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A new genus for the Neotropical species of *Aesalus* Fabricius, with descriptions of eight new species (Coleoptera: Lucanidae: Aesalinae)

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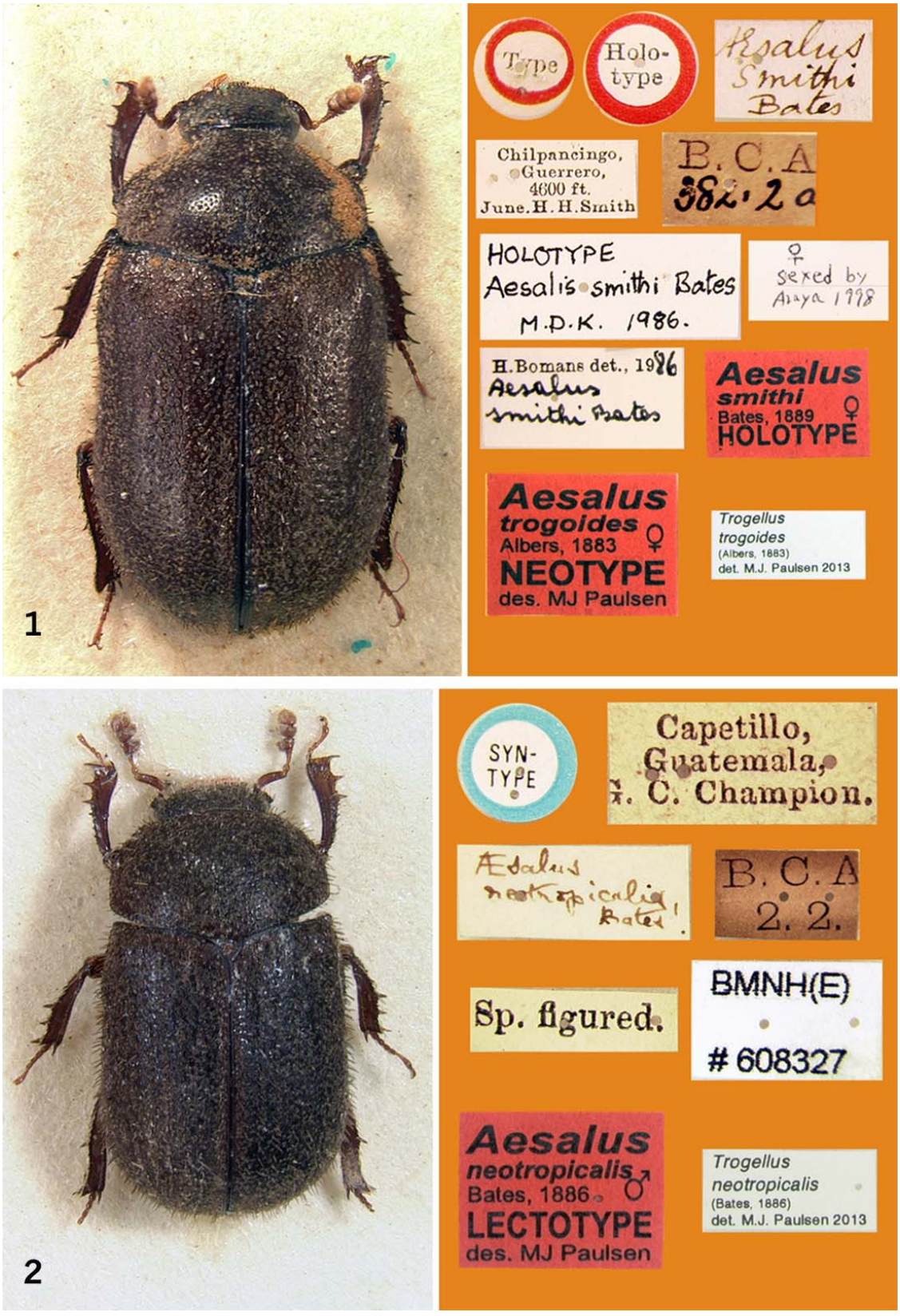
Abstract. The Neotropical members of the genus *Aesalus* Fabricius (Coleoptera: Lucanidae: Aesalinae) are transferred to a **new genus**, *Trogellus,* due to their morphological dissimilarity and molecular divergence from the Old World species of *Aesalus,* and the new genus is revised. A **neotype** is designated for *A. trogoides* Albers and a **lectotype** for *A. neotropicalis* Bates. *Aesalus smithi* Bates is placed into synonymy with *Aesalus trogoides*, **new synonymy**. Two **new combinations** result from the transfer of species formerly in *Aesalus*: *Trogellus trogoides* from Mexico and *Trogellus neotropicalis* from Guatemala. In addition to the two known species, eight **new species** are described: *T. catrachitus*, *T. chapinitus*, *T. hawksi*, *T. herrmanni*, *T. maesi*, *T. narizotus*, *T. ticiticus*, and *T. trifinius*. This brings the total number of species of Central American aesalines to ten. A phylogeny of Aesalini based on two gene regions of ribosomal DNA is presented. Due to clear morphological differences and large molecular divergence between species groups, two additional **new subgenera** of *Trogellus* are proposed: *Mayaesalus* and *Trogoides*.

Introduction

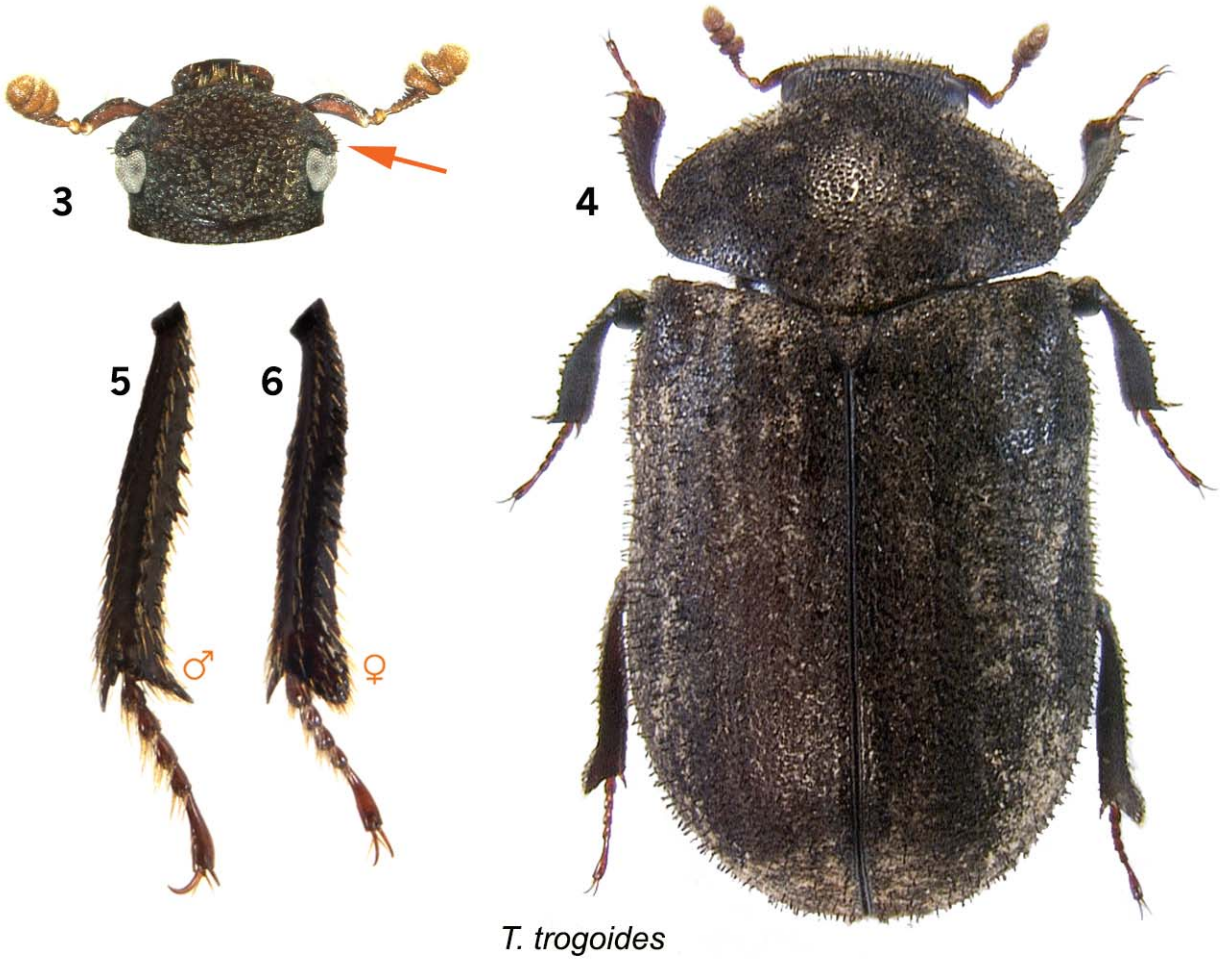
The genus *Aesalus* Fabricius (Coleoptera: Lucanidae: Aesalinae) is a group of small, atypical lucanids that are frequently overlooked or misidentified in collections. Albers (1883) described the first Mesoamerican species, *Aesalus trogoides,* comparing it to the Palearctic species *A. scarabaeoides* (Panzer), and indicating a length of 6 mm (see Fig. 1). Bates (1886) then described *A. neotropicalis* from Guatemala (Fig. 2) with a length of 4 mm and included both species in the Biologia Centrali-Americana (BCA). Bates distinguished his species by the presence of an ocular canthus, although he had not examined *A. trogoides,* and Albers had not indicated if a canthus was present in that species. In the supplement to the BCA, Bates (1889) described a third species, *A. smithi,* distinguishing it from *A. neotropicalis* by its shorter and broader ocular canthus but oddly not mentioning that it was also a much larger species at 5.9 mm (Fig. 1).

There was little comment on the taxonomy of the Mesoamerican species until Reyes-Castillo and Boucher (2003) indicated that they suspected *A. smithi* to be a synonym of *A. trogoides,* without formalizing the synonymy. Based on the canthus shape, distribution, and the larger size reported for *T. trogoides,* it is clear that Albers was referring to the same species as Bates' *A. smithi*. I have examined the holotype of *A. smithi* (BMNH), and it is conspecific with what has been considered *A. trogoides* by all authors. Albers' holotype of *A. trogoides* was destroyed in the bombing of Hamburg in 1943, where Paul Nagel had taken the specimen from its original depository at the Hannover Museum (Alexandra Eichler, Niedersächsisches Landesmuseum Hannover, communicated to Dr. Matthias Herrmann, MPI-Tübingen on my behalf). In this case there is an obvious need to tie Albers' name to a specific specimen to settle the synonymy with *A. smithi*, thus I am designating a neotype for *A. trogoides* below. Because no material is on hand from the original type locality of Oaxaca, I have chosen the specimen from the next closest locality, which is the holotype of *A. smithi* from Guerrero (Fig. 1). This results in *A. smithi* becoming an objective synonym of *A. trogoides*.

Recent collecting in Central America has resulted in the discovery of several new species that are described below. The genus is widely distributed in Central America in montane habitats, but these areas have been poorly sampled for this group. One method for collecting specimens is flight intercept traps in the appropriate habitat. I have also collected specimens at UV light and excavated adults and larvae from decaying pine logs. The larger series of historical specimens were beaten from dead branches (Bates 1886). Because all but one of the undescribed species are known from few specimens, it is highly likely that additional new species are yet to be discovered in isolated montane regions of Central America.



Figures 1-2. Existing primary types of Central American Aesalini, including labels. **1)** Holotype of *Aesalus smithi* Bates and neotype of *Aesalus trogoides* Albers. **2)** Lectotype of *Aesalus neotropicalis* Bates.

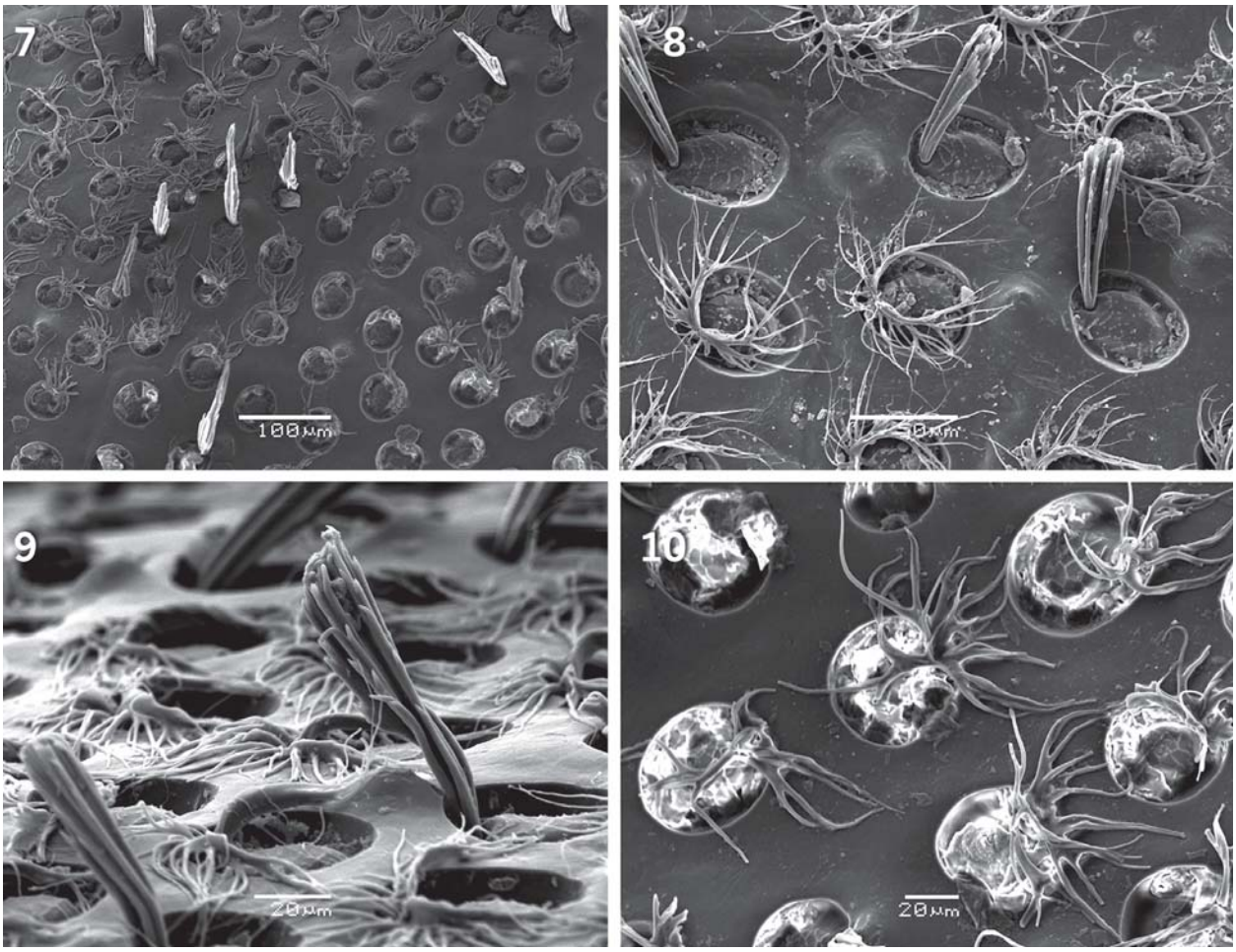


Figures 3-6. *Trogellus trogoides* (Albers). **3)** Head, with triangular clypeus, and with arrow indicating ocular canthus. **4)** Female habitus. **5)** Left metatibia of male showing acute apex (ventral view). **6)** Left metatibia of female showing tumid apex (ventral view).

Generic placement of the Central American Aesalini

Morphologically, the Mesoamerican aesaline species differ significantly from the type species of *Aesalus* Fabricius, the Palearctic *A. scarabaeoides*. That the Neotropical species had not been moved to their own genus in the hundred-plus years since their descriptions speaks to the paucity of specimens and lack of research on the group. Morphological differences between the Neotropical species and *A. scarabaeoides* are obvious and plentiful. In the Neotropical species the eyes are divided anteriorly by a large canthus, not entire (Fig. 3); the elytra have rows of bristles and minute, branching scales but lack clumps of large scales of differing colors; the protibiae are dentate, not serrate; the mandibles are small and not sexually dimorphic, lacking a dorsal tooth in males (Fig. 3); the punctures of the mesosternum and abdomen are oval, not elongate; the antennal clubs are entirely tomentose, not only on the distal faces; and abdominal segments 1–2 appear connate and are not separated by a deep furrow. For these reasons, I am removing the Central American species from *Aesalus*.

The Southeast Asian species of *Aesalus* differ greatly from that genus and were removed to the genus *Echinoaesalus* by Zelenka (1993). Furthermore, Krikken (2008) created the subgenus *Zelenkaesalus* for species with remarkably modified ventral surfaces (the presence of leg-shaped sulci that completely receive the legs). The Central American aesalines differ from species of the Southeast Asian genus *Echinoaesalus* Zelenka and its subgenus *Zelenkaesalus* Krikken in the following characters: ventral surface lacking sulci or furrows to receive legs or tarsi; epipleuron simple (not distinctly modified to



Figures 7-10. SEM microscopy of elytral surface and vestiture. **7)** *Trogellus herrmanni* n. sp., acute bristles. **8)** *T. trogoides*, blunt bristles with anterior tubercle, and branched scales. **9)** *T. trogoides*, detail of blunt bristle. **10)** *T. herrmanni* n. sp., detail of branched scales.

receive apices of meso- and metafemora); clumps of bristles and scales of differing colors lacking; meso- and metatibiae with strongly developed external teeth. The genus shares with *Echinoaesalus s.str.* the well-developed ocular canthus, lack of distinct sexual dimorphism in mandibular form, and entirely tomentose antennal club. Species of subgenus *Zelenkaesalus* possess a distinctive, short canthus that only slightly intrudes into the eye that suggests elevation to generic status may be warranted for *Zelenkaesalus*.

The Central American aesalines differ from the South American aesaline genus *Lucanobium* Howden and Lawrence by the lack of elytral patterning formed from differently colored circular scales and irregular clumps of bristles (Fig. 4). In addition, the clypeus of *Lucanobium* species is semicircular, not at all triangular, and the overall form more globose. In *Lucanobium,* the mesotibiae lack strongly developed external teeth. Finally, the male genitalia of *Lucanobium* have short parameres about 1/10 as long as the median lobe, not 1/2 to 1/4 as long as in the Mesoamerican species (Paulsen 2011).

Although the species treated here are morphologically conservative with respect to external characters, the group contains three distinct, definable subgenera based on differences in the male genitalia, protibial dentition, and dorsal vestiture. I have sequenced at least two members of each subgenus for molecular analyses, and the genetic divergence between them is similar to that between most other genera of Lucanidae, including other Aesalini (see phylogeny section). While formalizing each species hypothesis it has been useful to work within the framework of these subgenera. No larvae of the

Figures 11-14. Leg characters of subgeneric importance. **11)** Right protibia of *Trogellus herrmanni* n. sp. with large triangular teeth (dorsal view). **12)** Right protibia of *T. trogoides* with small peg-like teeth (dorsal view). **13)** Left metatibia of *T. trogoides* showing weak external teeth (ventral view). **14)** Left metatibia of *T. herrmanni* n. sp. showing strong external tooth at middle (ventral view).

Mesoamerican species have been described, and the characters discussed in this paper refer only to those of the adult beetles.

Material examined

Approximately 160 specimens from the following institutions and collections were examined for this study: (**BMNH**) Natural History Museum, London, UK; (**CASC**) California Academy of Sciences, San Francisco, CA; (**CMNC**) Canadian Museum of Nature, Ottawa, Canada; (**CNCI**) Canadian National Collection of Insects, Ottawa, Canada; (**IEXA**) Instituto de Ecología Xalapa, Veracruz, Mexico; (**INBIO**) Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica; (**FMNH**) Field Museum of Natural History, Chicago, IL; (**FSCA**) Florida State Collection of Arthropods, Gainesville, FL; (**MJPC**) M.J. Paulsen Collection, Lincoln, NE; (**RHTC**) Robert H. Turnbow, Jr. Collection, Ft. Rucker, AL; (**TAMU**) Texas A&M University Insect Collection, College Station, TX; (**UNAM**) Universidad Nacional Autónoma de México, Mexico City; (**UNSM**) University of Nebraska State Museum, Lincoln, NE; (**USNM**) United States National Museum of Natural History, Washington, D.C.; (**UVGC**) Universidad del Valle de Guatemala, Guatemala City, Guatemala; (**WBWC**) William B. Warner Collection, Chandler, AZ.

Conventions used in the description of morphological characters are as in Paulsen (2005) and Paulsen (2010). Because the salient characters of each subgenus are noted in the description for each and the species are relatively conservative externally, brief descriptions are provided that focus on the distinguishing characters for each species. These are reiterated in the Diagnosis/Remarks section. In many cases, characters of the male genitalia and dorsal vestiture best distinguish the species. Male specimens

can be easily identified without dissection by examination of the metatibial apex. Males have acute apices (Fig. 5), while in females the apices are tumid (Fig. 6).

Taxonomic Treatment

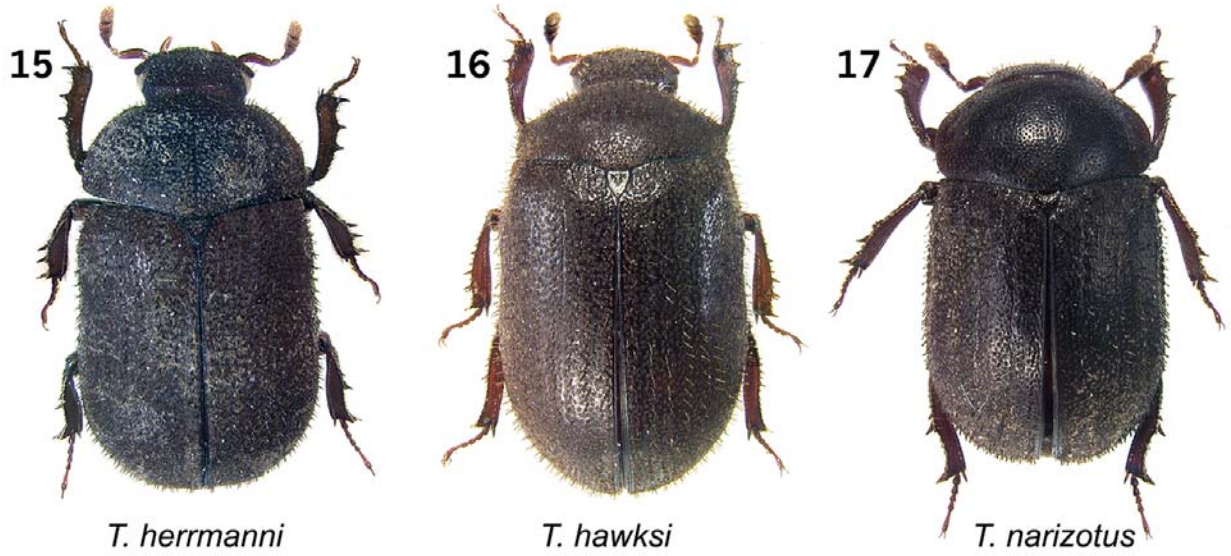
Trogellus Paulsen, new genus.

Type species: *Trogellus herrmanni* Paulsen, here designated.

Description. Coleoptera: Scarabaeoidea: Lucanidae: Aesalinae: Aesalini. ***Length*:** 3.7–6.5 mm. ***Width*:** 2.2–3.7 mm. ***Color*:** Body entirely dark brown, with testaceous to light brown bristles and minute branched scales (Fig. 7–10); surface often obscured by wood debris and residue. ***Head*:** Anterior margin of clypeus triangular or rounded. Mentum transversely subrectangular (nominal subgenus) to subquadrate, emarginate anteromedially, often bifoveate on disk. Eye canthus well developed (anterior margin of eye located on dorsal surface of head, per Holloway 1969), varying from short and broad to narrow and elongate. Antenna not geniculate; antennal club composed of 3 antennomeres in both sexes; club weakly asymmetrical, entirely tomentose. Mandibles small in both sexes, not distinctly sexually dimorphic, strongly incurved medially, approximately 1/3 length of head; form, simply falcate, right mandible with 1 strong internal tooth, left mandible with 1 weakly indicated to strong internal tooth; external margin with or without tooth-like process or angulation near middle. Labrum concealed by mandibles dorsally. ***Pronotum*:** Form convex, laterally explanate. Surface punctate, some punctures with erect bristles, bristled punctures with anterior tubercles, tubercles often well developed near posterior angles, occasionally indistinct. ***Elytra*:** Surface with two kinds of punctures, bristle (acute or blunt) or scale-bearing, with vestiture arising anteriorly in pit (*sensu* Holloway 1997); bristles erect, forming 8 rows on disc, each bristle with a small tubercle anterior to puncture; scales minute, multi-branched, appearing as brown scurfy covering usually with woody debris adhering, scale pits lacking anterior tubercle. ***Mesosternum*:** Mesosternal punctures oval, never lunate. ***Abdomen*:** Abdominal segments 1–2 appearing connate; segments 2–5 with deep furrow between segments. Segments 3–5 with scalloped anterior margin. Abdominal punctures predominantly oval with some more elongate punctures laterally (not furrow-like or sublinear), punctures containing setae (not scales). ***Legs*:** Anterior tibia dentate with 3–4 distinctly larger teeth, teeth broadly triangular (nominal subgenus; Fig. 11) or narrowly acute or peg-like (Fig. 12); teeth decreasing in size proximally; smaller teeth variably present in basal half. Mesotibia with 3–4 strong, external teeth in both sexes. Metatibia strongly, sexually dimorphic, with apex bulbous in females (Fig. 6) and acutely dentate in males (Fig. 5); Males with 0–2 strong external teeth at middle (Fig. 13–14), females with metatibial teeth smaller. ***Male genitalia*:** Parameres 1/2 to 1/4 as long as median lobe; median lobe variable, either simply cylindrical (nominal subgenus; Fig. 18–20), or with triangular lateral processes (Fig. 21–23), or asymmetrical and shell-shaped (Fig. 24–30).

Diagnosis/Remarks. *Trogellus* is distinguished from *Aesalus* by the characters outlined above. The most notable of these are the presence of an ocular canthus and the dorsal vestiture consisting of unicolorous bristles on the elytra with minute, intricately branched scales (Fig. 7–10). It is probable that the branched scales are associated with exudate that adheres wood debris to the elytral surface and results in a scurfy, camouflaging appearance. Members of the nominal subgenus differ in having acute elytral bristles (Fig. 7); distinctly broader, triangular protibial teeth (Fig. 11); a narrowly rectangular mentum without foveae; and simply cylindrical male genitalia.

Etymology. The generic name, gender masculine, is formed to approximate "little *Trox*". The name was chosen based on the close phylogenetic relationship between the Lucanidae and its sister family, Trogidae, which is morphologically most evident in the plesiomorphic aesaline stag beetles.



Figures 15–17. Habitus illustrations. **15)** *T. herrmanni* n. sp., male. **16)** *T. hawksi* n. sp., male. **17)** *T. narizotus* n. sp., male.

***Trogellus* (*Trogellus*) *herrmanni* Paulsen, new species**.

Type Material. Holotype male (INBIO) labeled: a) "Est. Pittier, Prov. Punta. COSTA / RICA / 1670m. 21–28 JUN 1995. M. / Moraga, / L_S_330900_577400 #5398"; b) INBIO barcode "COSTA RICA INBIO / CRI002 / 238296"; c) on red paper "*Trogellus* / *herrmanni* / [male symbol] / Paulsen, 2013 / HOLOTYPE". Allotype female (INBIO) labeled: a) "Est. Pittier, Prov. Punta. COSTA RICA / 1670m. 22–28 JUN 1995. A. Picado, / L_S_330900_577400 #5898"; b) INBIO barcode "COSTA RICA INBIO / CRI002 / 238292"; c) on red paper "*Trogellus* / *herrmanni* / [female symbol] / Paulsen, 2013 / ALLOTYPE".

Four male paratypes (INBIO) labeled as holotype except barcode numbers 238293, 238297, 238298, and 238305. Two female paratypes (INBIO) labeled as holotype except barcode numbers 238295, and 238300. Five male paratypes (INBIO) labeled as allotype except barcode numbers 321927, 321929, 321940, 321941, and 321942. Five female paratypes (INBIO) labeled as allotype except barcode numbers 321930, 321933, 321938, 321935, and 321937. One male, one female paratype (USNM) labeled: a) "PANAMA: Chiriqui / Bambito, 1770m; at Rio Chiriqui Viejo / 3 June 1983 / W. E. Steiner". One male paratype (CNCI) labeled: a) "PANAMA, Prov. Chiriqui / Cerro Punta, 8000 ft. / July 18–24, 1961 / J. M. Campbell"; b) "H. Bomans det. 19[85] / [*Aesalus* / *neotropicalis* / Bates]". Three male, four female paratypes (CMNC, MJPC) labeled: a) "PANAMA Chiriqui / Prov. 2km N Sta. / Clara, 1300m, 8° 51' N, / 82° 36' W Hartmann's / Finca 30–31.V.1977 / H. & A. Howden". One male paratype (CMNC) labeled: a) "PANAMA Chiriqui / Prov. 2km N Sta. / Clara, 1300m, 8° 51' N, / 82° 36' W Hartmann's / Finca ~~24–25.~~ [6.]V[I].1977 / H. & A. Howden"; One female paratype (CMNC) labeled: a) "PANAMA Chiriqui / Prov. 2km N Sta. / Clara, 1300m, 8° 51' N, / 82° 36' W Hartmann's / Finca 24–25.V.1977 / H. & A. Howden". One male, one female paratype (CMNC) labeled: a) "PANAMA, Chiriqui / Prov. 2km W Cerro / Punta 1720m 8° 51' N / 82° 36' W 25–29.V.77 / H. & A. Howden". One male paratype (CMNC) labeled: a) "PANAMA, Chiriqui / Prov. 2km W Cerro / Punta 1720m 8° 51' N / 82° 36' W 19–23.V.77 / H. & A. Howden". All paratypes with paratype labels on yellow paper: "*Trogellus* / *herrmanni* / [male or female symbol] / Paulsen, 2013/ PARATYPE".

Description. Holotype male. ***Length*:** 5.1 mm. ***Width*:** 2.5 mm. ***Head*:** Clypeus triangular with distinctly produced, tooth-like apex. Canthus elongate, length approximately 2× width. Mandibles with small but distinct external, median tooth at angulation. ***Pronotum*:** Surface posterolaterally densely punctate, lacking obvious tubercles; punctures mixed large and moderate in size, ocellate. ***Elytra*:** Surface with acute bristles (Fig. 7), bristles relatively short (distinctly shorter than canthus). ***Legs*:** Protibia tridentate, external margin between teeth slightly concave. Mesotibia with 3 strong external teeth (proxi-

mal tooth smaller) and acute apex. Metatibia with 1 large median tooth (Fig. 14) and strongly toothed apex (right metatibia also with second relatively large median tooth). ***Male genitalia*:** Parameres 1/4 as long as median lobe. Median lobe more or less symmetrical, robustly cylindrical for entire length, apex less sclerotized but not spatulate (Fig. 18).

Description. Allotype female. ***Length*:** 5.6 mm. ***Width*:** 2.8 mm. Differs from male holotype in the following: ***Legs*:** Protibia tridentate, external margin between teeth slightly concave. Mesotibia with 3 strong external teeth. Metatibia with median tooth smaller and apex tumid.

Paratypes vary as follows: ***Length*:** 4.8–5.6 mm. ***Width*:** 2.5–3.1 mm. Mandibles with external median tooth more or less obsolete to distinctly present at angulation. Mesotibia generally with 3 strong external teeth and proximal tooth small to obsolete. Metatibia with second median tooth variably absent in males; females with external teeth weaker.

Distribution. COSTA RICA: Puntarenas (18): Estación Pittier. **PANAMA: Chiriquí** (15): Bambito, Cerro Punto, Santa Clara/Hartmann's Finca.

Temporal Distribution. May (11), June (20), July (1).

Diagnosis/Remarks. This species is immediately recognizable due to its spiny, but relatively short, vestiture (see the remarks for the following species) and distinctive male genitalia. The Panama material from CMNC has non-validated holotype and paratype labels for a manuscript name that has not been made available and lack the putative author's name. According to CMNC registrar Nancy Boase (pers. comm.), the previous loan was granted 16 years ago, and was recalled after approximately a dozen years without resulting in a publication. For this reason, and because the labels indicate that the name was applied to specimens of two distinct species, I am ignoring the extraneous labels. They are not recorded here to prevent confusion.

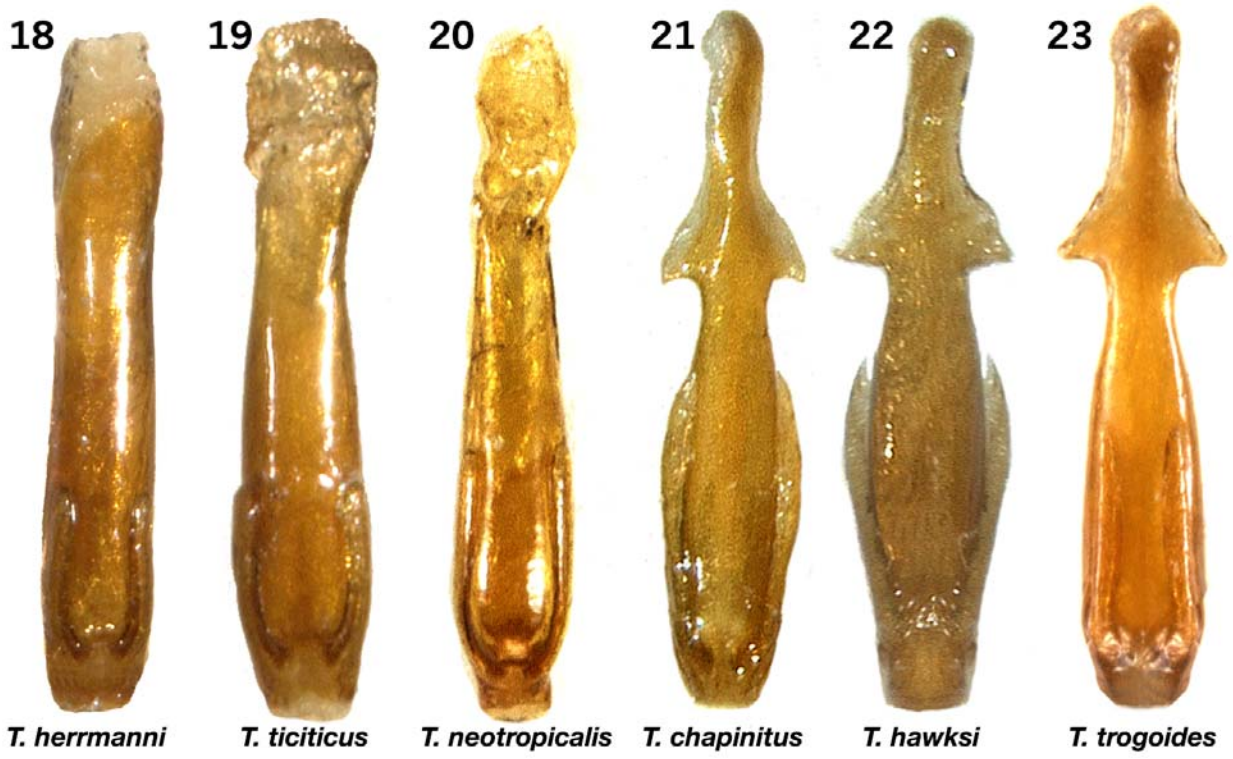
Etymology. This species is named for my friend and colleague Dr. Matthias Herrmann of Tübingen, Germany, in honor of his collecting prowess, love of beetles and books, and because he improves any trip by several orders of magnitude.

***Trogellus* (*Trogellus*) *ticiticus* Paulsen, new species**.

Type Material. Holotype male (CMNC) labeled: a) "COSTA RICA: Puntarenas / Monteverde, Estacion Biologica / Monteverde, 10°19'40"N / 84°49'08"W, 1540m, 9.VI.2001 / R. Anderson, at lights / 2001-101X"; b) orange paper "DNA VOUCHER / P006 2008 / MJ PAULSEN – UNSM"; c) on red paper "*Trogellus* / *ticiticus* / [male symbol] / Paulsen, 2013 / HOLOTYPE".

One male paratype (CMNC) labeled a) "COSTA RICA, 1560m / 4dung traps / 11–18.VI.83 / D.H. Lindeman"; b) "Aesalus howdeni" (sic). One male paratype (MJPC) labeled: a) "COSTA RICA. Punt. / Monteverde. 1400m / 26 May 1979 / H. & A. Howden". One female paratype (CNCI) labeled: a) "COSTA RICA. Punt. / Monteverde. 1400m / 31 May 1979 / H. & A. Howden". One paratype female (INBIO) labeled: a) "San Luis, 1040m, R.B. / Monteverde Prov. Punt- / arenas, Costa Rica, Jul / 1992. Z. Fuentes / L-N 250850, 449250; b) INBIO barcode "COSTA RICA INBIO / CRI000 / 730108". All paratypes with paratype labels on yellow paper: "*Trogellus* / *ticiticus* / [male or female symbol] / Paulsen, 2013 / PARATYPE".

Description. Holotype male: ***Length*:** 4.3 mm. ***Width*:** 2.3 mm. ***Head*:** Clypeus triangular with distinctly produced, tooth-like apex. Canthus elongate, length approximately 2× width. Mandibles without external median tooth at angulation. ***Pronotum*:** Surface densely punctate, lacking obvious tubercles; punctures moderate in size. ***Elytra*:** Surface with acute bristles, bristles relatively long (distinctly longer than canthus). ***Legs*:** Protibia more or less tridentate but with 2–3 smaller but distinct teeth giving a multidentate appearance, external margin between larger teeth slightly concave. Mesotibia with 3 strong



Figures 18–23. Male genitalia of *Trogellus* species, dorsal view. **18.** *T. herrmanni* n. sp. **19)** *T. ticiticus* n. sp. **20)** *T. neotropicalis*. **21)** *T. chapinitus* n. sp. **22)** *T. hawksi* n. sp. **23)** *T. trogoides*. The male genitalia of *T. maesi* n. sp. are unknown.

external teeth. Metatibia with 1 large median tooth and strongly toothed apex (left metatibia also with second relatively large median tooth). ***Male genitalia*:** Parameres 1/4 as long as median lobe. Median lobe more or less symmetrical, cylindrical, and tapering before spatulate, less sclerotized apex (Fig. 19).

Paratypes vary as follows: *Length*: 4.0–5.3 mm. ***Width*:** 2.2–2.8 mm. Mandibles with external angle rarely appearing toothed. Mesotibia generally with 3 strong external teeth. Metatibia of females with external tooth weak.

Distribution. COSTA RICA: Puntarenas (5): Monteverde.

Temporal Distribution. May (2), June (2), July (1).

Diagnosis/Remarks. This species is recognizable due to its long, spiny bristles on the elytra. Only three species have acute bristles, and in *T. ticiticus* they are distinctly longer than in *T. herrmanni* or *T. neotropicalis*. The male genitalia are unique in being more bulbous basally and narrowing before a spatulate apex of the median lobe (Fig. 19). In addition, the protibiae have more strongly developed secondary teeth in this species than in *T. herrmanni,* which results in the protibiae appearing less tridentate than multidentate.

Etymology. The specific epithet is a Latinized form of the term '*tico',* a colloquial name for Costa Ricans, with the diminutive suffix *-itico* used in that country, resulting in '*ticitico*' and meaning 'little *tico*'. It is used as a noun in apposition, and the gender is masculine.

***Trogellus* (*Trogellus*) *neotropicalis* (Bates, 1886), new combination.**

Aesalus neotropicalis Bates 1886: 2, original combination.

Type Material. Lectotype male (BMNH), *here designated*, labeled: a) blue-bordered, circular "SYNTYPE"; b) "Capetillo, / Guatemala, / G.C. Champion."; c) handwritten "*Æsalus* / *neotropicalis* / Bates"; d) "B.C.A. / 2.2"; e) "Sp. figured."; f) "BMNH(E) / #608327"; g) red paper "*Aesalus* / *neotropicalis* / Bates, 1886 [male symbol]/ LECTOTYPE / des. M.J. Paulsen".

Paralectotype [male or female symbol] pair (glued on card, BMNH) labeled: a) as lectotype; b) red-bordered circular "TYPE"; c–e) as b–d of lectotype; f) "H. Bomans det., 1986 / [*Aesalus* / *neotropicalis* / Bates"; g) yellow paper "*Aesalus* / *neotropicalis* / Bates, 1886 [male or female symbol] / PARALECTOTYPES / des. M.J. Paulsen". Paralectotype [male or female symbol] pair (glued on card, BMNH) labeled as previous pair but without label *b*. Paralectotype male (FMNH) labeled: "Guatemala / City / Champion."; b) handwritten "*Aesalus* / *neotropicalis* / co-type Bates"; c) "Chicago Nat Hist Mus / B. Benesh Colln. / Lucanidae (Benesh / Access No._); d) yellow paper "*Aesalus* / *neotropicalis* / Bates, 1886 [male symbol] / PARALECTOTYPE / des. M.J. Paulsen". Paralectotype female (CNCI) labeled: a) "Guatemala / City / Champion."; b) "B.C.A. / 2.2."; c) "COTYPE / [8234] / CNCNo. / [*A. neotropicalis* / Bates]"; d) [*Aesalus* / *neotropicalis* / Bates] / DET. at B.M. / H. F. Howden '62"; e) yellow paper, "*Aesalus* / *neotropicalis* / Bates, 1886 [female symbol]/ PARALECTOTYPE / des. M.J. Paulsen". All specimens with my determination label: "*Trogellus* / *neotropicalis* / (Bates, 1886) / det. M.J. Paulsen 2013".

Description. Lectotype male: ***Length*:** 4.1 mm. ***Width*:** 2.2 mm. ***Head*:** Clypeus triangular with distinctly produced, tooth-like apex. Canthus elongate, length approximately 2× width. Mandibles with external median tooth at angulation. ***Pronotum*:** Surface densely punctate, with fine tubercles evident anterolaterally; punctures moderate in size. ***Elytra*:** Surface with acute bristles, bristles relatively long (distinctly longer than canthus). ***Legs*:** Protibia tridentate, teeth triangular, sharp. Mesotibia with 2 strong, external teeth and acute apex. Metatibia with 1 large median tooth and acute apex. ***Male genitalia*:** Parameres 2/5 as long as median lobe. Median lobe more or less symmetrical, cylindrical and tapering before spatulate, less sclerotized apex (Fig. 20).

Variation in other specimens. ***Length*:** 3.8–4.2 mm. ***Width*:** 2.0–2.3 mm. ***Legs*:** Metatibia with external tooth weaker in females.

Distribution. GUATEMALA: Guatemala (3): Guatemala City. **Sacatepéquez** (5): Capetillo.

Temporal Distribution. No data (8).

Diagnosis/Remarks. At around 4mm in length, this species is distinctly smaller than most other species of *Trogellus*. It is immediately recognizable among the Guatemalan species due to its acute elytral bristles and stronger protibial teeth. Bates (1886) indicated that a series was collected by "beating the withered leaves and boughs of fallen forest trees". No recent specimens have been examined. Maes (1992) included Veracruz, Mexico in this species' distribution, but that specimen is part of a new species described below, and *T. neotropicalis* is not known from Mexico.

The lectotype male from the original syntype series in the BMNH has a label indicating that it was the specimen illustrated in the BCA by Bates (1886).

***Trogoides* Paulsen, new subgenus of *Trogellus*, Paulsen**

Type species: *Aesalus trogoides* Albers, here designated.

Description. This subgenus differs from the description given for *Trogellus* above by the presence of blunt bristles on the dorsal surface and narrower, peg-like protibial teeth (Fig. 12), and from both of the other genera by the male genitalia having triangular, lateral processes on the median lobe (Fig. 21–23).

Tubercles are generally present on the pronotum but vary from being weak and only present near the anterior angles in *T. trogoides* to being well developed laterally in the other species. Both sexes of *Trogoides* species have poorly developed metatibial teeth (Fig. 13), whereas males of both other subgenera have strongly developed teeth. Species of the subgenus *Trogoides* have a more elongate overall body form.

Etymology. The subgeneric name, gender masculine, is based on the specific epithet of its type species, tautonymically, and means 'resembling *Trox'*.

***Trogellus* (*Trogoides*) *chapinitus* Paulsen, new species.**

Type Material. Holotype male (FSCA) labeled: a) "GUATEMALA: Dept. Zacapa / Sierra de los Minas: "El Naranjo" / S slope below San Lorenzo Mine; / 15.07329, -89.68481; 1600–1770m / at light; 21–24.V.2010; oak forest; / P. Skelley, G. Steck, B. Sutton".

Paratype female (MJPC) labeled: a) "GUATEMALA: Dept. Zacapa / Sierra de los Minas: "El Naranjo" / S slope below San Lorenzo Mine; / 15.07329, -89.68481; 1600–1770m / FIT; 21–24.V.2010; oak forest; / P. Skelley, G. Steck, B. Sutton". Two paratype females (WBWC) labeled: a) "Guatemala: Izabal, SE of / Morales, Finca Firmesa 2 / 15°21'51"N, 88°41'28"W / elev. 3880', vi-21–22-2001"; b) "W.B. Warner, / J. Monzón-Sierra / & R. Cunningham / UV, MV & MH light".

Non-type specimens. One female (RHTC) labeled: a) "HONDURAS: Yoro / PN Pico Pijol / mv + bl, 22 July / 2001, R. Turnbow".

Description. Holotype male. ***Length*:** 5.0 mm. ***Width*:** 2.6 mm. ***Head*:** Canthus long, length approximately 2× width. Clypeus triangular, apex not distinctly produced. Mentum bifoveate. Mandibles weakly dentate externally at angulation. ***Pronotum*:** Surface densely punctate, with distinct tubercles posterolaterally at base of bristles; punctures moderate in size, ocellate. ***Metasternum*:** Punctures anterolaterally moderate in size. ***Elytra*:** Surface with blunt bristles, bristles moderately long (distinctly longer than 4th tarsomere). ***Legs*:** Protibiae tridentate, teeth narrow, weak; margin between teeth nearly flat (between 2 apical teeth more concave). Mesotibia with 3 external teeth (proximal tooth smaller) and acute apex. Metatibia straight, with 1 small median tooth and 1–2 smaller teeth proximally; apex acute. ***Male genitalia*:** Parameres broad and elongate, over 1/2 as long as median lobe, located on side of median lobe; median lobe symmetrical, with large triangular lateral processes at distal third, processes with distal margin curved towards base (Fig. 21).

Paratypes vary as follows: *Length*: 4.2–5.7 mm. ***Width*:** 2.4–3.0 mm. ***Legs*:** Mesotibia with 2–3 external teeth (proximal teeth smaller). Metatibia with external teeth almost obsolete, or 1–2 small teeth; metatibiae of females with tumid apex. ***Female genitalia*:** Styli long, peg-like, truncate at apex.

Distribution. GUATEMALA: Izabal (2): Morales- Finca Firmesa; **Zacapa** (2): Sierra de los Minas / San Lorenzo Mine. **HONDURAS: Yoro** (1): Pico Pijol.

Temporal Distribution. May (2), June (2), July (1).

Diagnosis/Remarks. This species is similar to *T. hawksi* externally, but it has smaller punctures on the metasternum. It is also similar to *T. maesi* but has straight metatibiae. The female genitalia are distinctive between the three species, although the known male genitalia vary only in the basal margin of the triangular processes being curved proximally or straight. An additional specimen from Pico Pijol, Honduras is not included in the type series but at present is referable to this species.

Etymology. The specific epithet is a Latinized form of the term '*chapin',* a colloquial name for Guatemalans, with the diminutive suffix *-ito* used in that country, resulting in '*chapinito*' and meaning 'little Guatemalan'. It is used as a noun in apposition, and the gender is masculine.

***Trogellus* (*Trogoides*) *hawksi* Paulsen, new species**.

Type Material. Holotype male (TAMU) labeled: a) "Mex: Chiapas, 3 / km. W. Jotolito / vi-7-1987, D.B. / Thomas & A. Mendoza"; b) "TAMU – ENTO / X0074298" barcode label; c) red paper: "*Trogellus* / *hawksi* [male symbol] / Paulsen, 2013 / HOLOTYPE".

One paratype female (WBWC) labeled: a) "MEX: Edo. Chiapas / Parque Laguna / Belgica, VI-4-87 / W.B. Warner"; b) handwritten "*Aesalus* / *sp.* / Det. W.B. Warner '92"; c) yellow paper: "*Trogellus* / *hawksi* [female symbol] / Paulsen, 2013 / PARATYPE". One paratype female (MJPC) labeled: a) "GUATEMALA: Such- / itepéquez, Finca / Tarrales, Volcan Atitlan / 9–13-VI-2012, 1340m / collector: J.B. Heppner".

Description. Holotype male. ***Length*:** 4.7 mm. ***Width*:** 2.5 mm. ***Head*:** Clypeus triangular, apex not distinctly produced. Canthus long, length approximately 2× width. Mandibles without external tooth at angulation. ***Pronotum*:** Surface densely punctate, with distinct tubercles posterolaterally at base of bristles, punctures large, ocellate. ***Metasternum*:** Anterolateral punctures large. ***Elytra*:** Surface with blunt bristles, bristles moderately long (distinctly longer than 4th tarsomere). ***Legs*:** Protibiae tridentate, teeth small, margin between teeth nearly flat. Mesotibia with 4 external teeth (proximal tooth smaller) and acute apex. Metatibia straight, with 1 small median tooth and 2–3 smaller teeth proximally; apex acute. ***Male genitalia*:** Parameres broad and elongate, over 1/2 as long as median lobe, located on side of median lobe; median lobe symmetrical, with large triangular lateral processes at distal third, processes with distal margin straight (Fig. 22).

Paratypes vary as follows: *Length*: 4.1–5.8 mm. ***Width*:** 2.3–3.1 mm. Female with external margin of protibiae slightly concave between teeth and mesotibial external tooth smaller. ***Legs*:** Metatibiae of females with tumid apex. ***Female genitalia*:** Styli moderately elongate, strongly hooked.

Non-type specimens. One male (CMNC) labeled: a) "Mexico, V.C. Volcan / San Martin, E. slope / B. & B. Valentine"; b) "beating el. / 49-5000' / 30-VII-59"; c) "[*Aesalus* / *neotropicalis* / Bates] / DET. / H.F. Howden [74]".

Distribution. GUATEMALA: Suchitepéquez (1): Finca los Tarrales/Volcan Atitlan. **MEXICO: Chiapas** (2)**:** Jotolito; Parque Laguna Belgica. **Veracruz** (1): Volcan San Martin Tuxtla, SE slope (CMNC);

Temporal Distribution. June (3), July (1).

Diagnosis/Remarks. The holotype is distinguished from the other Mexican species (*T. trogoides*) by its distinctly tuberculate head and pronotum; elongate, narrow ocular canthus; and much longer parameres. Specimens of *T. chapinitus* have smaller, weakly ocellate punctures on the metasternum.

An additional specimen from Veracruz is tentatively identified as *T. hawksi* because of the elongate ocular canthi and strongly tuberculate pronotum, but it is excluded from the type series. The Veracruz specimen is from the remote mountains of Tuxtla, an isolated montane area that is home to several endemic species, including two species and five subspecies of endemic birds (Winker et al. 1992). The male genitalia are similar to those of the holotype, but the parameres appear slightly larger, and the vestiture of the elytra appears coarser. A series of specimens from the locality would indicate whether the population is *T. hawksi* or an undescribed species. The specimen was identified and listed as *A.* near *neotropicalis* by Howden and Lawrence (1974), but as *A. neotropicalis* by Maes (1992).

Etymology. The species is named in honor of my friend and colleague, David C. Hawks, University of California, Riverside, California, for his unceasing efforts to bring some order to the chaos of scarabaeoid classification and the tremendous help he has provided me over the years.

***Trogellus* (*Trogoides*) *maesi* Paulsen, new species**.

Type Material. Holotype female (UNSM) labeled: a) "NICARAGUA: Matagalpa / Montaña Selva Negra / N13°00'01" W85°54'32" / VI-24/25-2002, FI Trap"; b) "BC Ratcliffe, ML Jameson, / FC Ocampo, MJ Paulsen / ABT Smith"; c) UNSM SCARAB DNA / VOUCHER SPECIMEN / [AS63 / SEPT.-2002];" d) red paper, "*Trogellus* / *maesi* [female symbol] / Paulsen, 2012 / HOLOTYPE".

Paratype female (MJPC) labeled: a, b as holotype; c) yellow paper, "*Trogellus* / *maesi* [female symbol] / Paulsen, 2013 / PARATYPE".

Description. Holotype female. ***Length*:** 4.7 mm. ***Width*:** 2.8 mm. ***Head*:** Clypeus triangular, apex not distinctly produced. Canthus long, length approximately 2× width. Mandibles with external tooth at angulation. ***Pronotum*:** Surface densely punctate, with distinct tubercles posterolaterally at base of bristles; punctures large, ocellate. ***Metasternum*:** Punctures anterolaterally moderate in size. ***Elytra*:** Surface with blunt bristles, bristles moderately long (distinctly longer than 4th tarsomere). ***Legs*:** Protibiae tridentate, teeth small, margin between teeth nearly flat. Mesotibia with 3 external teeth (proximal tooth smaller) and acute apex. Metatibia sinuate, with 2–3 small external teeth; apex tumid. ***Female genitalia*:** Styli short, strongly hooked.

Paratype varies as follows: *Length*: 5.8 mm. ***Width*:** 3.0 mm.

Distribution. NICARAGUA: Matagalpa (2): Selva Negra.

Temporal Distribution. June (2).

Diagnosis/Remarks. This species has a narrower, more elongate ocular canthus than *T. trogoides*. Externally, the species is similar to *T. hawksi* in the shape of the ocular canthus and the tuberculate pronotum, but the prosternum before the procoxae is distinctly narrower in *T. maesi* than in the remaining specimens of the subgenus, and the metatibiae are distinctly more sinuate. Furthermore, the styli of the female genitalia are shorter and more strongly hooked than in *T. hawksi,* and the metasternum has larger ocellate punctures. Both specimens were collected in a flight-intercept trap, and are female, so the male genitalia of the species remain unknown.

Etymology. The first, and only, stag beetle known from Nicaragua is named for Jean-Michel Maes of Leon, Nicaragua, in honor of his publications on Lucanidae and sympatry with the new species.

***Trogellus* (*Trogoides*) *trogoides* (Albers, 1883), new combination**.

Aesalus trogoides Albers 1883: 228, original combination.
Aesalus smithi Bates 1889: 382, **new synonymy.**

Type Material. Neotype of *Aesalus trogoides*, *here designated*, and holotype of *A. smithi* (BMNH) female labeled: a) "Chilpancingo, / Guerrero, / 4600 ft. / June. H. H. Smith"; b) "B.C.A. / [382, 2a]"; c) handwritten "*Aesalus* / *smithi* / Bates"; d) red-bordered, circular "Type"; e) red-bordered, circular "Holo- / type"; f) "H. Bomans det., 19[86] / [*Aesalus* / *smithi* Bates]"; g) handwritten "HOLOTYPE / "*Aesalis* (sic) *smithi* Bates / M.D.K. 1986"; h) handwritten [female symbol] / sexed by / Araya 1998"; i) "BMNH(E) / #608319"; i) red paper, "*Aesalus smithi* / Bates, 1889 / HOLOTYPE"; j) red paper, "*Aesalus trogoides* / Albers, 1883 / NEOTYPE / des. M.J. Paulsen"; k) "*Trogellus* / *trogoides* / (Albers, 1883) / det. M.J. Paulsen 2013". Justification for the designation of a neotype is presented in the Introduction above.

Description. Neotype female. ***Length*:** 5.9 mm. ***Width*:** 2.9 mm. ***Head*:** Clypeus triangular with distinctly produced, tooth-like apex. Canthus short, length approximately equal to width. Mandibles without external tooth at angulation. ***Pronotum*:** Lateral margin explanate in anterior view. Surface densely punctate, lacking obvious tubercles posterolaterally; punctures large, ocellate. ***Elytra*:** Surface with

blunt bristles, bristles short (distinctly shorter than 4th tarsomere). ***Legs*:** Protibia tridentate, external teeth small, margin between teeth slightly flat. Mesotibia with 4 external teeth (proximal tooth smaller). Metatibia with 1 small median tooth and tumid apex.

Other specimens vary as follows: ***Length*:** 4.9–6.5 mm. ***Width*:** 2.7–3.3 mm. Males with metatibial apex acute. ***Male genitalia*:** Parameres narrow, 2/5 as long as median lobe, located on dorsal surface of median lobe; median lobe symmetrical, with large triangular lateral processes at distal third, processes with distal margin straight (Fig. 23).

Distribution. MEXICO: Distrito Federal (37): Magdalena Contreras – Parque Nacional Los Dinamos (MJPC, UNAM); Tlalpan - La Venta (BMNH, CMNC, CASC, FMNH); **Guerrero:** Chilpancingo; Sierra de Taxco (Reyes-Castillo & Boucher 2003). **Hidalgo** (3): P.N. el Chico, Cam a la Peña del Cuervo; PN Los Marmoles, Zimapan, La Encarnacion Bosque de Encino (IEXA); Tenango de Doria (Reyes-Castillo & Boucher 2003); Tlanchinol (Delgado & Márquez 2006). **Jalisco** (2): Tecolotlan, Sierra de Quila; Zapotlán el Grande, Nevado de Colima (IEXA, UNAM). **Mexico** (1): Real de Arriba / Temescaltepec; Rio Frio (Reyes-Castillo & Boucher 2003). **Michoacan:** Pátzcuaro (Reyes-Castillo & Boucher 2003). **Morelos** (1): Tres Cumbres (CMNC). **Puebla:** Huauchinango (Reyes-Castillo & Boucher 2003). **Tamaulipas** (1): 6 mi W. Rio Sabinas near Encino (TAMU); Gómez Farías (Reyes-Castillo & Boucher 2003).

Temporal Distribution. April (1), June (3), July (30), August (1), October (1). No data (9).

Diagnosis/Remarks. This species is the largest in the genus and can immediately be recognized by the short and broad ocular canthus and by the absence of tubercles on the sides of the pronotum (instead being distinctly punctate with large, ocellate punctures). In other species of the subgenus *Trogoides* the tubercles of the posterior part of the pronotum are distinct. The parameres of the male genitalia are much shorter than in *T. hawksi,* the other species occurring in Mexico. According to the labels, the specimen from Tres Cumbres was collected as a larva in February and eclosed in April. Specimens have been taken in pine logs at high elevations.

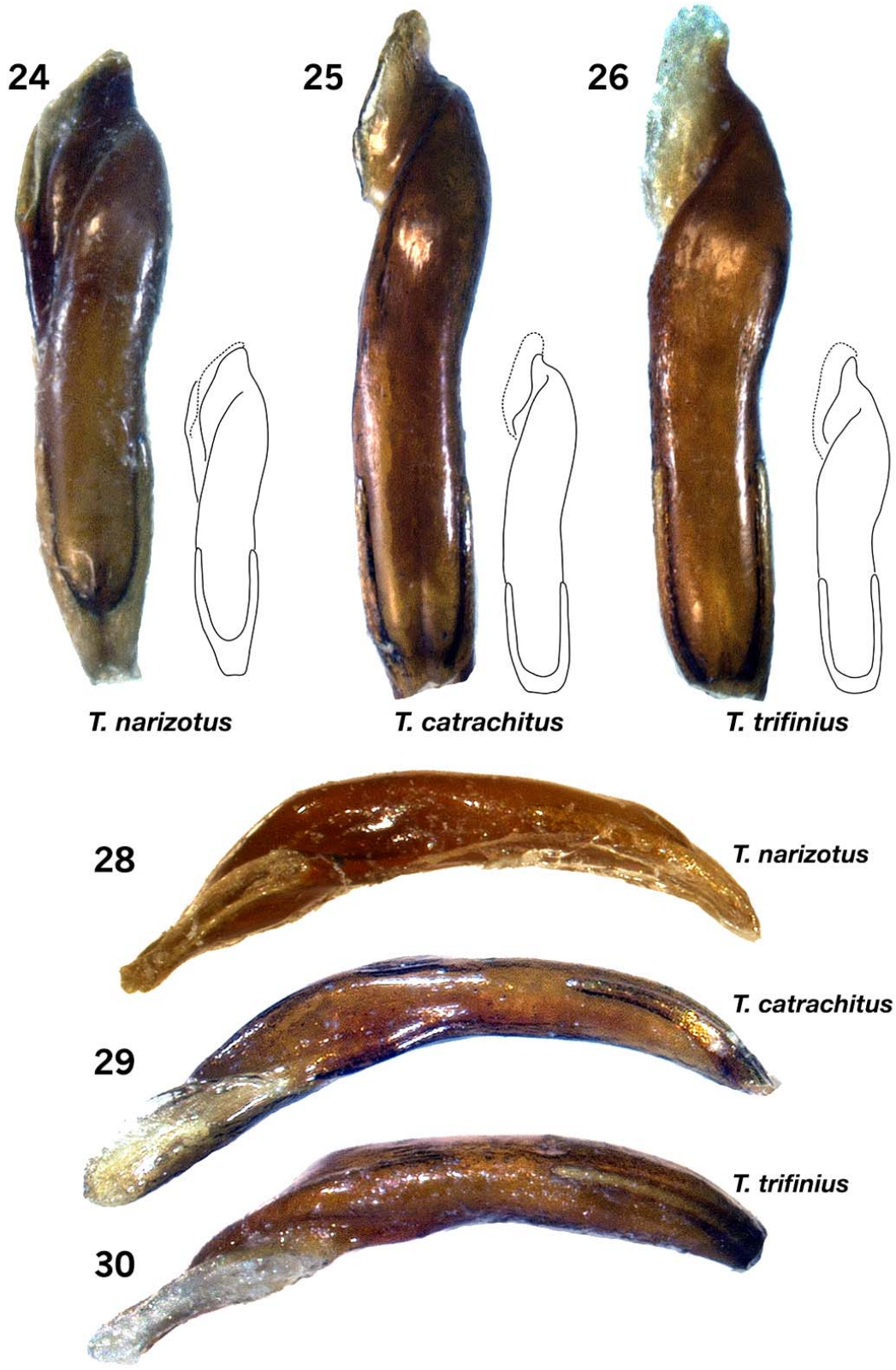
Reyes-Castillo and Boucher (2003) treated the species and provided a brief description and detailed distributional map. Howden and Lawrence (1974) listed specimens of *A.* near *trogoides* from the "state of Morelia, Mexico" (which probably refers to the *T. trogoides* specimen from Tres Cumbres, Morelos in the Howden Collection/CMNC), as well as from the "state of Tabasco". I have not encountered any specimens from Tabasco, which would be outside the known range of *T. trogoides*. Maes, in an undated web page (http://www.bio-nica.info/lucanidae/AESALUS%20TROGOIDES.htm, accessed 21.VIII.2013) construed this latter locality reference to mean the town of Tabasco in Zacatecas state. If that is correct, it would most likely refer to *T. trogoides,* although it would also be a significant extension of the known range.

This species has the largest distribution of any in the genus, but as with most other species, it is found at high elevations in pine and pine-oak forests. Reyes-Castillo and Boucher (2003) reported finding living and dead adults, larvae, and pupae in the dark reddish parts of decaying pine trunks and stumps from May to October. Other specimens have been taken in pine logs with lighter, crumbling decomposing wood (A.D. Smith, personal communication).

***Mayaesalus* Paulsen, new subgenus of *Trogellus,* Paulsen**.

Type species: *Trogellus narizotus* Paulsen, here designated**.**

Description. This subgenus is distinguished morphologically based on the rounded clypeal apex and the snail-shaped, asymmetrical median lobe of the male genitalia. The pronotum of species in this subgenus completely lack the tubercles that are found anterior to the scaled punctures in species of the other subgenera. Species of this subgenus have blunt dorsal bristles, not acute as in the nominal subgenus. The protibiae may be either tridentate or quadridentate, and the metatibiae of males have a strong external tooth. The body form is shorter (Fig. 17) than in species of the subgenus *Trogoides*.



Figures 24–30. Male genitalia of *Trogellus* subgenus *Mayaesalus* species, dorsal (Fig. 24–26) and right lateral (Fig. 28–30) views. Outlines of genitalia in dorsal view shown to the right of each. **24, 28)** *T. narizotus*, n. sp. **25, 29)** *T. catrachitus*, n. sp. **26, 30)** *T. trifinius*, n. sp.

***Trogellus* (*Mayaesalus*) *catrachitus* Paulsen, new species**.

Type Material. Holotype male (FSCA) labeled: a) "HONDURAS: Octoepe- / que (sic), El Portillo / 7 Oct. 1993 / R. Turnbow"; b) red paper, "*Trogellus* / *catrachitus* [male symbol] / Paulsen, 2012 / HOLOTYPE".

Description. Holotype male. ***Length*:** 5.8 mm. ***Width*:** 3.5 mm. ***Head*:** Frons flat, punctate; punctures large, separated by ¼ to 1 puncture diameter. Clypeus rounded, apex not produced. Frons not distinctly flattened. Canthus long, length approximately 2× width. Mandibles each with 1 strong internal tooth, externally lacking tooth at angulation. ***Pronotum*:** Lateral margin explanate in anterior view. Surface densely punctate, lacking tubercles at base of bristled punctures; punctures large. ***Elytra*:** Surface with blunt bristles, bristles long (as long as distance to next bristle in row). ***Legs*:** Protibiae quadridentate, teeth small, margin between teeth slightly concave. Mesotibia with 3 external teeth (proximal tooth smaller). Metatibia with 1 large, median tooth and 1 smaller tooth distally; apex acute. ***Male genitalia*:** Parameres narrow and short, 1/3 as long as median lobe; median lobe asymmetrical, cylindrical medially (not bulbous; Fig. 25, 29).

Distribution. HONDURAS: Ocotepeque (1): El Portillo.

Temporal Distribution. October (1).

Diagnosis/Remarks. The species is distinguished from *T. narizotus* by its less produced clypeus. It is similar to *T. trifinius* but differs in the structure of the median lobe of the male genitalia. In *T. catrachitus,* the median lobe is simply cylindrical medially, and the membranous apical portion smaller and more sclerotized. Also, the protibial teeth are smaller, the frons not strongly flattened, the elytral bristles are distinctly longer, and the ocular canthus more elongate.

Etymology. The specific epithet is a Latinized form of the term '*catracho',* a colloquial name for Hondurans, with the diminutive suffix *-ito* used in that country, resulting in '*catrachito*' and meaning 'little Honduran'. It is used as a noun in apposition, and the gender is masculine.

***Trogellus* (*Mayaesalus*) *narizotus* Paulsen, new species**.

Type Material. Holotype male (UNSM) labeled: a) "GUATEMALA: Sacatepéquez: / Antigua, Cerro Carmona, Finca / El Pilar; N14°32'16.9", / W90°41'43.1"; 2100m; ex pine / log, M.J. Paulsen; 4.VII.2009"; b) red paper, "*Trogellus* / *narizotus* [male symbol] / Paulsen, 2012 / HOLOTYPE".

Two paratype males, 1 paratype incomplete female (UVGC, MJPC) labeled a) as holotype; b) yellow paper, "*Trogellus* / *narizotus* [male or female symbol] / Paulsen, 2013 / PARATYPE".

Description. Holotype male (disarticulated). ***Length*:** 4.7 mm. ***Width*:** 3.0 mm. ***Head*:** Frons flat, punctate; punctures large, separated by 1/2 to 1 diameter. Clypeus rounded, apex distinctly produced (Fig. 31). Canthus short, length subequal to width. Mandibles each with 1 strong internal tooth, denticulate at external angulation. ***Pronotum*:** Lateral margin explanate in anterior view. Surface densely punctate, lacking tubercles at base of bristled punctures; punctures moderate in size. ***Elytra*:** Surface with blunt bristles, bristles short (shorter than distance to next bristle in row). ***Legs*:** Protibiae tridentate, teeth small, margin between teeth concave. Mesotibia with 2 strong, external teeth subequal in size. Metatibia with 1 large, median tooth with 1 smaller tooth distally; apex acute. ***Male genitalia*:** Parameres narrow and short, 1/3 as long as median lobe; median lobe asymmetrical, with elongated ostium (Fig. 24, 28).

Paratypes vary as follows: *Length*: 5.2–6.0 mm. ***Width*:** 3.0–3.3 mm. ***Legs*:** Metatibiae of female unknown (partial specimen missing metatibiae). ***Female genitalia*:** Styli short, peg-like.

Distribution. GUATEMALA: Sacatepéquez (4): Antigua- Cerro Carmona.

Figure 31. Head of *T. narizotus* n. sp., showing the rounded and produced clypeal apex.

Temporal Distribution. July (4).

Diagnosis/Remarks. This species is the most easily recognizable aesaline in Central America. The clypeal apex is produced and narrowly rounded (Fig. 31), whereas in the other species of the subgenus the apex is not produced and subtriangular. The shape of the male genitalia is also distinct (Fig. 24, 28). This is the only species in the subgenus for which a female is known, albeit from an incomplete specimen. The styli of the genitalia are much shorter than in those of other species studied, peg-like, and not hooked. I collected the entire series of one living and a few dead, disarticulated specimens and body parts in a decaying pine log.

Etymology. The specific epithet is a Latinized adjectival form of the Spanish term '*narizota',* meaning large nose. The gender is masculine.

***Trogellus* (*Mayaesalus*) *trifinius* Paulsen, new species**.

Type Material. Holotype male (UNSM) labeled: a) "EL SALVADOR: Santa Ana / Parq Nac Montecristo / VI-20–21-2002 2175m / N14°24'33" W89°22'20" / B. Ratcliffe, M. Jameson, R. Cave / A. Smith, F. Ocampo, M. Paulsen"; b) "UNSM SCARAB DNA / VOUCHER SPECIMEN / [AS62 / SEPT. / 2002"; c) "DNA VOUCHER / MAR07 MP334"; d) red label, "*Trogellus* / *trifinius* / Paulsen [male symbol] / HOLOTYPE".

Description. Holotype male. ***Length*:** 5.7 mm. ***Width*:** 3.2 mm. ***Head*:** Frons flat, punctate; punctures large, separated by 1/2 to 2 diameters. Clypeus subtriangular, rounded, apex not produced. Frons distinctly flattened, subconcave. Canthus short, length subequal to width. Mandibles each with 1 strong internal tooth, externally lacking tooth at angulation. ***Pronotum*:** Lateral margin explanate in anterior view. Surface densely punctate, lacking tubercles at base of bristled punctures; punctures large. ***Elytra*:** Surface with blunt bristles, bristles short (shorter than distance to next bristle in row). ***Legs*:** Protibiae quadridentate, teeth subtriangular and decreasing in size proximally, margin between teeth weakly concave. Mesotibia not present. Metatibia with 1 large median tooth; apex acute. ***Male genitalia*:** Parameres narrow and short, 1/3 as long as median lobe; median lobe asymmetrical, bulbous after middle (Fig. 26, 30).

Distribution. EL SALVADOR: Santa Ana (1): Parque Nacional Montecristo.

Figure 32. Distribution of *Trogellus* species. Subgenera are represented by icon shape, and the line from each name indicates the location of the type locality. *Trogellus* = triangles: *T. herrmanni* (green), *T. ticiticus* (red), and *T. neotropicalis* (white). *Trogoides* = squares: *T. trogoides* (yellow), *T. hawksi* (orange), *T. chapinitus* (blue), and *T. maesi* (white). *Mayaesalus* = circles: *T. narizotus* (green), *T. catrachitus* (red), and *T. trifinius* (yellow).

Temporal Distribution. June (1).

Diagnosis/Remarks. This species is distinguished from *T. narizotus* by its subtriangular clypeus. It shares a subtriangular clypeus with *T. catrachitus* but differs from that species in the structure of the median lobe of the male genitalia. In *T. trifinius,* the median lobe is bulbous medially, and the membranous apical portion is larger and less sclerotized. It also has distinctly stronger teeth on the protibia, shorter bristles on the elytra, a flattened frons, and a broader ocular canthus.

Etymology. The specific epithet is a Latinized form of the term '*Trifinio',* the name of the region around Montecristo Massif on the borders of El Salvador, Guatemala, and Honduras. It is used as a noun in apposition, and the gender is masculine.

Phylogeny of *Trogellus* and Aesalini

Taxonomic sampling and specimen vouchering

Sequences were analyzed for 47 taxa selected from a larger matrix examining the world Lucanidae (Paulsen and Hawks, in prep.), with 22 outgroup and 25 ingroup taxa (Aesalinae). The subfamily Aesalinae is represented by all three tribes and all nine genera. Of the ten species of *Trogellus,* only two could not

be included in the analyses: the most recent specimens of *T. neotropicalis* located were the original type series from 1888; I could not amplify DNA from the holotype and only known specimen of *T. catrachitus*. Outgroup taxa included Geotrupidae, Bolboceratidae, and Pleocomidae that were shown to be the sister group to the remaining Scarabaeoidea in Smith et al. (2006); Trogidae and Glaresidae, which comprise the sister group to Lucanidae according to Smith et al. (2006); and exemplars of the other three lucanid subfamilies (Lampriminae, Syndesinae, and Lucaninae). Outgroup taxa were chosen that had the most complete data for all gene regions in the study.

Sequenced specimens are identified by voucher labels and are currently housed in the MJPC, UNSM, or David C. Hawks Collection (Riverside, CA; DCHC). Holotype specimens that were sequenced are deposited at the institutions indicated in their descriptions. See Table S1 for a complete listing of included sequences and voucher locations.

DNA Extraction, Amplification and Sequencing

DNA extractions were performed at UCR and UNSM following a modified version of the ChelexH protocol (e.g., Paulsen 2010). Recent material was collected directly into alcohol, however most DNA was extracted from pinned museum specimens. In general, specimens from the last 15 years were sequenced, although usable sequences have been amplified from specimens more than 50 years old using this protocol. The non-destructive sampling technique generally involved removing the entire left middle leg and coxa for extraction, then reinserting the coxa when completed. Primer sequences for PCR amplification of 18S rDNA and the 28S rDNA D2, D3 and D4+D5 expansion regions are provided in Munro et al. 2011. The 28S rDNA expansion regions (D2, D3, and D4+D5) are contiguous. In some cases, a shorter version of 18S was amplified with internal primers (18Si; see Table 1), and because 18S is included to provide phylogenetic signal above the level of genera it was not amplified for all ingroup taxa. Sequencing was initially conducted at the San Diego State University Microchemical Core Facility until the closure of that facility in 2012, then at the UCR Genomics Core Facility. Sequences will be deposited on Genbank after a subsequent publication on the phylogeny of world Lucanidae (Paulsen and Hawks, in prep).

Sequence Alignment and Phylogenetic Analyses

Sequences were aligned manually ("by eye"), which generally is straightforward within Lucanidae and not unreasonable with a small dataset and relatively conserved gene regions. This resulted in a dataset with 3198 aligned base pairs. The alignment of length-variable ribosomal DNA sequences is a contentious topic (e.g., Munro et al. 2011; Klopfstein et al. 2013). As is desirable in molecular phylogenetic studies, the strongest phylogenetic signal is found in the unambiguously aligned regions of the matrix, which are (or should be) essentially invariant between the various presently available alignment methods. However, the only clear method by which to compare and assess alignment methodologies (computer-generated and manual) and their impact on and possible conflicts with unambiguous signal is to analyze matrices with regions of ambiguous alignment (RAAs) both included and excluded.

In these analyses four RAAs with a total of 67 base pairs were identified. Parsimony analyses were conducted using the maximum-parsimony optimality criterion in PAUP4.0ß10 (Swofford 2002) with 1000 random addition heuristic searches with TBR branch swapping, on matrices with RAAs either included or excluded. Gaps were treated as missing data, and all data were weighted equally. Branch support was evaluated using bootstrap analysis with 1000 random replicates and 50 random addition searches per replicate.

Because the removal of RAAs did not significantly affect the analyses (see below), Maximum Likelihood (ML) analyses and associated bootstrapping were conducted on the entire dataset with RAxML v.7.6.6 using a partitioned model on the XSEDE cluster via the CIPRES portal V2.2 (Miller et al. 2010). The two partitions used for analysis were 18S and 28S. A GTRGAMMA approximation of models was used for rapid ML bootstrapping and creating the final tree. Nodal supports were calculated using 1000 bootstrap iterations. Interpretation of bootstrap percentage follows Munro et al. 2011: a bootstrap per-

centage of >90% is considered very strong, 80–89% strong, 70–79% moderate, and 50–70% means low bootstrap support. Bootstrap values below 50% are considered unsupported and are not reported.

Phylogenetic Relationships and Interpretation

Maximum Parsimony (MP) analyses on the matrix with RAAs included resulted in four equally parsimonious trees of 1889 steps (RI = 0.64) that differed only in the relationships among the genera *Lucanobium*, *Aesalus*, and *Echinoaesalus*. In two of the four trees *Lucanobium* was the sister to the remaining Aesalini. The exclusion of RAAs resulted in a single most-parsimonious tree of 1787 steps (RI = 0.64), also with *Lucanobium* as the sister to the remaining Aesalini and with only a slight impact on branch lengths, mainly among the most highly divergent outgroup taxa. Both analyses resulted in a basal polytomy in Aesalini with no bootstrap support for the placement of these three genera. In the analysis with RAAs removed, all other nodes in the tree had 100% bootstrap support; the bootstrap support values from the analysis with RAAs included are indicated below the subtending branch on the best-scoring likelihood tree (Fig. 33). Because removal of the RAAs did not improve the resolution of Aesalini, the RAAs were not removed from the Maximum Likelihood analysis.

The best scoring likelihood tree is shown in Figure 33, and resulted in a nearly identical topology with the parsimony analyses, but is completely resolved with respect to the genera and tribes of Aesalinae (see below). Outgroup relationships agree with those of Smith et al. (2006), with Geotrupidae, Bolboceratidae, and Pleocomidae strongly supported as the sister group to the clade containing (Glaresidae + Trogidae) + Lucanidae. The monophyly of Lucanidae was recovered with very strong support. The subfamilies Lampriminae and Syndesinae are recovered as sister to the Aesalinae with very strong support. The subfamily Lucaninae (*sensu* Holloway 1969, Howden and Lawrence 1974, and Paulsen 2010) also was recovered with very strong support. The lucanine tribes Platycerini, Chiasognathini, Sclerostomini, Figulini, and Lucanini were included in these analyses. The tribe Platycerini has a checkered taxonomic history of being placed in the Aesalinae (Benesh 1946, 1960), and by subsequent works that merely copied Benesh's placement. Because this potentially impacts the composition of Aesalinae, the distant location of *Platycerus* on the tree is significant. This analysis demonstrates that a close relationship between Platycerini and Aesalinae is unsupportable molecularly, thus supporting Holloway's (1969) assertion that it is entirely untenable morphologically.

The three tribes of Aesalinae are recovered as monophyletic with strong to very strong support. Moderate support was obtained for the relationship of Aesalini + (Ceratognathini + Nicagini). Within Aesalini, the ML analysis resolved the relationships among genera, although with low bootstrap support. *Lucanobium* was recovered as the sister to the remaining genera, and *Aesalus* as the sister to *Echinoaesalus* + *Trogellus*. The two subgenera of *Echinoaesalus* demonstrate a high level of molecular divergence. Five Asian species of Aesalini provided for sequencing by Hao Huang (Shanghai, China) were removed from the matrix at his request, because he is currently preparing a paper that will address the relationships of these taxa. Future analyses with these taxa included will likely make the relationships between these genera clearer.

Trogellus is very strongly supported as a monophyletic, divergent sister group to the remaining genera of Aesalini, demonstrating that the Central American species were previously misplaced in *Aesalus*. As with previous analyses using 18S and 28s rDNA to elucidate relationships in Scarabaeoidea (Smith et al. 2006; Paulsen 2010), the gene regions chosen provide excellent resolution of relationships above the species level, which demonstrates the distinctness of *Trogellus* from the remaining genera of Aesalini, including *Aesalus*.

Within *Trogellus,* the three subgenera formed in this work are very strongly supported as monophyletic: *Trogellus* (clade A), *Mayaesalus* (clade B), and *Trogoides* (clade C). There was moderate support for the relationship *Trogoides* + (*Trogellus* + *Mayaesalus*). The morphological synapomorphies that unite *Trogellus* and *Mayaesalus* are merely the absence of the autapomorphies of *Trogoides* (shorter body form, strongly dentate metatibiae in males, etc.). *Trogellus* and *Mayaesalus* are fairly divergent (Fig. 33), and this, together with the lack of morphological synapomorphies in the two groups, supports the distinction between the two subgenera. *Trogoides* is highly divergent as shown by the length of the branch subtending node C. Within *Trogoides* the only species lacking distinct pronotal tubercles, *T. trogoides,* is

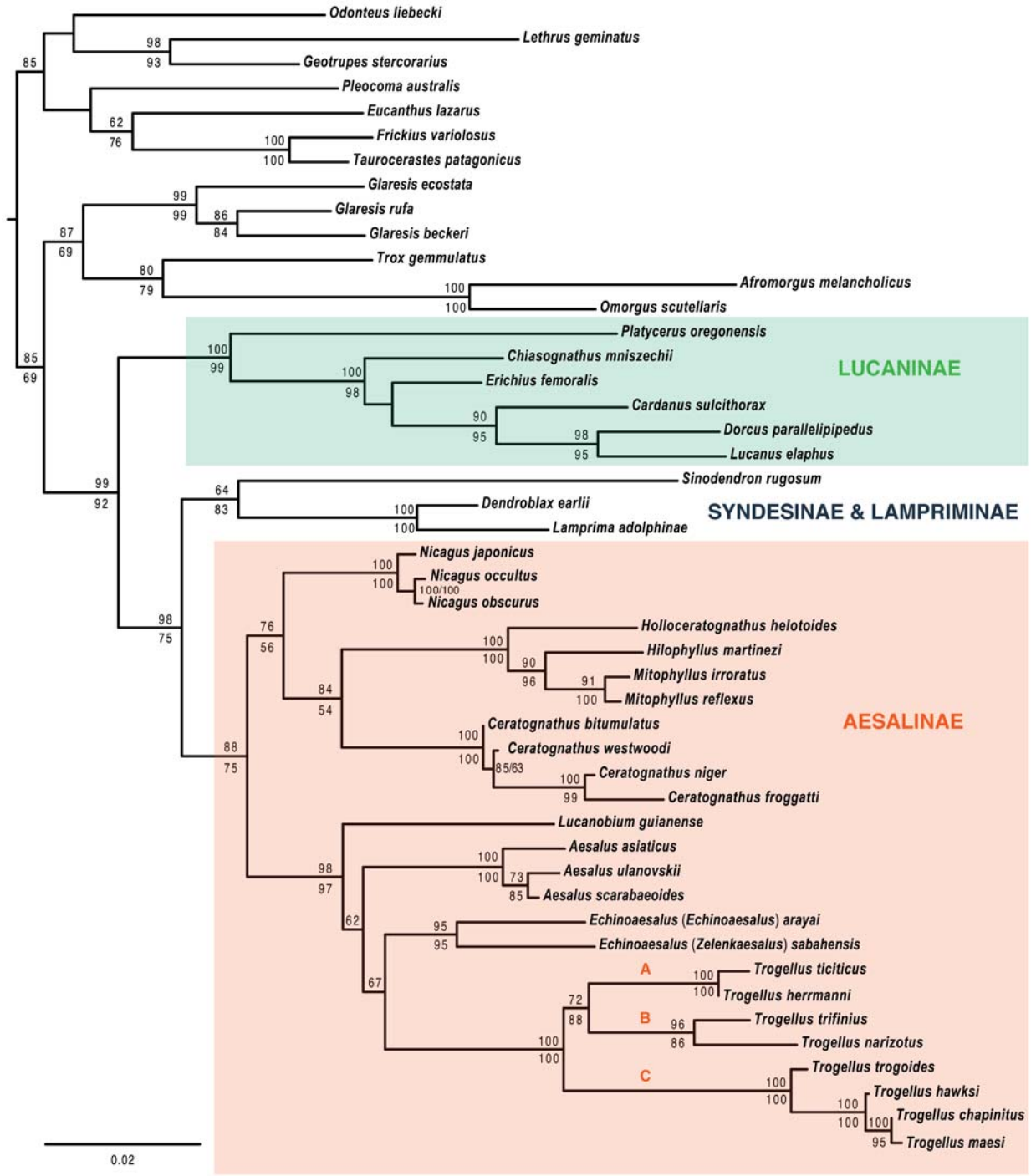


Figure 33. Aesalinae and *Trogellus* species maximum likelihood best tree from analysis of 18S rDNA and 28S rDNA D2, D3 and D4+D5 expansion regions, 3198 aligned base pairs. Bootstrap percentages for nodes over 50% are indicated above (ML) and below (MP) the subtending branch. Shading indicates two subfamilies of Lucanidae: Lucaninae (green) and Aesalinae (orange). Clades containing each subgenus are indicated with letters: A = *Trogellus*, B = *Mayaesalus*, and C = *Trogoides*. Bar indicates 0.02 nucleotide substitutions per site.

Table S1. Taxon, voucher number and depository, and gene regions sequenced.

Family	Taxon	Author	Voucher #	Depository	D2	D3	D4-5	18S1	18S2	18s3
Bolboceratidae	*Eucanthus lazarus*	(Fabricius)	S31	DCHC						
Bolboceratidae	*Odonteus liebecki*	Wallis	S32	DCHC						
Geotrupidae	*Geotrupes stercorarius*	(Linnaeus)	S571	DCHC						
Geotrupidae	*Lethrus geminatus*	Kraatz	S152	DCHC						
Geotrupidae	*Taurocerastes patagonicus*	Philippi	S494	DCHC						
Pleocomidae	*Pleocoma australis*	Fall	S488	DCHC						
Glaresidae	*Glaresis beckeri*	Solsky	S516	DCHC						
Glaresidae	*Glaresis ecostata*	Fall	S7	DCHC						
Glaresidae	*Glaresis rufa*	Erichson	MP486	MJPC						
Trogidae	*Afromorgus melancholicus*	(Fahraeus)	S701	DCHC						
Trogidae	*Omorgus scutellaris*	(Say)	S170	DCHC						
Trogidae	*Trox gemmulatus*	Horn	S92	DCHC						
Lucanidae	*Aesalus asiaticus*	Lewis	S287	DCHC						
Lucanidae	*Aesalus scarabaeoides*	(Panzer)	P235	MJPC						
Lucanidae	*Aesalus ulanovskii*	Ganglbauer	S518	DCHC						
Lucanidae	*Cardanus sulcithorax*	(Perty)	P342	MJPC						
Lucanidae	*Ceratognathus bitumulatus*	Carter	P27	ANIC						
Lucanidae	*Ceratognathus froggatti*	Blackburn	P28	ANIC						
Lucanidae	*Ceratognathus niger*	Westwood	MP63	CMNC						
Lucanidae	*Ceratognathus westwoodi*	Thomson	P26	ANIC						
Lucanidae	*Chiasognathus mniszechii*	Thomson	S182	DCHC						
Lucanidae	*Dendroblax earlii*	White	P100	MJPC						
Lucanidae	*Dorcus parallelipipedus*	(Linnaeus)	P392	MJPC						
Lucanidae	*Echinoaesalus arayai*	Huang & Imura	MP426	MJPC						
Lucanidae	*Echinoaesalus sabahensis*	Zelenka	P209	MJPC						
Lucanidae	*Erichius femoralis*	(Guérin-Méneville)	MP38	MJPC						
Lucanidae	*Frickius variolosus*	Germain	S180	DCHC						
Lucanidae	*Hilophyllus martinezi*	Paulsen & Mondaca	S581	MNNC						
Lucanidae	*Holloceratognathus helotoides*	(Thomson)	S150	DCHC						
Lucanidae	*Lamprima adolphinae*	(Gestro)	S146	DCHC						
Lucanidae	*Lucanobium guianense*	Paulsen	P244/MP427	MJPC						
Lucanidae	*Lucanus elaphus*	Fabricius	S69	DCHC						
Lucanidae	*Mitophyllus irroratus*	Parry	P5	MJPC						
Lucanidae	*Mitophyllus reflexus*	Broun	S149	DCHC						
Lucanidae	*Nicagus japonicus*	Nagel	S455	DCHC						
Lucanidae	*Nicagus obscurus*	(LeConte)	S38	DCHC						
Lucanidae	*Nicagus occultus*	Paulsen & Smith	S666	DCHC						
Lucanidae	*Platycerus oregonensis*	(Westwood)	S353	DCHC						
Lucanidae	*Sinodendron rugosum*	Mannerheim	S1	DCHC						
Lucanidae	*Trogellus chapinitus*	Paulsen, n. sp.	P204/P395	UNSM						
Lucanidae	*Trogellus hawksi*	Paulsen, n. sp.	P398	MJPC						
Lucanidae	*Trogellus herrmanni*	Paulsen, n. sp.	P338	MJPC						
Lucanidae	*Trogellus maesi*	Paulsen, n. sp.	AS63	UNSM						
Lucanidae	*Trogellus narizotus*	Paulsen, n. sp.	P396	MJPC						
Lucanidae	*Trogellus ticiticus*	Paulsen, n. sp.	P6	CMNC						
Lucanidae	*Trogellus trifinius*	Paulsen, n. sp.	MP334	UNSM						
Lucanidae	*Trogellus trogoides*	(Albers)	P15	MJPC						

Shading indicates gene regions used for each taxon: orange (complete sequence), green (partial sequence), or unshaded (not sequenced). Partial sequences for 18S2 are 18Si as described in the text. ANIC = Australian National Insect Collection; DCHC = David C. Hawks collection; MNNC = Museo National de Historia Natural, Santiago, Chile; other codens presented in Material Examined.

the sister to the remaining three more morphologically similar species. Consistently in these and other analyses of hundreds of species (Paulsen and Hawks, in prep.), no sequence variation is observed within lucanid or other scarabaeoid species for these regions. For this reason, the number of base pair differences seen between *Trogellus* species provides additional strong support for the distinctness of these taxa.

Checklist of New World Aesalinae

The following is a list of aesaline species of the Americas. All genera are exclusively American except for *Nicagus,* which includes *N. japonicus* Nagel from Japan.

Aesalinae
Aesalini

Lucanobium Howden and Lawrence, 1974.
Lucanobium guianense Paulsen, 2011. French Guiana.
Lucanobium squamosum Howden and Lawrence, 1974. Venezuela.

Trogellus Paulsen, new genus.
Trogellus (*Trogellus*) *herrmanni* Paulsen, **new species**. Costa Rica, Panama.
Trogellus (*Trogellus*) *neotropicalis* (Bates, 1886), **new combination.** Guatemala.
Trogellus (*Trogellus*) *ticiticus* Paulsen, **new species**. Costa Rica.
Trogellus (*Trogoides*) *chapinitus* Paulsen, **new species.** Guatemala, Honduras.
Trogellus (*Trogoides*) *hawksi* Paulsen, **new species**. Guatemala, Mexico.
Trogellus (*Trogoides*) *maesi* Paulsen, **new species**. Nicaragua.
Trogellus (*Trogoides*) *trogoides* (Albers, 1883), **new combination**. Mexico.
Trogellus (*Mayaesalus*) *catrachitus* Paulsen, **new species**. Honduras.
Trogellus (*Mayaesalus*) *narizotus* Paulsen, **new species**. Guatemala.
Trogellus (*Mayaesalus*) *trifinius* Paulsen, **new species**. El Salvador.

Ceratognathini

Hilophyllus Paulsen and Mondaca, 2006.
Hilophyllus argentinensis (Martínez, 1981). Argentina, Chile.
Hilophyllus martinezi Paulsen and Mondaca, 2006. Chile.
Hilophyllus penai (Martínez, 1976). Chile.

Nicagini

Nicagus LeConte, 1861.
Nicagus obscurus (LeConte, 1848). United States.
Nicagus occultus Paulsen and Smith, 2005. United States.

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