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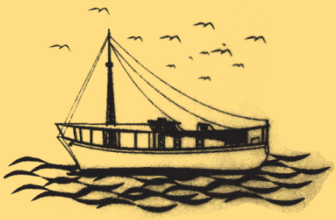

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Discovery of two new genera of detritivorous aquatic beetles Toneroides, in the Venezuelan Amazon (Coleoptera: Noteridae: Noterinae)

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ABSTRACT

Analysis of specimens of *Tonerus wheeleri* (MALUZ) reveals two distinct lineages. This finding led to the description of *Tonermorpha* gen. nov. with two species, *T. unguilonga* sp. nov. and *T. submersa* sp. nov. and *Tonerinus* gen. nov. with eight species: *Tonerinus amazonas* sp. nov., *T. amazonensis* sp. nov, *T. amazonicus* sp. nov., *T. hypognathus* sp. nov., *T. pemonus* sp. nov., *T. sazhnevi* sp. nov., *T. spangleri* sp. nov. and *T. toboganensis* sp. nov. *Tonerinus* gen. nov. differs from *Tonerus* Miller, 2009, in having serrate metatibial spurs, and other diagnostic features. *Tonermorpha* gen. nov. with long, slightly curved nails on each tarsus for a better grip on rocky stream substrates distinguishes it from both genera in addition to other diagnostic characters of its own. *Tonerinus* gen. nov. and *Tonermorpha* gen. nov. are distinguished by: Spines on the basal mandible margin and lacinia; microspinous margins on femurs and tibiae (very marked on the protibia of *Tonerinus*); a dorsoventral spur on the protibia; crenulate protarsal nails; serrate metatibial spurs (the posterior one doubly so); bitruncate (*Tonerinus*) or doubly sinuate (*Tonermorpha*) apical margin of the proventral process. A detritivorous and scavenging behavior is proposed for adults in all three genera, different from the predatory behavior generally associated with the family Noteridae, based on the spiny characteristics of the mandible and lacinia. All species are described and illustrated in detail, including habitus, genital terminalia, genital sclerites, sclerites

and cephalic appendages, locomotion sclerites. Finally the spatial distribution of Toneroides species in Venezuela is presented.

Key words: Amazonas, Coleoptera, new species, *Tonerus*, taxonomy, Venezuela.

Descubrimiento de dos nuevos géneros de escarabajos acuáticos detritívoros Toneroides, en el Amazona venezolano (Coleoptera: Noteridae: Noterinae)

RESUMEN

El análisis de ejemplares de *Tonerus wheeleri* (MALUZ) reveló dos linajes distintos. Este hallazgo dio lugar a la descripción de *Tonermorpha* gen. nov., con dos especie, *T. unguilonga* sp. nov., y *T. submersa* sp. nov.; y *Tonerinus* gen. nov., con ocho especies: *Tonerinus amazonas* sp. nov., *T. amazonensis* sp. nov., *T. amazonicus* sp. nov., *T. hypognathus* sp. nov., *T. pemonus* sp. nov., *T. sazhnevi* sp. nov., *T. spangleri* sp. nov. y *T. toboganensis* sp. nov. *Tonerinus* gen. nov. difiere de *Tonerus* Miller, 2009, por presentar los espolones metatibiales serrados, y otras características diagnósticas. *Tonermorpha* gen. nov., con uñas largas, ligeramente curvadas en cada tarso, para un mayor agarre en los sustratos rocosos de corrientes, lo distingue de ambos géneros; además de otros caracteres diagnósticos propios. *Tonerinus* gen. nov. y *Tonermorpha* gen. nov. se distinguen por: Espinas en el margen basal mandibular y lacinia; márgenes microespinosos en fémures y tibias (muy marcados en la protibia de *Tonerinus*); un espolón dorsoventral en la protibia; uñas protarsales crenuladas; espolones metatibiales serrados (el posterior doblemente); margen apical bitruncado (*Tonerinus*) o doblemente sinuado (*Tonermorpha*) de la apófisis proventral. Se propone un comportamiento detritívoro y carroñero para los adultos en los tres géneros, diferente al comportamiento depredador generalmente asociado a la familia Noteridae, basado en las características espinosas de la mandíbula y lacinia. Todas las especies se describen e ilustran en detalle, incluyendo *habitus*, terminalia genital, escleritos genitales, escleritos y apéndices cefálicos, escleritos de locomoción. Finalmente se presenta la distribución espacial de las especies Toneroides en Venezuela.

Palabras clave: Amazonas, Coleoptera, nuevas especies, taxonomía, *Tonerus*, Venezuela.

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INTRODUCTION

The tribe Tonerini, created by Miller in 2009, was based on a single species of aquatic beetle: *Tonerus wheeleri* endemic to the Amazon region of Venezuela. However, later studies (Baca *et al*. 2017) synonymized it, considering it a monotypic tribe and genus. The species was described from specimens collected at Tobogán de la Selva, on the banks of the Coromoto River, Amazonas State. In this paper, we present the description of two new genera that, although they share characteristics with the tribe Tonerini, they differ from the genus *Tonerus*.

The characterization of these new taxa is supported by a meticulous comparative study of the external morphology, both dorsal and lateral, complemented by a thorough analysis of the individual genitalia of each of the ten species involved in the new genera (García y Briceño 2023). The genital terminalia of both generic taxa are described in detail, as well as the cephalic sclerites, mouth appendages and locomotion sclerites (García y Briceño 2023). The described species represent new morphological stages with characteristic of both generic taxa, which justifies their separation from the genus *Tonerus*.

The new species are clearly distinguished from *Tonerus wheeleri* by a number of external and internal morphological features. Among these features are the shape of the cephalic, dorsal and ventral sclerites, the structure of the genitalia of the male and female, the morphology of the terminalia, the shape of the metatibial spurs, and the shape of the tarsal claws. The research assumes a detritivorous and scavenging behaviour for the adults of the genus, based on the spiny characteristics of the mandible and lacinia (Guzmán-Soto and Tamaris-Turizo 2014, Chará-Serma *et al*. 2010) which differs from the predatory behaviour generally associated with the family Noteridae. The objective of this research is the description of two new genera and ten new species brings the number of known species to eleven and the number of genera within the *Tonerus* group to three. This discovery represents a significant advance in the knowledge of the biodiversity of this group of beetles in Venezuela.

MATERIAL AND METHOD

The material was collected in the locality designated as “El Tobogán de la Selva”, a park or recreational resort located in the Ature municipality of Amazonas

state, south of Puerto Ayacucho (1A y 1B). This region is characterized by the presence of a tropical rainforest with a mean annual temperature of 25 °C and an annual rainfall of 2500 mm. Eleven specimens were analyzed.

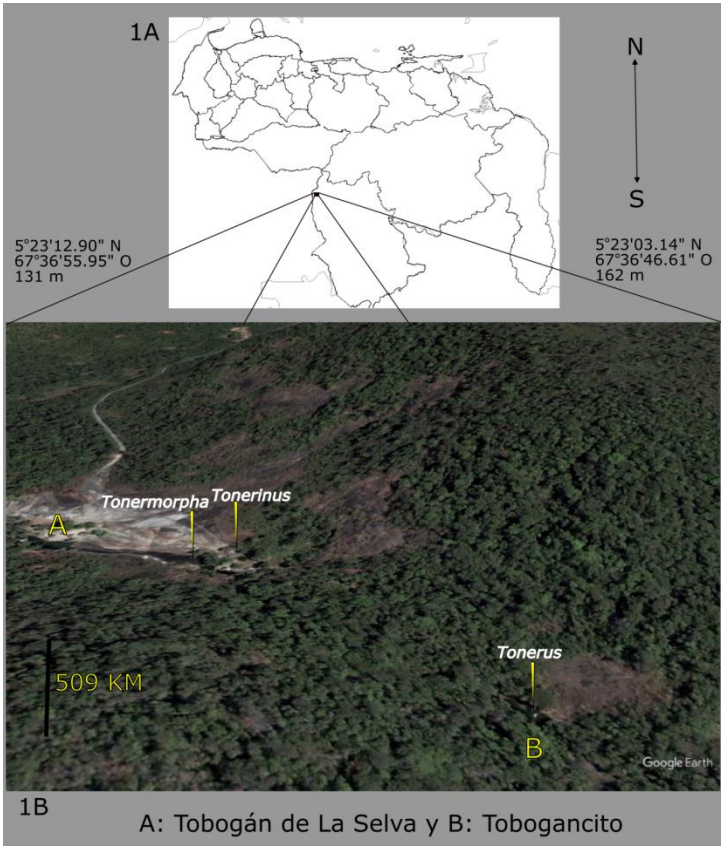

Figure 1A. Distribution of *Tonerus wheeleri* species group in Venezuela. Geographical location in the Amazonas state of the locality of the "Tobogán de la Selva" beach camp.
Figure 1B. Extraction of the local area or macrohabitat in which the three species of Tonerini are distributed: *Tonerinus* gen. nov., *Tonermorpha* gen. nov. and *Tonerus wheeleri* Miller, 2009; A) Collection area of the eight *Tonerinus* along the vegetation above the runoff on the rock on the left bank of the Río Coromoto, "Tobogán de la Selva" and collection site of the two *Tonermorpha* species in the "Tobogán de selva" S of Pto Ayacucho [Photo: Mauricio García, January-2003], the satellite image illustrates the point of collection of *Tonerinus* and *Tonermorpha* by the author(satellite image Google Earth, January, 2003); B) Tobogancito de la Selva. *Tonerus* specimens were collected in 2007 and provided on loan to Andrew Short and Kevin Miller.

Nine of the specimens were discovered in various natural habitats, including decomposing log debris, a *Madi* microhabitat, and superimposed on runoff from a hygrotrophic microhabitat, among the nascent grass accumulated on the north bank of the Coromoto River (García *et al*. 2016). The other two were collected on the rocky bank of the Rio Coromoto stream. All specimens were collected using a hand-held suction device at both habitat sites.

The identification and separation of the ten morphospecies was performed using a LEICA M10 stereo microscope with an 80x resolution objective, and a binocular compound microscope OPTIMA XSZ-207 was employed for microscopic observation. The genital sclerites were extracted according to the established protocol, which involves cleaning and removal of connective tissue with 10% potassium hydroxide (KOH) solution, followed by washing with distilled water. The sclerites were preserved in a double-mounted cardboard triangle containing the type specimen, using an alcohol-based entomological glue. The sclerites were then illustrated and enhanced in the digital design program Inkscape version 1.3.0. A combination of drawing and shading techniques was employed to create accurate and detailed illustrations of the sclerites. Satellite imagen was obtained from Google Earth Pro. A taxonomic key was constructed to differentiate the genus *Tonerus* from the newly identified taxa *Tonerinus* and *Tonermorpha*, as well as a map illustrating the zonation of the species within the tribe.

RESULTS

Taxonomic

Coleoptera Linnaeus, 1758
Adephaga Schellenberg, 1806
Noteridae Thomson, 1860
Noterinae Thomson, 1860
Tonerini Miller, 2009

Tonerinus García, **gen**. **nov**.
http://zoobank.org/urna:lsid:zoobank.org:act:9660A569-2E01-4C1E-92CA-D798F75A2817
(Figs. 2-5)

Type species. *Tonerinus amazonas* Garcia, **sp**. **nov**. by original designation.

Differential diagnosis. The genus *Tonerinus* gen. nov. is characterized by a robust body shape of the species, with a broad head, prognathous and hypognathous depending on the species, small eyes and a long labrum. The genus *Tonerinus* gen. nov. is characterized by a robust body shape of the species, with a broad head, prognathous and hypognathous depending on the species, small eyes and a long labrum.

Description. Species broad, greater width in humeral region. Lateral outline continuous between pronotum and elytron, with uniform curvature both anterior and posteriorly. Integral surface shiny and evenly covered with very fine isodiametric (squamous or microreticulate) epithelial cells. Pronotal ridge with lateral margin extending narrowly at posteroangular base, expanding and widening evenly towards anteroangular margin and along anterior margin. Head broader than long with labrum *prostratum* and *retroflectum* depending on species, broad and long, usually with flat surface (Fig. 2A). Mandible broad with two premolars; first premolar stout and broad, second premolar short with shaped surface of small teeth (molars); two-thirds of basal length with series of long and short, thick and thin spines in a row (Fig. 2B). Maxilla robust with coarsely spiny lacinia; maxillary palpus with the first three palpomeres similar, the fourth palpomere is long and rectangular with two small tactile sensors at the apex (Fig. 2C). Lip with two palpiferous openings in prementum; labial palp with three spatial palpomeres and basal palp inserting through palpiferous openings adjacent to the dorsal prementum; apical labial palpomere long and slender with two broad tactile sensoria, one preapical and one apical (Fig. 2D). Antenna short with bilobed scape, pedicel short, remaining rectangular antennomeres slightly shorter or longer than pedicel, each with superficial sensory; apical antennomere long and attenuate at apex with three sensory micropelons (Fig. 2E). Prosternum broad anteriorly, convex medially. Apophysis proventral extremely broad, flat and glabrous with bitruncate apex (Fig. 3). Metaventrite glabrous, medially broad and rounded. Platform noteroidal broad, glabrous, extended anteriorly towards metaventrite; metacoxal lobes with glabrous apices. Metacoxa and metafurca laterally fused to form a ring. Abdominal ventrites with glabrous surface; ventrite III+IV very broad; ventrites V and VI slender; ventrite VII glabrous, broad and long with rounded apex. Fore leg with broad, short femur, posterior margin with a row of short, thick spines bordering it; tibia very short and broad bordered with strong short, thick spines at the base and long, stout

spines in the apical half; protibial spur thick and slender, sparsely curved, pointed at the apex; protarsus long and thick with a medium-sized discoidal sucker at apex; tarsomere II long and thick with a small discoidal sucker at apex; tarsomeres III and IV slender with fine ventral spines; tarsomere V long and slender with a pair of long apical claws with crenulate ventral edge (Fig. 4A). Middle leg with broad femora slightly longer than femora, with two parallel rows of thick, short spines bordering anterior margin; mesotibia broad, one-third longer than protibia, anterior and posterior margins with long, stout spines bordering it, apex crowned with short, long, thin spines; tarsomere I very thick and long with a medium-sized discal sucker at the apex; tarsomere II short and broad with a small discoidal sucker at the apex; tarsomeres III and IV short with a thick, long spine at their apices; tarsomere V long with a pair of long, thin spines cleft in the middle (Fig. 4B).

Hind leg with femur broad at the base and attenuated at the apex, slightly longer than the mesofemur, bordered anteriorly with short, thick spines; metatibia broad one-third larger than mesotibia, bordered anteriorly and posteriorly with long, short, coarse spines and apex crowned with medium and coarse spines with the anterior spur long and coarse with the apical margin doubly serrate with coarse teeth at the apex, posterior spur short and broad with a row of short, fine serrations at the apex; metatarsus with the first tarsomere thick, long and cylindrical with spines at the apex, the remaining tarsomeres are short and cylindrical with spines at the apex and a pair of thin, straight single claws (Fig. 4C). Genital terminalia with the VIII abdominal sternite with slight sexual dimorphism, broad, long, longitumedially with a broad depression on dorsal face projecting on ventral face; dorsal surface densely setose; in anterior and posterior view forms an arc (Fig. 5); IX abdominal sternites short, broad and pseudo-rounded with varied rectangular basal margin (see species); gonocoxoesternites symmetrical and with sexual dimorphism (see species). Genital sclerite of female with short L-shaped laterotergites; laterotergal base extending beyond base along laterodorsal margin; gonocoxa flat with pointed apex. The median lobe on the genital sclerite of the male has a deep ventral groove that curves along its surface; viewed laterally, it shows a broad, bifurcated phallobase.

Etymology. The new epithet is a diminutive reference to the name *Tonerus*, preserving the root of the genus.

Tonerinus amazonas García, **sp**. **nov**.
(Figs. 1A-B, 2A, 6A-7A-8A-G)
http://zoobank.org/urna:lsid:zoobank.org:act:709009BC-A929-4ECD-B766-E432A87D54D7

Diagnosis. Seen dorsally *Tonerinus amazonas* sp. n. is widest at the humeral margin. In addition, the anterior margin of the pronotum in this species is greater than the cephalic width, making it wider anteriorly than posteriorly.

Location type. Tobogán de la selva, Ature, Amazonas, Venezuela.

Material type. Holotype ♂, from Venezuela, Amazonas, Ature, Tobogán de la selva, 20.i.2003, M. García and M. Balke cols., (5º 23'12.01" N and 67º 36'57.34" W), 125 m (MALUZ06649).

Description. Broad oval body shape with rounded anterior and posterior margin and apex as broad as anteriorly (Fig. 6A). In lateral view the dorsal convexity is slightly discontinuous between head and pronotum, with lobulation of the elytral margin between the first and second third followed by arching in the apical third (Fig. 7A). Length 2.15 mm and width 1.10 mm, widest at humeral margin. Dorsal colouration dark *fulvus* (brown) with dark longitudinal and transverse bands crosswise but diffuse in the central area which is less dark and a very diffuse arcuate band on the anterior elytral margin. Ventrally the colouring is fuliginosus (brownish black). Head prognathous wider than long with small eyes 3x its diameter apart; in lateral view narrowly convex; labrum long, convex and vertical or prostratum (Figs. 2A, 7A). Pronotum long, 1.5x head length, sparsely convex; lateral margin narrow with border almost straight 0.7x medial length, and continuous with elytral border (Fig. 7A). Elytra with dorsal surface fine and sparsely punctate; lateral margin slightly sinuous; viewed laterally the dorsum is convex andundulate at the lateral margin (Fig. 7A). IX abdominal sternite short and broad, subrectangular with very short, broad base and bilobed at basal margin with two micro-setae on each side; one membranous ventral side with sclerotised margins and one sclerotised dorsal side (Fig. 8F). Gonocoxoesternites bilobed with broad, rounded posterior margin and narrow anterior margin with rounded dorsal and ventral apodemas (Fig. 8G). IX sternite broad and short with rounded apex and broad base and with bilobed margin and several short fine setae on each lobe (Fig. 8F).

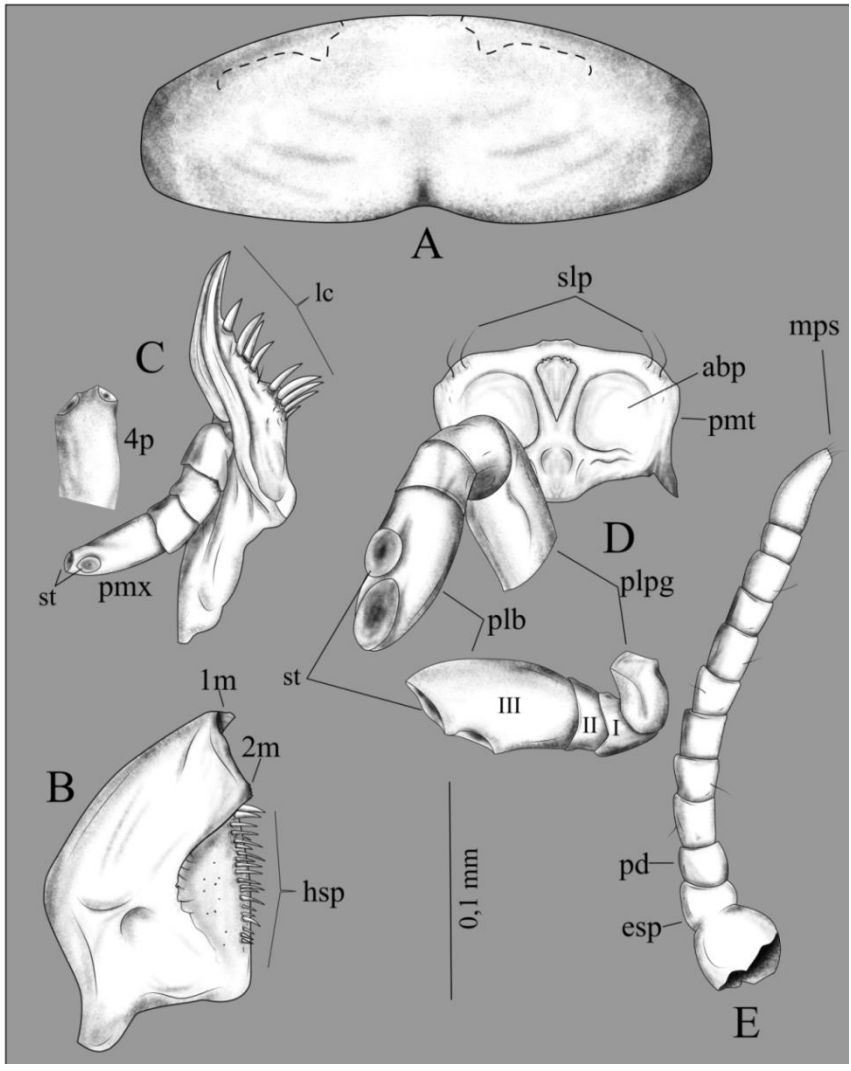

Figure 2. Cephalic sclerites and mouth appendages in species of *Tonerinus* **gen. nov**. A. Labrum, B. Left mandible, 1m = first molar, 2m = second molar, hsp = irregular row of mandibular spines, C. Left maxilla, lc = lacinia, pmx = maxillary palpus in anterior view, 4p = apex of fourth maxillary palpomere in lateral view, st = tactile sensory, D. Lip, abp = palpal aperture, pmt = prementum, slp = lateral setae of prementum, plb = labial palpus in anterior and lateral views, plpg = palpiger (basal palpomere of labial palpus fused behind prementum), E. Antenna, sp = scape, pd = pedicel.

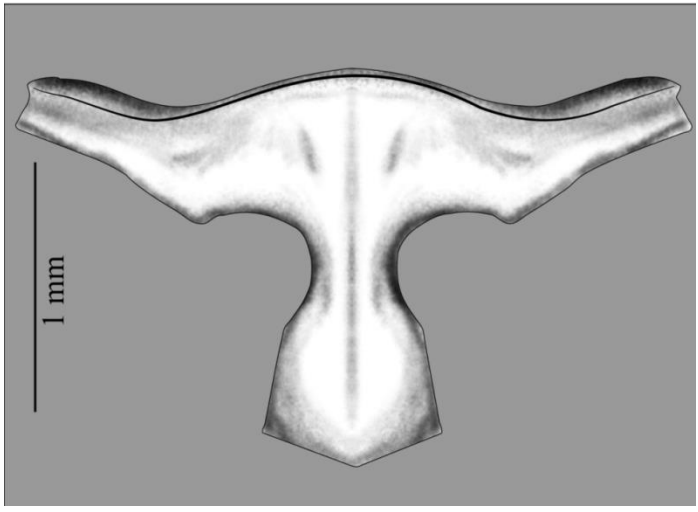

Figure 3. Apophysis proventralis of *Tonerinus* species **gen**. **nov**.

Gonocoxosternite with broad posterior end almost rounded and narrow anterior margin with rounded apodemes and series of short fine setae on basal lateral margin (Fig.8G). Male genital sclerite with median lobe curved from middle, attenuating to apex; broad bilobed phallobase with sinuous margin; right paramere short and broad with acute end and left paramere curved with acute L-shaped base and several apical setae (Figs. 8A-E).

Female. Unknown.

Etymology. The epithet refers to the local region in Venezuela and dedicates the species to the state of Amazonas.

Habitalogy. The species was collected in a microhabitat of the limnetic/lentic hydroecological system, "*Madis*" (García *et al*. 2016).

Distribution. Restricted to the locality of the Tobogán de la selva recreational park located in the riparian corridor of the Río Sipapo and Río Coromoto, Amazonas State.

Tonerinus amazonensis García, **sp**. **nov**.
(Figs. 1A-B, 2A, 6B-7B, 9A-C)
http://zoobank.org/urna:lsid:zoobank.org:act:C410B933-55DA-45F7-A228-390D3E37C469

Differential diagnosis. *Tonerinus amazonensis* sp. nov. resembles *T. amazonas*, but with a slightly shorter and less broad pronotum and a non-sinuate elytral lateral margin. However, *T. amazonensis* sp. n. differs in the elytral pattern. Instead of longitudinal and transverse bands, it has four very diffuse corner maculae with a central *fulvus* settlement darker than the rest of the elytral surface. In addition, *T. amazonensis* has a more extended head, similar to *T. amazonas.* Viewed laterally, the habitus of *T. amazonensis* is wavy with the lateral edge of the pronotum rounded and without elytral lobulation. In contrast, *T. amazonas* has a slightly rounded, almost straight elytral margin and an elytral lobulation almost in the middle.

Localidad tipo. Tobogán de la selva, Ature, Amazonas, Venezuela.

Material type. Holotype ♀, from Venezuela, Amazonas, Ature, Tobogán de la selva, 20.i.2003, M. García and M. Balke cols., (5º 23'12.01" N and 67º 36'57.34" W), 125 m (MALUZ06648).

Description. Body shape broad oval with discontinuous convexity between head and pronotum; rounded anterior and posterior margin and broad apex; with extended cephalic prognathism (Fig. 6B). In lateral view it is ventrally undulated without lobulation of the elytral margin followed by an arching in the apical third (Fig. 7B). Length 2.20 mm and width 1.10 mm, widest at humeral margin. Dorsal colouration fulvous with four slightly obscured corner maculae separated by a distinctly reddened blurred central area and a blurred arc on the anterior margin. Head broader than long, prognathous, with small eyes 3x its diameter apart; sparsely convex when viewed laterally with discontinuity between labium and clypeus; labium long convex and prostratum (Fig. 2A). Pronotum long 1.5x cephalic length, sparsely convex; broad lateral margin viewed laterally with rounded edge, of equal medial length and discontinuous with elytral margin. Elytra convex with fine, slightly punctate surface with thick ventral margin, and seen laterally straight in the first two elytral thirds, arcuate in the apical third (Fig. 7B). Gonocoxoesternite broad pseudo rectangular with rounded apodemes and a sharp lateral apodeme; dorsal mar-

gin with a series of basal setae (Fig. 9A). Female genital sclerite with very short laterotergite forming a basal lobe extending along laterodorsal margin of gonocoxa; small gonocoxa with broad apex with a row of setae extending to almost apical half of lateroventral margin, lobed anteriorly (Figs. 9 B, C).

Male. Unknown.

Etymology. The new epithet is dedicated to the gentilicio of origin or belonging of the species to the state of Amazonas.

Habitalogy. Similar to the previous species.

Distribution. Similar to the previous species.

Tonerinus amazonicus García, **sp**. **nov**.
(Figs. 1A-B, 2A, 6C-7C, 10A-G)
http://zoobank.org/urna:lsid:zoobank.org:act:B5D9896A-2E19-4039-B408-70F19757FD15

Differential diagnosis. This species is distinguished from those described above by unique characteristics. Firstly, the pronotal margin is narrower in the transverse half. This is because the lateral margins are not arched, but taper in the middle, almost forming a straight line. Secondly, the elytral pattern of perpendicular bands is very thick, more concise and not very blurred.

Locality type. Tobogán de la selva, Ature, Amazonas, Venezuela.

Material type. Holotype ♂, from Venezuela, Amazonas, Ature, Tobogán de la selva, 20.i.2003, M. García and M. Balke cols., (5º 23'12.01" N and 67º 36'57.34" W), 125 m (MALUZ06617).

Description. Body shape broad oval, convex with rounded anterior and posterior margins: viewed laterally there is discontinuity between head and pronotum (Fig. 6C). Lateral view convex with sinuous ventral margin (Fig. 7C). Length 2.25 mm and width 1.15 mm, widest at humerus. Dorsal colouration dark *fulvus* with elytral bands *fuliginosus*; ventrally colouration *fuliginosus*. Head large

prognathous, broader than long with small eyes 3x their diameter; labrum long, convex and prostratum discontinuous with clipeal margin (Fig. 2A); lateral view slightly flat surface. Pronotum long 1.5x cephalic length, surface slightly convex; lateral view pronotal margin equal to 0.8 x medial length with margin narrowing posteroangularly and widening posteriorly to anteroangular apex, rounded edge discontinuous with elytral margin. Elytra convex with finely punctate surface; ventral margin arcuate only in apical third. IX abdominal sternite broad, ovoid rounded with very short, lobed base (Fig. 10F). Gonocoxosternite short, broad, narrow anterior margin with broad, triangular apodemes; posterior margin very broad and sinuous with rows of lateral setae (Fig. 10G). Genital sclerite of male with broad median lobe, curved in apical half attenuated at apex; falobase broad and bilobed. Right paramere broad, turned in middle and left paramere long with two apical thirds broad and one basal third attenuate (Figs. 10A-E).

Female. Unknown.

Etymology. The epithet "*amazonicus*" is an adjective of Latin origin meaning "belonging to or relating to the Amazon" found in the Amazon basin.

Habitalogy. Similar to the previous species.

Distribution. Similar to the previous species.

Tonerinus hypognathus García, **sp**. **nov**.
(Figs. 1A-B, 2A, 6D-7D, 11A-G)
http://zoobank.org/urna:lsid:zoobank.org:act:485A5BFF-BD90-4952-A206-2D59A33A8BC8

Differential diagnosis. *Tonerinus hypognathus* sp. n. is distinguished from other species of the genus by a number of unique characteristics. It has a *hypognathous* head, i.e. it has a very downward sloping head. This means that only the vertex is visible in dorsal view, and the surface of the head is flattened in lateral view. *Tonerinus hypognathus* has a more robust and convex body shape from the labrum. The width and length of the pronotum are greater than in other species of the genus. The elytral banding pattern is more diffuse in the elytral half. In lateral view, the marginal margin of the pronotum is almost straight and is in line with the

elytral margin. These distinctive features allow differentiation of *T. hypognathus* from the other species of the genus *Tonerinus*.

Locality type. Tobogán de la selva, Ature, Amazonas, Venezuela.

Material type. Holotype ♂, from Venezuela, Amazonas, Ature, Tobogán de la selva, 20.i.2003, M. García and M. Balke cols., (5º 23'12.01" N and 67º 36'57.34" W) 125 m (MALUZ06650).

Description. Body shape robust, broad oval and very convex, with the anterior margin rounded, slightly discontinuous with the pronotal margin the apical end in less rounded and less broad (Fig. 6D); in lateral view it is very convex with the labrum completely inclined; the ventral margin is almost straight except for the somewhat arched elytral apex (Fig. 7D). Length 2.26 mm and width 1.15 mm, widest at humerus and posterior margin of pronotum. Testaceous colouration on dorsum with the cross pattern of elytral bands very blurred except for the apex of the longitudinal band. Head as broad as long, hypognathous, flattened in lateral view and long, convex labrum and prostratum below the longitudinal axis of the body (Fig. 2A); small eyes 4x its diameter apart. Pronotum long and broad, 2x cephalic length, convex; anteriorly with a row of small circles or beads along it and the posterior margin with a short C-shaped row of small ovals above the scutellar margin; in lateral view the pronotal margin is broad with straight edge, in line with the elytral margin and equals the medial length. Elytra very convex with finely punctate surface with ventral margin straight in first two thirds and arched at apex. IX abdominal sternite broad with sinuous apical margin and rounded lateral margins with short, bilobed base (Fig. 11F). Gonocoxosternite short and broad with narrow anterior margin and broad, short, rounded apodemes (Fig. 11G). Genital of male with broad median lobe of bilobed phalaobase with apical margin curved and attenuate at apex; left paramere broad in two apical thirds with one of the margins sinuous and one basal third attenuate and right paramere broad pseudo rectangular turned in the middle, apex and base attenuate (Figs. 11A-E).

Female. Unknown.

Etymology. The species is named "*hypognathus*" because of the inclined position of the head with the jaws vertical, different from the prognathous position of the previous species.

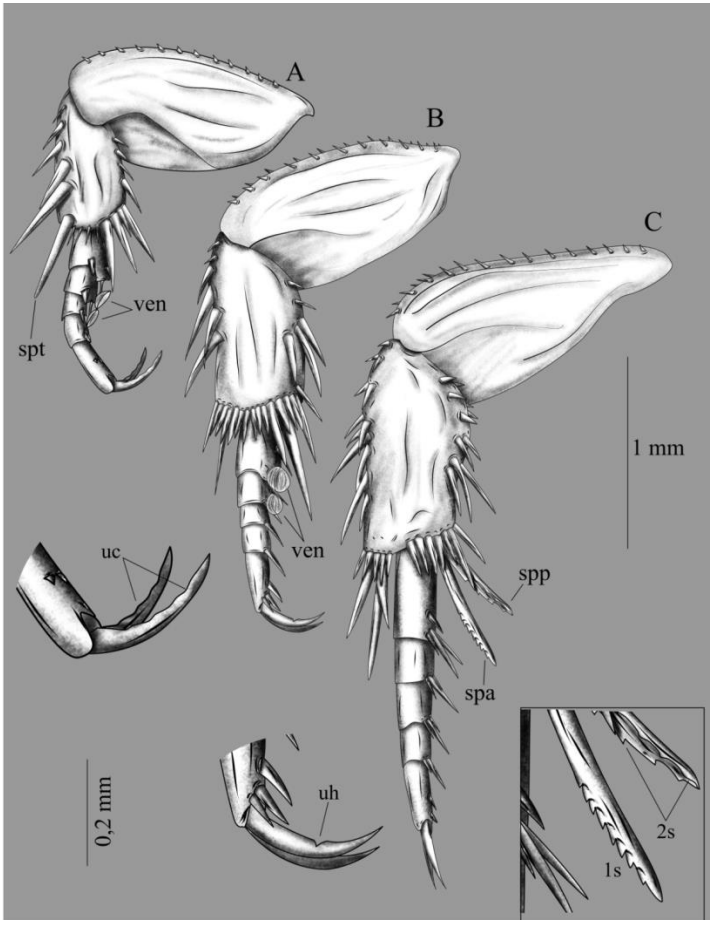

Figure 4. locomotion sclerites of *Tonerinus* gen. nov. species: A. Propata, B. Mesopata and C. Metapata. Metapata: spt = protibial spur, ven = protarsal and mesotarsal disc suckers, uc = protarsal nail with crenulated ventral edge and uh = mesotarsal nail with cleft ventral edge, spp = posterior spur doubly serrate at apical margin and spa = anterior spur serrate at apical margin, 2s = double row of teeth and 1s = single row of teeth.

Habitalogy. Similar to previous species.

Distribution. Similar to previous species.

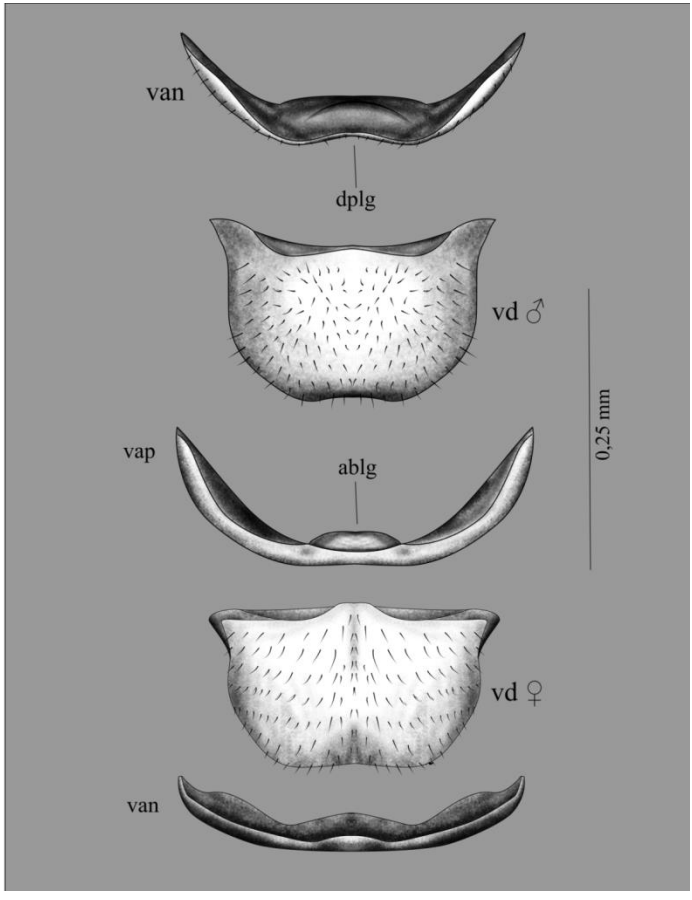

Figure 5. VIII abdominal sternite in *Tonerinus* species gen. nov.: vd = dorsal view of VIII abdominal sternite of male and female specimens, van = anterior view, dplg = dorsal longitudinal depression, vap = posterior view, ablg = ventral longitudinal bulge.

Tonerinus pemonus García, **sp**. **nov**.
(Figs. 1A-B, 2A, 6E-7E, 12A-G)
http://zoobank.org/urna:lsid:zoobank.org:act:3B977CA8-B3FC-4E35-BBE1-99D65730F620

Differential diagnosis. *Tonerus pemonus* sp. n. is related to *T. spangleri* sp. n., but differs from it in a number of key features. *Tonerinus pemonus* has bicoloured colouration on the head and pronotum, which is distinct from the elytral coloura tion. The design of the elytral bands in *T. pemonus* is different from that of *T. spangleri*.

In *T. pemonus* the elytral bands form a V-shape between the transverse maculae and the apical macula. In addition, the basal band is arched and joins longitudinally with the anterior transverse band. In contrast, *T. spangleri* has a cross-shaped pattern. In lateral view, *T. pemonus* is very broad and convex from labrum to apex, with a sinuous ventral margin. This characteristic distinguishes it from the other species described above.

Locality type. Tobogán de la selva, Ature, Amazonas, Venezuela.

Material type. Holotype ♂, from Venezuela, Amazonas, Ature, Tobogán de la selva, 20.i.2003, M. García and M. Balke cols., (5º 23'12.01" N and 67º 36'57.34" W), 125 m (MALUZ06647).

Description. Robust, highly convex oval shape with rounded anterior and posterior margins (Fig. 6E); in lateral view shows prominent arching without dorsal discontinuities and a doubly sinuous ventral margin (Fig. 7E). Length 2.20 mm and width 1.16 mm, greater width on humerus. Colouring of dorsum bicoloured with head and pronotum testaceous yellowish and elytra testaceous reddish with elytral bands forming a dark V in apical half a crescent in basal half connected longitudinally. Ventrally only the proventral process, metaventrite and noteroidal plate are fuliginosus, abdominal ventrites reddish testaceous and the rest of the sclerite yellowish testaceous. Head broader than long, robust and convex, slightly hypognathous or inclined with labrum below longitudinal axis of body; labrum long, convex and prostratum (Fig. 2A); eyes small, 3x their diameter apart. Pronotum long, 1.5x cephalic length; anterior margin with series of small circles or beads along it with some setose points and posterior margin with short row of small C-shaped ovals in front of scutellar margin; in lateral view convex and pronotal margin broad and rounded edge not in line with elytral margin, and equal to its medial length. Elytra with finely punctate surface and some setae spaced at apex; in lateral view very convex on dorsum and ventral margin sinuous, with a small broad lobulation between the first elytral thirds. IX abdominal sternite (Fig. 12F). Gonocoxosternite (Fig. 12G). Genitalia of male with median lobe broad in basal half and attenuate in apical half with curved, acute apex; falobase very broad with sinuous, bilobed margins; right paramere S-shaped twisted with bilobed base and left paramere of equal length to right with two broad apical thirds with long, thick setae at apex and attenuate basal third (Figs. 12A-E).

Female. Unknown.

Etymology. The new species is dedicated to the Pemon ethnic group.

Habitalogy. Similar to previous species.

Distribution. Similar to previous species.

Tonerinus sazhnevi García, **sp**. **Nov**.
(Figs. 1A-B, 2A, 6F-7F, 12A-G)
http://zoobank.org/urna:lsid:zoobank.org:act:20D5AB31-2C96-4493-9197-737B6D0A8B2C

Differential diagnosis. The species is similar to *T. amazonas* and differs from it only in lateral view, as it is wider and much more arched dorsally, has no dorsal discontinuity and the head is more inclined with respect to *T. amazonas*. Another difference is observed in the lateral margin of the pronotum which is pseudo-rounded at the edge in contrast to the straight edge of *T. amazonas*. This condition separates it from the rest of the species of the genus.

Locality type. Tobogán de la selva, Ature, Amazonas, Venezuela.

Material type. Holotype ♀, from Venezuela, Amazonas, Ature, Tobogán de la selva, 20.i.2003, M. García and M. Balke cols., (5º 23'12.01" N and 67º 36'57.34" W) 125 m (MALUZ06646).

Description. Body shape oval and broad with rounded anterior and posterior margins and lateral margin with a strong discontinuity between head and pronotum and slightly sinuous in the elytral region (Fig. 6F); in lateral view the dorsum is very convex and the ventral margin is doubly sinuous (Fig. 7F). Length 2.30 mm and width 1.18 mm, greatest width at the level of the humerus. Colouring of dorsum *fulvus* with diffusely darkened perpendicular elytral bands. Ventrally only the proventral process, metaventrite and noteroidal plate are *fuliginosus*, the abdominal ventrites reddish testaceous and the rest of the ventral sclerites yellowish testaceous. Head broader than long slightly inclined and slightly stout; labrum long and convex, *prostratum* (Fig. 2A); seen from side is convex, labrum and clypeus in line; eyes small 3x separated by 3x their diameter Pronotum long and broad; anterior margin with row of small circles or beads along it and posterior margin with short C-shaped

row of small ovals in front of scutellar margin; in lateral view margin narrow and pronotal margin lobed anteriorly and straight posteriorly in discontinuity with ventral elytral margin, and equal to medial length. Elytra with finely punctate surface with some scattered setose points at the apex; seen laterally it has a strong dorsal arching and the ventral margin is doubly sinuous with a long narrow lobulation between the two basal thirds, arched in the apical third. Gonocoxosternite very broad with the dorsal apodeme very broad relative to the ventral apodeme and a long rounded apodeme on the ventral lateral margin and a series of long setae on the dorsal margin (Fig. 13C). Genitalia of female with laterotergite very short, sinuous, with broad, rounded apex and base extending along laterodorsal margin in a thin, curved blade at end. Gonocoxa small and broad anteriorly and attenuate posteriorly with rounded apex, with a row of small, fine spines bordering the apex and extending almost to the middle of the lateroventral margin (Figs. 12A, B).

Male. Unknown.

Etymology. The name of the new species is dedicated to an invaluable scientist and scholar of aquatic coleoptera Dr. Alexey S. Sazhnev.

Habitat. Similar to the previous species**.**

Distribution. Similar to previous species.

Tonerinus spangleri García, **sp**. **nov**.
(Figs. 1A-B, 2A, 6G-7G, 14A-E)
http://zoobank.org/urna:lsid:zoobank.org:act:D9032DCD-04D2-48DD-B489-D2F8FC1D72CD

Differential diagnosis. In *T. spangleri* sp. nov., the elytral bands form a cross with diffusion in the centre. *Tonerinus spangleri* differs from the species described above by the curved shape of the pronotal margin and the elytral banding pattern. In lateral view, *T. spangleri* has a much broader and more convex head and no discontinuity in the dorsal convexity.

Locality type. Tobogán de la selva, Ature, Amazonas, Venezuela.

Material type. Holotype ♂, from Venezuela, Amazonas, Ature, Tobogán de la selva, 20.i.2003, M. García and M. Balke cols., (5º 23'12.01" N and 67º 36'57.34" W) 125 m (MALUZ06645).

Description. Body shape broad oval and convex, with rounded anterior and posterior margins (Fig. 6G); in lateral view it is observed as a perfect arch and a lobed ventral margin at pronotum level and slightly arched at level of elytra (Fig. 7G). Length 2.20 mm and width 1.10 mm, widest at humerus level. Dorsal colouring testaceous and a dark cross-banded pattern blurred in the centre. Ventrally proventral process, metaventrite and noteroidal plate *fuliginosus*, head, proventrite, abdominal ventrites reddish testaceous and legs yellowish testaceous. Robust head broader than long, prognathous with long, prostratum and convex labrum (Fig. 2A); small eyes 3x their diameter apart; lateral view convex and continuous with pronotum. Pronotum long and convex, 1.5x cephalic length; anterior margin with a series of small circles or beads along margin with some fine setose points; posterior margin with a short row of small C-shaped tegumental ovals above scutellar margin; lateral margin broad with rounded edge not continuous with elytral margin, and equals 0.8x medial length. Elytra convex with the elytral surface finely punctate with scattered setose points at the apex; in lateral view the ventral margin is slightly curved in the first two thirds somewhat accentuated in the last elytral third. IX sternite very broad and short pseudo rectangular with very short and sinuous base with several short fine setulae on margin (Fig. 14E). Gonocoxosternite short and slightly widened posteriorly and slightly narrowed at anterior margin with dorsal apodemes triangular and ventral apodemes rounded (Fig. 14D). Genital of male with median lobe widened in basal two-thirds and attenuated in apical one-third with acute apex; phallobase broadly bilobed (Figs. 14A-C).

Female. Unknown.

Etymology. The new of the species is dedicated to Dr. Paul Spangler (†) a great researcher of the aquatic Coleoptera of the world.

Habitalogy. Similar to previous species.

Distribution. Similar to previous species.

Tonerinus toboganensis García, **sp**. **nov**.
(Figs. 1A-B, 2A, 6H-7H, 15A-G)
http://zoobank.org/urna:lsid:zoobank.org:act:57B14576-750B-4321-A278-B5037E3EC851

Differential diagnosis. Although this species is remarkably similar to *T. amazonicus*, it is distinguished by a clearer colouration and a less defined and more

diffuse pattern of elytral bands. In lateral view, there is a greater width and a more pronounced arched profile, with a more robust head. The pronotal margin is more sloping and the ventral margin is lobed in the basal two thirds of the elytra. This arched feature clearly differentiates it from the rest of the species of the genus.

Locality type. Tobogán de la selva, Ature, Amazonas, Venezuela.

Material type. Holotype ♀, from Venezuela, Amazonas, Ature, Tobogán de la selva, 20.i.2003, M. García and M. Balke cols., (5º 23'12.01" N and 67º 36'57.34" W), 125 m (MALUZ06640).

Description. Body shape broad oval with anterior and posterior margins rounded (Fig. 6H); viewed laterally strongly convex on dorsum and doubly sinuous on ventral margin with a pronounced arcuate point between pronotum and elytra (Fig. 7H). Length 2.25 mm and width 1.15 mm, widest at humerus. Colouring of dorsum testaceous yellowish with diffuse elytral bands forming a Y in the apical half and a crescent in the basal half. Head broader than long, prognathous; in lateral view narrowly convex not in line with labrum, long and convex, prostratum (Fig. 2A); eyes small, 3x their diameter apart. Pronotum long and broad with small bead-like circles along anterior margin; posterior margin with a row of small ovals forming a C in front of scutellar margin; in lateral view convex with pronotal margin very broad and margin slightly rounded in discontinuity with ventral margin and equals medial length. Elytra with the surface finely punctate with some scattered setae; in lateral view very convex with the ventral margin gently lobed in the first two thirds of the elytra sloping towards the apex. IX abdominal sternite very broad and rounded with short base and straight margin (Fig. 15F). Gonocoxosternite short axe-shaped, anteriorly rounded with angular and very short apodemes almost imperceptible; posterior margin curved and acute at apex (Fig. 15G). Genitalia of male much widened at bilobed phallobase with attenuate apical one-third and acute apex; right paramere half-turned, with attenuate ends and rectangular left paramere with acute base and rows of long hairs on two apical thirds (Figs. 15A-E).

Female. Unknown.

Habitat. Similar to the previous species.

Distribution. Similar to the previous species.

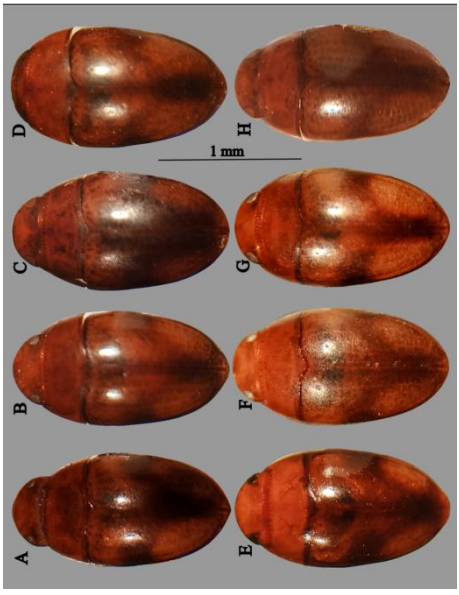

Figure 6. Dorsal *habitus* of *Tonerinus* species. A. *Tonerinus amazonas* **sp**. **nov**., B. *T. amazonensis* **sp**. **nov**., C. *T. amazonicus* **sp**. **nov**., D. *T. hypognathus* **sp**. **nov**., E. *T. pemonus* **sp**. **nov**., F. *T. sazhnevi* **sp**. **nov**., G. *T. spangleri* **sp**. **nov**., and H. *T. toboganensis* **sp**. **nov**.

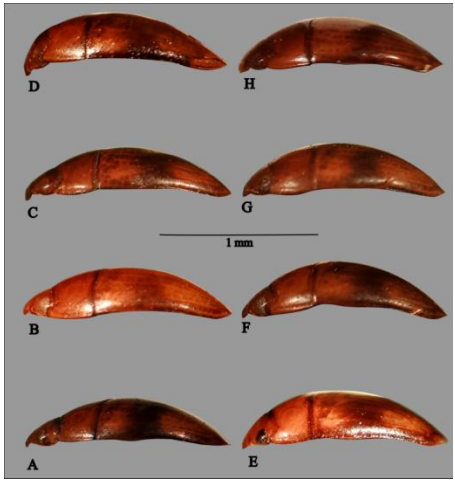

Figure 7. *Habitus* dorsal de las especies de *Tonerinus*. **A**. *Tonerinus amazonas* **sp**. **nov**., **B**. *T. amazonensis* **sp**. **nov**., **C**. *T. amazonicus* **sp**. **nov**., **D**. *T. hypognathus* **sp**. **nov**., **E**. *T. pemonus* **sp**. **nov**., **F**. *T. sazhnevi* **sp**. **nov**., **G**. *T. spangleri* **sp**. **nov**., y **H**. *T. toboganensis* **sp**. **nov**.

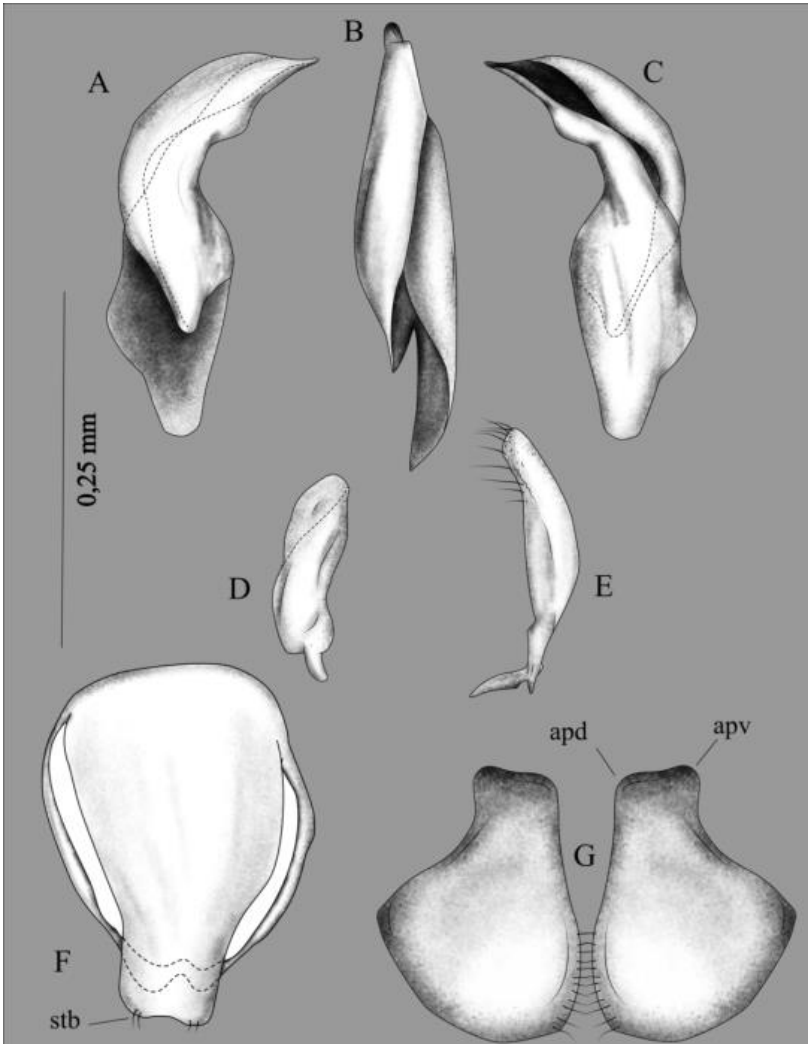

Figure 8. Male genitalia of *Tonerinus amazonas* **sp**. **nov**.: A. median lobe in right lateral view, B. median lobe in ventral view, C. median lobe in left lateral view, D. right paramere, E. left paramere, F. IX abdominal sternite in dorsal view, stb = two basal lateral setae and G: left lateral and right lateral male Gonocoxoesternites, apd = dorsal apodeme and apv = ventral apodeme.

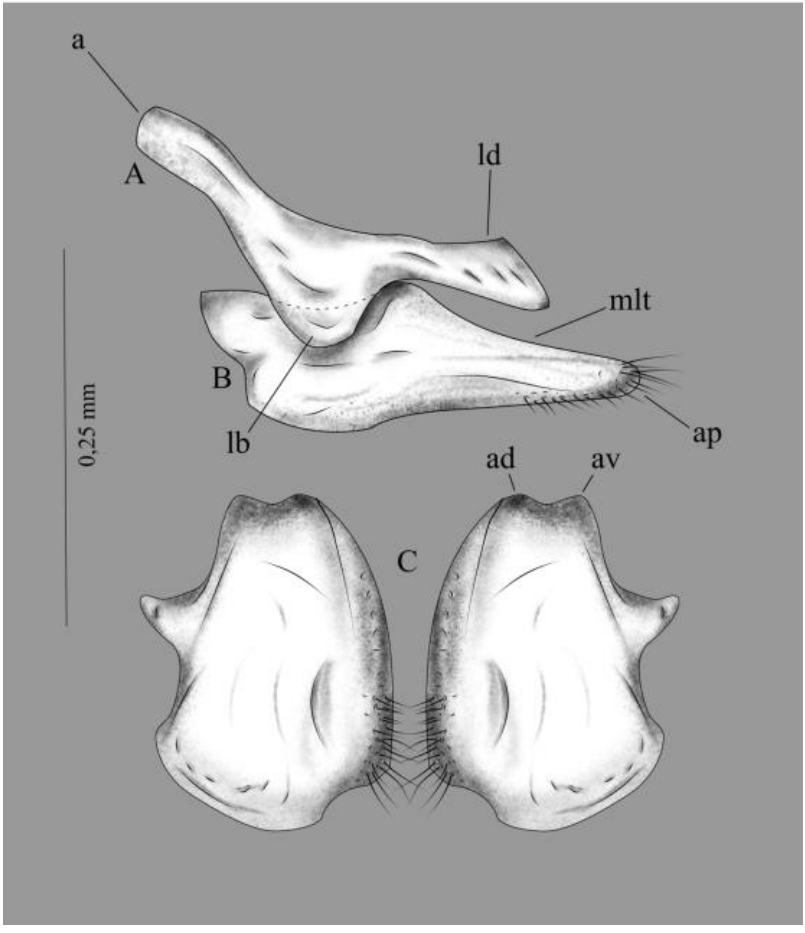

Figure 9. Female genitalia of *Tonerinus amazonensis* sp. nov.: A. Laterotergite in left lateral view, B. Gonocoxa in left lateral view, C. Gonocoxoesternite in dorso-ventral lateral view, ad = dorsal apodeme and av = ventral apodeme, lb = laterotergal basal lobe, a = laterotergalapex, ld = laterotergal dorsal lobe, mlt = laterodorsalmargin, ap = gonocoxalapex.

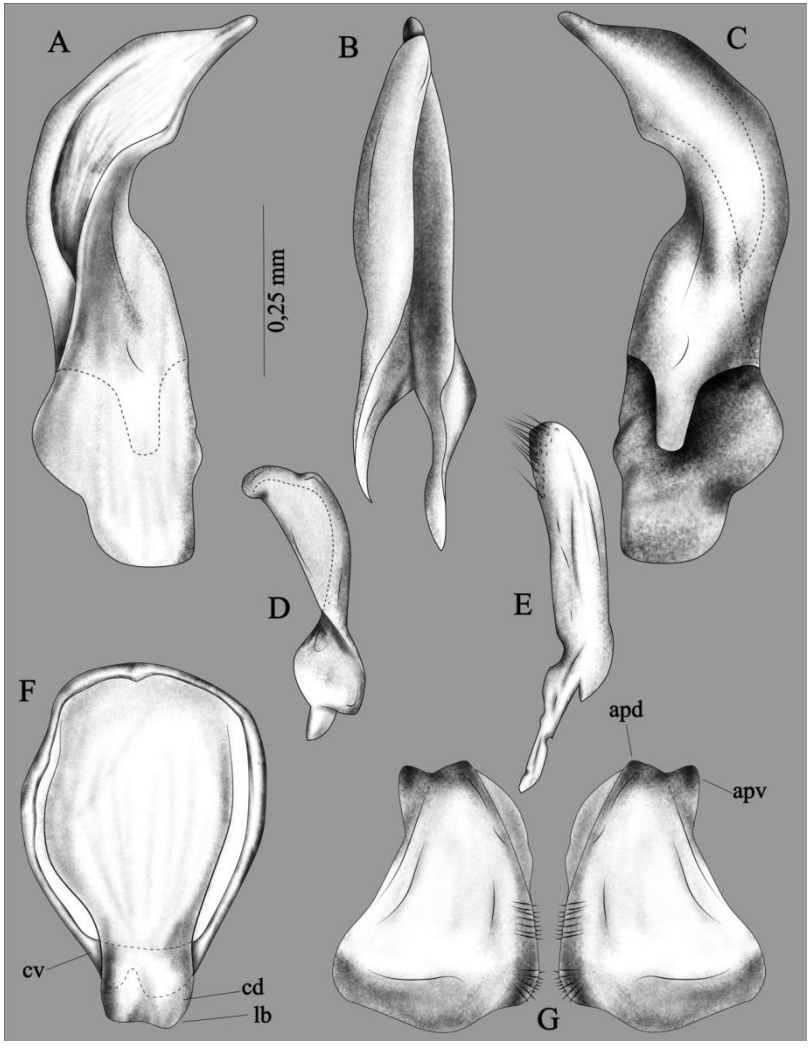

Figure 10. Male genitalia of *Tonerinus amazonicus* sp. nov.: A. Median lobe in right lateral view, B. Median lobe in ventral view, C. Median lobe in left lateral view, D. Right paramere, E. Left paramere, F. IX abdominal sternite in dorsal view, cd = dorsal face and cv = ventral face, lb = basal lobe and G. left lateral and right lateral male Gonocoxosternites, apd = dorsal apodeme and apv = ventral apodeme.

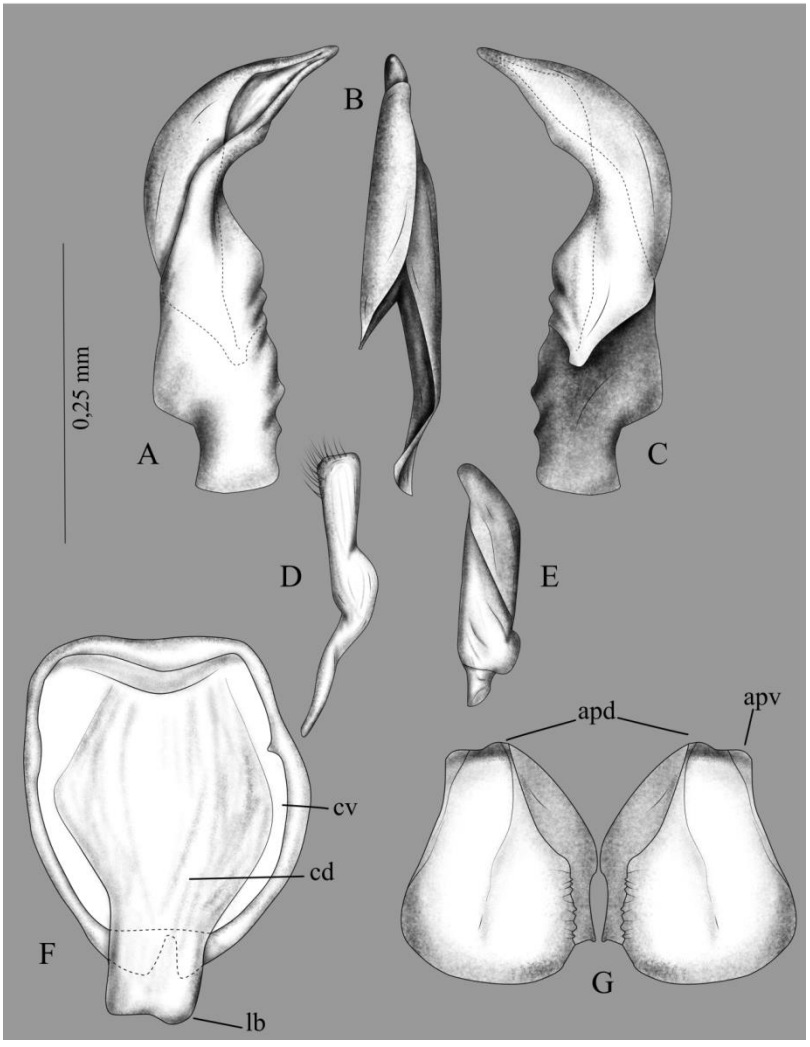

Figure 11. Male genitalia of *Tonerinus hypognathus* **sp**. **nov**.: A. median lobe in right lateral view, B. median lobe in ventral view, C. median lobe in left lateral view, D. left paramere, E. right paramere, F. IX abdominal sternite in dorsal view, cd = dorsal face and cv = ventral face, lb = basal lobes and G. left lateral and right lateral male gonocoxosternites, apd = dorsal apodeme and apv = ventral apodeme.

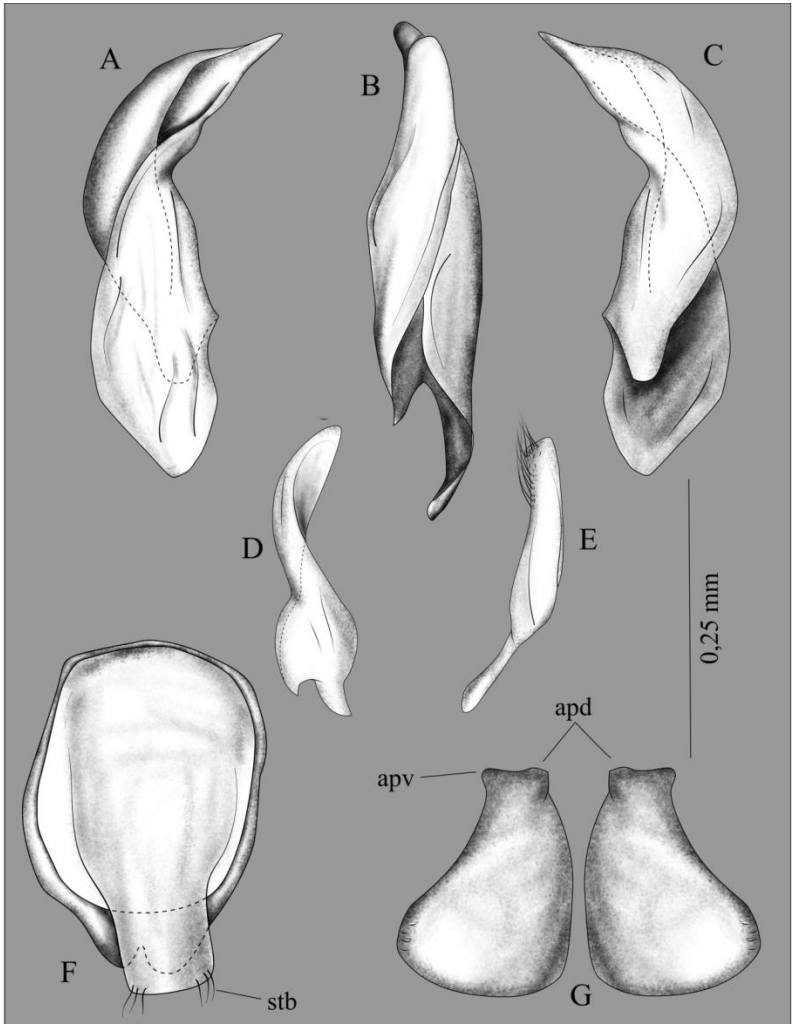

Figure 12. Male genitalia of *Tonerinus pemonus* **sp**. **nov**.: A. median lobe in right lateral view, B. median lobe in ventral view, C. median lobe in left lateral view, D. right paramere, E. left paramere, F. IX abdominal sternite in dorsal view, stb = three basal lateral setae and G: left lateral and right lateral male gonocoxosternites, apd = dorsal apodeme and apv = ventral apodeme.

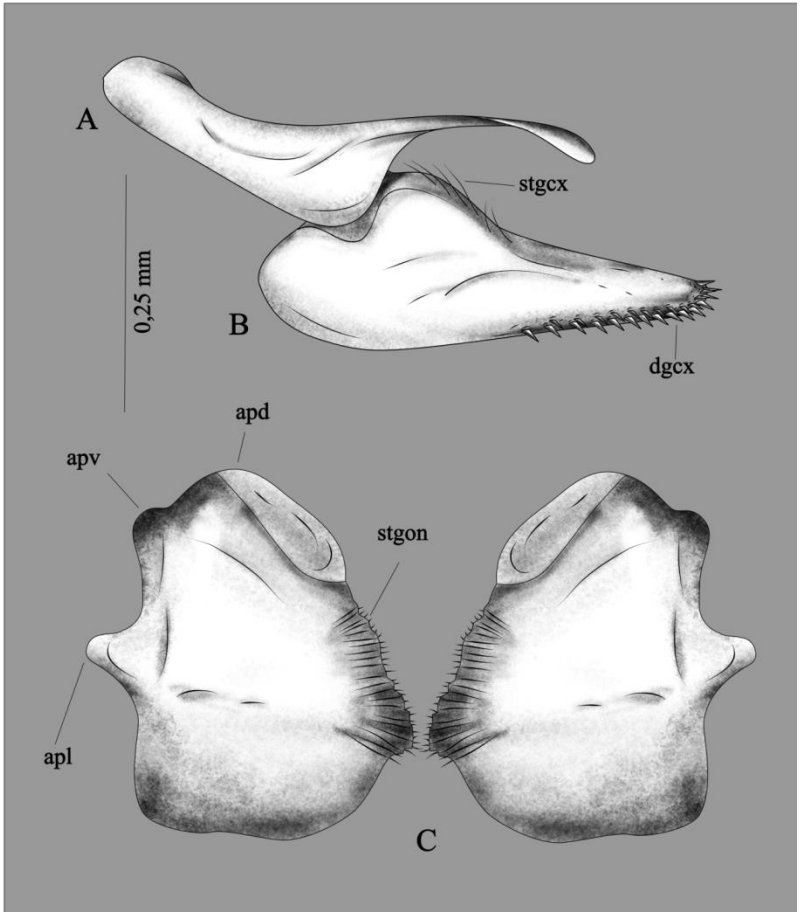

Figure 13. Female genitalia of *Tonerinus sazhnevi* sp. nov.: A. Laterotergite in left lateral view, B. Gonocoxa in left lateral view, stgcx = laterodorsalgonocoxal setae, dgcx = lateroventral and apical gonocoxal spines, C. Gonocoxosternite in right and left lateral view, ad = dorsal apodeme and av = ventral apodeme, apl = lateral apodeme, stegon = gonocoxosternal setae.

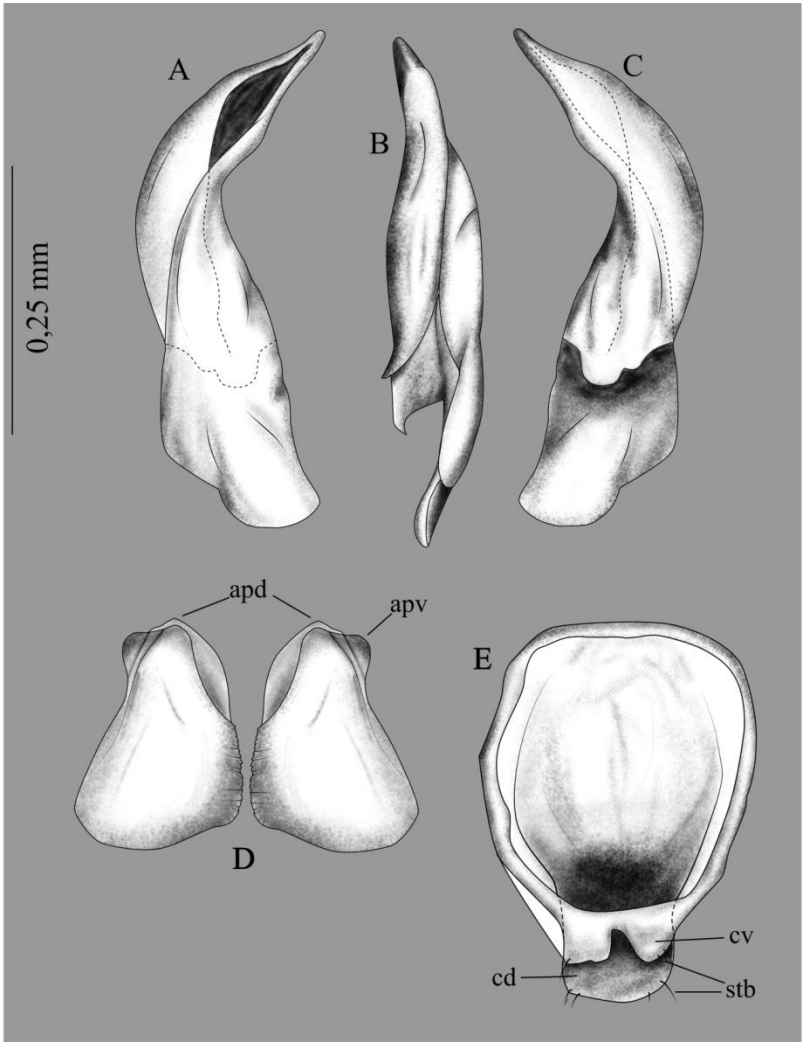

Figure 14. Male genitalia of *Tonerinus spangleri* **sp**. **nov**.: A. median lobe in right lateral view, B. median lobe in ventral view, C. median lobe in left lateral view, D. male left lateral and right lateral gonocoxosternites, E. IX abdominal sternite in ventral view, apd = dorsal apodeme and apv = ventral apodeme, E. IX abdominal sternite in ventral view, cv = ventral face and cd = dorsal face, stb = basal setae.

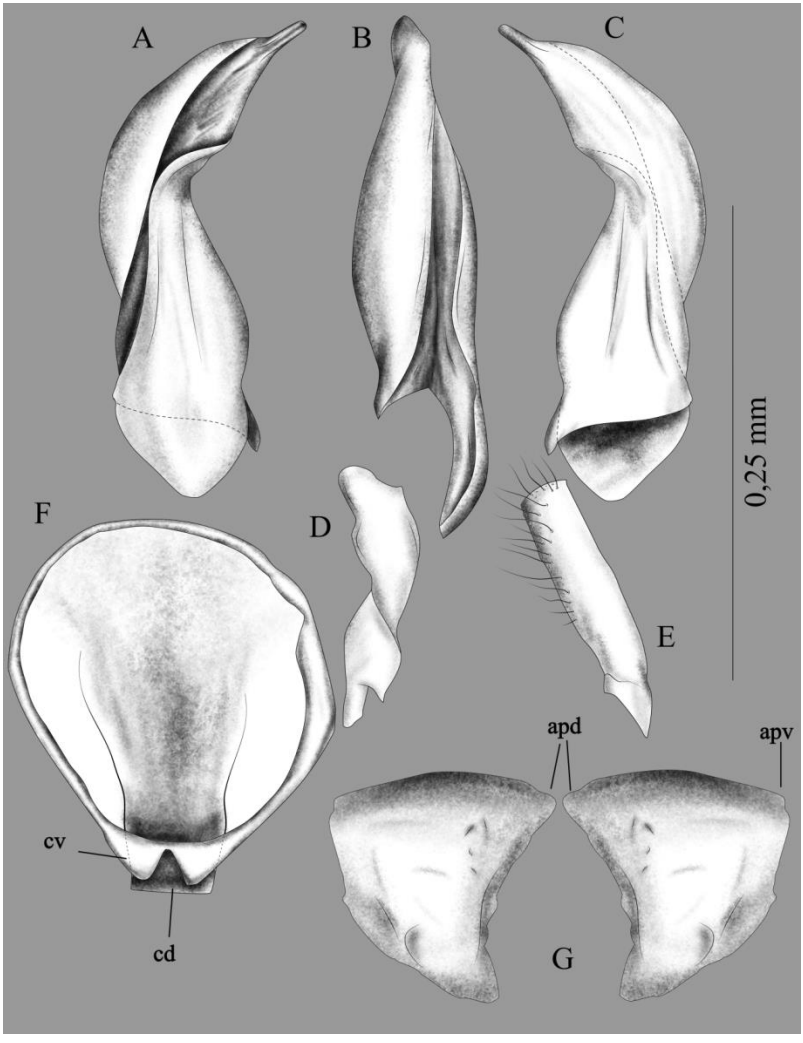

Figure 15. Male genitalia of *Tonerinus toboganensis* **sp**. **nov**.: A. median lobe in right lateral view, B. median lobe in ventral view, C. median lobe in left lateral view, D. right paramere, E. left paramere, F. IX abdominal sternite in ventral view, cv = ventral face and cd = dorsal face, G: left lateral and right lateral male gonocoxosternites, apd = dorsal apodeme and apv = ventral apodeme.

Tonermorpha García, **gen**. **nov**.
(Figs. 1A-B, 2A-B, E, 16-19)
http://zoobank.org/urna:lsid:zoobank.org:50A1AAAF-7A39-4E56-A449-6951FB01806E

Especie tipo. *Tonermorpha unguilonga* García, **sp**. **nov**. por designación original.

Differential diagnosis. The new taxon *Tonermorpha* gen. nov. differs from the genera *Tonerus* Miller and *Tonerinus* gen. nov. by a number of distinctive features. In terms of claw length, *Tonermorpha* has claws as long as tarsomere five on the anterior and middle tarsi and as long as the fourth and fifth together on the posterior tarsi, unlike *Tonerus* and *Tonerinus*, where the claws are shorter than tarsomere five. The shape of the apophysis is also distinctive: in *Tonermorpha*, the apophysis is doubly sinuate at the apex, whereas in *Tonerus* it is slightly curved with two slightly straight sides at the apex and in *Tonerinus* the apical margin of the apophysis is distinctly bitruncate. As for the serration of the metatibial spurs, *Tonermorpha* presents both metatibial spurs serrated, while in *Tonerus* the metatibial spurs are simple. Finally, the anterior and posterior margins of the protibia are less spiny in *Tonermorpha*, and strongly spiny in *Tonerinus*.

Description. Species broad, greater width in humeral region. Lateral outline continuous between pronotum and elytron, with uniform curvature both anteriorly and posteriorly. Integral surface shiny and evenly covered with very fine isodiametric (squamous or microreticulate) epithelial cells. Pronotal fold with lateral margin extending narrowly at posteroangular base, expanding and widening evenly towards anteroangular margin and along anterior margin. Head broader than long with labrumprostratum, broad and long, usually with flat surface (Fig. 2A). Mandible broad, with two premolars (Fig. 2A). Short second premolar with profiled surface of small teeth (molars); two-thirds of basal length with series of long and short, thick and thin spines in a row (Fig. 2B). Maxilla robust with coarsely spiny laciniae; maxillary palpus with the first three palpomeres similar, the fourth palpomere is long and rectangular with two small tactile sensors at the apex; its anterior margin is outlined by a thick carina along its entire length (Fig. 17). Labium with two palpiferous openings in the prementum; labial palpus with three spatial palpomeres and palpifer inserting through palpiferous openings and adjacent to the dorsal prementum; apical labial palpomere, one preapical and the other apical

separated by a convex space with the anterior margin outlined in a thickened carina along its entire length (Fig. 17). Antenna short with bilobed scape, pedicel short, remaining rectangular antennomeres slightly shorter or longer than pedicel, each with superficial sensory; apical antennomere long and attenuate at apex with three sensory micropelons (Fig. 2E). Proventrite broad and long longitumedially with anterior margin with a small apical cleavage convex medially; proventral apophysis extremely broad, flat, short and glabrous with bisinuate apex (Fig. 17). Metaventrite glabrous, medially broad and rounded. Platform noteroidal broad, glabrous, extended anteriorly towards metaventrite; metacoxal lobes with glabrous apices. Metacoxa and metafurca laterally fused to form a ring. Abdominal ventrites with glabrous surface; ventrite III+IV very broad; ventrites V and VI slender; ventrite VII glabrous, broad and long with rounded apex. Anterior femur short, broad, with narrow apex; anterior margin with series of short, thick spines bordering on apical half; posterior margin with series of very fine setae along entire length. Tibiae small, pseudo-rectangular with fine, short, sparse spaced setae; anterior margin with some long, thick spines on apical half; posterior margin with rows of short, thick spines on basal two-thirds and long, thick spines on apical third; apex slightly rounded with crown of short, thick spines and two long, slender, very sharp spurs, one at each end; protibial spur long and slender slightly curved at apex. Short tarsi gradually elongating with the fifth very long equivalent to the fourth and third combined; tarsal nail very long almost the length of the fifth tarsomere (Fig. 18a).

Mid femur long, broad and rectangular with glabrous surface except for a series of short, thick spines bordering the anterior margin along the entire length and a series of long, thin, widely spaced setae on the posterior margin; femoral base attenuated to form a narrow lobe and rounded femoral apex. Median tibia cylindrical with glabrous disc surface and margins strongly and thickly spiny, with retractile spines; apical margin with crown of thick, short, long spines, with long sharp spurs; median tarsi with broad tarsomeres I and II; long fifth tarsomere with widened apex of greater length than fourth and third combined, with pair of thin, very long, almost straight nails of similar length to fifth tarsomere (Fig. 18b). Hind femur short, broad, attenuate at base, broadened and rounded at apex; disc surface glabrous with a short series of short, fine spines on apical half of anterior margin. Hind tibia broad, pseudo-triangular with broad base and bitruncate apex bordered with short, coarse spines; disc surface glabrous with long, coarse spines on anterior and posterior margins; posterior metatibial spurs thick and long; anterior spur long with lateral

margin serrate at apex and posterior spur short and doubly serrate at apex (Fig. 18d). Posterior tarsomeres cylindrical, with the fifth less in length than the fourth and third combined, and a pair of very long claws greater in length than the fifth and fourth combined (Fig. 18c). VIII abdominal sternite with surface with scattered short, coarse setae; lateral margins with slight broad depressions; marginal margin sinuate; longitumedially depressed (Fig. 19A). Laterotergite very short, curved and thin at base and furrowed and broad at apex (Fig. 19B). Gonocoxa with laterodorsal lateroventral margins arched; apical lateroventral margin with series of short spines and rounded apex (Fig. 19B).

Etymology. "*Tonermorpha*" this generic name originates from the root "Toner-" this root comes from the name of the tribe Tonerini to which the genus belongs and the suffix '-morpha' indicating distinctive shape or appearance, which in context means "shaped like *Tonerus*".

Tonermorpha submersa García, **sp**. **nov**.
(Fig.1A-B, 16A-B)
http://zoobank.org/urna:lsid:zoobank.org:act:C4B782D3-D34F-47D5-9D4E-6C0DA3AED0EA

Diagnosis. This species present a greater diffusion of dark colouration on the elytral disc and by having the greatest width at the level of the humeral margin, below the pronotal base, in *T. unguilonga* the greatest width is at the level of the basal pronotal margin.

Locality type. Tobogán de la selva, Ature, Amazonas, Venezuela

Material type. Holotype ♂, from Venezuela, Amazonas, Ature, Tobogán de la selva, 20.i.2003, M. García and M. Balke cols., (5º 23'12.01" N and 67º 36'57.34" W), 125 m (MALUZ06660).

Description. Wide oval shape, very convex, with rounded anterior and posterior margin; seen laterally the dorsum is slightly discontinuous between the margin of the head and pronotum and very discontinuous between the lateral margin of head, pronotum and elytra. Length 2.25 mm and width 1.20 mm, greater width at the level of the humeral margin. *Fulvus* coloration with dark shades on the lateral of eyes, pronotum discal zone and on the elytra three rectangular dark spots, diffuse, on the scutellar margin and medial sides. Head wider than long; small eyes 3x diameter

apart; labrum curved, broad and short. Pronotum long 1.3x head length; lateral margin with slightly straight edge, 0.8x its total length. Elytra with sparsely punctate surface and widely spaced setae at level of apical third; in lateral view ventral margin slightly straight in first two thirds, with sinuosity in apical third. Genital sclerites and genital terminalia misplaced.

Female. Unknown.

Etymology. The new epithet refers to the aquatic environment based on the dimension of the long claws used for grasping the rocky substrate of currents: "*Submersus*" comes from the classical Latin "*submergere*, *submersus*" and means "*submerged*" or "sunken" the species does not have swimming hairs on the legs and it is thought that they are not adapted to swimming but walk on the rocky substrate of the Coromoto River littoral.

Habitalogy. The specimen was collected together with the other species in the group on the rocky bank of the Río Coromoto, a hygropetric horizontal run off microhabitat of a limnic/lotic hydroecological system (García *et al*. 2016).

Distribution. Restricted to the locality of the "Tobogán de la selva", a river side corridor of the Coromoto River, in the state of Amazonas.

Tonermorpha unguilonga García, **sp**. **nov**.
(Fig. 1A-B, 16C-D)
http://zoobank.org/urna:lsid:zoobank.org:act:8E078D37-A81F-4A38-86B7-C75792EB8429

Diagnosis. Pronotum broad with oval basal margin, widening markedly towards the humeri. Elytral surface of diffuse dark colouration on the central disc, forming four small square bands at the distal ends, significantly darker than the central region.

Locality type. Tobogán de la selva, Ature, Amazonas, Venezuela.

Material type. Holotype ♀, from Venezuela, Amazonas, Ature, Tobogán de la selva, 20.i.2003, M. García and M. Balke cols., (5º 23'12.01" N and 67º 36'57.34" W), 125 m (MALUZ06659).

Locality type. Tobogán de la selva, Ature, Amazonas, Venezuela.

Locality type. Tobogán de la selva, Ature, Amazonas, Venezuela.

Material type. Holotype ♀, from Venezuela, Amazonas, Ature, Tobogán de la selva, 20.i.2003, M. García and M. Balke cols., (5º 23'12.01" N and 67º 36'57.34" W), 125 m (MALUZ06659).

Description. Description. Broad oval shape with rounded anterior and posterior margins and continuous lateral margins between pronotum and elytra, with a small discontinuity at head and pronotal margin; in lateral view of uniform convexity from head to elytral apex. Length 2.20 mm and width 1.30 mm, greater width at pronotal and humeral margin. Coloration of the head fulvous with dark shades distributed on the inner margins of the eyes. Pronotum *fulvus* with dark shading on pronotal disc. Elytra fulvous with pseudo rectangular dark shading on lateral and apical ends illuding a V in elytral half; and a larger triangular dark shading on anterior margin, joined to dark shading of pronotal posterior margin. Ventrally with apophysis, metaventrite and abdomen blackish with *fulvus* shades; legs with light fulvous and dark shades. Head wider than long with small eyes separated by three times its diameter. Labrum flat, long, broad, *retroflectum* (Fig. 2); in lateral view continuous convexity with pronotum. Pronotum long 1.2x cephalic length; convexity continuous with elytra; in lateral view equivalent length 0.8x of central disc; rounded margin slightly discontinuous with elytral margin. Elytra convex; lateral view with ventral margin doubly sinuate to apex.

Male. Unknown.

Etymology. The new epithet is a combination of two words relating to the length of the tarsal nails: '*Unguis'* meaning nail and '*Longus'* meaning long, so the meaning in context is 'with long nails'.

Habitalogy. The specimen was collected together with the other species in the group on the rocky bank of the Río Coromoto, a hygropetric horizontal runoff microhabitat of a limnic/lotic hydroecological system (García *et a*l. 2016).

Distribution. Restricted to the locality of the 'Tobogán de la selva', a riverside corridor of the Coromoto River, in the state of Amazonas.

Taxonomic key to separate genera of Toneroides group.

(Fig. 20)

1.-Tarsal claws of the protarsus and mesotarsus equal in length to the fifth tarsomere and longer than the fifth and fourth combined on the metatarsus (Fig. 18)……*Tonermorpha* **gen**. **nov**.

-Tarsal claws of equivalent length shorter than the fifth tarsomere (Fig. 4)..... 2

2.-Metatibial spurs with serrate margins (Fig. 4c).....*Tonerinus* **gen**. **nov**.

- Simple metatibial spurs…….....*Tonerus* Miller.

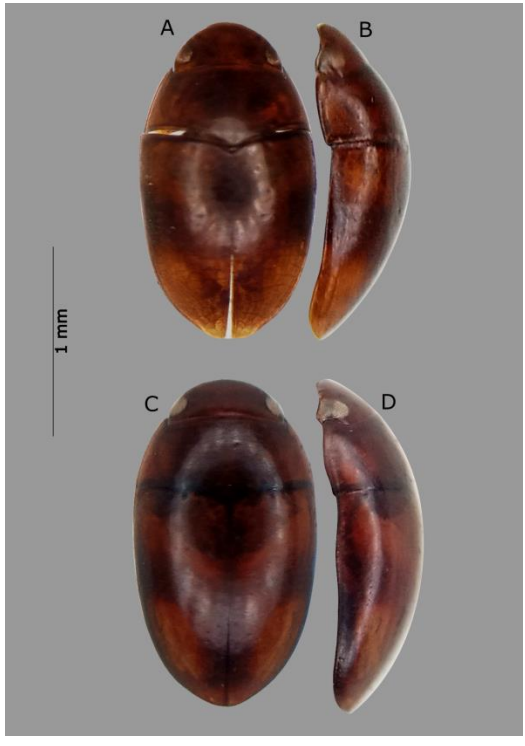

Figure 16. Dorsal and lateral *habitus* of *Tonermorpha* **gen**. **nov**. A. Dorsal and B. Lateral views of *Tonermorpha submersa* **sp**. **nov**. C and D. *Tonermorpha unguilonga* **sp**.**nov**.

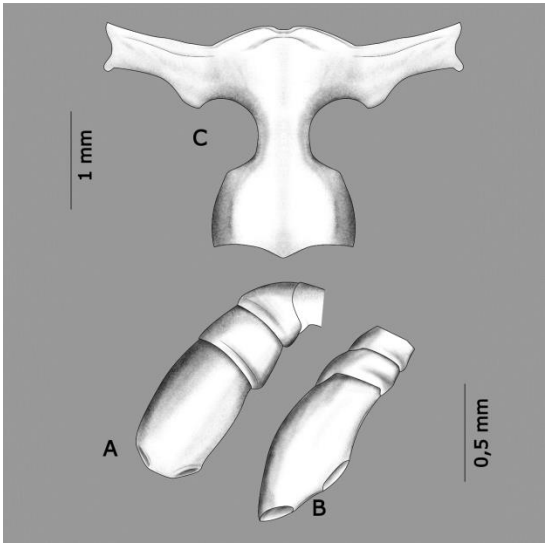

Figure 17. Cephalic and ventral sclerites of *Tonermorpha* gen. nov. A. maxilla palpus, B. labial palpus and C. Proventral apophyisis.

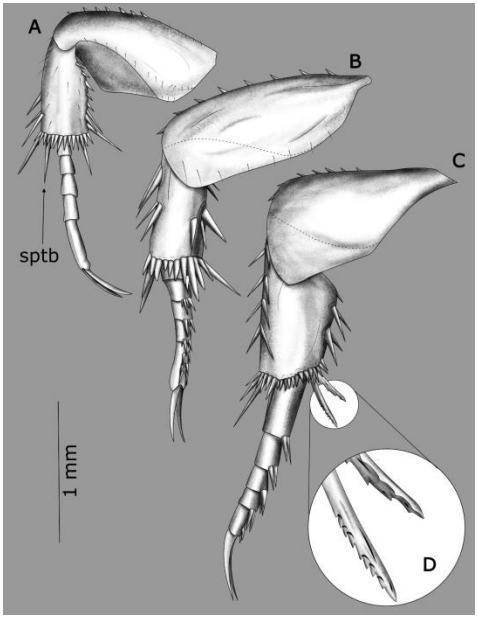

Figure 18. Locomotion sclerites of *Tonermorpha* species gen. nov. gen. nov. A. Propata, B. Mesopata, C. Metapata and D. Metatibial spurs, sptb = protibial spur.

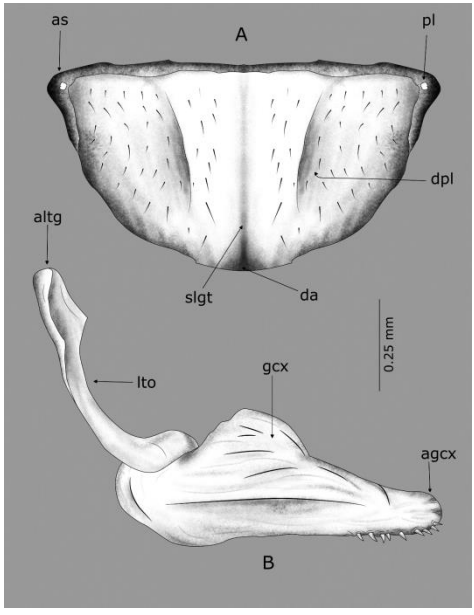

Figure 19. VIII abdominal sternite female genital sclerite of *Tonermorpha unguilonga* sp. nov. A. VIII sternite: as = lateral loop, pl = lateral pore, dpl = lateral depression, dp = apical depression, slgt = longitumedial groove, B. Genital sclerite: gcx = gonocoxa, lto = laterotergite, altg = laterotergal apex, agcx = gonocoxal apex.

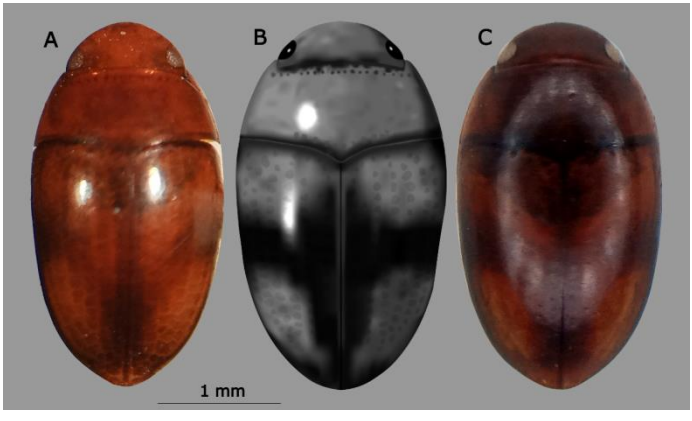

Figure 20. *Toneroides* group (Tonerini). A. *Tonerinus amazonicus* García, **gen**. *et***sp**. **nov**., B. *Tonerus wheeleri* Miller and C. *Tonermorpha unguilonga* García, **gen**. *et***sp**. **nov**.

DISCUSSION

Morphological features in both new genera suggest a primitive condition: the presence of cephalic characters such as mouth sclerites adapted to a passive diet (non-predatory) as a collector of organic particles or scraper of plant surfaces (Guzmán-Soto and Tamaris-Turrizo 2014; Chará *et al*. 2010), small eyes, legs with distinctive features, visible abdominal sternites, and a particular genital terminalia (sternites VIII, IX and gonocoxosternites) indicate an early evolutionary state.

A thorough analysis reveals significant differences between the two new genera and the genus *Tonerus*. Coloration patterns, dorsal and lateral view morphology allowed for the clear distinction of the nine species. Interspecific characters suggested the presence of two new genera. Tegumentary similarities point to a tribal distinction between the three genera: all species present flat isodiametric epithelial cells, similar to those of squamous tissue, which gives them a microrreticulated texture on their surface. This shared feature confirms that the three genera belong to a tribal taxon different from Noterini.

The Tonerini Tribe is retributable

According to Baca *et al*. (2017), DNA-based phylogenetic analyses do not place the Tonerini and Noterini tribes as separate monophyletic clades. This implies that they share an exclusive common ancestor and that both tribes possess numerous similar morphological features, suggesting synonymy between them. However, while Tonerini and Noterini share some similarities, there are distinctive morphological features that refute their synonymy.

The mandibles of *Tonerinus* gen. nov. and *Tonermorpha* gen. nov. (the author assumes they share the same character with the genus *Tonerus*) are not specialized for predation like those of Noterini. Instead, *Tonerinus* gen. nov. and *Tonermorpha* gen. nov. possess a robust apical molar for scraping or cracking shells, and a square second molar with a rough or granulated surface for grinding. Additionally, at the base of the mandible, *Tonerinus* gen. nov. and *Tonermorpha* gen. nov. have a row of fine spines on the basal third for scraping or picking over the surface of rocks, decaying wood, and even dead leaves. Lastly, *Tonerinus* gen. nov. and *Tonermorpha* gen. nov. possess a lacinia with coarse spines for scraping or collecting fine particles.

The differences in jaw structure and the presence of specific features such as spines and the spiny lacinia demonstrate that Tonerini and Noterini are not synonymous.

The species of *Tonerinus* gen. nov. and *Tonermorpha* gen. nov., as well as *Tonerus wheeleri*, are characterized by a robust build with large, wide heads. However, unlike members of Noterini, they have small eyes relative to their body size. This characteristic is not favorable for predation, as it limits visual capacity and, therefore, hunting accuracy and success. In contrast, the large eyes of Noterini provide them with better vision, allowing them to detect and pursue prey more effectively.

The tibiae of the genera *Tonerinus*, *Tonermorpha*, and *Tonerus* are considerably wide and have a prominent apicodorsal margin. This margin is bordered by long, thick spines, the number and size of which vary among the three genera: *Tonerinus* has strong spines, *Tonerus* has moderate spines, and *Tonermorpha* has sparse spines. At the apex of the tibia, a slightly curved spur is observed, in contrast to the robust, curved hook-shaped spur present in noterines. This latter spur has a very sharp apex, with the exception of the genus *Mesonoterus* Sharp (Miller 2009).

Regarding their legs, *Tonerinus* and *Tonermorpha* share short and wide femurs and tibias, with a spiny appearance and retractable spines on the tibias. However, the tarsal claws show notable differences between the two genera. In *Tonerinus*, the claws are short and curved in the pro- and mesotarsus, while in the metatarsus they are straight and cover the length of the fifth tarsomere. In *Tonermorpha*, the claws are long, equivalent to the combined length of the fifth and fourth tarsomere. In both genera, they are slightly curved in the pro- and mesotarsus and straight in the metatarsus.

Tonerinus species have ridges on the ventral margin of the front claws, an invagination on the middle tarsal claws and a simple shape on the metatarsal claws. In contrast to *Tonermorpha* species, all claws on the tarsi are simple. It is noteworthy that Miller (2009) does not mention any features on the tarsal claws of *Tonerus wheeleri*. In contrast, the claws of noterinids are serrate and have different formulae depending on the genus: (2-3-3), (2-2-3), (3-3-3), (3-3-2) or (1-1-1). The shape of the teeth on each claw also varies.

The metatibial spurs of the genus *Tonerinus* are characterized by their distinctly serrated edges. The anterior claw exhibits double parallel serrations, while the posterior claw only displays a serrated margin with long, slender teeth. In the case of *Tonermorpha*, only the posterior spur possesses a serrated edge. In contrast, *Tonerus wheeleri* exhibits simple metatibial spurs. Unlike Noterini, the metatibiae of *Tonerinus*, *Tonermorpha*, and *Tonerus* lack swimming hairs on their anterior and posterior margins, indicating their unsuitability for swimming. Conversely, Noterini does possess swimming hairs on its metatibiae, which facilitates its locomotion in water. The species of *Tonerinus*, *Tonermorpha*, and *Tonerus* are more adapted to locomotion on soils with a thin film of moisture. It is presumed that, due to the condition of long claws, the species of *Tonermorpha* are better adapted to walking clinging to rocky ground in streams.

The genital terminalia of *Tonerinus* are primitive in structure compared to Noterini. The VIII sternite is simple, while the IX sternite is short and broad. The gonocoxosternites have sparsely lobed apodemes and are absent in some species. In the genitalia of the female, the laterotergites are short, slender and L-shaped bilobed. The gonocoxae, on the other hand, are very small, flattened with pointed apices (in *Tonerus* they are thick with rounded apices). In contrast, the Noterini have a large pointed or lobed gonocoxal apex, which markedly differentiates their genitalia from those of Tonerini.

Tonerus, *Tonerinus* and *Tonermorpha* species are endemic and found in a single region of the Venezuelan Amazon, while Noterini has a much wider geographical distribution. This notable difference in distribution is an additional factor supporting the distinction between the two taxa.

In conclusion, the morphological differences and geographical distribution of Tonerini and Noterini suggest that they are not synonyms. The synonymy proposal of Baca *et al*. (2017) has not been accepted by all aquatic beetle specialists. Some authors argue that the molecular analysis presented is not conclusive and that the two tribes can still be distinguished based on specific morphological characters.

Specialized jaws ??

Tonerinus maxillae are characterized by robust laciniae with spines of variable size, giving them a rough and rugged texture. This morphological particularity sug-

gests one adaptation to scrape surfaces such as rocks or decaying wood present in surface runoff. Its use extends to biofilm, an algal film that forms on wet rocks, in areas where the water layer varies between 5 and 10 mm thick (Guzmán-Soto and Tamaris-Turrizo 2014; Chará *et al*. 2010). The combination of robust lacinia and strong spines would allow *Tonerinus*, *Tonermorpha*, and presumably, *Tonerus wheeleri* species to rasp these surfaces efficiently, accessing an alternative food source to predation.

The jaws of *Tonerinus* and *Tonermorpha* have a series of morphological characteristics that differentiate them from those of predatory species and adapt them to a diet based on organic detritus. In the apical region, we find a robust and specific molar for shredding or scraping coarse and hard particles. This feature contrasts with the sharp and strong molars present in predatory species. In the middle region, a coarse second molar is observed with an unrounded, rough or granulated rectangular apical surface as a series of small coarse teeth. These teeth are presumably used to demolish or pulverise coarse particles of detritus. On the basal part of the mandible, there is a long, compact row of fine spines distributed in a comb-like pattern. These spines could be used to collect small particles on the surface of moist soil or other soft surface.

In general, the morphological features of the mandibles of *Tonerinus* and *Tonermorpha* suggest an adaptation to a non-predatory diet based on detritus ingestion. This adaptation would allow species of both genera to exploit an ecological niche different from that of predatory species, expanding their success in environments with low prey availability.

All species of *Tonerinus* and *Tonerus wheeleri* were collected in specific habitats on the water film running over the rocks under decaying wood or under the vegetation layer on the runoff, while *Tonermorpha* species were collected in a sweep of the rocky substrate in the littoral zone of the Coromoto River stream. A striking feature of these species is the absence of swimming hairs on their metatibiae. Instead, they have large, thick, retractable spines, an adaptation for life in the leaf litter. This morphological feature indicates that they are not suitable for swimming, unlike other aquatic beetles.

The retractile spines of *Tonerinus* and metatibiae allow them to cling to leaf litter and other substrates present in their microhabitat. They move easily over the

surface of the water film and hold their position against the current of runoff. *Tonerinus* metatibiae represent a morphological adaptation to their particular lifestyle on leaf litter and water film. This adaptation allows them to exploit a unique ecological niche in shallow water environments with little current.

CONCLUSION

This study represents a significant advance in the knowledge of aquatic Coleoptera in Venezuela, particularly with regard to the systematics of the Tonerini tribe. The discovery of two new taxa, along with the genus *Tonerus*, has allowed for the recognition of new character states that fit the original taxonomic characteristics of the tribe. Thus, the reinstatement to its original status as a tribe distinct from Noterini is justified. These findings open up new avenues of research to better understand the diversity and evolution of aquatic Coleoptera in Venezuela and the Neotropical region.

In 2009, only one species of *Tonerus wheeleri* had been identified from more than 90 specimens within the then Tonerini tribe. The material analyzed in this research, collected in 2004, was not part of the original study of *Tonerus*. The analysis of coloration and *habitus*, characteristics that show great variability among the three genera, allowed us to recognize that the nine species described later were nothing more than different forms of *Tonerus* wheeleri, that is, hidden species within what was until then considered a single species. This hidden diversity led to the proposal of two new genera: *Tonerinus* **gen**. **nov**. and *Tonermorpha* **gen**. **nov**. These two new taxa, although less abundant than *Tonerus*, present greater morphological diversity. Overall, this evidence highlights the need for a thorough revision of the *Tonerus* wheeleri species in all available collections.

The findings of this study are highly relevant to the reinstatement of the original status of the Tonerini tribe in the near future. This finding significantly expands the knowledge on the taxonomy of the tribe Tonerini and its relevance for understanding the biodiversity of aquatic beetles of the family Noteridae. The novel information obtained on the diversity and distribution of the *Tonerus* genus group in Venezuela will significantly strengthen the understanding of the systematic and evolution of these aquatic beetles within the suborder Adephaga.

Note: Specimens of *Tonerus wheeleri* are not available at the Arthropod Museum of the University of Zulia (MALUZ) in Venezuela because they have not yet been returned.

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