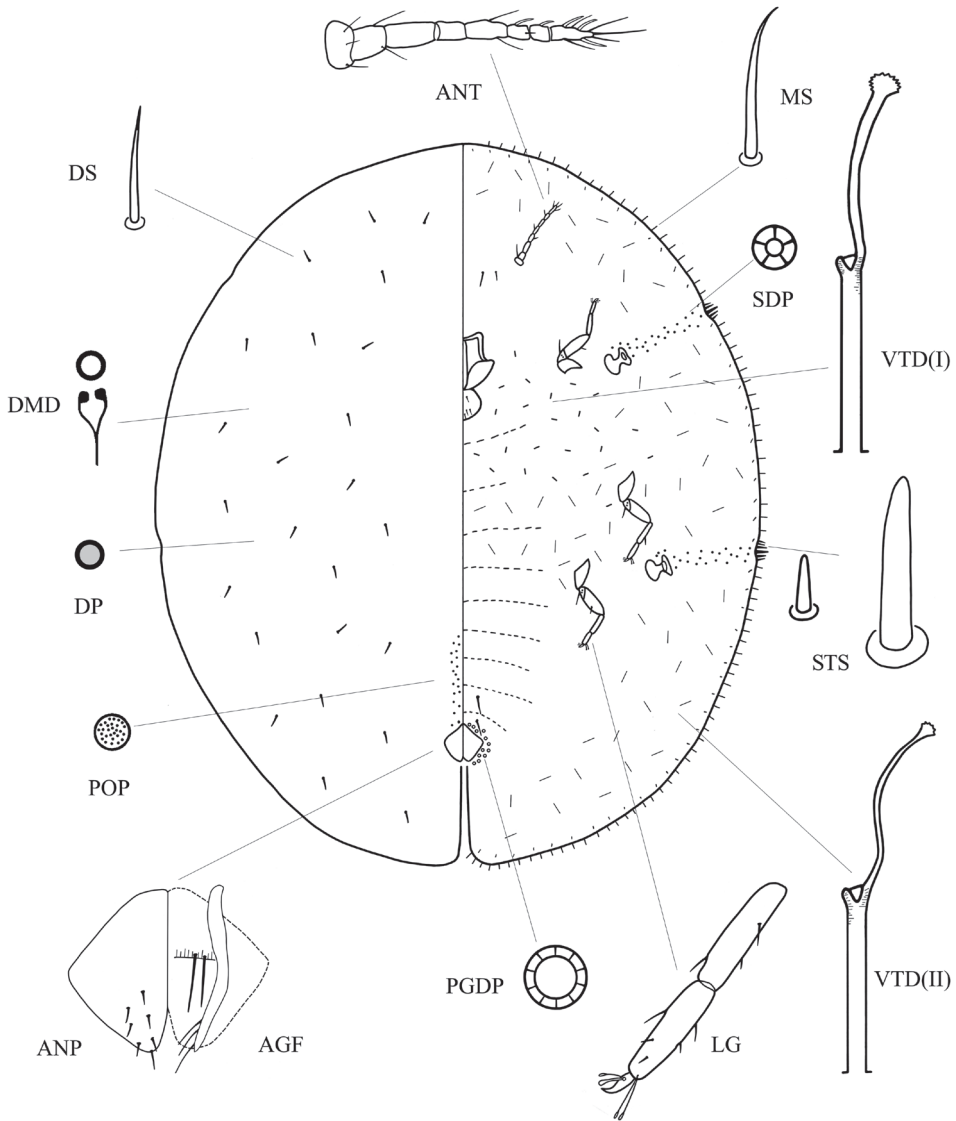


Figure 1. *Coccus multisetus* sp. n. ANT antenna; ANP anal plate; AGF ano-genital fold; DMD dorsal microduct; DP dorsal pore; DS dorsal seta; LG tibio-tarsus of hind leg; MS marginal seta; PGDP pregenital disc-pore; SDP spiracular disc-pore; STS stigmatic spines; VTD(I) ventral tubular duct of type 1; VTD(II) ventral tubular duct of type 2).

in both segments VI & VII, each 48–66 μm long; submarginal setae present in a single row, each 5–12 μm long; other ventral setae slender, each 6–12 μm long, quite sparsely distributed. Spiracles normal. Spiracular disc-pores each about 4–6 μm in diameter and mainly with 5 loculi; present in a band 2–4 pores wide between stigmatic cleft and each spiracle; with 26–38 pores in each anterior spiracle band and 34–44 pores in each posterior band. Pregenital disc-pores each about 5–7 μm in diameter and mainly

with 10 loculi; present around anal opening. Ventral tubular ducts of 2 types: 1) a duct with an elongate outer ductule, each about 15–24 μm long and 2–4 μm wide; an inner ductule about half width of outer ductule, each about 16–24 μm long and 2–3 μm wide; and with a well-developed terminal gland, each about 3–5 μm wide; present medially on head posterior to mouthpart and on prothorax; and 2) a duct with an elongate outer ductule, each about 18–24 μm long and 2–4 μm wide; an inner ductule slightly longer than outer ductule and narrower than that of type 1), each about 20–26 μm long and 1–2 μm wide; and with a well-developed terminal gland, each about 2–3 μm wide; forming a sparse submarginal band and also present medially on meso- and metathorax, extending laterally and mingling with type 1) ducts.

Distribution. China (Yunnan).

Etymology. The species epithet *multisetus* refers to the many setae on the dorsal surface of the anal plates.

Comments. Adult females of *C. multisetus* are superficially similar to those of *C. formicarii* (Green), which also had been collected in the nests of ants on *Mangifera indica*. The new species and *C. formicarii* (data from Hodgson, 1994, as *Taiwansaissetia formicarii*) share some distinct characteristics: 1) presence of setose dorsal setae; 2) lack of a tibio-tarsal articulatory sclerosis; 3) pregenital disc-pores restricted to around anal opening, and 4) lack of dorsal tubular ducts and submarginal tubercles. These distinct characteristics of the two species differ from those of typical *Coccus*, and might be due to their myrmecophilous habit and adaptation to living inside ant nests (Lin et al. in press).

However, *C. multisetus* can be distinguished by the possession of the following features (character states of *C. formicarii* in brackets): 1) 2 pairs of pregenital setae present (3 pairs); 2) 6 or 7 apical or subapical setae on each plate (3 or 4); 3) a submarginal band of ventral tubular ducts (absent); 4) dorsal setae nearly absent on median area (present), and 5) absence of a denticle on the claw (present). Although Hodgson (1994), when studying slide-mounted specimens considered to be *T. formicarii*, found their morphology to be rather variable, he noted none of the differences mentioned here, other than the presence of the denticle on the claw. It is thus considered that *C. multisetus* is an undescribed species which may be close to *C. formicarii*.

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Notes on the genus *Taridius* Chaudoir, 1875 (Coleoptera, Carabidae, Lebiini), with descriptions of six new species from Vietnam

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Abstract

Six new species of the genus *Taridius* Chaudoir, 1875 (Coleoptera, Carabidae) are described from Vietnam: *T. ornatus* **sp. n.**, *T. piceus* **sp. n.**, *T. fasciatus* **sp. n.**, *T. abdominalis* **sp. n.**, *T. coriaceus* **sp. n.**, and *T. disjunctus* **sp. n.**. The generic characters are redescribed, based on fresh material, with a key provided to all congeners.

Keywords

New species, *Taridius*, Carabidae, Coleoptera, Vietnam

Introduction

The genus *Taridius* Chaudoir, 1875, is a member of the subtribe Cimindidina Laporte de Castelnau, 1834, tribe Lebiini. Originally, it was established for a single species to which five more species were added afterwards (Bates 1892, Andrewes 1935, Emden 1937). Kirschenhofer (2010) contributed further five species to the genus, these being new or earlier described by him in the genera *Cymindis* Latreile, 1806, and *Perseus*

Kirschenhofer, 2003. He also downgraded the latter genus to a subgenus of *Taridius* and placed there all congeners, leaving the nominate subgenus monobasic. While the genus is widespread in the Oriental realm, its members have been recorded from type or few close localities, implying highly limited species ranges. Yet this does not seem to be the case because the adults of most of the species are winged and fly well.

The species diversity in the genus is unevenly distributed across the realm. In particular, five species have been reported from India, one from Myanmar, another one from Malay Peninsula, three from the Greater Sunda Isles (Java and Borneo), and only one species from Vietnam, Indochina. Several recent expeditions of the Joint Russia-Vietnam Tropical Center to southern Vietnamese provinces have shown that Vietnam actually supports a rich fauna of *Taridius*.

Six new species are described below from material taken during those expeditions, with a key to all congeners being provided to follow those of Andrewes (1935) and Kirschenhofer (2010). I also think it advisable to refine descriptions of the genus, as well as its two species, *T. sabahensis* and *T. wrasei*, by adding some important characters absent from the original descriptions. Indices used are based on the measurements as follows: total body length between the apices of the mandibles and elytra, length of the elytra from their basal margins to the apices, maximum widths of both the pronotum, elytra and head across eyes, as well as length of the pronotum along its mid-line.

Holotypes and some paratypes are deposited in the Zoological Museum of the Moscow State University, the other paratypes in the author's reference collection, A.N. Severtsov Institute of Ecology & Evolution, Russian Academy of Sciences (SIEE). A few specimens of *Taridius* have also been studied from the collection of the Moscow Pedagogical State University (MPSU). All the labels are typewritten, type ones also being red. These are uniform as follows: "HOLOTYPE or PARATYPE / *Taridius* / species name, sp. n. / D. Fedorenko des., 2011".

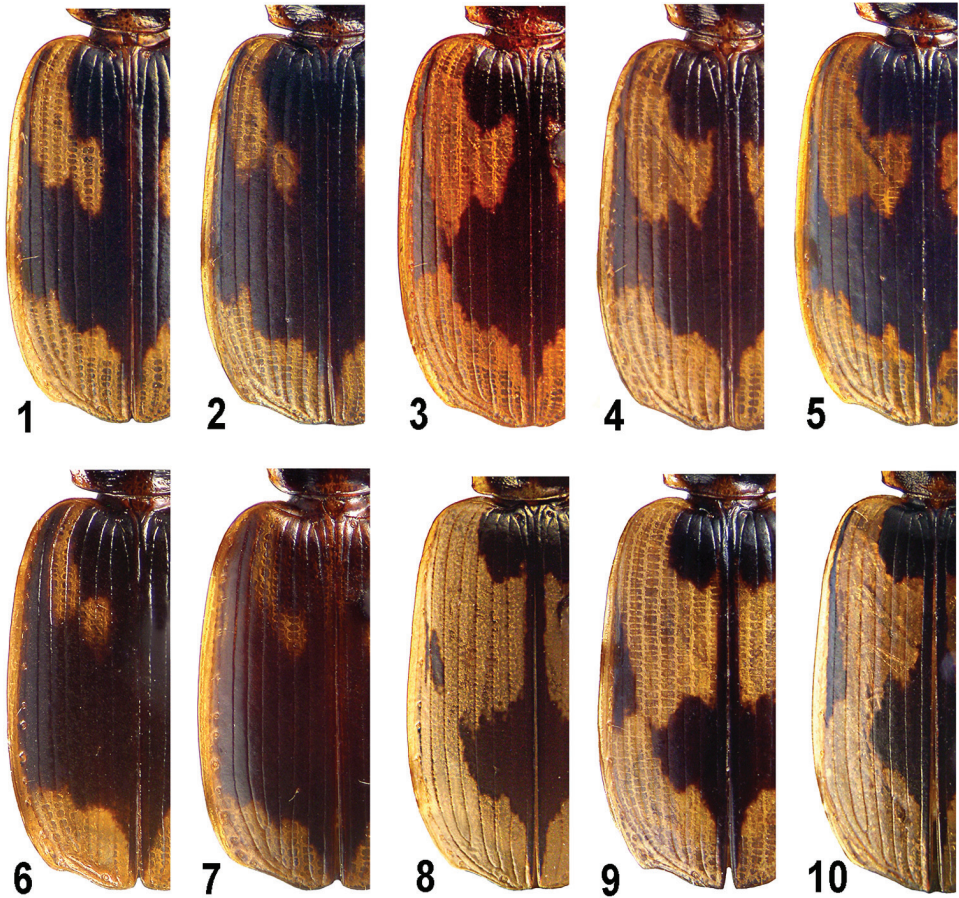
Taxonomy

Genus *Taridius* Chaudoir, 1875

<http://species-id.net/wiki/Taridius>

Type species: *Taridius opaculus* Chaudoir, 1875, by monotypy.

Redescription. Body medium-sized, subconvex to flattened. Dorsum glabrous, ventral surface glabrous or sparsely ciliate. Body dark brown to black, mouthparts, clypeus anteriorly, antennae, legs, propleura, reflexed side margin of pronotum, pronotal apex before site of front transverse impression, as well as base behind basal transverse impression mostly pale, yellow. Elytra black or dark brown, usually with a pale, yellow to pale brown, side border, epipleura and an ornate pattern which sometimes bears very slight bronzed reflexions over dark color. This pale pattern (Fig. 1) is generally composed of a



Figures 1–10. Genus *Taridius*, elytral pattern: *T. fasciatus* sp. n. (1, 2), *T. abdominalis* sp. n. (3, 4), *T. sababensis* (5), *T. ornatus* sp. n. (6), *T. piceus* sp. n. (7), *T. disjunctus* sp. n. (8), *T. wnasei* (9), *T. coriaceus* sp. n. (10).

large apical spot (PAS) and a humeral vitta (PHS) subdivided into two. Its external part, PHSe, long, running on intervals 6 and 7 and expanded onto 5th behind, while a shorter and smaller internal part, PHSi, occupying intervals 2 to 4 or 3 and 4 before middle. When increasingly extended backwards, PHSe makes a subequally wide, dark, subtransverse, medial fascia (DMF) constricted in interval 6 first (Figs 3–5) and divided into a common (post)median spot (DMS) and a submarginal strip (DLS) after (Figs 8–10). DLS runs on intervals 7 and 8, while tending to be reduced to a small patch at the middle and another one, vague to missing, behind shoulder. The remaining part of the dark pattern, a rounded to quadrate dark spot around scutellum on intervals 1 to 4–5 (DSS) is extended into a sutural strip (DSF) running on intervals 1–2 and tapering behind DMF or DMS. When entire, the dark pattern resembles a flying bird with open wings. Middle of prosternum, meso- and metaventrite mostly pale, reddish or reddish-yellow.

Microsculpture isodiametric on head and elytra, before anterior transverse impression and behind basal transverse impression of pronotum, as well as along its side margin and often also over its more or less wide, posterolateral area. Microsculpture on pronotal disc grated, composed of transverse, very wide and evenly rectangular meshes, rarely these being isodiametric (*T. coriaceus* sp. n.). Sometimes longitudinal meshes traceable along side margin between antero- and posterolateral setigerous pores (*T. piceus* sp. n.). Elytral microsculpture conspicuous, that on head and pronotal disc often obsolete. Head and pronotum minutely and sparsely punctate.

Eyes convex, genae short to rather long but not or barely projecting, head mostly broadest level to a little before 1/2 length of eye tubercle (eye and gena combined); frontal longitudinal carinae 2–5, rarely seven, on each side. Labrum rectangular, wider than long, very slightly emarginate at and sexsetose along front margin. Submentum bisetose, tooth of mentum stout, rather widely rounded apically, with two setae at middle. Ligula rather wide, truncate, bisetose, paraglossae adnate, slightly surpassing ligula, widely rounded apically. Penultimate labial palpomere plurisetose internally, apical joint fusiform to subtriangular. Antennae filiform, pubescent from antennomere 4 onwards, about last three joints surpassing elytral base, antennomeres 1, 3 and 4 subequally long, 3rd two thirds to nine tenths longer than 2nd; basal three joints with several cilia or very short hairs in addition to standard setae, 2nd mostly with three, preapical, lateral setae anteriorly.

Pronotum bisetose on each side, exceptionally trisetose anteriorly (*T. opaculus*), subcordate, broadest far before middle, with front margin slightly sinuate, front angles angles which barely projecting in the latter case. Anterior border interrupted medially, straight or barely sinuate before base; hind angles subrectangular to predominantly obtuse or highly so and rounded. Base oblique towards and often rounded at hind angles which hardly projecting in the latter case. Anterior border interrupted medially, basal border entire, sometimes weaker or interrupted in the middle. Side margin rather widely explanate and strongly reflexed, more so basad, often with more or less dense and large but shallow punctures throughout or only basally. Mid-line fine but moderately deep, extremities excluded, both front and basal transverse impressions weak to indistinct, basal foveae wide, shallow, mostly reduced to a small but rather deep pit just before basal border, giving rise to side gutter, basal transverse impression and a fine to indistinct paralateral line as internal border of basal fovea. A flattened area between this line (or its virtual forward extension) and side border rather densely transversely rugulose, sometimes coriaceous, a sparser and shallower rugosities over disc.

Elytra oblong-oval, humeri rounded, apical truncature slightly oblique, a little sinuate, with outer angle widely or obtusely rounded, apices truncate and mostly sharp, rectangular to slightly obtuse, with an almost indistinct re-entrant angle in the latter case. Angle between side and basal borders (humeral angle) absent or, exceptionally, highly obtuse opposite stria 7, basal border entire and slightly sinuate. Elytral striae moderately deep all along, impunctate or crenulate at base, intervals flat, sometimes (individual variability) odd narrower and a little more convex than even ones. Interval 8 sharply carinate internally in anterior three fourths. Dorsal setigerous

pores two, evenly spaced along stria 3, exceptionally (*T. nilgircus* Andrewes, 1935) serial on intervals 3 and 5. Umbilicate series uninterrupted and composed of *ca* 16 setigerous pores. Wings well-developed in all congeners examined but *T. piceus* sp. n. Metepisterna long.

Apical margin of last abdominal sternite (VII) bisetose in both sexes but quadrisetose in females of *T. disjunctus* sp. n., *T. wrasei* Kirschenhofer, 2010 and *T. andrewesi* Emden, 1937.

Profemur unisetose in the middle of postero-ventral edge, metacoxa bisetose along outer margin of its posterior part, metatrochanter unisetose, metafemur bisetose; meso- and metatibia dorsally with a more or less distinct, longitudinal sulcus, its edges carinate or at least sharp. Tarsi glabrous dorsally, claw joint setose beneath, claws pectinate. Meso- and metatarsomere 1 as long as the following two combined. Basal three protarsomeres of male dilated and furnished with adhesive vestiture.

Penis (Figs 17–28) in dorsal view mostly with a wide, premedian, swell on right side, apical lamella subtriangular to parallel-sided, widely rounded at tip. Parameres of similar shape in different species (Figs 29–32).

Female gonocoxite IX with two, inner (dorsal) and outer (ventral), ensiform setae varying in size between species. The best developed gonocoxite and setae, especially inner ones, tend to be reduced from *T. disjunctus* sp. n. to *T. coriaceus* sp. n. (Figs 39–46), inner seta becoming very small and invisible in some species (Figs 43–46).

Geographic distribution. Widespread in South and South-East Asia, from North India and Indochina in the north to Borneo and Java in the south.

Habits and habitats. The beetles occur at the altitudes of 150–1800 m asl where they dwell in leaf-litter of monsoon, broad-leaved, tropical or subtropical forests. Only two specimens of *T. ornatus* were taken in coniferous forests, among them a paratype collected in a *Pinus dalatensis* forest using pitfall traps and a female from Chu Yang Sin caught by hands in leaf-litter of an elfin wood under trees of *Chamaecyparis hodginsii* (Dunn, 1908). At higher altitudes, the adults were predominantly taken by pitfall trapping. This is true of *T. ornatus* and *T. piceus* found to occur syntopically. At low altitudes, beetles mostly flew to lights at night. These were *T. fasciatus* and *T. abdominalis* taken together, as well as a paratype of *T. disjunctus*. A specimen of *T. abdominalis* sp. n. was sifted from bamboo leaf litter and individual specimens of the other species (*T. coriaceus*, *T. disjunctus*, *T. wrasei*) were only occasionally collected by hand on the soil surface.

It follows also that up to five species can live sympatrically and at least two syntopically as well. The sympatric species were found to be as follows: (1) *T. ornatus*, *T. piceus*, *T. disjunctus*, *T. coriaceus* and *T. fasciatus* in the Bi Doup – Nui Ba Nature Reserve, (2) (1) *T. ornatus* and *T. disjunctus* in the Chu Yang Sin National Park, (3) *T. fasciatus* and *T. abdominalis* in the Bu Gia Map National Park.

In addition, the fact that different species or their groups show female styli of strongly different structure implies differences in the substrates, soil or leaf-litter of different kind, the larval stages inhabit.

Comments. (1) The congeners are all alike because of a great similarity in body shape. Yet, when combined, the color patterns of both the elytra and the ventral sur-

face of the hindbody are features sufficiently distinctive to discriminate most of the species with certainty.

(2) According to Kirschenhofer (2010), two structural characters, the shape of the last labial palpomere and the number of pronotal anterolateral setae, separate the subgenus *Perseus* from the nominate one which comprises *T. opaculus* only. In particular, a spindle-shaped palpomere and a single, standard, seta on the pronotum are peculiar to the former subgenus, whereas a subcylindric palpomere, combined with three anterolateral setae, to the latter. However, the palpomere has been found to be somewhat variable in shape. Firstly, it is subcylindric in males but fusiform in females. Secondly, the apically broadest palpomere is that of *T. piceus* sp. n., the species showing only one anterolateral seta on the pronotum. This leaves the polymerous anterolateral setae on the pronotum as the only support to an isolated position of *T. opaculus*. Yet, the support is weak because some other characters taken separate, *eg*, the serial dorsal setae on the elytra in the case of *T. nilgircus*, could also provoke the erection of a monobasic subgenus if necessary, polymerous pronotal and elytral setae are deemed hardly different for that purpose. Based on the above evidence, I refrain here from subdividing the genus into the subgenera pending a comparative analysis of male and female genitalia, as well as the number of setae on abdominal sternite VII of the female.

At least two lineages have been traced within the genus. The members of the first lineage share the last abdominal sternite bisetose in both sexes, as well as rather weak female styli supplied with strongly reduced ensiform setae. In addition, the dark elytral pattern is mostly entire, the facial carinae are more numerous, and often also the dorsal microsculpture is superficial on the head and pronotum. In the second lineage which includes *T. wrasei*, *T. disjunctus* sp. n., *T. andrewesi* and probably also *T. pahangensis* (Kirschenhofer, 2003), females are distinctive in showing four setae on the last abdominal sternite. A rather pale elytral pattern, conspicuous dorsal microsculpture, less numerous frontal carinae and strongly armed female styli, albeit this feature has been examined in but two species, are among additional characters of the lineage.

Key to species of *Taridius*

- 1(4) Elytra monochromous dark, with two discal setigerous pores on interval 3.
- 2(3) Small, 6.5 mm in length. Pronotal side margin bisetose, underside black, frons tricarinate on each side at best, elytra short, about three fourths longer than wide. (S-India)..... ***T. niger* Andrewes, 1935**
- 3(2) Large, 10–10.5 mm in length, anterolateral setae two or three on each side, elytra a half longer than wide, frontal carinae five or more on each side. (N-India, Myanmar) ***T. opaculus* Chaudoir, 1875**
- 4(1) Elytra bicolored, dark with a pale pattern.
- 5(6) Elytral discal setigerous pores about half-a-dozen in intervals 3 and 5. Elytral color pattern same as in Fig. 4. (S-India) ***T. nilgircus* Andrewes, 1935**
- 6(5) Only elytral interval 3 with two discal setigerous pores.

- 7(24) Pale spots, PHS and PAS, small, more or less widely separate medially; dark pattern entire (Figs 1–7), rarely with a vague posthumeral stroke detached from.
- 8(17) DMF subequally wide, with dark color subequally long on intervals 3 and 6 (Figs 1, 2, 6, 7). Female abdominal sternite VII bisetose.
- 9(12) DMF wide due to both pale spots small, PHS narrow, PAS short, transverse, occupying apical fourth of elytra at best.
- 10(11) Large, 8.5–9.6 mm in length. Microsculpture very sharp on head and elytra, conspicuous over pronotum, its angles highly obtuse and widely rounded. Mostly two long and one short frontal carina on each side. Elytral dark pattern black, increasingly pale forwards, at base slightly to barely darker than very small PHS (Fig. 7). Humeral angle highly obtuse but distinct. Wingless, elytra wide, 1.38–1.43 as long as wide 2. ***T. piceus* sp. n.**
- 11(10) Small, 7.4–8.4 mm in length. Microsculpture obsolete on head and pronotum. Frontal carinae four or five on each side. Elytral dark pattern black throughout, contrastingly darker than pale spots (Fig. 6). No angle between elytral side and basal borders. Winged, elytra longer, 1.44–1.53 as long as wide 1. ***T. ornatus* sp. n.**
- 12(9) Either DMF narrower (Figs 1, 2) or pale humeral vitta large, or both.
- 13(14) PHSe wide, running on intervals 5 to 8, frontal carinae on each side five. Large, 9 mm in length. (Myanmar) ***T. birmanicus* Bates, 1892**
- 14(13) PHSe narrow, reaching interval 7 only. Body length under 9 mm.
- 15(16) Frontal carinae on each side four or five; microsculpture traceable at least along basal and front margins of pronotum. Body small, 6.6–7.5 mm in length 3. ***T. fasciatus* sp. n.**
- 16(15) Frontal carinae three at best, body length 7.8–8.0 mm. (N-Vietnam) ***T. vietnamensis* (Kirschenhofer, 1996).**
- 17(8) DMF either reduced to a very narrow lateral process of large DMS between very large PHS and PAS or constricted in interval 6, with dark color 1/4–2/3 or still longer on interval 3 than on 6 (Figs 3–5).
- 18(19) PHS and PAS very large, with a very narrow DMF in-between, DLS reduced to a short posthumeral stroke on interval 8. Elytra short, 1.4 times as long as wide. Dorsal microsculpture conspicuous. Underside dark. Frontal carinae three on each side. Body length 7.8 mm. (NE-India) ***T. jendeki* Kirschenhofer, 2010**
- 19(18) PHS and PAS widely separated, DLS well-developed on outer intervals in anterior two thirds or at least in middle third. Elytra about half as long as wide. Abdomen often pale laterally or almost entirely.
- 20(21) Abdomen pale throughout but laterally. Elytral dark pattern with very slight bronzed tinge, DLS entire. Frontal carinae four or five on each side. Female abdominal sternite VII bisetose. Body small, 7.2–7.4 mm in length 4. ***T. abdominalis* sp. n.**
- 21(20) Abdomen either dark or with anterior two or three sternites pale laterally.

- 22(23) Abdomen entirely dark. Frontal carinae four on each side. Female abdominal sternite VII bisetose. Elytral pattern as in Fig. 5, a short posthumeral stroke detached from DLS. Body large, 8.5–9 mm in length. (Borneo) 5. *T. sabahensis* (Kirschenhofer, 2003)
- 23(22) Anterior two or three abdominal sternites pale laterally. Frontal carinae two or three on each side. Female abdominal sternite VII quadrisetose. Body length 7–8.5 mm. (Java) *T. andrewesi* Emden, 1937
- 24(7) PHS and PAS very large and adjoining on interval 6 or also on 5, sometimes vaguely separated, DLS separate or almost so (Figs 8–10). Dorsal microsculpture conspicuous and usually sharp. Very slight bronzed tinge mostly traceable on elytra.
- 25(30) Abdomen dark; frontal carinae two or three on each side.
- 26(29) DLS long, well-developed in anterior three fourths. Female abdominal sternite VII bisetose.
- 27(28) Body small, 7–8 mm in length. Elytral dark pattern without metallic tinge. (India) *T. stevensi* Andrewes, 1923
- 28(27) Body large, 8.6 mm in length. Elytral dark pattern with slight bronzed tinge. Pronotum with sharp and dense transverse rugosities over disc but its middle, and a very sharp microsculpture 6. *T. coriaceus* sp. n.
- 29(26) DLS reduced to a small and oblique spot in third sixth (Fig. 8); slight bronzed reflexions over dark color. Female abdominal sternite VII quadrisetose. Body large, 8.2–8.9 mm in length 7. *T. disjunctus* sp. n.
- 30(25) Abdominal sternites laterally pale. DLS well-developed in middle third but reduced anteriorly.
- 31(32) Frontal carinae mostly two on each side, with an additional and rather slight outer carina before anterior supra-orbital seta. Body length 7.2–8 mm. Female abdominal sternite VII quadrisetose. (Sabah, Borneo) 8. *T. wrasei* Kirschenhofer, 2010
- 32(31) Frontal carina one on each side. Body length 7.9 mm. (Pahang, Malay Peninsula) *T. pahangensis* (Kirschenhofer, 2003)

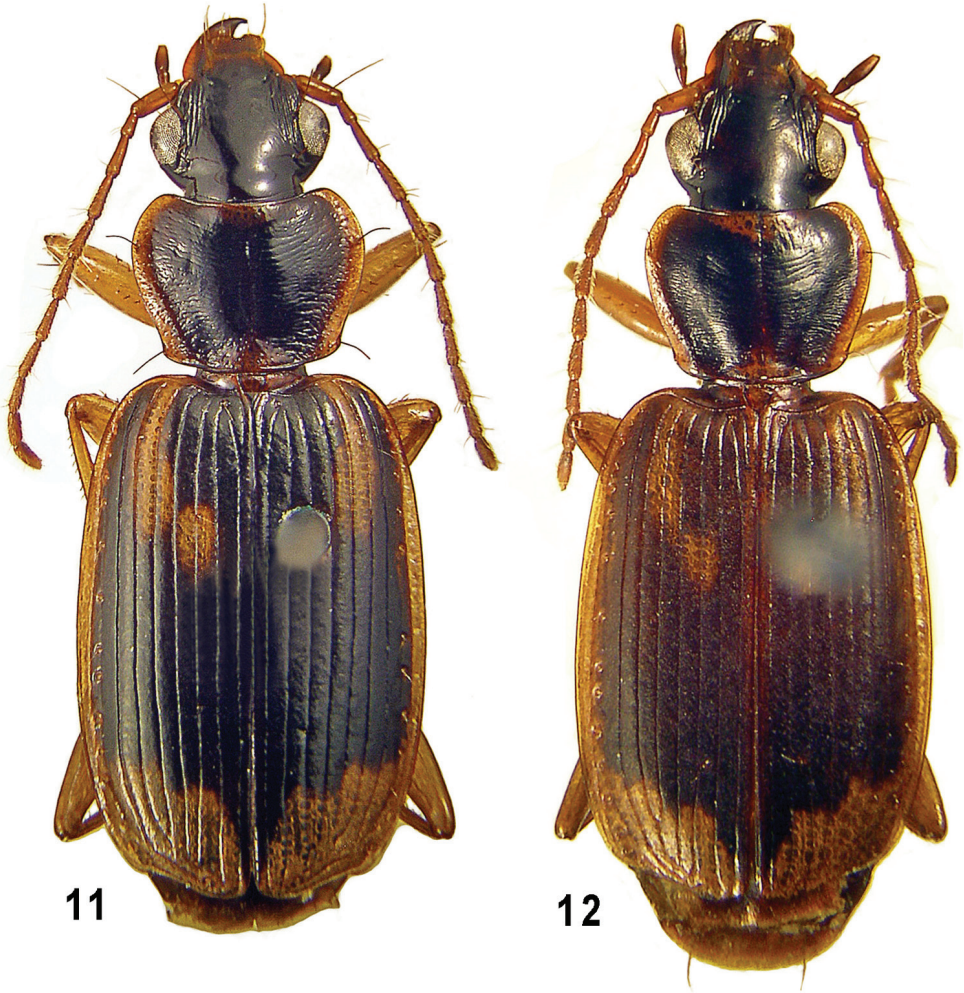
1. *Taridius ornatus* Fedorenko, sp. n.

urn:lsid:zoobank.org:act:4717ABE4-61DF-4EC2-873A-2A317259A5D7

http://species-id.net/wiki/Taridius_ornatus

Figs 6, 11, 20, 26, 37, 38, 43

Description. Body (Fig. 11), especially elytra, rather flat, 7.4–8.4 mm in length. DMF very wide (Fig. 6), outwardly extended to interval 9, PAS fairly short and transverse; PHSe short, expanded to interval 5 posteriorly and mostly also to interval 7 anteriorly, PHSi small, occupying intervals 3 and 4 posterior to PHSe, sometimes almost isolated. DSS transverse, mostly subangulate posterolaterally. Underside dark, middle of prosternum, meso- and metaventrite, as well as a narrow apical margin of abdominal sternite VII pale;



Figures 11–12. *Taridius ornatus* sp. n. (11) and *T. piceus* sp. n. (12), habitus.

outer half of metacoxae infusate. Microsculpture coarse on elytra, obliterate on both pronotum and back half of head, with almost indistinct traces here and there on pronotal disc.

Eyes slightly flattened, genae rather long and a little projecting, head broadest slightly behind $1/3$ eye tubercle length; frontal carinae on each side mostly four; of them, inner usually weaker, irregular, shortened at both extremities or only from behind, occasionally obsolete or duplicated. Vertex flattened, neck-constriction indistinct.

Pronotum 1.29–1.39 (mean 1.33, $n=8$) times as wide as head, 1.33–1.44 (mean 1.39) times as wide as long, base slightly convex backwards, a very small indentation between it and its lateral parts, the latter conspicuously oblique and increasingly curved forwards, sides subsinuate to nearly straight before base, hind angles highly obtuse and often rounded off, except for a small and blunt tooth bearing posterolateral seta. Front transverse impression obsolete or highly superficial, basal transverse impres-

sion shallow to moderately deep, slightly deeper at sides, basal foveae wide and shallow, at bottom each usually with a small, deep, transverse pit close to basal border, the latter interrupted or nearly so at middle. Anterior border widely interrupted at middle. Paralateral line obsolete or hardly traceable in basal half only. Coarse submarginal rugosities moderately dense and restricted to basal half. Coarse punctuation rather dense over reflexed side margin and adjacent parts of disc in its basal half.

Elytra oblong-oval, flat, 1.44–1.53 (mean 1.49) times as long as wide, 1.45–1.55 (mean 1.5) times as wide as pronotum. Striae impunctate, with almost invisible punctures at bottom, three or four inner striae distinctly shallower within DMF, intervals flat and subequally wide, rarely odd in basal third distinctly narrower than even ones. Last abdominal sternite bisetose along apical margin in both sexes.

Penis as in Figs 20 and 26, apical lamella moderately long, widely rounded at tip. Female gonocoxite IX long and narrow, ensiform setae small, dorsal one invisible in ventral view (Fig. 43).

Diagnosis. *T. ornatus* is distinguishable from a very similar species, *T. vietnamensis* (Kirschenhofer, 1996), in the more extensive dark pattern on the elytra, especially, in a wider and more transverse DMS, flattened eyes, a little projecting genae and rather flat elytra. In addition, the latter species has been taken at much lower altitudes, 620–750 m asl.

Variability. In a female from Chu Yang Sin (see below), the elytral DAS is slightly longer while the inner elytral striae within DMF are less shallow than in the type series.

Material. Holotype ♂: “S[outh] Vietnam, Lam Dong Prov. / Bi Doup – Nui Ba [Nature] Reserve / 12°07'N, 108°39'20"E / Bi Doup Mt., N. slope / h = 1700–1900 m [asl], 16.IV.2008, leg. D Fedorenko”. Paratypes, 5 ♂♂ and 4 ♀♀, taken together with holotype, as well as 12. and 19–22.IV.2008; 1 ♂, same locality, but env. Long Lanh / 12°10'44"N, 108°40'44"E / h = 1400–1600 m [asl], 29.III–20.IV.2008.

Additional material: ♀, Vietnam, Dak Lak Prov., Chu Yang Sin Natn. Park, 12°23'48"N, 108°20'59"E, Krong Kmar riv., upper flow, h = 1650 m [asl], 30.III–14.IV.2012, leg. D Fedorenko.

Geographic distribution. Known from three localities within Dalat Plateau, Lam Dong and Dak Lak Provinces, Vietnam.

2. *Taridius piceus* Fedorenko, sp. n.

urn:lsid:zoobank.org:act:29EC3746-78D5-4061-BFF7-E2C1E4A56FD0

http://species-id.net/wiki/Taridius_piceus

Figs 7, 12, 22, 28, 35, 36, 42

Description. Body (Fig. 12) flat, 8.5–9.6 mm in length. Dorsum rather dull due to a sharp microsculpture, with strong sericeous luster on elytra; head and pronotum dark brown to almost black, elytral dark pattern (Fig. 7) dark brown to black posteriorly while increasingly pale both forwards and outwards, thus being barely darker anteriorly than PHS and side border. Elytral color pattern as in *T. ornatus* in general, with PHS a little smaller and interval 9 mostly pale. Ventral surface same colored.

Eyes rather small, genae long and distinctly projecting at eye back margin, head broadest level to about 1/3 eye tubercle length; two, long, frontal carinae on each side, an additional, internal, mostly very short, occasionally well-developed, carina present before eyes, sometimes another, external, very fine and short one traceable. Vertex flattened, neck-constriction indistinct or almost so.

Pronotum 1.23–1.32 (mean 1.26, $n=8$) times as wide as head, 1.3–1.41 (mean 1.35) times as wide as long, base nearly straight, with lateral parts rather strongly oblique and rounded, sides posteriorly subsinuate to straight, hind angles mostly rounded off or barely traceable at posterolateral setigerous pore. Front transverse impression obsolete, basal transverse impression shallow to moderately deep, basal foveae each reduced to a deep pit at its bottom close to basal border, the latter shallower or subinterrupted at middle. Anterior border interrupted medially. Paralateral line shallow but traceable in basal three fourths, starting from basal pit. Rugosities fairly dense but not very sharp, denser over entire area outside paralateral line. Punctuation absent but very sparse minute punctures.

Wingless. Elytra flat, mostly reversely ovate, broadest behind middle, 1.38–1.43 (mean 1.4) times as long as wide, 1.52–1.62 (mean 1.58) times as wide as pronotum; with a highly obtuse, almost indistinct humeral angle opposite or just inside stria 7. Striae impunctate, even intervals flat, odd ones mostly slightly convex in basal third or half and often also a little narrower than even. Last abdominal sternite bisetose along apical margin in both sexes.

Penis (Figs 22, 28) regularly convex on right side, apical lamella long, parallel-sided, with a widely rounded tip forming a small capitulum in lateral view. Female gonosubcoxite IX stout, gonocoxite narrow, curved just before apex, dorsal ensiform seta small but distinct in ventral view (Fig. 42).

Diagnosis. The present species is easily recognizable due to a particular combination of large size, flat, wide and wingless body, dull dorsum, an extensive but rather pale dark pattern on the elytra, etc.

Material. Holotype ♂: “S[outh] Vietnam, Lam Dong Prov. / Bi Doup – Nui Ba [Nature] Reserve / 12°07'N, 108°39'20"E / Bi Doup Mt., N. slope / h = 1700–1900 m [asl], 12.IV.2008, leg. D Fedorenko”. Paratypes, 3 ♂♂ and 4 ♀♀, taken together with holotype, as well as 16. and 19–22.IV.2008.

Geographic distribution. Known from type locality only.

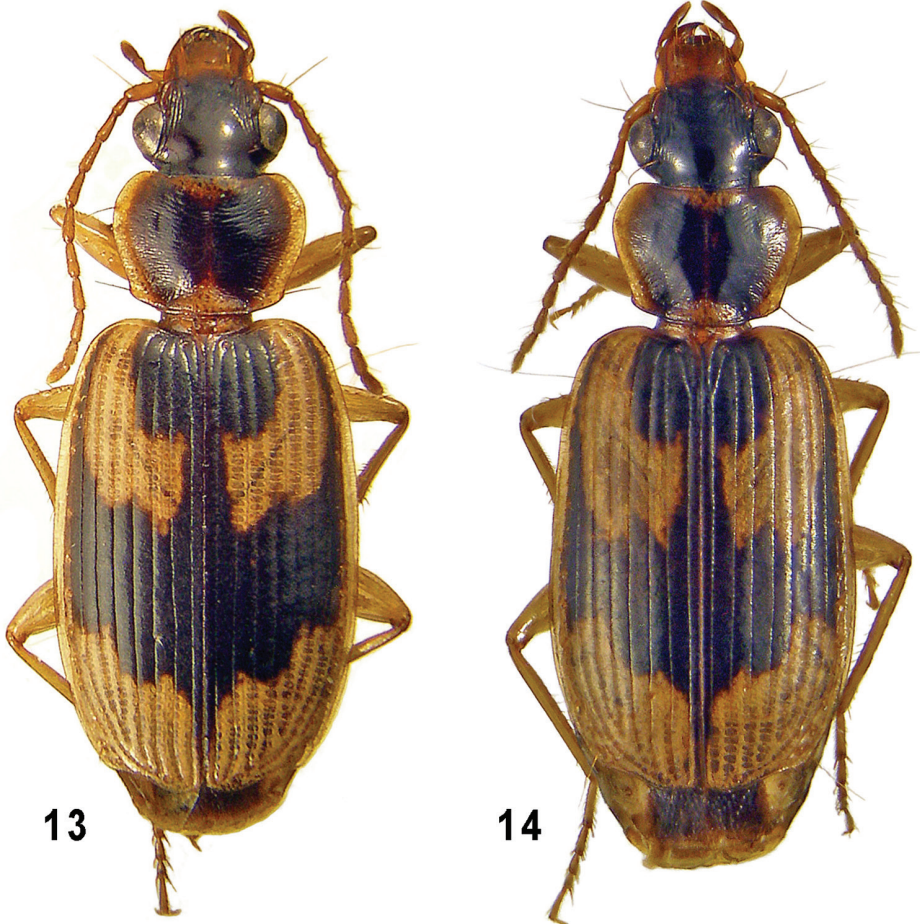
3. *Taridius fasciatus* Fedorenko, sp. n.

urn:lsid:zoobank.org:act:6B8F05A4-C0CF-47E1-A53B-FEC20252C2B2

http://species-id.net/wiki/Taridius_fasciatus

Figs 1, 2, 13, 17, 23, 31, 32, 44

Description. Body (Fig. 13) subconvex and small, 6.6–7.5 mm long. Dorsum black and shining, except for elytra. Pronotal pale pattern rather extensive along anterior and posterior margins. Elytral pale pattern (Figs 1, 2) fairly extensive as well, dark pattern entire, DMF moderately and subequally wide throughout, extended to interval 9 anteriorly and 8 posteriorly, with both front and back margins flexuose; its forward



Figures 13–14. *Taridius fasciatus* sp. n. (13) and *T. abdominalis* sp. n. (14), habitus.

extension along side margin (conformable to DLS) occupying intervals 8 and 9; DSS rounded laterally, on intervals 1 to 5 before while on 1 to 4 behind, mostly angulate posterolaterally, with a straight or concave back margin; one to two inner intervals involved in DSF, often one anteriorly and two just before DMF. PHS entire, PHSi about 1/2 its length posterior to PHSe, the latter extended to interval 7 at humerus. Sometimes PHSe very narrowly separated from PHSi or surpassing it, in the latter case DMF constricted in interval 6. PAS front margin oblique. Ventral surface colored as in previous two species. Microsculpture sharp on elytra, absent from or almost invisible on head, extremely fine on pronotum and obsolete either before its middle or over greater part of disc, posterolateral region excluded; microsculpture a little sharper in female as being very superficial but traceable over head and/or pronotum.

Eyes large and convex, together with genae almost semicircular in outline; frons with 4–5, more often four, carinae on each side, outer ones long, inner not surpassing anterior supraorbital seta; sometimes carinae unilaterally amplified in number to six,

irregular, or, otherwise, reduced to three, long ones. Vertex almost flat, neck-constriction barely traceable.

Pronotum 1.19–1.28 (mean 1.25, $n=8$) times as wide as head, 1.34–1.42 (mean 1.38) times as wide as long, basal margin slightly convex backwards or its almost straight medial part slightly produced, with lateral parts oblique towards and a little rounded at hind angles; anterior margin weakly sinuate, sides subsinuate to straight in basal half, mostly very shortly sinuate just before base, hind angles obtuse or very so, sharp to nearly indistinct. Front transverse impression obliterate, basal transverse impression shallow to moderately deep medially and deeper laterally, thus adjoining or forming a small, more or less deep, transverse pit at bottom of an almost reduced basal fovea, a very fine paralateral line traceable in basal third only. Basal border entire, anterior border very narrow, interrupted at middle. Rugosities rather dense and sharp, especially so posterolaterally, sparser and shallower in the middle of disc. Only reflexed side margin with large, sparse and shallow punctures combined with shorter rugosities.

Elytra flat, oblong-oval to reversely subovate, 1.44–1.57 (mean 1.51) times as long as wide, 1.57–1.71 (mean 1.63) times as wide as pronotum. Striae indistinctly crenulate, intervals subequally wide, flat or barely convex. Last abdominal sternite bisetose along apical margin in both sexes.

Penis as in Figs 17 and 23, its apical lamella subtriangular, more or less widely rounded at tip, the latter slightly curved upwards in lateral view. Female gonocoxite IX (Fig. 44) same as in *T. ornatus* sp. n.

Diagnosis. This insect is very similar to *T. vietnamensis* and *T. ornatus* sp. n., differing from both in the smaller body size and the dorsal microsculpture which is never totally absent from the pronotum. As compared to *T. vietnamensis*, the explanate side margin of the pronotum is narrower and less strongly reflexed, with a sharper side gutter, as well as the frontal carinae on each side are four or five instead of three.

Variability. Two additional specimens from higher altitudes (see below) are distinctive in a slightly larger body size and a posteriorly deeper side gutter of the pronotum due to its more strongly reflexed side margin. Furthermore, the male from Thailand shows the pronotum with transverse rugosities denser over the disc, especially along sides, a densely punctate side margin and almost straight lateral parts of the base, as well as the frontal carinae being still more numerous, six or seven, before. Besides this, the apical lamella of the penis is barely curved upwards in lateral view. Yet the endophallus is the same, implying that the differences are intraspecific, subspecific at best.

Material. Holotype ♂: “Vietnam, Binh Phuoc Prov. / Bu Gia Map Nat[ional] Park / 12°11'37"N, 107°12'21"E / h = 540 m [asl] / at light, 15.IV.2009, leg. D Fedorenko”. Paratypes, 20 ♂♂, 19 ♀♀, same data or 17–24. IV.2009.

Additional material: ♀ (MPSU), S-Vietnam, Dak Lak Prov., 75 km N of Phan Tiet, env. Gia Bac, h = 1100 m [asl], 18.IV.2007, leg. P Oudovichenko; ♂ (Collection of P. Bulirsch, Praha), Thailand, Mae Hong Son prov., Kiwlomm-pass near Soppong, 23.6.–2.7.2002, alt. 1400±50 m, WGS 84: 19°26'N, 098°19'E, lgt. Fouquè R. + H. & Kožich J.

Geographic distribution. S-Vietnam (Lam Dong and Dak Lak provinces), Thailand.

4. *Taridius abdominalis* Fedorenko, sp. n.

urn:lsid:zoobank.org:act:ABE5E05A-AB7C-42B0-9FD9-9A25A93FE947

http://species-id.net/wiki/Taridius_abdominalis

Figs 3, 4, 14, 18, 24, 29, 30, 45

Description. Very similar to the preceding species, except as follows: Body (Fig. 14) on average a little larger, 7.2–7.4 mm in length. Elytral dark pattern as in Figs 3 and 4, DSS with almost indistinct bronzed luster, PHSe long, its back margin level to or behind that of PHSi, DMF strongly constricted in interval 6; DSS rounded, occupying inner 4.5 intervals. Abdomen pale throughout but at sides; often also prosternum, meso- and metaventrites entirely pale. Microsculpture sharper, coarse on elytra, moderately deep over pronotum, superficial but traceable on head.

Frontal lateral carinae mostly four or five, sometimes almost three due to inner carina strongly reduced from behind.

Pronotum 1.23–1.3 (mean 1.26, n=6) times as wide as head, hardly broader, 1.37–1.45 (mean 1.4) times as wide as long; basal margin regularly convex backwards, mostly poorly rounded at hind angles, sides a little or barely sinuate before base, hind angles obtuse but rather sharp. Anterior border interrupted in the middle. Rugosities less sharp. Punctuation of base and reflexed side margin often moderately dense, punctures smaller and deeper.

Elytra, 1.5–1.52 times as long as wide, 1.55–1.63 (mean 1.58) times as wide as pronotum. Striae very finely punctate.

Penis (Fig. 24) with very short apical lamella. Female gonocoxite IX almost same as in previous species (Fig. 45).

Diagnosis. This species is distinctive among the others in the combination of elytral and ventral color patterns as described above, an almost entirely pale abdomen being found in no other species.

Material. Holotype ♂: “Vietnam, Binh Phuoc Prov. / Bu Gia Map Nat[ional] Park / 12°11'37"N, 107°12'21"E / h = 540 m [asl] / at light, 17–24. IV.2009, leg. D Fedorenko”. Paratypes, ♂, 3 ♀♀, same data.

Additional material: ♀, (SIEE): S-Vietnam, Dongnai Prov., Nam Cat Tien Natn. Park, *Dipterocarpus* forest, siefted from leaf-litter, 4.XII.2004, leg. A Anichkin.

Geographic distribution. Known from but two localities as above.

5. *Taridius sabahensis* (Kirschenhofer, 2003)http://species-id.net/wiki/Taridius_sabahensis

Figs 5, 41

Kirschenhofer, 2003: 9 (*Perseus*; Sabah, Borneo).

Description. Body subconvex, 8.5–9 mm long. Dorsum black, moderately shining. Elytral dark pattern (Fig. 5) entire, but for a small and vague posthumeral stroke

separated from DLS; DSS subrectangular, expanded onto interval 5 anteriorly and 4 posteriorly, with almost straight back margin, DSF running on interval 1 and barely expanded onto 2nd, DMF constricted on intervals 3 and 6, black color on 6th about two thirds longer than on 3rd, DLS occupying intervals 7 and 8 medially while only 8th anteriorly, terminating a fourth from base and two fifth from apex. Underside colored same as in *T. ornatus*. Microsculpture sharp on elytra, moderately sharp over pronotum, less conspicuous on head, very superficial on neck.

Eyes together with fairly long genae rather large, semicircular in outline; four fairly long frontal carinae present. Vertex slightly convex, neck-constriction very weak.

Pronotum 1.36–1.37 times as wide as head, 1.45–1.47 times as wide as long, basal margin a little convex backwards medially, lateral parts very slightly before, oblique forwards and increasingly curved outwards; sides barely sinuate before base, hind angles highly obtuse and almost indistinct; reflexed side margin widely explanate. Front transverse impression obliterate, basal transverse impression rather shallow, basal foveae large but nearly indistinct, each with a small oblique pit at bottom, paralateral line almost indistinct. Basal border entire, anterior border interrupted medially. Disc smooth with very sparse and weak transverse rugosities, very sparse punctures traceable only in basal foveae and close to side gutter just before them.

Elytra rather convex, 1.48–1.51 times as long as wide, 1.44–1.48 times as wide as pronotum, apices truncate and a little obtuse. Striae almost indistinctly crenulate, intervals subequally wide and flat. Last abdominal sternite bisetose in female.

Female gonocoxite IX narrow, ensiform setae moderately developed, dorsal seta distinct in ventral view (Fig. 41)

Material. ♀ (MPSU), E-Malaysia, Sabah, Mt. Kinabalu, Natn. Park, 1700 m asl, 16-30.07.2002, leg. Kurbatov & Zimina.

Geographic distribution. Known from a few localities in Sabah (Kirschenhofer 2010).

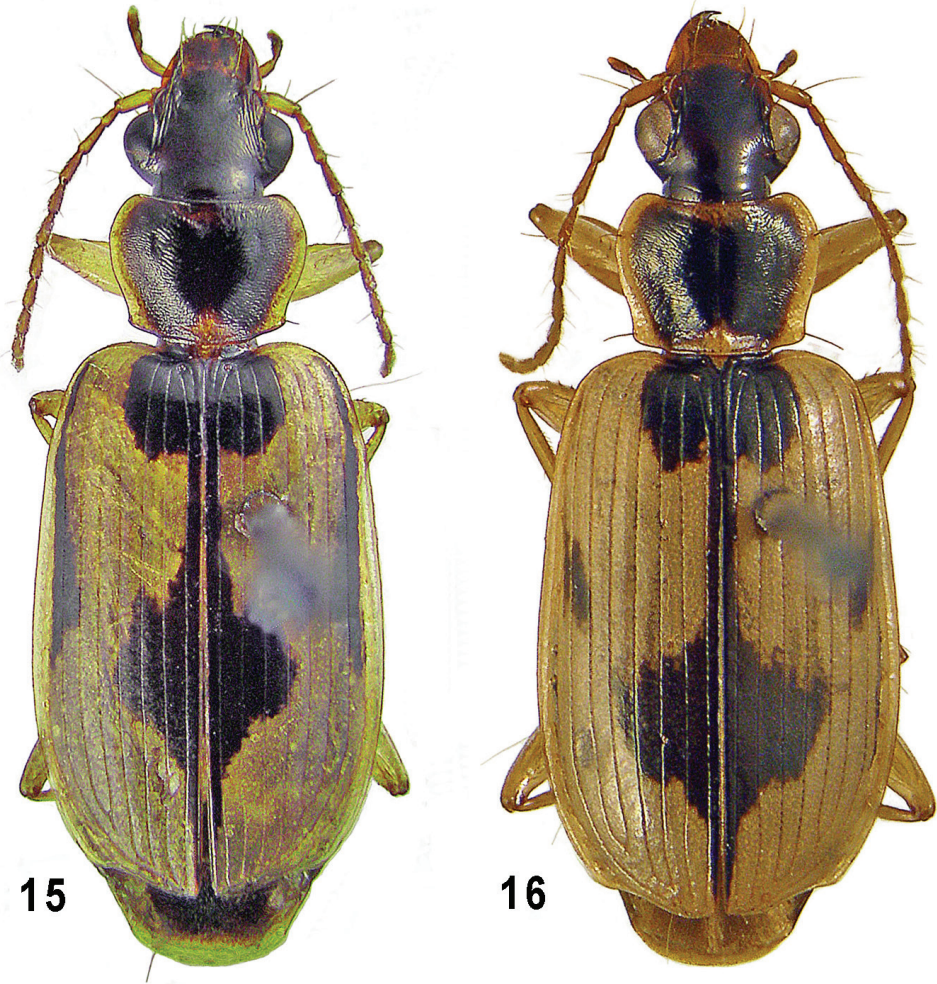
6. *Taridius coriaceus* Fedorenko, sp. n.

urn:lsid:zoobank.org:act:7CBAC243-A3D9-40CB-B75C-339CBF4D9CA8

http://species-id.net/wiki/Taridius_coriaceus

Figs 10, 15, 46

Description. Body (Fig. 15) subconvex, 8.6 mm in length. Dorsum black, a little shining due to a rather sharp microsculpture. Elytral dark pattern strongly reduced (Fig. 10): DSS occupying inner four intervals, slightly concave at back margin, sides and posterolateral angles both rounded, DSF occupying only sutural interval, DMS extended outwards as far as middle of interval 5, DLS separate on interval 8 in anterior three fifths, expanded onto 7th at middle and a little before. Underside black, metaventricle widely yellow medially, mesoventricle reddish at the extreme apex, prosternal process hardly paler between coxae, outer half of metacoxa infusate, abdomen black to dark brown, apical third of its last sternite yellow. Microsculpture sharp on elytra, very sharp, nearly granulate over pronotum, including reflexed side margin,

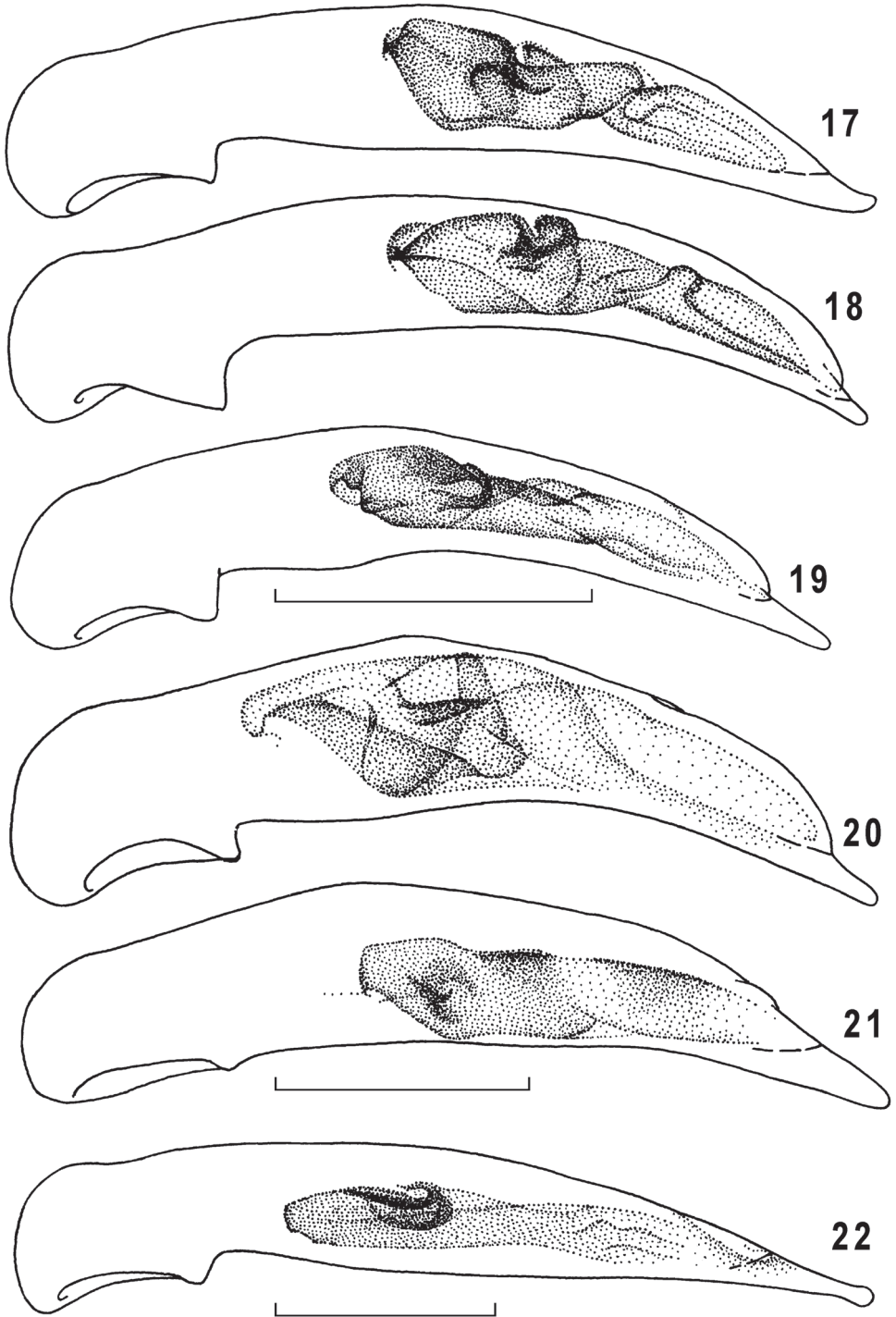


Figures 15–16. *Taridius coriaceus* sp. n. (**15**) and *T. disjunctus* sp. n. (**16**), habitus.

moderately deep, isodiametric or barely transverse, in the middle of disc, very distinct on head, superficial to obsolete on neck.

Eyes and genae combined almost semicircular in outline; frons on each side with three or four, anteriorly with four or five, carinae. Vertex almost flat, neck-constriction barely traceable.

Pronotum 1.17 times as wide as head, 1.39 times as wide as long, same as in as in *T. abdominalis*, but lateral parts of base nearly straight, sides distinctly sinuate before base, hind angles obtuse but rather sharp. Both front and basal transverse impressions, as well as basal foveae except at the very base, obsolete; paralateral line indistinct. A wide area between reflexed side margin and middle of disc coriaceous and dull from irregular, moderately deep and very dense rugosities accompanied by very sharp microsculpture in addition.



Figures 17–22. Genus *Taridius*, penis, left lateral aspect: *T. fasciatus* sp. n. (17), *T. abdominalis* sp. n. (18), *T. wrasei* (19), *T. ornatus* sp. n. (20), *T. disjunctus* sp. n. (21), *T. piceus* sp. n. (22); scale bar = 0.5 mm.

Elytra slightly convex, subovate, 1.56 times as long as wide, 1.79 times as wide as pronotum, broadest far behind middle, apices truncate and subrectangular. Striae impunctate, intervals subequally wide and almost flat. Last abdominal sternite bisetose along posterior margin.

Female gonocoxite IX long, parallel-sided, widely rounded apically, ensiform setae almost totally reduced, dorsal setae invisible in ventral view (Fig. 46).

Diagnosis. The species is certain to belong to the group which members share the last abdominal sternite bisetose in both sexes. From all of them, it differs by separate, dark, elytral DLS, peculiar pronotal sculpture and microsculpture, as well as by a particular structure of the female gonocoxite IX. A similar elytral pattern is observed in *T. stevensi* which is in contrast smaller and devoid of bronzed luster over dark color. Well-developed DLS and a dark abdomen are uncharacteristic of *T. wrasei* and *T. pahangensis*, the former species showing a quadrisetose abdominal sternite VII. The latter, according to its original description, is distinctive in having only one frontal carina on each side and a transverse pronotal microsculpture.

Material. Holotype ♀, S[outh] Vietnam, Lam Dong Prov. / Bi Doup – Nui Ba [Nature] Reserve / env. Long Lanh / 12°10'44"N, 108°40'44"E / h = 1400–1600 m [asl], V.2009 / leg. D Fedorenko.

Geographic distribution. Known from type locality only.

7. *Taridius disjunctus* Fedorenko, sp. n.

urn:lsid:zoobank.org:act:ACD9C0D6-0176-448B-BDD8-9EEC25080770

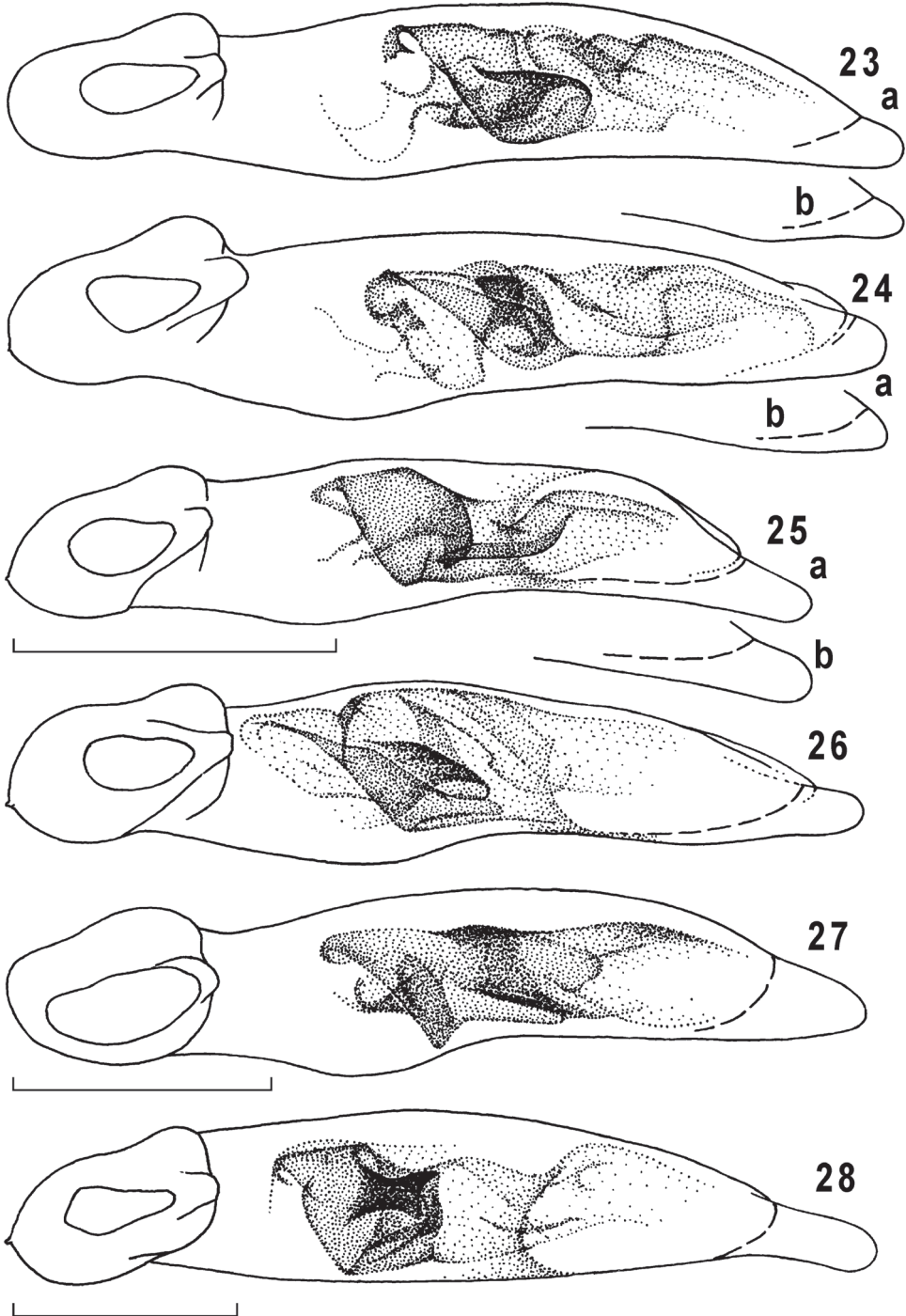
http://species-id.net/wiki/Taridius_disjunctus

Figs 8, 16, 21, 27, 39

Description. Body (Fig. 16) subconvex, 8.2–8.9 mm in length. Dorsum black, moderately shining. Elytral dark pattern (Fig. 8) with slight but distinct bronzed luster, strongly reduced laterally: DSS rounded, with inner four intervals involved in, emarginate at DSF which running on sutural interval only, DMS expanded outwards as far as stria 5, DLS reduced to a very small median patch on interval 7 or also on 8. Underside colored as in *T. ornatus*. Microsculpture sharp on elytra, moderately sharp over pronotum and head, superficial to obsolete on neck.

Eyes slightly reduced, genae rather long and oblique but not projecting, head broadest in anterior third of eye tubercle length; frontal carinae mostly three, among them inner one shorter and shallower anteriorly. Vertex rather convex, neck-constriction distinct.

Pronotum 1.16–1.23 (mean 1.19, n=3) times as wide as head, 1.31–1.36 (mean 1.33) times as wide as long, basal margin a little convex backwards or its straight medial part slightly surpassing lateral parts, these oblique and increasingly curved forwards; sides sinuate or barely so before obtuse or highly obtuse hind angles. Front transverse impression obliterate, basal transverse impression rather deep, wide, deeper laterally, forming a rather deep, oblique pit at bottom of fairly large basal fovea which is separated from disc by a paralateral line traceable in basal half to two thirds. Both basal and



Figures 23–28. Genus *Taridius*, penis, ventral aspect: *T. fasciatus* sp. n. (23a), *T. abdominalis* sp. n. (24a), *T. wrasei* (25a), *T. ornatus* sp. n. (26), *T. disjunctus* sp. n. (27), *T. piceus* sp. n. (28); variations of penial apex (b); scale bar = 0.5 mm.

anterior borders entire. Transverse rugosities rather dense and sharp, more so in basal foveae. Punctuation invisible or very sparse along reflexed side margin only.

Elytra rather convex, 1.47–1.55 (mean 1.52) times as long as wide, 1.77–1.89 (mean 1.84) times as wide as pronotum, apices truncate and a little obtuse; apical truncature conspicuously sinuate before rather distinct though obtusely rounded outer angles. Striae indistinctly crenulate, intervals subequally wide and almost flat. Last abdominal sternite quadrisetose in female.

Penis (Figs 21, 27) with a very large, triangular, apical lamella (the penis is poorly sclerotized because of an immature condition of the only male examined). Female gonocoxite and gonosubcoxite IX stout, the former with strong ensiform setae (Fig. 39).

Diagnosis. This species is close to *T. wrasei* and perhaps also *T. pahangensis*, with which it shares such characters as similar body shape and elytral color pattern, as well as a conspicuous dorsal microsculpture. Yet it differs from both in the larger body, entirely black abdomen and strongly reduced, almost indistinct, DLS, from the former also in the smaller eyes with oblique genae, the more convex elytra and a particular structure of both male and female genitalia.

Material. Holotype ♀, S[outh] Vietnam, Lam Dong Prov. / Bi Doup – Nui Ba [Nature] Reserve / 12°07'N, 108°39'20"E / Bi Doup Mt., N. slope / h = 1700–1900 m [asl], 10.IV.2008 / leg. D Fedorenko. Paratypes, ♂, same locality, but env. Long Lanh, 12°10'44"N, 108°40'44"E / h = 1400–1600 m [asl], V.2009; ♀, Vietnam, Dak Lak Prov. / Chu Yang Sin Natn. Park / 12°23'48"N, 108°20'59"E, Krong Kmar riv., upper flow / h = 1000 m [asl], at light, 30.III–14.IV.2012 / leg. D Fedorenko.

Geographic distribution. Lam Dong and Dak Lak provinces, Vietnam.

8. *Taridius wrasei* Kirschenhofer, 2010

http://species-id.net/wiki/Taridius_wrasei

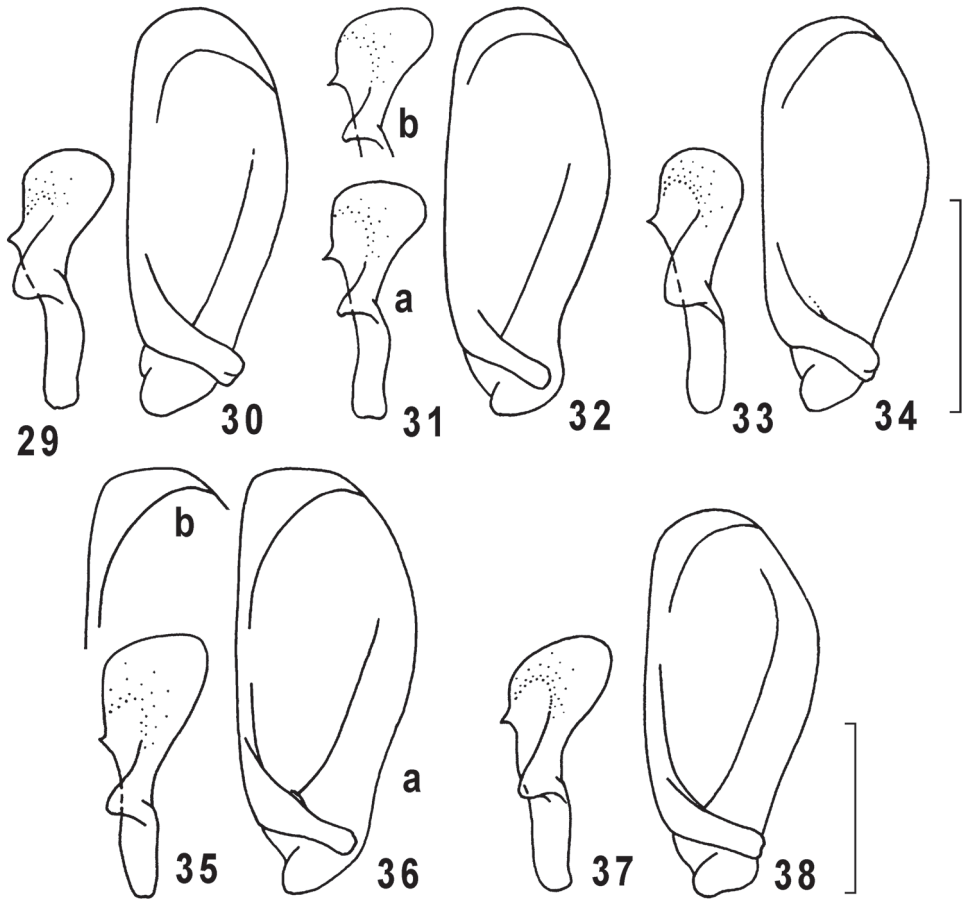
Figs 9, 19, 25, 33, 34, 40

Kirschenhofer, 2010: 25 (Sabah, Borneo).

Description. Similar to the previous species, except for as follows: body smaller, 7.2–8 mm in length. No bronzed luster over elytral dark pattern, DSS rounded and occupying intervals 1 to 4 and usually also expanded onto 5th, DLS much larger, triangular, on intervals 7 and 8, terminating one forth and three fifths from base and apex, respectively (Fig. 9). Pale color more strongly developed on ventral surface, including metacoxae, metaventre mesal to the line between mesocoxa and outer tip of metacoxa, as well as sides of first three abdominal sternites. Microsculpture rather sharp throughout.

Eyes larger, together with short genae more convex, semicircular in outline, head broadest level to about middle of eye tubercle length; usually two, long, frontal carinae on each side and a weak outer one. Vertex fairly flat, neck-constriction almost indistinct.

Pronotum 1.2–1.26 (mean 1.24, n=3) times as wide as head, 1.34–1.4 (mean 1.37) times as wide as long, basal margin slightly and regularly convex backwards or with me-

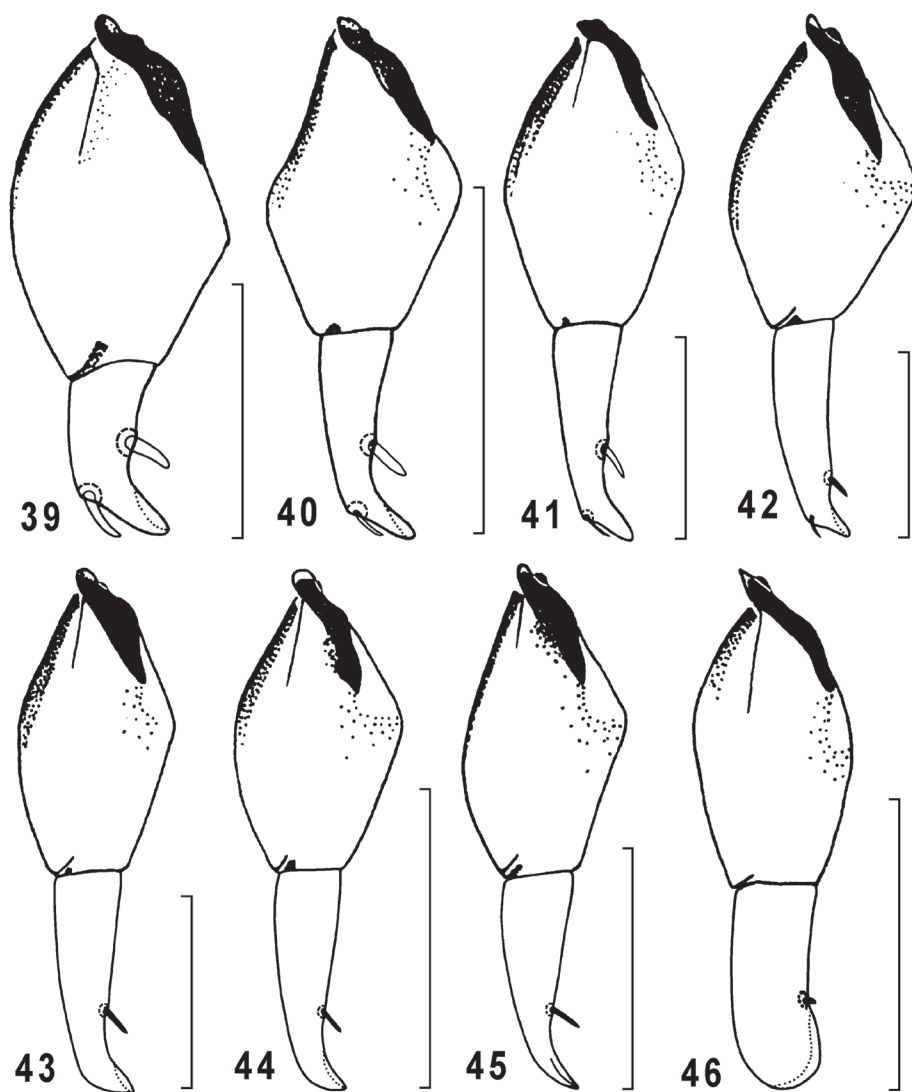


Figures 29–38. Genus *Taridius*, right (29, 31, 33, 35, 37) and left (30, 32, 34, 36, 38) parameres: *T. abdominalis* sp. n. (29, 30), *T. fasciatus* sp. n. (31 a, b, 32), *T. wrasei* (33, 34), *T. piceus* sp. n. (35, 36 a, b), *T. ornatus* sp. n. (37, 38); scale bar = 0.3 mm.

dial part slightly surpassing lateral ones, these being oblique forwards and nearly straight; sides barely to distinctly sinuate before obtuse to subrectangular and rather sharp hind angles. Front transverse impression obliterate or very shallow, basal transverse impression rather shallow as well, a rather deep pit at bottom of fairly large basal fovea, paralateral line hardly traceable in basal third. Basal border entire, anterior border interrupted medially. Transverse rugosities dense and fairly sharp throughout, sparser and shallower only in the middle of disc. Punctuation absent from disc and almost so over reflexed side margins.

Elytra rather flat, 1.47–1.53 (mean 1.5) times as long as wide, 1.70–1.77 (mean 1.73) times as wide as pronotum.

Penis as in Figs 19 and 25, apical lamella fairly long, parallel-sided, widely rounded at tip; left paramere with a short and widely rounded apex (Fig. 33). Female gonocoxite and gonosubcoxite IX (Fig. 40) more slender, and with smaller ensiform setae than in the previous species.



Figures 39–46. Genus *Taridius*, female left gonocoxite & gonosubcoxite IX, ventral aspect: *T. disjunctus* sp. n. (39), *T. wrasei* (40), *T. sabahensis* (41), *T. piceus* sp. n. (42), *T. ornatus* sp. n. (43), *T. fasciatus* sp. n. (44), *T. abdominalis* sp. n. (45), *T. coriaceus* sp. n. (46); scale bar = 0.3 mm.

Material. ♂, ♀ (SIEE), E-Malaysia, Sabah, Mt. Kinabalu, Natn. Park, 1700 m asl, 16–30.07.2002, leg. Kurbatov & Zimina; ♂, same data, but road Kota – Kinabalu – Tambunan, km 52, 1600–1800 m asl (MPSU).

Geographic distribution. Sabah, Borneo.

Comments. According to Kirschenhofer (2010), this species is barely different from *T. pahangensis* from Pahang, Malay Peninsula, mainly in a sharper dorsal micro-sculpture. If so, the latter species may have two or three frontal carinae on each side of the head instead of only one as specified originally.

Acknowledgments

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A new species of blunt-headed vine snake (Colubridae, *Imantodes*) from the Chocó region of Ecuador

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‡ [urn:lsid:zoobank.org:author:4F85DEF3-9AA1-4621-8566-1FE501361DA5](https://zoobank.org/4F85DEF3-9AA1-4621-8566-1FE501361DA5)

§ [urn:lsid:zoobank.org:author:C908E3FA-0D77-4342-B0B6-E05DF6F75B0E](https://zoobank.org/C908E3FA-0D77-4342-B0B6-E05DF6F75B0E)

| [urn:lsid:zoobank.org:author:2FA1D2DC-BF35-4FF1-B272-F9D30F3FD39D](https://zoobank.org/2FA1D2DC-BF35-4FF1-B272-F9D30F3FD39D)

¶ [urn:lsid:zoobank.org:author:A6080521-DD0E-4020-8842-37BA772B1D65](https://zoobank.org/A6080521-DD0E-4020-8842-37BA772B1D65)

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[urn:lsid:zoobank.org:pub:3D17FC43-0134-484D-8FC4-77F201AE2C02](https://zoobank.org/pub/3D17FC43-0134-484D-8FC4-77F201AE2C02)

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Abstract

We describe a new species of *Imantodes* from the Chocó region of northwestern Ecuador. The new species differs most significantly from all other congeners in lacking a loreal scale. We analyze the phylogenetic relationships among species of *Imantodes* based on two mitochondrial genes, and postulate that the new species and *I. lentiferus* are sister taxa. A key to the species of *Imantodes* from Ecuador is presented.

Keywords

Chocó, Dipsadinae, Ecuador, *Imantodes*, snakes, systematics

Introduction

The New World colubrid snake clade Dipsadinae Bonaparte 1838 includes more than 400 extant species assigned to approximately 25 taxa traditionally ranked as genera (Daza et al. 2009; Zaher et al. 2009). Most members of the Dipsadinae have unilobed (or nearly unilobed), unicapitate hemipenes, with the *sulcus spermaticus* dividing distally (Zaher et al. 2009). One of the most remarkable dipsadine genera is *Imantodes*. Its long, thin body, disproportionately slender neck, and blunt head, makes easy to distinguish *Imantodes* from all other New World snakes. This genus includes six currently recognized species (*I. cenchoa*, *I. gemmistratus*, *I. inornatus*, *I. lentiferus*, *I. phantasma*, and *I. tenuissimus*) commonly known as blunt-headed vine snakes, occurring from Mexico to Argentina (Myers 1982).

Studies on phylogenetic relationships and species limits among dipsadines are scarce. However, recent work provides strong evidence from DNA sequence data for a clade containing *Imantodes* and *Leptodeira*, although monophyly of *Imantodes* remains controversial (Daza et al. 2009; Mulcahy 2007). Furthermore, *I. gemmistratus* as currently circumscribed appears to be paraphyletic (Daza et al. 2009; Mulcahy 2007). Future studies with increased taxon and character sampling will probably clarify the phylogenetic relationships and species limits within *Imantodes*.

Three species of blunt-headed vine snakes are known from Ecuador; *I. inornatus* and *I. lentiferus* occur west and east of the Andes, respectively, whereas *I. cenchoa* is known from both versants (Torres-Carvajal and Salazar-Valenzuela 2012). In this paper we describe a new species of *Imantodes* from northwestern Ecuador and infer its phylogenetic affinities to other species in the genus as currently circumscribed.

Materials and methods

Morphological data

All type specimens of the new species described in this paper are listed in the type series below, and were deposited at the Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito (QCAZ), the Museo Ecuatoriano de Ciencias Naturales, Quito (DHMECN), and the Amphibian & Reptile Diversity Research Center at The University of Texas at Arlington, USA (UTA). Specimens of other species of *Imantodes* examined in this study are listed in the appendix. Snout-vent length (SVL) and tail length (tL) measurements were recorded to the nearest millimeter. All other measurements were made with digital calipers and recorded to the nearest 0.01 mm. Sex was determined by noting the presence of hemipenes, everted or by tail dissection. Partially everted hemipenes were prepared following standard techniques (Pesantes 1994; Zaher 1999). Differences in scale counts between the new species and other species of *Imantodes* were evaluated with t-tests for normally distributed variables (i.e., Shapiro-Wilk test, $P > 0.05$), all of which had equal variances (i.e., F-test, $P > 0.001$). We used the program PAST 2.15 (Hammer et al. 2001) for all statistical tests.

DNA Sequence Data

Total genomic DNA was digested and extracted from liver or muscle tissue using a guanidinium isothiocyanate extraction protocol. Tissue samples were first mixed with Proteinase K and lysis buffer and digested overnight prior to extraction. DNA samples were quantified using a Nanodrop® ND-1000 (NanoDrop Technologies, Inc), re-suspended and diluted to 25 ng/ul in ddH₂O prior to amplification.

We amplified 1674 nucleotides (nt) encompassing two mitochondrial loci, NADH dehydrogenase subunit 4 (ND4, 651 nt) and cytochrome b (cyt-b, 1023 nt) from five individuals of *I. cenchoa*, three of *I. lentiferus*, three of the new species described herein and one of *Leptodeira septentrionalis*. Cyt-b was amplified using the primers Gludg, L14910, and H16064 (Burbrink et al. 2000; Parkinson et al. 2002), whereas ND4 was amplified using the primers ND4, LEU and ND412931L (Arévalo et al. 1994; Blair et al. 2009). Additionally, we used sequences of *I. cenchoa*, *I. gemmistratus*, *I. inornatus*, *I. lentiferus* and *L. septentrionalis* from GenBank. Although monophyly of *Imantodes* has not been rigorously tested yet (see Discussion), for the purposes of this study we assume that *Imantodes* forms a clade and root our tree with *L. septentrionalis*. Gene regions of taxa included in phylogenetic analyses along with their GenBank accession numbers and locality data are shown in Table 1. Amplification of genomic DNA consisted of an initial cycle at 94 C for 3.5 min, 42 C for 1 min, and 68 C for 1.5 min, followed by 40 cycles of a denaturation at 94 C for 30 s, annealing at 52 C for 30 s, and extension at 72 C for 60 s, as well as a final extension at 72 C for 15 min.

Table 1. Vouchers, locality data, and GenBank accession numbers of taxa and gene regions included in this study. Asterisks indicate new sequences obtained for this study.

Taxon	Voucher	Locality	Genbank accession number	
			Cyt-b	ND4
<i>Imantodes cenchoa</i>	MPEGLJV 5763	Brasil: Para	EF078556	EF078508
<i>I. cenchoa</i>	JMD 1616	Colombia: Chocó	GQ334486	GQ334587
<i>I. cenchoa</i>	MHUA R-14290	Colombia: Antioquia	GQ334484	GQ334585
<i>I. cenchoa</i>	MHUA R-14500	Colombia: Antioquia	GQ334485	GQ334586
<i>I. cenchoa</i>	MVZ 149878	Costa Rica: Limón	EF078553	EF078505
<i>I. cenchoa</i>	QCAZ 11115	Ecuador: Santo Domingo de los Tsáchilas	*KC176244	*KC176256
<i>I. cenchoa</i>	QCAZ 6300	Ecuador: Esmeraldas	*KC176248	*KC176260
<i>I. cenchoa</i>	QCAZ 4207	Ecuador: Orellana	*KC176247	*KC176259
<i>I. cenchoa</i>	UTA R-42360	Guatemala: Izabal	EF078554	EF078506
<i>I. cenchoa</i>	SIUCR 03724	Panama: Cocolé	EF078555	EF078507
<i>I. cenchoa</i>	CORBIDI 3794	Peru: Tumbes	*KC176245	*KC176257
<i>I. cenchoa</i>	CORBIDI 8823	Peru: San Martín	*KC176246	*KC176258
<i>I. chocoensis</i> sp. n.	QCAZ 7978	Ecuador: Esmeraldas	*KC176249	*KC176261
<i>I. chocoensis</i> sp. n.	QCAZ 7984	Ecuador: Esmeraldas	*KC176250	*KC176262
<i>I. chocoensis</i> sp. n.	UTA R-60205	Ecuador: Esmeraldas	*KC176254	*KC176266
<i>I. gemmistratus</i>	UTA R-45922	Guatemala: San Marcos	GQ334487	GQ334588
<i>I. gemmistratus</i>	LSUMZ 39541	Mexico: Sonora	EF078558	EF078510

Taxon	Voucher	Locality	Genbank accession number	
			Cyt-b	ND4
<i>I. gemmistratus</i>	UTA R-51979	Mexico: Sinaloa	EF078557	EF078509
<i>I. inornatus</i>	MHUA R-14540	Colombia: Antioquia	GQ334488	GQ334589
<i>I. inornatus</i>	ASL 307	Costa Rica	GQ334489	GQ334590
<i>I. inornatus</i>	MVZ 204109	Costa Rica: Cartago	EF078559	EF078511
<i>I. inornatus</i>	MVZ 204110	Costa Rica: Heredia	EF078560	EF078512
<i>I. lentiferus</i>	MPEGLJV 5581	Brazil: Para	EF078562	EF078514
<i>I. lentiferus</i>	MPEGLJV 6880	Brazil: Amazonas	EF078561	EF078513
<i>I. lentiferus</i>	QCAZ 8377	Ecuador: Pastaza	*KC176251	*KC176263
<i>I. lentiferus</i>	QCAZ 8488	Ecuador: Zamora Chinchipe	*KC176252	*KC176264
<i>I. lentiferus</i>	QCAZ 9187	Ecuador: Morona Santiago	*KC176253	*KC176265
<i>Leptodeira septentrionalis</i>	MHUA R-14403	Colombia: Antioquia	GQ334528	GQ334632
<i>L. septentrionalis</i>	QCAZ 10550	Ecuador: Esmeraldas	*KC176243	*KC176255

Phylogenetic analyses

Editing, assembly, and alignment of sequences were performed with Geneious Pro™ 5.3 (Drummond et al., 2010). Phylogenetic relationships were assessed under a Bayesian approach in MrBayes 3.2.0 (Ronquist and Huelsenbeck, 2003). The model of character evolution for each gene was obtained in JModeltest (Posada, 2008) under the Akaike information criterion. Genes were combined into a single dataset with two partitions, one per gene. Four independent analyses were performed to reduce the chance of converging on a local optimum. Each analysis consisted of five million generations and four Markov chains with default heating values. Trees were sampled every 1000 generations resulting in 5000 saved trees per analysis. Stationarity was confirmed by plotting the log-likelihood scores per generation in the program Tracer 1.2 (Rambaut and Drummond, 2003). Additionally, the standard deviation of the partition frequencies and the potential scale reduction factor (Gelman and Rubin, 1992) were used as convergence diagnostics for the posterior probabilities of bipartitions and branch lengths, respectively. Adequacy of mixing was assessed by examining the acceptance rates for the parameters in MrBayes and the effective sample sizes (ESS) in Tracer. After analyzing convergence and mixing, 500 trees were discarded as “burn-in” from each run. We then confirmed that the four analyses reached stationarity at a similar likelihood score and that the topologies were similar, and used the resultant 18,000 trees to calculate posterior probabilities (PP) for each bipartition on a 50% majority rule consensus tree.

Results

The taxonomic conclusions of this study are based on the observation of morphological features and color patterns, as well as inferred phylogenetic relationships. We consider this information as species delimitation criteria following the general species concept of de Queiroz (1998, 2007).

***Imantodes chocoensis* sp. n.**

Proposed standard English name: Chocoan blunt-headed vine snakes

Proposed standard Spanish name: Cordoncillos del Chocó

urn:lsid:zoobank.org:act:D47B3B06-B8B2-4FDC-A54E-3A1F99091044

http://species-id.net/wiki/Imantodes_chocoensis

Holotype. – QCAZ 7984 (Figs. 1,2), an adult male from 4 km N Durango, 1.0283°N; -78.5950°W (DD), 253 m, Provincia Esmeraldas, Ecuador, collected on 24 April 2007 by E. Carrillo-Ponce, I. G. Tapia, and E. E. Tapia.

Paratypes (6). – ECUADOR: Provincia Carchi: DHMECN 6753, Río San Juan, 1.1858°N, -78.5006°W (DD), 243 m, collected on 12 September 2009 by M. Yáñez-Muñoz, L. Oyagata, and M. Altamirano; DHMECN 6757, Sendero Awa, 1.1643°N, -78.5071°W (DD), 257 m, collected on 16 September 2009 by M. Yáñez-Muñoz, L. Oyagata, and M. Altamirano. Provincia Esmeraldas: UTA R-60205, San Lorenzo-Santa Rita, 1.0321°N, -78.7138°W (DD), 115 m, collected on 21 March 2008 by M. Alcoser, R. Betancourt, P. Loaiza L., L. Oyagata, S. Ramírez J., J. W. Streicher, C. Tobar, and E. N. Smith; QCAZ 7978, same collection data as holotype; QCAZ 10185, 4 km W Alto Tambo, 0.91241°N, -78.5809°W (DD), collected on 18 December 2009 by S. Poe, L. Gray, and I. Latella; QCAZ 10710, Playa de Oro, Estero Pote and Estero Angostura, lower part of Cotacachi Cayapas Ecological Reserve, 0.8285°N, -78.7220°W (DD), collected on 27 November 1994 by E. Toral-Contreras, V. Ortiz, and F. Nogales.

Diagnosis. *Imantodes chocoensis* differs from all other known congeners in lacking a loreal scale. It can be further distinguished from its sister species (see Phylogenetic relationships) *I. lentiferus* by having 17 longitudinal rows of dorsal scales at midbody and at nearly one head length anterior to the cloaca (15 in *I. lentiferus*), more ventrals ($t = 7.27$, $P < 0.001$), more subcaudals ($t = -4.31$, $P < 0.001$), more postoculars (2–3, mean = 2.43 ± 0.51 ; 1–2, mean = 1.81 ± 0.39 in *I. lentiferus*), more infralabials (12–15, mean = 13.21 ± 0.80 ; 9–12, mean = 10.68 ± 0.60 in *I. lentiferus*), and smaller dark blotches on dorsum (Fig. 3). Among other species of *Imantodes* known from Ecuador, the new species differs further from *I. inornatus* ($N = 2$ –3) in having more ventrals ($t = 6.74$, $P < 0.001$), more subcaudals ($t = -5.05$, $P = 0.002$), more infralabials (9–11, mean 10.00 ± 0.89 in *I. inornatus*), a longer head (head length/width 1.54–1.71, mean = 1.63 ± 0.07 in *I. chocoensis* sp. n.; 1.29–1.61, mean = 1.45 ± 0.16 in *I. inornatus*), and dark blotches on dorsum (dark spots and flecks in *I. inornatus*; Fig. 3). The new species can also be distinguished from *I. cenchoa* by having a single anal scale (vrs. two), fewer ventrals ($t = 7.73$, $P < 0.001$), fewer subcaudals ($t = -4.04$, $P < 0.001$), more infralabials (7–12, mean 9.92 ± 0.85 in *I. cenchoa*), and dorsal dark blotches that include two or fewer vertebral scales and do not extend laterally onto ventrals (blotches are larger in *I. cenchoa* and extend onto lateral tips of ventrals; Fig. 3). Scale counts and measurements of species of *Imantodes* from Ecuador are presented in Table 2.

Description of holotype. Male (Figs. 1,2); SVL = 66.30 mm; tail length = 30.40 mm; head width = 7.98 mm; head length = 13.26 mm; head height = 5.37 mm.



Figure 1. Holotype of *Imantodes chocoensis* sp. n. in dorsal (left) and ventral (right) views. Photographs by OTC.

Short, blunt head 1.7 times longer than broad and 2.5 times longer than deep; head abruptly distinct from neck, three times wider than thinnest part of neck and also slightly wider than greatest width of body; eye large and protuberant, occupying 27% of length of head, with elliptical pupil visible from anterior, lateral, dorsal, and ventral aspects; rostral 1.6 times wider than high, concave in anterior view, and narrowly visible from above; paired prefrontals extending anteroventrally to level of center of eye, each in contact with its mate and with frontal, supraocular, preocular, nasal, and internasal; frontal pentagonal, 1.6 times longer than wide (greatest width), and about 1.2 times longer than distance from its anterior edge to tip of snout; supraocular anteriorly narrow and posteriorly nearly as wide as greatest frontal width; broad parietals, about 1.3 times longer than wide; interparietal suture 1.2 times longer than length of frontal, and 1.4 times longer than distance from frontal to tip of snout; nasal plate single, centrally pierced by large naris (0.79 mm in diameter), in contact with rostral anteriorly, internasal dorsally, prefrontal posterodorsally, preocular posteriorly, and first and second supralabials ventrally; loreal absent; one large and high preocular; two postoculars (an extra tiny scale on left side ventrally), the lower somewhat less than half the size of the upper; temporals 2+2+3; supralabials 9, first and second in contact with nasal, fourth in contact with preocular, and fourth to seventh bordering the orbit; infralabials 13, with first six in contact with anterior genial, and sixth to eighth touching posterior genial; first pair of infralabials in contact medially behind mental; anterior and posterior genials nearly equal in length; gular scales with posterolateral apical pit.

Body higher than wide, rounded ventrolaterally; dorsal scales smooth, juxtaposed or subimbricate; dorsal body scales in 17 rows throughout; scales of vertebral row



Figure 2. Head of holotype of *Imantodes chocoensis* sp. n. in dorsal (top), lateral (middle) and ventral (bottom) views. Photographs by OTC.

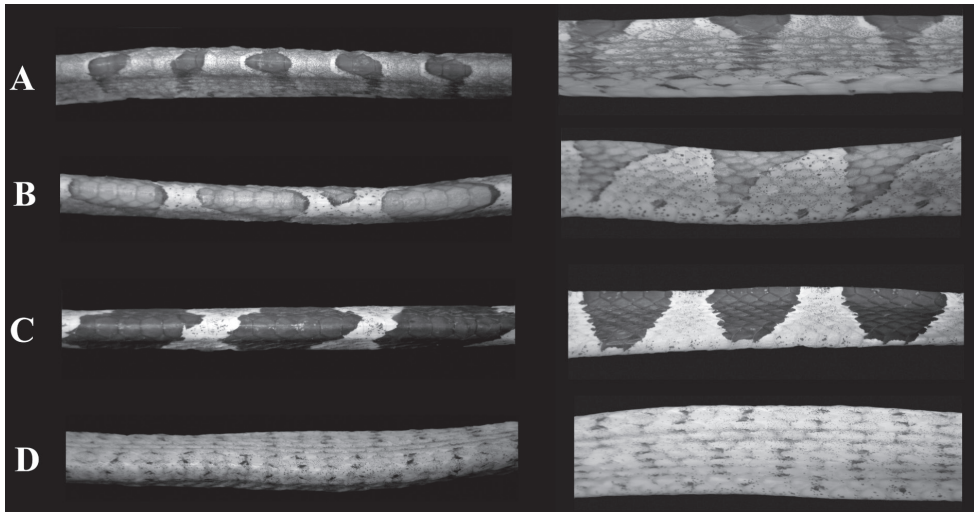


Figure 3. Body segments of species of *Imantodes* from Ecuador in dorsal (left) and lateral (right) views. **A** *Imantodes chocoensis* sp. n. (DHMECN 6753, paratype) **B** *I. lentiferus* (DHMECN 8345) **C** *I. cenchoa* (DHMECN 7826) **D** *I. inornatus* (DHMECN 5661). Photographs by MYM.

conspicuously enlarged, 2.5 times wider than adjacent dorsals, with concave posterior margins; ventrals 242; anal plate single; subcaudals 161.

Color in preservative of holotype (Figs 1,2). Dorsal background light brown, with a longitudinal series of 63 dark brown middorsal blotches from head to cloaca; dark middorsal blotches longer anteriorly, 2–3 vertebral scales long, than posteriorly, 1–2 vertebral scales long, and extending laterally 1–3 (anteriorly) or more (posteriorly) dorsal scale rows, but never reaching ventral scales; each dark middorsal blotch irregularly bordered anteriorly and posteriorly by thin cream line; ventral aspect of body yellowish cream with dark brown spots and flecks; ventral aspect of tail yellowish cream with spots concentrating midventrally; dorsal surface of head light brown with several dark brown spots and two short dark stripes extending from posterior aspect of parietals to a point just posterior to head; ventral surface of head whitish cream.

Hemipenes (Fig. 4). The right hemipenis of the paratype DHMECN 6753 of *Imantodes chocoensis* was removed, fully everted and expanded (Fig. 4). The organ is bulbous and relatively long, 11.2 mm in length, and when adpressed to the outside of the tail it extends from the cloaca to the sixth subcaudal scale. The organ is longer than wide (width 46% of length), unilobed, symmetrical, calyculate, capitate, and arched towards the sulcal side. The sulcus spermaticus is simple, linear, semicentripetal, and thin, demarcated by thick bordering tissue at the base, particularly at the anterior border, and ending on the surface of the capitulum facing medially. The capitulum is ornamented with papillated calyces, spinulated proximally. The capitulum, approximately 45% the length of the hemipenis, is slightly demarcated by a groove, more prominent on the sulcal side and joining the sulcus spermaticus. In the asulcate side the base of the capitulum has more prominent spines. Truncus covered by large spines, on the sulcate

Table 2. Scale counts and measurements of species of *Imantodes* from Ecuador. Range (first line) and mean \pm SD (second line) are presented when appropriate. Sample size is presented in parentheses if different from that in heading.

Character	<i>I. cenchoa</i> N = 42	<i>I. inornatus</i> N = 6	<i>I. lentiferus</i> N = 30	<i>I. chocoensis</i> sp. n. N = 7
Longitudinal scale rows on neck	17	17	15–17 15.07 \pm 0.37	17
Longitudinal scale rows at midbody	17	17	15	17
Longitudinal scale rows anterior to cloaca	17	13–15 13.67 \pm 1.03	15	17
Ventrals	249–280 262.62 \pm 6.22	203–219 210.67 \pm 5.99	216–237 226.80 \pm 5.03	232–251 243.14 \pm 5.84
Subcaudals	155–189 (37) 165.95 \pm 8.01	109–126 (5) 117.80 \pm 6.18	130–151 (27) 139.85 \pm 5.89	140–161 (6) 151.83 \pm 7.41
Anals	2	1–2 1.17 \pm 0.41	1	1
Anterior temporals	1–3 2.13 \pm 0.51	1–2 1.08 \pm 0.29	1	1–2 1.43 \pm 0.51
Posterior temporals	2–5 2.80 \pm 0.53	1–2 1.92 \pm 0.29	1–3 2.07 \pm 0.36	2
Loreals	1	1	1	0
Preoculars	1–3 1.36 \pm 0.53	1–2 1.25 \pm 0.45	1–2 1.03 \pm 0.18	1
Postoculars	1–4 2.11 \pm 0.38	2–3 2.08 \pm 0.29	1–2 1.81 \pm 0.39	2–3 2.43 \pm 0.51
Supralabials	7–9 7.99 \pm 0.33	8	7–9 8.05 \pm 0.34	9
Infralabials	7–12 9.92 \pm 0.85	9–11 10.00 \pm 0.60	9–12 10.68 \pm 0.60	12–15 13.21 \pm 0.80
Genials	2	2	2 (28)	2
Head length/width	1.35–1.80 1.56 \pm 0.11	1.29–1.62 1.51 \pm 0.13	1.37–1.91 1.62 \pm 0.14	1.54–1.71 1.63 \pm 0.07
Tail length/Total length	0.28–0.33 (37) 0.30 \pm 0.01	0.27–0.30 (5) 0.28 \pm 0.01	0.28–0.34 (27) 0.31 \pm 0.01	0.29–0.32 (6) 0.31 \pm 0.01
Maximum SVL (cm)	107.90	64.00	70.30	74.40
Maximum Total length (cm)	152.10	91.50	101.40	107.50

and asulcate and surfaces, 23 in total, 13 to the right of the sulcus spermaticus and 10 to the left, and has a few rows of small spines, two at the base on the asulcate side and two to three rows just right of the sulcus spermaticus.

Variation. Intraspecific variation in scale counts and measurements in *Imantodes chocoensis* sp. n. is presented in Table 2. Color in life of paratypes UTA R-60205 and DHMECN 6753 (Fig. 5) is similar to color in preservative of holotype; iris copper brown. Middorsal blotches from head to cloaca vary between 55–66; one specimen (UTA R-60205) had one middorsal blotch covering five vertebral scales.

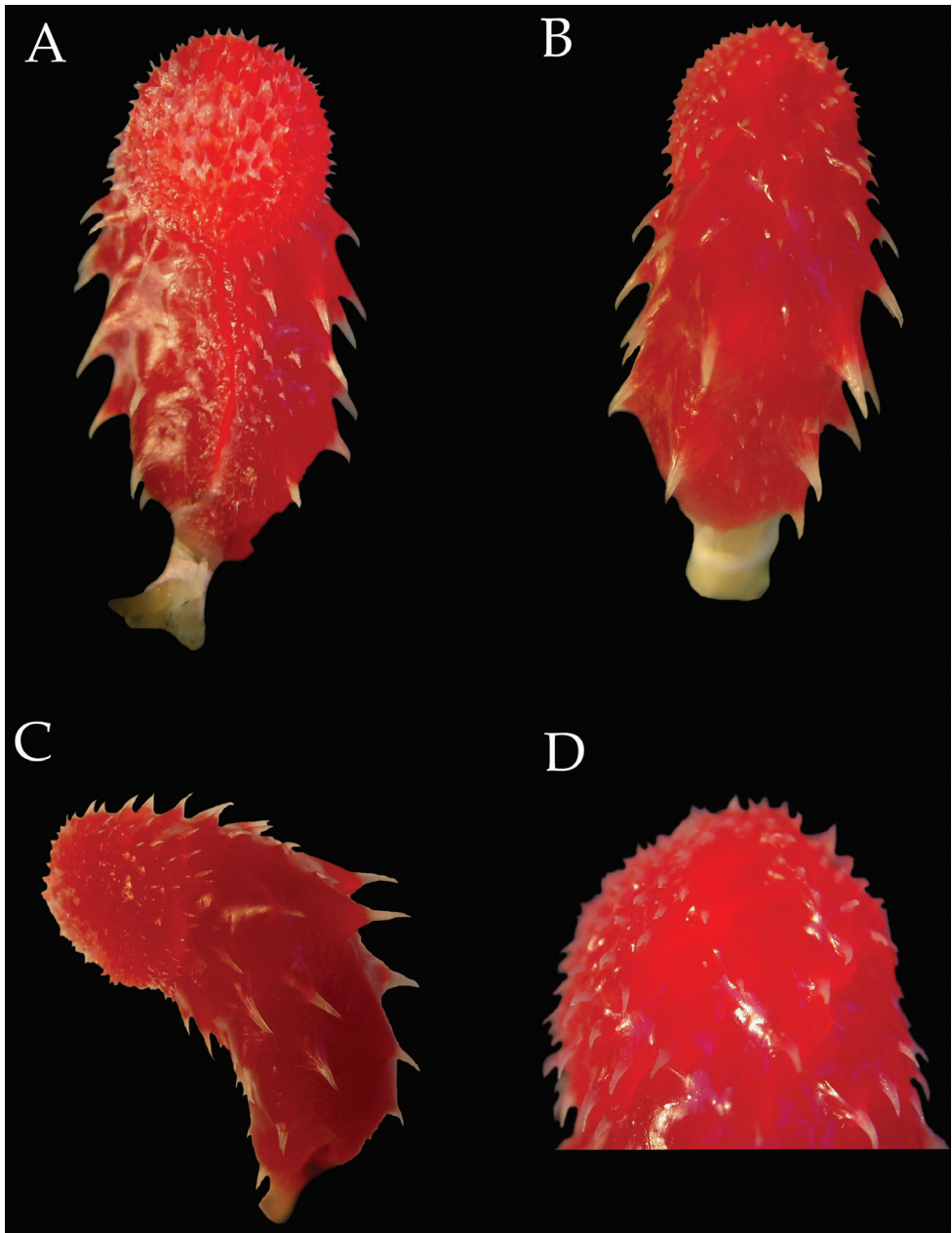


Figure 4. Right hemipenis of *Imantodes chocoensis* sp. n. (DHMECN 6753, paratype) in sulcal (A), asulcal (B), and lateral (C) views D close-up of distal end showing spines interrupted by sulci. Photographs by MYM.

Distribution and ecology. *Imantodes chocoensis* inhabits Chocoan rainforests on the Pacific coast in northern Ecuador (Fig. 6). It occurs in lowland evergreen forest (Cerón et al. 1999) at elevations of 115–260 m in the provinces of Carchi and Esmeraldas. This new species has been collected in sympatry with *I. cenchoa* in Esmeraldas,



Figure 5. Paratypes of *Imantodes chocoensis* sp. n. UTA R-60205 (top), DHMECN 6753 (bottom). Photographs by ENS and MYM.

and most likely also shares its distribution with *I. inornatus*. Other colubrid snakes collected in Tobar Donoso (Carchi) are *Chironius grandisquamis*, *Clelia clelia*, *Dendrophidion clarkii*, *Leptophis ahaetulla*, *Mastigodryas* sp., *Ninia atrata*, *Oxyrhopus petola*,

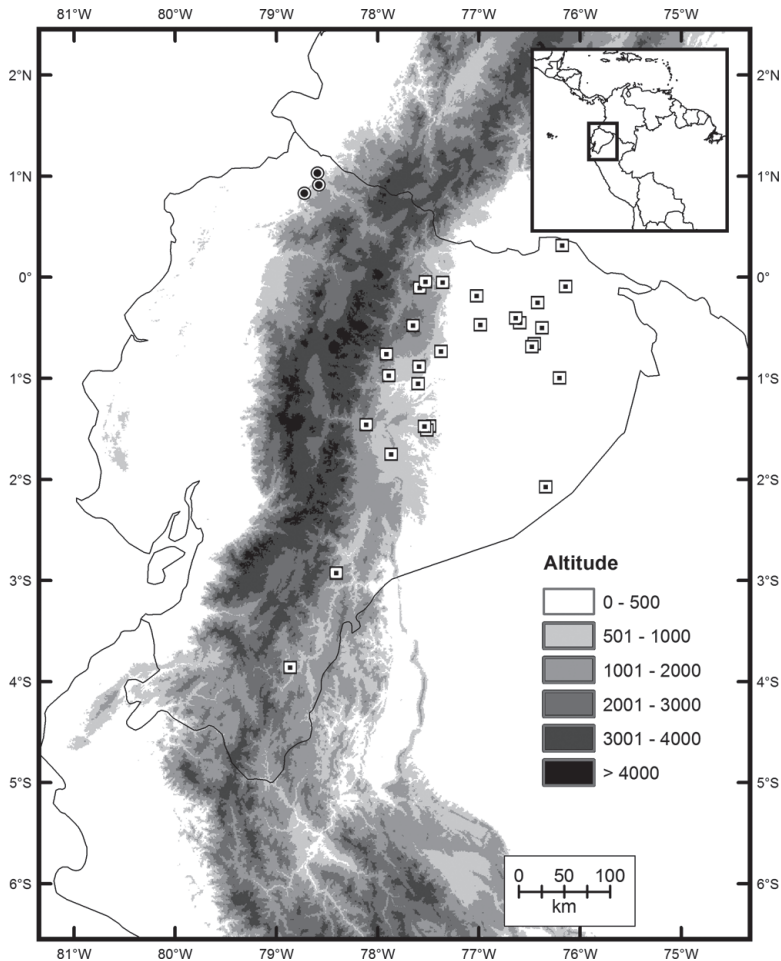


Figure 6. Distribution of *Imantodes chocoensis* sp. n. (circles) and its sister species *I. lentiferus* (squares) in Ecuador.

Pseustes shropshirei, *Sibon nebulatus*, *Synopsis bicolor*, *Tantilla melanocephala*, and *Xenodon rabdocephalus*. The known localities of *I. chocoensis* lie in close proximity to the Ecuador-Colombia border and we expect for it to be found in neighboring Colombia.

Etymology. The specific epithet *chocoensis* is an adjective derived from Chocó, the very humid tropical region comprising the Pacific coast of northern Ecuador, Colombia and Panama (Morrone 2001). This region is part of the 274,597 km² Tumbes-Chocó-Magdalena hotspot as defined by Conservation International, which includes more than 320 species of reptiles.

Phylogenetic relationships. Selected models of evolution for sampled fragments of ND4 and cyt-b genes were HKY+I+G and TPM2uf+I+G, respectively. The resulting 50% majority rule consensus tree (Fig. 7) supports strongly (PP=1) a sister taxon relationship between *Imantodes chocoensis* sp. n. and *I. lentiferus*, as well as the exclusivity (Rieppel 2010) of both species. Similarly, *I. inornatus* and *I. cenchoa* are recovered as

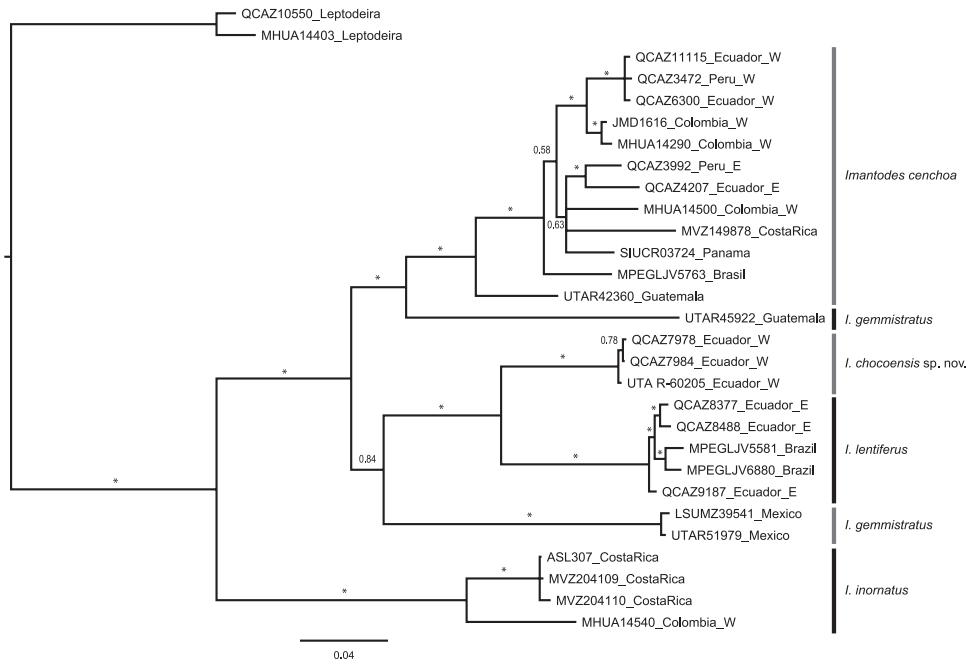


Figure 7. Majority rule (50%) consensus tree of 18,000 trees obtained from a Bayesian analysis of two mitochondrial genes (cyt-b, ND4) and 29 specimens. Asterisks correspond to posterior probability values > 0.99. Voucher numbers followed by country of collection are indicated for each terminal. E: east of the Andes, W: west of the Andes.

exclusive clades with strong support (PP=1). Noteworthy the *I. cenchoa* clade includes samples from Guatemala, Costa Rica, Panama, Brasil, and Colombia, Ecuador and Peru on both sides of the Andes. In agreement with previous hypotheses, *I. gemmistratus* is paraphyletic; of three samples included in this study, one from Guatemala is sister to the *I. cenchoa* clade with strong support (PP=1), whereas the other two, from Mexico, are weakly supported as sister to the *I. chocoensis* sp. n. and *I. lentiferus* clade.

Discussion

Myers (1982) distinguished two monophyletic groups within *Imantodes* – *lentiferus* and *cenchoa* – based on hemipenial characters, maxillary dentition, relative tongue length, and coloration. According to Myers, the *lentiferus* group included *I. lentiferus* and *I. phantasma* as sister taxa, as well as *I. inornatus*, whereas the *cenchoa* group included *I. cenchoa*, *I. gemmistratus* and *I. tenuissimus*. Since the phylogenetic tree presented in this paper does not include all species of *Imantodes*, we cannot rigorously test Myers' hypothesis of phylogenetic relationships within *Imantodes*. Nonetheless, two major differences are worth noting. First, in our phylogenetic tree *I. inornatus* is sister to all other species of *Imantodes* (but see below). Second, in agreement with previous

work (Daza et al. 2009), we recover a paraphyletic *I. gemmistratus*, with specimens from Guatemala closely related to *I. cenchoa* as postulated by Myers (1982), and specimens from Mexico in a clade with *I. lentiferus* and the *I. chocoensis* sp. n. (Fig. 7).

Monophyly of *Imantodes* remains controversial, but we refrained from testing it without better taxon and character sampling. Previous phylogenetic studies based on DNA sequence data have failed to support the monophyly of *Imantodes* as currently circumscribed (Daza et al. 2009; Mulcahy 2007). Except for a tree including only two species of *Imantodes* (Fig. 6 in Daza et al. 2009) and a Maximum Parsimony tree (Fig. 5 in Mulcahy 2007), these studies suggest that *I. inornatus* is sister to a clade containing *Imantodes* and *Leptodeira* as sister taxa. Furthermore, the phylogenetic tree presented in this paper is congruent with this hypothesis (Fig. 7), suggesting that *I. inornatus* might belong to a clade different from *Imantodes*. In fact, this species differs from other *Imantodes* in several morphological (e.g., no prominent dorsal blotches, or conspicuously enlarged vertebral scales; Fig. 3) and behavioral (e.g., head-flaring) features (Mulcahy 2007; Myers 1982).

Key to the species of *Imantodes* from Ecuador

- 1 Longitudinal scale rows at midbody 17 **2**
- Longitudinal scale rows at midbody 15 ***I. lentiferus***
- 2 Vertebral scales 2.5–4 times wider than adjacent dorsal scales; dorsal color pattern with conspicuous dark blotches (Fig. 3) **3**
- Vertebral scales similar in size or slightly wider than adjacent dorsal scales; dorsal color pattern with dark spots and speckles (Fig. 3) ***I. inornatus***
- 3 Loreal present; dorsal blotches include more than two vertebral scales and extend onto edge of ventrals (Fig. 3) ***I. cenchoa***
- Loreal absent; dorsal blotches include two or less vertebral scales and do not extend laterally onto ventrals (Fig. 3) ***I. chocoensis***

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Appendix

Specimens examined

Imantodes cenchoa – COLOMBIA: *Meta*: UTA R-3364–65, Serranía de la Macarena, peak near Caño Sardinata, 30 Km WSW Vista Hermosa, 1300 ft; COSTA RICA: *Limón*: UTA R-12903, Approximately 17 km WSW Puerto Limón, between Río Blanco and Río Toro, 150 m; ECUADOR: *Carchi*: QCAZ 4419–20, Chical, road to San Pablo, 0.9211°N, 78.1809°W, 1248 m; *Cotopaxi*: QCAZ 1203, San Francisco de las Pampas, 0.4332°S, 78.9667°W, 1600 m; QCAZ 2771–72, 6 km west of Guasaganda, 0.8206°S, 79.1171°W, 350 m; QCAZ 8888, Naranjito, Bosque Integral Otonga (BIO), 0.4147°S, 79.0007°W; *Esmeraldas*: QCAZ 2248, La Mayronga, Lagarto, 1.0420°N, 79.2800°W; QCAZ 6669, Alto Tambo, El Placer, La Carolina, 0.7044°N, 78.2011°W, 500 m; QCAZ 7589–90, Bilsa, 0.6201°N, 79.9307°W; QCAZ 7930, Reserva Ecológica Bilsa, 0.3588°N, 79.7180°W, 590 m; UTA R-55946, road Alto Tambo - San Lorenzo, 1.33311°N, 78.61687°W, 336 m; UTA R-55947, road Lita - San Lorenzo, 1.07750°N, 78.65785°W, 91 m; UTA R-55948, Tunda Loma Lodge, 1.18333°N, 78.75349°W, 37 m; QCAZ 7979–81, 4 km N Durango 1.0283°N, 78.5950°W, 253 m; QCAZ 10203, near Lita, 0.8886°N, 78.5288°W; QCAZ 10706, lowlands of Reserva Ecológica Cotacachi Cayapas, Playa de Oro, Pote and Angostura estuaries, 0.8284°N, 78.7220°W; *Guayas*: QCAZ 9118, Bosque Protector Cerro Blanco, 2.1758°S, 80.0216°W, 213 m; *Morona-Santiago*: UTA R-37985–86, Limón; *Napo*: QCAZ 8422–23, río Hollín, 0.6950°S, 77.7307°W; *Orellana*: QCAZ 1742, 1752, Parque Nacional Yasuní, Block 16, Maxus road between Pompeya south and Iro, 0.6755°S, 76.3552°W, 110 m; QCAZ 3423, Parque Nacional Yasuní, km 80 road to Pompeya-Iro, Belle river bridge area, 0.8401°S, 76.3017°W; QCAZ 3650, Parque Nacional Yasuní, Estación Científica Yasuní, 0.6750°N, 76.3892°W, 220 m; QCAZ 8920–21,

Florencia, 0.8966°S, 75.4370°W; QCAZ 9141, 9143, Parque Nacional Yasuní, road to Pompeya - Iro, km 10, 0.4598°S, 76.5931°W, 271 m; QCAZ 9528, southern bank of río Napo, Eden, 0.4983°S, 76.0711°W, 216 m; QCAZ 9551, northern bank of río Napo, San Vicente, 0.6790°S, 75.6511°W, 196 m; QCAZ 1738, Parque Nacional Yasuní, Block 16, Maxus road between Pompeya south and Iro, 0.6755°S, 76.3552°W, 100 m; *El Oro*: QCAZ 8992, Bella María, near Valle Hermoso, 3.5116°S, 79.8202°W, 282 m; *Pastaza*: QCAZ 4255, road to El Triunfo, Arajuno, 1.2325°S, 77.6876°W, 800 m; QCAZ 8161, around Villano, AGIP petroleum camp, K4, 1.4706°S, 77.4868°W; QCAZ 8378, around Villano, AGIP petroleum camp, K10 Unidad 3, 1.4727°S, 77.5359°W, 430 m; QCAZ 8914, Bataburo Lodge, 1.2500°S, 76.6667°W, 220 m; UTA R-15852, Río Cononaco, S side, within a few km of Perú border; *Pichincha*: EPN 1315354, Los Bancos, sector Milpe; *Santo Domingo de los Tsáchilas*: QCAZ 11048, La Concordia, Bosque Protector la Perla, 0.0570°S, 79.3590°W; QCAZ 11115, Hostería Tinalandia, near Alluriquín, 0.2965°S, 79.0523°W; *Sucumbios*: QCAZ 1488–89, Reserva de Producción Faunística Cuyabeno, 0.2597°S, 75.8886°W; QCAZ 2564, Reserva de Producción Faunística Cuyabeno, research station (PUCE), 0.0018°S, 76.1755°W; GUATEMALA: *Alta Verapaz*: UTA R-46623, Finca Rubelpec, 650 m; UTA R-46624, Finca San Juan, 590 m; UTA R-46625, Finca San Juan, 550 m; UTA R-26194, N slope Sierra de las Minas, Finca Pueblo Viejo, W slope Río Tinajas/Río Chiquito divide, 5.25 air km SSE, 1200–1500 m; UTA R-26193, N slope Sierra de las Minas, Finca Pueblo Viejo, 4.0 air km SE Pueblo Viejo, 0 m; UTA R-26195, Vicinity of Pueblo Viejo; *Baja Verapaz*: UTA R-42430, Purulhá, Finca Sabó, 15°14.87'N, 090°9.87'W, 1170 m; *Escuintla*: UTA R-28376, Finca Medio Monte, 720 m; UTA R-22804, 26198, S slope Volcán de Agua, Finca Rosario Vista Hermosa; *Huehuetenango*: UTA R-44705, 44716, Barillas, Finca Chiblac Buena Vista, 15°53.18'N, 091°14.73'W, ca. 930 m; UTA R-45491, Barillas, Finca Chiblac Buena Vista camino a Las Nubes, 15°52.12'N, 091°13.95'W, 1330 m; UTA R-42305, Sierra de Los Cuchumatanes, Finca Chiblac Buena Vista (now Aldéa Buenos Aires), 15°52.97'N, 091°14.80'W, 975 m; *Izabal*: UTA R-28373, E slope Montañas del Mico, 12.0 km WSW Puerto Santo Tomás, 786 m; UTA R-28375, E slope Montañas del Mico, along Río San Ramoncito, above Las Escobas, 226 m; UTA R-26205, El Estor, El Chupón, 2.0 m; UTA R-26206, El Estor, El Zapotillo, 2 m; UTA R-38217, Livingston, Aldéa La Libertad, Km 285 a Petén, 75 m; UTA R-39234, Livingston, Sierra de Santa Cruz, Cerro 1019, 940 m; UTA R-39536, Los Amates, Quirigua, Sitio Arqueológico; UTA R-29871, Los Amates, Sierra del Espiritu Santo, Aldéa San Antonio; UTA R-32996, Los Amates, Sierra del Espiritu Santo, Aldéa San Antonio, ca. 500 m; UTA R-28381, Los Amates, Sierra del Espiritu Santo, S side Cerro del Nylon, 725 m; UTA R-29870, Montañas del Mico, 11.6 km WSW Puerto Santo Tomás, 744 m; UTA R-16022–23, Montañas del Mico, 5.1 km WSW Puerto Santo Tomás, Las Escobas, 104 m; UTA R-20833–34, Montañas del Mico, 5.1 km WSW Puerto Santo Tomás, Las Escobas, 150–250 m; UTA R-28374, Montañas del Mico, 5.1 km WSW Puerto Santo Tomás, Las Escobas, 150 m; UTA R-29868–69, Montañas del Mico, 8 km WSW Puerto Santo Tomás, 457 m; UTA R-46686, Montañas del Mico, Crest of Cerro Las Escobas, near Guatel Tower,

860 m; UTA R-38216, 39535, Morales, Sierra de Caral, Aldéa Negro Norte, ca. 1150 m; UTA R-42358, Morales, Sierra de Caral, Aldéa Negro Norte, ca. 1100 m; UTA R-32998, Morales, Sierra de Caral, Aldéa Negro Norte, Cerro Negro Norte, 1180 m; UTA R-37240, Morales, Sierra de Caral, Carretera entre Quebradas y La Firmeza, 190 m; UTA R-42360, Morales, Sierra de Caral, Carretera Quebradas-La Firmeza, 990 m; UTA R-32997, Morales, Sierra de Caral, Cerro Bonillistas, 300 m; UTA R-38215, Morales, Sierra de Caral, La Firmeza, 825 m; UTA R-37241, Morales, Sierra de Caral, San Miguelito, 450 m; UTA R-37242, Morales, Sierra de Caral, San Miguelito, 470 m; UTA R-37243, Morales, Sierra de Caral, San Miguelito, 600 m; UTA R-37244, Morales, Sierra de Caral, San Miguelito, 550 m; UTA R-37245, Morales, Sierra de Caral, San Miguelito, 560 m; UTA R-46687, Morales: Sierra de Caral: Finca “San Silvestre”, 475m; UTA R-37239, Municipio de Morales, Sierra de Caral, along tributary of Río Bobos, E of San Miguelito, 625 m; UTA R-37238, Municipio de Morales, Sierra de Caral, road between Quebradas and San Miguelito, 100 m; UTA R-20832, Near Mariscos, 20 m; UTA R-46685, Polochic Valley, 4 mi w El Estor, 30 m; UTA R-42361, Quebrada El Branchi, 2.0–4.0 km NE Aldéa La Libertad, 50 m; UTA R-22805, Sesbán, 900 m; UTA R-26207, Sierra de Santa Cruz, Cerro 1019, 980; UTA R-46681, Sierra de Santa Cruz, Exmibal Forest (first crest on road from El Estor to Finca Semuc) just W of El Estor, 560 m; UTA R-46682, Sierra de Santa Cruz, Exmibal Forest (first crest on road from El Estor to Finca Semuc) just W of El Estor, 650 m; UTA R-46683, Sierra de Santa Cruz, Exmibal Forest (first crest on road from El Estor to Finca Semuc) just W of El Estor, 650 m; UTA R-46684, Sierra de Santa Cruz, Exmibal Forest (first crest on road from El Estor to Finca Semuc) just W of El Estor, 805 m; UTA R-28377, Sierra de Santa Cruz, Finca Chacchilá, El Coco, ca. 300 m; UTA R-22168, 32999, Sierra de Santa Cruz, Finca Semuc; UTA R-28379, Sierra de Santa Cruz, Finca Semuc headquarters, ca. 500 m; UTA R-26199, Sierra de Santa Cruz, Finca Semuc, 1.0 km S headquarters, 445 m; UTA R-28378, Sierra de Santa Cruz, Finca Semuc, 1.0 km S headquarters; UTA R-29875, Sierra de Santa Cruz, Finca Semuc, 2 km S headquarters, Río Semuc, 400 m; UTA R-42359, Sierra de Santa Cruz, Finca Semuc, Casco, ca 450 m; UTA R-26196, Sierra de Santa Cruz, Finca Semuc, Chinamococh, 650 m; UTA R-26197, Sierra de Santa Cruz, Finca Semuc, Chinamococh, 600 m; UTA R-26200, Sierra de Santa Cruz, Finca Semuc, Chinamococh, 675 m; UTA R-29874, Sierra de Santa Cruz, Finca Semuc, S side Cerro Serujijá, 700 m; UTA R-29872, Sierra de Santa Cruz, Finca Semuc, S side Semococh, 580 m; UTA R-29873, Sierra de Santa Cruz, Finca Semuc, S side Semococh, 860 m; UTA R-26201, Sierra de Santa Cruz, S side Cerro Cana Tomasa, 475 m; UTA R-26202–04, Sierra de Santa Cruz, S side Cerro Cana Tomasa, 400 m; UTA R-26208–10, Sierra de Santa Cruz, Xiacam, 980 m; *Petén*: UTA R-39231, 7.9 km SW (by road) El Cruce, 740 m; UTA R-39233, ca. San José, N shore Lago Petén-Itzá; UTA R-50300, Gringo Perdido, NE side of Lago Petén-Itzá, near El Remate, 140 m; UTA R-46124, La Libertad, Parque Nacional, Sierra Lacandón, Distrito Yaxchilán; UTA R-39232, Near El Caoba, 400 m; UTA R-50299, on trail starting 1.6 km S of Tikal Visitor’ S Center; *Quezaltenango*: UTA R-20835, 22802–03, S slope Volcán Santa María, Finca El Faro, ca 4 km N El Palmar, 875 m;

San Marcos: UTA R-42285, Area La Trinidad-Aldéa La Fraternidad, 1200–1940 m; UTA R-45685, Malacatán, Finca San Ignacio, 14°56.75'N, 092°2.50'W, 610–760 m; UTA R-39510, Municipio Esquipulas Palo Gordo, Aldéa Fraternidad, Finca La Esperanza, 1550–1890 m; UTA R-39329–35, San Rafael Pie de la Cuesta, Finca America El Vergel, ca. 1500 m; UTA R-45683–84, San Rafael Pie de la Cuesta, Finca America El Vergel, 14°56.30'N, 091°53.48'W, 1600 m; *Sololá*: UTA R-45687, San Lucas Tolimán, Finca Santo Tomás Pachuj, 14°36.53'N, 091°7.40'W, 1340 m; *Zacapa*: UTA R-32994, Sierra del Merendón, Finca San Enrique, Sur del Casco; UTA R-32995, Sierra del Merendón, Finca San Enrique, Sur del Casco, 800 m; UTA R-32993, Sierra del Merendón, Finca San Enrique, Sur del Casco, Cerro La Palmichera, 890 m; *Unknown*: UTA R-22167, No specific locality; HONDURAS: *Olancho*: UTA R-53268, Sierra de Agalta, 14.945N, 86.151W, 1195 m; *Unknown*: UTA R-24863, 25040–45, 24860–62, No specific locality; MEXICO: Nayarit: UTA R-53413, 12.4 road miles N of Las Varas, 21.21270°N, 104.99162°W, 749 m; *Oaxaca*: UTA R-2461, 13.5 from Veracruz-Oaxaca state line, 52 mi N La Ventosa, 17°10.80'N, 095°3.60'W; UTA R-52643, Municipio La Soledad, Piedra Ancha, 16.75417N, 95.45699W, 1135 m; UTA R-25819, Sierra Juárez, between Metates and Vista Hermosa, 17°40.20'N, 096°19.20'W, 900–1500 m (1200 m); UTA R-12336, Sierra Juárez, Metates, 17°42.00'N, 096°18.60'W, 902 m; UTA R-14148, Sierra Juárez, Metates, 17°42.00'N, 096°18.60'W; UTA R-12337, Sierra Juárez, Metates, 17.7 km S Valle Nacional, 17°42.00'N, 096°18.60'W, 914 m; *Quintana Roo*: UTA R-53411, Mex 180D, 21.05151°N, 87.06756°W, 13 m; *San Luis Potosí*: UTA R-4673, Hwy 85, 8.0 mi S Antigua Morelos; *Tamaulipas*: UTA R-4672, Hwy 80, 1.0 mi E Nuevo Morelos; *Veracruz*: UTA R-3013, 0.2 mi N Los Mangos, 18°16.20'N, 095°7.20'W, 400 m; UTA R-3011, 0.2 mi N of Encinal, 18°15.00'N, 095°6.60'W, 370 m; UTA R-9410, 1.8 mi S Juan Diaz Covarrubias, 18°7.80'N, 095°9.60'W; UTA R-3017, 10 mi S Catemaco (bridge), 18°17.40'N, 095°7.20'W, 450 m; UTA R-3015, 2.4 mi S Los Mangos, 270 m; UTA R-3012, 3.2 mi S Catemaco (bridge), 18°22.20'N, 095°7.20'W, 400 m; UTA R-3016, 7.8 mi N Juan Diaz Covarrubias, 18°12.60'N, 095°7.20'W.

Imantodes gemmistratus – COSTA RICA: *Guanacaste*: UTA R-44972, Liberia, Santa Rosa National Park; GUATEMALA: *Escuintla*: UTA R-22807, Finca Medio Monte, ca. 500 m; UTA R-22169–70, 22806, S slope Volcán de Agua, Finca Rosario Vista Hermosa; *San Marcos*: UTA R-45922, Malacatán, Finca San Ignacio, 14°56.75'N, 092°2.50'W, 610–760 m; UTA R-28380, San Pablo, Finca Palmira; *Santa Rosa*: UTA R-45651, Taxisco, Aldéa Madre Vieja (entre Monterrico and Ixtapa), 0 m; *Sololá*: UTA R-4496, San Juan Obispo; *Unknown*: UTA R-4706, No specific locality; MEXICO: *Guerrero*: UTA R-53968, Carretera Marquelia - San Luis Acatlán, 16.68388°N, 98.78722°W; *Jalisco*: UTA R-53967, Carretera Puerto Vallarta - La Cumbre Mex 200, 19.4 road miles S of Puerto Vallarta Plaza; *Nayarit*: UTA R-53539, Carretera Puerto Vallarta - Tepic, Mex 200, 21.20688°N, 104.95229°W, 86m; UTA R-53540, MX Hwy 200 S of Tepic, just S of Las Varas, 21.08391°N, 105.20233°W, 24 m; UTA R-53966, Carretera Tepic Las Vacas, Mex 200. 17.3 road miles N of Las Vacas, 21.21319°N, 104.94702°W, 879 m; *Oaxaca*: UTA R-52646, Camino

Niltepec-El Palmar, 16.6808N, 94.57074W, 230 m; UTA R-6638, Cerro Baúl, 16°33.60'N, 094°10.20'W, 1700 m; UTA R-2460, 23.3 mi E La Ventosa, 16°33.60'N, 094°36.60'W; UTA R-8828, 5.9 mi S El Tejocotes, 17°13.20'N, 097°3.00'W; UTA R-6072, 8.0 km NE Tapanatepec, 16°24.60'N, 094°9.60'W, 274 m; *Sinaloa*: UTA R-4823, 3.6 mi E Concordia; UTA R-4376, 5.0 mi SE Villa Unión, 100 ft; *Veracruz*: UTA R-3014, 5.5 mi S Catemaco (bridge), 18°21.00'N, 095°6.60'W, 540 m; UTA R-3074, Los Tuxtlas, 3.6 mi S Catemaco, 18°22.80'N, 095°7.20'W, 390 m; UTA R-3081, On way back from Encinal; UTA R-6869, 2.1 mi N Juan Diaz Covarrubias, 18°9.60'N, 095°9.60'W; UTA R-6865, 4.4 mi N Juan Diaz Covarrubias, 18°10.20'N, 095°8.40'W; UTA R-9411, 5.4 mi S Juan Diaz Covarrubias, 18°10.80'N, 095°7.80'W; *Yucatan*: UTA R-53969, Mex 180D, 20.74248°N, 88.21232°W.

Imantodes inornatus – COSTA RICA: *Cartago*: UTA R-12904, 2.0 km W Pavones de Turrialba, 500 m; ECUADOR: *Esmeraldas*: QCAZ 3843, La Chiquita protected forest, 30 km San Lorenzo-Ibarra, 1.2333°N, 78.7600°W; DHMECN 5661, road San Lorenzo-Lita, 1.1979°N, 78.7305°W, 60 m; UTA R-55930–31, road San Lorenzo-Lita, 1.26219°N, 78.79528°W, 40 m; *Manabí*: EPN 8978, Maicito on road to Chone.

Imantodes lentiferus – COLOMBIA: *Vaupés*: UTA R-5175, Timbó; ECUADOR: *Morona Santiago*: QCAZ 9187, General Leonidas Plaza Gutiérrez (Limón), Napinaza, Quebrada río Napinaza, 2.9230°S, 78.4080°W; *Napo*: QCAZ 284–85, El Reventador, 0.0412°S, 77.5268°W; DHMECN 4591, Archidona, Cotundo, Narupa Biological Reserve, Fundación Jocotoco, 0.7583°S, 77.9103°W, 1800 m; *Orellana*: QCAZ 8476, Pata 3 and Chontayacu, Huataracu community, 0.1811°S, 77.0201°W, 346 m; QCAZ 10110, Parque Nacional Yasuní, 1 km E road to Maxus, km 38, 0.6539°S, 76.4518°W; *Pastaza*: QCAZ 8170, around Villano, AGIP petroleum camp, K4 Unidad 1, 1.4722°S, 77.4864°W; QCAZ 8197, around Villano, AGIP petroleum camp, K4 Unidad 3, 1.4697°S, 77.4874°W; QCAZ 8276, around Villano, Kurintza community, Kurintza Unidad 3, 1.5100°S, 77.5141°W, 387 m; QCAZ 8377, around Villano, AGIP petroleum camp, K10 Unidad 3, 1.4727°S, 77.5359°W, 430 m; DHMECN 4368, Montalvo, Nuevo Corrientes, Kurintza, 2.0721°S, 76.3397°W, 300 m; EPN 1276, Mera, 1.4567°S, 78.1114°W; EPN 6256, Arajuno, Parroquia Curaray, caserío Chuyayacu, 0.4744°S, 77.6505°W; EPN 6482, Arutam, 1.7500°S, 77.8666°W; EPN 8974, Shell, Taigsha; EPN 897677, no specific locality; *Sucumbíos*: EPN 11531, 11617, Gonzalo Pizarro, Lumbacui, Aguarico protected Forest, 0.0492°S, 77.3567°W; DHMECN 160, Lago Agrio, Tarapoa, San Pablo de Kantesiya, 0.2499°S, 76.4166°W, 300 m; DHMECN 1572, Shushufindi, Limoncocha, 0.3999°S, 76.6333°W, 300 m; DHMECN 8345, Putumayo, Santa Elena, Block 27, 0.3667°N, 76.1869°W, 264 m; *Zamora Chinchipe*: QCAZ 8488, Guadalupe, Afluente del río Piuntza, Finca de Mesías San Martín, 3.8564°S, 78.8646°W, 1154 m; [*Pichincha*]: EPN 8975, Pachijal (in error), 0.1300°S, 78.7264°W; NO SPECIFIC POLITICAL UNIT: *Oriente*: EPN 897273, No locality data: EPN 9585.

Imantodes tenuissimus – MEXICO: *Quintana Roo*: UTA R-53970, Mex Hwy180D, 21.07407°N, 87.02190°W, 17 m; *Yucatan*: UTA R-53412, Carretera Yaxacalba - Tah-zibichen, 20.52230°N, 88.82845°W, 33 m.