ZooKeys 381: 1–10 (2014)
doi: 10.3897/zookeys.381.6832
www.zookeys.org

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

The oribatid mite genus *Papillocepheus* (Acari, Oribatida, Tetracondylidae), with description of a new species from southern Vietnam

Sergey G. Ermilov[1,3,†], Alexander E. Anichkin[2,3,‡], Andrei V. Tolstikov[1,§]

1 *Tyumen State University, Tyumen, Russia* **2** *A.N. Severtsov Institute of Problems of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia* **3** *Joint Russian-Vietnamese Tropical Research and Technological Center, Hanoi-Ho Chi Minh, Vietnam*

† *http://zoobank.org/89063E86-8DB6-4477-9F4E-6E0DA7E3BCBB*
‡ *http://zoobank.org/FD60CA89-3F8A-4225-A0BA-C9780C05516A*
§ *http://zoobank.org/905DB7C2-26A0-45FA-8EFA-9BDB3A20B96B*

Corresponding author: *Sergey G. Ermilov* (ermilovacari@yandex.ru)

Academic editor: *V. Pesic* | Received 17 December 2013 | Accepted 5 February 2014 | Published 18 February 2014

http://zoobank.org/9707F737-DFA9-4998-A02A-2CF0C9760983

Citation: Ermilov SG, Anichkin AE, Tolstikov AV (2014) The oribatid mite genus *Papillocepheus* (Acari, Oribatida, Tetracondylidae), with description of a new species from southern Vietnam. ZooKeys 381: 1–10. doi: 10.3897/zookeys.381.6832

Abstract

The genus *Papillocepheus* is recorded in the Oriental region for the first time. A new species, *Papillocepheus primus* **sp. n.**, is described from southern Vietnam; the description is based on specimens collected from semidecayed leaves and litter of Dong Nai Biosphere Reserve and Bu Gia Map National Park. The new generic diagnosis of *Papillocepheus* and an identification key to the known species of this genus are given.

Keywords

Oribatid mites, new species, description, *Papillocepheus*, generic diagnosis, new record, key, Vietnam

Introduction

Papillocepheus (Acari, Oribatida, Tetracondylidae) is the genus of oribatid mites that was proposed by Balogh and Mahunka (1966) with *Papillocepheus heterotrichus* Balogh & Mahunka, 1966 as type species. Currently, this genus comprises nine species, which are collectively distributed in the Ethiopian and Australian regions, Yemen and Chile. These

species are as follows: *P. areolatus* Mahunka, 1987 (Mahunka 1987; recorded from Kenya), *P. decoratus* Mahunka, 1994 (Mahunka 1994; Madagascar), *P. decorus* (Hammer, 1966) (Hammer 1966; New Zealand), *P. deficiens* J. & P. Balogh, 1983 (Balogh and Balogh 1983; Australia); *P. heterotrichus* Balogh & Mahunka, 1966 (Balogh and Mahunka 1966; South Africa), *P. longisetosus* Mahunka, 2009 (Mahunka 2009; Yemen), *P. neotropicus* (P. Balogh, 1988) (Balogh and Balogh 1988; Chile), *P. reductus* Mahunka, 1994 (Mahunka 1994; Madagascar) and *P. tuberculatus* (Mahunka, 1978) (Mahunka 1978; Mauritius).

In the course of taxonomic identification of Vietnamese oribatid mites collected in October and November 2013 we found one new species, belonging to the genus *Papillocepheus*. Hence, the genus is recorded in Vietnam and the Oriental region for the first time. The main purpose of our paper is to describe and illustrate this species.

Also, the new generic diagnosis of *Papillocepheus* and an identification key to the known species of this genus are provided.

Material and methods

Specimens of *Papillocepheus primus* sp. n. were collected by A.E. Anichkin and S.G. Ermilov in southern Vietnam. Holotype, female: Dong Nai Province, Dong Nai Biosphere Reserve, 11°26'N, 107°26'E, 120 m a.s.l., semidecayed leaves of the Moracea family in a monsoon semideciduous tropical forest on sandy soils near (0.5 m) Dong Nai river, 25.X.2013. Paratype, female: Binh Phuoc Province, Bu Gia Map National Park, 12°11'N, 107°12'E, 539 m a.s.l., leaf litter on ferralitic soils (sifting) in Palm forest on slope of a hill near small river, 14.XI.2013.

All specimens were studied in lactic acid, mounted in temporary cavity slides for the duration of the study, and then stored in 70% ethanol in vials. Body measurements are presented in micrometers. The body length was measured in lateral view, from the tip of the rostrum to the posterior edge of the ventral plate. Notogastral width refers to the maximum width in dorsal aspect. Lengths of body setae were measured in lateral aspect. Formulae for leg setation are given in parentheses according to the sequence of trochanter–femur–genu–tibia–tarsus (famulus included). Formulae for leg solenidia are given in square brackets according to the sequence of genu–tibia–tarsus. Terminology used in this paper mostly follows that of Norton and Behan-Pelletier (2009).

Systematics

Genus *Papillocepheus* Balogh & Mahunka, 1966
http://species-id.net/wiki/Papillocepheus

=*Clavazetes* Hammer, 1966

Type species. *Papillocepheus heterotrichus* Balogh & Mahunka, 1966

New generic diagnosis (based partially on data from: Balogh and Mahunka 1966; Hammer 1966).

Tetracondylidae with the following combination of characters: costulae dorsal or dorso-lateral, reach the insertions of lamellar setae; transcostula present or absent; rostral, lamellar and interlamellar setae well developed, setiform or weakly dilated distally or medio-distally; sensilli with short stalk and clavate head; exobothridial setae absent; notogaster with 8–10 pairs of setae, all medium size or short; majority of notogastral setae clearly dilated in distal or medial part, phylliform or willow leaf shaped; medial prodorsal and notogastral condyles usually absent, when present, separated; epimeral formula 3–1–3–3, sometimes some setae absent or represented by alveoli; genital plates with three setae; aggenital setae present or absent; anal plates with two pairs of setae; three pairs of adanal setae present; adanal setae ad_3 located in lateral or preanal position; localization of adanal lyrifissures different among types; setae *u* of all leg tarsi setiform.

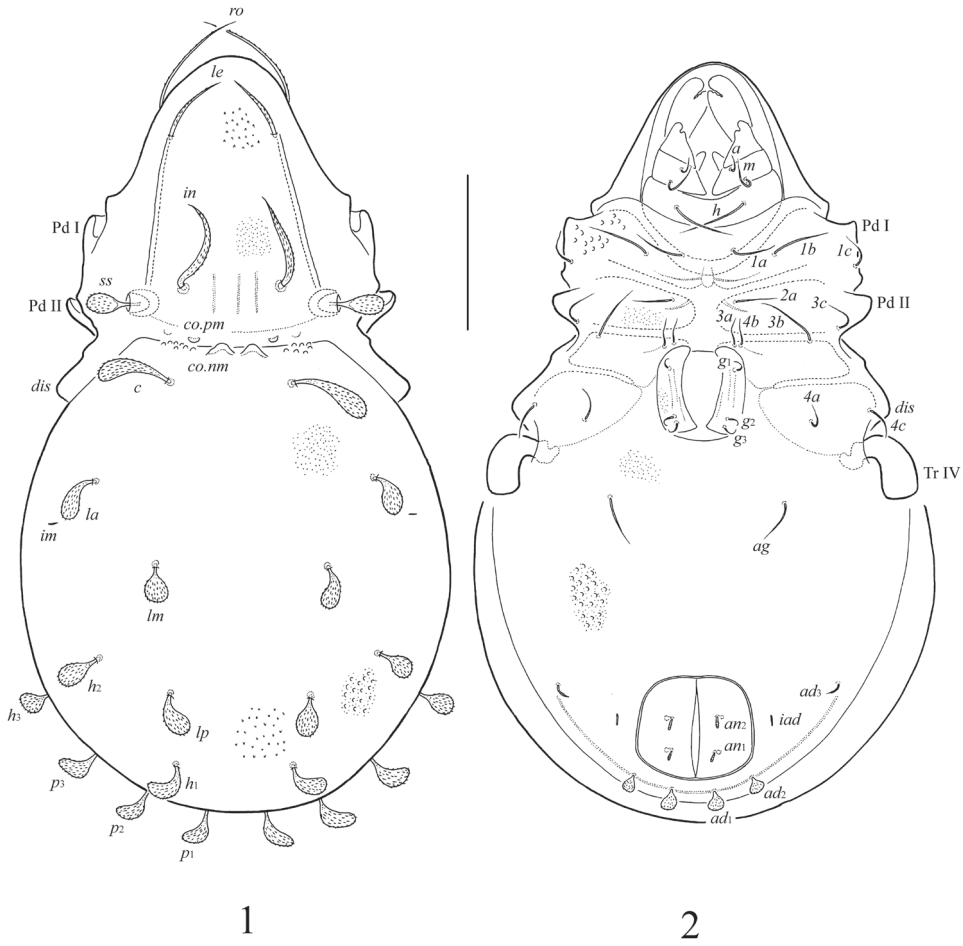
Papillocepheus primus **Ermilov, Anichkin & Tolstikov, sp. n.**
http://zoobank.org/CB231C4F-387C-46BE-9C54-0A71399761AD
http://species-id.net/wiki/Papillocepheus_primus
Figs 1–5

Diagnosis. Body size 498 × 273–282. Rostral setae simple, barbed; lamellar setae shorter, thickened, barbed; interlamellar setae thick, willow leaf shaped, densely barbed. Sensilli with barbed head. Medial prodorsal and notogastral condyles present, notogastral ones located close to each other; lateral prodorsal and notogastral condyles absent. Notogaster with 10 pairs of phylliform setae. Epimeral setal formula: 3–1–3–3. Anal setae dilated in medial part. Adanal ad_1, ad_2 phylliform; ad_3 slightly thickened in medial part, inserted in lateral position. Adanal lyrifissures located in paraanal position, distanced from the anal plates. Most setae on leg tarsi smooth, with swelling in tip.

Description. *Measurements*. Body length 498 (holotype and paratype: both female); body width 273 (holotype), 282 (paratype).

Integument. Body color yellow-brownish. Body surface and legs covered by granular cerotegument; granules conical (length up to 4). Body surface (including genital and anal plates) densely microfoveolate (diameter of foveolae up to 1). Lateral parts of prodorsum, notogaster and anogenital region additionally with larger foveolae (diameter of foveolae up to 6). Lateral region of body near to pedotecta II and anterior margin of notogaster partially tuberculate (diameter of tubercles up to 8).

Prodorsum. Rostrum simple, widely rounded. Costulae well developed, thin. Transcostula absent. Rostral setae (*ro*, 69–77) setiform, barbed, inserted laterally. Lamellar setae (*le*, 49–57) shorter, slightly thicker and more densely barbed than rostral setae, inserted dorso-laterally near the end of costulae. Interlamellar setae (*in*, 77–86) thick, willow leaf shaped with attenuate tip, densely barbed. Sensilli (*ss*, 32–36) short, with barbed head. Medial prodorsal condyles (*co.pm*) small, rounded distally. One

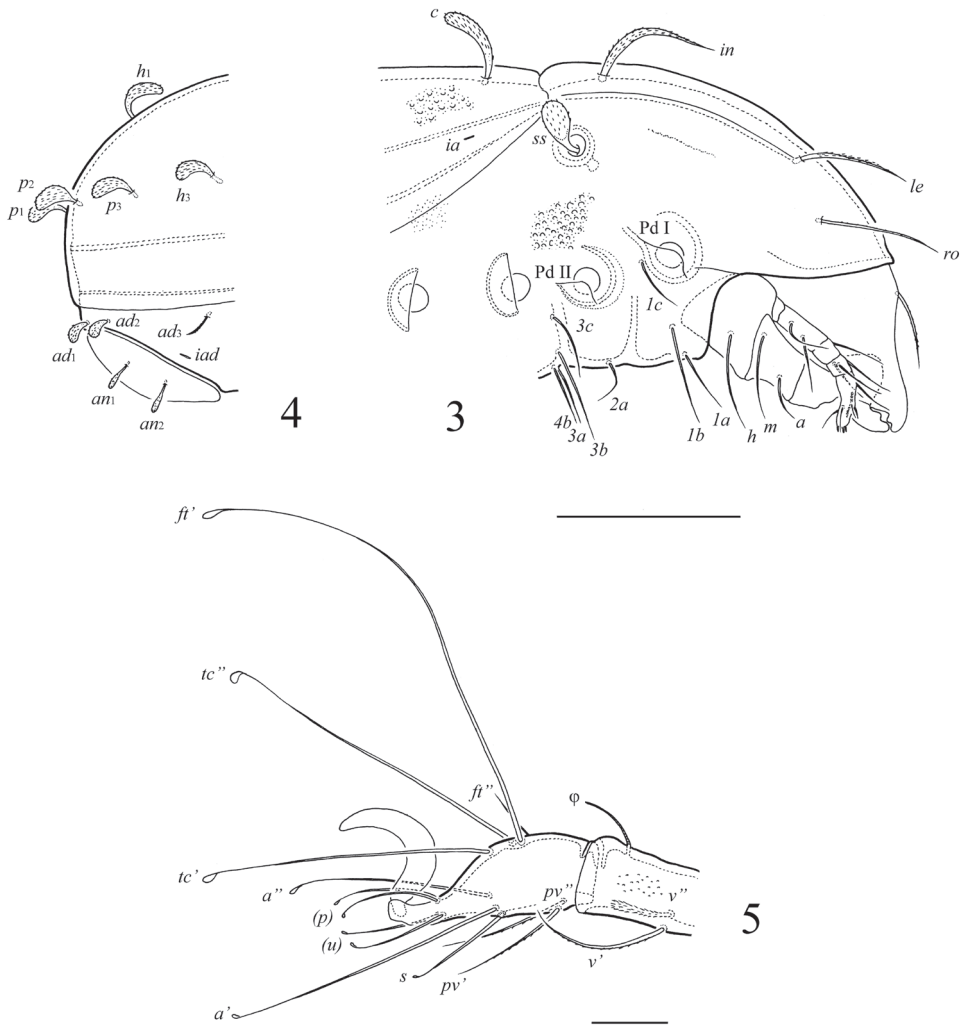


Figures 1–2. *Papillocepheus primus* sp. n., adult: **1** dorsal view **2** ventral view (legs except trochanters IV not illustrated). Scale bar 100 μm.

indistinct tubercle located laterally to each medial condyle, possibly, it is the second pair of medial prodorsal condyles. Lateral prodorsal condyles absent. Distinct tutorial lines absent.

Notogaster. Medial notogastral condyles (*co.nm*) of medium size, weakly triangular distally, located close to each other, between prodorsal medial condyles. Lateral notogastral condyles absent. Notogaster with 10 pairs of notogastral setae. All setae widely phylliform; *c* (45–49) longer than others (32–36). Opisthonotal gland openings and lyrifissures *ip*, *ih*, *ips* poorly visible.

Gnathosoma. Subcapitulum longer than wide: 123 × 94. Subcapitular setae setiform, smooth; *h* and *m* (both 57) longer than *a* (24). Adoral setae absent. Palps (length 82) with setation 0–2–1–3–8(+ω). Solenidion thickened, blunt-ended, pressed to the

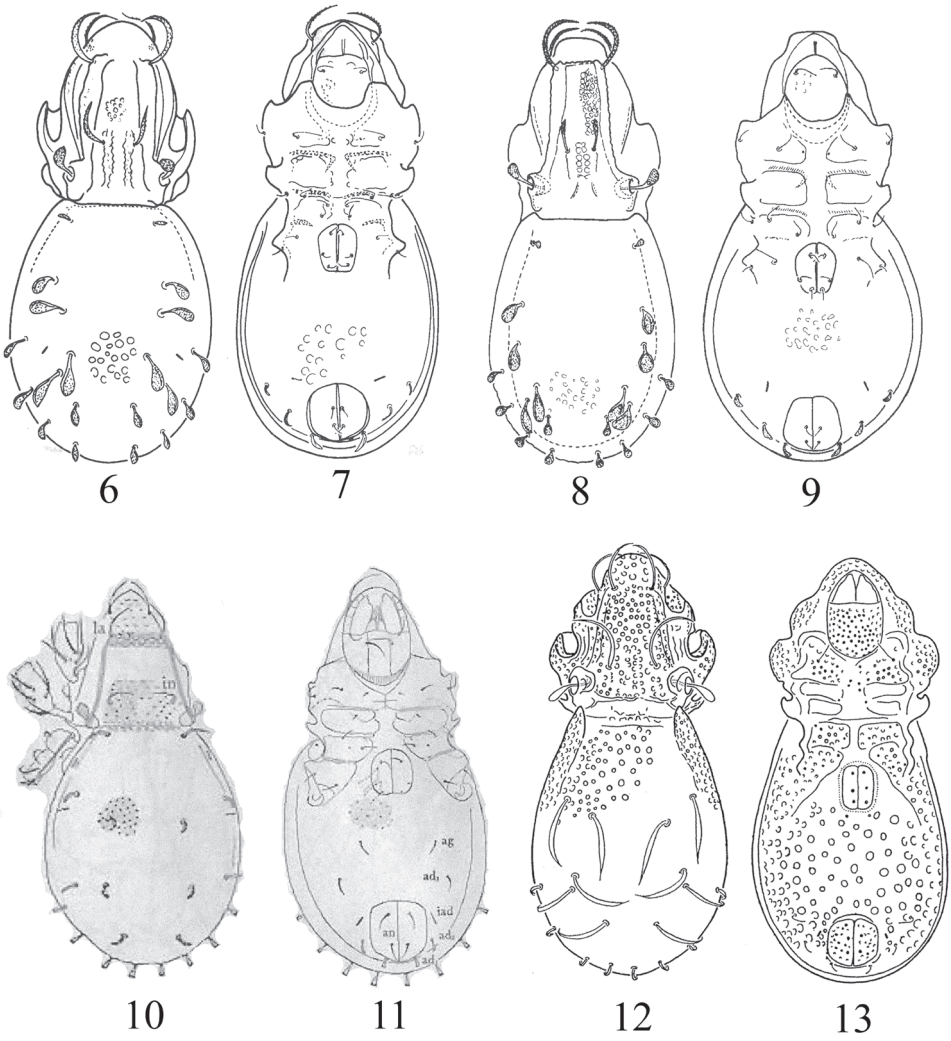


Figures 3–5. *Papillocepheus primus* sp. n., adult: **3** lateral view of prodorsum and anterior part of notogaster (legs not illustrated) **4** lateral view of posterior part of notogaster **5** tarsus and anterior part of tibia of leg I, right, antiaxial view. Scale bar (**3, 4**) 100 μm, (**5**) 20 μm.

palptarsus surface, not attached with eupathidium. Chelicerae (length 139) with one barbed seta *cha* (45); seta *chb* not evident. Trägårdh's organ conical.

Lateral podosomal and epimeral regions. Epimeral setal formula: 3–1–3–3. All setae setiform, smooth. Setae *1b*, *3b* (57–61) longer than other setae (36–41). Discidia (*dis*) rounded.

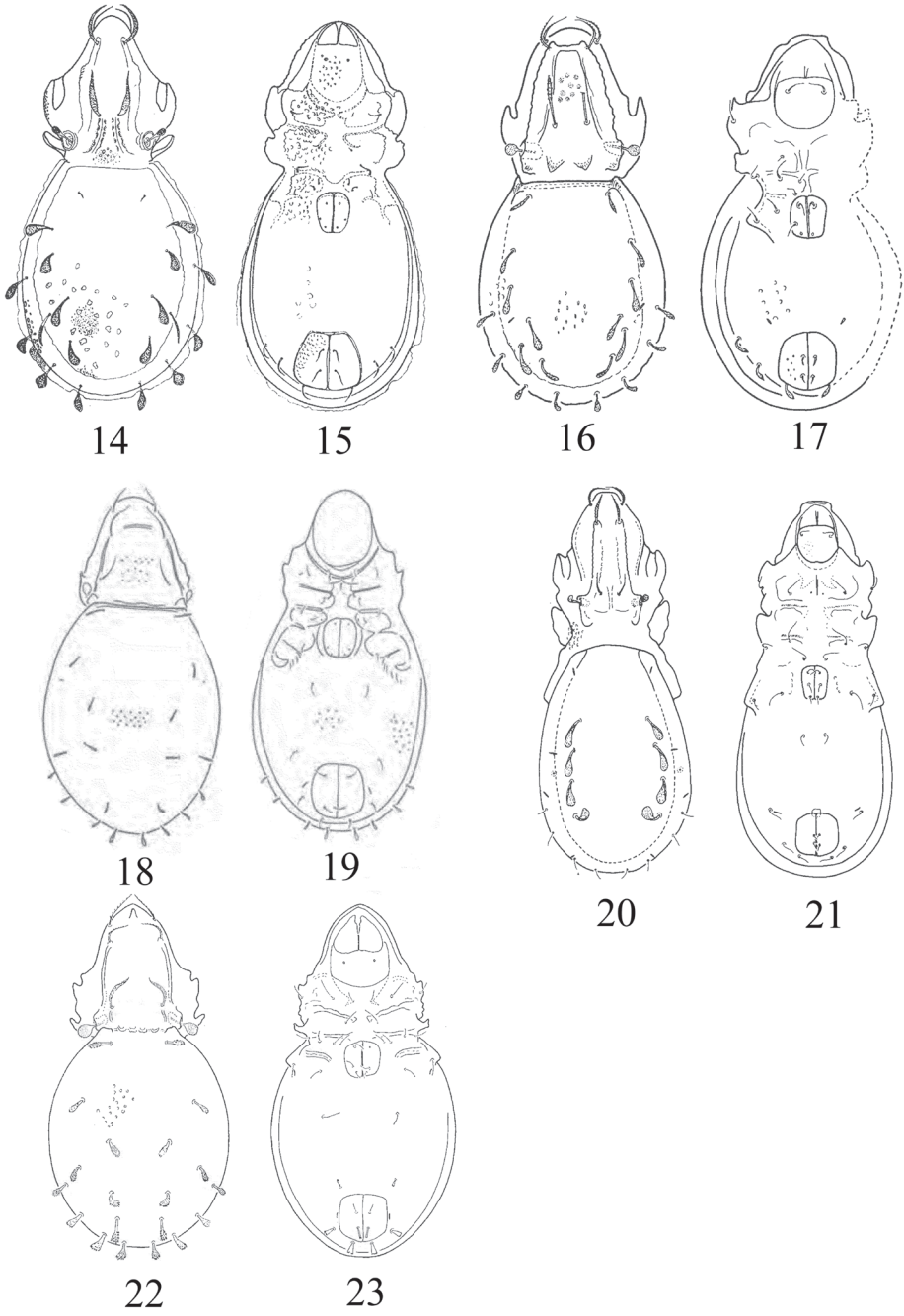
Anogenital region. Three pairs of genital (g_1–g_3, 18–20) and one pair of aggenital setae (*ag*, 32–36) setiform, smooth. Two pairs of anal setae (an_1, an_2, 18–20) thickened, dilated in medial part, barbed. Three pairs of adanal setae present: ad_1, ad_2 (16) phylliform, inserted in postanal position; ad_3 (16–18) slightly thickened in medial part,



Figures 6–13. Species of the genus *Papillocepheus*, adult (**6, 8, 10, 12** dorsal view; **7, 9, 11, 13** ventral view): **6, 7** *P. areolatus* Mahunka, 1987 **8, 9** *P. decoratus* Mahunka, 1994 **10, 11** *P. decorus* (Hammer, 1966) **12, 13** *P. deficiens* J. & P. Balogh, 1983. Figures from: Mahunka 1987, 1994; Hammer 1966; Balogh and Balogh 1983, accordingly. Scale bars absent in original descriptions.

barbed, inserted in lateral position. Adanal lyrifissures *iad* located in paraanal position, distanced from the anal plates.

Legs. Generally, morphology of leg segments typical for Tetracondylidae (Grobler 1995; Ermilov et al. 2010). Claw of each tarsus smooth. Tarsi without teeth. Formulae of leg setation (including famulus) and solenidia: I (1–4–3–4–16) [1–2–2], II (1–4–3–3–15) [1–1–2], III (2–3–0–2–14) [1–1–0], IV (1–2–1–2–13) [0–1–0]; homology of setae and solenidia indicated in Table 1. Most setae on tarsi smooth, with swelling



Figures 14–23. Species of the genus *Papillocepheus*, adult (**14, 16, 18, 20, 22** dorsal view; **15, 17, 19, 21, 23** ventral view): **14, 15** *P. heterotrichus* Balogh & Mahunka, 1966 **16, 17** *P. longisetosus* Mahunka, 2009 **18, 19** *P. neotropicus* (P. Balogh, 1988) **20, 21** *P. reductus* Mahunka, 1994 **22, 23** *P. tuberculatus* (Mahunka, 1978). Figures from: Balogh and Mahunka 1966; Mahunka 2009; Balogh and Balogh 1988; Mahunka 1994, 1978, accordingly. Scale bars absent in original descriptions.

Table 1. Leg setation and solenidia of adult *Papillocepheus primus* sp. n.

Leg	Trochanter	Femur	Genu	Tibia	Tarsus
I	*v'*	*d*, *(l)*, *bv"*	*(l)*, *v'*, σ	*(l)*, *(v)*, φ_1, φ_2	*(ft)*, *(tc)*, *(it)*, *(p)*, *(u)*, *(a)*, *s*, *(pv)*, *e*, ω_1, ω_2
II	*v'*	*d*, *(l)*, *bv"*	*(l)*, *v'*, σ	*l'*, *(v)*, φ	*(ft)*, *(tc)*, *(it)*, *(p)*, *(u)*, *(a)*, *s*, *(pv)*, ω_1, ω_2
III	*l'*, *v'*	*d*, *l'*, *ev'*	σ	*(v)*, φ	*ft"*, *(tc)*, *(it)*, *(p)*, *(u)*, *(a)*, *s*, *(pv)*
IV	*v'*	*d*, *ev'*	*d*	*(v)*, φ	*(ft)*, *(tc)*, *(p)*, *(u)*, *(a)*, *s*, *(pv)*

Roman letters refer to normal setae (*e* to famulus), Greek letters to solenidia. Single prime (') marks setae on anterior and double prime (") setae on posterior side of the given leg segment. Parentheses refer to pair of setae.

in tip. Other setae setiform, barbed (except *v"* on tibia IV, dilated distally and densely barbed). Seta *ft'* absent on tarsi III, *ft'* present on tarsi IV. Seta *l'* absent on genua III, IV. Famulus short, straight. Solenidia simple.

Type deposition. The holotype is deposited in the collection of the Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia; one paratype is in the collection of the Tyumen State University Museum of Zoology, Tyumen, Russia.

Etymology. The specific name "*primus*" refers to the first species of *Papillocepheus* recorded in the Oriental region.

Comparison. *Papillocepheus primus* sp. n. can be distinguished from all known species of the genus *Papillocepheus* by the key, which is presented below.

Key to known species of the genus *Papillocepheus*

1 Eight or nine pairs of notogastral setae present **2**

– Ten pairs of notogastral setae present **3**

2 Eight pairs of notogastral setae present (*c* and h_1 absent); notogastral setae *la*, *lm*, *lp*, h_2 well dilated distally, phylliform, setae p_1–p_3, h_3 simple; setae *lm* located posterior to *la*; adanal lyrifissures in direct apoanal position; body size: 565–620 × 206–261 ..... ***P. reductus*** **Mahunka, 1994**

– Nine pairs of notogastral setae present (*c* absent); all notogastral setae weakly dilated in medial part, willow leaf shaped; *lm* located medio-posterior to *la*; adanal lyrifissures almost transversely oriented; body size: 503 × 230 ..... ***P. deficiens*** **J. & P. Balogh, 1983**

3 Medial prodorsal or/and medial notogastral condyles developed **4**

– Medial prodorsal and medial notogastral condyles not developed **6**

4 Translamella present; *lm* located posterior to *la*; aggenital setae absent; adanal lyrifissures in preanal position; body size: 582 × 290 ..... ***P. longisetosus*** **Mahunka, 2009**

– Translamella absent; *lm* located medio-posterior to *la*; aggenital setae present; adanal lyrifissures in paraanal position **5**

5 Medial notogastral condyles not developed; adanal setae ad_3 in preanal position; adanal lyrifissures located close to the anal plates; body size: 436–471 × 202–224 ..... ***P. tuberculatus*** **(Mahunka, 1978)**

– Medial notogastral condyles developed; adanal setae ad_3 in lateral position; adanal lyrifissures distanced from the anal plates; body size: 498 × 273–282... .....***P. primus* sp. n.**

6 Notogastral setae *lm* located dorsally on notogaster, medio-posterior to *la*; aggenital setae present.....**7**

– Notogastral setae *lm* located dorso-laterally on notogaster, posterior to *la*; aggenital setae absent.....**8**

7 Adanal setae ad_1, ad_2 simple; aggenital setae located closer to genital plates than to anal plates; body length: 470 .....***P. neotropicus* (P. Balogh, 1988)**

– Adanal setae ad_1, ad_2 dilated distally, phylliform; aggenital setae halfway between genital and anal plates; body length: 500...***P. decorus* (Hammer, 1966)**

8 Notogastral setae *c* minute, thin; notogastral setae p_1–p_3, h_3 similar in size to other notogastral setae (except *c*); adanal setae simple; body size: 715–720 × 353–358 ..... ***P. heterotrichus* Balogh & Mahunka, 1966**

– Notogastral setae *c* well developed, phylliform; notogastral setae p_1–p_3, h_3 smaller than other notogastral setae (except *c*); some adanal setae phylliform.....**9**

9 Translamella present; interlamellar setae straight, weakly dilated distally; adanal lyrifissures longitudinal oriented; body size: 482–517 × 221–266 ....***P. decoratus* Mahunka, 1994**

– Translamella absent; interlamellar setae curved, willow leaf shaped; adanal lyrifissures transversely oriented; body size: 549–590 × 246–279 .... ***P. areolatus* Mahunka, 1987**

Acknowledgements

We cordially thank Dr. Elizabeth A. Hugo-Coetzee (National Museum, Bloemfontein, South Africa) and Prof. Dr. Gerd Weigmann (Free University of Berlin, Institute of Zoology, Berlin, Germany) for the valuable comments. We are thankful to the staff of Dong Nai Biosphere Reserve and Bu Gia Map National Park for support during the field work. The reported study was supported by RFBR, research project No. 14-04-31183 mol_a.

References

Balogh J, Balogh P (1983) Data to the oribatid fauna of Australia (Acari). II. Acta Zoologica Academiae Scientiarum Hungaricae 29(4): 283–301.

Balogh J, Balogh P (1988) Oribatid mites of the Neotropical region. I. Akadémiai Kiadó Press, Budapest, 335 pp.

Balogh J, Mahunka S (1966) New oribatids (Acari) from South Africa. Acta Zoologica Academiae Scientiarum Hungaricae 12(1–2): 1–23.

Ermilov SG, Sidorchuk EA, Rybalov LB (2010) A new species of *Dolicheremaeus* (Acari: Oribatida: Tetracondylidae) from Ethiopia. Systematic and Applied Acarology 15(3): 235–243.

Grobler L (1995) New species of the genus *Plenotocepheus* Hammer, 1966 (Acari, Oribatida, Otocepheidae) from South Africa, I. Navorsinge van die Nasionale Museum, Bloemfontein 11(2): 13–36.

Hammer M (1966) Investigations on the oribatid fauna of New Zealand. Part I. Det Kongelige Danske Videnskabernes Selskab Biologiske Skrifter 15(2): 1–108.

Mahunka S (1978) Neue und interessante milben aus dem Genfer museum XXXIV. A compendium of the oribatid (Acari) fauna of Mauritius, Reunion and the Seychelles Is. II. Revue Suisse de Zoologie 85(2): 307–340.

Mahunka S (1987) Studies on the oribatid fauna of Kenya (Acari: Oribatida) I. Miscellanea Zoologica Hungarica 4: 71–91.

Mahunka S (1994) Oribatids from Madagascar II. (Acari: Oribatida) (new and interesting mites from Geneva Museum LXXIX). Revue Suisse de Zoologie 101(2): 47–88.

Mahunka S (2009) Oribatid mites from the Arabian Peninsula, including further records from Socotra (Acari: Oribatida). Revue Suisse de Zoologie 116(2): 257–274.

Norton RA, Behan-Pelletier VM (2009) Oribatida. Chapter 15. In: Krantz GW, Walter DE (Eds) A Manual of Acarology, 3rd edition. Texas Tech University Press, Lubbock, 430–564.

ZooKeys 381: 11–78 (2014)
doi: 10.3897/zookeys.381.6772
www.zookeys.org

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

New genera and species of Neotropical Exosternini (Coleoptera, Histeridae)

Michael S. Caterino[1,†], Alexey K. Tishechkin[1,2,‡]

1 *Department of Invertebrate Zoology, Santa Barbara Museum of Natural History, 2559 Puesta del Sol, Santa Barbara, CA 93105 USA* **2** *Louisiana State Arthropod Museum, Department of Entomology, Louisiana State University, 404 Life Sciences Building, Baton Rouge, LA 70803 USA*

† *http://zoobank.org/F687B1E2-A07D-4F28-B1F5-4A0DD17B6490*
‡ *http://zoobank.org/341C5592-E307-43B4-978C-066999A6C8B5*

Corresponding author: *Michael S. Caterino* (mcaterino@sbnature2.org)

Academic editor: *C. Majka* | Received 10 December 2013 | Accepted 28 January 2014 | Published 18 February 2014

http://zoobank.org/AFD0E4A6-F366-4D0C-B093-D7D6CE60F188

Citation: Caterino MS, Tishechkin AK (2014) New genera and species of Neotropical Exosternini (Coleoptera, Histeridae). ZooKeys 381: 11–78. doi: 10.3897/zookeys.381.6772

Abstract

We describe the following 8 new genera and 23 new species of Neotropical Exosternini. *Conocassis* **gen. n.** (*Conocassis minor* **sp. n.** [type species], *Conocassis dromedaria* **sp. n.**, *Conocassis trisulcata* **sp. n.**, and *Conocassis invaginata* **sp. n.**), *Enkyosoma* **gen. n.** (*Enkyosoma rockwelli* **sp. n.**), *Pluricosta* **gen. n.** (*Pluricosta onthophiloides* **sp. n.**), *Pyxister* **gen. n.** (*Pyxister devorator* **sp. n.** [type species] and *Pyxister labralis* **sp. n.**), *Chapischema* **gen. n.** (*Chapischema doppelganger* **sp. n.**), *Scaptorus* **gen. n.** (*Scaptorus pyramus* **sp. n.**), *Lacrimorpha* **gen. n.** (*Lacrimorpha glabra* **sp. n.** [type species], *Lacrimorpha balbina* **sp. n.**, *Lacrimorpha subdepressa* **sp. n.**, and *Lacrimorpha acuminata* **sp. n.**), *Crenulister* **gen. n.** (*Crenulister grossus* **sp. n.** [type species], *Crenulister explanatus* **sp. n.**, *Crenulister dentatus* **sp. n.**, *Crenulister impar* **sp. n.**, *Crenulister umbrosus* **sp. n.**, *Crenulister simplex* **sp. n.**, *Crenulister paucitans* **sp. n.**, *Crenulister spinipes* **sp. n.**, and *Crenulister seriatus* **sp. n.**) These all represent highly distinctive and phylogenetically isolated forms, almost invariably known from very few specimens. All but one species have been collected only by passive flight intercept traps, and nothing significant is known about the biology of any of them.

Keywords

Histeridae, Histerinae, Exosternini, predator, Neotropical region

Introduction

In the course of revising all known New World Exosternini, hundreds of new species have been discovered. Many of these new species have been more or less readily assignable to known genera (including *Operclipygus* Marseul: Caterino and Tishechkin 2013; *Kaszabister* Mazur: Dégallier et al. 2012; *Mecistostethus* Marseul: Caterino et al. 2012; *Baconia*: Caterino and Tishechkin 2013b; *Hypobletus* Schmidt: Tishechkin and Caterino in prep.; *Yarmister* Wenzel: Tishechkin and Caterino in prep.). However, many have not. Phylogenetic analyses of all species of New World Exosternini, and representatives of nearly all World genera utilizing diverse morphological and molecular characters have attempted to place these numerous enigmatic species, succeeding in many cases but failing in others (Caterino and Tishechkin in review). Here we describe a number of the most distinctive and phylogenetically isolated lineages in this group, recognizing eight new genera, together containing 23 species, all of them previously undescribed.

All but one of these new species have been collected exclusively through the use of flight interception traps. While this this type of trapping is extremely valuable in biodiversity surveys, it unfortunately provides little information about the natural history of these exceptionally attractive and unusual species. We can only hope that by calling attention to their existence that our colleagues may help us to scour appropriate microhabitats to uncover the natural histories of these species.

Materials and methods

Conventional imaging was done using a Visionary Digital's, 'Passport' portable imaging system, which incorporates a Canon 7D with MP-E 65mm 1-5× macro zoom lens. Images were stacked using Helicon Focus software. SEM imaging was done on a Zeiss EVO 40 scope. Most specimens were sputter coated with gold but some uncoated specimens were examined in 'variable pressure' mode. We present only selected images as necessary to identify the species in this paper. However, multiple photographs of all species have been archived in MorphBank (www.morphbank.net), and are also available through the Encyclopedia of Life (www.eol.org). Following histerid conventions, total body length is measured from the anterior margin of the pronotum to the posterior margin of the elytra (to exclude preservation variability in head and pygidial extension), while width is taken at the widest point, generally near the elytral humeri.

Much of the morphological terminology used is based on Wenzel and Dybas (1941), but modified to follow more recent treatments by Helava et al. (1985), Ôhara (1994), Kanaar (1997) and Lawrence et al. (2011). We have presented an extensive discussion of Exosternini-specific morphological terminology in Caterino and Tishechkin (2013a) and refer the reader to the labeled illustrations there.

We present extensive descriptions for the majority of species. At the same time, we term most of these 'diagnostic descriptions', to emphasize the fact that they focus on those character systems in which differences among species are typically found.

They are not intended to be exhaustive descriptions of each species' morphology. We have attempted to make most descriptions consistent in character content and order, facilitating comparison as well as their reuse in other contexts, such as in species pages and other media, which we encourage. The 'remarks' sections highlight the few most important key characters of each species.

Material examined lists provide verbatim data only for holotypes and summary data for all other material, whether paratypes or non-types. Within verbatim records, data are enclosed in double quotes, with data on separate labels separated by a slash '/'. The summary data generally avoids excessive repetition: each record begins with the number of specimens exhibiting identical data; records separated by commas are largely identical, differing only in the datum presented, most frequently distinct dates or collectors; distinct localities are separated by semicolons, and records from distinct countries are separated by periods (full-stops).

Collection abbreviations

CEMT Coleção de Entomologia, Universidade Federal do Mato Grosso, Cuiabá, Brazil
CHND Nicolas Degallier Collection, Paris
CMNC Canadian Museum of Nature, Ottawa, Canada
FMNH Field Museum, Chicago, USA
LSAM Louisiana State Arthropod Museum, Baton Rouge, USA
MNHN Museum National d'Histoire Naturelle, Paris, France
MSCC Michael Caterino Collection, USA
NZCS National Zoological Collection of Suriname, Paramaribo, Suriname
SEMC Snow Entomology Museum, University of Kansas, Lawrence, USA
UFPR Universidade Federal do Paraná, Curitiba, Brazil
USNM National Museum of Natural History, Washington, USA

Taxonomy

***Conocassis* gen. n.**
http://zoobank.org/8B5DA462-CDB0-4DE2-AE74-82D21121AD5D
http://species-id.net/wiki/Conocassis

Type species. *Conocassis minor* sp. n.

Description. ***Size range****:* Length 1.7–2.0 mm; width 1.2–1.5 mm; ***Body***: rufescent to rufobrunneus, somewhat narrowly elongate, widest at humeri, abruptly narrowed anteriorly at pronotal middle, with exaggerated sculpturing throughout. ***Head***: head deflexed relative to anterior pronotal margin; frons flat, sides weakly rounded, longitudinally strigose, with fine setigerous punctures between strigae, setae minute; frontal stria complete along margin of eye and across front, prom-

inent, descending onto epistoma anteriorly, subangulate at middle; supraorbital stria absent; epistoma narrowed to front, apex rather narrowly emarginate, with lateral striae meeting frontal stria, convergent, nearly meeting anterad; labrum small, about twice as wide as long, apex weakly emarginate; mandibles with incisor edges evenly curved to apex, basal teeth inconspicuous; submentum broadly triangular, weakly produced into base of oral cavity, sparsely setose; mentum subtrapezoidal, apex weakly sinuate; labial palpifers prominent; labial palps 3-segmented, with basal palpomere very short, apical palpomere widest near base, subacute; maxillary cardines short, semicircular, glabrous, stipes with two setae along lateral margin; maxillary palpi 4-segmented with basal palpomere very short, palpomeres 2 and 3 similar in length and breadth, ultimate palpomere about twice as long as penultimate, widest near base, narrowed apically; antennal scape stout, anterior surface becoming longitudinally carinate in apical half, with few apical setae; funicle widening slightly to short, disclike 8th antennomere; antennal club about 2.5× as long as wide, densely setose, with indistinct, denser subapical setose sensory patches on dorsal and ventral surfaces. ***Pronotum***: widest near base, sides sinuate, strongly narrowed anterad midpoint, basal margin uneven; lateral marginal pronotal stria complete around lateral and anterior margins, though strongly sinuate at sides, submarginal stria present along sides, not parallel to marginal, joining it near anterior corner; pronotal disk with prominent dorsal process arising from entire anterior margin, narrowing and arcing more or less evenly to middle of posterior margin, sides of process longitudinally creased to deeply invaginated, dorsal surface of process coarsely reticulostrigose, sides more or less smooth; pronotal gland openings, if present, obscured by sculpturing, possibly incorporated into lateral invaginations of pronotal process. ***Elytra***: elytron with striation generally carinate and exaggerated; epipleuron with complete marginal stria and additional stria along upper edge, paralleling outer subhumeral stria, continuing around elytral apex, variably meeting apices of dorsal striae; outer subhumeral, inner subhumeral, and dorsal striae 1-4 all complete, increasingly more strongly impressed toward suture, apices meeting apical marginal elytral suture; elytral intervals smooth to strongly microsculptured. ***Prosternum***: prosternal keel rather narrow, base weakly produced, carinal striae complete, subparallel, united basally, meeting presternal suture anteriorly, which varies from indistinct to deeply impressed; lateral striae diverging to sides, delimiting anterior leg depression; prosternal lobe extremely reduced, no longer at midline than at sides, marginal stria obsolete. ***Mesoventrite***: mesoventrite short, shallowly emarginate at middle, with complete marginal stria; mesometaventral stria paralleling or diverging anterad from mesometaventral suture at middle. ***Metaventrite***: postmesocoxal and lateral metaventral striae parallel, arching toward metacoxa then anterad to metepisternum; metaventral disk weakly depressed at middle. ***Abdomen***: 1st abdominal ventrite with anterior marginal stria continued to posterior margin by lateral striae, disk rather simply and finely punctate; propygidium slightly to distinctly wider than long, rather strongly convex, sparsely to densely reticulostrigose; propygidium apparently with single pair of gland openings very close to

anterior corners (obscured by sculpturing in most species); pygidium longer than basal width, sculptured as propygidium, generally smoother apicomedially. ***Legs***: each trochanter with single seta; profemur subparallel-sided to expanded at middle of anterior margin, with anterior marginal stria delimiting microsculptured marginal area; protibiae widened from base, sides subparallel to slightly narrowing, bearing 3–5 marginal setae in apical half; protarsal groove very weakly developed; meso- and metafemora rather large, produced beyond epipleurae in repose, broad, variously widened along posterior margins; meso- and metatibiae long, widened apically, bearing 3–4 longitudinal striae on anterior surfaces; mesotibia only bearing 2–4 characteristic long, thin subapical setae, at least one of which is inserted on the posterior surface; all tarsi laterally compressed, bearing simple ventral setae, with relatively large weakly curved claws. ***Male genitalia*** (Fig. 4): Paired accessory sclerites present; T8 with broad basal and narrower apical emarginations, line of basal membrane attachment complete, just distad basal emargination, ventral apodemes well developed, nearly meeting along midline; S8 with halves separated, apical guides moderately and evenly developed from base to apex, each apex with single prominent seta; 9th tergite with very weak ventrolateral apodemes, apices narrow, subacute; T10 completely divided; S9 broad at base, narrowest near apex, head broad, subquadrate apically, with small apical emargination, more strongly sclerotized along midline; tegmen broad basally, strongly narrowed to apex, narrowly divided apically, median foramen basad apical narrowing, moderately to strongly curved ventrad in apical half; basal piece about one-third tegmen length; median lobe short, simple, from one-fourth to one-third tegmen length. ***Female genitalia****:* T8 forming a single plate, apically emarginate; S8 tripartite, basal baculi convergent proximally; S9 elongate, articulated with strap-shaped extension from apex of S8; T10 entire; overall ovipositor rather short; valvifers paddle-shaped, paddles nearly one-half total length; coxites strong, slightly longer than broad, two-thirds length of valvifers, strongly bidentate, with strengthening ridge on inner face; gonostyle present; bursa copulatrix membraneous, weakly expanded; spermatheca gradually expanded, apically bulbous, with slightly expanded spermathecal gland attached near its base.

Diagnosis. This highly distinctive genus scarcely needs a diagnosis. Its prominent pronotal process (Figs 1, 2) is unique and unmistakable. Its assignment perhaps to tribe could be problematic, as it exhibits no hint of an emargination of the prosternal keel (Fig. 3A–B). However, both male and female genitalia, as well as DNA sequences place it unambiguously as deeply nested within the neotropical Exosternini.

Remarks. Phylogenetic analyses to date place *Conocassis* as the sister group of *Kaszabister*, a group of 4 species which are inquilines of fire ants (*Solenopsis* spp.) (Caterino and Tishechkin in review). There are few obvious similarities between these apart from generally exaggerated surface sculpturing (to a much lesser degree in *Kaszabister*). We were very fortunate to have collected a DNA quality specimen of *Conocassis minor* during our own fieldwork, its sequence providing some confidence in its general placement.

Kaszabister, on the other hand, has not yet been sequenced, so a more rigorous test of their close relationship remains to be carried out.

Etymology. The genus name means 'conical helmet' referring to the anterior process of the pronotum. The gender of the name is feminine.

Key to species of *Conocassis*

1 Sides of pronotal shield with at least one deep invagination (Fig. 2A–C); mesometaventral stria narrowly arched anterad at middle, departing from mesometaventral suture (Fig. 3B); larger, darker species **2**

– Sculpturing of sides of pronotal shield more superficial (Fig. 1A); mesometaventral stria barely departing anteriorly from mesometaventral suture (Fig. 3A); smaller, paler species ..... ***Conocassis minor***

2 Basal half of 4th elytral stria strongly bulged outward, interval deeply excavate medially (Fig. 1B, D) **3**

– Basal half of 4th elytral stria more or less evenly arcuate from base to apex, interval not so deeply excavate medially (Fig. 1C) ..... ***Conocassis trisulcata***

3 Pronotal shield in lateral profile evenly curved from anterior to posterior margins (Fig. 2B) ..... ***Conocassis dromedaria***

– Pronotal shield in lateral profile straight in basal half, abruptly curving downward from near midpoint to apical margin (Fig. 2C) ... ***Conocassis invaginata***

***Conocassis minor* sp. n.**
http://zoobank.org/27475A8C-6617-4B8C-BABF-C099F0CF575D
http://species-id.net/wiki/Conocassis_minor
Figs 1A, 3A, C, E, 4A–F, Map 1

Type locality. BRAZIL: Distrito Federal, Reserve IBGE [15.95°S, 47.88°W].

Type material. Holotype male: "**BRASIL: Dist. Federal,** Brasilia, Res. Ecol. de IBGE, 15°5.5'S, 47°53'W, Lin. 1, Pto. 3. Armad. janela, area queimada. 20.i.1998" / "Caterino/Tishechkin Exosternini Voucher EXO-00099" (UFPR). **Paratypes** (2): same data as type (CHND, FMNH).

Other material: **BRAZIL: Mato Grosso do Sul**, cerradão fragment nr. Selviria, 20.3354°S, 51.4095°W, flight intercept trap [FIT], 30.xi-3.xii.2011, M.S. Caterino & A.K. Tishechkin, DNA extraction #MSC-2273, voucher EXO-00932 (MSCC).

Diagnostic description. Length: 1.6–1.7 mm, width: 1.1–1.2 mm; as in generic description, with the following specific characters: body rufescent; frontal stria extending only to base of epistoma; apical margin of epistoma deeply emarginate; side of pronotal process with two longitudinal creases, neither deeply invaginated; pronotal disk lacking basolateral carina; pronotal process more or less evenly rounded in lateral profile; pronotal disk very finely alutaceous behind median process; all elytral

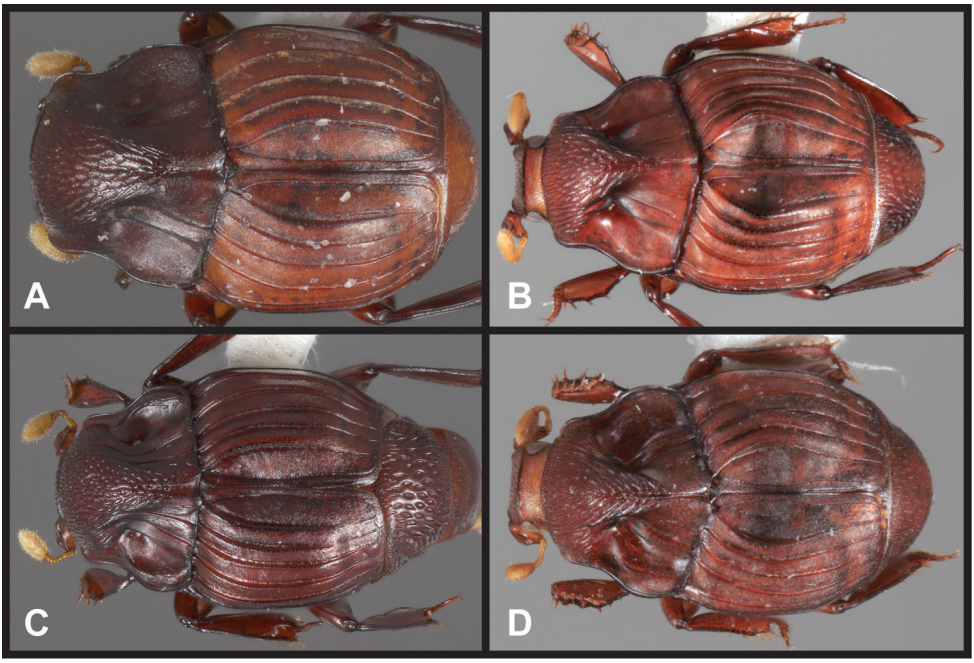
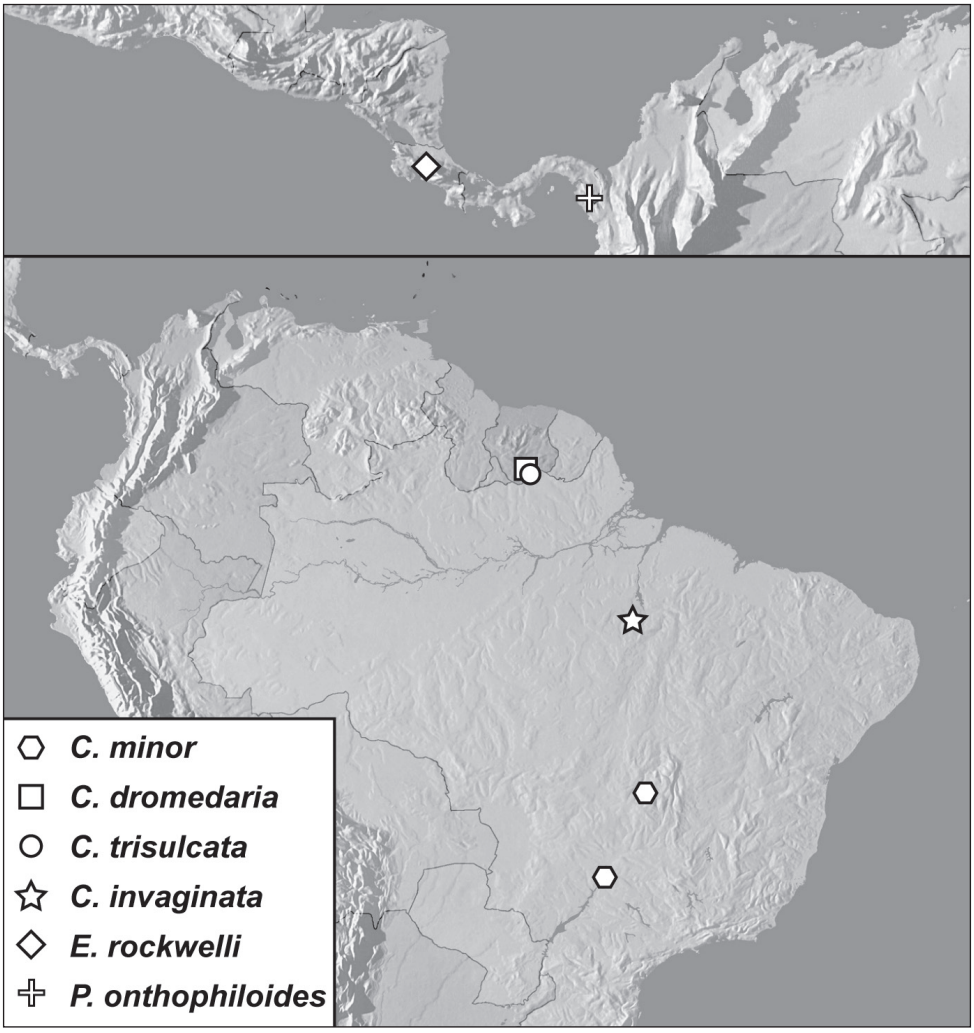


Figure 1. *Conocassis* spp. dorsal habitus. **A** *Conocassis minor* **B** *Conocassis dromedaria* **C** *Conocassis trisulcata* **D** *Conocassis invaginata.*

striae rather weakly carinate; median elytral interval shallowly depressed in basal half, texture of median interval finely granular throughout; no trace of 5th dorsal stria present in median interval; texture of outer intervals finely granulate basally, smoother apically; epipleural margin granulate but not strigose; presternal suture not impressed across middle, carinal striae only vaguely extended to sides; protibiae slightly narrowed in apical half, apex rounded; protibial spurs inconspicuous; abdominal ventrites 2-4 faintly and shallowly punctate at sides; propygidium moderately convex, slightly shorter than pygidium along midline; propygidial punctures elongate, only moderately deep, more so at sides, punctures faintly alutaceous within; pygidium finely strigose in basal third, finely punctate apically; male genitalia (Fig. 4A–F) as for generic description except tegmen widest just distad midpoint, ventral curvature rather even in apical half.

Remarks. This species is easily distinguished from the other three species in this genus. It is distinctly smaller and paler in color, and generally has the dorsal sculpturing less exaggerated (Fig. 1A). The elytral striae are rather simply carinate, and the lateral creases on the sides of the pronotal process are not at all invaginated as they are in the following three species.

Etymology. This species name refers to the fact that it is the smallest known member of the genus.



Map 1. Specimen records of *Conocassis* spp., *Enkyosoma rockwelli*, and *Pluricosta onthophiloides*.

***Conocassis dromedaria* sp. n.**
http://zoobank.org/95C4F58A-408D-4946-B12D-B943DF5136C7
http://species-id.net/wiki/Conocassis_dromedaria
Figs 1B, 2A, 4G–H, Map 1

Type locality. SURINAME: Sipaliwini, upper Palumeu River [2.4770°N, 55.6294°W].

Type material. Holotype male: "**SURINAME: Sipaliwini**, CI-RAP Survey camp 1, upper Palumeu, 225m, 2.47700°N, 55.62941°W, Flight intercept. 10–16.iii.2012, A.E.Z. Short, SR12-0310-TN1" / "Caterino/Tishechkin Exosternini Voucher EXO-03047" (NZCS).

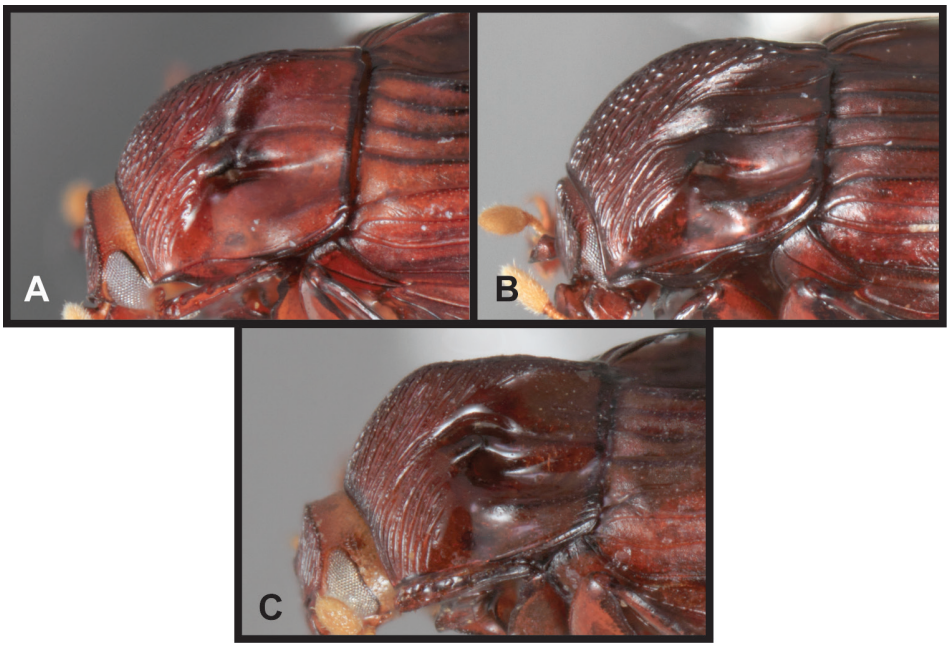


Figure 2. *Conocassis* spp., lateral view of pronotum. **A** *Conocassis dromedaria* **B** *Conocassis trisulcata* **C** *Conocassis invaginata.*

Diagnostic description. Length: 1.9 mm, width: 1.4 mm; as for generic description, with the following specific characters: body rufobrunneus; frontal stria extending only onto base of epistoma; side of pronotal process with two distinct creases, the lowermost narrowly, deeply invaginated; pronotal disk lacking carina extending anterad from basolateral corner; pronotal process rather evenly rounded from base to apex in lateral profile; pronotal disk very finely alutaceous behind median process; median elytral interval strongly depressed in basal half, the 4th dorsal stria strongly elevated and displaced laterad, texture of median interval finely granular throughout; texture of outer intervals finely alutaceous basally, becoming smooth posteriorly; epipleural margin granulate but not strigose; no trace of 5th dorsal stria present; presternal suture deeply impressed, especially at middle; abdominal ventrites 2-4 with sparse, oblique strigae at sides; propygidium strongly convex, about as long as pygidium along midline; propygidial punctures very elongate, coarse and deep, especially at sides, alutaceous within; pygidium strigose in basolateral corners, becoming simply, finely punctate apicomedially; male genitalia (Fig. 4G–H) as for generic description except tegmen widest just basad midpoint, apices long and narrow, ventral curvature moderate to near apex where it is abruptly bent ventrad.

Remarks. This species and the following two are very similar, closely related, and difficult to separate. All are larger, darker, and more strongly sculptured than *C. minor*, and can easily be separated from it. However, differences among them are more subtle. *Conocassis dromedaria* and *C. invaginata* appear most similar, with the strong basal depression

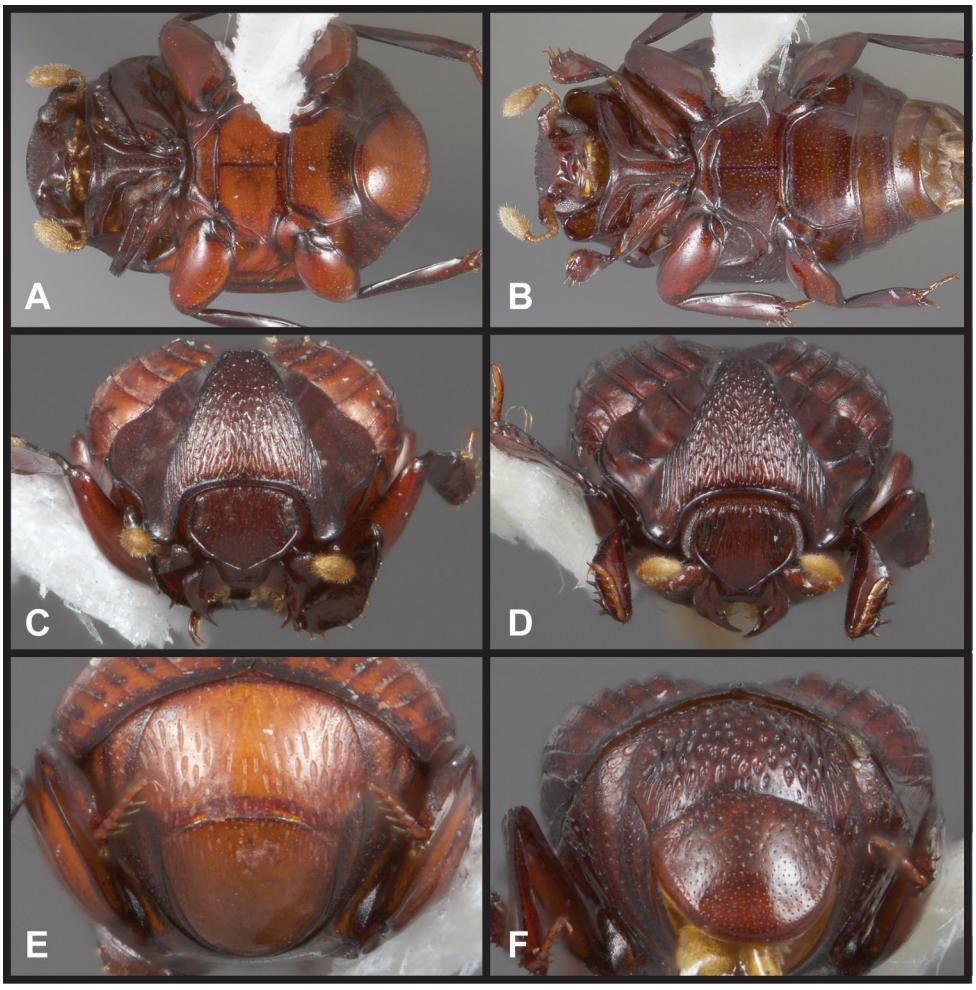


Figure 3. *Conocassis* spp. **A** *Conocassis minor*, ventral view **B** *Conocassis trisulcata*, ventral view **C** *Conocassis minor*, anterior view **D** *Conocassis trisulcata*, anterior view **E** *Conocassis minor*, posterior view of pygidia **F** *Conocassis trisulcata*, posterior view of pygidia.

in the median elytral interval (Fig. 1B, D), and the 4th stria very strongly elevated and displaced laterad. These two can be separated by the narrowly open lower pronotal invagination, and poorly developed upper pronotal invagination of *C. dromedaria* (Fig. 2A). This species also lacks a basolateral carina on the pronotal disk that the other two share. The more completely granulate elytral intervals of *C. invaginata* (Fig. 1D) also set it apart from both the others, in which the intervals are distinctly smoother apically. With *Conocassis dromedaria* and *C. trisulcata* represented only by single specimens, and only *C. dromedaria* represented by a male, their status will have to be reassessed later in light of more material.

Etymology. This species is named for the camel-like hump on the pronotum, from the specific name of the one-humped dromedary.

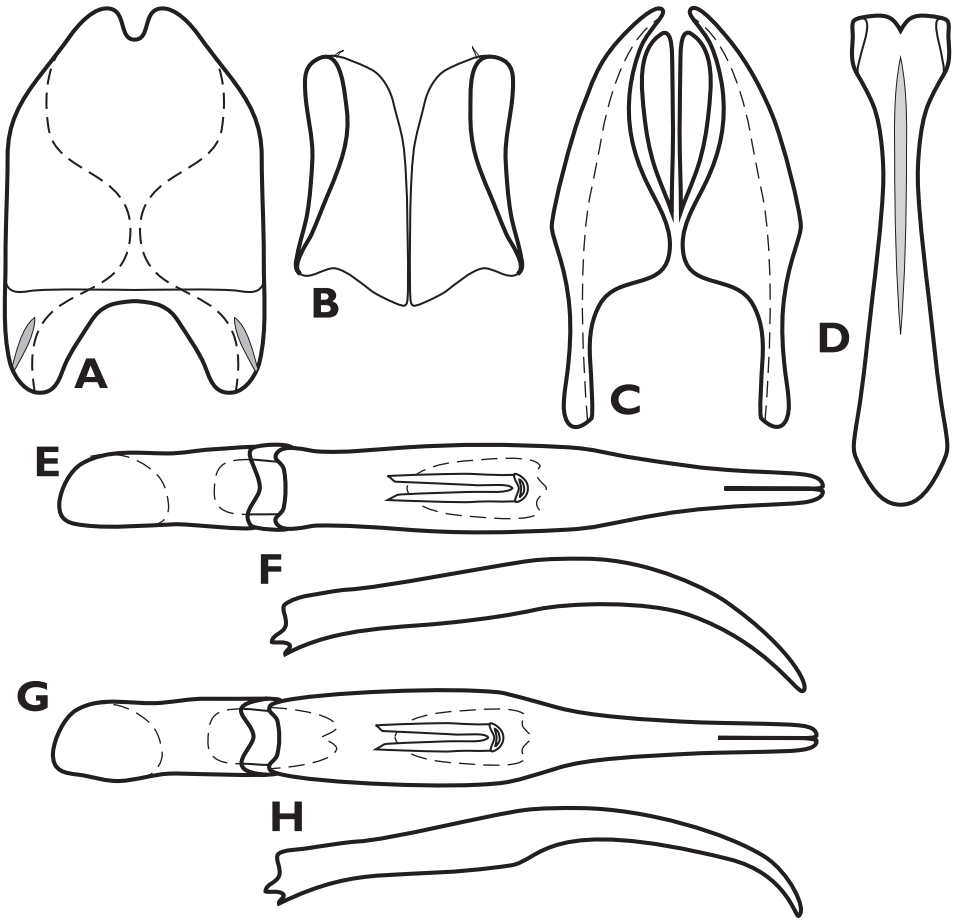


Figure 4. *Conocassis* spp., male genitalia. **A-F** *Conocassis minor* **A** 8th tergite **B** 8th sternite **C** 9th and 10th tergites **D** 9th sternite **E** Aedeagus, dorsal view **F** Aedeagus, lateral view **G–H** *Conocassis dromedaria* **G** Aedeagus, dorsal view **H** Aedeagus, lateral view.

***Conocassis trisulcata* sp. n.**
http://zoobank.org/0AB37D8D-A738-4067-BB58-855BFEC48639
http://species-id.net/wiki/Conocassis_trisulcata
Figs 1C, 2B, 3B, D, F, Map 1

Type locality. SURINAME: Sipaliwini, upper Palumeu River [2.4770°N, 55.6294°W].

Type material. Holotype female: "**SURINAME: Sipaliwini**, CI-RAP Survey camp 1, upper Palumeu, 225m, 2.47700°N, 55.62941°W, Flight intercept. 10-16. iii.2012, A.E.Z. Short, SR12-0310-TN1" / "Caterino/Tishechkin Exosternini Voucher EXO-02504" (NZCS).

Diagnostic description. Length: 2.0 mm, width: 1.5 mm; as for generic description, with the following specific characters: body rufobrunneus; frontal stria

extending to middle of epistoma; side of pronotal process with three distinct creases, only the lowermost narrowly, deeply invaginated; pronotal disk with distinct carina extending anterad from basolateral corner toward median invagination; pronotal process rather evenly rounded from base to apex in lateral profile; pronotal disk very finely alutaceous behind median process; median elytral interval only moderately depressed in basal half, the 4th dorsal stria not displaced laterad, only weakly arcuate throughout length, texture of median interval finely granular throughout; texture of outer intervals finely alutaceous basally, becoming smooth posteriorly; epipleuron vertically strigose on and above marginal bead; no trace of 5th dorsal stria present; presternal suture marked by anteriorly divergent prosternal carinal striae at sides, not impressed across middle; abdominal ventrites 2-4 only very faintly strigose at sides; propygidium strongly convex, about as long as pygidium along midline; propygidial punctures coarse and deep, slightly elongate, only slightly more so at sides, punctures largely smooth within; pygidium strigose in basolateral corners, becoming simply, finely punctate apicomedially.

Remarks. In addition to the characters remarked under the preceding species, this species' relatively shallow median elytral depression (Fig. 1C), and simply carinate and arcuate 4th dorsal stria will separate it, as will the presence of three distinct lateral creases on the pronotal process (Fig. 2B), only the lowermost of which is distinctly invaginated. This species also lacks an indication of the presternal suture at the middle (Fig. 3B).

Etymology. This species is named for the three distinct lateral pronotal creases.

***Conocassis invaginata* sp. n.**
http://zoobank.org/7987E394-93FB-4AA5-BCF5-BBD6707EDD1B
http://species-id.net/wiki/Conocassis_invaginata
Figs 1D, 2C, Map 1

Type locality. BRAZIL: Pará, Carajas [6.06°S, 50.2°W].

Type material. Holotype female: "Octobre 1984, piége d'interception CARAJAS, PARÁ, N. DEGALLIER" / "Caterino/Tishechkin Exosternini Voucher EXO-00008" (UFPR). **Paratype female**: **BRAZIL: Pará,** Carajas, S. Norte, xi.1984, N. Degallier (CHND).

Diagnostic description. Length: 1.9 mm, width: 1.4 mm; as for generic description, with the following specific characters: body rufobrunneus; frontal stria extending to near apex of epistoma; side of pronotal process with two distinct creases, the lowermost deeply invaginated, more broadly open, the second, more dorsal crease also rather deeply invaginated; pronotal disk with carina extending anterad from basolateral corner toward median invagination; pronotal process abruptly rounded to apex only from middle in lateral profile; pronotal disk very finely alutaceous behind median process; median elytral interval strongly depressed in basal half, the 4th dorsal stria strongly elevated and displaced laterad, texture of median interval finely granular

throughout; fragments of 5th dorsal stria present in median interval; texture of outer intervals finely granulate throughout, not smoother apically; epipleural margin granulate but not strigose; presternal suture impressed across middle; abdominal ventrites 2-4 with sparse, oblique strigae at sides; propygidium strongly convex, about as long as pygidium along midline; propygidial punctures very elongate, coarse and deep, especially at sides, alutaceous within; pygidium strigose in basolateral corners, becoming simply, finely punctate apicomedially.

Remarks. As noted under the preceding two species, this species is best recognized by the presence of only two lateral creases on the pronotal process (Fig. 2C), both of which are deeply invaginated. The completely granulate elytral intervals and presence of fragments of the 5th dorsal stria (Fig. 1D) are also unique.

Etymology. This species is named for the fact that it has the deepest pronotal invaginations in the genus.

***Enkyosoma* gen. n.**
http://zoobank.org/514A6CCE-FA73-4B93-8E75-6A076491AE53
http://species-id.net/wiki/Enkyosoma

Type species. *Enkyosoma rockwelli* sp. n.

Description. This genus differs from other Exosternini in the following combination of characters: body widest behind middle, subdepressed, somewhat flattened dorsally, metaventrite rather abruptly convex ventrally, glabrous, lacking secondary punctation, and almost entirely lacking typical striae; frons more or less coplanar with vertex; labrum broad, apically emarginate, lateral margins with conspicuous setal fringe; mandibles with short incisor edges; antennal scape elongate, slender, curving posteroventrad beneath eye; funicle about as long as scape, weakly widened distally, the 8th antennomere cupuliform, no shorter than preceding antennomeres; antennal club elongate oval, completely tomentose, with two nearly complete setose annuli more distinctly interrupted on dorsal surface, only slightly curved basad at middle; eye substantially reduced; pronotum lacking prescutellar impression, though fine prescutellar fovea may be present, with three median gland openings on each side, one in anterior angles, one behind eye about one funicle width behind anterior margin, one displaced posterad on disk; three distinct gland openings also present along lateral pronotal margin; elytra with few striae extremely fine, inconspicuous; prosternal keel depressed, rather broad, produced at base; prosternal lobe deflexed; mesoventrite anteriorly emarginate; metaventrite strongly convex posteriorly, posterior margin arcuate; propygidium transverse, with single gland openings in anterolateral corners; pygidium large, apically rounded, without gland openings or marginal striae; trochanter with 2-3 short apical setae; femora moderately broad, slightly flattened; protibia subtriangular, with outer edge weakly outwardly rounded, not distinctly toothed, with numerous distinct marginal spines; two small protibial spurs present; all tarsi rather long and curving, with numerous ventral spines, those of protarsus (of male only?) strongly

spatulate; mesotibia moderately expanded toward apex, metatibia less so, both with nearly complete series of marginal spines; male genitalia (Fig. 6) with paired accessory sclerites present; apices of S8 bearing only very fine, inconspicuous setae; T10 completely divided; S9 with head broad, subquadrate, with complete apical flange; tegmen narrow and elongate, sides parallel in basal half, narrowed to thin, ventrally curved apex, median foramen basad apical narrowing, ventral surface with basal tooth formed by thin median keel; Female not known.

Remarks. This genus is easily recognized by its relatively large, rounded, subdepressed body form (Figs 5A-C), and its complete lack of elytral striae. Its spinose, slightly dilated tibiae and strongly convex metaventrite are also unique features.

In our recent analysis of Exosternini relationships (Caterino and Tishechkin in review) *Enkyosoma* is resolved as closely related to *Scaptorus* and *Chapischema*, the three of them forming the sister group to *Operclipygus*. However, only three characters change on the branch supporting this group (loss of 5th dorsal elytral stria, reduction to a single seta on the protrochanter, and the differentiation of the proximal apodemes of the male median lobe), and none are particularly substantial or unique. In gross morphology there are no obvious similarities among the three.

Etymology. From the Greek, literally 'pregnant body', referring to the strongly convex metaventrite.

***Enkyosoma rockwelli* sp. n.**
http://zoobank.org/B2A17604-CE7D-4383-8BB4-4742770CD804
http://species-id.net/wiki/Enkyosoma_rockwelli
Figs 5, 6, Map 1

Type locality. COSTA RICA: Puntarenas, Monteverde [10.3194°N, 84.8158°W].

Type material. Holotype male: "**COSTA RICA: PUNTARENAS**, Monteverde, Estacion Biologica Monteverde 10°19'10"N, 84°48'57"W, 1730m, 12.VI.2001 R.Anderson, montane forest litter, 2001-107H" / "Caterino/Tishechkin Exosternini Voucher EXO-00175" (CMNC).

Description. ***Size range:*** Length 3.0 mm; width 2.7 mm; ***Body***: body elongate ovoid, widest behind middle, subdepressed, dorsally somewhat flattened, more convex ventrally, dark rufescent, glabrous, with conspicuous ground punctation throughout, lacking secondary punctation, and almost entirely lacking typical striae. ***Head:*** frons elongate, largely coplanar with vertex, weakly depressed at middle; frontal and supraorbital striae absent; epistoma wide, somewhat deflexed, weakly emarginate apically; labrum large, about one-third as long as wide, apical margin deeply emarginate, lateral margins with conspicuous setal fringe; mandibles with short incisor edges, left bearing prominent basal tooth, right mandible with weaker basal tooth; submentum wide, slightly depressed relative to surrounding genae, anterior margin weakly outwardly arcuate; mentum trapezoidal, narrowed anteriorly, apical margin more or less entire; labial palps three segmented, basal segment short, penultimate and ultimate palop-

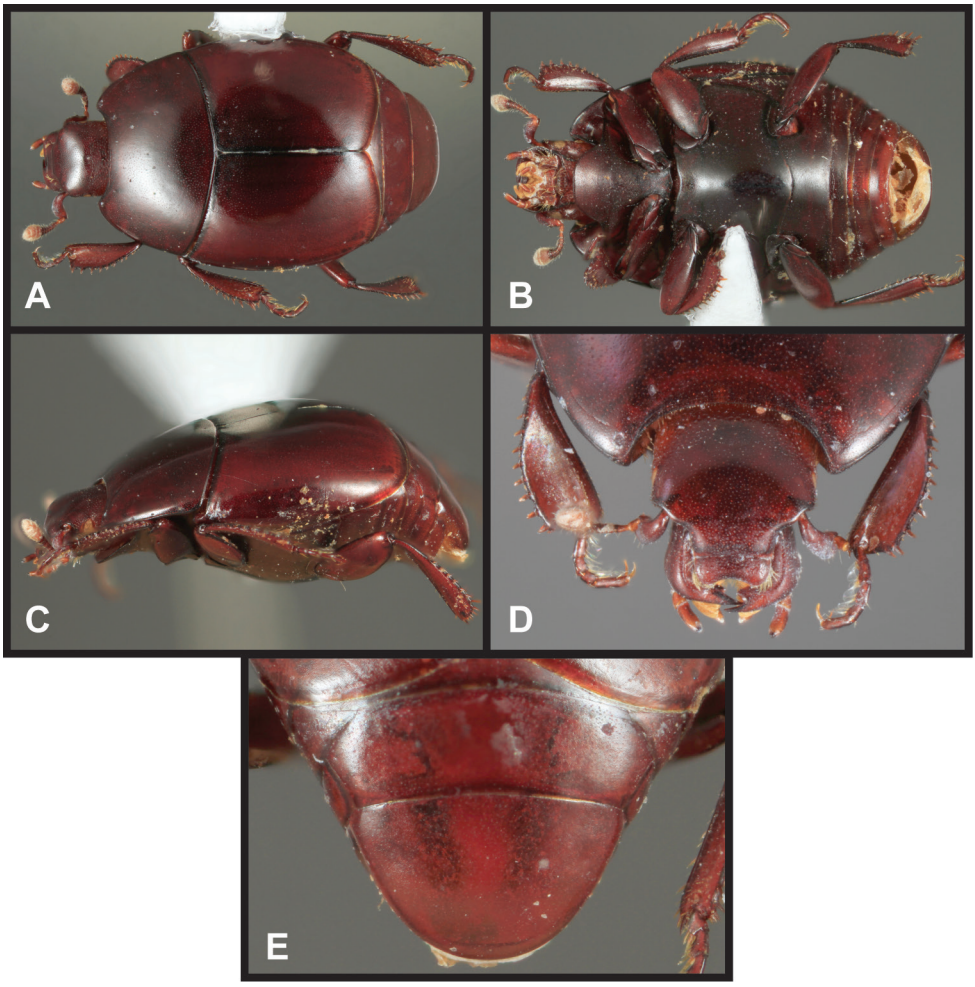


Figure 5. *Enkyosoma rockwelli*. **A** Dorsal habitus **B** Ventral habitus **C** Lateral habitus **D** Anterior view of head **E** Posterior view of pygidia.

meres elongate; submentum and mentum bearing numerous elongate setae; maxillary cardo shining, glabrous, stipes microsculptured and with numerous long setae; maxillary palp four segmented, rather stout; antennal scape elongate, not markedly widened apically, curving posteroventrad beneath somewhat reduced compound eye; funicle about as long as scape, weakly widened distally, the 8th antennomere cupuliform, no shorter than preceding antennomeres; antennal club elongate oval, completely tomentose, with two nearly complete setose annuli more distinctly interrupted on dorsal surface, only slightly curved basad at middle. ***Pronotum****:* pronotum weakly convex, sides faintly arcuate from base to apices; prescutellar impression absent, though fine prescutellar fovea may be present; pronotal disk with three median gland openings on each side, one in anterior angles, close to corner, one behind eye about one funicle width

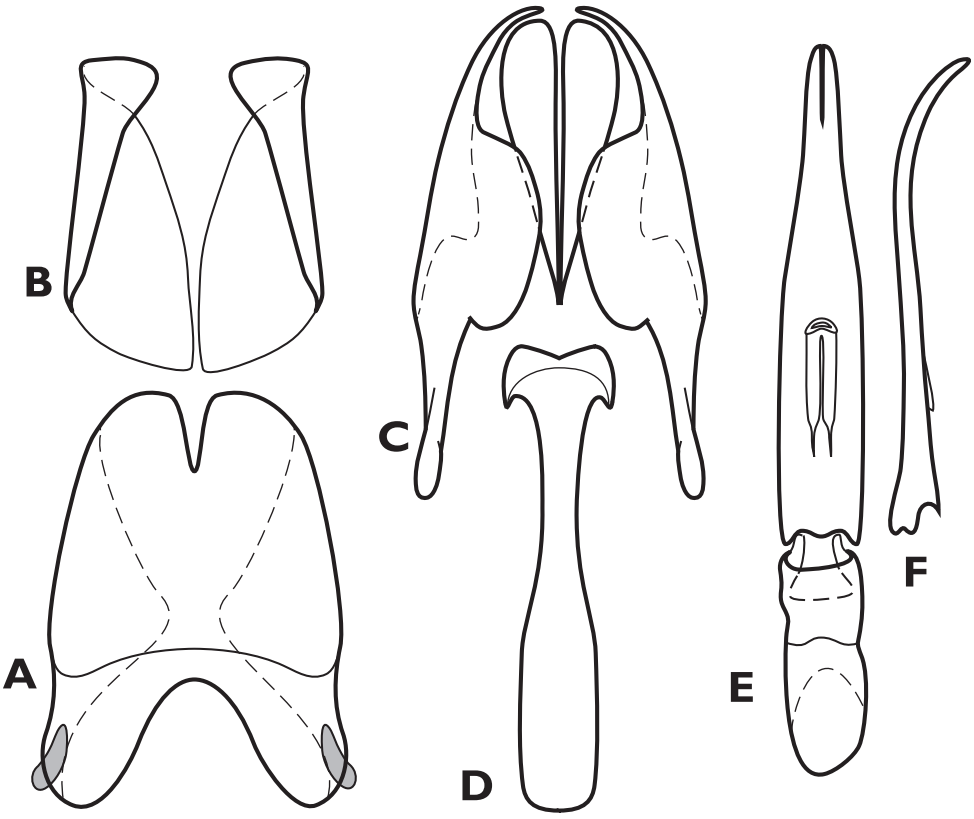


Figure 6. *Enkyosoma rockwelli*, male genitalia. **A** 8th tergite **B** 8th sternite **C** 9th and 10th tergites **D** 9th sternite **E** Aedeagus, dorsal view **F** Aedeagus, lateral view.

behind anterior margin, one directly posterad this one, just behind pronotal midpoint; three distinct gland openings also present along lateral pronotal margin; marginal stria complete along lateral and anterior margins; fragments of lateral submarginal stria visible near anterior corners. ***Elytra***: elytra with few striae extremely fine, inconspicuous; epipleuron with single complete marginal stria and fragments of additional epipleural striae detectable, oblique humeral stria visible near base, 1st dorsal stria finely impressed in apical two-thirds, 2nd stria visible in basal half, slightly abbreviated from base, 3rd stria present in basal third, 4th, 5th and sutural striae entirely absent; elytral disk with very fine granular microsculpture faintly impressed toward apices. ***Prosternum***: prosternal keel depressed, rather broad, produced at base, lacking striae; prosternal lobe about three-fourths length of keel, deflexed, lacking marginal stria; both prosternal keel and lobe rather densely microsculptured. ***Mesoventrite***: mesoventrite broad, subquadrate, anterior margin emarginate, marginal stria faintly impressed. ***Metaventrite***: metaventrite strongly convex posteriorly, posterior margin arcuate; mesometaventral, postcoxal and inner lateral metaventral striae absent, metaventral disk smooth at middle, more distinctly microsculptured at sides. ***Abdomen***: abdominal ventrites 1-4 lack-

ing striae, more or less distinctly microsculptured throughout; propygidium short, transverse, with single gland openings in anterolateral corners; pygidium large, apically rounded; propygidium and pygidium with very fine ground punctation and transverse waves of microsculpture. ***Legs***: each trochanter with 2-3 short apical setae; femora moderately broad, slightly flattened; protibia subtriangular, with outer edge weakly outwardly rounded, not distinctly toothed, but set with about 9 distinct marginal spines; two small protibial spurs present; all tarsi rather long and curving, with numerous ventral spines, those of protarsus (of male only?) strongly spatulate; mesotibia moderately expanded toward apex, metatibia much less so, both with nearly complete series of marginal spines. ***Male genitalia*** (Fig. 6): Paired accessory sclerites present; T8 with broad basal and narrower apical emarginations, line of basal membrane attachment complete distad basal emargination, ventral apodemes well developed, narrowing ventrally, slightly separated along midline; S8 with halves approximate at base, apical guides widening from base to apex, apices narrowly rounded, bearing only very fine, inconspicuous setae; T9 with base of dorsal flaps rather protuberant above proximal apodemes, ventrolateral apodemes well developed, T9 apices narrow, convergent subacute; T10 elongate, completely divided; S9 with sides subparallel in basal half, narrowest distad midpoint, head broad, subquadrate apically, with complete apical flange, apex not emarginate; tegmen narrow and elongate, sides parallel in basal half, narrowed to thin, ventrally curved apex, median foramen basad apical narrowing, ventral surface with basal tooth formed by thin median keel; basal piece nearly one-half tegmen length; median lobe about one-third tegmen length, proximal arms thinned basally. ***Female***: not known.

Remarks. This species is only known from the type specimen.

Etymology. We name this species for Mr. Marvin Rockwell, one of the original Quaker founders of the Costa Rican community of Monteverde, who has helped many visitors (the senior author included) better appreciate the biodiversity of Costa Rica.

***Pluricosta* gen. n.**

http://zoobank.org/521A7B18-FA66-4C18-9D6F-0B29AC444B56
http://species-id.net/wiki/Pluricosta

Type species. *Pluricosta onthophiloides* sp. n.

Description. This genus differs from other Exosternini in the following combination of characters: body round, strongly convex, with strong elytral ridges, rufescent, glabrous; frons and epistoma depressed along midline, frontal stria present; labrum wide, shallowly emarginate apically; mandibles with weakly arcuate incisor edges lacking basal teeth; antennal scape slightly wider near base, narrowed apically, with longitudinal carina along inner anterior edge; funicle shorter than scape, weakly widening apically, antennomere 8 short, cupuliform, not disc-like; antennal club slightly elongate oval, largely tomentose, with only indistinct subapical sensory patches; pronotum rather strongly convex, with two gland openings on each side, anterior opening

simple, along anterior margin behind eye, posterior opening with secondary annulus, displaced posterad to near middle of disk; prescutellar impression absent; elytra with strong longitudinal ridges, apparently corresponding to alternate interstriae; prosternal keel emarginate at base; prosternal lobe short, apically truncate; mesoventrite narrowly produced at middle; propygidium slightly shorter than pygidium along midline, with gland openings near anterolateral corners; pygidium equilaterally subtriangular, apex rounded, simple; each trochanter with single long seta; femora narrow; protibia rounded apically, lacking marginal teeth, with marginal spines inserted only along apical half of edge; protibial spurs present, reduced; meso- and metatibiae thin, simple, with single longitudinal stria along inner edge, completely lacking teeth or spines along outer margin; all tarsi slightly compressed, with slightly spatulate ventral setae; male not known; female T8 divided; S8 forming a single plate, basal baculi articulated with basolateral corners, convergent, separate at base; S9 not evident, though elongate articulating strap from median apex of S8 is present; T10 not observed; valvifers paddle-shaped, basal paddles just over one-third entire valvifer length; coxites over two-thirds valvifer length, apically tridentate, with lateral teeth rather weak; gonostyle slightly shorter than median tooth, setose; bursa copulatrix membraneous, lacking sclerites, not obviously expanded; spermatheca forming a gradually enlarged, elongate sac, an elongate, slightly kinked spermathecal gland inserted near its midpoint.

Remarks. This genus is unmistakable in its elevated, longitudinal elytral ridges (Fig. 7). In our recent analysis of Exosternini relationships (Caterino and Tishechkin in review), it is placed as sister to a group containing *Mecistostethus* and *Lacrimorpha*, described below.

Etymology. The name of this genus refers to the series of ridges on the elytra; feminine.

***Pluricosta onthophiloides* sp. n.**
http://zoobank.org/501486D6-3BB6-45A5-91D6-D63EE18914C7
http://species-id.net/wiki/Pluricosta_onthophiloides
Fig 7, Map 1

Type locality. PANAMA: Darién, Cana Biological Station [7.755°N, 77.685°W].

Type material. Holotype female: "PANAMA: Darién, Cana Biological Station, Serranía de Pirre, 1250 m, 7°45'18"N, 77°41'6"W, 07-09 Jun 1996; J.Ashe, R.Brooks, PAN1AB96 110 ex: flight intercept trap" / "SM0034338 KUNHM-ENT" (SEMC).

Description. ***Size range:*** Length 1.7 mm; width 1.5 mm; ***Body:*** body round, strongly convex, with strong elytral ridges, rufescent, glabrous. ***Head:*** frons slightly longer than wide, depressed along midline, smooth, with complete frontal stria more or less rounded across front; epistoma depressed along midline, weakly emarginate apically; labrum about 4× as wide as median length, shallowly emarginate apically; mandibles with weakly arcuate incisor edges lacking basal teeth; antennal scape slightly wider near base, narrowed apically, with longitudinal carina along inner anterior edge;

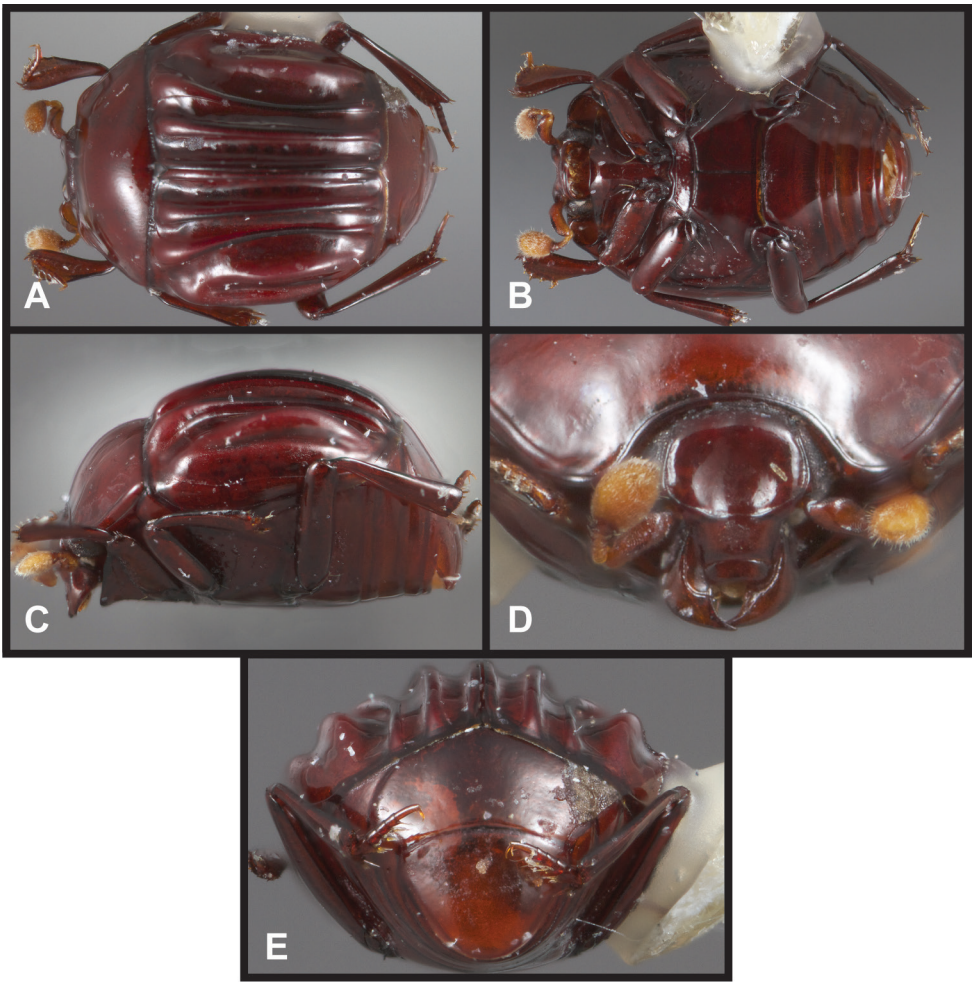


Figure 7. *Pluricosta onthophiloides*. **A** Dorsal habitus **B** Ventral habitus **C** Lateral habitus **D** Anterior view of head **E** Posterior view of pygidia.

funicle shorter than scape, weakly widening apically, antennomere 8 short, cupuliform, not disc-like; antennal club slightly elongate oval, largely tomentose, with only indistinct subapical sensory patches. ***Pronotum****:* pronotum rather strongly convex, sides narrowed evenly from base to apex, only faintly sinuate at base and middle; marginal pronotal stria complete along lateral and apical margins; sublateral stria present along entire lateral margin, just curving mediad anteriorly, pronotal disk shallowly depressed along its inner edge; pronotal disk with two gland openings on each side, anterior opening simple, along anterior margin behind eye, posterior opening with secondary annulus, situated directly posterad anterior opening, just in front of midline; prescutellar impression absent; posterior margin of disk simple. ***Elytra***: elytra dominated by several strong longitudinal ridges, epipleuron with single submarginal stria, contin-

ued along apical margin to apex of 2nd dorsal stria; outer subhumeral stria complete; other dorsal striae very fine, running near upper edge of elevated ridges, clearly visible only near apices; apices of 3rd-4th, and 5th-sutural striae joined along posterior margin. ***Prosternum***: prosternal keel shallowly but subacutely emarginate at base, carinal striae obsolete basally, joined by anterior arch short of presternal suture; prosternal lobe less than half as long as keel, apically truncate, lacking marginal stria. ***Mesoventrite***: mesoventrite narrowly produced at middle, with complete marginal stria, disk shallowly depressed behind. ***Metaventrite***: mesometaventral stria well impressed, coincident with mesometaventral suture; postcoxal stria directed laterad toward middle of metepisternum, ending freely; lateral metaventral stria running obliquely toward outer third of metacoxa, slightly abbreviated apically. ***Abdomen***: 1st abdominal ventrite with complete anterior marginal stria continued by postmetacoxal stria which curves laterad behind coxa, ending freely; ventrites 2-4 impunctate; propygidium only slightly shorter than pygidium along midline, smooth, with inconspicuous gland openings near anterolateral corners; pygidium similar in basal width and midline length, apex rounded, simple. ***Legs***: each trochanter with single long seta; femora rather narrow, metafemur particularly elongate; protibia gradually widened to rounded apical half, lacking marginal teeth, with marginal spines inserted only along apical half of edge; protibial spurs present, slightly reduced; meso- and metatibiae thin, simple, with single longitudinal stria along inner edge, completely lacking teeth or spines along outer margin; all tarsi slightly compressed, with slightly spatulate ventral setae. ***Male:*** not known.

Remarks. This species is known only from the female type specimen. Capture of a male would be very helpful to assessing its relationships.

Etymology. The name of this species refers to its superficial resemblance to the histerid genus *Onthophilus* Leach, owing to the parallel ridges on the elytra.

Pyxister **gen. n.**
http://zoobank.org/EFD5583E-6027-4D18-A2D6-177C65F1DA89
http://species-id.net/wiki/Pyxister

Type species. *Pyxister devorator* sp. n.

Description. ***Size range:*** Length 2.4–2.8 mm; width 1.6–1.9 mm; ***Body***: body elongate, subcylindrical, sides parallel, rufobrunneus, variably punctate, glabrous. ***Head:*** frons weakly to strongly depressed at middle, subangulate at sides in front of eyes, frontal stria complete to strongly reduced, supraorbital stria present, detached; epistoma and labrum varied; mandibles strongly toothed; mouthparts rather strongly recessed in oral cavity; submentum flat, produced in front; mentum subquadrate, nearly as long as broad, bearing sparse long setae; ultimate labial palpomeres elongate, slightly compressed; cardo glabrous, stipes with few long setae on lateral margin; ultimate maxillary palpomere slightly compressed; antennal scape elongate, curved, widest near midpoint; funicle shorter than scape, widening from antennomere 4-8, 8th antennomere cupuliform, more or less disclike; antennal club short, tomentose, with single,

slightly elongate, axial sensory patch on ventral surface and longer patch on dorsal surface. ***Pronotum****:* pronotal sides more or less straight, slightly convergent to apex; prescutellar impression faintly impressed to obsolete; pronotal disk with two median gland openings on each side, one very close to margin behind eye, one posterad just behind pronotal midpoint; marginal pronotal stria present on lateral and anterior margins, may be complete or interrupted at sides; submarginal pronotal stria may be present at sides. ***Elytra***: elytra slightly depressed along suture; epipleuron with single, complete marginal stria, outer subhumeral stria interrupted at middle, inner subhumeral stria absent, striae 1-5 present, 1 and 5 may be abbreviated, sutural stria complete. ***Prosternum***: prosternal keel emarginate at base, carinal striae present, more or less complete, convergent anterad, joined in anterior arch; prosternal lobe short, slightly deflexed, marginal stria present. ***Mesoventrite***: mesoventrite wide, short, with marginal stria fine, close to edge, may be interrupted; mesometaventral stria strongly angulate forward nearly to margin. ***Metaventrite***: postmesocoxal stria poorly developed, short; lateral metaventral stria extending from inner corner of mesocoxa toward middle of metacoxa, abbreviated or not. ***Abdomen***: 1st abdominal ventrite with single, oblique lateral stria; propygidium slightly convex, about two-thirds length of pygidium, gland openings may be visible near anterolateral corners; pygidium moderately to strongly convex, apical margin rounded. ***Legs***: trochanters with single long seta; femora moderately elongate; protibia with outer margin rounded, moderately strongly dentate, with 5-6 spinose teeth; two protibial spurs present, meso- and metatibiae narrow to moderately widened to apex, mesotibia with entire margin spinose, metatibia spinose toward apex; protarsi (of male only?) with spatulate ventral setae. ***Male genitalia****:* accessory sclerites absent; T8 with narrow subacute apical emargination, ventral apodemes well developed but separated beneath, basal membrane attachment line intersecting slightly sinuate basal emargination; S8 with halves approximate in basal half, apical guides increasingly wide toward apex, rather abruptly narrowed to narrowly rounded apices, with only very fine inconspicuous setae; T9 with basal apodemes short, apex narrowly subacute, ventrolateral apodeme weakly hooked; T10 undivided; S9 desclerotized along midline, with deep apical emargination, apical flange interrupted, apical corners produced; tegmen with sides subparallel in basal two-thirds, slightly widened to subquadrate, subtruncate apex, lacking medioventral process; median lobe simple, about one-third tegmen length; basal piece short, with strong apicoventral articulating process. ***Female genitalia****:* T8 entire, with narrow apical emargination; S8 undivided, only emarginate apicolaterally, basal baculi strongly, arcuately convergent at base; S9 present, short, connected to S8 by sclerotized strap; T10 entire; valvifers gradually expanded to base, paddles about half total length; coxites large, about two-thirds valvifer length, strongly bidentate; gonostyle slightly shorter than median tooth, setose; bursa copulatrix entirely membraneous, weakly expanded; spermatheca globose; spermathecal gland not evident in preparation.

Remarks. The cylindrical body shape of *Pyxister* (Fig. 9A–B) will help separate it from most other Neotropical Exosternini. However, there are scattered species in many larger genera, as well as a few genera (*Yarmister* Wenzel and *Megalocraerus* Lewis, in ad-

dition to the new genus *Chapischema* described below), in which a similar body form can be found. The genus can be separated from these by the combination of subangulate frons (Fig. 9C–D), dentate mandibles, antennal club lacking annuli but with small longitudinal sensory patch (Fig. 8E), second median pronotal gland openings strongly displaced posterad, sutural elytral interval impressed, prosternal keel distinctly emarginate (Fig. 9G–H), and the mesometaventral stria nearly reaching anterior mesoventral margin, disrupting or interrupting marginal stria. It is unfortunate that the male is known for only one of the species, but unusual genitalic characters (Fig. 10) include the lack of accessory sclerites, apically broadened tegmen, lack of medioventral tegmenal process, and strong apicomedial process of the basal piece. In the female (only *P. labralis*), the undivided 8th sternite is unusual among Neotropical Exosternini. In our recent analysis of Exosternini relationships (Caterino and Tishechkin in review), *Pyxister* emerges from within the poorly-defined 'scutellar impression group', close to species with which it shares few obvious characters. Its relationships remain to be fully resolved.

Etymology. Pyxis = canister or casket, referring loosely to the cylindrical body form, masculine.

Key to species of *Pyxister*

1 Lateral submarginal pronotal stria present, complete along side; labrum flat, emarginate (Fig. 9C) ..... ***Pyxister devorator***

– Lateral submarginal pronotal stria absent; labrum strongly swollen (Fig. 9D) ... . ***Pyxister labralis***

***Pyxister devorator* sp. n.**
http://zoobank.org/2A6B1DE9-A768-4F79-B0B2-038457E20A67
http://species-id.net/wiki/Pyxister_devorator
Figs 8, 9A, 10, Map 2

Type locality. BRAZIL: Rio de Janeiro, 17km E Nova Friburgo [22.3844°S, 42.5583°W]

Type material. Holotype male: "**BRASIL: RIO DE JANEIRO**, 17km E Nova Friburgo, 22°23'04"S, 42°33'30"W, 750m, 29.I.2000, F.Génier & S. Ide, secondary mountain Atlantic for. ex. f.i.t., day 4-9, **FG2000-58**" / "Caterino/Tishechkin Exosternini Voucher EXO-00159" (CMNC). **Paratypes** (4): 1: same data as type; 3: same locality as type, but 21.i.2000, FG2000-09 (CMNC, MSCC).

Diagnostic description. Length: 2.5–2.8 mm, width: 1.6–1.8 mm; as for generic description, with the following specific characters: frontal disk depressed at middle, with fine ground punctation especially at sides, with very few larger secondary punctures intermingled; frontal stria complete, slightly sinuate anteriorly; frontoclypeal suture indicated by fine, complete impressed line; epistoma broad, more or less flat, apical margin straight; labrum about twice as wide as long, slightly narrowed to weakly rounded apex, basally flat, but increasingly broadly depressed toward apex; pronotal

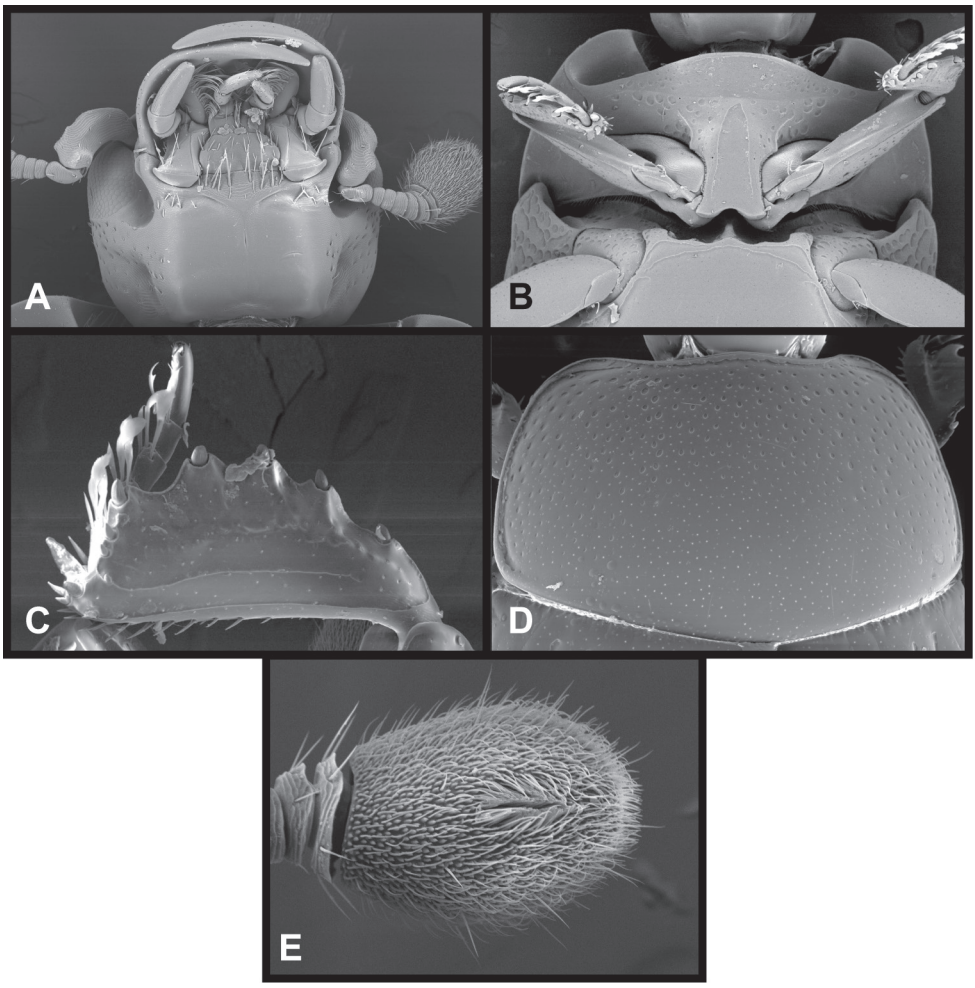


Figure 8. *Pyxister devorator*, SEMs showing generic characters. **A** Head, ventral view **B** Pro- and mesosterna **C** Protibia and protarsus, posterior view **D** Pronotum **E** Antennal club, dorsal view.

sides weakly outwardly rounded, anterior emargination very faintly produced at middle, with marginal stria complete along lateral and anterior margins, submarginal stria complete along side, curving inward at front, coarsely crenulate throughout; pronotal disk with secondary punctures almost throughout, absent only mediobasally, separated by approximately their diameters; elytral epipleuron with single, complete epipleural stria rather distant from lateral margin, outer subhumeral stria more or less complete but interrupted near middle and slightly abbreviated at base, inner subhumeral stria absent, 1st dorsal stria obsolete in apical third, 2nd–4th striae complete, 5th stria obsolete in basal half, sutural stria complete, rather deeply impressed along suture; marginal mesoventral stria complete or nearly so, though weak medially and crowded by meso-metaventral stria; meso- and metatibiae widened to apex, apical width about 3× basal

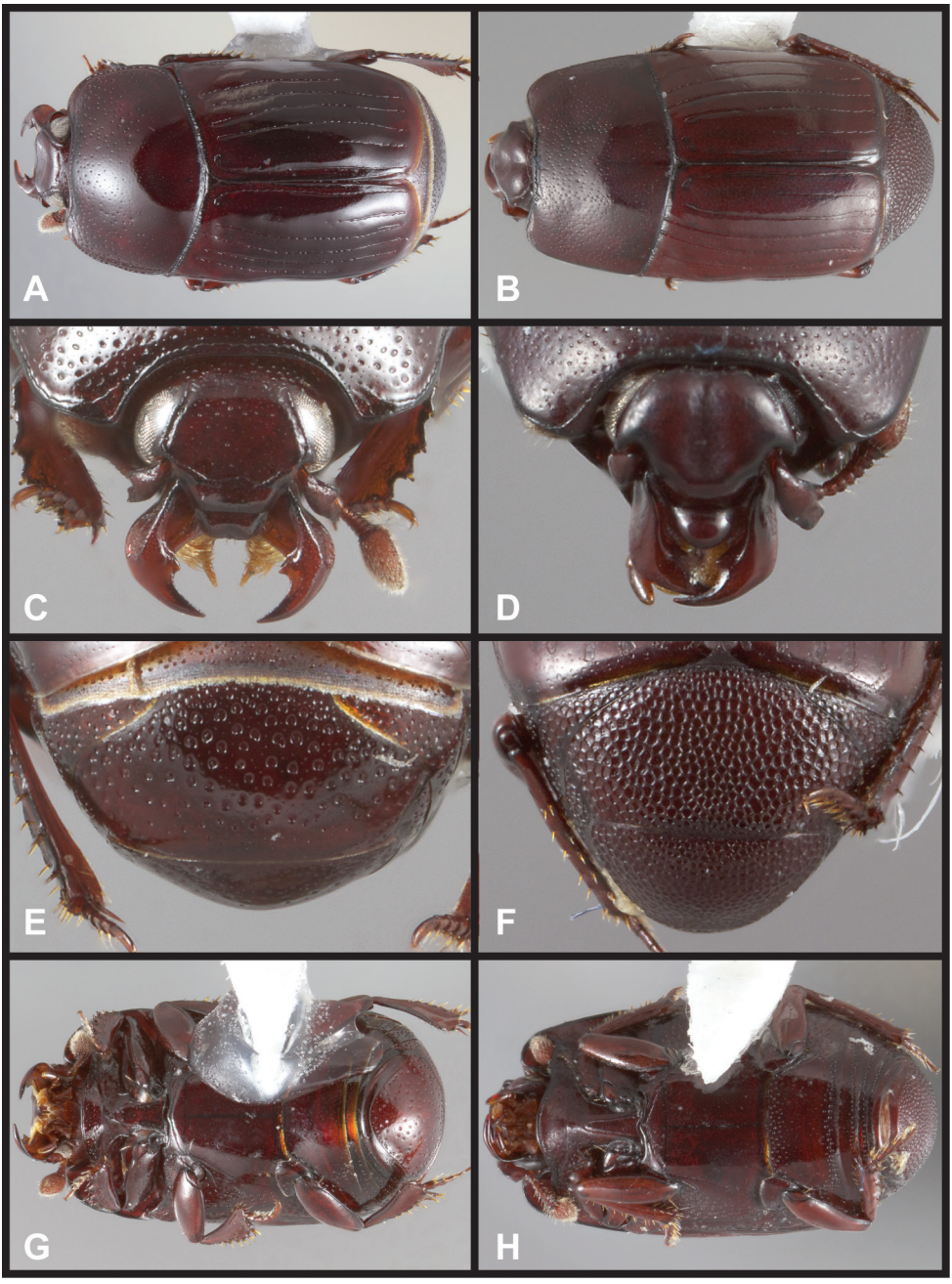


Figure 9. *Pyxister* spp. **A** *Pyxister devorator*, dorsal habitus **B** *Pyxister labralis*, dorsal habitus **C** *Pyxister devorator*, head, anterior view **D** *Pyxister labralis*, head, anterior view **E** *Pyxister devorator*, pygidia, posterior view **F** *Pyxister labralis*, pygidia, posterior view **G** *Pyxister devorator*, ventral habitus **H** *Pyxister labralis*, ventral habitus.

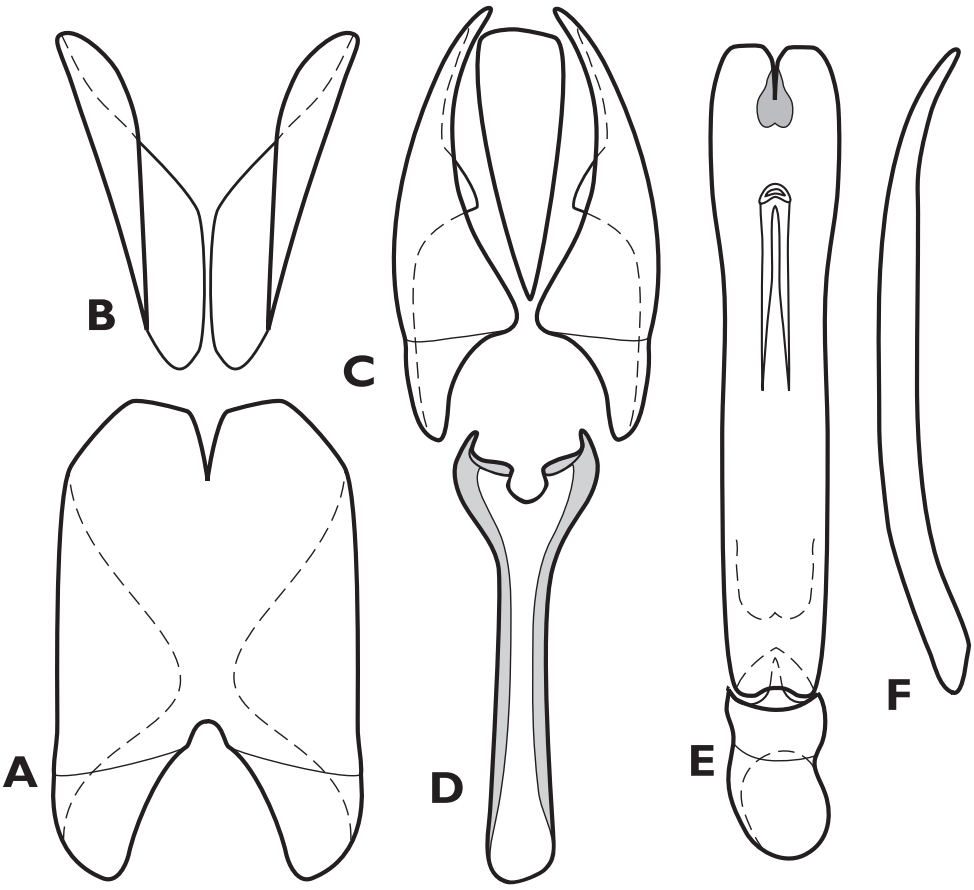
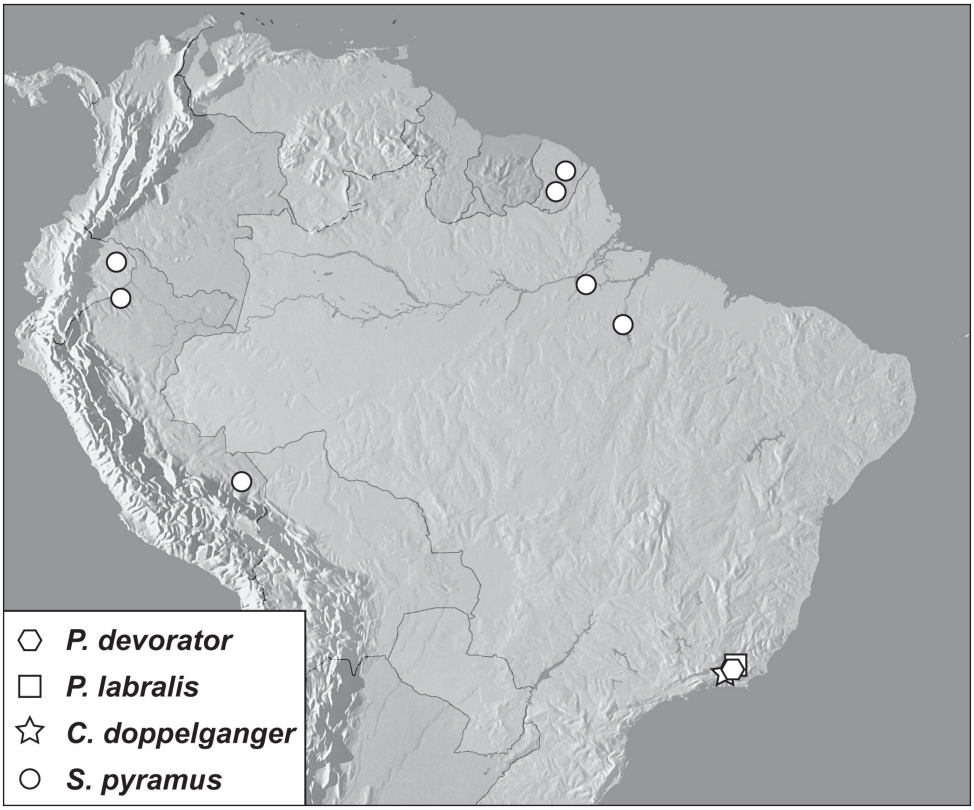


Figure 10. *Pyxister devorator*, male genitalia. **A** 8th tergite **B** 8th sternite **C** 9th and 10th tergites **D** 9th sternite **E** Aedeagus, dorsal view **F** Aedeagus, lateral view.

width, both strongly spinose; propygidium with fine ground punctation interspersed with secondary punctures irregularly separated by 1–1.5× their diameters; pygidium with secondary punctures generally smaller and sparser, tending to be concentrated and more deeply impressed along lateral margins.

Remarks. The two species of *Pyxister* appear clearly related, but at the same time show some remarkable differences, particularly in the structure of the head. The convex frons and strongly swollen labrum of *P. labralis* (Fig. 9D) are not at all indicated in *P. devorator*, which has a more or less flat frons, and a labrum which is slightly depressed and emarginate apically (Fig. 9C). Other distinguishing characters of *P. devorator* are its complete lateral submarginal pronotal stria, apically abbreviated 1st dorsal elytral stria, and its sparsely punctate pygidia (Fig. 9E).

Etymology. The name of this species means 'devourer', alluding to its strong mandibles.



Map 2. Specimen records of *Pyxister* spp., *Chapischema doppelganger*, and *Scaptorus pyramus.*

***Pyxister labralis* sp. n.**
http://zoobank.org/119C0416-4BD1-44CC-86E0-2F9507259043
http://species-id.net/wiki/Pyxister_labralis
Figs 9B–D, Map 2

Type locality. BRAZIL: Rio de Janeiro, Sans Souci [22.2833°S, 42.5206°W].

Type material. Holotype female: "Brasil, Rio de Janeiro, Nova Friburgo, Sans Souci, 9-15/XI/2009, E. Grossi (*leg.*)" / "Interceptação de vôo (FIT)" / "Caterino/ Tishechkin Exosternini Voucher EXO-00749" (UFPR).

Diagnostic description. Length: 2.4 mm, width: 1.7 mm; as for generic description, with the following specific characters: frons strongly transversely produced along anterior margin, depressed along midline basad anterior ridge, with antennal insertions deeply incised, frontal stria present only along inner margins of eyes, frontal disk impunctate; frontoclypeal suture not evident; epistoma recessed below frontal margin; labrum very strongly swollen, produced anterad; pronotal sides straight, parallel; marginal pronotal stria interrupted behind eyes, submarginal pronotal stria absent; pronotum very weakly tuberculate at posteromedian gland openings, disk with small secondary

punctures almost throughout, absent only mediobasally, separated by approximately their diameters; elytral epipleuron with single, complete epipleural stria rather distant from lateral margin, outer subhumeral stria more or less complete but interrupted near middle and slightly abbreviated at base, inner subhumeral stria absent, 1st-4th dorsal striae complete, 5th stria obsolete in basal half, sutural stria complete, sutural intervals weakly depressed; mesoventrite with marginal stria distinctly interrupted; meso- and metatibiae rather slender, no more than twice as wide apically than basally, finely spinose; propygidium and pygidium completely coarsely reticulopunctate.

Remarks. This species is easy to distinguish from its only congener by the unique shape of the frons and especially the labrum (Fig. 9D), both being strongly produced. In addition, *P. labralis* lacks a submarginal pronotal stria, has the 1st dorsal elytral stria entire, and has the propygidium and pygidium densely reticulopunctate (Fig. 9F).

Etymology. This species' name refers to its very distinctive, strongly convex labrum.

***Chapischema* gen. n.**
http://zoobank.org/536DA99C-5A83-4696-95CD-7F128E8746C5
http://species-id.net/wiki/Chapischema

Type species. *Chapischema doppelganger* sp. n.

Description. This genus differs from other Exosternini in the following combination of characters: body elongate, cylindrical, parallel-sided, glabrous; frons subangulate in front of eyes, moderately produced above antennal insertions, weakly depressed at middle; epistoma convex, apex truncate; labrum about twice as wide as long; left mandible with outwardly arcuate incisor edge, right mandible with small acute basal tooth; submentum slightly depressed, outwardly arcuate along anterior margin; mentum subtrapezoidal, very narrowly emarginate apically, sparsely setose; cardo glabrous, smooth; stipes with few long setae; all palpi relatively stout, ultimate palpomeres, particularly maxillary palps, thickened and with numerous conspicuous punctures; antennal scape elongate, sides sinuate, narrowed at middle in anterior aspect; funicle gradually but slightly widened to apex, 8th antennomere as long as preceding antennomeres; antennal club small, about as long as preceding 4 antennomeres, lacking complete annuli, sensoria poorly defined, apparently with two widely interrupted annuli close to dorsal apex; pronotal disk with only single distinct pair of gland openings, present between anterior margin and anterior submarginal stria; prescutellar impression absent; prosternal keel very shallowly emarginate at base; prosternal lobe slightly deflexed; anterior margin of mesoventrite broadly emarginate, but very weakly produced at center; propygidium rather long, more or less flat, with small gland openings near anterolateral corners; pygidium slightly longer than propygidium along midline, apical margin simple, rounded; protrochanter glabrous, meso- and metatrochanters each with two very short apical setae; femora simple; protibia with outer margin rounded, weakly dentate, strongly spinose; protibial spurs very short; protarsus with ventral setae simple; meso- and metatibiae elongate, outer margins with spinose, mesotibia faintly

dentate; meso- and metatarsi short, each with single pair apicoventral spines; male genitalia with accessory sclerites present; T8 rather short; S8 halves approximate only at base, inner margins divergent to apex, apically with very fine, inconspicuous setae; T9 with prominent, strongly hooked ventrolateral apodemes, dorsal lobes more strongly sclerotized along sides; T10 divided; S9 with apical emargination distinct, apical flange interrupted; tegmen with very large medioventral process; median lobe simple; female not known.

Remarks. In body form *Chapischema* is generally very similar to the preceding new genus, *Pyxister* (and likewise to *Megalocraerus*, and various other rare cylindrical Neotropical Exosternini). Among such taxa, it can best be recognized by its carinate frontal stria (Fig. 11C), abbreviated epipleural stria, and mesoventral margin, which is simultaneously broadly emarginate and narrowly produced at the middle (Fig. 11B). Generic status is supported principally by its unique male genitalia, with a very prominent medioventral tooth on the tegmen (Fig. 12F). It is resolved as closely related to *Scaptorus* and *Enkyosoma* in our forthcoming analysis of Exosternini relationships (Caterino and Tishechkin in review). However, the three are very different in appearance and this result cannot be regarded with great confidence. *Chapischema* shows no phylogenetic affinity with the superficially very similar *Pyxister*.

Etymology. The name of this genus is from the Greek, meaning 'pill-shaped'; feminine.

***Chapischema doppelganger* sp. n.**
http://zoobank.org/F9C0BCD3-D1F0-4E95-A822-7A1ADDDC4C92
http://species-id.net/wiki/Chapischema_doppelganger
Figs 11–12, Map 2

Type locality. BRAZIL: Rio de Janeiro, 17km E Nova Friburgo [22.3844°S, 42.5583°W].

Type material. Holotype male: "**BRASIL: RIO DE JANEIRO**, 17km E Nova Friburgo, 22°23'04"S,42°33'30"W, 750m, 29.I.2000, F.Génier & S. Ide, secondary mountain Atlantic for. ex. f.i.t., day 4-9, **FG2000-58**" / "Caterino/Tishechkin Exosternini Voucher EXO-00013" (CMNC).

Description. ***Size range:*** Length 2.2 mm; width 1.3 mm; ***Body***: body elongate, cylindrical, parallel-sided, rufobrunneus, ground punctation rather inconspicuous, glabrous. ***Head:*** frons rather broad, subangulate at sides in front of eyes, moderately produced in front above antennal insertions, beneath complete, subangulate frontal stria, weakly depressed at middle, with sparse ground punctures and very faint microsculpture within frontal depression; supraorbital stria weak but complete, narrowly detached from frontal stria at sides; epistoma convex, apex truncate; labrum about twice as wide as long, apex arcuate, but dorsal surface increasingly depressed to apex, making it appear somewhat emarginate; mandibles coarsely punctate on sides. ***Pronotum:*** pronotal sides subparallel in basal half, slightly arcuately narrowing to apex; marginal pronotal stria present on lateral and anterior margins, but narrowly interrupted behind eye, anterior portion continuous with lateral submarginal stria, which

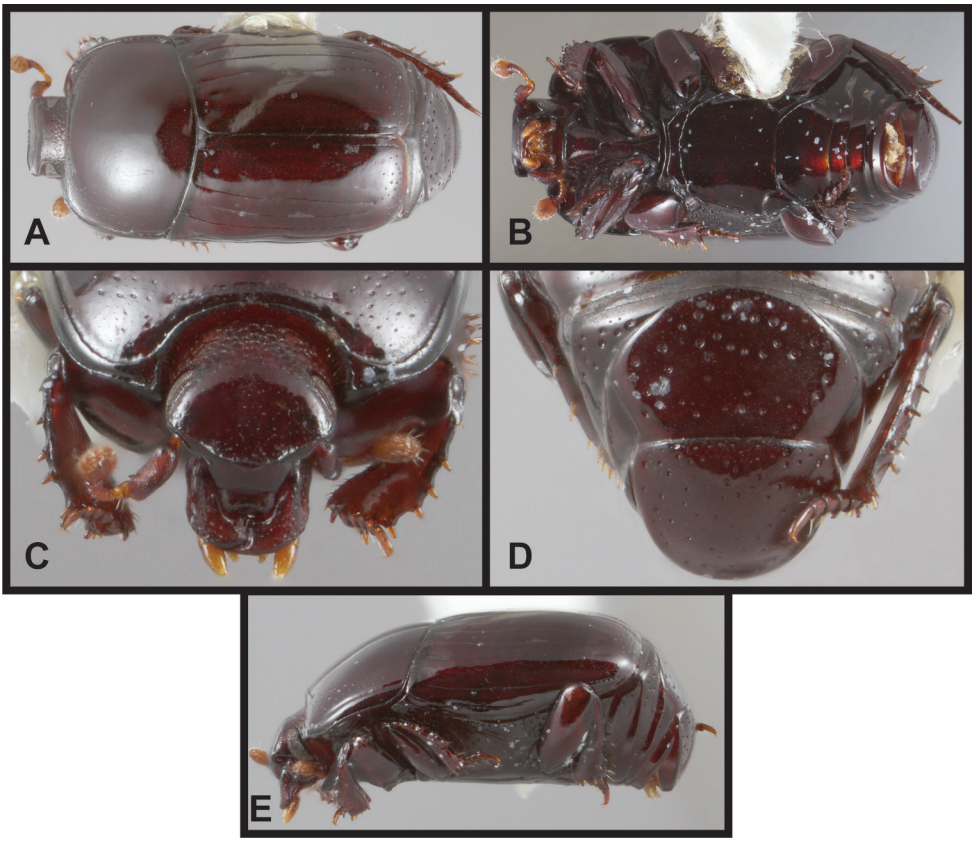


Figure 11. *Chapischema doppelganger*. **A** Dorsal habitus **B** Ventral habitus **C** Head, anterior view **D** Pygidia, posterior view **E** Lateral habitus.

is complete and deeply impressed along sides; detached anterior submarginal stria transversely impressed behind head; pronotal disk with only single distinct pair of gland openings, located between anterior margin and free ends of transverse anterior submarginal stria; pronotal disk rather strongly convex, with few, small sparse secondary punctures near anterolateral corners; prescutellar impression absent. ***Elytra***: elytral epipleuron with single epipleural stria present in basal half only, obsolete apically, outer subhumeral stria complete, inner subhumeral stria absent, dorsal striae 1-3 complete, rather crowded toward side, 4th and 5th striae absent, sutural stria thin, fragmented, obsolete in basal half; elytral disk with sparse secondary punctures in basal eighth. ***Prosternum***: prosternal keel very shallowly emarginate at base, carinal striae complete, close together at middle, divergent anteriorly and posteriorly, free at base, united in narrow arch in front; short secondary striae present between carinal striae and procoxae; lateral prosternal striae weakly divergent; prosternal lobe very slightly deflexed, about two-thirds as long as keel, marginal stria present medially, divergent from edge, abbreviated at sides. ***Mesoventrite***: anterior margin of mesoventrite broadly emar-

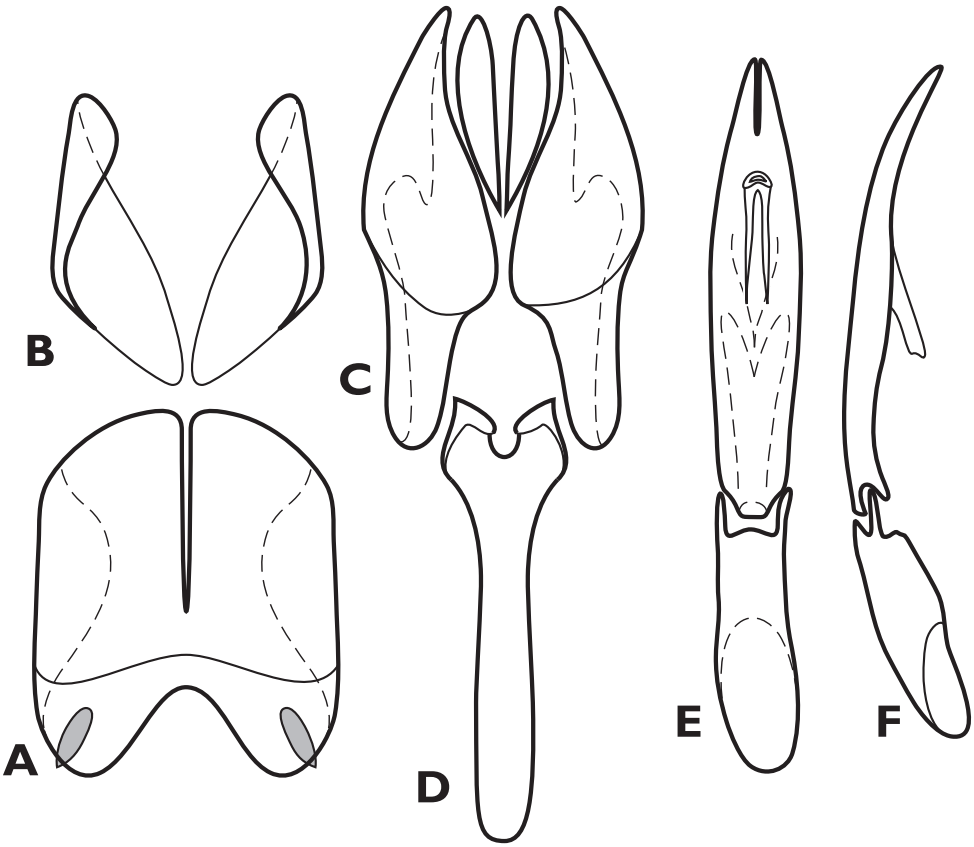


Figure 12. *Chapischema doppelganger*, male genitalia. **A** 8th tergite **B** 8th sternite **C** 9th and 10th tergites **D** 9th sternite **E** Aedeagus, dorsal view **F** Aedeagus, lateral view.

ginate, but very weakly produced at center, marginal stria complete; mesometaventral stria coarsely crenulate, arched slightly forward onto basal third of mesoventrite. ***Metaventrite***: postmesocoxal stria curved loosely behind coxa, extending nearly to mesepimeral-metepisternal corner; lateral metaventral stria curved laterad posteriorly toward posterior sixth of metepisternum; metaventral disk impunctate at middle, with few coarse secondary punctures at sides. ***Abdomen***: 1st abdominal ventrite with lateral striae obliquely impressed along inner edge of metacoxa; ventrites 2-4 with few coarse punctures only at extreme sides; propygidium rather long, about two-thirds as long as broad, more or less flat, with small gland openings near anterolateral corners, disk with few small, very irregularly sparse secondary punctures; pygidium elongate, about one third longer than basal width, slightly longer than propygidium along midline, apical margin rounded, disk weakly depressed along sides, punctation similar to but finer and sparser than that of propygidium. ***Legs***: protrochanter glabrous, meso- and metatrochanters each with two very short apical setae; femora simple; protibia with outer margin rounded, weakly 5-dentate, each tooth with moderately strong spine; posterior

surface rather coarsely dimpled; protibial spurs very short; protarsus with ventral setae simple; meso- and metatibiae elongate, widened apically to about twice basal width, outer margins with 4-5 rather strong spines, mesotibia in particular faintly dentate; meso- and metatarsi short, each with single pair apicoventral spines. ***Male genitalia*** (Fig. 12): accessory sclerites present; T8 rather short, with sides subparallel, apex very deeply, narrowly emarginate, basal membrane attachment line complete distad basal emargination, ventrolateral apodemes moderately developed, well separated beneath; S8 halves approximate only at base, inner margins divergent to apex, apical guides widest near apex, with very fine inconspicuous setae; T9 with broad basal apodemes, prominent, strongly hooked ventrolateral apodemes, dorsal lobes more strongly sclerotized along sides; T10 weakly sclerotized, completely divided; S9 with sides sinuate, subparallel, apical emargination distinct, rounded, apical flange interrupted, apical corners moderately prominent; tegmen widest near middle, slightly narrowed to base, more strongly narrowed to apex, with very large medioventral process; median lobe simple, about half tegmen length; basal piece long, about two-thirds tegmen length.

Remarks. The superficial similarity of this species with *Pyxister devorator*, also exclusively known from the same collecting event near Nova Friburgo, Brazil, is remarkable. Despite the apparent similarity, they do differ in several external characters, and the male genitalia differ in numerous substantial characters. Their external similarity must be considered an extreme convergence.

Etymology. This species' name refers to its extreme similarity to the sympatric *Pyxister devorator.*

***Scaptorus* gen. n.**
http://zoobank.org/4B2498BC-56C0-4E99-9AFC-51866CB77347
http://species-id.net/wiki/Scaptorus

Type species. *Scaptorus pyramus* sp. n.

Description. This genus differs from other Exosternini in the following combination of characters: body elongate, sides subparallel, distinctly convex; frons widened to rounded anterior corners produced over antennal bases; epistoma bituberculate along anterior margin; labrum with apical margin truncate, weakly produced and carinate; left mandible with straight, edentate incisor edge, right mandible curved to apex, with small, acute basal tooth; submentum rather short, slightly depressed, weakly produced anteriorly into oral cavity; mentum broadly subquadrate, weakly emarginate apically, labial palpi 3-segmented, basal palpomere very short, penultimate and ultimate palpomeres rather thin and elongate; maxillary cardines very smooth, stipes faintly microsculptured, with few scattered setae, maxillary palpi 4-segmented, basal palpomere short, 2nd and 3rd palpomeres subequal, ultimate palpomere about twice as long as penultimate, simply fusiform; antennal scape elongate, very slightly widened toward apex, with few setae on anterior surface; funicle slightly shorter than scape, widened slightly to cupuliform 8th antennomere; antennal club elongate oval, about

as long as funicle, tomentose, with median and subapical annuli crowded into apical half, both interrupted on dorsal surface, free ends enlarged into sensory patches, the apical-most more so; pronotal gland openings not evident; pronotal sides subparallel, abruptly bent to apical corners; transverse elevated carina present behind and parallel to anterior pronotal margin, curving posterad briefly at sides, abruptly bent to lateral margin behind anterior corner; prosternal keel overlapped at base by projecting mesoventrite, weakly convex, short, anteriorly displaced by prominent prosternal lobe, which is strongly produced, deflexed, with raised median ridge; mesoventrite subtrapezoidal, projecting anteriorly; mesometaventral stria absent; propygidium transverse, with small gland openings in anterolateral corners; pygidium about one third wider than long, apical margin simply rounded; protrochanter lacking setae, meso- and metatrochanters with pair of very short setae near apex of posterior edge; profemur rather narrow, anterior edge sinuate; protibia narrow at base, outer margin more or less rounded apically, weakly dentate, strongly spinose; protibial spurs present, short; protarsus somewhat laterally compressed, bearing spatulate ventral setae in both sexes; meso- and metafemora narrow; meso- and metatibiae slightly widened to apices, bearing few thin spines toward apex of outer margins; male genitalia with paired accessory sclerites present; T8 with ventral apodemes nearly meeting along midline; S8 with halves divergent apically, apical guides well developed, with subapical setae; T9 with broad, blunt ventrolateral apodemes; T10 completely divided; S9 head broad, with prominent lateral flanges, apical flange low, continuous, not interrupted medially; tegmen lacking medioventral tooth or process; median lobe long, basal processes strongly differentiated; female T8 forming a single plate; S8 tripartite, basal baculi narrowly articulated with lateral plates, thin and convergent proximally; S9 well developed, about twice as long as broad, articulated with strap-shaped extension from apex of S8; T10 entire; valvifers about as long as coxites, weakly paddle-shaped, weakly expanded in basal third; coxites nearly three times as long as wide, bidentate, with median apical tooth rather thin and elongate, outer tooth weakly developed, the two well separated; gonostyle flattened, shorter than median tooth, apically setose; bursa copulatrix membranous, barely expanded; spermatheca rather short, sausage-shaped, with basal stem short, with slightly thin, very elongate spermathecal gland attached near its base.

Remarks. *Scaptorus* is characterized by numerous unique features. The transverse carina of the pronotum (Figs 13A, 14A–B) is the most obvious, immediately separating this from other Neotropical Exosternini. But in addition the bituberculate epistomal margin, projecting mesoventral margin (overlapping the reduced prosternal keel), and longitudinally ridged prosternal lobe (Fig. 13B) are also very unusual. A somewhat comparable mesosternum can be found in *Mecistostethus* Marseul, but this is almost certainly convergence; the two genera share little else. It is instead resolved as closely related to *Enkyosoma* and *Chapischema* in our recent analysis of Exosternini relationships (Caterino and Tishechkin in review).

Etymology. The name of this genus translates to 'shoulder ridge' referring to its most diagnostic feature.

***Scaptorus pyramus* sp. n.**
http://zoobank.org/02EDCF2F-50F2-44DA-85CA-B9C54FD7F423
http://species-id.net/wiki/Scaptorus_pyramus
Figs 13–15, Map 2

Type locality. FRENCH GUIANA: Belvèdére de Saül [3.01°N, 53.21°W].

Type material. Holotype male: **GUYANE FRANÇAISE**: Belvèdére de Saül, point de vue. 3°1'22"N, 53°12'34"W. Piège vitre 31.xi.2010. SEAG leg." / "Caterino/ Tishechkin Exosternini Voucher EXO-01763" (MNHN). **Paratypes** (6): 5: same data as type, except 2: 24.i.2011, 2: 10.xii.2010, 1: 17.i.2011; 1: Rés. des Nouragues, Camp Inselberg, 4°05'N, 52°41'W, 8.x.2010, FIT, SEAG (CHND, FMNH, MSCC).

Other material. 1: **ECUADOR**: **Orellana**, Yasuní Res. Stn. on mid. Rio Tiputini. 0°40.5'S, 76°24'W, FIT, 23–30.vi.1999, A.Tishechkin (LSAM), 1: 28.vi–5.vii.1999 (LSAM). 1: **PERU**: **Loreto**: Campamento San Jacinto, 2°18.75'S, 75°51.77'W, 175–215m, 7.vii.1993, FIT, R. Leschen (SEMC); 1: **Madre de Dios**: CICRA Field Station, 12.55261°S, 70.11008°W, 295m, 11–13.vii.2010, blue pan trap, Chaboo Team (SEMC). 1: **BRAZIL: Pará:** Tucuruí, 3°45'S, 49°40'W, FIT, 27.x-9.xi.1985 (CHND); Melgaço Dist., Rio Marinau, 1°51.5'S, 51°20'W, FIT, 29.x-13.xi.1993 (CHND).

Description. ***Size range****:* Length 2.2-2.5 mm; width 1.9-2.1 mm; ***Body***: body rufobrunneus, elongate, sides subparallel, distinctly convex. ***Head****:* frons nearly as long as broad, more or less flat, weakly depressed in middle, sides widened very slightly to rounded anterior corners produced over antennal bases; frontal stria fine, present close to sides and along anterolateral edges, absent from middle; supraorbital stria absent; frontal disk with fine but conspicuous ground punctation throughout, with few coarser punctures along dorsal margin, faintly microsculptured; epistoma bituberculate along anterior margin, tubercles subtended by weak carinae to ends of frontal stria, epistomal disk depressed along midline; labrum about one-third as long as broad, apical margin truncate, weakly produced and carinate above flattened supraoral surface. ***Pronotum***: pronotal sides subparallel in basal two-thirds, abruptly bent to apical corners; pronotal gland openings not evident; marginal stria complete along lateral and anterior margins; sinuate, transverse elevated carina present one-fourth behind and parallel to anterior pronotal margin, curving posterad briefly at sides, abruptly bent to lateral margin one-third from anterior corner; ground punctation of disk fine posterad carina, markedly denser anterad carina, with few coarser, shallow punctures at sides; prescutellar impression absent. ***Elytra***: convexity of elytra slightly greater than that of pronotum, i.e., lateral profile not a smooth curve; epipleuron smooth, with single, complete marginal stria; outer subhumeral stria carinate, forming distinct lateral margin to dorsal surface, inner subhumeral stria present only in basal half, striae 1-4 complete, 5th stria obsolete in basal one-third, rarely complete, sutural stria obsolete in basal one-third; all dorsal striae rather shallowly impressed, but 4th, 5th and sutural striae broad, at least apically, delimited on inner and outer edges. ***Prosternum***: prosternal keel overlapped at base by projecting mesoventrite, lacking carinal striae, weakly convex, short, anteriorly

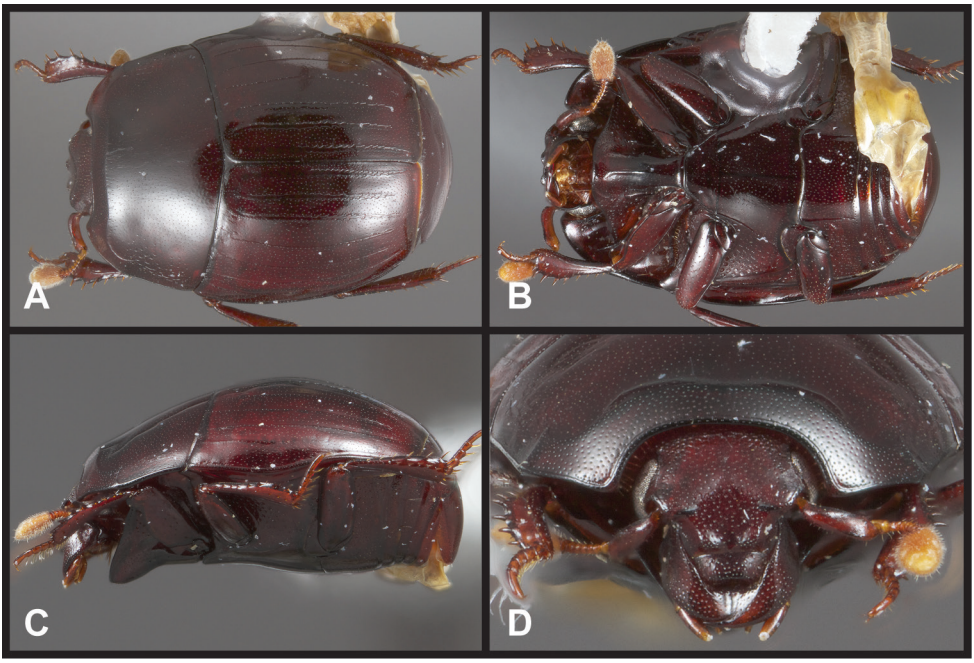


Figure 13. *Scaptorus pyramus*. **A** Dorsal habitus **B** Ventral habitus **C** Lateral habitus **D** Head, anterior view.

displaced by prominent prosternal lobe, which is strongly produced, deflexed, with raised median ridge, marginal stria absent. ***Mesoventrite***: mesoventrite subtrapezoidal, narrowed, projecting anteriorly, lacking marginal stria; mesometaventral stria absent. ***Metaventrite***: postcoxal stria present, curved around mesocoxa to middle of mesepimeron; lateral metaventral stria extending from inner corner of mesocoxa toward middle of metacoxa, bent laterad apically toward metepisternum; metaventral punctation fine and sparse at middle, with few coarser punctures at sides. ***Abdomen***: 1st abdominal ventrite with ground punctation rather dense, with parallel lateral striae along inner edge of metacoxa; ventrites 2-4 simply punctate, lacking transverse striae; propygidium wide, rather short, with small gland openings in anterolateral corners; pygidium about one third wider than long, apical margin simply rounded. ***Legs***: protrochanter lacking setae, meso- and metatrochanters with pair of very short setae near apex of posterior edge; profemur rather narrow, anterior edge sinuate, partial stria along posterior margin; protibia narrow at base, outer margin widened to more or less rounded apical half, weakly dentate, each tooth bearing thin but rather long spine; protibial spurs present, short; protarsus somewhat laterally compressed, bearing spatulate ventral setae in both sexes; meso- and metafemora narrow, slightly elongate; meso- and metatibiae slightly widened to apices, bearing few thin spines toward apex of outer margins. ***Male genitalia*** (Fig. 15): Paired accessory sclerites present; T8 with broad basal and narrower apical emarginations, line of

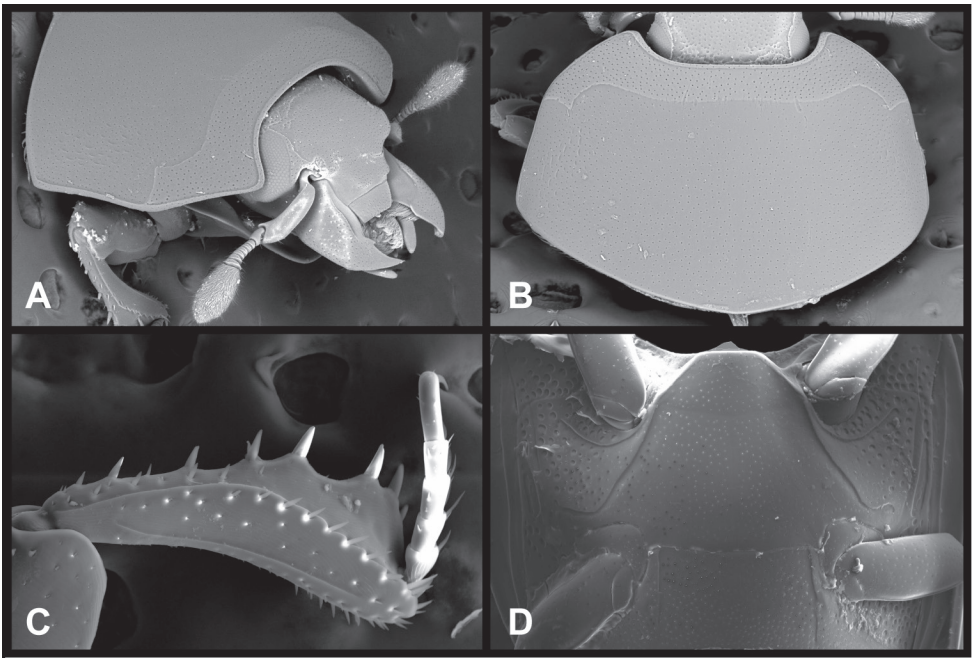


Figure 14. *Scaptorus pyramus*, SEMs. **A** Head and pronotum, anterolateral view **B** Pronotum **C** Protibia, anterior view **D** Meso- and metaventrites.

basal membrane attachment complete, distad basal emargination, ventral apodemes well developed, nearly meeting along midline; S8 with halves nearly meeting only at base, divergent apically, apical guides well developed from base to near apex, rather abruptly narrowed to subacute apex, each side with single inconspicuous subapical seta; T9 with broad, blunt ventrolateral apodemes, apices narrow, obliquely subtruncate; T10 completely divided; S9 broad, truncate at base, narrowed toward apex, head broad, with prominent lateral flanges, apical flange low, continuous, not interrupted medially; tegmen rather narrow, widest at middle, evenly narrowed to base and apex, weakly curved in lateral aspect, lacking medioventral tooth or process; basal piece about one-third tegmen length; median lobe almost half tegmen length, gonopore rather wide, basal processes strongly differentiated, with thin proximal arms over half overall length.

Remarks. The majority of specimens of this unusual species appear to bear witness to some interesting aspect of its biology. Most show distinct longitudinal scratches on the pronotal disk behind the transverse carina (Fig. 14B). What might be causing this is unclear, but we would suggest ant mandibles as a possibility. We limit the type series to those specimens from French Guiana, due to the lack of males from other localities with which to confirm identity.

Etymology. The name of this species refers to pyramidal swellings on the apex of the epistoma.

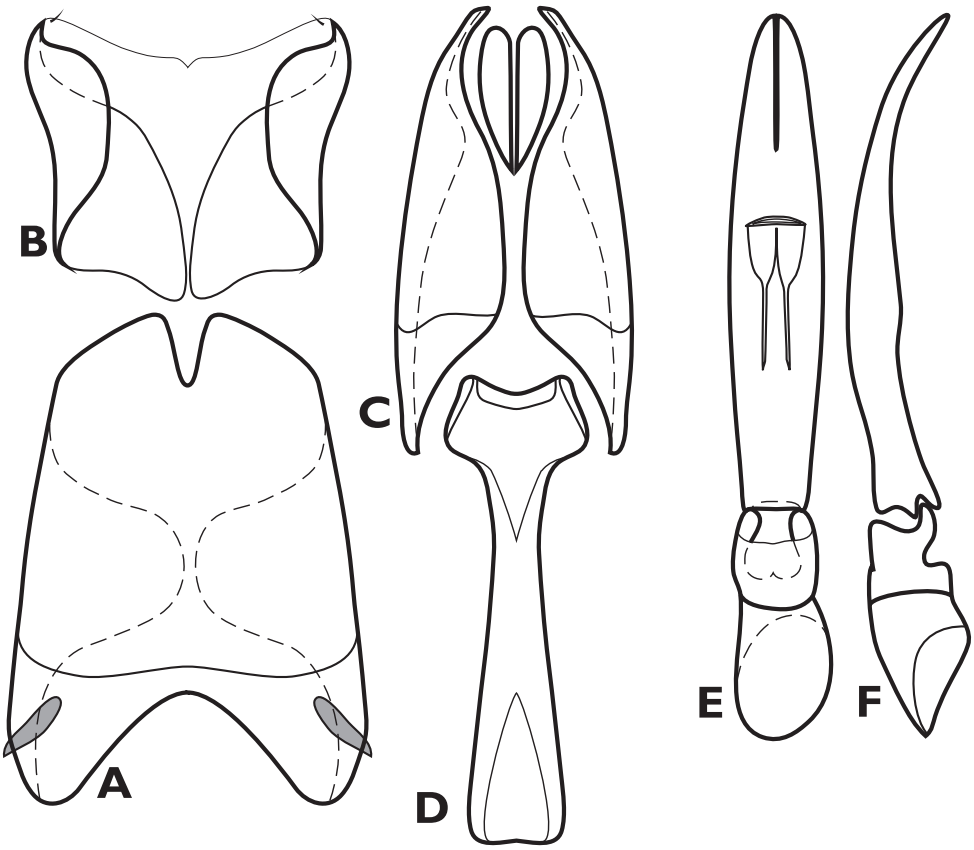


Figure 15. *Scaptorus pyramus*, male genitalia. **A** 8th tergite **B** 8th sternite **C** 9th and 10th tergites **D** 9th sternite **E** Aedeagus, dorsal view **F** Aedeagus, lateral view.

***Lacrimorpha* gen. n.**
http://zoobank.org/1339536E-A1A2-42D6-A0CE-73B092CEE826
http://species-id.net/wiki/Lacrimorpha

Type species. *Lacrimorpha glabra* sp. n.

Description. ***Size range:*** Length 1.8–2.2 mm; width 1.5–1.8 mm; ***Body:*** body depressed, sublimuloid, with sides rounded and pygidia variably prolonged, generally lightly colored, rufescent to rufo-brunneus, smooth, with fine ground punctation but very little secondary punctation. ***Head:*** frons and epistoma convex, prominent, frons rather broad with frontal stria complete, weakly recurved at middle; supraorbital stria fine, usually detached at sides; epistoma weakly emarginate apically; labrum short inwardly arcuate, about 4× wider than long; mandibles rather short, basal denticles on incisor very small to obsolete; submentum transversely depressed, posterolateral margins raised, apical margin produced slightly into base of oral cavity; mentum about twice as wide as midline length, sides narrowed, apex weakly emarginate; maxillary cardo glabrous, stipes with two setae along

lateral margin, basal palpomere short, 2nd and 3rd palopmeres short, subequal, ultimate palpomere narrowed apically, about 1.5× as long as penultimate; antennal scape weakly expanded to apex, weakly carinate along inner margin, funicle narrow at base, weakly widened to 7th and disc-like 8th antennomere; antennal club tomentose, basal annulus obsolete, middle annulus with slightly basally expanded sensory patch on upper surface, simple on lower surface, apical annulus poorly defined, transverse. ***Pronotum****:* pronotal sides arcuate, strongly convergent to anterior corners; prescutellar impression absent; median pronotal gland openings very fine, one pair along anterior margin laterad eye, one pair behind eye about two-thirds pronotal length from anterior margin; marginal pronotal stria complete and continuous along lateral and anterior margins; submarginal stria complete laterally, not extending mediad behind head, very close to marginal stria, intervening disk narrowly convex. ***Elytra***: elytral striation strongly reduced, single epipleural stria present, complete, diverging from margin in anterior half, outer subhumeral stria complete, nearly meeting 1st dorsal stria apically, inner subhumeral stria absent, oblique humeral stria faint, 1st dorsal stria more or less complete, may be slightly abbreviated basally, may be extended mediad along posterior margin of elytron, 2nd and third dorsal striae weakly impressed, present in basal half or less, 4th and 5th striae completely absent, sutural stria usually represented only by extremely short striole at posteromedian corner of elytron, may be extended laterad by apical marginal stria. ***Prosternum***: prosternal keel narrow, acutely emarginate at base, carinal striae weak to absent; prosternal lobe about half as long as keel, marginal stria present or absent. ***Mesoventrite***: mesoventrite acutely produced in front, marginal stria complete, with varied fine strioles in anterolateral corners; mesometaventral stria absent. ***Metaventrite***: mesoventrite with postmesocoxal stria present, varied in length, lateral metaventral stria absent; median portion of metaventral disk with fine ground punctation only, grading to coarser punctures laterad coxae, punctures along metaventral-metepisternal suture may coalesce into stria; metepisternum often with longitudinal stria. ***Abdomen***: 1st abdominal ventrite with single faint to abbreviated stria along inner margin of metacoxa, generally curved laterad behind coxa, disk faintly strigose at sides; ventrites 2-4 with posterior marginal stria along lateral thirds or more; ventrite 5 variously prolonged, apical margin strongly arcuate; propygidium flat or faintly depressed at sides, with basal marginal stria, complete or not; propygidial disk without obvious gland openings; pygidium with apex subacute to very prolonged and acuminate, with lateral marginal striae or not. ***Legs***: all femora flattened and slightly expanded, arcuate on anterior and posterior edges; each trochanter with single seta; protibia with inner and especially outer edges arcuate, narrowing apically, the outer edge bearing 6-7 strong spines, denser near apex, lacking emarginations between, two apical protibial spurs present, strongly reduced, anterior surface of protibia with tarsal groove almost obsolete; protarsus of both sexes bearing spatulate ventral setae; meso- and metatibiae very narrow, parallel-sided, bearing a few thin spines toward apex of inner and outer edges; meso- and metatarsi as long or longer than corresponding tibia, with long, ventral setae that may be vaguely spatulate. ***Male genitalia***: accessory sclerites present, basal; T8 with weakly developed ventrolateral apodemes, apical margin may be slightly desclerotized, basal membrane attachment line intersecting basal emargination; S8 divided, inner edges divergent in apical half, lateral guides weakly to moderately developed,

apices narrowed, bearing a few conspicuous setae near apical corners; T9 with ventrolateral apodemes only very weakly developed, not hooked, apices narrowed, acute at inner corners; T10 weakly sclerotized, completely divided; S9 broad, sclerotized along edges, with small apical emargination and weak apical flanges; tegmen flattened, moderately broad basally, slightly narrowed apically, lacking ventromedial process; median lobe more than half as long as tegmen, with proximal apodemes prominent, abruptly narrowed at extreme proximal end; basal piece long, about half as long as tegmen, with prominent apicoventral point. ***Female genitalia***: T8 forming a single plate, apically desclerotized, with shallow, arcuate basal emargination; S8 tripartite, with median sclerite weakly divided from lateral sclerties, basal baculi narrowly attached to lateral sclerites, evenly convergent proximally; S9 weakly sclerotized, elongate, articulated with strap-shaped extension from apex of S8; T10 broad, apically arcuate; valvifers paddle-shaped, paddles nearly one-half total length; coxites elongate, two-thirds length of valvifers, tridentate, with very prominent median tooth dwarfing teeth on either side; gonostyle long, bisetose, inserted between two lateralmost apical teeth; bursa copulatrix membranous, weakly expanded; spermatheca weakly sclerotized, approximately spherical, borne on long thin stalk inserted at base of common oviduct, with elongate, weakly spiraled spermathecal gland attached near its base.

Diagnosis. This genus is easy to recognize based on its sublimuloid shape (Fig. 16), with the body depressed, the sides rounded, and the pygidium variably prolonged and subacute. Its convex frons is also unusual, as are the rounded, spinose protibiae, the very narrow meso- and metatibiae, the reduced elytral striation, and the almost complete lack of secondary punctation. *Lacrimorpha* is resolved as the sister group of the genus *Mecistostethus* in our recent analysis of Exosternini relationships (Caterino and Tishechkin in review).

Etymology. The name of this genus means 'tear-drop shaped', resulting from its tapered posterior end. The genus is feminine.

Key to species of *Lacrimorpha*

1	Postmesocoxal stria ending freely behind coxa	**2**
–	Postmesocoxal stria recurved anterad to mesepimeron	**3**
2	Lateral edge of metaventrite lacking stria near metepisternal suture; prosternal keel with weak carinal striae; marginal stria of prosternal lobe well developed at middle	***Lacrimorpha glabra***
–	Lateral edge of metaventrite with stria along anterior half of metepisternal suture; prosternal keel lacking carinal striae; marginal stria of prosternal lobe fragmented to absent	***Lacrimorpha subdepressa***
3	Basal propygidial stria complete; lateral edge of metaventrite with stria along metepisternal suture; apex of pygidium subacute, pygidium more or less equilateral, lacking lateral striae	***Lacrimorpha balbina***
–	Basal propygidial stria interrupted; lateral edge of metaventrite lacking stria near metepisternal suture; pygidium strongly prolonged, apex acuminate, with lateral strioles	***Lacrimorpha acuminata***

***Lacrimorpha glabra* sp. n.**
http://zoobank.org/D7C3978A-F7C9-49FF-AB69-89D1DEA948E1
http://species-id.net/wiki/Lacrimorpha_glabra
Figs 16A, E, H, 17A–B, E, G–I, Map 3

Type locality. BRAZIL: Pará: Tucuruí [3.75°S, 49.67°W].

Type material. Holotype male: "Tucurui 49°40'W, 3°45'S, PARA BRESIL" / "16-29/7/1985, piége d'interception, N. Degallier" / "Caterino/Tishechkin Exosternini Voucher EXO-00189" (UFPR).

Diagnostic description. Length: 2.0 mm, width: 1.8 mm; as for generic description, plus the following specific characters: body rufescent; mandibles lacking basal incisor teeth; apices of first and sutural elytral striae connected by apical marginal elytral stria; basal propygidial stria nearly complete, only narrowly interrupted at middle; fine ground punctation of pygidia relatively conspicuous; pygidium equilaterally subtriangular, apex bluntly subacute; prosternal keel with weak carinal striae in basal half only; prosternal lobe with well impressed marginal stria along middle portion; postmesocoxal stria bent laterad behind coxa, ending freely; only few punctures along metepisternal margin subserially arranged, without marginal stria on edge of mesoventrite; metepisternum itself with fragmented longitudinal stria; postmetacoxal stria not distinguishable from lateral strigosity of 1st abdominal ventrite.

Remarks. This species has its pygidial apex subacute (Fig. 16A), but not particularly prolonged. This in combination with the posteriorly abbreviated postmesocoxal stria and lack of lateral marginal metaventral stria will distinguish it from its congeners.

Etymology. This species' name refers to its very smooth, glabrous body surface.

***Lacrimorpha subdepressa* sp. n.**
http://zoobank.org/341A2D9F-B60C-44D2-BCF3-9F11984026C3
http://species-id.net/wiki/Lacrimorpha_subdepressa
Figs 16C, F, Map 3

Type locality. FRENCH GUIANA: Rés. des Nouragues [4.0834°N, 52.6833°W].

Type material. Holotype female: "Rés. Natur. des Nouragues, Camp Inselberg, 4°05'N, 52°41'W, Piège vitre, 30.ix.2010, SEAG leg." (MNHN). **Paratypes** (4 females): 3: same locality as type, 30.xi.2010, 16.ix.2010, and 25.i.2011; 1: Rés. Natur. des Nouragues, Saut Pararé, 4°02'N, 52°41'W, FIT, 20.iv.2010, SEAG. (CHND, LSAM, MSCC).

Diagnostic description. Length: 1.9–2.1 mm, width: 1.6–1.8 mm; as for generic description, plus the following specific characters: body rufobrunneus; right mandible with weak basal incisor tooth; apical marginal elytral stria absent; propygidium with basal marginal stria broadly interrupted at middle; pygidium with apex bluntly subacuminate, with sides slightly narrowed toward apex, barely longer than basal width; prosternal keel lacking carinal striae; prosternal lobe with at most weak fragments of marginal stria, may be obsolete; postmesocoxal stria bent lat-

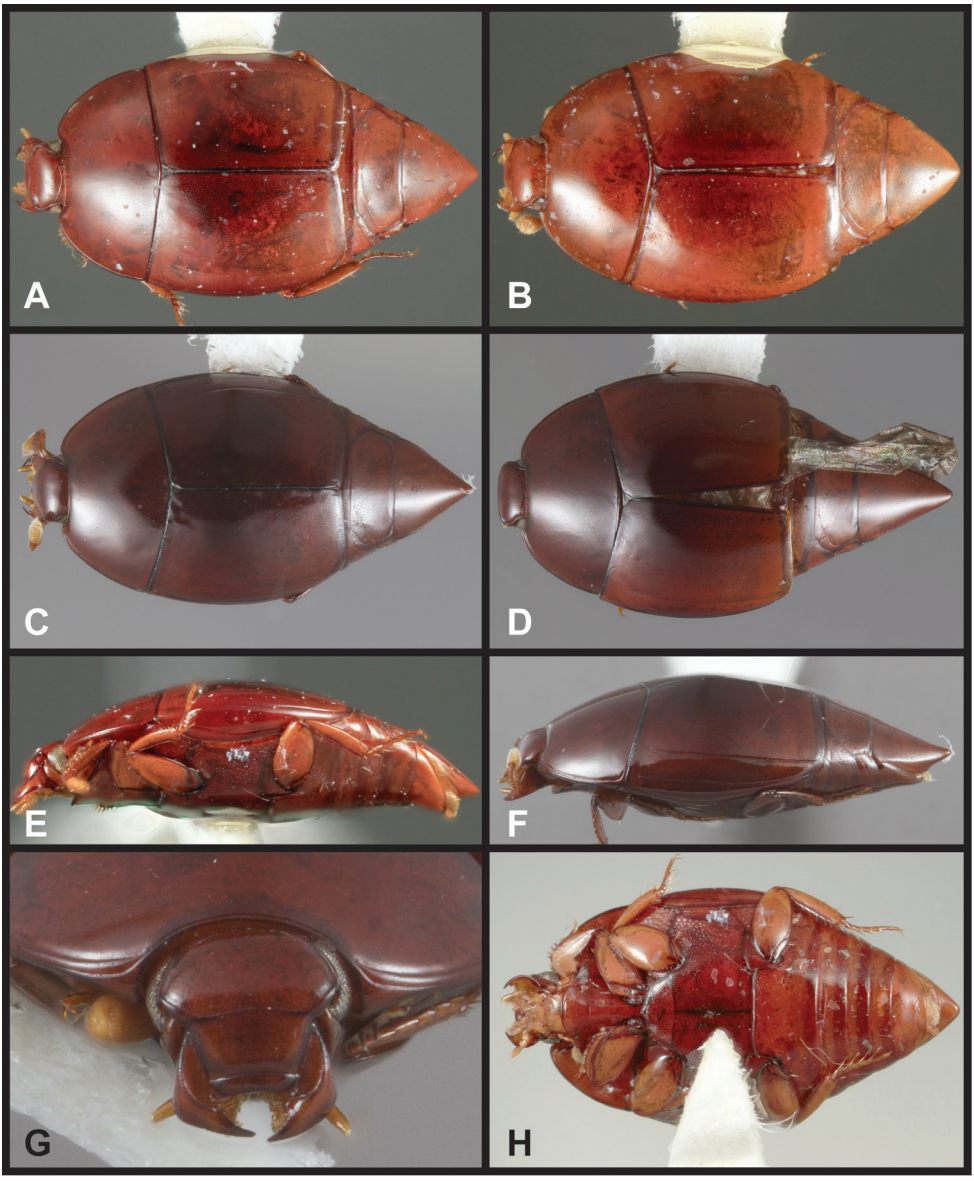
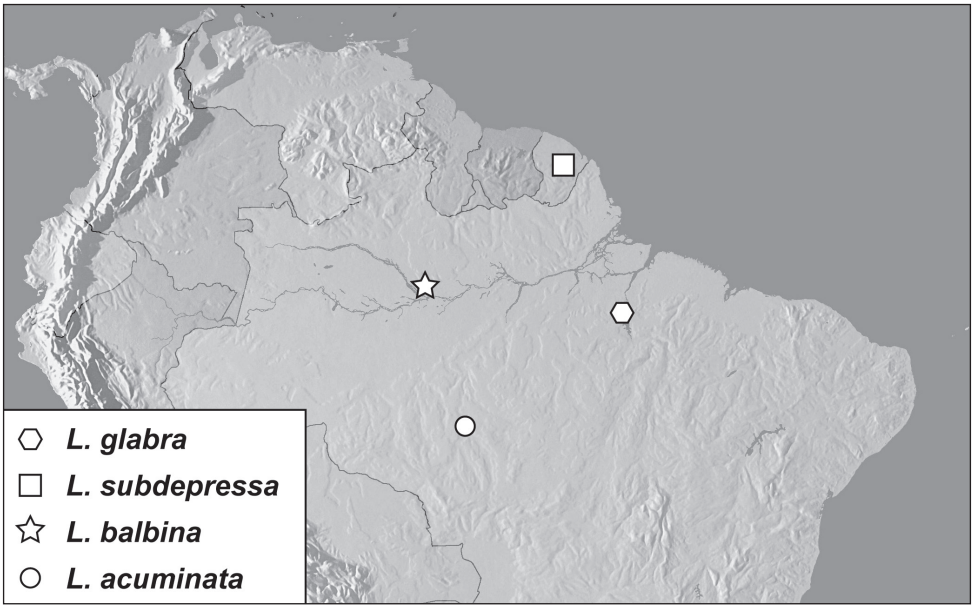


Figure 16. *Lacrimorpha* spp. **A** *Lacrimorpha glabra*, dorsal habitus **B** *Lacrimorpha balbina*, dorsal habitus **C** *Lacrimorpha subdepressa*, dorsal habitus **D** *Lacrimorpha acuminata*, dorsal habitus **E** *Lacrimorpha glabra*, lateral habitus **F** *Lacrimorpha subdepressa*, lateral habitus **G** *Lacrimorpha acuminata*, head, anterior view **H** *Lacrimorpha glabra*, ventral habitus.

erad behind coxa, ending freely; metaventral disk with distinct stria along basal half to two-thirds of metepisternal suture; longitudinal metepisternal suture well developed; postmetacoxal stria not distinguishable from lateral strigosity of 1st abdominal ventrite.



Map 3. Specimen records of *Lacrimorpha* spp.

Remarks. This species can be separated from the others in the genus *Lacrimorpha* by its slightly darker color (Fig. 16C), presence of half to two-thirds of the lateral metaventral stria, weak prosternal lobe stria, and absence of carinal striae of the prosternal keel.

Etymology. The name of this species refers to its moderately subdepressed body form.

***Lacrimorpha balbina* sp. n.**
http://zoobank.org/F88C3135-5E9D-4966-99AE-E0B7E2E9841B
http://species-id.net/wiki/Lacrimorpha_balbina
Fig 16B, Map 3

Type locality. BRAZIL: Amazonas, Balbina [1.9553°S, 59.4580°W].

Type material. Holotype female: "20-30/IV/88 FIT BALBINA Amazonas, Brésil" / "Caterino/Tishechkin Exosternini Voucher EXO-00190" (UFPR).

Diagnostic description. Length: 1.8 mm, width: 1.6 mm; as for generic description, plus the following specific characters: body rufescent; mandibles lacking basal incisor teeth; apical marginal elytral stria absent, apical sutural striole strongly reduced; basal propygidial stria complete and close to basal margin; ground punctation of propygidium slightly more conspicuous than that of pygidium; pygidium subtriangular, slightly shorter than basal width, apex bluntly subacute; prosternal keel with weak carinal striae in basal half; prosternal lobe with fragment of marginal stria at middle; postmesocoxal stria recurved around coxa to mesepimeron; secondary punctation of

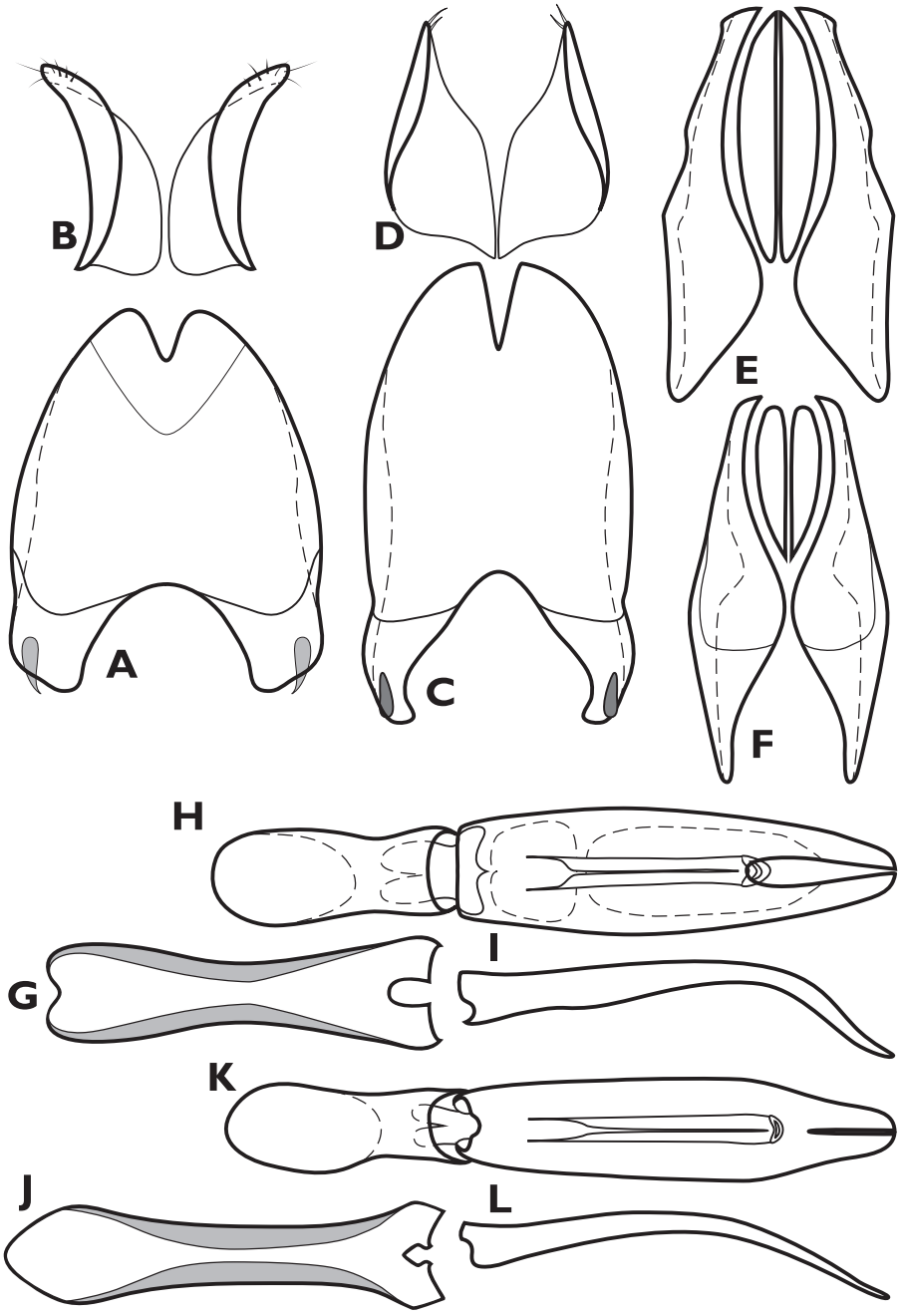


Figure 17. *Lacrimorpha* spp., male genitalia. **A** *Lacrimorpha glabra*, 8th tergite **B** *Lacrimorpha glabra*, 8th sternite **C** *Lacrimorpha acuminata*, 8th tergite **D** *Lacrimorpha acuminata*, 8th sternite **E** *Lacrimorpha glabra*, 9th and 10th tergites **F** *Lacrimorpha acuminata*, 9th and 10th tergites **G** *Lacrimorpha glabra*, 9th sternite **H** *Lacrimorpha glabra*, aedeagus, dorsal view **I** *Lacrimorpha glabra*, aedeagus, lateral view **J** *Lacrimorpha acuminata*, 9th sternite **K** *Lacrimorpha acuminata*, aedeagus, dorsal view **L** *Lacrimorpha acuminata*, aedeagus, lateral view.

sides of metaventrite very shallow and sparse; lateral stria present along metepisternal margin; metepisternum with complete longitudinal stria; 1st abdominal ventrite with lateral stria present along inner edge of metacoxa and bending laterad behind coxa.

Remarks. This species can be distinguished from the others in the genus by the combination of: relatively weakly produced pygidial apex (Fig. 16B), complete basal propygidial stria, and completely recurved postmesocoxal stria.

Etymology. This species is named for its type locality, close to the dam of this name northeast of Manaus.

***Lacrimorpha acuminata* sp. n.**
http://zoobank.org/8D6F599D-6DDB-427A-805A-4775E213E61C
http://species-id.net/wiki/Lacrimorpha_acuminata
Figs 16D, G, 17C–D, J–L, Map 3

Type locality. BRASIL: Mato Grosso, Fazenda São Nicolau [9.859°S, 58.215°W].

Type material. Holotype male: "**BRASIL**: **Mato Grosso**: Mpio. Cotriguaçu, Fazenda São Nicolau, Prainha, 9°51.6'S, 58°12.9'W, flight intercept, Oct. 2009, F.Z.Vaz-de-Mello" / "Caterino/Tishechkin Exosternini Voucher EXO-01301" (CEMT).

Diagnostic description. Length: 2.0 mm, width: 1.8 mm; as for generic description, plus the following specific characters: body rufescent, with ground punctation very fine and sparse; right mandible with small, acute basal incisor tooth; apical marginal elytral stria absent, apical sutural striole strongly reduced; basal propygidial stria interrupted for about one-fifth width of propygidium; ground punctation of propygidium slightly more conspicuous than that of pygidium; pygidium about one-third longer than basal width, with lateral marginal striae in basal half, apex bluntly subacute; prosternal keel lacking carinal striae; prosternal lobe with marginal stria well impressed in middle; postmesocoxal stria recurved around coxa to mesepimeron; secondary punctures of sides of metaventrite small and uniform but rather dense; lateral stria absent from metepisternal margin; metepisternum with complete longitudinal stria; 1st abdominal ventrite with lateral stria difficult to distinguish from ground strigosity.

Remarks. This species' most distinctive character is its very distinctly prolonged pygidial apex (Fig. 16D). It also, like the preceding species, has its postmesocoxal stria recurved completely to the mesepisternum, but has its basal propygidial stria interrupted medially.

Etymology. This species' name refers to the acuminate pygidium.

***Crenulister* gen. n.**
http://zoobank.org/0B3C5374-EC9F-4A51-BA6A-FE8CF8FD7C6E
http://species-id.net/wiki/Crenulister

Type species. *Crenulister grossus* sp. n.

Description. ***Size range:*** Length 1.7–3.2 mm; width 1.5–2.8 mm; ***Body:*** body rather broadly ovoid, variably subdepressed to rather strongly depressed, rufescent to rufopiceous. ***Head:*** frons broad, frontal corners rounded, rather prominent over antennal bases; frontal disk depressed in common with epistoma, frontal stria recurved dorsad within depression, usually complete; sides of epistoma variably ridged, carinate and/or striate; labrum broad, apical margin generally carinate, truncate to weakly emarginate; mandibles with small or no basal teeth on incisor edge; submentum flat to slightly depressed, sparsely setose; mentum about half as long as wide, arcuately narrowed anteriorly, apical margin acutely emarginate; cardo smooth and glabrous, stipes with few setae along lateral margin; ultimate palpomeres fusiform; antennal scape elongate, curved, weakly carinate along anterior margin; funicle weakly widened beyond 5th antennomere, 8th antennomere slightly shorter than preceding; antennal club elongate, widest just beyond midpoint, tomentose, with interrupted basal annulus near midpoint and complete annulus between midpoint and apex, slightly enlarged basad at middle, particularly on dorsal surface. ***Pronotum***: pronotal sides weakly arcuate, convergent to anterior corners, slightly to distinctly explanate at sides, marginal stria usually complete along lateral and apical margins, submarginal stria present very close to sides, absent across front, weakly crenulate; pronotum with pair of gland openings very close to anterior margin behind eye and glands variably displaced posterad onto pronotal disk, usually multiplied along a visible track bearing up to 5 distinct openings along its length; pronotal disk with secondary punctures, when present, strongly concentrated across basal half. ***Elytra***: elytral disk weakly to moderately convex, all striae coarsely impressed, each stria comprising two alternating series of interconnected punctures, appearing chain-like at their most dense; epipleuron usually with one complete marginal stria, with fragments of a second in posterior half or not, inner subhumeral stria usually complete, dorsal striae 1-4 complete, 5th and sutural striae rarely obsolete basally, bases of 4th or 5th and sutural striae rarely connected by weak basal arch; ground punctation of elytral disk fine to coarse, with at least a few coarse secondary punctures usually present in most interstriae. ***Prosternum***: prosternal keel generally distinctly, subacutely emarginate at base, with complete carinal striae usually united in narrow anterior arch, short secondary lateral strioles frequently present between carinal striae and procoxae; lateral prosternal striae present, divergent in front of coxae; prosternal lobe one-half to two-thirds length of keel, apically rounded to subtruncate, with marginal stria present at middle, variably obsolete at sides. ***Mesoventrite***: mesoventrite subacutely produced at middle, with complete marginal stria smooth to crenulate; mesometaventral stria crenulate, usually strongly arched to angulate anterad onto middle of mesoventral disk, disk frequently with sparse secondary punctures. ***Metaventrite***: metaventral disk with coarse secondary punctures usually over most of surface, postmesocoxal stria present, recurved anterad to mesepimeron or ending freely posterolaterad coxa, lateral metaventral stria sinuate, extending from inner corner of mesocoxa toward middle of metacoxa, frequently abbreviated apically; coarse punctures of metepisternum may coalesce into vague to distinct striae. ***Abdomen***: ventrites mostly coarsely punctate, punctures tending to coalesce into striae along apical mar-

gins of ventrites 2-4; 1st ventrite with poorly developed lateral stria along inner edge of metacoxa, abbreviated or curving laterad behind coxa; propygidium transverse, 2-3× as wide as long, with single gland opening on each side, often borne on weak convexity behind anterolateral corner, sometimes associated with weak oblique striole, disk generally sparsely covered with shallow secondary punctures, punctures often sparser in apical half; pygidium more or less equilateral, apex rounded to weakly subacute, gland openings generally present near lateral margin one-fifth to one-fourth from base, these often associated with lateral marginal pygidial striae; marginal stria when present rarely complete around apex; pygidial disk variably punctate. ***Legs***: all trochanters bearing single long seta; profemur rather dilated at middle, narrowed, slightly emarginate at inner apex, protibia generally rounded, strongly spinose, tibial margin only rarely emarginate between to form marginal teeth; protibial spurs present but generally weak; protarsus of both sexes with strongly spatulate setae; meso- and metafemora weakly dilated basad middle, with complete posterior marginal stria; meso- and metatibiae similar, weakly widened to apex, with series of long, rather thin marginal spines; meso- and metatarsi with 4 ventral spines along apical margins only. ***Male genitalia***: accessory sclerites vestigial or absent; T8 with sides evenly tapered to subtruncate apex, basal membrane attachment line generally tangential to deep, rounded basal emargination, ventrolateral apodemes produced most strongly at base, narrowed apically, separated by about one-third T8 width beneath; S8 short along midline, with longer divergent lateral guides bearing several strong setae along apicoventral margin, with weak membraneous velum across entire apex; T9 with ventrolateral apodemes not strongly tapered, inner apices subquadrate beneath, T9 apices subacute to obliquely subtruncate; T10 entire, may be emarginate basally and/or apically; S9 rather short, with broad truncate to emarginate base, head variably subquadrate, apically emarginate, with apical flanges separate; aedeagus rather broad, flattened, sides rounded, apical division conspicuous, apices often distinctly separate, medioventral process strong, produced beneath near midpoint; basal piece one-fourth to one-third tegmen length, with distinct medioventral tooth; median lobe short, proximal arms strongly narrowed basally. ***Female genitalia***: T8 forming single broad plate; S8 forming separate median and lateral plates, basal baculi thin, narrowly attached to lateral sclerites, convergent proximally; S9 slightly elongate, articulated with strap-shaped extension from apex of S8; T10 weakly sclerotized; valvifers paddle-shaped, paddles rather short, about one-third valvifer length; coxites 2.5–3× as long as wide, tridentate, with weak inner tooth, prominent median tooth, and intermediate lateral tooth; gonostyle nearly as long as median tooth, setose; bursa copulatrix membranous, lacking sclerites, weakly expanded; spermatheca weakly sclerotized, globose, borne on long thin stalk inserted at base of common oviduct, with elongate, spiraled spermathecal gland attached near its midpoint.

Diagnosis. In most respects this genus is highly distinctive. However, many of the distinguishing characters vary considerably within the group, in addition to appearing in unrelated species, and it is only through a combination of external characters and male genitalia can an unambiguous diagnosis be provided. For most species, the pattern of pronotal punctation, with coarse punctures restricted to the

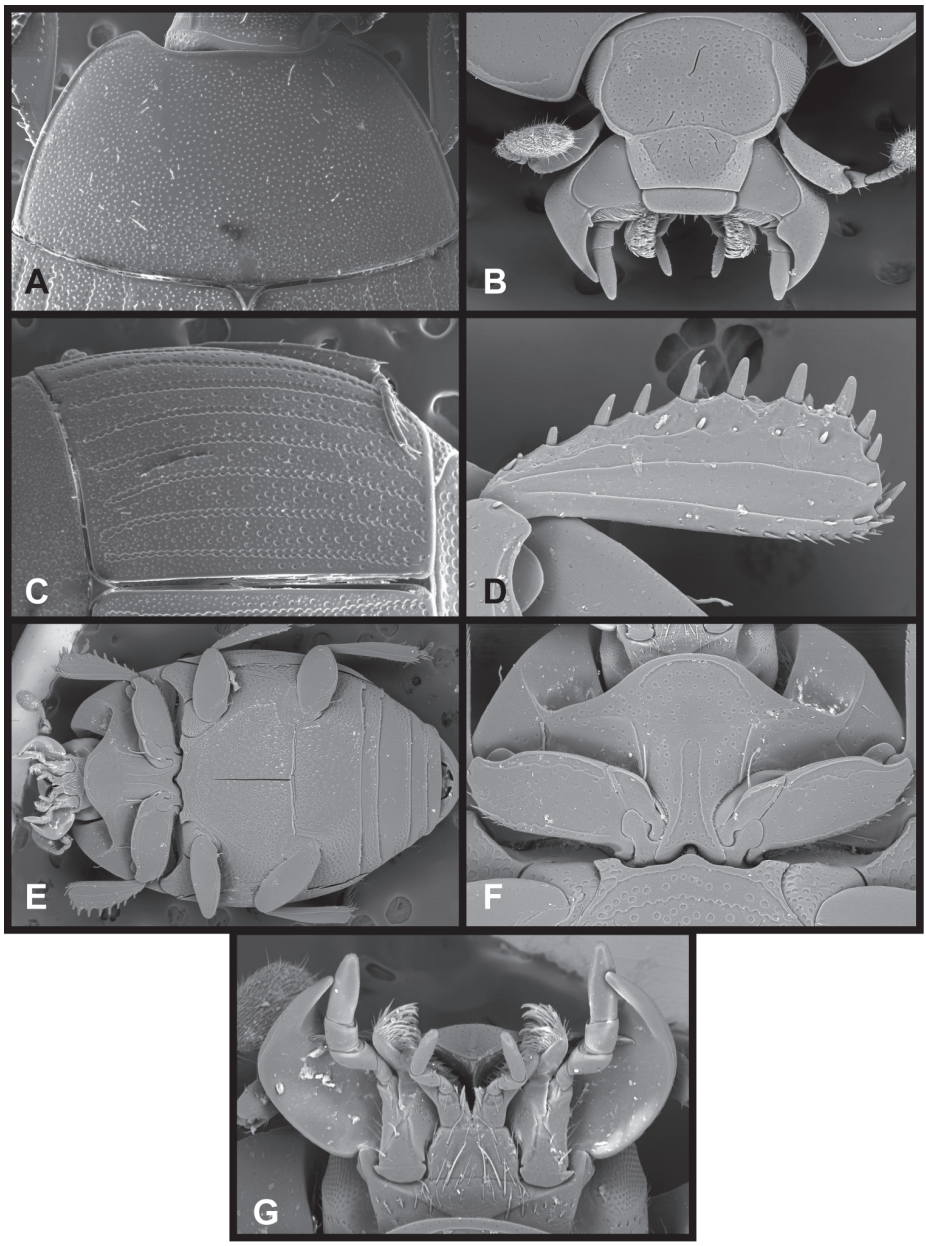


Figure 18. *Crenulister umbrosus*, SEMs showing generic characters. **A** Pronotum **B** Head, anterior view **C** Right elytron **D** Protibia, posterior view **E** Ventral habitus **F** Prosternum and mesoventrite **G** Head, ventral view.

basal half of the pronotal disk (Figs 18A, 19A, C, 22A, 23A), is distinctive, and this in combination with coarsely impressed elytral striae (Fig. 18C) and sparse secondary punctures in the elytral interstriae will separate most species. The longitudinal

tracks of multiplied pronotal gland openings (Fig. 19G) are also very unusual, and will put most species here easily. If the above are true, and the protarsi have spatulate setae, the diagnosis is unambiguous. Finally, the male genitalia of *Crenulister* also exhibit several distinctive characteristics, in particular the rather broad, flat aedeagus, with strong, acute ventromedial process (see Fig. 20E), frequently with the tegmen apices separated, the few strong setae at the apex of the 8th sternite (Fig. 20B), and the broad, medially subquadrate ventrolateral apodeme of the 9th tergite (Fig. 20C). A single (undescribed) species in a distantly related group shares all of these external characters, and represents an amazingly similar overall body form. The only good characters to distinguish it are its lack of spatulate protarsal setae, and its entirely different male genitalia, with its aedeagus strongly narrowed and hooked apically, completely unlike the short, broad and flattened aedeagus of *Crenulister*.

Phylogenetically, *Crenulister* emerges from within a diverse group of mostly undescribed taxa that we loosely term the 'scutellar impression group', particularly a small subgroup related to the named species *Phelister blairi* Hinton.

Etymology. The genus name refers to the ubiquitously crenulate elytral striae found in the species of this genus, in conjunction with the common histerid ending -ister. The gender of the genus is masculine.

Key to species of *Crenulister*

1 5th and sutural striae obsolete in basal third..... ***Crenulister simplex***
– 5th and usually sutural striae complete to base of elytra, at least as basal fragments..... **2**
2 Inner subhumeral stria obsolete in basal fourth..... ***Crenulister seriatus***
– Inner subhumeral stria reaching base of elytron **3**
3 Punctures of metepisternum coalescing into distinct longitudinal stria half or more the length of the sclerite; marginal pygidial stria generally present, if substantially fragmented **4**
– Punctures of metepisternum discrete, or at most one or two coalescing into very short striole; marginal pygidial stria generally absent **6**
4 Darker species; pygidial punctures denser near pygidial apex; epipleuron generally with second marginal stria well developed in posterior half..... **5**
– More rufescent species; pygidial secondary punctures less dense toward apex, with few secondary punctures along midline in general; epipleuron with only a single, complete epipleural stria..... ***Crenulister impar***
5 Larger species; prescutellar impression obsolete; marginal pygidial stria rather well impressed, may be interrupted apically, but rarely fragmented..... ..... ***Crenulister spinipes***
– Smaller species; small prescutellar impression evident among basal pronotal punctures, usually outlined by several punctures; marginal pygidial stria less regular, fragmented in apical third..... ***Crenulister umbrosus***

6 Pronotal disk very coarsely punctate in most of basal half, secondary punctures reaching midline at least in the middle; elytral striae deeply and coarsely impressed..... ***Crenulister grossus***

– Pronotal disk with secondary punctures smaller and sparser, more or less restricted to basal third; elytral striae varied, but generally less strongly impressed..... **7**

7 Larger (>3mm PE length), dark rufescent species, with moderately coarse punctures restricted to basal one-fourth of pronotum ***Crenulister paucitans***

– Smaller (<2.5mm), more pale rufescent species, with secondary pronotal punctures smaller, sparser, and not as discretely limited to posterior one-fourth of pronotal disk..... **8**

8 Outer protibial margin with emarginations between spines deep and distinct, nearly or fully as deep as the marginal spines are long; sutural stria complete to base ..... ***Crenulister dentatus***

– Outer protibial margin with emarginations between spines shallow, much shallower than length of marginal spines; sutural stria weakened to obsolete at base..... ***Crenulister explanatus***

***Crenulister grossus* sp. n.**
http://zoobank.org/6815E9BF-4D58-4FDB-B838-BED962A0C02C
http://species-id.net/wiki/Crenulister_grossus
Figs 19A–B, 20, Map 4

Type locality. BRAZIL: Mato Grosso, Fazenda São Nicolau [9.8386°S, 58.2508°W].

Type material. Holotype male: "**BRASIL: Mato Grosso:** Mpio Cotriguaçu, Fazenda São Nicolau, Matinha. 9°50.3'S, 58°15.05'W. Flight intercept Oct 2009. F.Z.Vaz-de-Mello" / "Caterino/Tishechkin Exosternini Voucher EXO-03022" (CEMT). **Paratypes** (6): 1 same data as type, 2: same locality as type, but xii.2010; 3: **Mato Grosso**: Mpio Cláudia, 11°24.5'S, 55°19.5'W, FIT, 17–27.x.2010, A.F.Oliveira (CEMT, UFPR, FMNH, MSCC).

Diagnostic description. Length: 2.6–3.2 mm, width: 2.4–2.8 mm; as for generic description, with the following diagnostic characters: body rufopiceous, elongate ovoid, moderately convex; frontal stria fine but complete across middle, frontal disk rather strongly depressed, with a few sparse secondary punctures, mostly toward vertex; epistoma with oblique lateral ridges delimiting median depression, but not striate; labrum about 5× wider than long, apical margin shallowly, broadly emarginate; pronotum with gland opening track extending posterad just beyond midpoint, with 3-4 openings along its length, substriate; pronotal sides moderately explanate along smooth, non-crenulate lateral submarginal stria; pronotal disk with numerous, large secondary punctures in basal third, most strongly concentrated and extending slightly further forward at middle, sides almost entirely smooth; prescutellar impression not evident; elytron with single, complete, crenulate epipleural stria, all dorsal striae complete, very coarsely impressed, appearing chain-

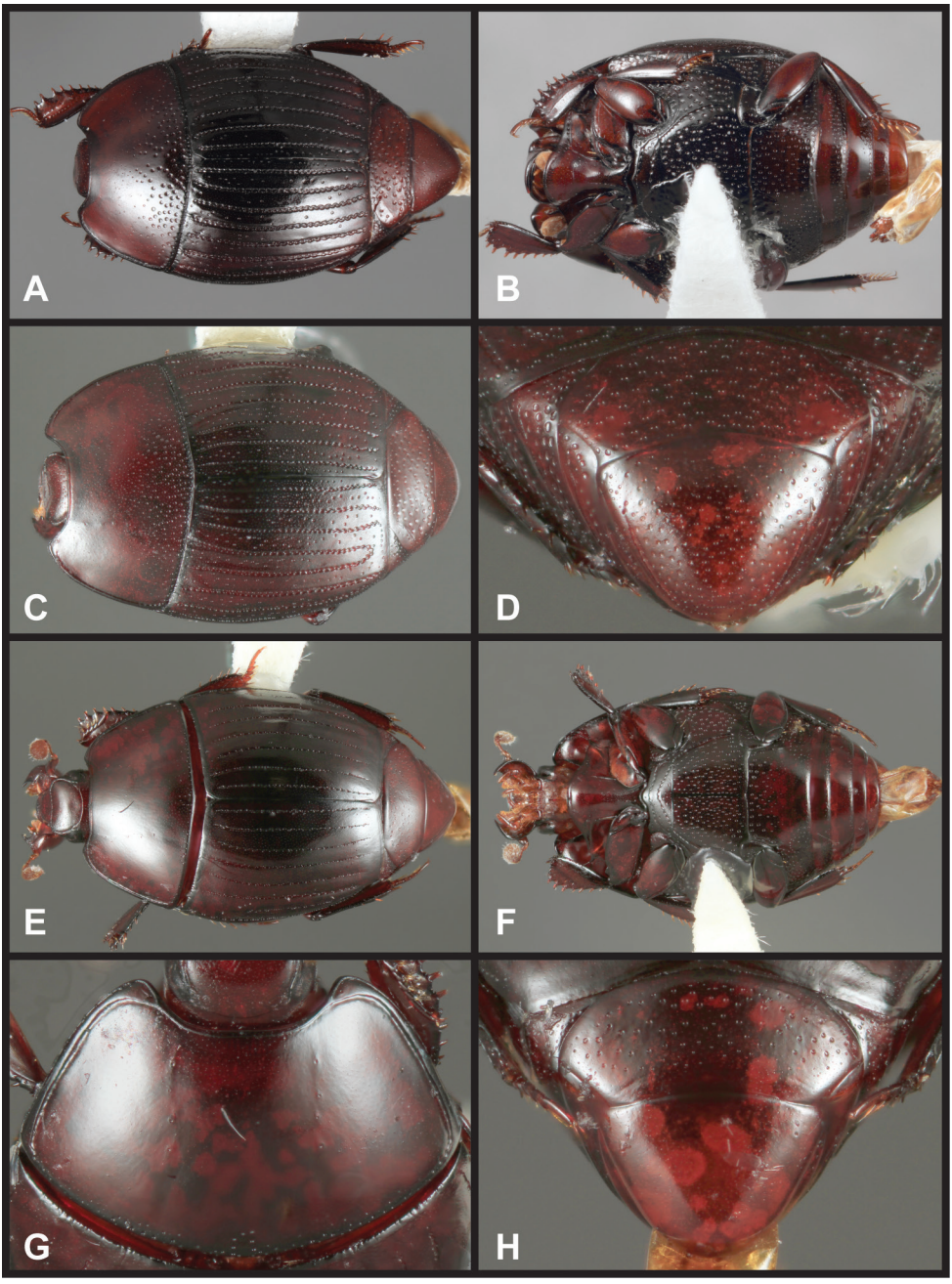


Figure 19. *Crenulister* spp. **A** *Crenulister grossus*, dorsal habitus **B** *Crenulister grossus*, ventral habitus **C** *Crenulister spinipes*, dorsal habitus **D** *Crenulister spinipes*, pygidia, posterior view **E** *Crenulister seriatus*, dorsal habitus **F** *Crenulister seriatus*, ventral habitus **G** *Crenulister seriatus*, pronotum **H** *Crenulister seriatus*, pygidia, posterior view.

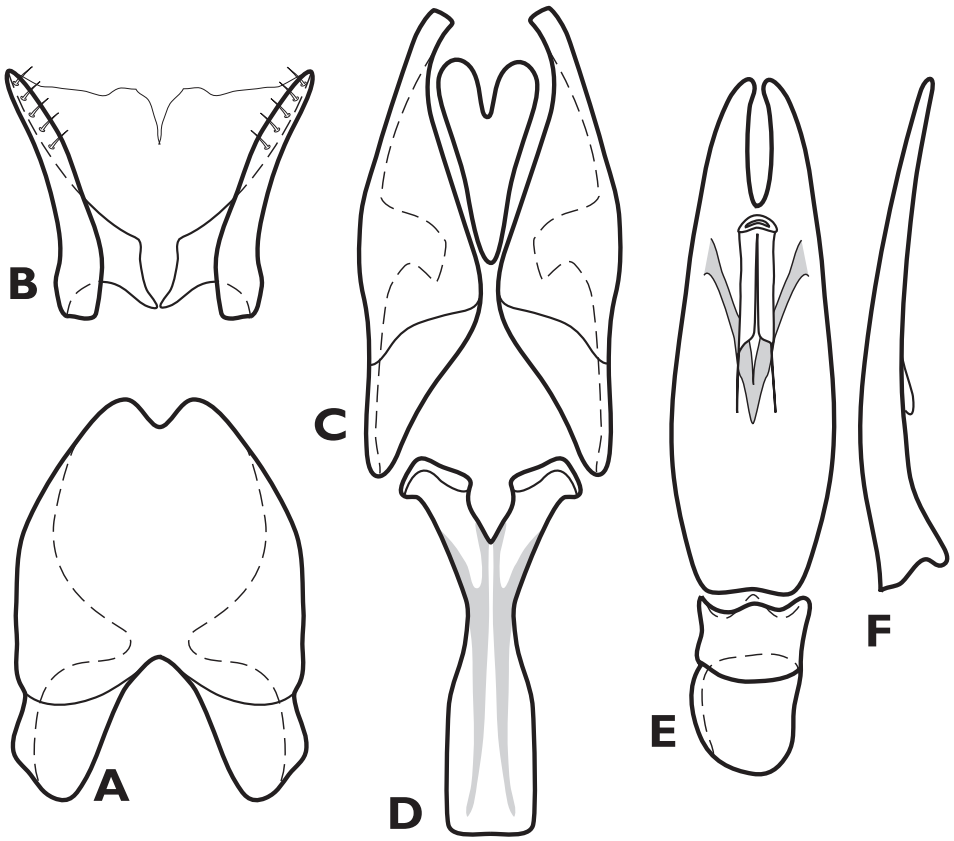
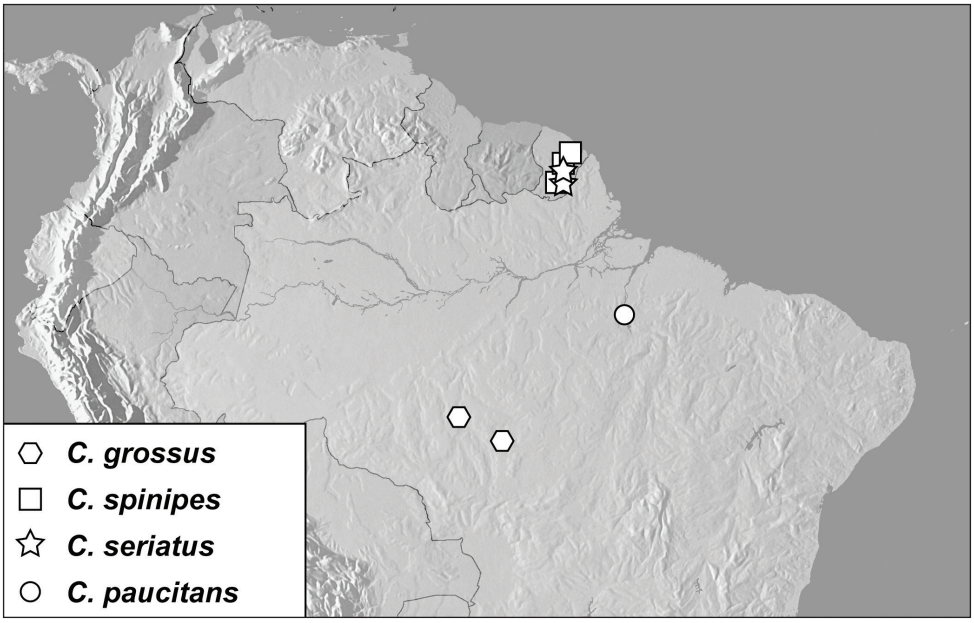


Figure 20. *Crenulister grossus*, male genitalia. **A** 8th tergite **B** 8th sternite **C** 9th and 10th tergites **D** 9th sternite **E** Aedeagus, dorsal view **F** Aedeagus, lateral view.

like; elytral intervals very sparsely, irregularly punctate, most intervals with 4-6 punctures; prosternal keel with faint secondary striae alongside complete, anteriorly united carinal striae; prosternal lobe deflexed in apical half, with marginal stria present only at middle; mesoventrite with marginal stria weakly crenulate, mesometaventral stria more coarsely so and arched forward just beyond mesoventral midpoint; postmesocoxal stria recurved anterad around mesocoxa but ending short of mesepimeron; lateral metaventral stria crenulate, reaching middle of metacoxa, recurved mediad apically in some individuals; mesoventrite entirely and more or less uniformly coarsely punctate; metepisternal punctures independent, not forming a stria; punctures of 1st abdominal ventrite mostly uniform, only transversely elongate along posterior margin; marginal punctures of ventrites 2–4 similarly elongate, but mostly separate, not or only intermittently coalescing into marginal striae; protibia 7-spined, with marginal dentation very weakly developed; meso- and metatibiae with 4-5 spines each, mainly in apical half; propygidium with secondary punctures shallow, very sparse, separated by 1-3× their diameters, densest in basal half; propygidial gland opening associated with very weak oblique striole in anterior corners; pygidial



Map 4. Specimen records of *Crenulister* spp.

punctation weak, punctures much smaller and sparser than those of propygidium, more or less uniformly separated by about 4× their diameters throughout; pygidial gland openings evident at sides about one-fourth from base, marginal striae absent. Male (Fig. 20): accessory sclerites absent; T8 with ventrolateral apodemes strongly narrowed beneath; S8 with halves meeting only at basal corner, inner margins short and strongly divergent, with about 5 strong setae toward apex; T9 with apices obliquely truncate; T10 apically emarginate; S9 truncate, quadrate at base, apex narrowly and rather deeply emarginate; tegmen widest in basal third, narrowed to apex, apices slightly separated, medioventral process produced beneath about one-fourth from base; median lobe about one-third tegmen length, basal piece short, about one-fourth tegmen length.

Remarks. This is the largest species of *Crenulister*, and between its size (Fig. 19A–B), coarse punctation, and very coarsely impressed elytral striae, one of the easiest to recognize.

Etymology. This species name refers to its relatively large size, and secondarily its occurrence in Mato Grosso, Brazil.

***Crenulister spinipes* sp. n.**
http://zoobank.org/B93E12E9-34CC-4548-80C7-4A68545CCF94
http://species-id.net/wiki/Crenulister_spinipes
Figs 19C–D, Map 4

Type locality. FRENCH GUIANA: Réserve des Nouragues [4.038°N, 52.673°W].

Type material. Holotype female: "**GUYANE FRANÇAISE:** Régina, Réserve des Nouragues, 4°2.27'N, 52°40.35'W, Piége d'interception, 28 Jan 2010. SEAG leg." / "Caterino/Tishechkin Exosternini Voucher EXO-00181" (MNHN). **Paratypes** (2): 1: Belvèdére de Saül, point de vue, 3°1'22"N, 53°12'34"W, 4.i.2011, FIT, SEAG (CHND); 1: Montagne des Chevaux, 4°43'N, 52°24'W, 26.xii.2008, FIT, SEAG (FMNH)

Diagnostic description. Length: 2.4–2.6 mm, width: 2.2–2.4 mm; as for generic description with the following diagnostic characters: body rufobrunneus, elongate ovoid, moderately convex; frontal stria fine but complete across middle, frontal disk rather strongly depressed, with sparse secondary punctures rather evenly distributed on frons and epistoma; epistoma with oblique lateral ridges delimiting median depression bearing faint traces of striae basally; labrum about 4× wider than long, apical margin shallowly, broadly emarginate; pronotum with gland opening track extending posterad just beyond midpoint, with 3-4 openings along its length; pronotal sides moderately explanate along very weakly crenulate lateral submarginal stria; pronotal disk with numerous, large secondary punctures in basal third, most strongly concentrated at middle, sides largely smooth; prescutellar impression not evident; elytron with one complete, crenulate epipleural stria and second incomplete stria closer to margin in posterior half, all dorsal striae complete, moderately coarsely impressed, appearing chain-like; elytral intervals sparsely, irregularly punctate, most intervals with 12–18 punctures; prosternal keel with complete, narrowly anteriorly united carinal striae; prosternal lobe with marginal stria present only at middle; mesoventrite with marginal stria weakly crenulate, mesometaventral stria similarly so, subangulately arched forward just beyond mesoventral midpoint; postmesocoxal stria slightly recurved anterad around mesocoxa but ending short of mesepimeron; lateral metaventral stria crenulate, reaching middle of metacoxa; mesoventrite entirely and more or less uniformly coarsely punctate; metepisternal punctures coalescing into a short longitudinal stria; punctures of 1st abdominal ventrite mostly uniform, slightly obliquely elongate posterad metacoxa, transversely elongate along posterior margin, intermittently coalesced into marginal strioles, as are those of ventrites 2–4; protibia 7–8-spined, with marginal dentation very weakly developed; meso- and metatibiae with 4–5 spines each, mainly in apical half; propygidium with secondary punctures shallow, sparse, separated by 1–2× their diameters throughout; propygidial gland opening associated with weak oblique striole in anterior corners; pygidial punctation sparse, punctures slightly smaller than those of propygidium, more or less uniformly separated by 2–3× their diameters throughout; pygidial gland openings evident at sides about one-fourth from base, marginal striae present along sides, broadly interrupted at apex. Male: not known.

Remarks. This species and *C. grossus* are very similar and evidently closely related. The smaller size, less coarsely impressed elytral striae (Fig. 19C), and semistriate metepisternum, abdominal ventrites and propygidium (Fig. 19D) will distinguish this species readily. Although both are larger than average for the genus, *C. grossus* is still markedly larger.

Etymology. The name of this species refers to its conspicuously spinose protibiae.

***Crenulister seriatus* sp. n.**
http://zoobank.org/6A69B05A-9B17-48B4-B74E-D95D8B5770F7
http://species-id.net/wiki/Crenulister_seriatus
Figs 19E–H, 21, Map 4

Type locality. FRENCH GUIANA: Belvèdére de Saül [3.01°N, 53.21°W].

Type material. Holotype male: "**GUYANE FRANÇAISE**: Bélvédère de Saúl, point de vue. 3°1'22"N, 53°12'34"W. Piège vitre, 20.xii.2010. SEAG leg." / "Caterino/Tishechkin Exosternini Voucher EXO-01768" (MNHN). **Paratypes** (5): 4: same locality as type, 7.i.2011, 24.i.2011, 31.i.2011, and 2.ix.2011 (CHND, FMNH, MSCC); 1: Régina, Réserve des Nouragues, 4°2.27'N, 52°40.35'W, 3.ix.2009, FIT, SEAG (CHND).

Diagnostic description. Length: 2.7–3.0 mm, width: 2.2–2.4 mm; as for generic description with the following diagnostic characters: body dark rufobrunneus, elongate oval, weakly convex; frontal stria fine, complete, frontal disk shallowly depressed, with few or no secondary punctures; epistoma with weak lateral ridges delimiting median depression bearing weak basal strioles; labrum about 4× wider than long, apical margin weakly outwardly arcuate; pronotum with gland opening track extending posterad behind middle, with 4 more or less evenly spaced openings; pronotal sides weakly depressed along smooth, raised lateral submarginal stria; pronotal disk with only a single series secondary punctures along basal margin, with a few encircling weak prescutellar impression, sides impunctate; elytron with one complete, crenulate epipleural stria and second, incomplete stria closer to margin in posterior half, inner subhumeral stria variably obsolete in about basal third, all other dorsal striae complete, moderately coarsely impressed, appearing chain-like; interstriae almost entirely lacking secondary punctures; prosternal keel with complete carinal striae slightly divergent anteriorly, not connected, faint secondary carinal stria present between carinal stria and procoxa; prosternal lobe deflexed in anterior half, with marginal stria present only at middle; mesoventrite with marginal stria weakly crenulate, mesometaventral stria crenulate, subangulately arched forward just beyond mesoventral midpoint; postmesocoxal stria slightly recurved anterad around mesocoxa, nearly reaching mesepimeron; lateral metaventral stria not crenulate, reaching inner third of metacoxa; metaventrite with secondary punctation largely uniform, but median punctures slightly smaller than those at sides; metepisternal punctures vaguely coalesced into a short stria; lateral stria of 1st abdominal ventrite well impressed along inner edge of metacoxa, with a separate transverse striole behind metacoxa; punctures of 1st abdominal ventrite limited to anterior third of median part of disk, with few oblique punctures posterad metacoxa; posterior margins of ventrites 1-4 very narrowly striatopunctate; protibia 7-8-spined, with marginal dentation weakly developed; mesotibia with 6-8 spines along margin, metatibia with fewer spines, present mainly along apical half; propygidium with secondary punctures quite small, sparse, separated by 2-4× their diameters, becoming obsolete in apical fourth; propygidial disk lacking anterolateral strioles; pygidium lacking secondary punctures; pygidial gland openings distinct about one-sixth from anterior margin,

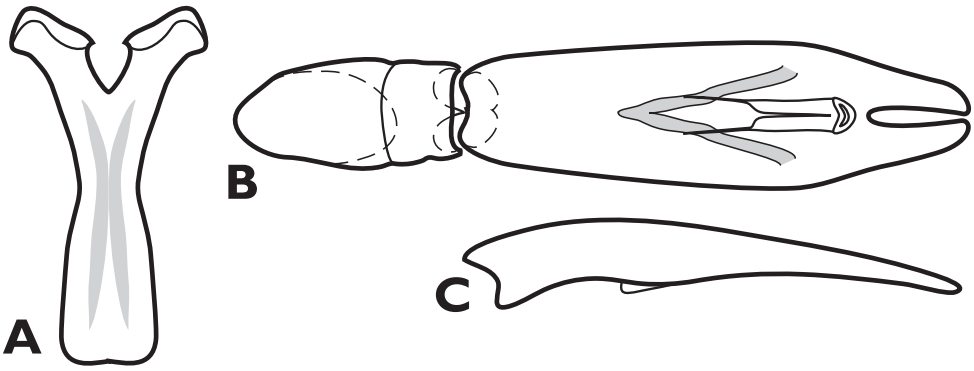


Figure 21. *Crenulister seriatus*, male genitalia. **A** 9th sternite **B** Aedeagus, dorsal view **C** Aedeagus, lateral view.

equidistant from lateral margin; pygidial margin lacking striae. Male (T8, S8, T9 as in *C. grossus*; see Fig. 20): accessory sclerites absent; T8 with ventrolateral apodemes strongly narrowed beneath; S8 with halves meeting only at basal corner, inner margins short and strongly divergent, with about 7 strong setae toward apex; T9 with apices narrowly obliquely truncate; T10 desclerotized along much of midline, only undivided at middle; S9 short, broad, widened to weakly emarginate base, apex broadly emarginate (Fig. 21A); tegmen (Fig. 21B–C) with sides weakly rounded, widening to just beyond midpoint, narrowed to apex, apices slightly separated, medioventral process produced beneath about one-third from base; median lobe about one-third tegmen length, basal piece just over one-third tegmen length.

Remarks. This species is quite distinguishable by its relative lack of secondary punctures (Fig. 19E). Those of the pronotum occur only along the basal margin; those of the interstriae are essentially lacking; the 1st abdominal ventrite is punctate only in the anterior third; and the pygidium (Fig. 19H) is devoid of secondary punctures. Among the larger, darker species, these features readily diagnose it.

Etymology. This species' name refers to its particularly conspicuous series of pronotal gland openings, against a largely impunctate background.

***Crenulister paucitans* sp. n.**
http://zoobank.org/CDD37AA2-5C9E-485F-BF2D-6C45BF1BE97A
http://species-id.net/wiki/Crenulister_paucitans
Fig 22, Map 4

Type locality. BRAZIL: Pará: Tucuruí [3.75°S, 49.67°W].

Type material. Holotype female: "**BRASIL: Pará:** Tucuruí, 3°45'S, 49°40'W. Piège d'interception. 27.x-9.xi. 1985" / "Caterino/Tishechkin Exosternini Voucher EXO-00180" (UFPR).

Diagnostic description. Length: 3.1 mm, width: 2.6 mm; as for generic description with the following diagnostic characters: body rufobrunneus, elongate ovoid,

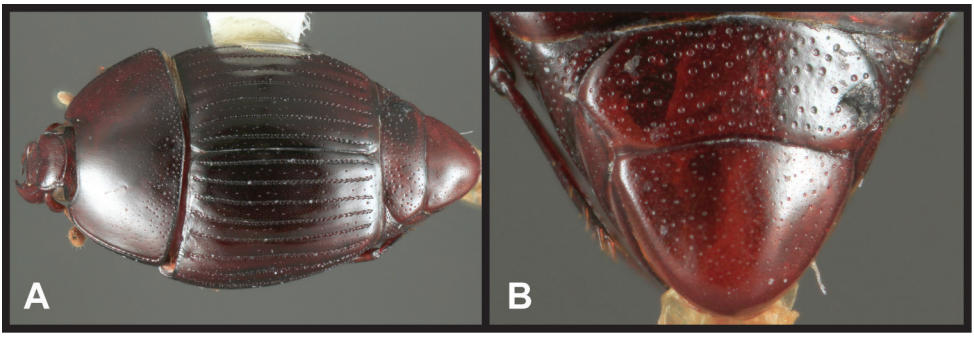


Figure 22. *Crenulister paucitans*. **A** Dorsal habitus **B** Pygidium, posterior view.

moderately convex; frontal stria fine, very narrowly interrupted at middle, frontal disk moderately depressed, with very sparse secondary punctures barely larger than background punctation; epistoma with weak lateral ridges delimiting median depression; labrum about 4× wider than long, apical margin more or less straight across; pronotum with gland opening track extending posterad to about midpoint, with 3 openings lying within weak striole in its posterior half; pronotal sides explanate along crenulate lateral submarginal stria; pronotal disk with secondary punctures restricted to basal margin, the smallest barely extending beyond the basal fourth, sides largely smooth; prescutellar impression not evident; elytron with one complete, crenulate epipleural stria and posterior fragments of second incomplete stria closer to margin, all dorsal striae complete, moderately coarsely impressed, appearing chain-like; elytral intervals very sparsely, irregularly punctate, most intervals with 8-12 small punctures; prosternal keel with complete carinal striae slightly separated anteriorly; prosternal lobe slightly deflexed, with marginal stria present only at middle; mesoventrite with marginal stria smooth, mesometaventral stria crenulate, subangulately arched forward just to about mesoventral midpoint; postmesocoxal stria slightly recurved anterad around mesocoxa, but ending short of mesepimeron; lateral metaventral stria weakly crenulate, reaching middle of metacoxa; metaventrite with secondary punctures larger and denser in posterior half; metepisternal punctures not coalesced into a short stria; lateral stria of 1st abdominal ventrite well impressed along inner edge of metacoxa, with a separate transverse striole behind metacoxa; punctures of 1st abdominal ventrite rather small, finer and sparser posterad, slightly obliquely elongate posterad metacoxa, transversely elongate along posterior margin, intermittently coalesced into marginal strioles, as are those of ventrites 2-4; protibia 7-8-spined, with marginal dentation weakly developed; mesotibia with 6 spines along margin, metatibia with 4 spines, mainly in apical half; propygidium with secondary punctures shallow, sparse, separated by 1-3× their diameters throughout; propygidial disk lacking anterolateral strioles; pygidial punctation very sparse and fine, almost obsolete along midline; pygidial gland openings slightly tuberculate, evident near sides about one-fifth from base; pygidial margin lacking striae. Male: not known.

Remarks. Given the existence of only a single specimen, it seems likely that many apparently distinct features may become less so in light of individual variation. How-

ever, this species can generally be distinguished by the strong limitation of pronotal punctures to the basal fourth (Fig. 22A), the association of the pronotal gland openings with a distinct longitudinal striole, the diminished punctation in the anterior half of the metaventral disk, and the lack of marginal pygidial stria (Fig. 22B).

Etymology. The name of this species refers to the relative paucity of punctures in the elytral interstriae.

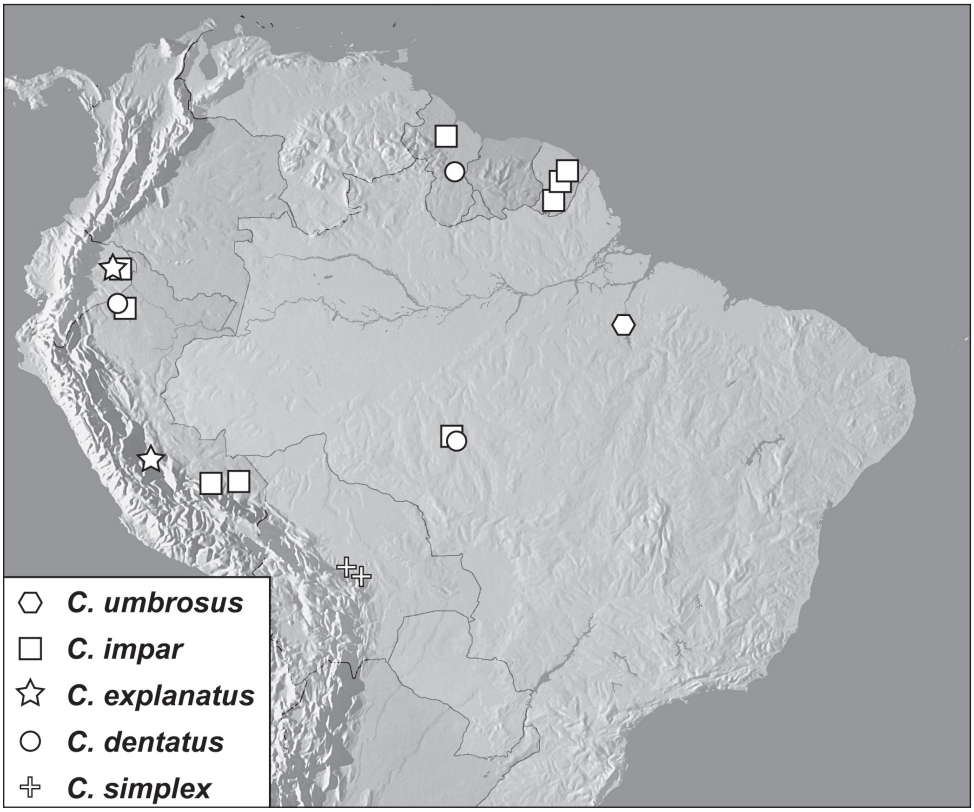
***Crenulister umbrosus* sp. n.**
http://zoobank.org/BC4A74B9-1E52-4549-825A-F4B591B52FB7
http://species-id.net/wiki/Crenulister_umbrosus
Figs 18A–G, 25E–G, Map 5

Type locality. BRAZIL: Pará: Tucuruí [3.75°S, 49.67°W].

Type material. Holotype male: "**BRASIL: Pará**, Tucurui, 3°45'S, 49°40'W. Piège d'interception. IV.1985" / "Caterino/Tishechkin Exosternini Voucher EXO-03005" (UFPR). **Paratypes** (3): same locality as type, 2: 10-29.vii.1985 (CHND, MSCC, FMNH), 1: 9-17.xii.1985 (CHND).

Other material. Same locality as type, 9–17.xii.1985 (CHND).

Diagnostic description. Length: 1.9–2.0 mm, width: 1.7–1.8 mm; as for generic description with the following diagnostic characters: body rufopiceous, elongate ovoid, slightly more parallel-sided than most, subdepressed; frontal stria fine, complete, frontal disk moderately depressed, with fine, dense punctation consisting of ground punctation and barely larger secondary punctation; epistoma with lateral ridges delimiting median depression bearing weak fragments of lateral striae; labrum about 4× wider than long, apical margin weakly emarginate; pronotum with gland opening track nearly reaching midline, with 3-4 openings lying within the impunctate track; pronotal sides with weakly crenulate, complete lateral submarginal stria; secondary punctures of pronotal disk rather small, mostly restricted to basal fourth; weak prescutellar impression present; elytron with complete, crenulate epipleural stria and secondary stria in posterior half; all dorsal striae complete, coarsely impressed; elytral interstriae irregularly but distinctly punctate, intervals with 20–25 coarse punctures; prosternal keel deeply emarginate at base, with carinal striae slightly abbreviated anteriorly, united; prosternal lobe slightly deflexed, marginal stria present only at middle; mesoventrite with marginal stria weakly crenulate, mesometaventral stria crenulate, arched forward to basal third of mesoventral disk; postmesocoxal stria recurved anterad around mesocoxa, ending short of mesepimeron; lateral metaventral stria rather weakly crenulate, ending short of metacoxa; metaventral disk with secondary punctures slightly smaller and sparser anteromedially; metepisternal punctures coalesced into a short stria; lateral stria of 1st abdominal ventrite fragmentary along inner edge of metacoxa, curving laterad behind metacoxa; secondary punctures of median portion of 1st abdominal ventrite smaller and sparser in posterior half, with slightly oblique punctures toward sides behind metacoxa; punctures along posterior



Map 5. Specimen records of *Crenulister* spp.

margins of ventrites 1–2 transversely elongate but separate, those of ventrites 3–4 intermittently coalesced into marginal strioles; protibia 5–6-spined, with marginal dentation weakly developed; meso- and metatibia with thin, elongate spines, mainly along apical half of margin; propygidium with secondary punctures shallow but rather large, uniformly separated by 1–1.5× their diameters; propygidial gland openings borne on faint tubercles in anterolateral corners; propygidial strioles absent; pygidium with secondary punctures more conspicuous at sides and apex; pygidial gland openings present near sides about one-fourth from base; pygidial margin with fragmentary striae along apical two-thirds, not complete around apex. Male (Figs 25E-G): accessory sclerites absent; T8 with ventrolateral apodemes strongly narrowed beneath; S8 with halves meeting along short inner margins apices moderately strongly divergent, with about 5 strong setae; T9 with apices narrow, obliquely truncate; T10 weakly desclerotized along midline; S9 slightly widened to weakly emarginate base, apex rather deeply emarginate; tegmen with sides very weakly rounded, widest toward apex, apices rather narrow and slightly separated, medioventral process produced beneath about one-fourth from base; median lobe nearly one-half tegmen length, basal piece about one-third tegmen length.

Remarks. This species is the darkest of the smaller species. Its coloration in combination with complete elytral striation, conspicuous interstrial punctation (Fig. 18C), and fragmentary marginal pygidial stria will fairly readily distinguish it from other species in the genus. The single specimen excluded from the type series is slightly larger and more coarsely punctate, especially ventrally, than the other specimens, despite being collected in the same locality (and even same dates).

Etymology. This species' name refers to its relatively dark coloration.

***Crenulister impar* sp. n.**
http://zoobank.org/2DFA0072-A31C-48B5-8871-DCC23E0B38FB
http://species-id.net/wiki/Crenulister_impar
Figs 23A, 24, Map 5

Type locality. FRENCH GUIANA: Belvèdére de Saül [3.01°N, 53.21°W].

Type material. Holotype male: "**GUYANE FRANÇAISE**: Bélvédère de Saúl, point de vue. 3°1'22"N. 53°12'34"W. Piège vitre, 2.ix.2011. SEAG leg." / "Caterino/ Tishechkin Exosternini Voucher EXO-03016" (MNHN). **Paratypes** (12): 1: same locality as type, 20.xii.2010 (CHND); 4: **FRENCH GUIANA:** Rés. Natur. des Nouragues, Camp Inselberg, 4°05'N, 52°41'W, 30.ix.2010, FIT, SEAG (MNHN, CHND, FMNH, MSCC), 1: 20.viii.2010 (LSAM), 1: 22.ix.2010 (CHND), 1: 9.xi.2010 (CHND), 1: 25.i.2011 (CHND), 1: 8.x.2010 (CHND); 1: Matoury, 41.5 km SSW on Hwy N2, 4°37'22"N, 52°22'35"W, 50m, 26-28.v.1997, J. Ashe & R. Brooks, FIT (SEMC). 1: **GUYANA: Cuyuni-Mazaruni:** Kartabo, 24.ix.1920, W.M.Mann (USNM).

Other material. 1: **PERU: Madre de Dios:** Tambopata, Reserva Cuzco Amazonico, 15km NE Pto. Maldonado, 12°33'S, 69°03'W, 200m, 22.vi.1989, FIT, J. Ashe & R. Leschen (SEMC), 1: 24.vi.1989 (SEMC); 1: **Loreto:** 1.5km N Teniente Lopez, 2°35.66'S, 76°06.92'W, 210–240m, 20.vii.1993, FIT, R. Leschen (SEMC); 1: **Cusco:** Villa Carmen Field Station, 12.8925°S, 71.4192°W, 24-26.v.2011, FIT (SEMC). 1: **BRAZIL: Mato Grosso**, Cotriguaçu, Fazenda São Nicolau, Matinha, 9°50.3'S, 58°15.05'W, xii.2009, FIT, F.Z. Vaz-de-Mello (CEMT). 1: **ECUADOR: Orellana:** Tiputini Biodiversity Station, 0.6376°S, 76.1499°W, 4–9.vi.2011, FIT, M.S. Caterino & A.K. Tishechkin, DNA extraction voucher MSC-2129 (MSCC).

Diagnostic description. Length: 1.8–2.2 mm, width: 1.6–2.0 mm; as for generic description with the following diagnostic characters: body rufescent to rufobrunneus, elongate ovoid, subdepressed; frontal stria fine, usually complete, rarely narrowly interrupted, frontal disk moderately depressed, with fine but relatively dense punctation consisting of ground punctation and barely larger secondary punctation; epistoma with lateral ridges delimiting median depression bearing weak lateral striae basally; labrum about 4× wider than long, apical margin weakly emarginate; pronotum with gland opening track reaching approximately to midline, with 3-4 openings along its length; pronotal sides with crenulate, slightly elevated lateral submarginal stria; pronotal disk with small secondary punctures conspicuous in basal half, as well as at sides,

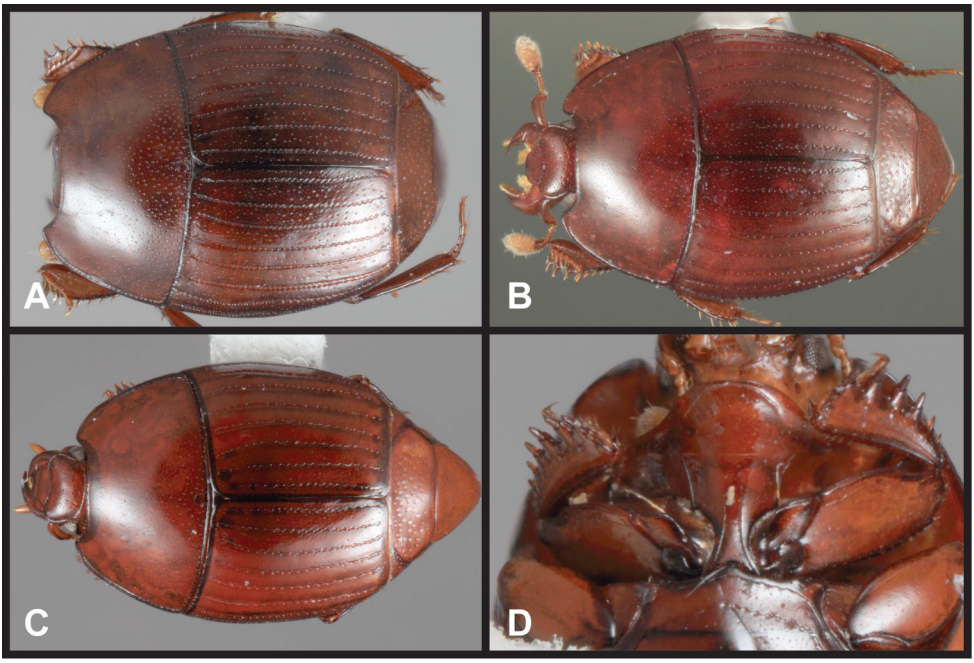


Figure 23. *Crenulister* spp. **A** *Crenulister impar*, dorsal habitus **B** *Crenulister explanatus*, dorsal habitus **C** *Crenulister dentatus*, dorsal habitus **D** *Crenulister dentatus*, prosternum and protibiae.

anteromedial portion of disk with only fine ground punctation; weak prescutellar impression present; elytron with one complete, crenulate epipleural stria rather distant from margin, especially posteriorly, all dorsal striae complete, shallowly but coarsely impressed; all elytral interstriae sparsely, irregularly punctate, with 18-30 secondary punctures, generally more in the 5th-sutural interval; prosternal keel deeply emarginate at base, carinal striae complete, narrowly united anteriorly; prosternal lobe slightly deflexed, marginal stria present only at middle; mesoventrite with marginal stria fine to weakly crenulate, mesometaventral stria crenulate, angulately arched forward to basal third of mesoventral disk; postmesocoxal stria recurved anterad around mesocoxa, ending short of mesepimeron; lateral metaventral stria crenulate, ending short of metacoxa; metaventral disk punctate throughout, secondary punctures slightly smaller and sparser anteromedially; metepisternal punctures coalesced into distinct stria; lateral stria of 1st abdominal ventrite present along inner edge of metacoxa, curving laterad behind metacoxa, occasionally interrupted; secondary punctures of median portion of 1st abdominal ventrite larger and denser in basal half, with slightly oblique punctures toward sides behind metacoxa; punctures along posterior margins of ventrites 1-4 transversely elongate, intermittently coalesced into marginal strioles; protibia ~6-7-spined, with marginal dentation weak; meso- and metatibia with 3-5 thin, elongate spines, mainly along apical half of margin; propygidium with secondary punctures shallow but rather large, fairly uniformly separated by about their diameters throughout; pro-

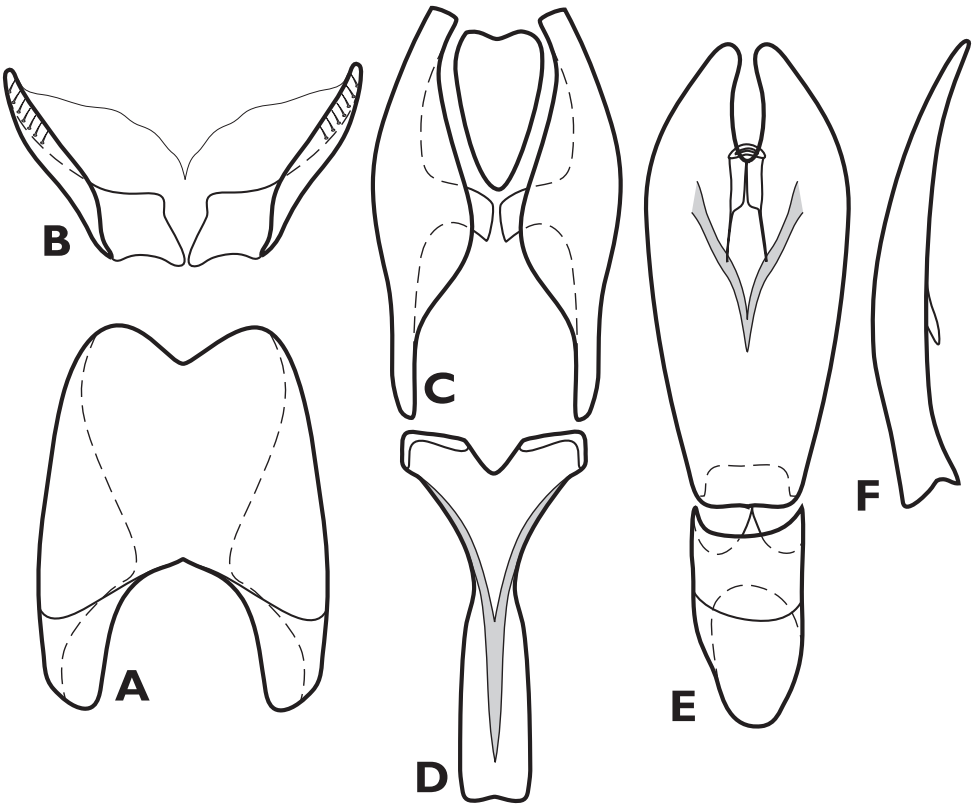


Figure 24. *Crenulister impar*, male genitalia. **A** 8th tergite **B** 8th sternite **C** 9th and 10th tergites **D** 9th sternite **E** Aedeagus, dorsal view **F** Aedeagus, lateral view.

pygidial gland openings very faintly tuberculate in anterolateral corners, propygidial strioles absent; pygidium with sparse secondary punctation mainly along sides; pygidial gland openings evident near sides about one-fourth from base; pygidial margin with striae along most of apical two-thirds, usually interrupted at apex. Male (Fig. 24): accessory sclerites absent; T8 with ventrolateral apodemes strongly narrowed beneath; S8 short with halves meeting only at basal corner, inner margins short and strongly divergent, with 6-8 strong setae toward apex; T9 with apices obliquely truncate; T10 weakly emarginate at apex; S9 quadrate at base, apex emarginate; tegmen widest in apical third, apex more or less rounded, apices slightly separated, medioventral process produced beneath about one-third from base; median lobe short, basal piece about one-third tegmen length.

Remarks. This species is somewhat difficult to characterize, in part because there's, relatively more material than for most, from a wider area, and individual variation is accordingly more evident. Among the smaller, more rufescent species of the genus, the complete elytral striae (Fig. 23A), presence of distinct secondary punctures on most of the basal half of the pronotal disk, the pronotal gland track reaching to the pronotal

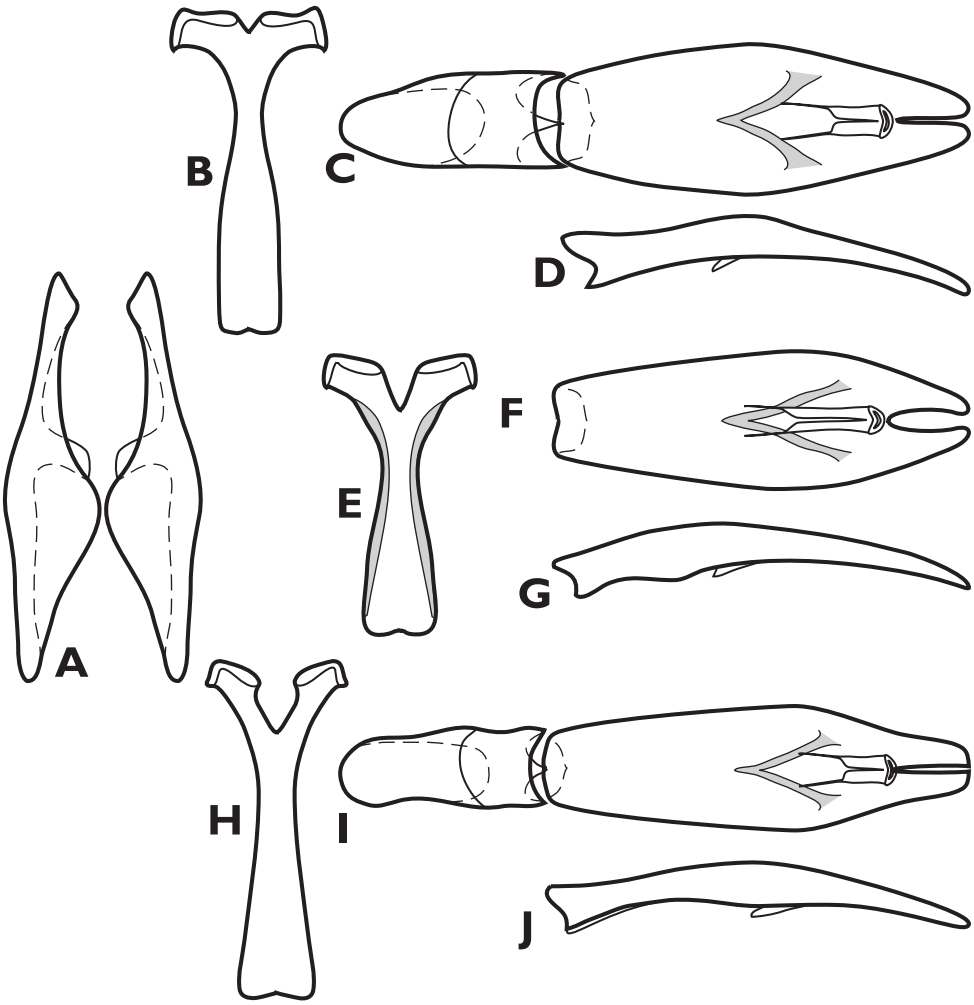


Figure 25. *Crenulister* spp., male genitalia. **A** *Crenulister dentatus*, 9th tergite **B** *Crenulister explanatus*, 9th sternite **C** *Crenulister explanatus*, aedeagus, dorsal view **D** *Crenulister explanatus*, aedeagus, lateral view **E** *Crenulister umbrosus*, 9th sternite **F** *Crenulister umbrosus*, aedeagus, dorsal view **G** *Crenulister umbrosus*, aedeagus, lateral view **H** *Crenulister dentatus*, 9th sternite **I** *Crenulister dentatus*, aedeagus, dorsal view **J** *Crenulister dentatus*, aedeagus, lateral view.

midpoint, and the presence of (usually) well developed marginal pygidial striae will generally distinguish it. The apically widened aedeagus (Fig. 24E) is distinctive, and consistent among males examined. However, we restrict the type locality to the Guianas due to some uncertainty about species assignment of all populations. Additional material from the southern and Andean parts of the range may reveal more consistent patterns of external variation and justify further splitting.

Etymology. This species' name refers to the 'unequal' distribution of pronotal punctures, distinctly increasing in density posterad.

***Crenulister explanatus* sp. n.**
http://zoobank.org/4E3D496A-4682-430E-873A-EE533BD83C3E
http://species-id.net/wiki/Crenulister_explanatus
Figs 23B, 25B–D, Map 5

Type locality. ECUADOR: Orellana, Yasuní Research Station [0.674°S, 76.398°W].

Type material. Holotype male: "**ECUADOR:** Napo, mid.Rio Tiputini, Yasuní Res. Stn. 0°40.5'S, 76°24'W, FIT#1, 23-30 Jun 1999. AKT#032, C.Carlton & A.Tishechkin" / "LSAM0045737" (FMNH).

Other material. 1: same locality as type, 26.vii–4.viii.1999 (LSAM); 1: **PERU: Junin**, ~16km NW Satipo, Rio Venado, 11°11.677'S, 74°46.137'W, 1150m, 3-8.iii.2010, A.V. Petrov (LSAM).

Diagnostic description. Length: 1.8–2.1 mm, width: 1.6–1.9 mm; as for generic description with the following diagnostic characters: body rufescent, elongate ovoid, subdepressed; frontal stria fine, complete, frontal disk moderately depressed, frontal stria fine, complete, disk with few rather conspicuous secondary punctures against fine background punctation; epistoma with rather well-developed lateral and anterior marginal striae; labrum about 4× wider than long, apical margin subtruncate; pronotum with single median gland opening about one-third from anterior margin; pronotal sides with fine, slightly raised lateral submarginal stria; secondary punctures of pronotal disk small, sparse, slightly larger and denser in basal third; prescutellar impression small but distinct; elytron with single, complete, crenulate epipleural stria; subhumeral and dorsal striae 1-4 complete, 4th weakly arched to the sutural at base, 5th stria barely abbreviated basally, sutural stria largely obsolete in basal fourth, may be represented by few serial punctures, all striae shallowly but coarsely impressed; inner elytral interstriae irregularly, sparsely punctate, with 8-10 punctures, fewer in outer intervals; prosternal keel acutely but not too deeply emarginate at base, with carinal striae narrowly united anteriorly; prosternal lobe weakly deflexed, marginal stria present only at middle; mesoventrite with marginal stria fine, mesometaventral stria crenulate, subangulate to basal third of mesoventrite; postmesocoxal stria recurved anterad around mesocoxa, reaching mesepimeron; lateral metaventral stria weakly crenulate, abbreviated in front of metacoxa; metaventral disk with secondary punctures smaller and sparser anteromedially; metepisternal punctures separate, not coalesced into a stria; lateral stria of 1st abdominal ventrite weakly impressed along inner edge of metacoxa; secondary punctures of median portion of 1st abdominal ventrite becoming obsolete in posterior half, with slightly oblique punctures toward sides behind metacoxa; punctures along posterior margins of ventrites 1-4 transversely elongate, intermittently coalesced into marginal strioles; protibia 5-6 spined, marginal dentation weakly developed; meso- and metatibia with 4-5 thin, elongate spines, mainly along apical half of margin; propygidium with secondary punctures shallow but rather large, uniformly separated by about half their diameters in basal half, sparser in posterior half; propygidial gland openings present in anterolateral corners; propygidial strioles absent; pygidium with few small secondary punctures, more conspicuous at sides; pygidial gland openings not evident; pygidial

margin lacking striae. Male (Fig. 25B–D): accessory sclerites weakly sclerotized, present; T8 with ventrolateral apodemes rather broad beneath, narrowing to apex; S8 with halves meeting only at basal corner, inner margins short and strongly divergent, with about 3 strong setae toward apex; T9 with apices subacute; T10 apically entire; S9 weakly emarginate, quadrate at base, apex narrowly and shallowly emarginate; tegmen widest near midpoint, apices only very narrowly separated, medioventral process produced beneath about one-third from base; median lobe about one-third tegmen length, basal piece nearly half tegmen length.

Remarks. This species is closely related to the following, with simple pronotal gland openings, the elytral interstrial punctures largely restricted to the inner intervals, the postmesocoxal stria reaching the mesepimeron, and the metepisternum nonstriate. This species does not have the protibial margin appearing as strongly dentate, and has the sutural stria basally obsolete. The three specimens we assign to this species in fact vary considerably in size, coloration, and sculpturing, and we exclude two of them (females) from the type series due to associated uncertainty, regardless the fact that one is from the same locality as the holotype.

Etymology. This species' name refers to the slightly explanate lateral pronotal margins (Fig. 23B).

***Crenulister dentatus* sp. n.**
http://zoobank.org/87F03327-D81B-4ED0-9539-943F66D08A2B
http://species-id.net/wiki/Crenulister_dentatus
Figs 23C–D, 25H–J, Map 5

Type locality. GUYANA: Potaro-Siparuni (Region 8), Iwokrama Forest [4.2844°N, 58.5097°W].

Type material. Holotype male: "GUYANA: Region 8, Iwokrama Forest, Kabocalli Field Stn., 60m, 4°17'4"N, 58°30'35"W, 3–5 JUN 2001 R. Brooks,Z.Falin GUY1BF01 146 ex: flight intercept trap" / "SM0573091 KUNHM-ENT [barcode label]" (SEMC).

Other material. 1: **BRAZIL: Mato Grosso:** Cotriguaçu, Fazenda São Nicolau, Prainha, 9°51.6'S, 58°12.9'W, x.2009 (CEMT); 1: **PERU: Loreto:** Campamento San Jacinto, 2°18'44.85"S, 75°51'46"W, 175-215m, 3-12.vii.1993, R. Leschen, FIT (SEMC).

Diagnostic description. Length: 1.9–2.0 mm, width: 1.6–1.8 mm; as for generic description with the following diagnostic characters: body rufescent, elongate ovoid, subdepressed; frontal stria well impressed, complete, frontal disk moderately depressed, with few rather conspicuous secondary punctures against fine background punctation; epistoma with lateral ridges delimiting median depression bearing very weak fragments of lateral striae; labrum about 4× wider than long, apical margin weakly emarginate; pronotum with single median gland opening about one-third from anterior margin; pronotal sides with weakly crenulate, slightly raised lateral

submarginal stria; secondary punctures of pronotal disk small, sparse, slightly larger and denser in basal half; weak prescutellar impression present; elytron with single complete crenulate epipleural stria; all dorsal striae complete, coarsely impressed; elytral interstriae irregularly, sparsely punctate, inner intervals with 8–10 punctures, fewer in outer intervals; prosternal keel deeply emarginate at base, with carinal striae slightly abbreviated, separate anteriorly; prosternal lobe deflexed, marginal stria present only at middle; mesoventrite with marginal stria weakly crenulate, mesometaventral stria crenulate, subangulate to near mesoventral midpoint; postmesocoxal stria recurved anterad around mesocoxa, reaching mesepimeron; lateral metaventral stria rather weakly crenulate, extending nearly to middle of metacoxa; metaventral disk with secondary punctures distinctly smaller and sparser anteromedially; metepisternal punctures separate, not coalesced into a stria; lateral stria of 1st abdominal ventrite weakly impressed along inner edge of metacoxa; secondary punctures of median portion of 1st abdominal ventrite smaller and sparser in posterior half, with slightly oblique punctures toward sides behind metacoxa; punctures along posterior margins of ventrites 1–2 transversely elongate but separate, those of ventrites 3–4 intermittently coalesced into marginal strioles; protibia 5–6-spined, with marginal dentation rather well-developed; meso- and metatibia with 4–5 thin, elongate spines, on metatibia mainly along apical half of margin; propygidium with secondary punctures shallow but rather large, uniformly separated by less than half their diameters in basal half, rather discretely obsolete in posterior half; propygidial gland openings present in anterolateral corners but difficult to distinguish from secondary punctures; propygidial strioles absent; pygidium largely lacking secondary punctures; pygidial gland openings not evident; pygidial margin lacking striae. Male (Fig. 25A, H–J): accessory sclerites absent; T8 with ventrolateral apodemes broad, widely separated ventrally; S8 with halves meeting only at basal corner, inner margins short and strongly divergent, apices very narrow, without setae or membranous velum; T9 with apices subacute; T10 deeply, narrowly emarginate at apex; S9 widened to weakly emarginate base, apex narrowly and rather deeply emarginate; tegmen widest just beyond middle, narrowed to apex, apices barely separated, medioventral process produced beneath near midpoint; median lobe about one-third tegmen length, basal piece about half tegmen length.

Remarks. This species is defined by the relatively well developed protibial marginal teeth (Fig. 23D), with deep emarginations between spine insertions. In addition to this character, the species lacks a marginal pygidial stria and secondary pygidial punctures. Its pronotal gland openings are not multiplied, exhibiting only single openings on each side about one-third the pronotal length from the anterior margin, and the sub-basal pygidial gland openings appear to be absent (this is difficult to ascertain). The three specimens attributed here agree in all these characters. However, they also exhibit considerable differences, with the two specimens excluded from the type series showing finer punctation in general, especially more or less lacking elytral interstrial punctures. The Peruvian individual is further distinguished by a rather distinctly explanate pronotal margin. However, as the type is the only male among them, we tentatively

lump them together for the present. This will clearly need to be revisited if and when additional material becomes available.

Etymology. This species is named for its distinctively dentate protibiae.

***Crenulister simplex* sp. n.**
http://zoobank.org/66B616D7-522B-4429-9821-8A956025C163
http://species-id.net/wiki/Crenulister_simplex
Figs 26–27, Map 5

Type locality. BOLIVIA: Cochabamba, Valle de Sajta Biological Station [17.1092°S, 64.7978°W].

Type material. Holotype male: "BOLIVIA: Cochabamba, Cochabamba, 67.5km NE, Est. Biol. Valle del Sajita[sic], Univ. de San Simon, 300m, 17°6'33"S, 64°47'52"W, 9-13 FEB 1999, R.Hanley, BOL1H99 078, ex. flight intercept trap" / "SM0159345, KUNHM-ENT [barcode label]" (SEMC). **Paratype** (1): **BOLIVIA: Santa Cruz**, 4-5km SSE Buena Vista, Hotel Flora y Fauna, 17°29'S, 63°33'W, FIT, 29.iv-6.v.2004, A.R. Cline (LSAM).

Diagnostic description. Length: 1.7–1.8 mm, width: 1.5–1.6 mm; as for generic description with the following diagnostic characters: body rufescent, elongate ovoid, subdepressed; frontal stria fine, complete or narrowly interrupted, frontal disk moderately depressed, with relatively dense punctation consisting of ground punctation and barely larger secondary punctation; epistoma with lateral ridges delimiting median depression bearing weak lateral striae basally; labrum about 4× wider than long, apical margin weakly emarginate; pronotum with gland opening track not quite reaching midline, with 2 openings lying within the impunctate track; pronotal sides weakly explanate, particularly in front; lateral submarginal stria fine, subcarinate, merging with margin just behind anterior corner; pronotal disk with secondary punctures very small and sparse, most evident along basal margin, almost indistinguishable from background punctation elsewhere; weak prescutellar impression present; elytron with one complete, crenulate epipleural stria rather distant from margin, especially posteriorly, both subhumeral striae and dorsal striae 1–4 complete, 5th and sutural striae obsolete in basal third, striae shallowly but coarsely impressed; elytral intervals very sparsely, irregularly punctate, inner intervals with 2–6 very small secondary punctures; prosternal keel deeply emarginate at base, carinal striae slightly abbreviated, divergent anteriorly, not connected; prosternal lobe slightly deflexed, marginal stria present only at middle; mesoventrite with marginal stria fine, not crenulate, mesometaventral stria crenulate, angulately arched forward just short of mesoventral midpoint; postmesocoxal stria recurved anterad around mesocoxa to mesepimeron; lateral metaventral stria rather fine, only weakly crenulate, ending short of metacoxa; metaventral disk with secondary punctures almost obsolete in anterior half and along midline, coarser posterolaterally; metepisternal punctures coalesced into a short stria; lateral stria of 1st abdominal ventrite finely impressed, oblique along inner edge of metacoxa, curving

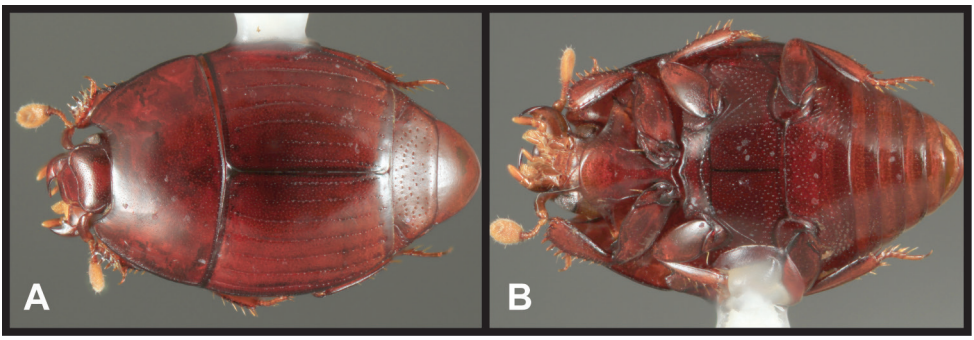


Figure 26. *Crenulister simplex*. **A** Dorsal habitus **B** Ventral habitus.

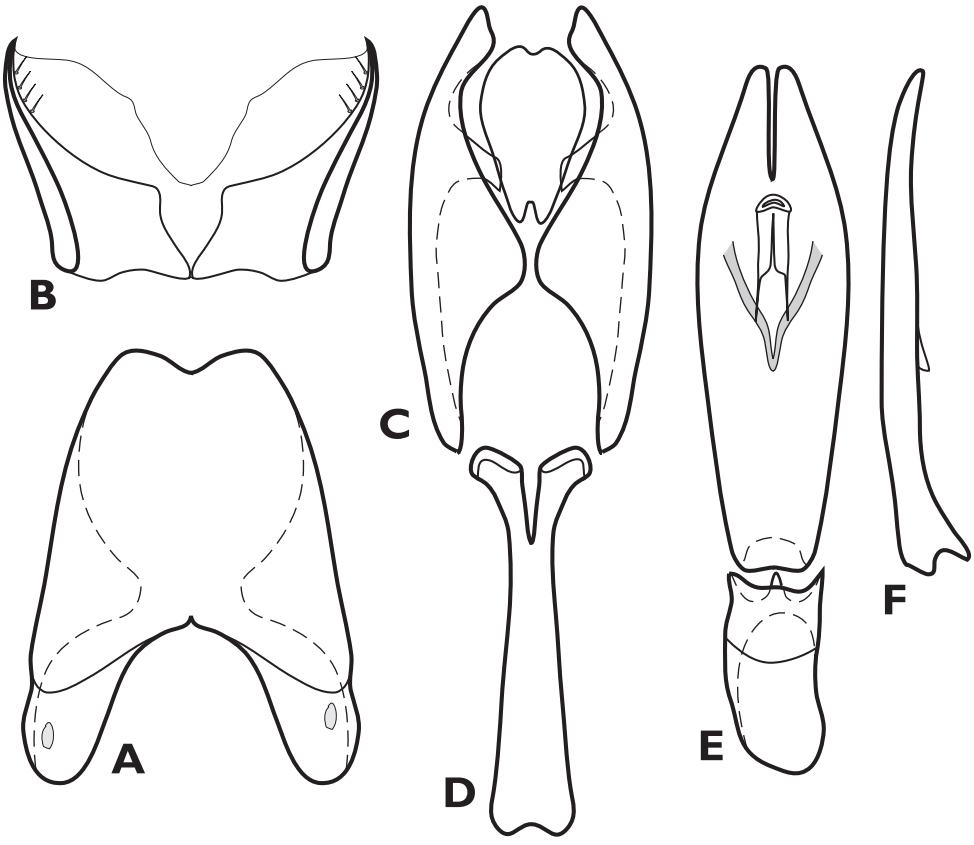


Figure 27. *Crenulister simplex*, male genitalia. **A** 8th tergite **B** 8th sternite **C** 9th and 10th tergites **D** 9th sternite **E** Aedeagus, dorsal view **F** Aedeagus, lateral view.

laterad behind metacoxa; secondary punctures of median portion of 1st abdominal ventrite largely restricted to basal third, with slightly oblique punctures toward sides behind metacoxa; punctures along posterior margins of ventrites 1–4 transversely elongate, intermittently coalesced into marginal strioles; protibia ~6-spined, with marginal

dentation weakly developed; meso- and metatibia with thin, elongate spines, mainly along apical half of margin; propygidium with secondary punctures shallow but rather large, separated by 1–2× their diameters in basal half, smaller and sparser apically; propygidial gland openings present just mediad lateral corners, nearly one-half behind anterior margin, propygidial strioles absent; pygidium lacking secondary punctation; pygidial gland openings slightly tuberculate, evident near sides about one-fourth from base; pygidial margin with striae along most of apical two-thirds, but interrupted at apex. Male (Fig. 27): accessory sclerites reduced, vestigial; T8 with ventrolateral apodemes slightly narrowed ventrally; S8 with halves meeting only at basal corner, inner margins short and strongly divergent, apices narrow, with three strong setae; T9 with apices subacute; T10 apex entire; S9 widened to bulbous, emarginate base, apex narrowly and deeply emarginate; tegmen widening slightly from base just beyond middle, narrowed to apex, apices narrowly separated, medioventral process produced beneath about one-third from base; median lobe about one-fourth tegmen length, basal piece about one-third tegmen length.

Remarks. The basally obsolete 5th and sutural striae (Fig. 26A) in this species are largely adequate to distinguish it. The only other species in the genus with basally weakened striae (*C. explanatus*) has the pronotum and elytral interstriae much more conspicuously punctate. Both are very weakly and finely punctate in this species.

Etymology. This species' name refers to its relatively impunctate, simple external sculpturing.

Acknowledgments

We are very grateful to colleagues who provided specimens and data, including Fernando Vaz-de-Mello (CEMT), Robert Anderson and François Genier (CMNC), Margaret Thayer, Al Newton, and James Boone (FMNH), Chris Carlton and Victoria Bayless (LSAM), Thierry Deuve and Azadeh Taghavian (MNHN), Zack Falin and Andrew Short (SEMC), Lúcia Massutti de Almeida, Paschoal Grossi, and Fernando Leivas (UFPR), Gary Hevel, David Furth, and Terry Erwin (USNM), Stéphane Brûlé, Pierre-Henri Dalens, Eddy Poirier and Julien Touroult (SEAG - Société entomologique Antilles-Guyane), Alexander Petrov, and Nicolas Dégallier. For assistance with fieldwork and permits we thank Kelly Swing, Hernan Alvarez and the staff of the Tiputini Biodiversity Station, Carlos Flechtmann and his students (Silvia Tanabe, Julius Cerqueira, and Bruno Ferreira), Lúcia Massutti de Almeida and her students (Fernando Leivas, Daniel Moura, Kleber Mise, and Paschoal Grossi) and Fernando Vaz-de-Mello. We are grateful for the laboratory assistance of Erik Shafer and Hunter McCrea. We appreciate the reviews by Tomáš Lackner and Peter Kovarik that greatly improved this paper. This project was supported by National Science Foundation grant DEB 0949790; partial support came from the Louisiana State University Agricultural Center and NSF grants DEB 9815394 and DEB 0516311, as well as the Schlinger Foundation.

References

Caterino MS, Tishechkin AK, Dégallier N (2012) A revision of the genus *Mecistostethus* Marseul (Coleoptera: Histeridae). ZooKeys 213: 63–78. doi: 10.3897/zookeys.213.3552

Caterino MS, Tishechkin AK (2013a) A systematic revision of the genus *Operclipygus* Marseul. ZooKeys 271: 1–401. doi: 10.3897/zookeys.271.4062

Caterino MS, Tishechkin AK (2013b) A systematic revision of the genus *Baconia* Lewis. ZooKeys 343: 1–297. doi: 10.3897/zookeys.343.5744

Caterino MS, Tishechkin AK (in press) Phylogeny and generic limits in New World Exosternini (Coleoptera: Histeridae: Histerinae). Systematic Entomology.

Dégallier N, Mazur S, Tishechkin AK, Caterino MS (2012) A revision of the genus *Kaszabister* Mazur. ZooKeys 199: 71–89. doi: 10.3897/zookeys.199.3245

Helava JVT, Howden HF, Ritchie AJ (1985) A review of the New World genera of the myrmecophilous and termitophilous subfamily Hetaeriinae (Coleoptera: Histeridae). Sociobiology 10(2): 127–382.

Kanaar P (1997) Revision of the genus *Paratropus* Gerstaecker. Zoologische Verhandelingen 315: 1–185.

Lawrence JF, Ślipiński A, Seago AE, Thayer MK, Newton AF, Marvaldi AE (2011) Phylogeny of the Coleoptera based on morphological characters of adults and larvae. Annales Zoologici 61(1): 1–217. doi: 10.3161/000345411X576725

LeConte JE (1845) A monography of the North American Histeroides. Boston Journal of Natural History 5: 32–86.

Ôhara M (1994) A revision of the superfamily Histeroidea of Japan (Coleoptera). Insecta Matsumurana, New Series 51: 1–283.

Wenzel RL, Dybas HS (1941) New and little known Neotropical Histeridae (Coleoptera). Fieldiana, Zoology 22(7): 433–472.

ZooKeys 381: 79–111 (2014)
doi: 10.3897/zookeys.381.6445
www.zookeys.org

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

A cornucopia of cryptic species - a DNA barcode analysis of the gobiid fish genus *Trimma* (Percomorpha, Gobiiformes)

Richard Winterbottom[1,2], Robert H. Hanner[3], Mary Burridge[1], Margaret Zur[1]

1 *Department of Natural History, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, M5S 2C6, Canada* **2** *Department of Ecology & Evolutionary Biology, University of Toronto, 25 Willcocks Street, Toronto, Ontario, M5S 3B2, Canada* **3** *Centre for Biodiversity Genomics, University of Guelph, Guelph, Ontario, N1G 2W1, Canada*

Corresponding author: *Richard Winterbottom* (rickw@rom.on.ca)

Academic editor: *N. Bogutskaya* | Received 16 October 2013 | Accepted 23 January 2014 | Published 18 February 2014

Citation: Winterbottom R, Hanner RH, Burridge M, Zur M (2014) A cornucopia of cryptic species - a DNA barcode analysis of the gobiid fish genus *Trimma* (Percomorpha, Gobiiformes). ZooKeys 381: 79–111. doi: 10.3897/zookeys.381.6445

Abstract

A genetic analysis of partial mitochondrial 5' cytochrome *c* oxidase I gene (DNA barcode) sequences of 473 specimens assigned to 52 morphological species (including four known, but not formally named, species) of the gobiid genus *Trimma* revealed the presence of 94 genetic lineages. Each lineage was separated by > 2% sequence divergence. Thus there were an additional 42 haplogroups recognizable as provisional candidate species given that a value of > 2% difference is typical of different species of fishes. Such a high degree of apparently different cryptic species is, in our experience, virtually unprecedented among vertebrates. These results have precipitated further morphological research in a few cases, which has uncovered subtle differences independently corroborating the genetic results. However, such efforts are limited by the dearth of traditional systematists available to undertake the necessary time-consuming, and highly detailed, morphological research. In some cases, the genetic results we present are consistent with, and confirm, minor taxonomic distinctions based on morphology and/or colour pattern. In other instances, what had been recognized as a single species consists of several genetic lineages - up to eight in, for example, what we have identified based on morphology as *Trimma okinawae*. The increase from 52 to 94 potential species in our sampling raises the predicted total number of species in this genus from about 110 to nearly 200 (versus the 73 valid described species currently recognized).

Keywords

Trimma, gobies, mtDNA, COI, cryptic species, Indo-West Pacific ocean

Introduction

Descriptions of new species of the small (average 2 cm SL), often colourful, Indo-Pacific pygmy gobies of the genus *Trimma* Jordan & Seale, have exploded during the last 30 years or so – from 17 species recognized as being valid prior to Winterbottom's (1984) publication to the 73 valid species recognized today. Numerous additional species of these coral reef inhabitants have been recognized as morphologically distinct from those already described, and await publication. One of us (RW) estimates the current number of known, morphologically distinctive, species to be about 110 (approximately 37 undescribed).

Previous studies of the 5' mitochondrial cytochrome c oxidase subunit I (COI; the animal "DNA Barcode") gene in other goby genera have frequently uncovered or documented hidden diversity (e.g. Baldwin et al. 2009, Tornabene et al. 2010, Victor 2010). Tornabene et al. (2010) studied western Atlantic members of *Bathygobius* Bleeker. At the time of their study, there were three recognized species, but matters were complicated by numerous proposed subspecies, and many nominal species. Nonetheless, their study revealed the presence of eight discreet genetic lineages, of which at least two do not appear to have available names (one of two lineages of *B. soporator* (Valenciennes), 2.9% difference; and one of two lineages of *B. geminatus* Tornabene et al., 2.1% difference). The mean interspecific genetic differences between the lineages in the western Atlantic varied between 2.1–17.2% (the latter value between *B. antilliensis* Tornabene et al. and *B. lacertus* (Poey)). Similarly, a study by Baldwin et al. (2009) on the Western Atlantic and Caribbean species of *Coryphopterus* Gill revealed 12 genetic lineages for which 11 species names were available. One described species (*C. punctipectophorus* Springer) was not available for their study, and the single Curacao specimen that forms a separate lineage from *C. alloides* Böhlke & Robins, is under further study and has not yet been formally named. The mean differences between lineages recorded by Baldwin et al. (2009) were generally greater than those recorded by Tornabene et al. (2010) for *Bathygobius*, ranging from 7.1% (*C. hyalinus* Böhlke & Robins vs. *C. personatus* (Jordan & Thompson)) to 27.9% (*C. glaucofraenum* Gill vs. *C. kuna* Victor). A similar situation at a smaller scale has been documented by Victor (2010), who found that *Elacatinus multifasciatus* (Steindachner) contained three genetic lineages, two of which he described as new. Both of these differed by about 11% from specimens from the type locality of *E. multifasciatus*, but only *E. rubrigenis* Victor exhibited a trenchant morphological difference. The other new species, *E. panamensis* Victor, is very similar in external appearance to *E. multifasciatus*, yet is separated from *E. rubrigenis* by only 3% of the COI gene, suggesting a lack of congruence between genetic and morphological divergence in this group. In earlier studies of *Elacatinus*, Taylor and Hellberg (2005, 2006) suggested that, for this genus of 34 currently recognized species (Froese and Pauly 2013), speciation was consistent with a model of regional but recurrent adaptive radiations driven by a combination of colouration and ecological differentiation. However, we note that Hsu et al. (2011) provide evidence that, at least in *Siganus* Forsskål, 1775, species defined by colour differences do not necessarily equate with genetic lineages.

Such cryptic diversity among small reef fishes is not, apparently, confined to gobies. Baldwin et al. (2011) described seven new species of the labrisomid *Starksia* Jordan & Evermann following a barcode analysis of 13 of the currently recognized Caribbean species. Their Neighbour-Joining network (Baldwin et al. 2011, fig. 1) shows numerous other apparently distinct genetic lineages that may well represent discreet species among their samples, although most of these had only a few available specimens. In a more wide-ranging biogeographical study of fishes, Hubert et al. (2012) compared 141 apparent con-specifics between the Indian and Pacific oceans. They found no difference in COI in 44% of the species, but uncovered two (47% with genetic differences ranging from 1–12%) or more (9% with distances varying between 3–22%) haplogroups in the other con-specifics. In a study of 207 marine fishes from Australian waters, Ward et al. (2005) reported an average within species variation of 0.4% and a between species variation of 9.9%.

In order to document the extent of cryptic diversity in *Trimma*, we performed a barcode analysis based on 473 specimens of this genus, most of them from the fish tissue collections of the Royal Ontario Museum.

Materials and methods

The ROM specimens used in our analysis (catalogue number prefixed by "T") were collected using overdoses of various anaesthetics (e.g. clove oil, quinaldine), and the whole fish was placed in a vial containing either a saturated salt solution (Seutin et al. 1990; specimens collected prior to 1998) or 95% ethyl alcohol (after 1998). These specimens were subsampled for genetic analysis. In collections made prior to 2006, the samples retained for genetic analysis were seldom photographed immediately after collection, although photographs of a specimen from the same lot as the tissue specimen were frequently taken. In the collections made in 2011, all tissue specimens were photographed. Values given in the tables are rounded to the nearest decimal point. We use the term "variance" to denote the percentage of sequence divergence within a group. For undescribed but known species, we use a system of numbering the species prefixed by 'RW'. These numbers are unique and consistent for a given undescribed species pending its formal description. The system allows the specimens to be catalogued in museum collections, and obviates the problems frequently found in checklists and books on Indo-Pacific fishes where species are simply numbered sequentially, with the same number nearly always denoting different species between different, and sometimes the same, author(s).

Voucher specimen information and digital images (where applicable) were deposited in the Barcode Of Life Database (BOLD, http://www.barcodedsystems.org; Ratnasingham and Hebert 2007) following recommendations of the FISH-BOL campaign (Ward et al. 2009) and related collaborators protocol (Steinke and Hanner 2011) in a publicly accessible data project (titled "Trimma12" ; DOI: doi: 10.5883/DATASET-TRIMMA12).

DNA was extracted using a Qiagen DNeasy Blood & Tissue Kit (QIAGEN) following the manufacturer's instructions with some exceptions: after adding AW2, spin columns were dried through a final centrifugation at 17,000× g for 5 minutes; sample DNA was eluted with 50 µL of AE buffer and centrifuged at 6,000× g for 1 minute, and the same 50 µL of AE buffer was then re-eluted with a final centrifugation at 6,000× g for 1 minute in order to increase the DNA concentration. Each 12.5 µL PCR reaction consisted of 2 µL of template DNA, 6.25 µL 10% trehalose, 2 µL ddH2O, 0.625 µL MgCl2 [50 mM], 0.0625 µL dNTPs [10 mM], 0.06 µL Platinum Taq (Invitrogen), 0.10 µL [0.01 mM] each of the universal fish COI cocktail primers C_FishF1t1 and C_FishR1t1 (Ivanova et al. 2007) and 1.25 µL 10X PCR buffer (Invitrogen). PCR thermocycling conditions were an initial hot start of 94 °C for 2 min, 25 cycles of denaturation at 94 °C for 30 s, annealing at 52 °C for 40 s and extension at 72 °C for 1 min, with a final extension at 72 °C for 10 min. PCR products were visualised using 2% agarose gel E-Gel96 Pre-cast Agarose Electrophoresis System (Invitrogen). Only amplicons with single, intense bands were sequenced.

Each sequencing reaction consisted of 1 µL of PCR product along with 1 µL BIG DYE 3.1 reagent (Applied Biosystems, Inc), 1 µL M13F/M13R primer (Messing 1983), 10 µL ddH20 and 1 µL 5X sequencing buffer (Invitrogen). The thermocycling profile was an initial hot start 96 °C for 2 min, followed by 30 cycles of denaturation at 96 °C for 30 s, annealing at 55 °C for 15 s, and an extension at 60 °C for 4 min. PCR products were bi-directionally sequenced and run on an ABI 3730 capillary sequencer (Applied Biosystems). Sequencher 4.05 (GeneCodes) was used to trim primers, assemble and manually edit bidirectional contigs from raw trace files.

Sequence assemblies and supporting electropherogram "trace" files were uploaded to BOLD (and submitted to GenBank, accession numbers: KJ202257–KJ202608) and combined with other available *Trimma* sequences using a Hidden Markov Model alignment of translated COI amino acid sequences (Ratnasingham and Hebert 2007). Aligned sequences of > 500 bp in length were used to generate pairwise or p-distances to infer a Neighbour-Joining phenogram of sequence divergences using BOLD in order to provide a visual depiction of the barcode variation among and between species. Sequence data from an updated data set were also parsed into molecular operational taxonomic units (MOTUs) using the RESL (Refined Single Linkage Analysis) algorithm and subsequently annotated with Barcode Index Numbers (BINs), as implemented on version 3 of BOLD (Ratnasingham and Hebert 2007). This approach combines single linkage clustering and Markov clustering to recognize gaps in sequence space that correlate with species boundaries by optimizing MOTU partitions using the Silhouette index and uniquely labelling each MOTU with a Barcode Index Number or BIN (detailed in Ratnasingham and Hebert (2013)). The value of 2% used here is approximately equivalent to the more sophisticated RESL analysis used to distinguish haplogroup clusters that are subsequently enumerated with Barcode Index Numbers or BINs as promulgated by Ratnasingham and Hebert (2013, see above).

Results

The presentation of the results follows the sequence of appearance of the species names in the main barcode phenogram (Fig. 1), except where there are several haplogroups differing by > 2% sequence divergence under a single species name, or where a few such names alternate within such groups. In these cases, all such haplogroups are discussed under a single heading. Species which appear to form well defined monospecific entities and which have < 2% within species variance are listed below, and are not discussed further. These include (in the order in which they appear in Fig. 1): *T. maiandros* Hoese et al., *T. rubromaculatum* Allen & Munday, *T. habrum* Winterbottom, *T. anaima* Winterbottom, *T. imai* Suzuki & Senou, *T. agrena* Winterbottom & Chen, *T. hotsarihiensis* Winterbottom, *T. sheppardi* Winterbottom, *T. haimassum* Winterbottom, *T.* RW sp. 24, *T. yanoi* Suzuki & Senou, *T. papayum* Winterbottom, *T. kudoi* Suzuki & Senou, *T. halonevum* Winterbottom, *T. tauroculum* Winterbottom & Zur, *T. haima* Winterbottom, *T.* RW sp. 97, *T.* RW sp. 98, *T. preclarum* Winterbottom, *T. necopinum* (Whitley), *T. mendelssohni* (Goren), *T. corallinum* (Smith), *T. cana* Winterbottom, *T. fucatum* Winterbottom & Southcott, *T. annosum* Winterbottom, *T. hoesei* Winterbottom, *T. randalli* Winterbottom & Zur, and *T. flavatrum* Hagiwara & Winterbottom. However, it seems significant that, of these 27 taxa, all but six are represented from a single geographic locality in our material. The exceptions are: *T. anaima* (2, Timor and Raja Ampat), *T. halonevum* (8, Bali, Raja Ampat, Timor and Vanu Atu), *T. annosum* (14, Great Barrier Reef, Palau, Raja Ampat and Taiwan), *T. haimassum* (6, Rabaul and Raja Ampat), *T. hoesei* (4, Palau and Raja Ampat), and *T. yanoi* (6, Palau, Rabaul and Raja Ampat). All the others consist of more problematic species and groups discussed below, and these, too, are treated in the order that they appear in colour-coded labeled blocks in Fig. 1. The results are presented under subheadings where we felt the complexity of the analysis warranted such treatment for the sake of clarity.

The *Trimma tevegae* group

Figs 1A, 2–4, 13; Tables 1–2

Note. This is the most taxonomically complex of all the groups within *Trimma*. It contains four nominal species, all of which appear to be valid (Winterbottom 2011), and is made up of at least 11 different, and often widely divergent, haplogroups in our barcode analysis (Fig. 1). The species for which the group is named, *Trimma tevegae* Cohen & Davis, 1969, was described from specimens collected at the Dawapia Rocks in Rabaul Harbour, New Britain (see map, Fig. 2). Yoshino and Araga (1975) described *T. caudomaculatum* (as *T. caudomaculata*) from the Okinawa Island, part of the Ryukyu Islands, Japan. Winterbottom (2005a) compared these two nominal taxa morphologically based on material from throughout the western Pacific (including type specimens of both nominal species). He concluded that, while there was considerable morphological and colour variation present

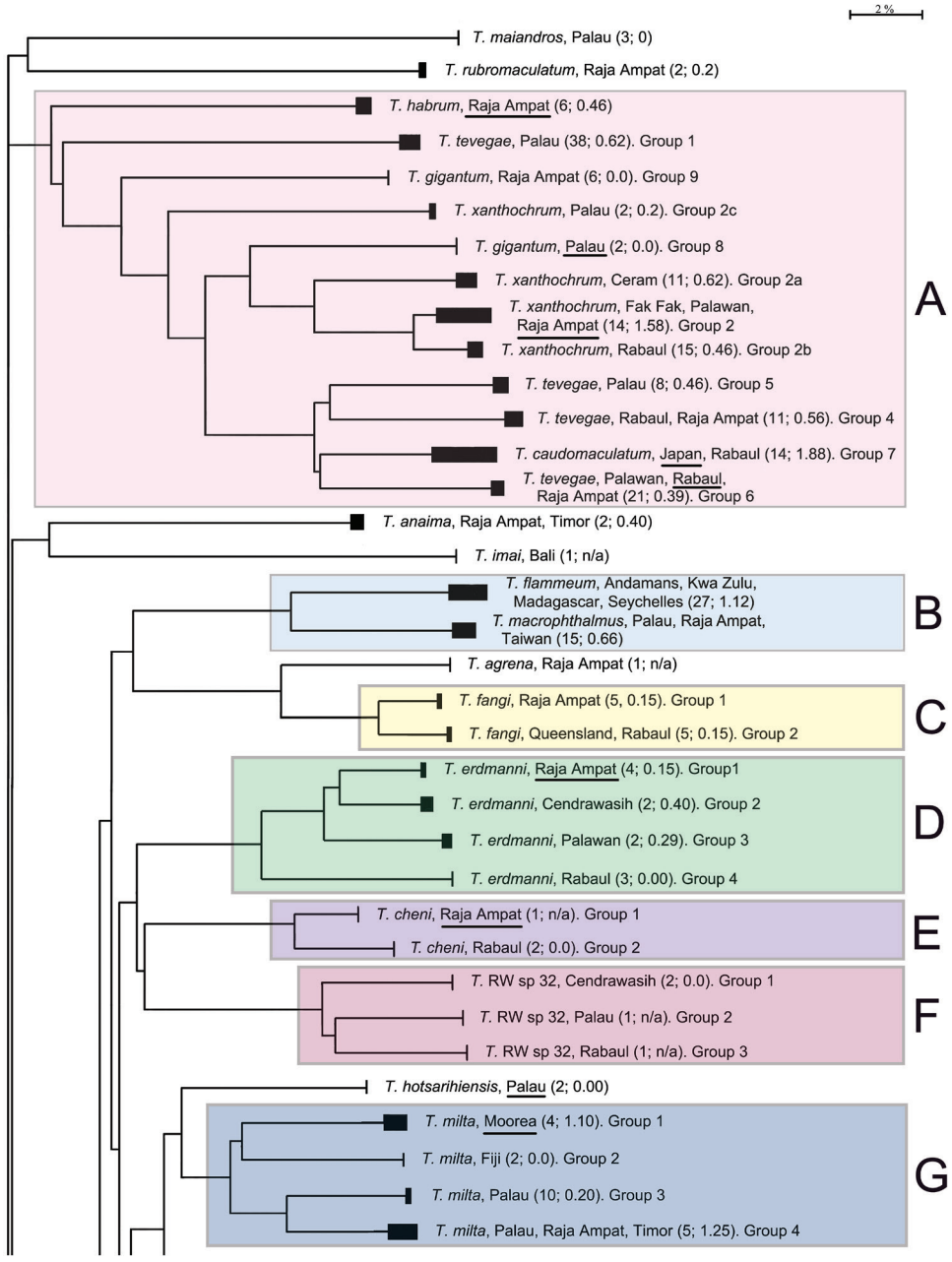


Figure 1. Condensed Neighbour-Joining network of the COI gene based on an analysis of 473 specimens of *Trimma*. Solid bars represent approximate within group variation. Species names/numbers are followed by the locality of the specimens, with the number of specimens followed by the percentage variation within the group in parentheses. Scale bar: 2% genetic distance. Coloured boxes and their alphabetical notations refer to the sequential groups discussed in the text. Type localities for each species are underlined where such samples were available. "Queensland" is used in lieu of "Great Barrier Reef".

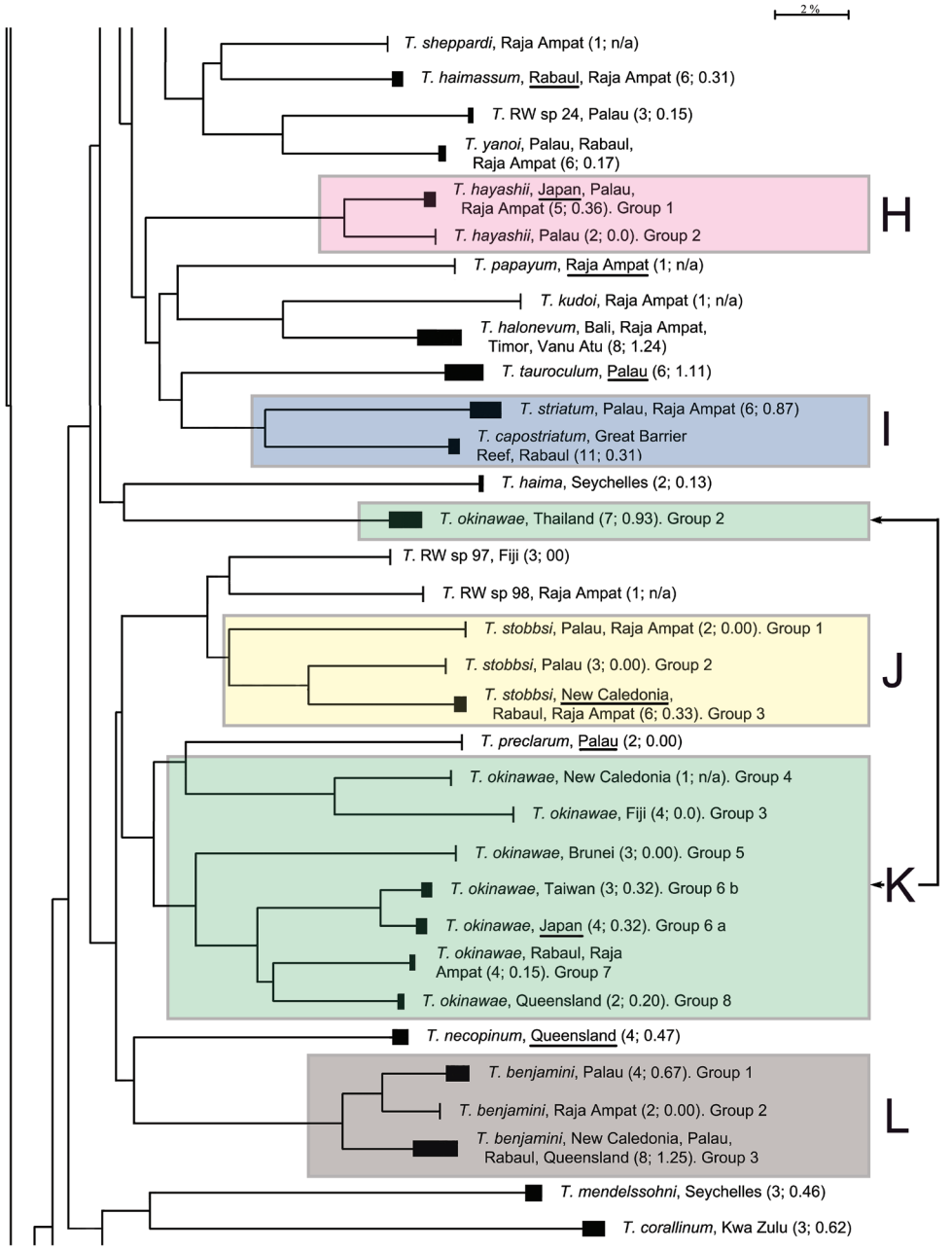


Figure 1. Continued.

in the material, all the specimens represented a single species, since he could find no consistent patterns in the variation he described. Winterbottom and Zur (2007) described *T. gigantum* from relatively deep collections (57–73 m) made in Palau by Patrick Colin. They

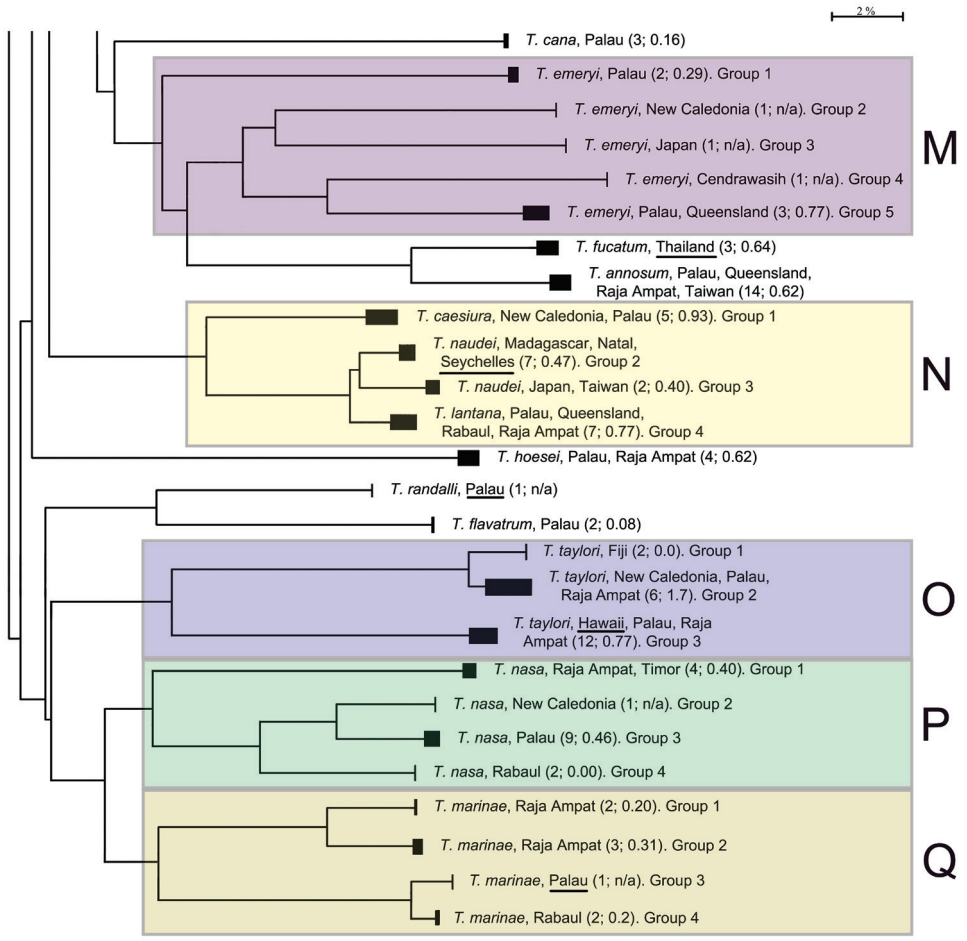


Figure 1. Concluded.

compared their new species to *T. fishelsoni* (Goren), currently known only from the Red Sea, and did not include any detailed reference to *T. tevegae*, since their new species clearly differed from other members of that complex in lacking any trace of a dark caudal blotch. In 2011, Winterbottom described *T. xanthochrum* from the Raja Ampat Province of Indonesia. In the discussion section of that description, he reversed his opinion (Winterbottom 2005a) that *T. tevegae* and *T. caudomaculatum* represented the same species, and hinted at morphological and colour differences that could be used to separate them from each other and from *T. xanthochrum*. He also suggested, based on barcode analyses done up to that time, that there were several other haplogroups in the *T. tevegae* complex that warranted more detailed morphological investigation to see whether any characters could be found to support this limited genetic evidence. One problem that he mentioned was the lack of genetic material from the type locality of *T. tevegae*, a situation since rectified by a two week collecting trip he made to Rabaul, New Britain in November, 2011.

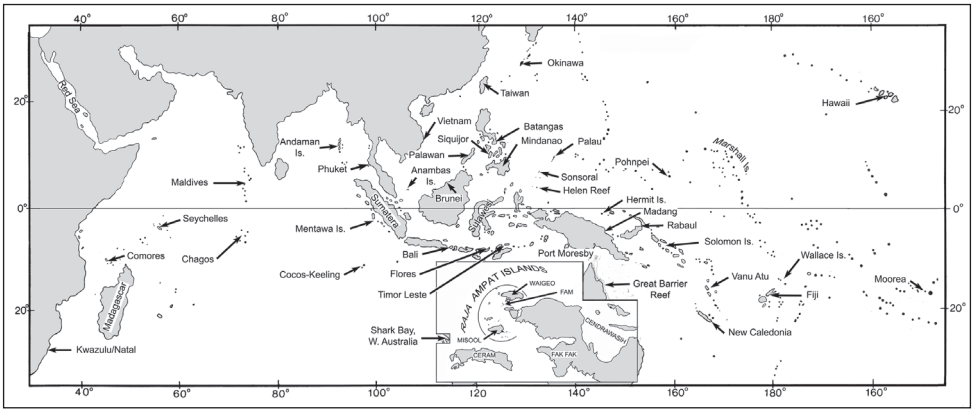


Figure 2. Map of the Indo-Pacific, showing localities where samples were collected. Inset - details of the Raja Ampat islands and Bird's Head region of Papua New Guinea.

Analysis. A) Although the most basal taxon associated with this group is *T. habrum* (Fig. 13A), we have not included it in the following analysis. The most phenetically divergent member of *T. tevegae* group in terms of its COI gene is from Palau, and was originally identified as *T. tevegae*. It is very similar in overall morphology to the rest of the *T. tevegae* group which possess a dark caudal blotch (Fig. 13B), and is listed as Group 1 in Fig. 1, section A. It differs from all the other haplogroups by a minimum of 17.7% of the COI base pairs (see Table 1).

Comments. Further morphological work initiated as a result of this study suggests that Group 1 is separable from the others based on a combination of four blotches (made up of melanophores) around the eye at 3, 4:30, 6 and 9 o'clock positions (only visible in well-preserved material, although the elongate blotch below the eye is usually apparent), the second spine of the first dorsal fin somewhat elongate, reaching to the base of the 4th to 7th ray of the second dorsal fin when adpressed, 13 unbranched pectoral-fin rays, and a single row of 6–7 cheek scales. The freshly collected colour pattern is based on a colour slide of a single, damaged 14.4 mm SL female specimen (Fig. 13B) that is probably of this haplogroup (i.e. it fits the above morphological criteria above). It is a relatively drab fish, being darkish red below the midlateral septum and lighter above. In preservative, the dorsum is darkened by melanophores, especially around the scale pockets, and by a scattering of large brown chromatophores which decrease in number towards the midline. The ventrum has a slightly greater concentration of large brown chromatophores, and few, if any, melanophores, and the combination gives the impression of a moderately dark fish with a somewhat lighter diffuse lateral stripe. It appears to be a small species (maximum recorded SL of 17.3 mm), and is only present in our analysis from the main islands of Palau. All but one of the 38 specimens we processed are from a single collection. Further work is underway to formally describe this new species (Winterbottom in prep.).

Table 1. Results from a barcode analysis of 142 specimens of *Trimma tevegae* group, giving number of specimens per group, the maximum variation within each group, followed by the minimum distances between groups (as percentages). Specific names under Group # are the names used in the networks; locality abbreviations are: FF, Fak Fak Peninsula; P, Palawan; Ra, Rabaul; and RA, Raja Ampat.

Group #	Locality	n	Var.	Minimum distance between groups									
				2	2a	2b	2c	4	5	6	7	8	9
1 (as *T. tevegae*)	Palau	38	0.6	17.7	21.3	19.3	19.7	21.5	21.1	22.4	20.8	21.6	18.1
2 (as *T. xanthochrum*)	FF/P/RA	14	1.6	–	7.7	2.5	16.1	14.7	14.0	14.2	13.8	10.7	15.2
2a (as *T. xanthochrum*)	Ceram	11	0.6		–	7.8	16.3	15.8	14.8	16.2	13.9	12.0	17.3
2b (as *T. xanthochrum*)	Rabaul	15	0.5			–	16.7	16.2	14.6	15.1	14.4	10.3	14.6
2c (as *T. xanthochrum*)	Palau	2	0.0				–	15.8	14.9	15.2	14.6	15.6	15.9
4 (as *T. tevegae*)	RA/Ra	11	0. 6					–	9.2	9.5	9.1	15.1	17.0
5 (as *T. tevegae*)	Palau	8	0.5						–	9.5	9.1	14.7	18.5
6 (as *T. tevegae*)	P/Ra/RA	21	0.4							–	7.9	14.5	16.8
7 (as *T. tevegae*)	Japan/Ra	14	1.7								–	14.1	16.8
8 (as *T. gigantum*)	Palau	2	0.0									–	16.7
9 (as *T. gigantum*)	RA	6	0.0										–

B) Morphologically, specimens identified as *T. gigantum* can easily be distinguished from the other members of the group by the lack of a large dark blotch at the base of the caudal peduncle. However, the barcode analysis widely separates two distinct geographic entities, both originally identified as this species. The two specimens from Palau used in our analysis were collected together with the holotype and 21 paratypes at Uchelbeluu Reef in Palau (Winterbottom and Zur 2007, labeled as *T. gigantum* Group 8 in Figs 1, 13E). These specimens nest phenetically with the members of the *T. xanthochrum* subgroup (q.v.), but are separated from them by a minimum distance of 10.3% of the COI base pairs. The second lot of samples provisionally identified as this species (Fig. 13C; 6 specimens from the Raja Ampat islands of Indonesia, labeled as *T. gigantum* Group 9 in Fig. 1A) show no variation in COI among themselves, but are separated from all other haplogroups in the group by a minimum of 14.6% sequence divergence.

Comments. A preliminary analysis of morphology between these two haplogroups did not reveal any obvious differences, and further work is clearly necessary if we are going to be able to distinguish between them (especially preserved museum material).

C) Four haplogroups are identifiable among what we call the *T. xanthochrum* subgroup (Fig. 1A). Of these four, *T. xanthochrum* Group 2c, from Palau (Fig. 13D), is the most different in its COI (a minimum of 16.1% sequence divergence from any other group) and in having a brownish, rather than yellow, overall colouration. *Trimma gigantum* from Palau (see above) is placed phenetically at the next node, forming the congruent level group with groups 2a (Ceram – no image available), 2 (Fak Fak Peninsula, Raja Ampat – the type locality of *T. xanthochrum*, and Palawan; Fig. 13F) and 2b (Rabaul; Fig. 13G). Group 2a (Ceram) is separated by a minimum of 7.8% sequence divergence from its nearest neighbour, and Group 2b shows a 2.5% minimum difference from specimens included here as Group 2. The relationships of this latter

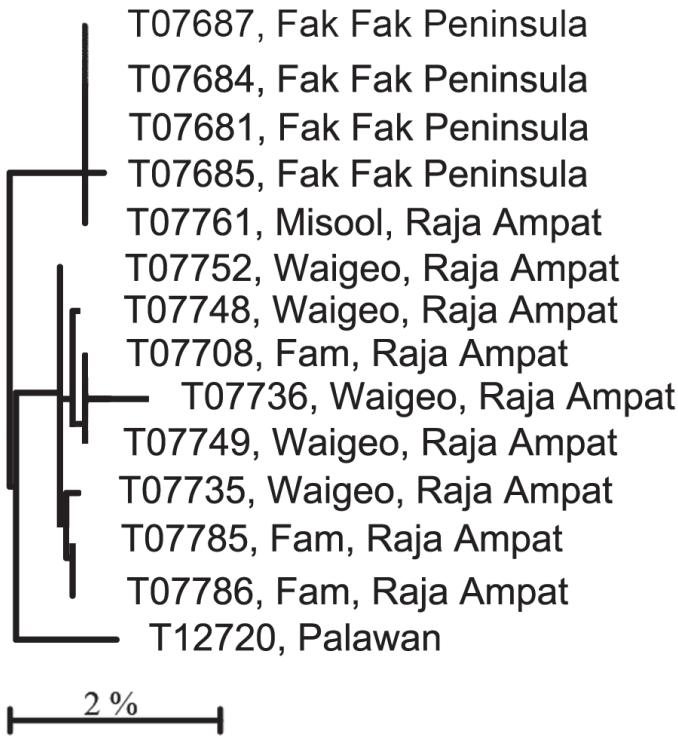


Figure 3. Relationships of 14 specimens of the *T. xanthochrum* Group 2, based on COI.

group are complex, and, based on current sampling, show some geographic variation (Fig. 3, Table 2). Specimens from southern Misool Island and from the southern side of the Fak Fak Peninsula vary from each other by 0.2%, and by a minimum of 1.1% from others in this assemblage. The eight specimens from the Raja Ampat Islands to the north have a variance of just 0.4%, and are separated from a single specimen from Palawan by a minimum of 1.2%. Group 2 differs from Group 2b (15 specimens from Rabaul, variance 0.5%) by a minimum value of 2.5%.

Comments. Morphologically, all these fishes possess a large dark blotch on the caudal peduncle and base of the caudal fin, a generally yellowish to brownish body, and have two or more sensory papillae in vertical rows beneath the eye and transversely in the interorbital row (part of row *p*: see description and figures of *T. xanthochrum* in Winterbottom 2011). No further morphological work has yet been undertaken to search for characters that might support the separation of the *T. xanthochrum* haplogroups.

D) The *T. tevegae* – *T. caudomaculatum* subgroup contains four haplogroups (identified as *T. tevegae* Groups 4, 5, 6 and 7 in Figs 1 and 4). Group 4 (Rabaul and Raja Ampat, 11 specimens, variance 0.6%; Fig. 13I) differs by a minimum of 9.2% from Group 5 (Palau, 8 specimens, variance 0.5%; Fig. 13H); these two together differ from the remaining two haplogroups by a minimum of 9.1% (see Table 1). The remaining two haplogroups, Group 6 (Palawan, Rabaul and Raja Ampat, 21 specimens, 0.4%

Table 2. Results from a barcode analysis of 14 specimens of *Trimma xanthochrum* Group 2, giving maximum variation within each group followed by the minimum and maximum distances between groups (as percentages). These values are typical of intraspecific barcode divergences among fishes.

Locality	n	Variation	Min./max. distance between groups	
			Raja Ampat	Palawan
Fak Fak/Misool	5	0.2	0.9/1.1	1.6
Raja Ampat	8	0.5	0	1.2/1.6
Palawan	1	n/a	-	0

variance; Fig. 13K) differs from Group 7 (Japan and Rabaul, 14 specimens, 1.9% variance; Fig. 13J) by a minimum of 7.9%. There is virtually no geographic structure discernible among the samples in Group 6, which is somewhat surprising to us given the relatively extensive geographic distribution of the samples.

Comments. There is currently no reliable way to distinguish between Groups 4 and 5 based on morphology despite fairly extensive data analyses, and further work is needed. The fishes in Group 6 differ morphologically from most others in the complex in having a relatively short second dorsal spine (reaching posteriorly between the interspace between the two fins to the base of the second dorsal-fin ray when adpressed), a single papilla in rows 3 and 4 below the eye (row *c*), row *p* in the interorbital region also consisting of single papillae, nearly always 13 unbranched pectoral-fin rays, usually a diffuse dark blotch just behind the symphysis of the lower jaw, and larger, darker brown spots among the brown chromatophores on the dorsal surface of the snout. In all these characters, these specimens match the types of *T. tevegae*, and we are relatively confident that the Group 6 haplotype represents the true *T. tevegae*. In the case of *T. caudomaculatum* (Group 7) there appears to be a clear cut difference of between 1.7–1.9% between the Japanese samples (11 specimens, variance 1.7%) and the three specimens from Rabaul (0.0% variance). We have here simply regarded these populations as the same species, since the maximum difference value between them is < 2%. However, we note that the RESL algorithm places the Japanese and Rabaul populations in separate BINs – the only difference between the two criteria (i.e. < 2% threshold vs RESL) that was present in our data set. Our specimens from Japan were collected off the north coast of Ie-jima Island, which lies just off the northern margin of Okinawa Island, the type locality of *T. caudomaculatum*. They appear to agree with the description and type specimens of *T. caudomaculatum*, a species apparently characterized in life by a bright blue lateral stripe from the upper orbit to the upper peduncle, another in the mid-dorsal region from the anterior snout to the base of the dorsal fins, a blue bar on the cheek just below the eye, and a mauve to magenta flush above and below the caudal spot which continues posteriorly onto the basal half of the caudal fin. This species has a very elongate second spine in the first dorsal fin, which often reaches to or beyond the end of the second dorsal fin when adpressed, and the head papillae are as in *T. tevegae* (Group 6). In preserved specimens, the marking under the eye is normally

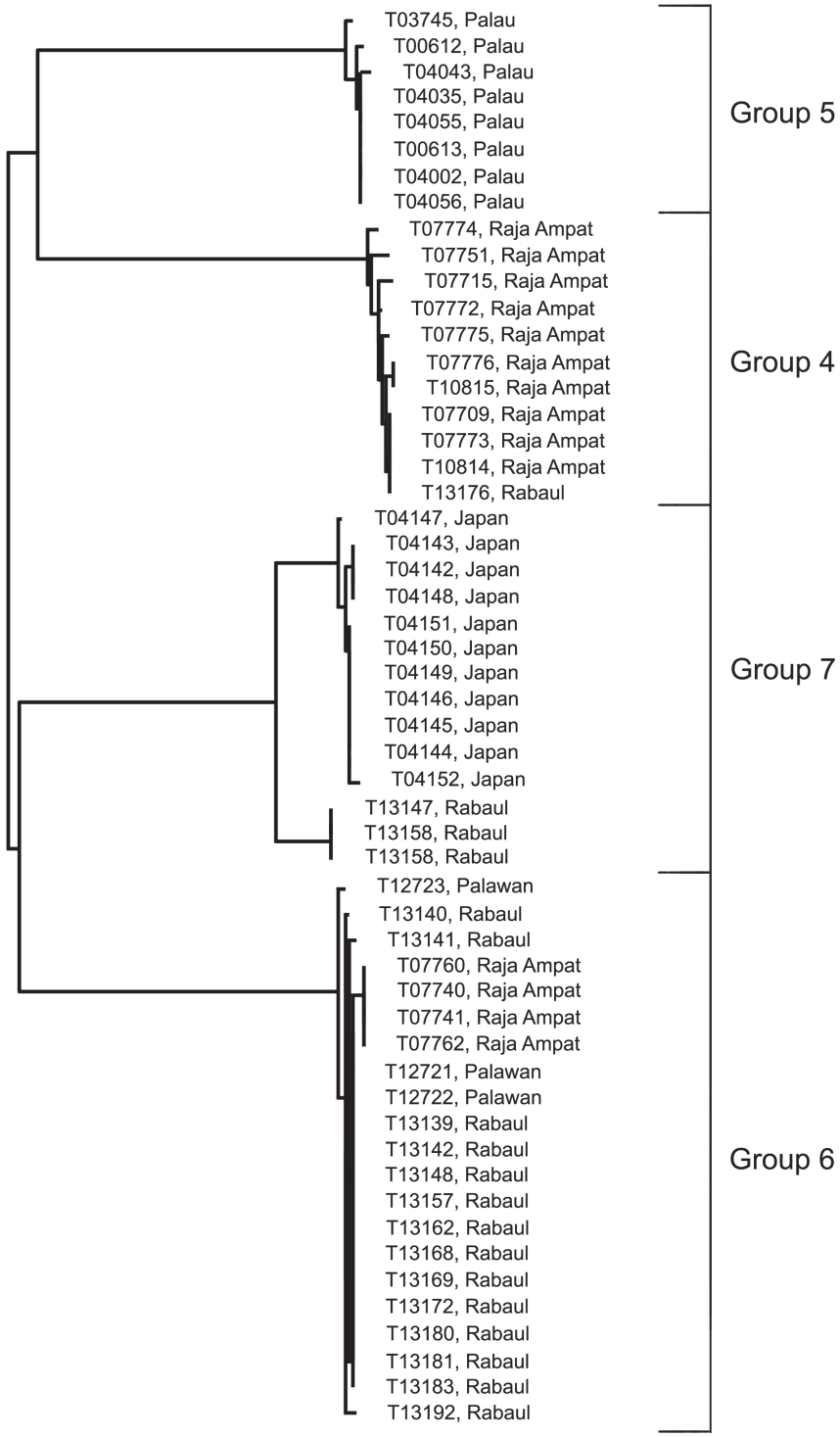


Figure 4. Relationships of 54 specimens of the *T. tevegae* – *T. caudomaculatum* group based on COI.

present as a well-developed dark stripe, the top of the snout is very dark and heavily pigmented, and there is often scattered dark pigment on the undersurface of the head. Specimens recently collected by Mark Erdmann in Timor Leste and at Port Moresby, Papua New Guinea, include two specimens each for DNA analysis (both samples received too late for inclusion here) of what appear, both in morphology and in live colour pattern, to be *T. caudomaculatum*. Live specimens exhibiting the blue lateral stripe have been photographed at several localities in the western Pacific, and may be this species, or there may prove to be more than one taxon involved. Large specimens of both Group 4 and Group 5 may have blue lateral and dorsal stripes. In addition, there is undoubtedly more than just a single species of this group in Japanese waters (see, e.g. the images in Senou et al. 2004, and various websites such as http://fishpix.kahaku.go.jp/fishimage-e/search.html). Among the specimens from Raja Ampat, tissue samples falling into Group 2 were twice collected with tissue voucher specimens from Group 4, and once together with the tissue voucher from Group 6, so these forms are syntopic. All Palau specimens were from contiguous island groups except for Group 5, which consists of three specimens from the main islands of Palau (from both the east and the west coasts), and five specimens from Helen Reef in the South West Islands, some 570 kilometers (350 miles) to the south-west. Group 5 was the only haplogroup represented in the samples from Helen Reef, whereas the main Palauan islands had representatives of Groups 1, 2c and 5. Variance for Group 5 was 0.5%, without any correlation with geographic origin. Among the Palauan samples, the only coincident sampling involved the simultaneous collection of a specimen from each of Groups 1 and 2c at 20–28 m on Uchelbeluu Reef near Koror on the east coast of the main islands. The collections made at Rabaul differed from those made elsewhere in that each individual site sampled was kept separate from all the others made during that dive, with the precise depth recorded. Each such collection was made at a specific substation (overhang, small cave, fissure, etc.) on the reef. We here report only on the specimens from which tissues were taken because there are still some difficulties in separating preserved specimens into groups based on morphology. Four haplogroups were present at Rabaul, although only three were collected at Dawapia Rocks (the type locality of *T. tevegae*). The fourth haplogroup represented, here reported as *T. tevegae* Group 4 (otherwise known at present only from Raja Ampat), was represented by a single specimen from Little Pigeon Island, some 18 km ESE of Dawapia Rocks and outside Simpson Bay. The three haplogroups at the type locality were *T. xanthochrum* Group 2, *T. caudomaculatum* Group 7 and *T. tevegae* Group 6. All three tissue samples of *T. caudomaculatum* were taken on the same dive, but at three different places and depths on the reef. Tissue samples of *T. tevegae* Group 6 were collected at two of these same substations, so these two haplogroups are syntopic at the micro-scale. Although tissue samples of *T. tevegae* Group 6 (n=14) and *T. xanthochrum* Group 2 (n=15) were not retained from exactly the same microhabitats, morphological identifications of the non-tissue specimens suggests that the two do co-occur in the same micro-habitat on occasion. Depth information based solely

on the tissue samples indicates that *T. tevegae* Group 6 generally occurs at 13–29 m (mean 21 m), and that most *T. xanthochrum* Group 2 are found a little deeper (20–45, mean 32 m).

The *Trimma flammeum*/*T. macrophthalmus* group

Fig. 1B

Analysis. *Trimma flammeum* (Smith) (variance 1.1%) and *T. macrophthalmus* (Tomiyama) (variance 0.7%) differ from each other by a minimum of 9.0% sequence divergence. Morphologically, and in colour pattern, these two species are virtually identical with only a slight variation in colour pattern (Winterbottom and Hoese in prep.), and their status as separate species has been unsupported empirically.

Comments. These two species are well represented in terms both of number of specimens (27 and 15 respectively) and in breadth of geographic range. The minimum 9.0% difference between the two haplogroups, suggests that the two are, in fact, distinct species. The only morphological difference that has been noted is that the spots on the pectoral fin base of *T. flammeum* are red in life and pale in preservative, while those in *T. macrophthalmus* are reddish-brown or dusky in life and dark in preservative (Winterbottom and Hoese in prep.). *Trimma flammeum* ranges from the south-western Indian Ocean (Kwazulu/Natal) to the Andaman Islands in the north-eastern Indian Ocean, while *T. macrophthalmus* occurs from the Cocos-Keeling Islands in the south-eastern Indian Ocean to Fiji in the east and north to Japan. It is currently unknown which species, if either, occurs at the Mentawa Islands off the west coast of Sumatera, as well as on Sumatera itself. These areas lie in the potential contact zone between the two species.

The *Trimma fangi* group

Fig. 1C

Analysis. The 10 specimens in this group are all currently identified as *T. fangi* Winterbottom & Chen on the basis of morphology and colour pattern. Our barcode analysis, however, distinguishes two haplogroups separated by 3.5% sequence divergence, one from Raja Ampat (variance 0.2%) and the other from the Great Barrier Reef and Rabaul (variance 0.2%).

Comments. The type locality for this species is the Anambas Islands, in the South China Sea between mainland Malaysia and the island of Borneo, and we have no specimens with genetic material available for genetic analysis from this area. It is therefore unknown whether the specific name applies to either of the haplogroups, or whether it applies to a third group. Further morphological work is needed to clarify the situation.

The *Trimma erdmanni* group

Figs 1D, 5; Table 3

This species was recently described based on specimens collected in the Raja Ampat islands by Winterbottom (2011), who commented that specimens attributable to this species were known from Sulawesi, the Hermit Islands, and Madang, and that there were photographs of specimens from Palawan, Mindanao and Batangas in the Philippines. Since that time, we have accumulated specimens identified morphologically as *T. erdmanni* from Cendrawasih Bay, Palawan and Rabaul in addition to the tissue specimens from the type locality in Raja Ampat.

Analysis. The specimens from Raja Ampat (Group 1; 4; 0.2% variance) are phenetically closest to those from Cendrawasih (Group 2; 2; 0.4% variance) but differ by 4.5% (Table 3). The next closest are the specimens from Palawan (Group 3; 2; 0.3% variance) which differ from these two groups by a minimum of 5.1%, followed by those from Rabaul (Group 4; 3; 0.0% variance), with a minimum distance of 8.4%.

Comments. Mark Erdmann (pers. comm.) has informed us of several subtle colour and ecological differences he observed among specimens initially identified as this species, but these have yet to be quantified and compared to the barcode results. Additional morphological data needs to be gathered and analyzed along with the colour differences.

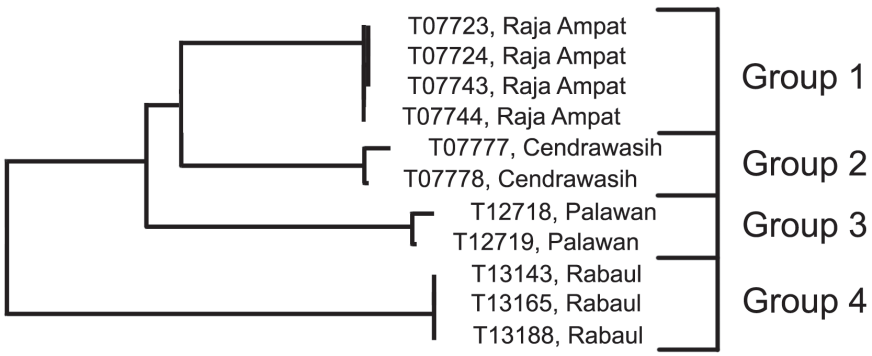


Figure 5. Relationships of 11 specimens of the *Trimma erdmanni* group based on COI.

Table 3. Results from a barcode analysis of 11 specimens of *Trimma erdmanni*, giving maximum variation within each group followed by the minimum distances between the groups (as percentages).

Group#	Locality	n	Variation	Min. Distance		
				2	3	4
1	Raja Ampat	4	0.2	4.5	5.1	8.4
2	Cendrawasih	2	0.4	0	6.5	10.1
3	Palawan	2	0.3	–	0	10.6
4	Rabaul	3	0.0	–	–	0

The *Trimma cheni* group

Fig. 1E

This species was also recently described by Winterbottom (2011) from Raja Ampat, with additional records from the Philippines, Palau, Flores, Sulawesi and Ceram. Tissue specimens were only available from Raja Ampat (n=1) and from Rabaul (n=2), where the barcode analysis found two haplogroups differing by 4.5% sequence divergence. The specimen from Raja Ampat (Group 1) was collected with four paratypes of the species, and we assume that this specimen belongs to the same haplogroup as the holotype.

The *Trimma* RW sp. 32 group

Fig. 1F

This informal name has been used for an undescribed species, characterised by a very large ocellated black spot in the first dorsal fin. Specimens with this distinctive marking are known from various localities in the western Pacific, including the Philippines and Wallace Island, as well as the tissue samples analysed here from Cendrawasih (Group 1; 2; 0.0% variance), Palau (Group 2; 1; n/a) and Rabaul (Group 3; 1; n/a). According to our analysis, each of these localities contains a distinct haplogroup, with samples from Cendrawasih differing from the others by a minimum of 7.4% sequence divergence, while the Palau and Rabaul specimens differ by a minimum of 7.1%. This clearly suggests that any formal descriptions of new species from within this group should be based on specimens from a single geographic locality, and that comparative material from other localities be examined minutely for potential morphological variations.

The *Trimma milta* group

Figs 1G, 6; Table 4

Analysis. The *Trimma milta* Winterbottom group contains four discreet haplogroups (Figs 1, 6). Group 1(intra-group variation 1.1%) is from the type locality (Moorea, Society Islands), and differs by 7.9% from Group 3 (variance 0.2%) from Palau. Group 2, from Fiji (variance 0%) differs by 8.7% sequence divergence from Group 1, and by over 10% from the other two haplogroups (Table 4). Group 3, from the main islands of Palau and the northernmost of the South West Islands (Sonsorol) differs by 6.7% from Group 4, which is unusual among the *T. milta* haplogroups in having representatives from three major geographical localities (Palau, Raja Ampat and Flores) while exhibiting only modest variance (1.3%).

Comments. Group 3 presents a complex picture. Ten specimens from Palau have a variance of 0.2%. Two samples, excluded here because their sequences exhibit several

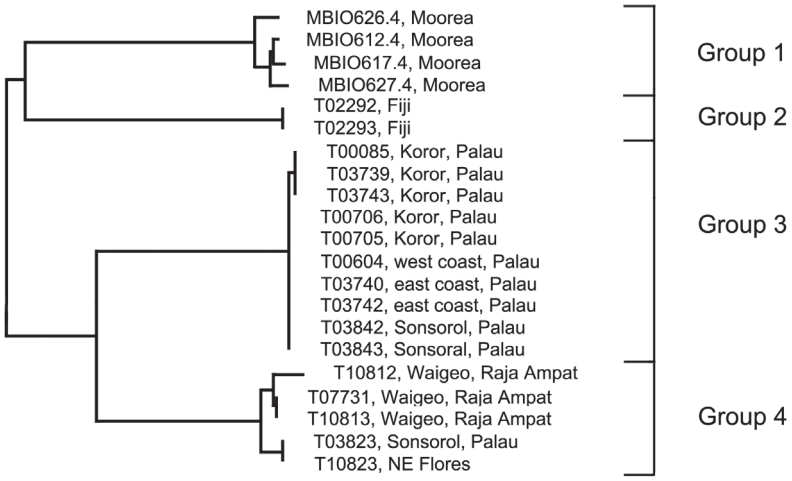


Figure 6. Relationships of 21 specimens of the *T. milta* group based on COI.

Table 4. Results from a barcode analysis of 21 specimens of *Trimma milta*, giving maximum variation within each group followed by the minimum distances between the groups (as percentages). Pal/RA/Flores – Palau, Raja Ampat and north-eastern Flores.

Group #	Locality	n	Variation	Min. Distance			
				1	2	3	4
1	Moorea	4	1.1	0	8.7	7.9	9.0
2	Fiji	2	0	–	0	10.2	10.1
3	Palau	10	0.2	–	–	0	6.2
4	Pal/RA/Flores	5	1.3	–	–	–	0

anomalies (including stop codons), differed by a minimum distance of 3.9% from the others. To date, no work has been undertaken to test the barcode results morphologically. The only observations made were on the images from the various localities. Specimens from Moorea tend to be overall dark red to orange (although a few specimens are orange-yellow), those from Raja Ampat are pinkish with less obviously outlined scale pockets, while those from Palau are predominantly yellow, with a few of them having diffuse darker bars below the eye. Clearly there is a need for a thorough examination of specimens currently assigned to this species throughout its apparent range.

The *Trimma hayashii* group

Fig. 1H

The species was described by Hagiwara and Winterbottom (2007) from the Ryukyu Islands, Japan, with additional type specimens from Palau and Pohnpei. Our barcode

analysis of 7 specimens shows two haplogroups, one from Japan, Palau and Raja Ampat (Group 1; 5; 0.4% variance) and the other represented by specimens from Palau (Group 2; 2; 0.0% variance). These two groups are separated by 4.7% sequence divergence. It is interesting that the two specimens in the second group are from Helen Reef, the isolated southern-most of the South West Islands of Palau (Fig. 2), while the three Palauan specimens in the first group are from the main Palauan islands to the north. Closer morphological analysis of the Helen Reef material assigned to this species is clearly indicated.

The *Trimma striatum*/*T. capostriatum* group

Fig. 1I

These two species have long been considered synonyms (e.g. Winterbottom 1984). *Trimma striatum* was described from the Philippines by Herre (1945, as *Coronogobius*), and *T. capostriatum* was described by Goren (1981, as *Zonogobius*) from New Caledonia. Recent work by Hoese (as part of Winterbottom and Hoese in prep.) has enumerated colour pattern differences between the two nominal species suggesting that they are distinct species, and that conclusion is bolstered by our barcode data. Specimens of *T. striatum* from Palau and Raja Ampat (6; 0.9% variance) differ from specimens identified as *T. capostriatum* from the Great Barrier Reef and Rabaul (11; 0.3% variance) by a minimum of 9.3% sequence divergence. These two species were identified from the same collection made in the lagoon at Helen Reef, South-West Islands of Palau using colour pattern criteria, and this syntopy further supports their distinctiveness.

The *Trimma stobbsi* group

Fig. 1J

Trimma stobbsi was described by Winterbottom (2001) from New Caledonia (type locality), with paratypes listed from the Maldives, Indonesia, Papua New Guinea, the Philippines and the Solomon Islands. Our barcode analysis of 11 specimens is divided into three haplogroups. The first, from Palau and Raja Ampat (Group 1; 2; 0.0% variance), differs from the other two by a minimum of 12.4%; the second group (from Palau only, Group 2; 3; 0.0% variance) differs from the third group from New Caledonia, Rabaul and Raja Ampat (Group 3; 6; 0.3% variance) by 7.9% sequence divergence. This third group probably represents the same haplogroup as the holotype. The data thus suggests that there are at least two other undescribed species in this complex. More detailed examination of the morphology and colour patterns of these specimens is needed.

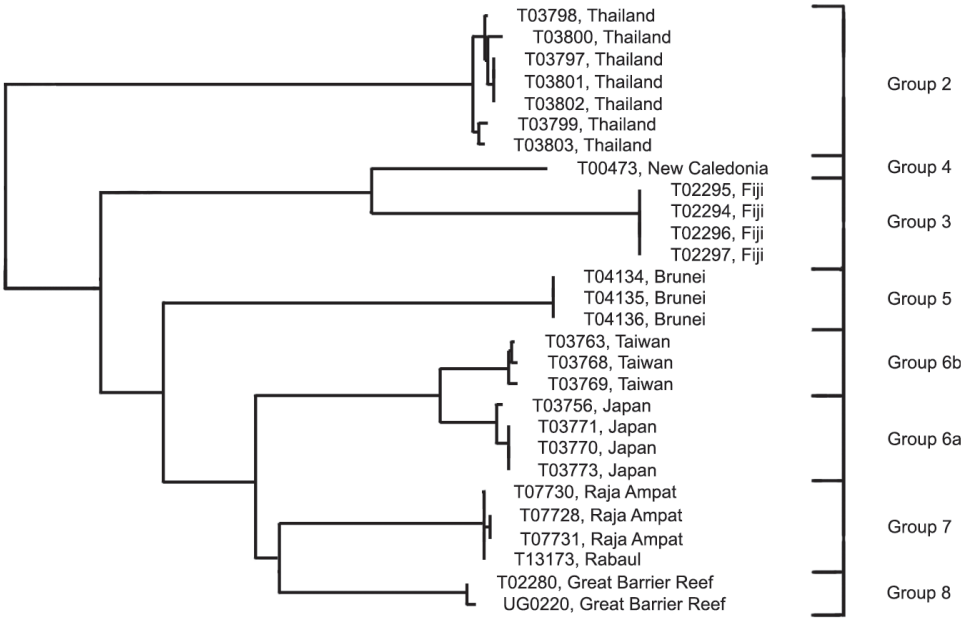


Figure 7. Relationships of 28 specimens of the *T. okinawae* group based on COI.

The *Trimma okinawae* group

Figs 1K, 7; Table 5

Trimma okinawae was described by Aoyagi (1949:173) as a new subspecies, *Eviota caesiura okinawae*, from three specimens from Japan (the holotype, a 24 mm SL male, from Itoman, Okinawa Island). All the type specimens are apparently lost (D.F. Hoese pers. comm.).

Specimens identified morphologically as *T. okinawae* proved to consist of eight discreet haplogroups according to our analysis, second only to the *T. tevegae* group in number of haplogroups previously ascribed to a single species. A single specimen identified as this species from Palau was included in our original analysis (as Group 1, ROM T00075), but the subsample we used for sequencing appears to have been contaminated, as it was closely grouped with 10 specimens of another gobiid, *Priolepis cincta*, from several western Pacific localities. We have omitted this specimen from further consideration here, assuming that contamination of the sample has occurred.

Analysis. The phenetically most distinctive haplogroup (n=7, variance 0.9%) was from Phuket, Thailand (Group 2), and this group was separated from the cluster including all the other specimens originally identified as this species in the barcode phenogram (Fig. 1). They differed from their nearest neighbour, identified as *T. okinawae* (Group 7, from Rabaul and Raja Ampat) by a minimum of 16.5%, and from the most divergent group (Group 3, from Fiji) by a minimum of 19.9% (Fig. 7, Table 5). Groups 3 (Fiji) and 4 (New Caledonia) are nearest neighbours and differ from each

Table 5. Results from a barcode analysis of 28 specimens of *Trimma okinawae*, giving number of specimens, maximum variation within each group followed by the minimum distances between the groups (as percentages). Abbreviations: GBR, Great Barrier Reef; New Caledonia; Ra/RA, Rabaul and Raja Ampat.

Group#	Locality	n	Var.	Minimum distance between groups						
				3	**4**	**5**	**6a**	**6b**	**7**	**8**
2	Thailand	7	0.9	19.9	19.3	17.9	17.8	18.2	16.5	17.8
3	Fiji	4	0.0	–	7.9	17.9	16.8	16.3	17.0	16.2
4	New Cal.	1	n/a		–	16.4	14.8	14.6	15.6	15.3
5	Brunei	3	0.0			–	13.7	13.3	13.1	11.6
6a	Japan	4	0.3				–	2.4	8.9	7.9
6b	Taiwan	3	0.3					–	8.9	7.8
7	Ra/RA	4	0.2						–	7.1
8	GBR	2	0.2							–

other by 7.9% and from the remaining five groups by a minimum of 14.6%. Of the latter, the specimens from Brunei (Group 5) are the most divergent, with a minimum distance of 11.6% from the remaining four groups, which are divided into two pairs, separated by a minimum of 7.8% from each other. Specimens from Japan (the type locality) differ from those from Taiwan by a minimum of 2.4%, while the specimens from Raja Ampat and Rabaul differ from those from the Great Barrier Reef by a minimum of 7.1%.

Comments. Although some morphological variation in the extent of predorsal scalation, depth of interiorbital groove, length of second spine of first dorsal fin, and colour pattern—especially the vertical markings on the cheek and opercle and the overall base colour—have been noticed (D.F. Hoese pers. comm.; RW pers. obs.), no consistent differences have been recorded or published to date. However, it is planned to describe the Great Barrier Reef population as a discreet species (Winterbottom and Hoese in prep.). Again, further work, both morphological and genetic, is sorely needed to resolve the issues raised by our barcode analysis.

The *Trimma benjamini* group

Fig. 1L

This species was described based on type specimens from the Philippines (Winterbottom 1996), and specimens identified on the basis of morphology as this species have been recorded from throughout most of the western Pacific and out onto the Pacific plate (Marshall Islands). Unfortunately, no specimens from the Philippines were available for genetic analysis. Among the 14 specimens that were available, there appear to be three haplogroups. The minimum percentage differences between these groups, while above the typical 2% sequence divergence threshold delineating different species of fishes (e.g. April et al. 2013), are relatively low compared to those found in many

other haplogroups identified as a single species of *Trimma*. A group of specimens from Palau (Group 1; 4; 0.7% variance) differs from those from Raja Ampat (Group 2; 2; 0% variance) by 3.4% sequence divergence. These two groups differ from a third group from the Great Barrier Reef, New Caledonia, Palau and Rabaul (Group 3; 8; 1.3% variance) by a minimum of 5.2%. Much of the intra-group variation in the latter is encompassed between the two specimens from Rabaul, so that there appears to be little or no geographical structuring of that variation. However, further morphological work is needed to explore the apparent structure described above.

The *Trimma emeryi* group

Fig. 1M, 8; Table 6

Trimma emeryi was described by Winterbottom (1985) based on numerous specimens from the Chagos Archipelago, central Indian Ocean. We have been unable to obtain specimens from the type locality for genetic analysis. The barcode analysis reveals five haplogroups identified as this species for specimens from the western Pacific, for three of which we have only a single specimen. These five groups are separated by large genetic distances.

Analysis. The two specimens from Palau in Group 1 are the most divergent in COI, being separated from the other four groups by a minimum of 17.9%. Groups 2 and 3 are nearest neighbours and differ from each other by 16.1%, and from Groups 4 and 5 by a minimum of 17.2%. The latter two groups are phenetically closest to each other, differing by 13.8% (Fig. 8, Table 6). Group 5 is the only group to contain specimens from more than one locality (the Great Barrier Reef and Palau).

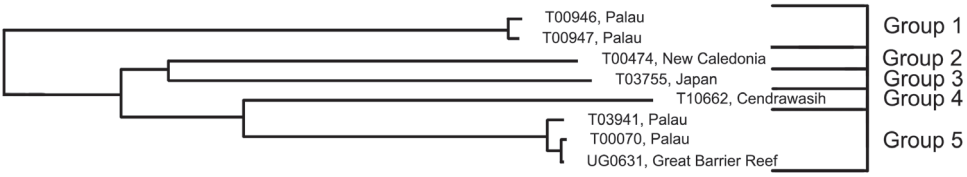


Figure 8. Relationships of 8 specimens of the *T. emeryi* group based on COI.

Table 6. Results from a barcode analysis of 8 specimens of *Trimma emeryi*, giving number of specimens, maximum variation within each group followed by the minimum distances between the groups (as percentages). Abbreviations: GBR, Great Barrier Reef; New Cal., New Caledonia.

Group #	Locality	n	Var.	Minimum Distance			
				2	3	4	5
1	Palau	2	0.5	20.1	21.9	19.7	17.9
2	New Cal.	1	n/a	–	16.1	17.2	18.8
3	Japan	1	n/a		–	18.3	18.9
4	Cendrawasih	1	n/a			–	13.8
5	GBR/Palau	3	0.8				–

Comments. The specimens from which genetic samples of Group 1 were taken were noted in the field as being paler in overall colouration than is usually the case for specimens identified as this species. Winterbottom (1985) had noted that specimens from Fiji differed somewhat morphologically from the Chagos type material, and suggested that further studies were necessary. Those studies have not yet been undertaken, but are obviously necessary given the barcode results presented above.

The *Trimma caesiura* group

Figs 1N, 9, 14; Table 7

This complex was reviewed morphologically by Winterbottom and Villa (2003). In that paper, the authors included several species that are widely separated from *T. caesiura* (Jordan & Seale) in the barcode phenogram. We will here only consider the species currently identified as *T. caesiura*, *T. lantana* Winterbottom & Villa and *T. naudei* Smith.

Analysis. *Trimma caesiura* (5; 0.9% variance; Fig. 14A) is separated by a minimum of 10.1% from the other three groups (Fig. 9, Table 7), while *T. lantana* (7; 0.8% variance; Fig. 14D) is separated from *T. naudei* (Groups 2 and 3) by between 2.3% (Group 2, western Indian Ocean; Fig. 14B) and 4.0% (Group 3, Japan/Taiwan; Fig. 14C). The specimens identified as *T. naudei* from the western Indian Ocean are separated from those from Japan and Taiwan by 3.0%. Interestingly, the former of these exhibits a closer phenetic similarity to *T. lantana* than it does to the Japan/Taiwan specimens identified as *T. naudei*.

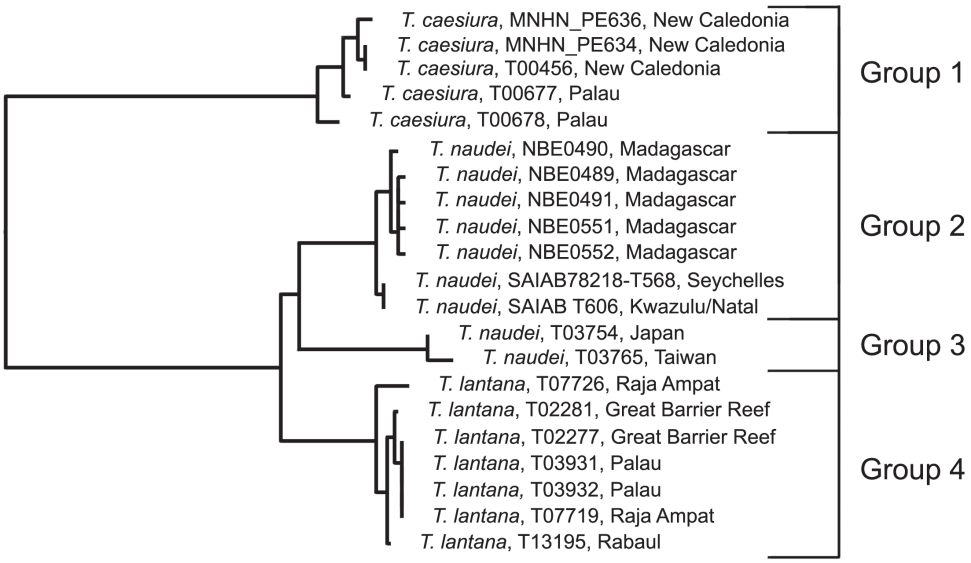


Figure 9. Relationships of 21 specimens of the *T. caesiura* group based on COI.

Table 7. Results from a barcode analysis of 21 specimens of the *Trimma caesiura* group, giving maximum variation within each group followed by the minimum distances between the groups (as percentages). Abbreviations: GBR/Pal/RA, Great Barrier Reef, Palau, Raja Ampat; NC, New Caledonia; WIO, Western Indian Ocean.

Group #	Locality	n	Variation	Min. distance		
				2	3	4
1 (*T. caesiura*)	NC/Palau	5	0.9	10.5	10.7	10.1
2 (*T. naudei*)	WIO	7	0.5	0	3.0	2.3
3 (*T. naudei*)	Japan/Taiwan	2	0.4	–	0	4.0
4 (*T. lantana*)	GBR/Pal/RA	7	0.8	–	–	0

Comments. Specimens identified as *T. naudei* range from the Comores Islands in the western Indian Ocean, through Thailand and Vietnam to Japan, and throughout Indonesia to Sulawesi and north to the Philippines. Unfortunately, we have no material for genetic analysis from these other western Pacific localities. *Trimma lantana* shows considerable morphological variation across the north of Australia from the Great Barrier Reef to as far west as Shark Bay in Western Australia. Our only genetic samples from Australia come from the Great Barrier Reef. Specimens north of the Great Barrier Reef to Raja Ampat, Rabaul, and Helen Reef (South West Islands of Palau) appear to be very uniform in colour pattern and morphology.

The *Trimma taylori* group

Figs 1O, 10; Table 8

Trimma taylori was described from specimens collected off Oahu in the Hawaiian Islands (Lobel 1979). Specimens identified as this species based on morphology have been found from the northern Red Sea and Comores in the west through the Great Barrier Reef to the Society Islands in the east, and north to the Philippines.

Analysis. The barcode analysis suggests three haplogroups (Fig. 10) for specimens identified as this species on the basis of morphology and colour pattern. One of these, Group 1 (Fiji) is only marginally separated from Group 2 from New Caledonia, Palau and Raja Ampat (2.4% variance; Table 8). However, these two groups are widely separated from Group 3 from Hawaii, Palau and Raja Ampat (minimum of 17.6%).

Comments. The four specimens from Hawaii in our analysis were collected from the same island (Oahu) that the type series is from, and Group 3 undoubtedly represents the species name. It is therefore likely that Group 2 represents an undescribed species, but there are no morphological criteria currently known that would allow

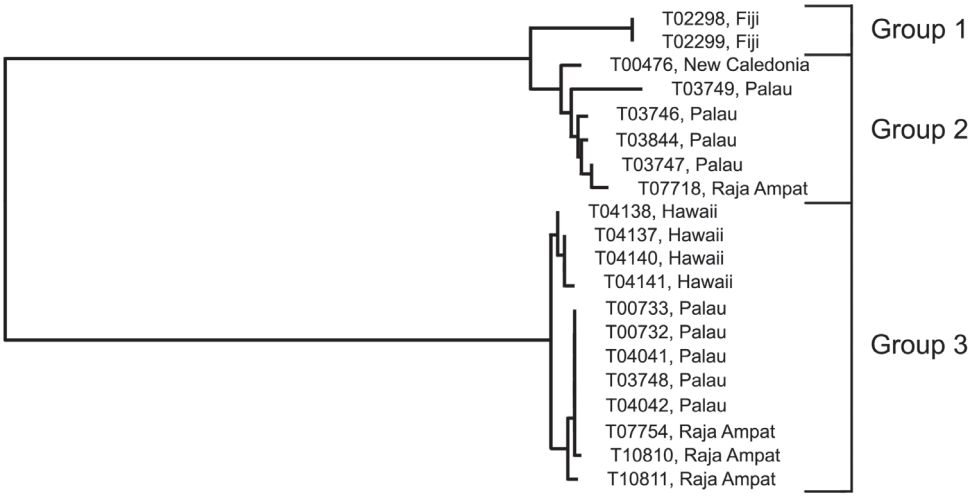


Figure 10. Relationships of 20 specimens of the *T. taylori* group based on COI.

Table 8. Results from a barcode analysis of 20 specimens of the *Trimma taylori* group, giving maximum variation within each group followed by the minimum distances between the groups (as percentages). Abbreviations: NC, New Caledonia; Pal, Palau; RA, Raja Ampat.

Group #	Locality	n	Variation	Min. distance	
				2	3
1	Fiji	2	0.0	2.4	18.8
2	NC/Pal/RA	6	1.7	–	17.6
3	Hawaii/Pal/RA	12	0.8		–

specimens to be identified from museum collections. Whether the Fijian samples (here separated as Group 1) represent the same or a different species as the remaining members in Group 2 also needs to be closely examined.

The *Trimma nasa* group

Figs 1P, 11, 14; Table 9

Trimma nasa was described by Winterbottom (2005b) based on specimens from the Philippines (type locality: Siquijor Island) plus one large lot from the Solomon Islands (Guadalcanal). Additional non-type material listed was from Fiji, the Great Barrier Reef, Indonesia, New Caledonia, Papua New Guinea, Palau and Vanu Atu. Material available for this paper consisted of specimens from Raja Ampat and Timor (Indonesia: Group 1), New Caledonia (Group 2), Palau (Group 3) and Rabaul (Papua New Guinea: Group 4). Unfortunately, no specimens from the type locality were available, so it is unknown as to which, if any, of the four haplogroups recovered

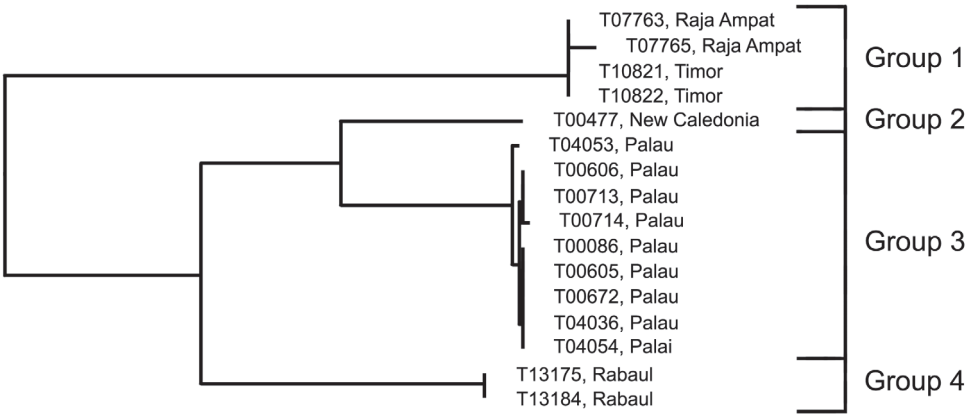


Figure 11. Relationships of 16 specimens of the *T. nasa* group based on COI.

Table 9. Results from a barcode analysis of 16 specimens of the *Trimma nasa* group, giving maximum variation within each group followed by the minimum distances between the groups (as percentages).

Group #	Locality	n	Variation	Min. Distance		
				2	3	4
1	Raja Ampat/Timor	4	0.4	16.0	16.8	15.9
2	New Caledonia	1	n/a	0	5.5	9.0
3	Palau	9	0.5	–	0	9.3
4	Rabaul	2	0.0	–	–	0

by our barcode analysis the types belong to. Although all our specimens are from single political entities, there may be large distances between samples. For example, specimens from Indonesia (Raja Ampat and Timor) are separated by a straight-line distance of about 1,000 kms, and those from Palau (main islands to Helen Reef) by about 570 kms (Fig. 2).

Analysis. Group 1 (Raja Ampat and Timor, 4; 0.4% variance; Fig. 14E) is separated from the other three groups by a minimum of 15.9% of COI (Fig. 11, Table 9). Groups 2 (New Caledonia; Fig. 14F) and 3 (Palau, 9; 0.5% variance; Fig. 14G) are nearest phenetically, and differ from each other by 5.5%, and from Group 4 (from Rabaul, 2; 0.0% variance; Fig. 14H) by a minimum distance of 9.0%.

Comments. The original description of *T. nasa* noted that the specimens examined from Palau and New Caledonia essentially lacked the dark nasal stripe characteristic of specimens from other areas (we note in passing that specimens from these two areas have the least distance between them of any of the haplogroups uncovered in our analysis). However, further work is needed to try to uncover morphological characters that may allow for separation among the four haplogroups uncovered in our barcode analysis.

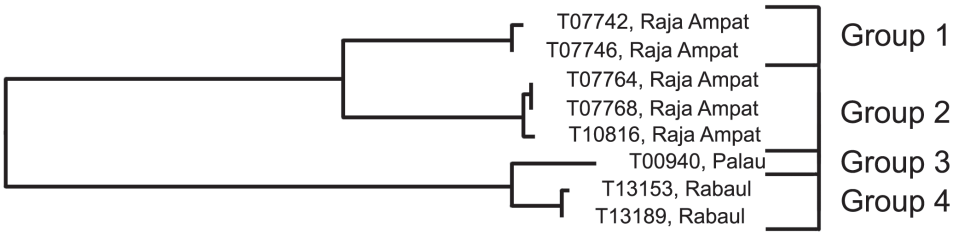


Figure 12. Relationships of 8 specimens of the *T. marinae* group based on COI.

Table 10. Results from a barcode analysis of 8 specimens of the *Trimma marinae* group, giving maximum variation within each group followed by the minimum distances between the groups (as percentages).

Group #	Locality	n	Variation	Min. Distance		
				2	3	4
1	Raja Ampat	2	0.2	4.8	15.0	15.0
2	Raja Ampat	3	0.3	0	15.6	15.3
3	Palau	1	n/a	–	0	2.0
4	Rabaul	2	0.2	–	–	0

The *Trimma marinae* group

Figs 1Q, 12; Table 10

Trimma marinae was described in the same paper as *T. nasa* (Winterbottom 2005b), based on specimens from Palau. Winterbottom (2005b) included Japan and New Britain in the distribution of the species, based on underwater photographs, and the range has since been extended to Raja Ampat (Dimara et al. 2010). Our barcode results suggest that there are four haplogroups currently identified as this species.

Analysis. The single sample (Group 3, Fig. 12) from the type locality, Palau, differs from those from Rabaul (Group 4; 2; 0.2% variance) by 2.0%, which is identical to the degree of difference suggesting discreet species. These two groups differ from specimens from Raja Ampat by a minimum of 15.0%. The latter are divided into two haplogroups. Group 1 (2; 0.2% variance) differs from Group 2 (3; 0.3% variance) by 4.8% sequence divergence.

Comments. There are currently no known morphological or colour pattern differences supporting these different haplogroups.

Discussion

The results we have presented suggest that there are nearly double the number of 'species' originally recognized in our analysis (52 versus 94) if one accepts the guideline that a 2% barcode sequence divergence between two groups roughly equates to different species

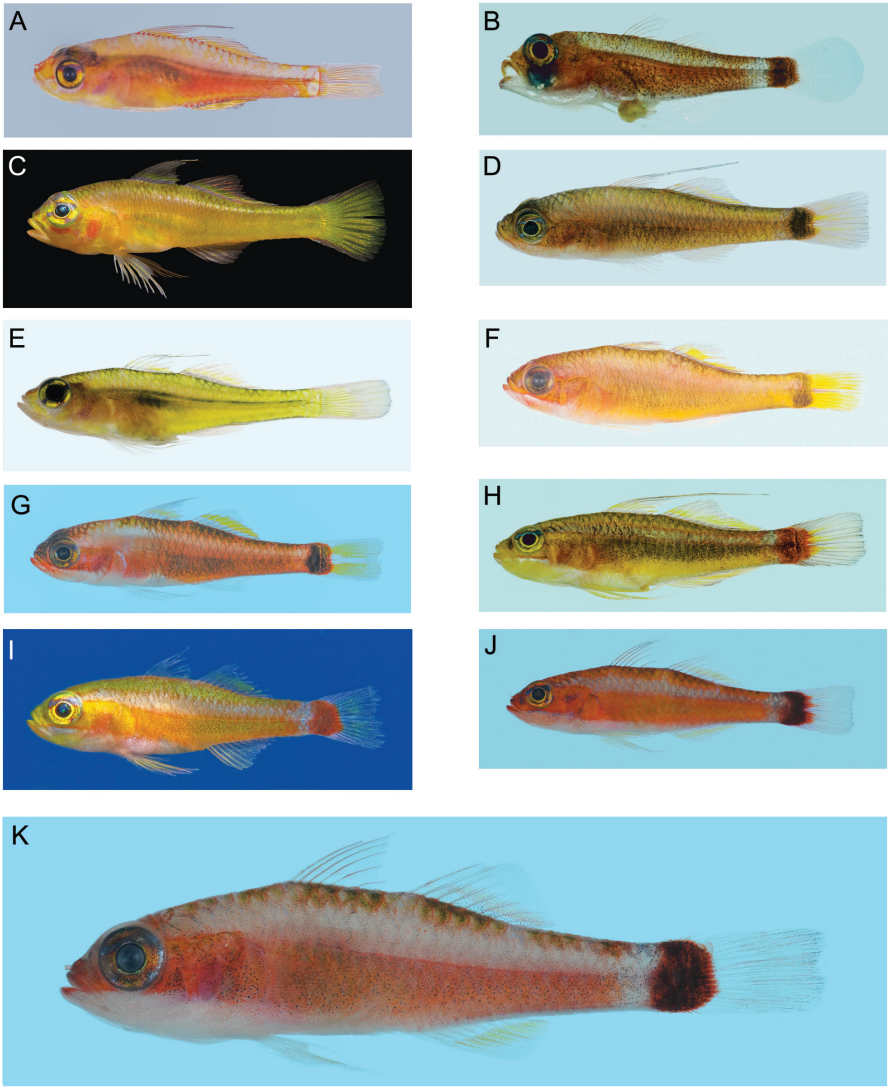


Figure 13. Left lateral views of freshly collected specimens of 10 of the 11 haplogroups forming the *Trimma tevegae* group (no image available for *T. xanthochrum* Group 2a, from Ceram), plus the phenetically basal taxon, *T. habrum*. All images by R. Winterbottom, except for C and I (courtesy of Mark V. Erdmann). Standard length, sex, locality and catalogue number given where available. **A** *Trimma habrum*, 16.8 male, Penemu I., Raja Ampat, ROM 84881 **B** *Trimma tevegae* (Group 1), 14.4 female, Uchelbeluu Reef, Palau, ROM 80390 (note prolapsed intestine) **C** *Trimma gigantum* (Group 9), Fam Is., Raja Ampat **D** *Trimma xanthochrum* (Group 2c), 19.8 male, Uchelbeluu Reef, Palau, ROM 93075 **E** *Trimma gigantum* (Group 8), 27.7 female, Uchelbelu Reef, Palau, ROM 80353 **F** *Trimma xanthochrum* (Group 2), 22.0 female, Penemu I., Raja Ampat, ROM 84885 **G** *Trimma xanthochrum* (Group 2b), 18.4 female, Rabaul, New Britain, ROM 88170 **H** *Trimma tevegae* (Group 5), 22.5 male, Koror, Palau, ROM 80312 **I** *Trimma tevegae* (Group 4), SE Misool, Raja Ampat **J** *Trimma caudomaculatum* (Group 7), 21.5 female, Rabaul, ROM 92109 (Note broken tip of second spine of first dorsal fin) **K** *Trimma tevegae* (Group 6), 16.0 male, Rabaul, ROM 92319 (group 6 is believed to represent the 'true' *T. tevegae*).

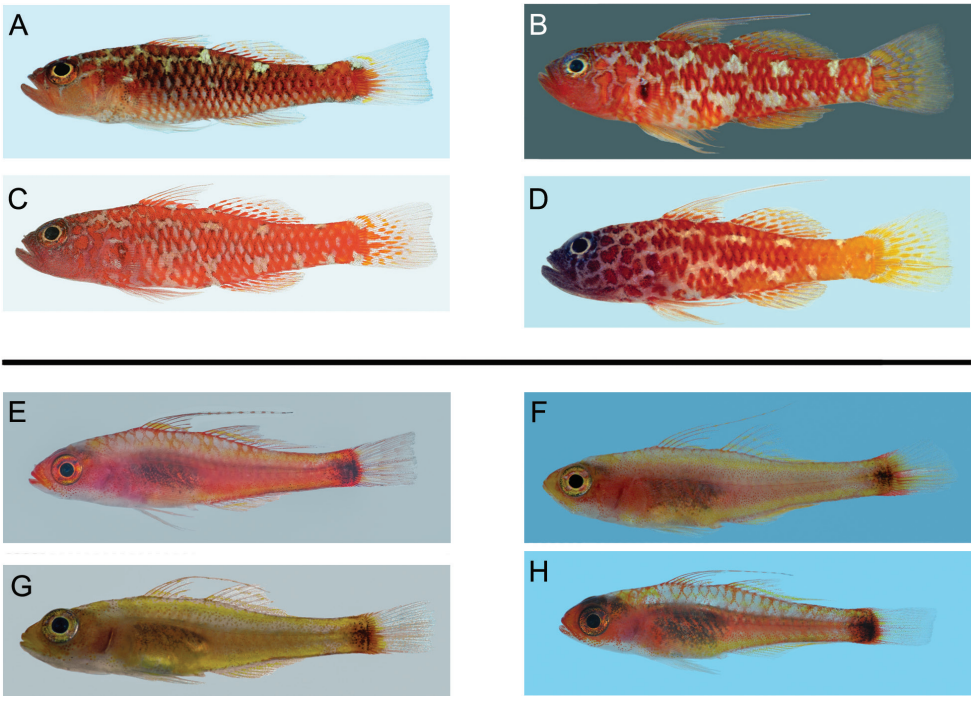


Figure 14. Left lateral views of freshly collected specimens of the four haplogroups forming the *Trimma caesiura* group (above), and the four haplogroups of the *Trimma nasa* group (below). All images by R. Winterbottom. Standard length, sex, locality and catalogue number follow the species name. **A** *Trimma caesiura*, 24.0 male, Babeldaob I., Palau, ROM 76105 **B** *Trimma naudei*, 26.7 male, Comores, ROM 59796 **C** *Trimma naudei*, 23.3 female, Nha Trang, Vietnam, ROM 73199 **D** *Trimma lantana*, 22.6 male, Helen Reef, Palau, ROM 83077 **E** *Trimma nasa*, 19.5 female, Kepotsol I., Raja Ampat, ROM 85321 **F** *Trimma nasa*, 22.6 female, New Caledonia, ROM 63925 **G** *Trimma nasa*, 16.5 female, Uchelbeluu Reef, Palau, ROM 80392 **H** *Trimma nasa*, 16.7 female, Rabaul, New Britain, ROM 92157.

(April et al. 2013). Our results differ somewhat from previous barcode studies in other genera of gobies. For example, although our findings are comparable in the magnitude of the differences we found among *Trimma* lineages (despite the fact that we used minimum distances between lineages rather than the mean distances reported by both Tornabene et al. 2010 and Baldwin et al. 2009), we often uncovered a greater percentage of cryptic species within the groups analysed above (e.g. for *T. okinawae*). This is not surprising, given the far larger area encompassed by the Indo-Pacific (vs. the Caribbean), and the more intensive traditional systematic studies of the latter area. We note that our results based on recognizing groups based on a 2% or greater difference in COI differ from a RESL/BIN analysis we performed on an updated data set in only one case. This was the recognition by the latter method of two groups of what we consider here to be *T. caudomaculatum* – one from Rabaul, and the other from Japan. Interestingly, 5 of the paratypes of this species from Japan have a few branched rays in the pectoral fin (2–5 branched, mean 3.0, n=5) whereas these rays are all unbranched in the Rabaul specimens (n=4).

Our study included samples identified as belonging to 48 named and four unnamed species. The barcode results suggest that there are 94 haplogroups separated by 2% or more sequence divergence. If future research bears out the barcode results, and assuming further that RW's estimate of the undescribed species is relatively accurate, the final number of species in the genus would be of the order of 200. Given that intensive sampling for both morphological and genetic samples of *Trimma* is lacking for the majority of Indo-Pacific coral reefs, even this number (200) may be a significant underestimate. We were unable to obtain specimens of 25 of the recognized described species (34%), and therefore we do not feel it appropriate to present the statistics found in other studies for comparative purposes (e.g. average distance between closest taxa). We are also loathe to further dissect the distance data between members of the groups we recognize above, both because these groups are not necessarily monophyletic (our analysis is based on a Neighbour-Joining network, which cannot provide phylogenetic inferences), and because we are convinced that many, if not most, of these groups contain as yet unsampled lineages which could reduce the distance values we obtained. The lack of comprehensive sampling over the vast area of the tropical Indo-Pacific, while understandable, is nevertheless frustrating.

The problem of cryptic species has been a long-standing one for biologists. With the advent of barcoding, the BOLD platform and BINs, hints of their existence have become more easily uncovered and thus available for further exploration. While the results presented in this paper may be preliminary, there are simply not enough taxonomists to check the large number of questions raised by our analysis against morphological attributes. However, our study has revealed a plethora of often very different haplogroups currently masquerading under a single specific name. The differences between these genetic lineages frequently exceeds (sometimes dramatically so) the guide-lines of a 2% difference in the barcode sequence as being equivalent to a species. Our purpose, then, is to draw attention to the magnitude of the problem facing any inventory of gobiid species (especially of *Trimma*, and potentially other small and very speciose genera such as *Eviota*), and to expose the exciting potential that further and more wide-ranging research into certain recalcitrant groups within these genera could provide in terms of biogeograpy, evolution and conservation biology.

Acknowledgments

We would like to express our appreciation for the assistance of many people in assembling the materials used in this study. In addition to the teams involved in RW's field work (identified in many of the papers cited herein), we are especially grateful to N. Delventhal (University of Manitoba, Canada), M. Erdmann (Conservation International, Indonesia), W. Holleman (South African Institute of Aquatic Biology), R. Langston and K. Cole (University of Hawaii), U. Satapoomin (Phuket Marine Biological

Laboratory), and H. Senou (Kanagawa Prefectural Museum of Natural History, Japan) for collecting and/or providing specimens of species especially targeted for this analysis. We also thank A. Bentley (Biodiversity Institute, University of Kansas), P. Bouchet (Muséum National d'Histoire Naturelle), N. Hubert (Indonesian Institute of Sciences), M. Mwale (South African Institute for Aquatic Biodiversity), S. Planes (CNRS), D. Steinke (University of Guelph), and R. Ward (CSIRO) for access to additional unpublished *Trimma* records on BOLD that were included in this study. We thank H. Braid, R. Breese, N. Serrao and J. Zhang for assistance with barcoding in the Hanner lab. We also acknowledge the BOLD team, particularly C. Steinke, for informatics support and members of the Advanced Analysis Centre (AAC) and Canadian Centre for DNA Barcoding (CCDB) at the University of Guelph for sequencing support.

Grants for field work expenses to obtain specimens used herein and the subsequent research that led to this paper was provided by NSERC Discovery Grant 7619, the ROM Foundation, the ROM's Department of Natural History (all to RW).

Lastly, we acknowledge P.D.N. Hebert for informatics and sequencing support provided to BOLD, the CCDB and the international Barcode of Life (iBOL.org) project via the Ontario Ministry of Research and Innovation, NSERC and Genome Canada (through the Ontario Genomics Institute).

References

Aoyagi H (1949) Studies on the coral reef fishes of the Riu-Kiu Islands. V. The Zooological Magazine, The Zoological Society of Japan (Tokyo) 58(9): 171–173.

April J, Hanner RH, Dion-Côté AM, Bernatchez L (2013) Glacial cycles as an allopatric speciation pump in north-eastern American freshwater fishes. Molecular Ecology 22(2): 409–422. doi: 10.1111/mec.12116

Baldwin CC, Castillo CI, Weigt LA, Victor BC (2011) Seven new species within western Atlantic *Starksia atlantica*, *S. lepicoelia*, and *S. sluiteri* (Teleostei, Labrisomidae), with comments on congruence of DNA barcodes and species. ZooKeys 79: 21–72. doi: 10.3897/zookeys.79.1045

Baldwin CC, Weigt LA, Smith DG, Mounts JH (2009) Reconciling genetic lineages with species in Western Atlantic *Coryphopterus* (Teleostei: Gobiidae). Smithsonian Contributions to the Marine Sciences (38): 111–138.

Dimara R, Fauzan A, Lazuardi M, Pada D, Allen GR, Erdmann MV, Huffard CL, Katz LS, Winterbottom R (2010) Pisces, Teleostei, Gobiidae, illustrated list of additions to the fauna of the Raja Ampat Islands, Indonesia. Check List 6(4): 619–625.

Froese R, Pauly D (2013) FishBase. www.fishbase.org [accessed on 10/2013]

Goren M (1981) Three new species and three new records of gobies from New Caledonia. Cybium, 3e ser. 5(3): 93–101.

Hagiwara K, Winterbottom R (2007) Two new species of *Trimma* from the western Pacific. Bulletin of the National Museum of Natural Science (Tokyo), ser. A., Suppl. 1: 163–174.

Herre AWCT (1945) Notes on fishes in the Zoological Museum of Stanford University. XIX. Two new Philippine gobies, with key to the genera of gobies with vomerine teeth. Proceedings of the Biological Society of Washington 58: 77–82.

Hsu T-H, Adiputra YT, Burridge CP, Gwo JC (2011) Two spinefoot colour morphs: mottled spinefoot *Siganus fuscescens* and white-spotted spinefoot *Siganus canaliculatus* are synonyms. Journal of Fish Biology 79: 1350–1355. doi: 10.1111/j.1095-8649.2011.03104.x

Hubert N, Meyer CP, Bruggemann HJ, Guérin F, Komeno RJL, Espiau B, Causse R, Williams JT, Planes S (2012) Cryptic diversity in Indo-Pacific coral-reef fishes revealed by DNA-Barcoding provides new support to the Centre-of-Overlap hypothesis. PLoS ONE 7(3): e28987. doi: 10.1371/journal.pone.0028987

Ivanova NV, Zemlak TS, Hanner RH, Hebert PDN (2007) Universal primer cocktails for fish DNA barcoding. Molecular Ecology Notes 7: 544–548. doi: 10.1111/j.1471-8286.2007.01748.x

Lobel PS (1979) Description of a new Hawaiian gobiid fish of the genus *Trimma*. Breviora, Museum of Comparative Zoology (456): 1–15.

Messing J (1983) New M13 vectors for cloning. Methods in Enzymology 101: 20–78. doi: 10.1016/0076-6879(83)01005-8

Ratnasingham S, Hebert PDN (2007) BARCODED: The Barcode of Life Data System. (www.barcodinglife.org). Molecular Ecology Notes 7: 355–364. doi: 10.1111/j.1471-8286.2007.01678.x

Ratnasingham S, Hebert PDN (2013) A DNA-Based Registry for All Animal Species: The Barcode Index Number (BIN) System. PLoS ONE 8(8): e66213. doi: 10.1371/journal.pone.0066213

Senou H, Suzuki T, Shibukawa K, Yano K (2004) A Photographic Guide to the Gobioid Fishes of Japan. Heibonsha Publishers, Japan, 534 pp. [in Japanese]

Seutin G, Bagley P, White BN (1990) Preservation of avian blood and tissue samples for DNA analyses. Canadian Journal of Zoology 69: 82–90. doi: 10.1139/z91-013

Steinke D, Hanner RH (2011) The FISH-BOL collaborator's protocol. Mitochondrial DNA 22(S1): 10–14. doi: 10.3109/19401736.2010.536538

Taylor MS, Hellberg, ME (2005) Marine radiations at small geographic scales: speciation in neotropical reef gobies (*Elacatinus*). Evolution 59(2): 374–385.

Taylor MS, Hellberg ME (2006) Comparative phylogeography in a genus of coral reef fishes: biogeographic and genetic concordance in the Caribbean. Molecular Ecology 15: 695–707. doi: 10.1111/j.1365-294X.2006.02820.x

Tornabene L, Baldwin CC, Weigt LA, Pezold F (2010) Exploring the diversity of western Atlantic *Bathygobius* (Teleostei: Gobiidae) with cytochrome *c* oxidase-I, with descriptions of two new species. aqua, Journal of Ichthyology and aquatic Biology 16(4): 141–170.

Victor B C (2010) The Redcheek Paradox: the mismatch between genetic and phenotypic divergence among deeply-divided mtDNA lineages in a coral-reef goby, with the description of two new cryptic species from the Caribbean Sea. Journal of the Ocean Science Foundation 3: 1–16.

Ward RD, Hanner R, Hebert PDN (2009) The campaign to DNA barcode all fishes, FISH-BOL. Journal of Fish Biology 74(2): 329–356. doi: 10.1111/j.1095-8649.2008.02080.x

Ward RD, Zemlak TS, Innes BH, Last PR, Hebert PDN (2005) DNA barcoding Australia's fish species. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 360: 1847–1857. doi: 10.1098/rstb.2005.1716

Winterbottom R (1984) A review of the gobiid fish genus *Trimma* from the Chagos Archipelago, Central Indian Ocean, with the description of seven new species. Canadian Journal of Zoology 62: 695–715. doi: 10.1139/z84-101

Winterbottom R (1985) Two new fish species (in *Priolepis* and *Trimma*) from the Chagos Archipelago central Indian Ocean. Canadian Journal of Zoology 63: 748–754. doi: 10.1139/z85-109

Winterbottom R (1996) A new species of gobiid fish, *Trimma benjamini*, from the western Pacific. Revue Française d'aquariologie 23: 57–60.

Winterbottom R (2001) Two new gobiid fish species in *Trimma* and *Trimmatom* (Teleostei: Gobiidae) from the Indian and Western Pacific Oceans. aqua, Journal of Ichthyology and aquatic Biology 5(1): 19–24.

Winterbottom R (2005a) On the status of *Trimma tevegae* and *Trimma caudomaculata* (Gobiidae). aqua, International Journal of Ichthyology 10(2): 51–56.

Winterbottom R (2005b) Two new species of the *Trimma tevegae* species group from the western Pacific (Percomorpha; Gobiidae). aqua, International Journal of Ichthyology 10(1): 51–56.

Winterbottom R (2011) Six new species of the genus *Trimma* (Percomorpha; Gobiidae) from the Raja Ampat Islands, Indonesia. aqua, International Journal of Ichthyology 17(3): 127–162.

Winterbottom R, Villa CA (2003) A new species of the *Trimma caesiura* complex (Gobiidae, Teleostei) from the north-eastern margin of the Australian Plate, with a redescription of the other nominal species in the complex. aqua, Journal of Ichthyology and aquatic Biology 7(1): 13–28.

Winterbottom R, Zur M (2007) Three new species of the *Trimma* from Palau, Western Pacific (Percomorpha; Gobiidae). aqua, International Journal of Ichthyology 13(1): 13–24.

Yoshino T, Araga C (1975) In: Masuda H, Araga C, Yoshino T (Eds) Coastal Fishes of Southern Japan. Tokai University Press, Tokyo, 382 pp.