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Beneath the bark – Complicated taxonomy: Revision of the darkling beetle genus *Phrenapates* Gray, 1832 (Tenebrionidae: Phrenapatinae)

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Abstract. A revision of the Neotropical darkling beetle genus *Phrenapates* Gray, 1832 (Tenebrionidae: Phrenapatinae) is conducted. The genus previously contained six species ranging from Central to South America. Nearly 350 specimens of *Phrenapates* were examined to define morphology and evaluate previously published species. The genus is redescribed with its taxonomic history and classification summarized. Two new species are described: *Phrenapates gilloglyi* Rincon & Smith sp. nov. from the Cerro Jefe Mountain located within Cerro Azul, Panama; and *Phrenapates fortunaensis* Rincon & Smith sp. nov. from the Fortuna Forest Reserve in Panama. A replacement name, *Phrenapates erratus* Rincon, Lumen & Kamiński nom. nov., is introduced for *Phrenapates latreillei* Gebien, 1910 to avoid homonymy with *Phrenapates latreillei* Lacordaire, 1859. Lectotypes are designated for *Phrenapates bennettii* Gray, 1832, *P. dux* Gebien, 1910, *P. educator* Gebien, 1910, *P. erratus*, *P. latreillei*, and *P. ohausi* Gebien, 1910, to stabilize species concepts. *Phrenapates mandibularis* Gebien 1910 is treated as a junior synonym of *Phrenapates latreillei* Lacordaire, 1859. As a result, a total of eight species is now recognized (*P. bennettii, P. ohausi, P. dux, P. latreillei, P. educator, P. erratus, P. gilloglyi,* and *P. fortunaensis*). Distribution maps and a key to the species of *Phrenapates* are provided. Dissections confirmed that unlike most other Tenebrionidae, female *Phrenapates* lack well-sclerotized ovipositors, with only coxite 4 and paraproct remaining for oviposition. This reduction is potentially attributed to their unusual life history, as *Phrenapates* live in subsocial colonies inside dead wood and may not need to inject eggs into substrate.

Keywords. Darkling beetles, Neotropical, Panama, new species, nomen novum.

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Introduction

Phrenapatinae Solier, 1834 is a diverse subfamily of Tenebrionidae Latreille, 1802 containing 25 genera and ca 150 described species of saproxylic darkling beetles distributed across the Afrotropical, Australasian, Indomalayan, Nearctic, Neotropical, and Palearctic regions (Watt 1974; Matthews *et al.* 2010; Rosas-Ramos 2020; Bouchard *et al.* 2021). To accompany their subcortical lifestyle, phrenapatines express an array of cuticular head armaments and variable mandible morphology. Current taxonomy has been focused on alpha level contributions (Schawaller & Bouchard 2019; Iwan & Raś 2020; Jiang *et al.* 2020; Iwan *et al.* 2023). The type genus for the subfamily, *Phrenapates* Gray, 1832, was last treated by Gebien (1911), who also provided additional descriptions and illustrations.

The distribution of *Phrenapates* spans from Central to South America (Doyen 1979). They largely live in colonies inside logs and stems of dead trees (ex. *Bombax* Linnaeus, 1753 also known as silk-cotton trees), with larvae developing within lateral chambers and depending upon the frass generated by adults (Ohaus 1909; Watt 1974). *Phrenapates* superficially resemble beetles in the family Passalidae Leach, 1815 (Fig. 1) who also exhibit parental feeding behavior and live in subcortical colonies (Shuster & Shuster 1985, 1997). The bauplan of *Phrenapates* resembles that of lagriioid Tenebrionidae (see Tschinkel & Doyen 1980), with the distinguishing character being the first segment of the antennae being as long as the following 3, as well as the last 3 segments forming a club and having elongated mouthparts (e.g., projecting mandibles, galea longer than lacinia) (Solier 1834; Watt 1974; Doyen & Lawrence 1979).

George Gray (in Griffith & Pidgeon 1832) provided the first valid species description of the genus using an unpublished account by William Kirby (*Phrenapates bennettii* Gray, 1832). In his subsequently published work, Kirby (1837) described the similarity of *Phrenapates* to Passalidae and Bostrichidae Latreille, 1802, using the following characters: body plan similar to Passalidae, spurious joint between the claws of the tarsi, and all tibiae possessing spines. Solier (1834) placed *Phrenapates* in a new tribe Phrépatides within the Heteromeres (now Tenebrionidae), using the number of antennomeres (11) and the number of tarsomeres on the fore, mid, and hind tarsus (5-5-4) as uniting characters. In 1859, Lacordaire published a catalog of Tenebrionidae mentioning Kirby's description of *P. bennettii* and providing a description for *P. latreillei* Lacordaire, 1859, erroneously attributing it to Dejean. Gebien in 1910 re-

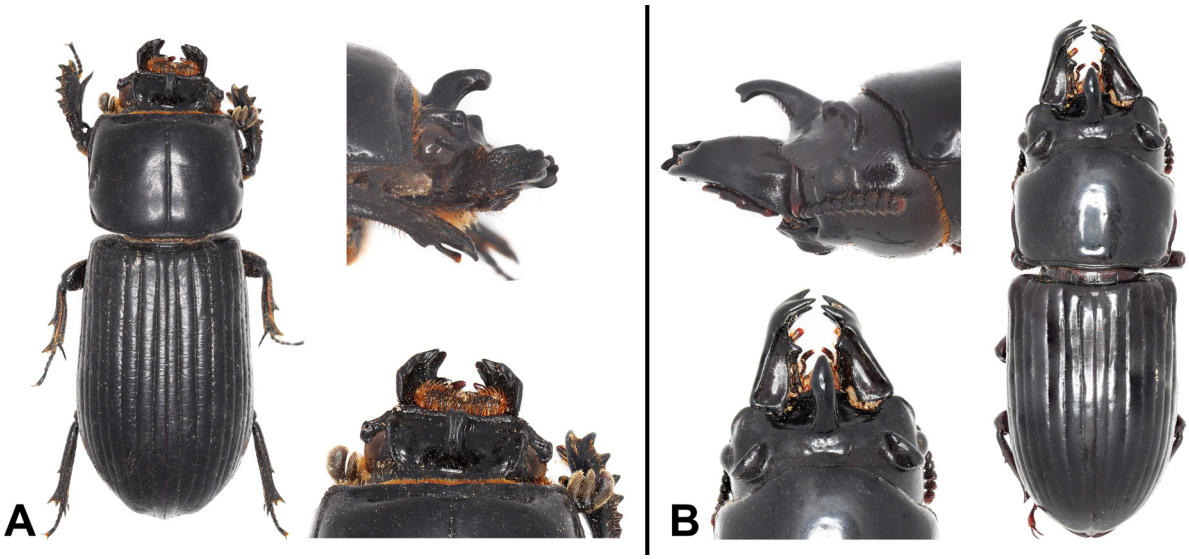

Fig. 1. Convergent morphology of Passalidae Leach, 1815, and *Phrenapates* Gray, 1832. **A**. Passalidae Leach, 1815 (MIZPAN). **B**. *Phrenapates bennettii* Gray, 1832 (MIZPAN).

described *P. bennettii* and five additional species, bringing the total species count to six. In 1911, Gebien provided further descriptions and illustrations in a second publication. Watt in 1974 elevated Phrenapatinae to subfamily status and placed *Phrenapates* into the tribe Phrenapatini Solier, 1834.

To reassess, organize, and identify current and undescribed species, 346 specimens were loaned from eleven institutions, including type material from all previously known species. A morphological revision was conducted to test the taxonomic stability of the genus, as well as to describe new species. The last treatment of *Phrenapates* was over 100 years ago, and since its original description(s), more material has become available to evaluate species concepts, making a revision of the type genus of the subfamily Phrenaptinae (and tribe Phrenapatini) possible.

Material and methods

Institutional abbreviations

The following collections graciously loaned specimens for this study.

AAAG = Alan and Anita Gillogly (private coll.), Caldwell, Idaho; Alan Gillogly
AMNH = American Museum of Natural History, New York, USA; Lee Herman
BMNH = The Natural History Museum [formerly British Museum (Natural History)], London, UK; Max Barclay
CASC = California Academy of Sciences, San Francisco, California, USA; Christopher Grinter
FMNH = Field Museum of Natural History, Chicago, Illinois, USA; Julia Snyder
MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; Crystal Maier
MIZPAN = Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw, Poland; Dariusz Iwan
MNHN = Muséum national d'Histoire naturelle, Paris, France: Antoine Mantilleri
NHMB = Naturhistorisches Museum, Basel, Switzerland; Christoph Germann
PERC = Purdue Entomological Research Collection, Purdue University, West Lafayette, Indiana, USA; Aaron D. Smith
SEMC = Snow Entomological Museum, University of Kansas, Lawrence, Kansas, USA; Kirsten Jensen
TAMU = Texas A & M University, College Station, Texas, USA; Karen Wright

This revision is based on morphological and georeference data acquired from 346 adult specimens of *Phrenapates*. Of these, subsets of each species were measured for size (total of 105 specimens). Dissection followed the methodology of Iwan & Kamiński (2016). Specimens were soaked in a warm KOH solution to soften connective tissue before dissection. Morphological terminology follows that of Gebien (1911), Doyen (1966), and Matthews *et. al* (2010). Material identified via comparison with type material had their mouthparts removed and mounted on cards or points. The KOH method was also used to dissect reproductive structures. Dissected tissue was then included in a vial or paper point/card on the pin beneath the specimen. Images of specimens were taken using a Passport Imaging system (https://www.visionarydigital.com), and mounted images assembled using Helicon Focus ver. 5.3 (https://www.heliconsoft.com). Backgrounds were cleaned in Adobe Photoshop CS6. Measurements were taken digitally using the ruler tool in Photoshop on images with known measurements based on the camera body, lens, and magnification used. Smaller parts of specimens were photographed, montaged, and measured using a Leica M165 stereo microscope with the accompanying Leica software (https://www.leica-microsystems.com). Body length was measured along the midline from the apex of mandibles to the apex of elytra. Body width was measured across the widest point of the elytra. Color was determined under fiber optic illumination and from images. Distributional data from specimen labels

were used to generate maps using QGIS ver. 3.16, with vector layers downloaded from the Natural Earth web page (https://www.naturalearthdata.com).

Results

The majority of specimens examined were misidentified or lacked species level identifications. Upon examination of pinned material and comparison of type and more recently collected specimens, it was clear that most differences between species are restricted to the head. Further, the original diagnoses and descriptions were often vague or inaccurate (e.g., uninformative reproductive morphology at the species level or subtle differences between similar taxa such as *Phrenapates educator* vs *P. erratus* Rincon, Lumen & Kamiński nom. nov.). As such, a new generic definition outlining the variation of morphology within the group is provided in the taxonomy section below, as well as newer treatments at the species level for previously described species. Specifically, type designations for previously described species are provided where necessary (e.g., lectotypes), along with brief diagnostic redescriptions as well as focused diagnoses to provide stability to the revised species concepts presented here.

Taxonomy

Class Insecta Linnaeus, 1758
Order Coleoptera Linnaeus, 1758
Suborder Polyphaga Emery, 1886
Family Tenebrionidae Latreille, 1802
Subfamily Phrenapatinae Solier, 1834
Tribe Phrenapatini Solier, 1834

Genus ***Phrenapates*** Gray, 1832

Phrenapates Gray, 1832: 91.
Phrepates Solier, 1834: 488 [incorrect subsequent spelling of genus name].

Type species

Phrenapates bennettii Gray, 1832; by monotypy.

Diagnosis

In terms of body size, *Phrenapates* is the largest genus in the subfamily by a large margin (18–39 mm long vs Archaeoglenini Watt, 1974 < 5 mm and Penetini Lacordaire, 1859 < 10 mm). Additionally, *Phrenapates* is the only genus in the subfamily to possess both clypeal horns and supraorbital tubercles in males and females; other examples of armature in the subfamily include projections on the head (e.g., *Peneta* Lacordaire, 1859) and/or mandibles (*Molion* Champion, 1886). The only other genus in the tribe Phrenapatini, *Delognatha* Lacordaire, 1859, can be differentiated based on the following characteristics: clypeal horns and supraorbital tubercles absent, smaller (less than 8 mm), and mandibles less projected (< the length of the head). Archaeoglenines can be differentiated from *Phrenapates* by the following characters: extremely small size (< 5 mm), procoxal cavity closed laterally by meso- and metaventrites, mesotrochantin not visible; prothorax with distinct anterolateral antennal cavities (Iwan *et al.* 2015). *Phrenapates* can be differentiated from penetines as they have mesocoxae with exposed trochantins and prominent mandibles (Watt 1974; Doyen & Lawrence 1979).

Etymology

No etymology was given in the original description. It potentially derives from the Greek roots 'Phren-' ('place of thought' / 'head/mind') and '-apata' ('deceitful' / 'cheat'), possibly referencing the head's morphological similarity to passalids.

Redescription

Measurements. Length 18–39 mm, width 6–13 mm, specimens measured (n = 105). Color nitidus dark brown to black. Body sub-cylindrical.

Head. Antennae clavate 11-segmented with last three antennomeres forming club, each with sensilla on apices. Subgenal ridge slightly dilated distally, tapering near mentum. Mandibles protruding and tridentate, equal to or greater than length of head, medial edge with or without teeth, inner margin crenulate or not. Mandibles with or without small setae on dorsal surface. Galea long and cylindrical with cluster of bristles situated near midpoint or toward apex. Mentum rectangular, slightly widening towards apex, strongly to weakly sculptured, apex with medial notch or not; lateral apices produced or not (Fig. 2). Clypeus apex dilated or not, all species with clypeal horn in both sexes. Clypeal horn variously shaped (Fig. 3) and occasionally slightly twisted or bent to left or right. Supraorbital tubercles present or absent. Eyes generally larger in males than females, roughly circular, undivided, and slightly protuberant.

Prothorax. Pronotum rectangular, micro-punctate, lateral margin carinate. Posterior of head capsule tucked slightly beneath anterior margin.

Pterothorax. Scutellum sub-triangular. Elytral striae with large punctures evenly spaced and interstices with small irregularly spaced punctures. Macropterous. Metaventral groove shallow and broad.

Legs. Tibiae armed with 0–5 spines, apex with four pointed spines where tarsi attach. Sparse setae on apices of tibiae and on tarsi. Protibiae with cluster of long apical setae. Pulvilla with four setae.

Abdomen. Glabrous, shining, and impunctate. Hind margins of abdominal ventrites three and four with membranes exposed. Aedeagus bipartite, parameres slightly dilated apically in lateral view, rounded apically in dorsal view with 4–5 setae on each paramere (Fig. 4). Median lobe exits ventrally. Ovipositor reduced to sclerotised coxite 4 and weakly sclerotised paraproct (Fig. 5).

Remarks

For information on larvae and pupae, see descriptions by Doyen & Lawrence (1979) and pupal descriptions by Bouchard (2019).

Status

Member of the subfamily Phrenapatinae in tribe Phrenapatini, which is unified by the mesocoxae lacking exposed trochantins and the possession of prominent mandibles (Watt 1974). Phrenapatini includes two genera, *Phrenapates* and *Delognatha*.

Species included

Phrenapates bennettii Gray, 1832, *P. dux* Gebien, 1910, *P. educator* Gebien, 1910, *P. erratus* Rincon, Lumen & Kamiński nom. nov., *P. fortunaensis* Rincon & Smith sp. nov., *P. gilloglyi* Rincon & Smith sp. nov., *P. latreillei* Lacordaire 1859, *P. ohausi* Gebien, 1910.

Distribution (Figs 6–7)

Central America: Costa Rica, Guatemala, Honduras, Nicaragua, Panama; South America: Bolivia, Brazil, Chile, Colombia, Ecuador, Guyana, Peru, Venezuela.

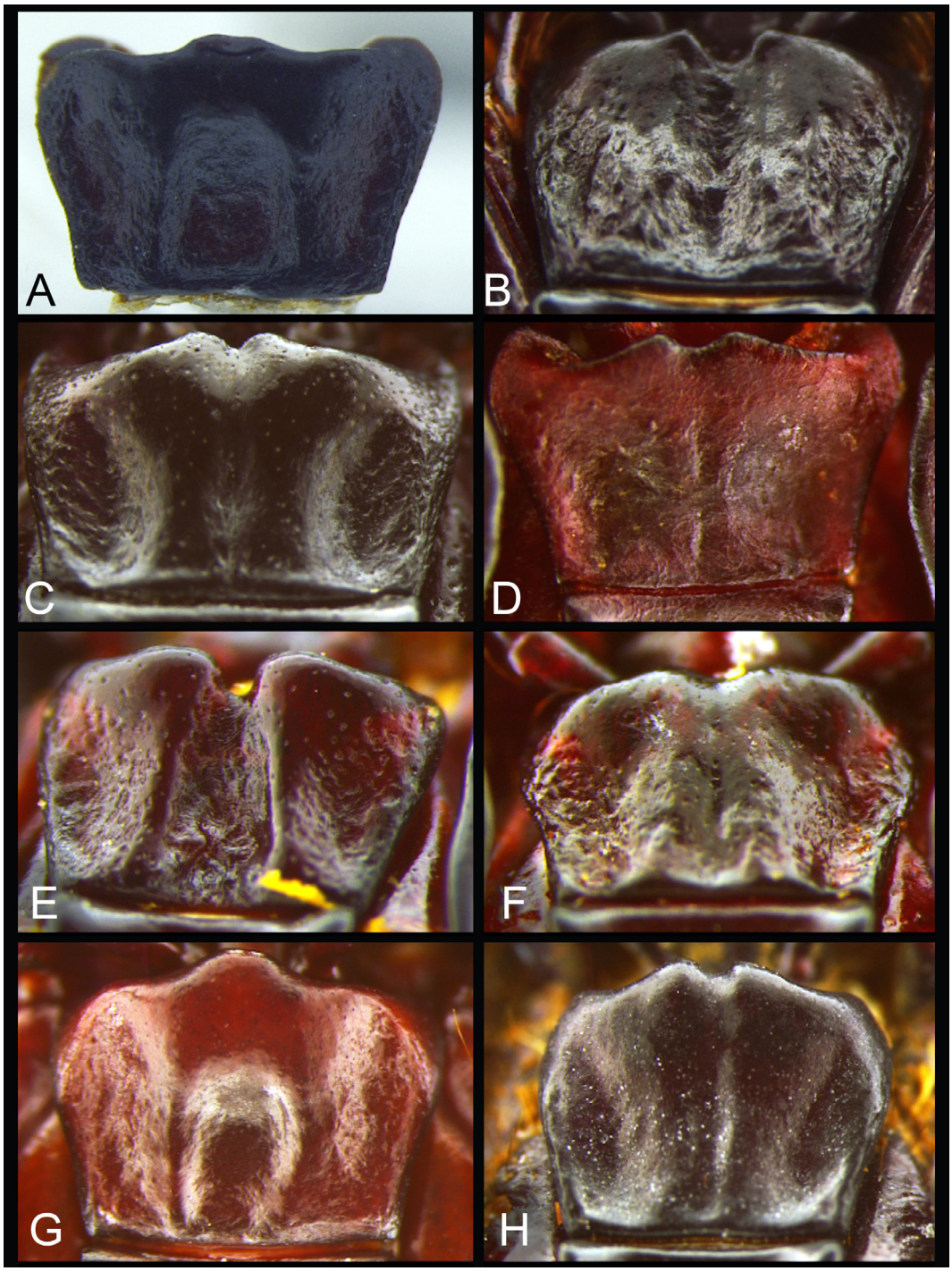

Fig. 2. Different menta morphologies of the species of *Phrenapates* Gray, 1832. **A**. *Phrenapates bennettii* Gray, 1832, lectotype, ♂ (Teneb_base 23170, BMNH). **B**. *Phrenapates gilloglyi* Rincon & Smith sp. nov., holotype, ♂ (Teneb_base 23367, PERC). **C**. *Phrenapates dux* Gebien, 1910, (Teneb_base 23242, PERC). **D**. *Phrenapates erratus* Rincon, Lumen & Kaminski nom. nov., lectotype, ♂ (Teneb_base 23168, NHMB). **E**. *Phrenapates mandibularis* Gebien 1910 [*Phrenapates latreillei* Lacordaire], holotype, ♂ (Teneb_base 23167, NHMB). **F**. *Phrenapates educator* Gebien, 1910, lectotype, ♂ (Teneb_base 23175, NHMB). **G**. *Phrenapates fortunaensis* Rincon & Smith sp. nov., holotype, ♂ (Teneb_base 23482, PERC). **H**. *Phrenapates ohausi* Gebien, 1910, lectotype, ♂ (Teneb_base 22810, BMNH).

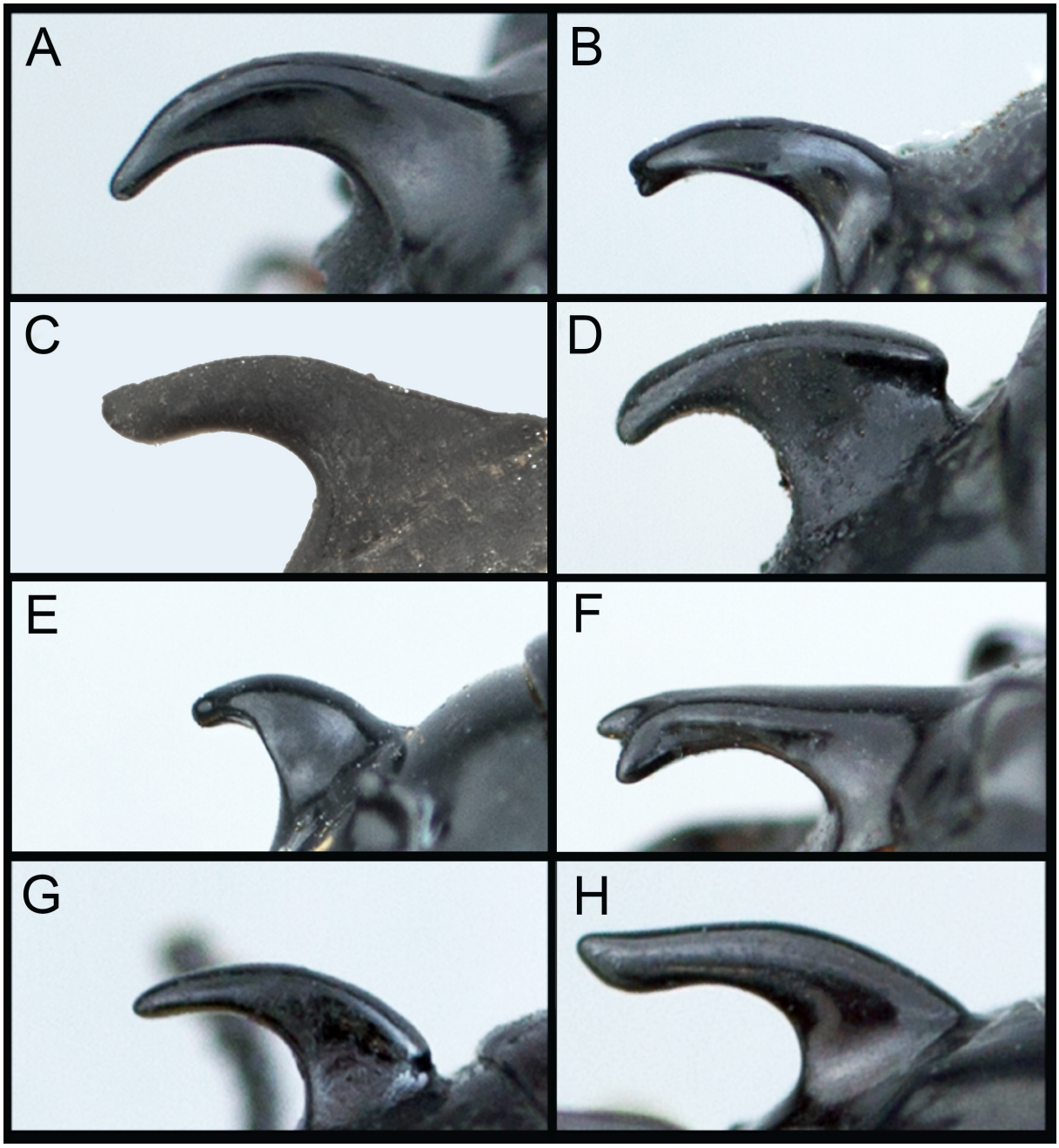

Fig. 3. Clypeal horn morphology, lateral views. **A**. *Phrenapates ohausi* Gebien, 1910 (Teneb_base 23212, CASC). **B**. *Phrenapates bennettii* Gray, 1832 (Teneb_base 22972, AAAG). **C**. *Phrenapates erratus* Rincon, Lumen & Kamiński nom. nov., lectotype, ♂ (Teneb_base 23168, NHMB). **D**. *Phrenapates dux* Gebien, 1910 (Teneb_base 23215, AAAG). **E**. *Phrenapates fortunaensis* Rincon & Smith sp. nov., holotype, ♂ (Teneb_base 23482, PERC). **F**. *Phrenapates gilloglyi* Rincon & Smith sp. nov., holotype, ♂ (Teneb_base 23367, PERC). **G**. *Phrenapates latreillei* Lacordaire, 1859, ♂ (Teneb_base 22740, AAAG). **H**. *Phrenapates educator* Gebien, 1910 (Teneb_base 23286, MNHM)

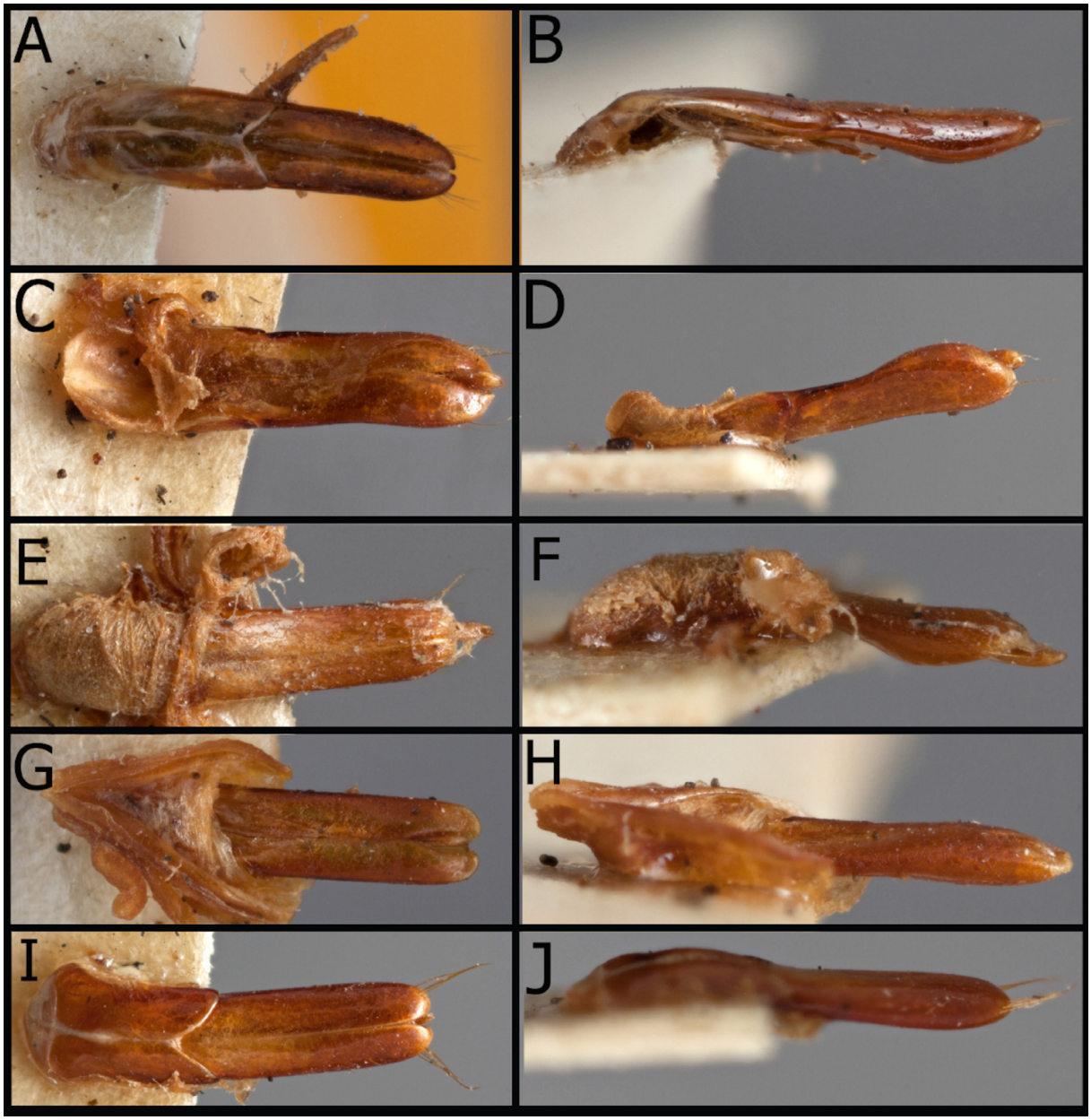

Fig. 4. *Phrenapates* Gray, 1832, adeagi, dorsal and lateral views. **A–B**. *Phrenapates bennettii* Gray, 1832, ♂ (Teneb_base 23186, NHMB). **C–D**. *Phrenapates dux* Gebien, 1910, lectotype, ♂ (Teneb_base 23166, NHMB). **E–F**. *Phrenapates educator* Gebien, 1910, lectotype, ♂ (Teneb_base 23175, NMHB). **G–H**. *Phrenapates mandibularis* Gebien 1910 [*Phrenapates latreillei*], holotype, ♂ (Teneb_base 23167, NHMB). **I–J**. *Phrenapates ohausi* Gebien, 1910, ♂ (Teneb_base 23165, NHMB).

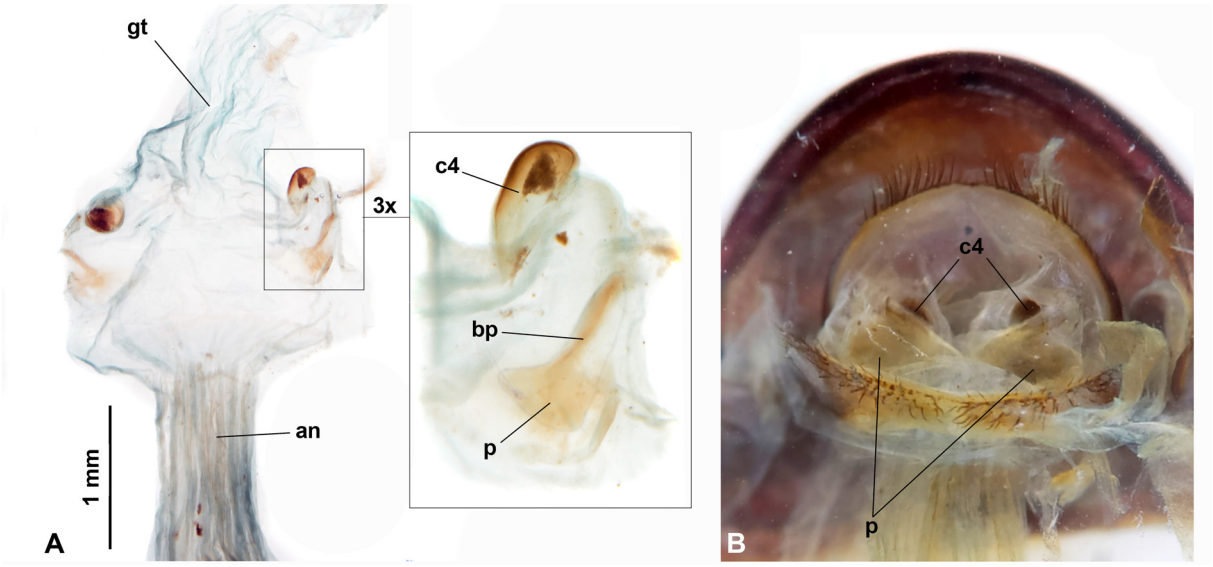

Fig. 5. Female terminalia of two species of *Phrenapates* Gray, 1832. **A**. *Phrenapates bennettii* Gray, 1832 (MIZPAN). **B**. *Phrenapates dux* Gebien, 1832 (MIZPAN). Abbreviations: an = anus; bp = baculus of paraproct; c4 = coxite 4; gt = genital tubes; p = paraproct.

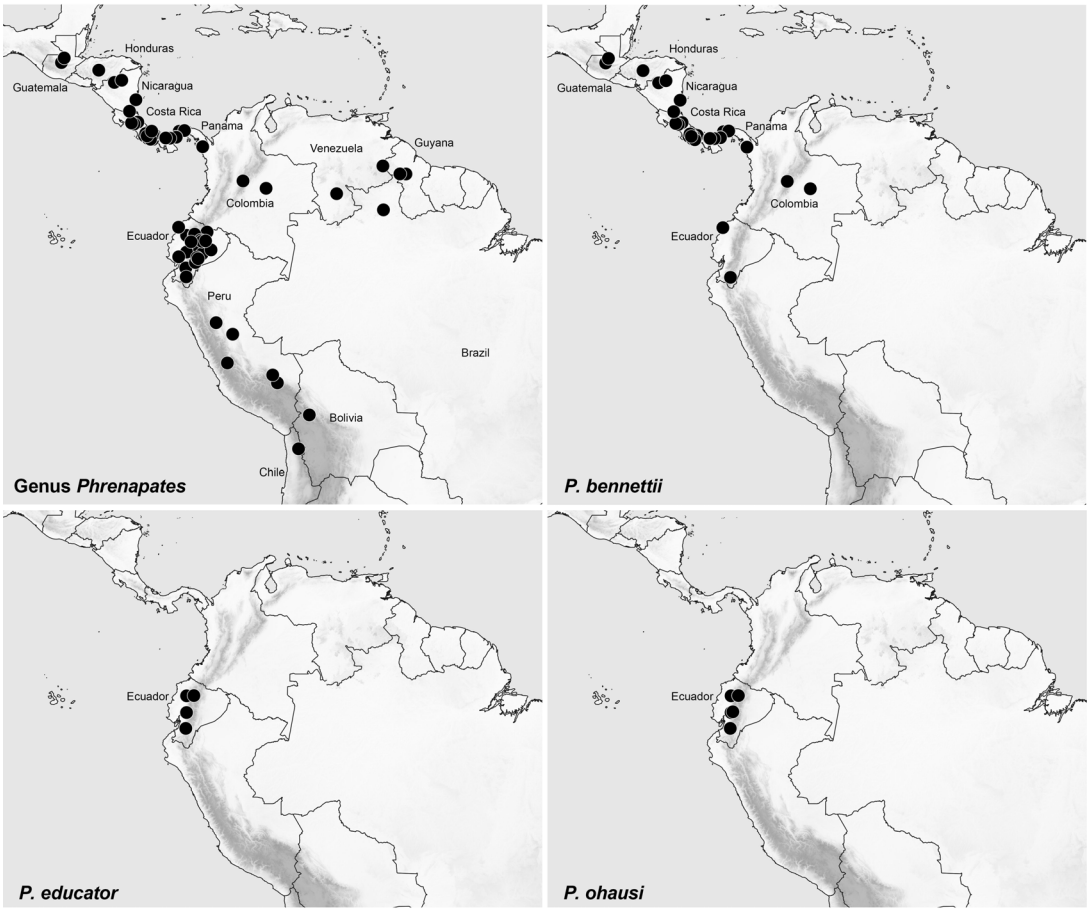

Fig. 6. Distribution of the genus *Phrenapates* Gray, 1832, *Phrenapates bennettii* Gray, 1832, *Phrenapates educator* Gebien, 1910, and *Phrenapates ohausi* Gebien, 1910.

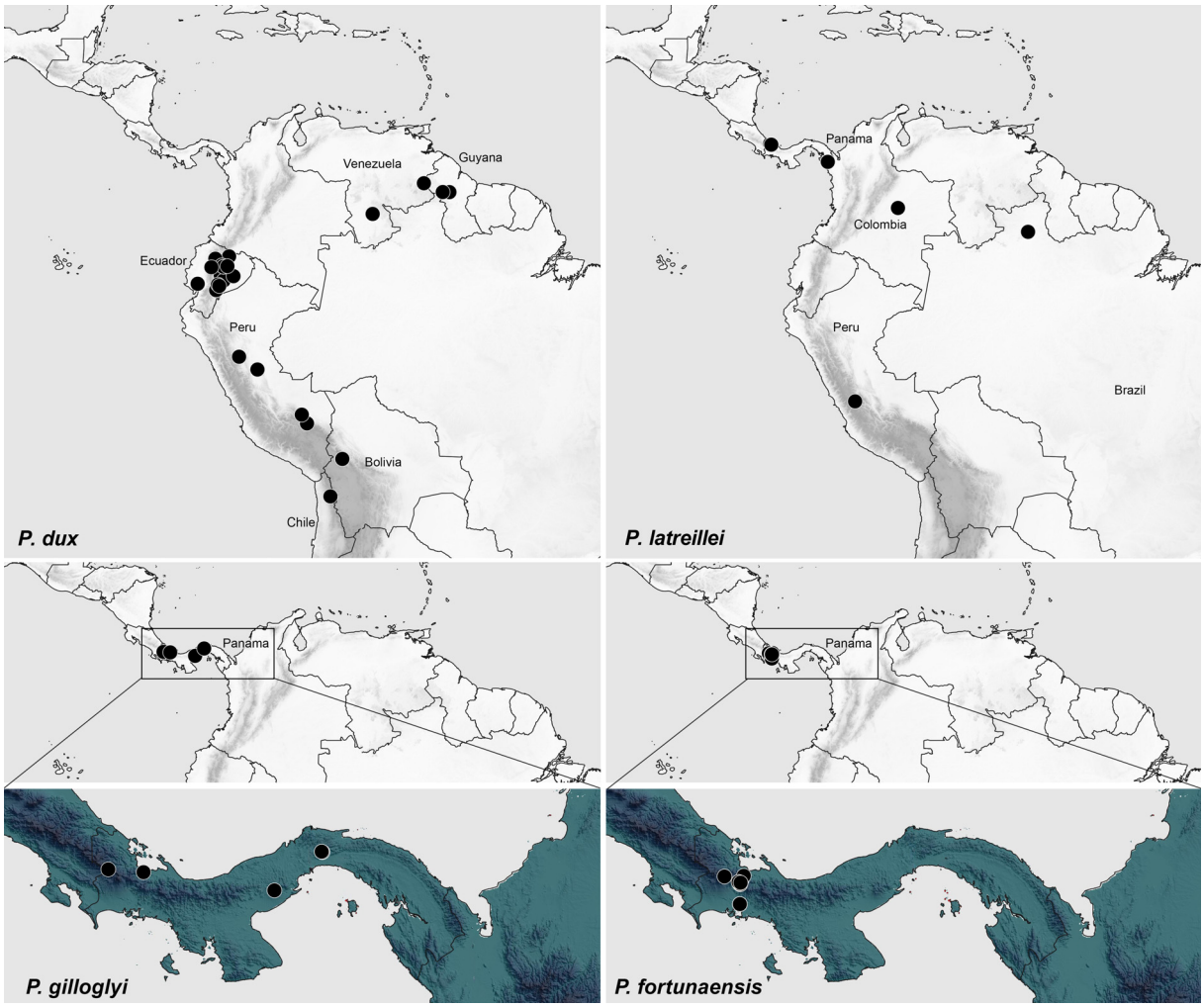

Fig. 7. Distribution of the *Phrenapates dux* Gebien, 1910, *Phrenapates latreillei* Lacordaire, 1859, *Phrenapates gilloglyi* Rincon & Smith sp. nov., and *Phrenapates fortunaensis* Rincon & Smith sp. nov.

Key to the species of *Phrenapates* Gray, 1832

1. Two supraocular tubercles on the head (Fig. 8A–F) 2
– Lacking supraocular tubercles (Fig. 8G–H) 5

2. Clypeal horn tapered to a point (Fig. 3A); mandibles without crenulation or tooth on the inner margin (as in Fig. 9C); supraorbital tubercles height subequal to width (Fig. 8A–B), mentum with rounded front angles (Fig. 2H) .....***P. ohausi*** Gebien, 1910
– Clypeal horn with end either blunted or with three points (Fig. 3B, F); mandibles with or without crenulations or tooth on the inside edge; supraorbital tubercles taller than wide or shorter than wide (Fig. 8C–F), mentum with lateral apices produced (as in Fig. 2A, C–D) 3

3. Clypeal horn ending in three points (Fig. 3F); supraorbital tubercles taller than wide; inner mandible smooth, without crenulated teeth (as in Fig. 9C) .....***P. gilloglyi*** Rincon & Smith sp. nov.
– Clypeal horn with single, blunt ending (Fig. 3B, E); supraorbital tubercles not as tall as wide (Fig. 8C–D); mandible with crenulations on inner margin (Fig. 9B) 4

4. Lateral apices of mentum rounded (Fig. 2G); clypeal horn short (not or barely arced) (Fig. 3E); mandibles with tooth on inner margin (as in Fig. 9A) ..... ***P. fortunaensis*** Rincon & Smith sp. nov.
– Lateral apices of mentum produced (Fig. 2A); clypeal horn arced (on rare occasions short) (Fig. 3B); mandibles without tooth and with crenulations on inner margin (Fig. 9B) ... ***P. bennettii*** Gray, 1832

5. Clypeal horn with slightly enlarged base laterally, tapering in center, with broad and flattened top (Fig. 3D); never with tooth on mandible (Fig. 9C); large species (27–32 mm long) ....***P. dux*** Gebien, 1910
– Clypeal horn not as above; with or without tooth on mandible (as in Fig. 9A, C); generally smaller species (< 28 mm long) 6

6. Mandibles with tooth on inner margin (as in Fig. 9A); clypeal horn curved in strong, circular arc (Fig. 3G); small bundle of bristles placed near midpoint of galea ..... ***P. latreillei*** Lacordaire, 1859
– Mandibles without tooth on inner margin (Fig. 9C); clypeal horn weakly or not at all curved downward (Fig. 3C, H); small bundle of bristles placed nearer to apex of galea (Fig. 10A, C) 7

7. Carinate ridge near attachment point of mandible, dorsal depression semi-rugose and with setae, mentum sinuate on sides, ratio of distance from clump of bristles on galea to tip and to base is 1:2 (Fig. 10A), Ecuador .....***P. educator*** Gebien, 1910
– Carinate ridge near attachment point of mandible weaker, dorsal depression not semi-rugose but punctate and without setae, mentum arctuate on sides, ratio of distance from clump of bristles on galea to tip and to base is less than 1:2 (Fig. 10C), Columbia .... ***P. erratus*** Rincon, Lumen & Kamiński nom. nov.

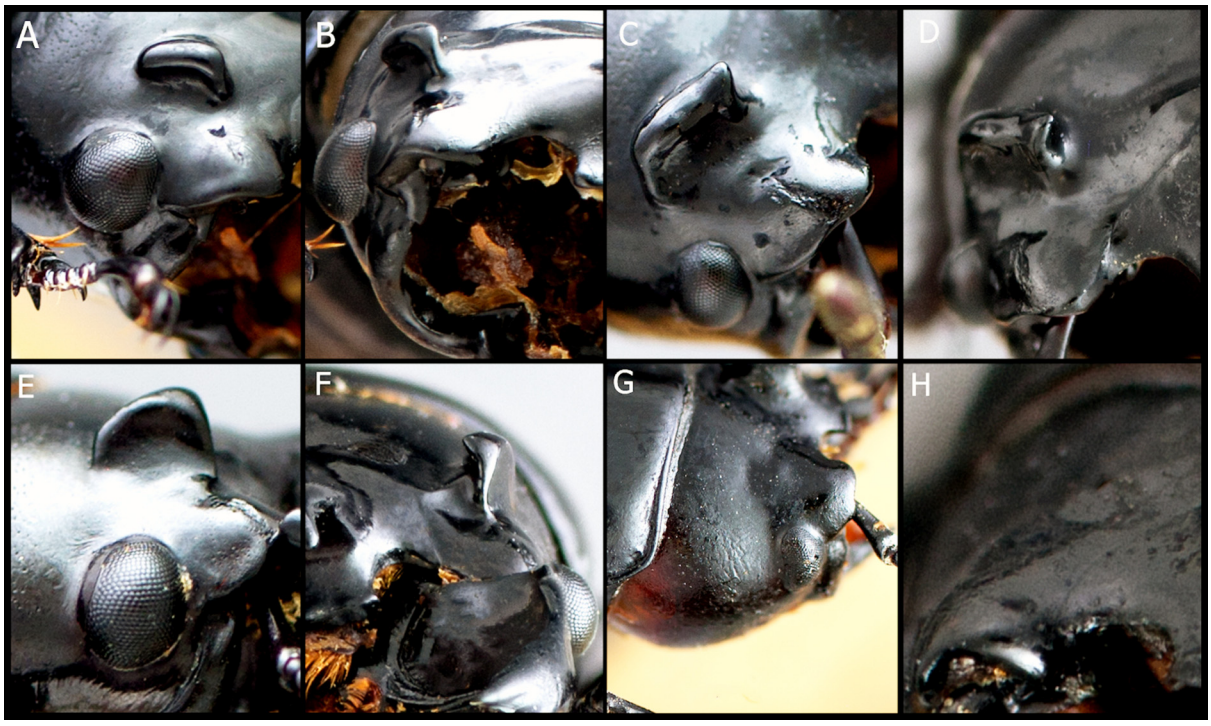

Fig. 8. Supraorbital tubercles of *Phrenapates* Gray, 1832. **A–B**. *Phrenapates ohausi* Gebien, 1910, (Teneb_base 23212, CASC). **C–D**. *Phrenapates bennettii* Gray, 1832, (Teneb_base 22972, AAAG). **E–F**. *Phrenapates gilloglyi* Rincon & Smith sp. nov., holotype, ♂ (Teneb_base 23367, PERC). **G–H**. Absence of supraorbital tubercles in *Phrenapates dux* Gebien, 1910, (Teneb_base 23215, AAAG).

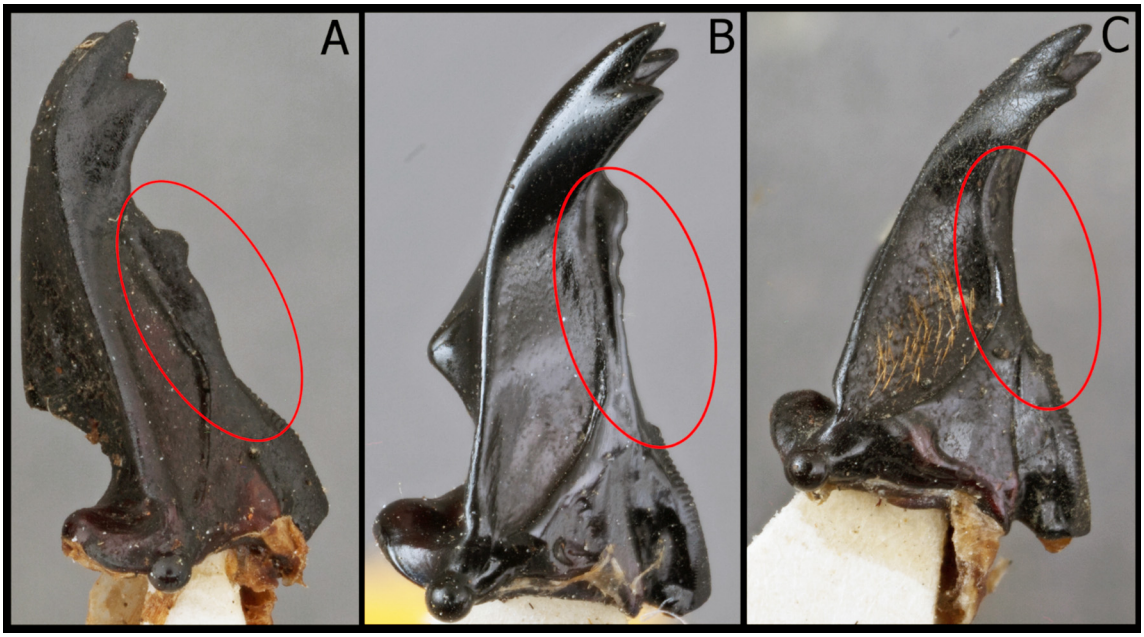

Fig. 9. Mandible crenulations and teeth in *Phrenapates* Gray, 1832. **A**. Tooth, no crenulations in *Phrenapates mandibularis* Gebien 1910 [*Phrenapates latreillei*], holotype, ♂ (Teneb_base 23167, NHMB). **B**. Crenulations, no tooth, in *Phrenapates bennettii* Gray, 1832, ♂ (Teneb_base 23186, NHMB). **C**. No crenulations or tooth in *Phrenapates dux* Gebien, 1910 (Teneb_base 23215, AAAG)

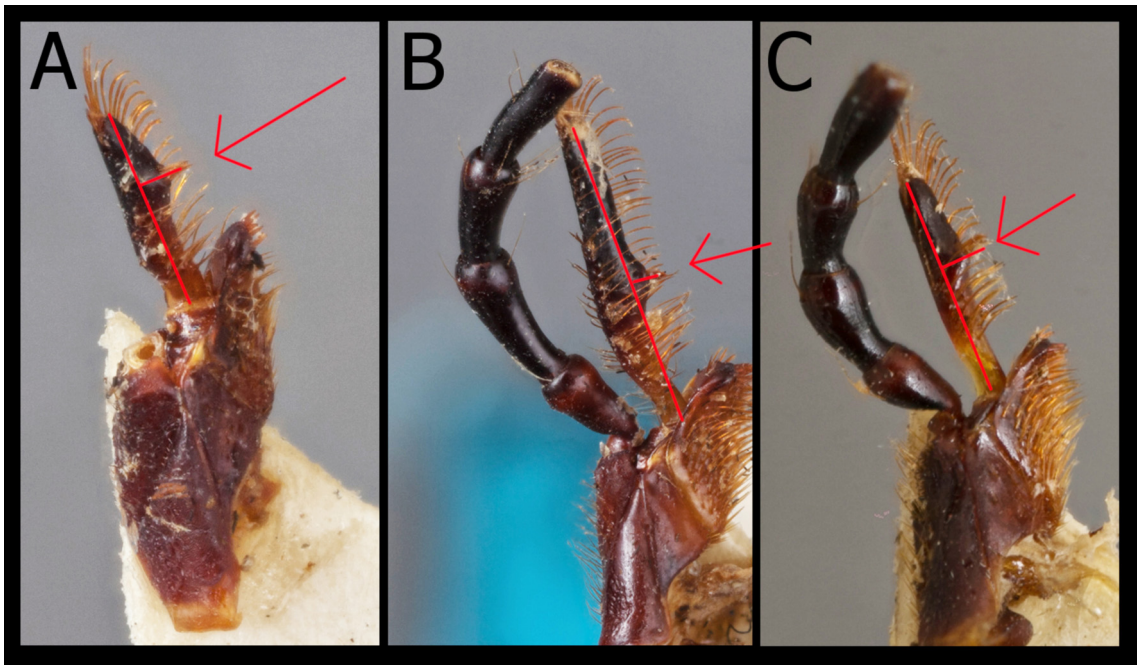

Fig. 10. Position of galea setae cluster in *Phrenapates* Gray, 1832. **A**. Near the apex (ratio tip to clump of bristle to tip to end 1:2) as in *Phrenapates educator* Gebien, 1910, lectotype, ♂ (Teneb_base 23175, NMHB). **B**. Centered as in *Phrenapates ohausi* Gebien, 1910, ♂ (Teneb_base 23165, NHMB). **C**. Galea ratio less than 1:2 in *Phrenapates erratus* Rincon, Lumen & Kamiński nom. nov., lectotype, ♂ (Teneb_base 23168, NHMB).

Phrenapates bennettii Gray, 1832
Figs 1B, 2A, 3B, 4A–B, 5A, 6, 8C–D, 9B, 11

Phrenapates bennettii Gray, 1832: 91.

Diagnosis

Phrenapates bennettii can be separated from all other known congeners based on the following characters: supraorbital tubercles present, separating this species from *P. dux, P. latreillei*, *P. educator,* and *P. erratus* Rincon, Lumen & Kamiński nom. nov. The supraorbital tubercles in *P. bennettii* are shorter than wide (Fig. 8C–D), separating them from *P. gilloglyi* (tubercles are taller than wide) and *P. ohausi* (tubercles are as tall as wide). Clypeal horn ends in a blunted point, unlike the smooth tapered horn in *P. ohausi*, short horn in *P. fortunaensis*, and three-pointed horn in *P. gilloglyi*. Mandibles have crenulations on the inside margin, which differs from *P. gilloglyi* and *P. ohausi*. *Phrenapates bennettii* have variation in the shape of their mentum but never have a notch like that of *P. gilloglyi* or *P. ohausi* (Fig. 2B, H); the mentum has produced lateral apices which differs from *P. fortunaensis* with rounded lateral apices.

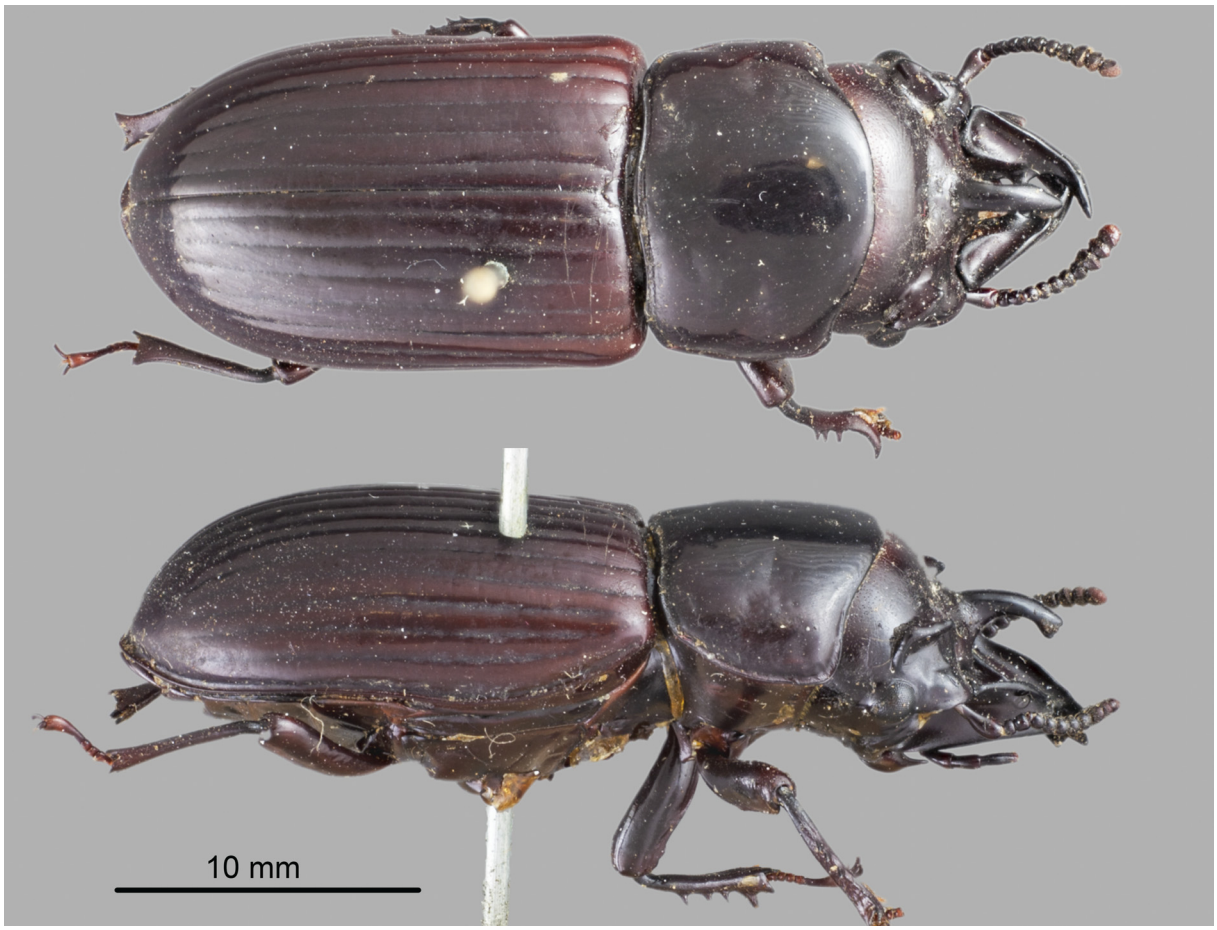

Fig. 11. *Phrenapates bennettii* Gray, 1832, lectotype, ♂ (Teneb_base 23170, BMNH), dorsal (top) and lateral (bottom) views.

Type material

Lectotype (designated here)
COLUMBIA • ♂; "*Phrenapates* / *Bennettii* / Kirby, Columbia // F. Bates / 81.19 // (red label) LECTOTYPE / *Phrenapates* / *bennettii* / Gray 1832 // (blue label) Tenebrionid Base / Aaron D. Smith / Catalog # 23170"; Teneb_base 23170; BMNH.

Paralectotypes
The two additional specimens from Kirby's material should be considered paralectotypes. However, we were unable to locate them during this study.

Other material examined

COLUMBIA • 1 spec.; Bogota; 1924; Teneb_base 23174; NHMB.

COSTA RICA • 2 specs; Puntarenas, Cote Brus, Est Biol. Las Alturas; 8°57' N, 82°52' W; 26 Mar. 2002; in rotten logs; A. Cline and A. Tishechkin leg.; Teneb_base 22871 to 22872; AAAG • 1 spec.; Provincia de Puntarenas, Canton Coto Brus. Agua Caliente; Aug. 1986; Nick Zakharoff gift to Cal. Acad. Soi. Coll.; Teneb_base 23263; CASC • 1 spec.; Cartago 15 km NE of Turrialba; 18–21 Apr. 1981; E. Giesbert leg.; Teneb_base 23261; CASC • 1 spec.; Bebedero [Underwood, 94]; Teneb_base 23265; MNHN • 1 spec.; San Carlos [78 Plesiotype 161]; Teneb_base 23186; NHMB • 1 spec.; Puntarenas 8 km S of San Vito; 25 May 1983; Dan Heffern leg.; Teneb_base 23262; TAMU.

ECUADOR • 2 specs; Cachabe. [low c.]; Nov. [96]; Rosenberg leg.; Teneb_base 23254 to 23255; MNHN • 1 spec.; Equateur Loja Abbé Guajon; Teneb_base 23253; MNHN.

GUATEMALA • 3 specs; Teneb_base 23250 to 23252; MNHN • 3 specs; St Cristobal, Verapaz; Teneb_base 23156 to 23158; NHMB • 1 spec.; s. loc.; Teneb_base 23172; NHMB.

HONDURAS • 1 spec.; [Coll. Nonfried]; Teneb_base 23256; MNHN • 1 spec.; s. loc.; Teneb_base 23171; NHMB.

NICARAGUA • 18 specs; Jinotega, Cerro Kilambé; 1000 m a.s.l.; Jul. 2001; col. M.A. Guatemala; Teneb_base 23249, 22901, 22903 to 22916, 22935 to 22936; AAAG • 6 specs; Zelaya, Cerro Saslaya; 500 m a.s.l. (Bosque); 7–14 Jul. 1999; B. Hernandez leg.; Teneb_base 22937 to 22942; AAAG • 1 spec.; San Carlos, Rio San Juan, Est. Biol. [Bartola] Selva alta perenfolia; 30 m a.s.l.; 10°58' N, 84°20' W; 11 Sep. 2000; J. Marquez leg.; en troncos caidos; Teneb_base 22943; AAAG • 1 spec.; Bluefields; 1–3 Apr. 1949; L.E. Long leg.; Teneb_base 23264; FMNH.

PANAMA • 10 specs; Chiriqui prov., 5 km NE of Santa Clara, Hartmann's; 1515 m a.s.l.; 8°50.68' N, 82°44.58' W; 23 Aug. 2008; A. Gillogly leg.; Teneb_base 22838 to 22847; AAAG • 1 spec.; 9.7 km W of Volcan Chiriqui prov.; 28 Dec. 1991; 1400 m a.s.l.; A.Gillogly and J.H. White leg.; Teneb_base 22880; AAAG • 2 specs; Cocle Prov., 3 km N of El Yalle, La Mesa; 930 m a.s.l.; 8°38'13" N, 80°07'28" W; 21 Jul. 1999; A.R. Gillogly leg.; Teneb_base 22848, 22867; AAAG • 2 specs; Cocle Prov., 3 km N of El Valle; Teneb_base 22868 to 22869; AAAG • 1 spec.; La Mesa, NE side of Cerro Gaital, Cocle Prov.; 850–900 m a.s.l.; 13 Oct. 1991; A.R. Gillogly leg.; Teneb_base 22870; AAAG • 4 specs; Cocle Prov., NE side of La Mesa, Cerro Gaital; 900 m a.s.l.; 1 Mar. 1992; A.R. Gillogly leg.; Teneb_base 22876 to 22879; AAAG • 1 spec.; 10 km N of El Cope, Cocle Prov.; 750 m a.s.l.; 21 Dec. 1991; Teneb_base 22881; AAAG • 22 specs; Darien Prov. Cana, Pirre Ridge; 1650 m a.s.l.; 7°45.825' N, 77°43.325' W; 5 May 2008; A.R Gillogly and M. Seid leg.; Teneb_base 22944 to 22948, 23248, 23332 to 23347; AAAG • 25 specs; Darien Prov. Cana, Pirre Trail; 1560 m a.s.l.; 5 Jun. 1996; A.R Gillogly leg.; Teneb_base 22969 to 22984, 23348 to 23355, 22902; AAAG • 6 specs; Panama Prov. Cerro Jefe; 894 m a.s.l.

9°13.339' N, 79°22.257' W; 18 Aug. 2008; Gillogly and Smith leg.; Teneb_base 22832 to 22837; AAAG • 2 specs; Veraguas Prov., 8 km W of Santa Fe Cerro Tute; 950 m a.s.l.; 8°30'26" N, 81°6'49" W; 24 Jul. 1999; A.Gillogly leg.; Teneb_base 22873 to 22874; AAAG • 1 spec.; Veraguas Prov. 4km N of Alto de Piedra, NW Sta Fe.; 900 m a.s.l.; 10 Apr. 1993; A.R. Gillogly leg.; Teneb_base 22875; AAAG • 1 spec.; 4.8 km NNE of Santa Fe Veraguas, Panama Prov.; 700 m a.s.l.; 8 Dec. 1991; Teneb_base 22882; AAAG •1 spec.; Chiriqui, Powerline cut N of Lago, Fortuna; 1163 m a.s.l.; 8°44.75' N, 82°13.94' W; 31 Aug. 2008; A.D. Smith leg.; Teneb_base 18779; ADSC • 1 spec.; Barro Colorado, C.Z.; 3 Feb. 1936; W.J. Gertsch leg.; Teneb_base 23300; AMNH • 1 spec.; Barriles, Chiriqui; 31 Jan. 1931; Teneb_base 23302; CASC • 1 spec.; Potrerilles; 25 Jan. 1935; Teneb_base 23303; CASC • 1 spec.; Bocas Del Toro, 10 km NE of Fortuna Dam; 1036 m a.s.l.; 23–26 May 1984; E. Giesbert leg.; Teneb_base 23301; CASC • 1 spec.; Chiriqui; Champion ex. Gordon and Salvin leg.; Teneb_base 23299; MCZ • 1 spec.; Chiriqui; Teneb_base 23304; MNHN • 10 specs, Museum Paris ex coll. E. Oberthur; V. de Chiriqui m de Mathan; 1901; Teneb_base 23305 to 23314; MNHN • 1 spec.; Cocle Prov. Cerro, Gaitai; 1000 m a.s.l.; 8°36' N, 80°10' W; 11 Nov. 1992; P. Jolivet leg.; Teneb_base 23260; MNHN • 4 specs; Chiriqui; Teneb_base 23162 to 23164, 23178; NHMB • 1 spec.; Chiriqui; Teneb_base 23173; NHMB • 1 spec.; [Chiriqui 59]; Teneb_base 23177; NHMB.

UNKNOWN • 3 specs; patria; Teneb_base 23159 to 23161; NHMB.

Redescription

Measurements. Length 26–39 mm, width 9–13 mm, specimens measured (n = 20).

Head. Medial edge of mandibles without tooth, inner margin crenulated. Galea with cluster of bristles situated near midpoint. Mentum weakly sculptured, apex without medial notch; lateral apices produced. Clypeal apex not dilated. Supraorbital tubercles present; shorter than wide. Clypeal horn arced (in lateral view); ending bluntly at tip.

Status

Gray in Griffith and Pidgeon (1832) did not designate a holotype from the type series of Kirby's three specimens from Choco, Columbia. Therefore, a lectotype designation is needed to stabilize the taxonomic status of the species and genus. There is one specimen from Kirby's collection held by the Natural History Museum in London (BMNH) with the correct locality, which is hereby designated as the lectotype.

Distribution

Central America: Costa Rica, Guatemala, Honduras, Nicaragua, Panama; South America: Colombia, Ecuador (Fig. 6).

Phrenapates dux Gebien, 1910
Figs 2C, 3D, 4C–D, 5B, 6–7, 8G–H, 12

Phrenapates dux Gebien, 1910: 504.

Diagnosis

Phrenapates dux (27–36 mm) can be separated from the other large species *P. bennettii* (26–39 mm) and *P. ohausi* (28–39 mm) by its lack of supraorbital tubercles. Other species which lack supraorbital tubercles can usually be separated by size (*P. dux* 27–36 mm vs 18–28 mm and 21–26 mm in *P. latreillei* and *P. educator*, respectively). *Phrenapates dux* can be separated from *P. latreillei* through the presence of a tooth on the inner margin of the mandibles (present in *P. latreillei*, absent in *P. dux*). The horn in

P. dux is especially unique within the genus, being constricted at the base, dorsally flattened on the top, and having an angular arc. Other species without supraorbital tubercles are differentiated by clypeal horns with strong, circular arcs (*P. latreillei*), or with weak arcs (*P. educator*). The lateral apices of the mentum are produced in *P. dux*, rather than rounded of *P. ohausi*. The dorsal ridge next to the clypeus is not dilated as in *P. educator*. Mandibles without the crenulations seen in *P. bennettii*.

Type material

Lectotype (designated here)
ECUADOR • ♂; (green label) "O. Ecuador. / Macas // *Phrenapates* / *dux* / X Geb (red label) Cotype! / No. 166 // Sammlung / H Gebien // (blue label) Tenebrionid Base / Aaron D. Smith / Catalog # 23166"; Teneb_base 23166; NHMB.

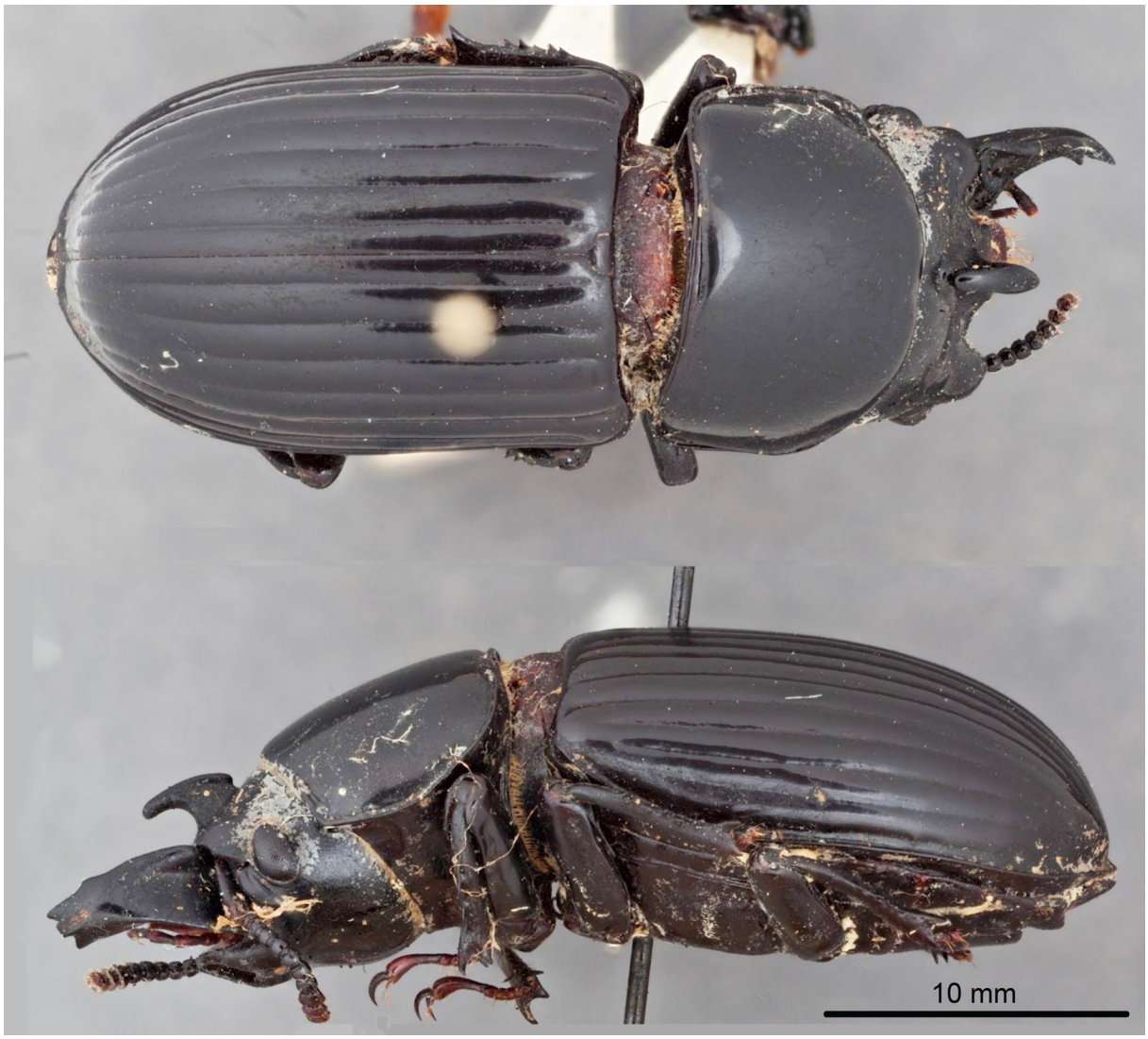

Fig. 12. *Phrenapates dux* Gebien, 1910, lectotype, ♂ (Teneb_base 23166, NHMB), dorsal (top) and lateral (bottom) views.

Other material examined

BOLIVIA • 1 spec.; Yungas de La Paz; Teneb_base 23191; NHMB • 1 spec.; Yungas de LePaz, 1000m; H. Rolle Berlin S.W.N. leg.; Teneb_base 23184; NHMB.

CHILE • 1 spec.; [northern] Chili; 29 Dec. 1973; [C]. G. Minet leg.; Teneb_base 23259; NHMB.

ECUADOR • 1 spec.; Napo, 3 km E of Huaticocha; 0°45.22' S; 77°27.84 W; 19 Aug. 1997; A.R. Gillogly leg.; Teneb_base 22949; AAAG • 2 specs; Napo Prov. Archidona, Rio Hollin; 21 Dec. 2001; P. Bravo and E. Vasquez leg; collection R. Diaz; Teneb_base 23214 to 23215; AAAG • 3 specs; Zatzayacu Oriente; 10 Nov. 1932; Teneb_base 23222 to 23224; AMNH • 5 specs; El Partidero; 17–27 Nov. 1935; Teneb_base 23225 to 23228, 23233; AMNH • 1 spec; Zatzayacu Oriente; 10 Nov. 1932; Teneb_base 23229; AMNH • 1 spec; [East] Ecuador Jivaria; 17 Nov. 1905; Ohaus leg.; Teneb_base 22809; BMNH • 2 specs; Quito F4724; Teneb_base 23220 to 23221; CASC • 1 spec.; Macas er.; Teneb_base 23275; CASC • 1 spec.; Guayaquil SA; Teneb_base 23199; CASC • 4 specs; 3–12 m N of Puyo, Napo Pastaza; 935 m a.s.l.; 9 Nov. 1955; E.I. Schlinger and E.S. Ross leg.; Teneb_base 23192 to 23195; CASC • 1 spec.; Lumbaqui; 23 Sept. 1977; Teneb_base 23201; FMNH • 3 specs; Arajuno; Oct. 1960; L.E. Pena coll. acc. 17-422; Teneb_base 23196 to 23198; FMNH • 1 spec.; Pastaza Jibaria Shurupe; 7 Nov. 1987; Mike Huybensz leg.; Teneb_base 23202; FMNH • 1 spec.; 1853; Museum Paris Chimborazo, and Pichincha MANDEVILLE; Teneb_base 23273; MNHN • 1 spec.; 1922; Teneb_base 23274; MNHN • 2 specs; [East] Ecuador Macas No. 166; Zuña on Huilca MUSEUM PARIS de Macas Cap D'espanay Mars; Teneb_base 23189 to 23190; NHMB • 2 specs; same location as for preceding; Teneb_base 23179 to 23180; NHMB • 1 spec.; Panelos(?) [illegible]; Teneb_base 23185; NHMB • 8 specs; Napo Prov. Archidona; Rio Hollin; 21 Dec. 2001; R. Diaz, P.Bravo and E. Vasquez leg.; Teneb_base 23234 to 23241; TAMU.

GUYANA • 1 spec.; Reg 8, Potaro River, 5°18' N, 59°54.635' W [WGS84]; 5 Jun. 2012; R.A. Koch leg.; Teneb_base 23242; PERC.

PERU • 1 spec.; Upper Rio Huallaga; 1 Jan. 1926; Teneb_base 23230; AMNH • 1 spec.; same data as for preceding; Oct. 1929; Teneb_base 23231; AMNH • 1 spec.; Rio Huallaga; Oct. 1930; Teneb_base 23232; AMNH • 1 spec.; same location as for preceding; Teneb_base 23243; AMNH • 3 specs; Kaieteur, BG.; 6 Aug. 1911; Teneb_base 23217 to 23219; AMNH • 2 specs; Marcapata; Teneb_base 23187 to 23188; NHMB • 1 spec.; Cusco Dept. Villa Carmen field station, 1.2 km N of cafeteria; 12.87753° S, 71.40153° W; 525–1000 m a.s.l.; 27 May 2011; D.J. Bennett leg.; hand collecting; PER-11-DJB-036.; Teneb_base 18774; SEMC.

VENEZUELA • 1 spec.; Mt Duida, 1158 m a.s.l., Amazonas; Feb. 1968; J. Rivero; MCZ-Ent 00753334; Teneb_base 23244; MCZ • 1 spec.; La Escalera Bolivar, on rotten log near a stream; 1000 m a.s.l.; 22 Mar. 1968; J.A.Rivero leg.; MCZ-ENT 000753333; Teneb_base 23216; MCZ.

Redescription

Measurements. Length 27–36 mm, width 10–12 mm, specimens measured (n = 20).

Head. Medial edge of mandibles without tooth, inner margin without crenulation. Galea with cluster of bristles situated near midpoint. Mentum weakly sculptured, apex with medial notch; lateral apices produced. Clypeal apex not dilated. Supraorbital tubercles absent. Clypeal horn with wide base, arced (in lateral view); dorsal surface flattened, ending bluntly at tip.

Status

While the original description does not provide a specific number of specimens examined; it does indicate that there were multiple individuals by providing a size range. Therefore, we designate here a lectotype from the presumed syntype series (see above for label data).

Distribution

South America: Bolivia, Chile, Ecuador, Guyana, Peru, Venezuela (Fig. 7).

Phrenapates educator Gebien 1910
Figs 3F, H, 4E–F, 6, 10A, 13

Phrenapates educator Gebien, 1910: 504.

Diagnosis

The three species *P. erratus* Rincon, Lumen & Kamiński nom. nov., *P. educator*, and *P. latreillei* are noticeably smaller than the other five species (21–28 mm in length vs 26–39 mm in larger species).

Fig. 13. *Phrenapates educator* Gebien 1910, lectotype, ♂ (Teneb_base 23175, NMHB), dorsal (top) and lateral (bottom) views.

Phrenapates erratus was only represented here by the lectotype (Fig. 14), and no additional material was found during this revision. Gebien (1911) noted that *P. erratus* is very similar to *P. educator*. Characters he listed were: *P. educator* displays a strongly concave lower lip (clypeal apex) vs *P. erratus*, mandibles that are more deeply hollowed out, and the slightly weaker humeral angles of the elytra that show the epipleural keel (which is covered in *P. erratus*). Upon comparison of *P. erratus* vs *P. educator*, many of these characters were either difficult to delineate, or found to include some variation within *P. educator*. *Phrenapates educator* is best separated from *P. erratus* by the distinct carina near the attachment point of the mandible, *P. erratus* has, instead, a weak carinate bump. The dorsal depression on the mandible is deeply punctate without setae, while the mandible of *P. erratus* is semi-rugose and has setae. The mentum, though variable, tends to be arcuate in *P. erratus* and sinuate in *P. educator*.

Type material

Lectotype (designated here)
ECUADOR • ♂; (green label) "W. Ecuador / Pucay 300m / (Ohaus) XI.05. // *Phrenapates* / *educator*/ X Geb // (red label) Type / No. 163 // Sammlung / H Gebien // (blue label) Tenebrionid Base / Aaron D. Smith / Catalog # 23175"; Teneb_base 23175; NHMB.

Other material examined

COLOMBIA • 1 spec.; Aguaral; Teneb_base 23183; NHMB.

ECUADOR • 1 spec.; St Domingo, Colorados; Jun. 1981; G. Onoré leg.; Teneb_base 23245; CASC • 4 specs; Balzapampa Route de Quita Prov. de Bolivar; Sep.–Oct. 1893; M.de Mathan leg.; Teneb_base 23285 to 23288; MNHN • 2 spec.; 1922; Museum Paris Quito Cap D'Espinay; Teneb_base 23289 to 23290; MNHN • 1 spec.; W. Ecuador Pucay; 300 m a.s.l.; Nov. 1905; Ohaus leg.; Teneb_base 23169; NHMB.

Redescription

Measurements. Length 21–26 mm, width 7–8 mm, specimens measured (n = 6).

Head. Medial edge of mandibles without tooth, inner margin without crenulation. Galea with cluster of bristles situated toward apex. Mentum moderately sculptured, apex with medial notch; lateral apices produced. Supraorbital tubercles absent. Clypeal horn weakly arced (in lateral view); ending bluntly at tip.

Status

While the original description does not provide a specific number of specimens examined; it does indicate that there were multiple individuals by providing a size range (Gebien 1910). Therefore, we designate here a lectotype from the presumed syntype series (see above for label data).

Distribution

South America: Ecuador, Columbia (Fig. 6).

Phrenapates erratus Rincon, Lumen & Kamiński nom. nov.
Figs 2D, 3C, 6, 10C, 14

Phrenapates latreillei Gebien, 1910: 504 [junior primary homonym of *Phrenapates latreillei* Lacordaire, 1859: 315].

Diagnosis

For separation of *Phrenapates erratus* Rincon, Lumen & Kamiński nom. nov. from larger species and from *P. latreillei* see the diagnoses for *P. latreillei* and *P. educator*, respectively. Morphologically, *P. erratus* can be difficult to differentiate from *P. educator*. *Phrenapates erratus* is best separated from *P. educator* in the weak carinate bump near the attachment point of mandible, *P. educator* has a distinct carina in the proximal end. The dorsal depression on mandible is rugose and has setae in *P. erratus* while in *P. educator* the dorsal depression is deeply punctate and does not have setae. The mentum, though variable, tends to be arcuate in *P. erratus* while it is sinuate in *P. educator*.

Etymology

Named in reference to remedying or editing previously authored taxon names.

Type material

Lectotype (designated here)
UNKNOWN LOCATION • ♂; (green label) "Nov. Granada // *Phrenapates* / *Latreillei* / Geb // (red label) Type / No. 166 // Sammlung / H Gebien // (blue label) Tenebrionid Base / Aaron D. Smith / Catalog # 23168"; Teneb_base 23168; NHMB.

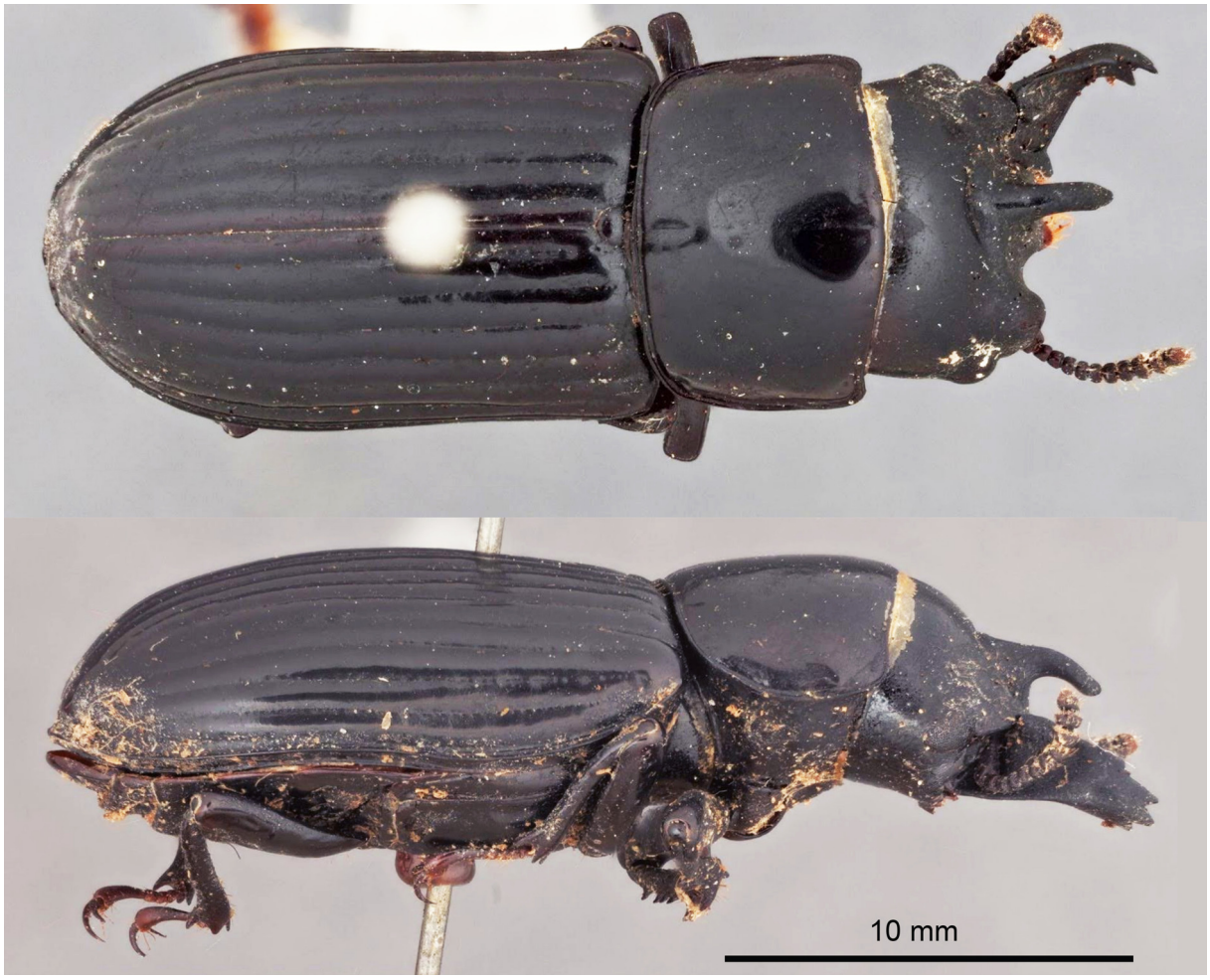

Fig. 14. *Phrenapates erratus* Rincon, Lumen & Kamiński nom. nov., lectotype, ♂ (Teneb_base 23168, NHMB), dorsal (top) and lateral (bottom) views.

Redescription

Measurements. Length 23 mm, width 8 mm (n = 1).

Head. Medial edge of mandibles without tooth, inner margin without crenulation. Galea with cluster of bristles situated toward apex. Mentum strongly sculptured, apex with medial notch; lateral apices produced. Clypeal apex dilated. Supraorbital tubercles absent. Clypeal horn bent weakly downward (in lateral view); ending bluntly at tip.

Status

Gebien's first treatment (1910) of *Phrenapates* presents *P. latreillei* as a new species in preparation for a subsequent treatment. In 1911, Gebien attempted to stabilize the nomenclature by officially introducing the name *Phrenapates latreillei* for specimens available to him that were, in his opinion, fitting the species concept. Gebien's (1910, 1911) treatments appear to be based on the presumption that "in litt." attributions to Dejean (i.e. Gebien 1911, Gemminger and Harold 1870) and Lacordaire's (1859) species description were invalid. His initial description was based on more than a single specimen (inferred from size range provided) from New Granada (Gebien 1910); however, in 1911 when providing a more detailed redescription of this species, he stated that only a single specimen was available to him, which is here designated as the lectotype to stabilize the concept of the species (see label data above). Furthermore, in the same paper, Gebien (1911) also attributed this species to Dejean ("in litt."), introducing organizational chaos in the nomenclature. Reevaluation of the literature has revealed that Lacordaire's (1859) description of *Phrenapates latreillei* does, in fact, meet the requirements of the ICZN (1999) and should be treated as valid. As such, Gebien's *Phrenapates latreillei* should be treated as a junior primary homonym of Lacordaire's (1859) name. A replacement name, *Phrenapates erratus* Rincon, Lumen & Kamiński nom. nov., is hereby introduced for *Phrenapates latreillei* Gebien, 1910.

Finally, verification of historical type material shows that Gebien's (1910) concept of *P. latreillei* does not match the concept presented by Lacordaire (1859). As such, *P. erratus* Rincon, Lumen & Kamiński nom. nov. is hereby treated as a separate species. The investigation conducted here supports a close relation between this species and *Phrenapates educator*; however, *P. erratus* remains diagnosable via the weak carina near the proximal end of the mandible and the rugosity of the mandible and the presence of setae. More material is needed to fully test the status of *Phrenapates erratus*. Finally, we designate a specimen identified as *P. latreillei* by Gebien in NHMB as the lectotype for *Phrenapates erratus* (see Type Material of *P. erratus* above).

Distribution

South America: the label information cannot be georeferenced as it refers to a large geographic region (New Granada), which includes areas of Columbia, Ecuador, Panama, and Venezuela.

Phrenapates fortunaensis Rincon & Smith sp. nov.
urn:lsid:zoobank.org:act:92CCAB44-7C22-4F30-A36F-79139C448612
Figs 2G, 3E, 6–7, 15

Diagnosis

Phrenapates fortunaensis Rincon & Smith sp. nov. can be separated from all other known congeners based on the following characters: supraorbital tubercles present, separating this species from *P. dux, P. latreillei, P. educator,* and *P. erratus* Rincon, Lumen & Kamiński nom. nov. The supraorbital tubercles are wider than tall, similar to *P. bennettii*, but different than in *P. gilloglyi* Rincon & Smith sp. nov. Mandibles with crenulations on inside margin, as well as with an extra tooth as in *P. bennettii,* which

differs from the smooth inner margin of *P. gilloglyi*. The mentum lacks an apical medial notch, instead possessing a small projection, giving the appearance of a trilobate mentum (Fig. 2G).

Etymology

Species named after the Fortuna Mountains where the specimens were found.

Type material

Holotype

PANAMA • Chiriqui Prov., Reserva Fortuna, 3rd Nov. Trail; 8°45.468′ N, 82°15.671′ W; 1234–1280 m a.s.l.; 1 Sep. 2008; A.R. Gillogly leg.; Teneb_base 23482; PERC.

Other material examined

PANAMA • 1 spec.; Boca d. Toro Prov., 3 km NW of Fortuna Hwy border station; 900 m a.s.l.; 1 Aug. 1997; A.R. Gillogly leg.; Teneb_base 23331; AAAG • 2 specs; Bocas del Toro Prov., La Culebra Trail, 5 km N of Boquete; 1500 m a.s.l.; 16 Jul. 1995; A.R. Gillogly leg.; Teneb_base 23468 to 23469; AAAG • 1 spec.; Chiriqui Prov. Reserva la Fortuna Cont. Div. Trail; 1300 m a.s.l.; 8°47' N, 82°13' W; 18 Jan. 1992; A.R. Gillogly leg.; Teneb_base 23324; AAAG • 4 specs; Chiriqui Prov, Reserva Fortuna, 3rd Nov. Trail; 1234–1280 m a.s.l.; 8°45.468' N, 82°15.671 W; 1 Sep. 2008; A.R. Gillogly leg.; Teneb_base 23482 to 23485; AAAG • 3 specs; Chiriqui Prov. Rsva la Fortuna Cont. Div.Trail; 1200 m a.s.l.; 27 Apr. 1996; A.R. Gillogly leg.; Teneb_base 23323, 23466 to 23467; AAAG • 10 specs; Chiriqui Prov. Reserva

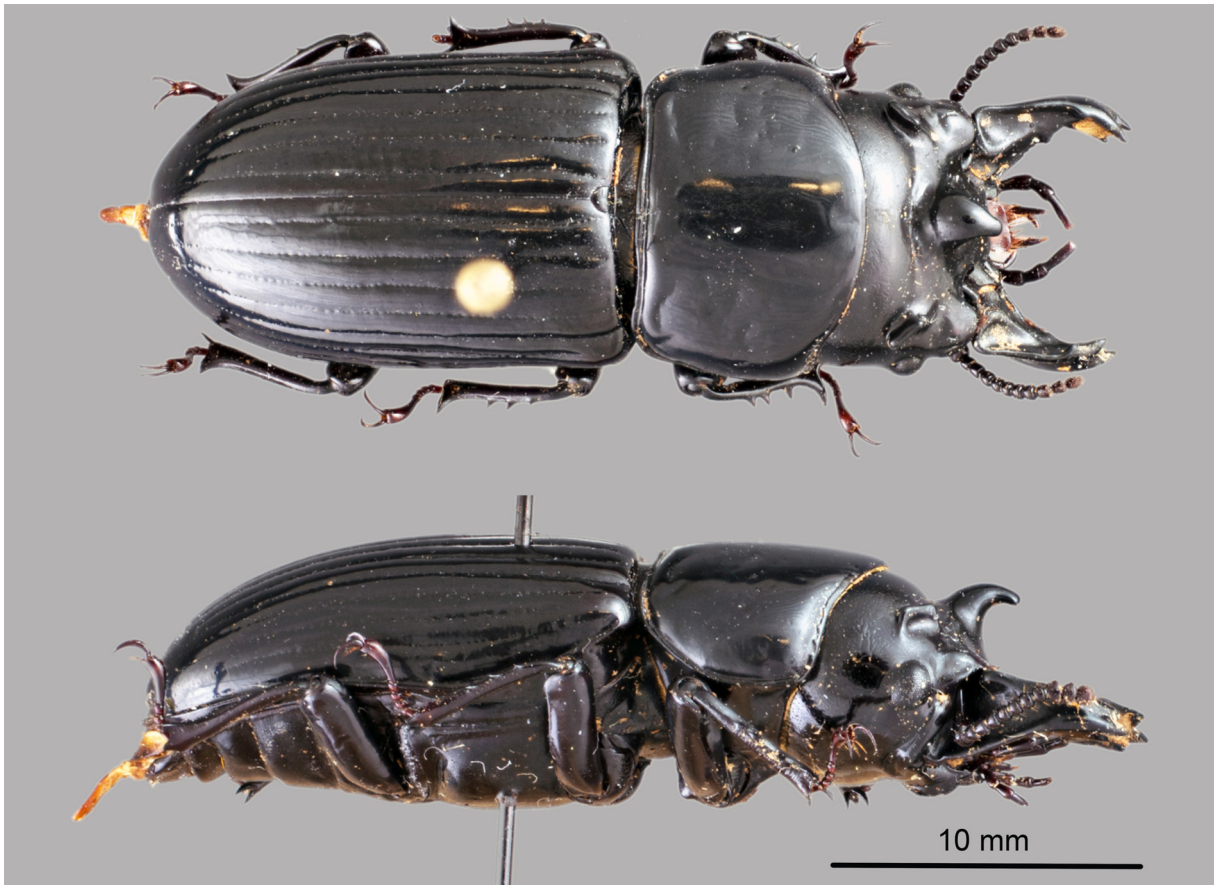

Fig. 15. *Phrenapates fortunaensis* Rincon & Smith sp. nov., holotype, ♂ (Teneb_base 23482, PERC), dorsal (top) and lateral (bottom) views.

Fortuna, Fortuna Hwy, N of Dam; 1151 m a.s.l.; 8°24.840' N, 82°14.562' W; 30 Aug. 2008; Gillogly and Smith leg.; Teneb_base 23472–23481; AAAG • 2 specs; Chiriqui Prov. Reserva la Fortuna, powerline cut; 1145 m a.s.l.; 8°44.80' N, 82°13.90' W; 31 Jul. 2008; A.Gillogly and A. Smith leg.; Teneb_base 23486 to 23487; AAAG • 5 specs; Chiriqui Prov. Rsva Fortuna, 1.7 km N of Dam; 1152 m a.s.l.; 8°44.829' N, 82°14.572' W; 25 Apr. 2009; A. Gillogly and D. Ward Jr. leg.; Teneb_base 23317 to 23321; AAAG • 2 specs; Chiriqui Prov. Rsva Fortuna, 3rd Nov. Trail; 1527 m a.s.l.; 8°45.768' N, 82°15.358' W; 28 Apr. 2009; A. Gillogly and D. Ward leg.; Teneb_base 23315 to 23316; AAAG • 2 specs; Chiriqui Prov. Rsva Fortuna, Samudio Trl.; 1090 m a.s.l.; 8°44.1' N, 82°14.8' W; 27 Apr. 2009; A.Gillogly and D.Ward Jr. leg.; Teneb_base 23470 to 23471; AAAG • 3 specs; Chiriqui Reserva la Fortuna, Est. Biologica; 1200 m a.s.l.; 8°43'18" N, 82°14'17" W; 8 Jul. 1999; A.R. Gillogly leg.; Teneb_base 23330, 23464 to 23465; AAAG • 1 spec.; Chiriqui, 3rd Nov. Trail, on rotten logs; 8°45.47' N, 82°15.67' W; 1227 m a.s.l.; 1 Sep. 2008; A.D. Smith leg.; Teneb_base 18775; ADSC • 6 specs; Chiriqui, Powerline cut; 1 km NW of Charchita; 8°24.840' N, 82°14.562' W; 1151 m a.s.l.; 30 Aug. 2008; A.D. Smith leg.; Teneb_base 18766, 18769 to 18773; ADSC • 2 specs; Chiriqui, Powerline cut, N of Lago, Fortuna: 1163 m a.s.l.; 8°44.75' N, 82°13.94' W; 31 Aug. 2008; A.D. Smith leg.; Teneb_base 18777 to 18778; ADSC • 1 spec.; Chiriqui Fortuna; 82°15' W, 8°44' N; 20 May 1978; O'Briens and Marshall leg.; Teneb_base 22814; CASC • 3 specs; Chiriqui Reserva La Fortuna, Hydrographic sta. trail; 28 May 1993; E.G. Riley; Teneb_base 22811–22813; TAMU.

Description

Measurements. Length 26–33 mm, width 9–11 mm, specimens measured (n = 20).

Head. Medial edge of mandibles with tooth, inner margin crenulated. Galea with cluster of bristles situated near midpoint. Mentum moderately sculptured, apex without medial notch; lateral apices rounded. Clypeal apex not dilated. Supraorbital tubercles present; shorter than wide. Clypeal horn very short, weakly arced (in lateral view) and weakly tapered to blunt point.

Distribution

Central America: Panama.

Phrenapates gilloglyi Rincon & Smith sp. nov.
urn:lsid:zoobank.org:act:76CB49A2-518F-406D-B9CE-F161967E351A
Figs 2B, 3F, 6–7, 8E–F, 16

Diagnosis

Phrenapates gilloglyi Rincon & Smith sp. nov. can be separated from all other known congeners based on the following characters: supraorbital tubercles present, separating this species from *P. dux, P. latreillei, P. educator,* and *P. erratus* Rincon, Lumen & Kamiński nom. nov. Supraorbital tubercles with a height greater than or equal to the width, separating them from *P. bennettii* and *P. fortunaensis* Rincon & Smith sp. nov. Clypeal horn ending in three points, unlike the smoothly tapered horn in *P. ohausi*. Mandibles with no crenulations or teeth on inside margin, which differs from *P. bennettii* and *P. fortunaensis*. Mentum with apical notch, unlike in *P. fortunaensis* or *P. bennettii*.

Etymology

The species is named after the passalid taxonomist Dr Alan Gillogly for his donation of specimens and valuable insight.

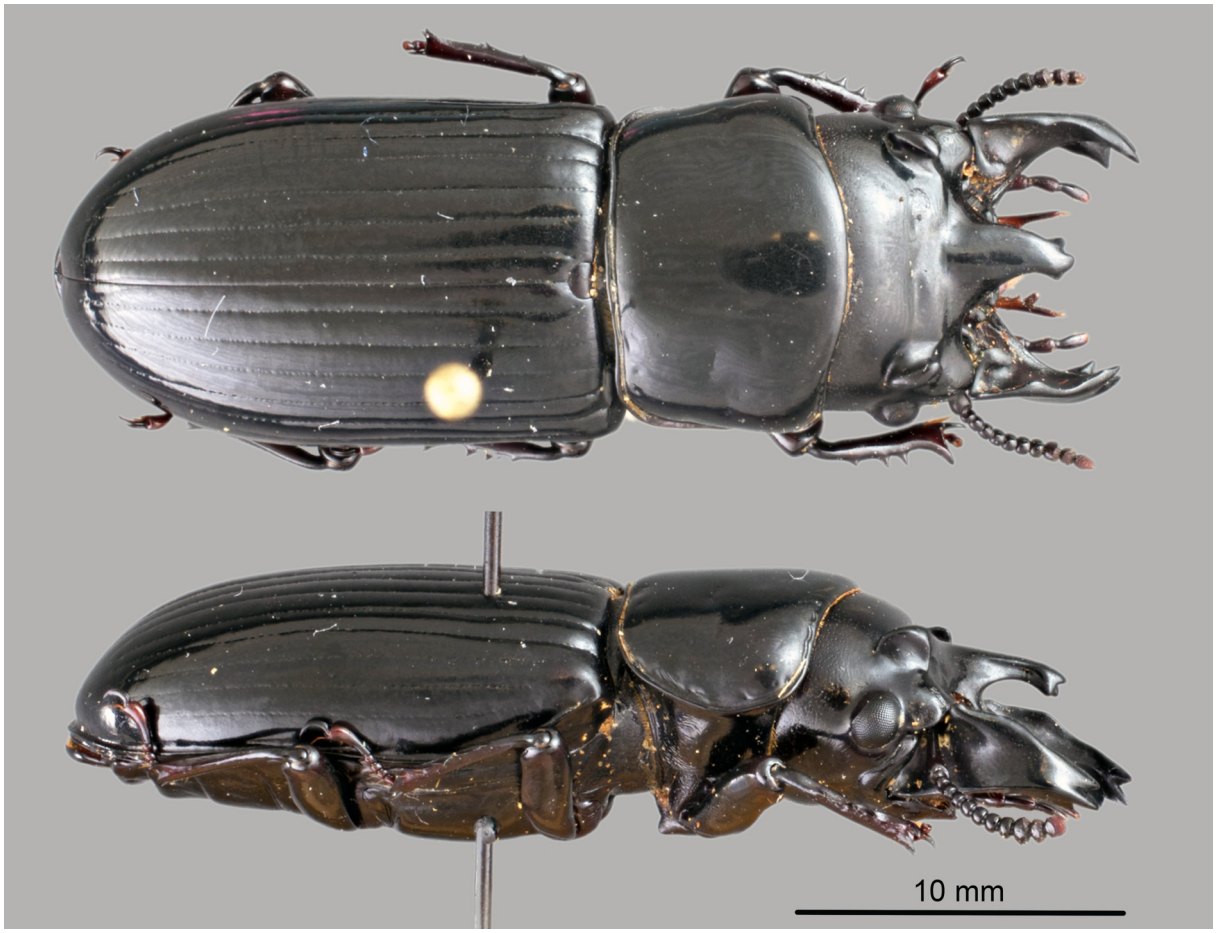

Fig. 16. *Phrenapates gilloglyi* Rincon & Smith sp. nov., holotype, ♂ (Teneb_base 23367, PERC), dorsal (top) and lateral (bottom) views.

Type material

Holotype

PANAMA • ♂; "Panama, Cocle Prov., 3 km N of El Valle, Cerro Gaital; 900 m a.s.l.; 21 Jul. 1999; A. Gillogly leg.; 8°37′35″ N, 80°6′53″ W; Teneb_base 23367; Tenebrionid Base / Aaron D. Smith / Catalog # 23367"; Teneb_base 23367; PERC.

Other material examined

PANAMA • 3 specs; Panama Prov. Cerro Jefe; 894 m a.s.l.; 9°13.339' N, 79°22.257' W; 18 Aug. 2008; Gillogly and Smith leg.; Teneb_base 23364 to 23366; AAAG • 2 specs; Cocle Prov., 3 km N of El Valle Cerro Gaital; 900 m a.s.l.; 8°37'35" N 80°6'53" W; 21 Jul. 1999; A. Gillogly leg.; Teneb_base 23367 to 23368; AAAG • 1 spec.; Cocle Prov. El Valle, Cerro Gaital; 850 m a.s.l.; Jun. 2008; Daniel Curoe leg.; Teneb_base 23369; AAAG • 1 spec.; Bocas d. Toro Prov. Tank Hill, 5 km S of Chiriqui Grande; 750 m a.s.l.; 1 Aug. 1997; A.R. Gillogly leg.; Teneb_base 23370; AAAG • 1 spec.; Cerro Jefe road to Altos de Pacora; 894 m a.s.l.; 9°13.34' N, 79°22.26' W; 18 Aug. 2008; A.D. Smith leg.; Teneb_base 18780; ADSC • 1 spec.; Cerro Jefe summit, Panama Prov.; 8–10 May 1985; F.T. Hovore leg.; Teneb_base 22950; CASC • 3 specs; Cerro Jefe; 700–800 m a.s.l.; 26 Oct 1969; B. Malkin leg.; Teneb_base 23356 to 23358; FMNH • 1 spec.; Rio Changena Bocas del Toro R.PAN; Sep. 1961; G.B. Fairchild leg.; Teneb_base 23322; MCZ.

Description

MEASUREMENTS. Length 26–33 mm, width 9–11 mm, specimens measured (n = 12).

HEAD. Medial edge of mandibles without tooth, inner margin without crenulation. Galea with cluster of bristles situated near midpoint. Mentum weakly sculptured, apex with medial notch; lateral apices rounded. Supraorbital tubercles present; height greater than width. Clypeal horn straight to weakly arced (in lateral view); ending in three, raised blunt points.

Distribution

Central America: Panama (Fig. 7).

Phrenapates latreillei Lacordaire, 1859
Figs 2E, 3G, 4G–H, 6–7, 9A, 17

Phrenapates latreillei Lacordaire, 1859: 315.
Phrenapates mandibularis Gebien, 1910: 504. **Syn. nov.**

Diagnosis

Phrenapates latreillei has no supraorbital tubercles, separating it from *P. bennettii*, *P. ohausi*, *P. gilloglyi* Rincon & Smith sp. nov. and *P. fortunaensis* Rincon & Smith sp. nov. The horn of *P. latreillei* (Fig. 3G) differs from the unique form of *P. dux* (Fig. 3D). *Phrenapates latreillei* (as well as *P. educator*) can usually be separated from *P. dux* (length 27–36 mm) as sizes range from 18–28 mm. The closest species morphologically to *P. latreillei* is *P. educator*. *Phrenapates latreillei* has a horn with a stronger arc than *P. educator* (Fig. 3G–H, respectively). Additionally, there is a tooth on the mandible which is absent in *P. educator*. The mentum has stronger paramedial ridges and a deeper medial excavation in *P. latreillei* vs the less sculptured mentum in *P. educator*. Though not always consistent, the apex of the labrum is often more convex in *P. latreillei*, whereas it tends to be straight/slightly concave in *P. educator*.

Type material

Holotype [*Phrenapates mandibularis* **syn. nov.**]
COLOMBIA • ♂; (green label) "00; // *Phrenapates* / *mandibularis* / X Geb // (red label) Type / No. 165 // Sammlung / H Gebien // (blue label) Tenebrionid Base / Aaron D. Smith / Catalog # 23167"; Teneb_base 23167; NHMB.

Lectotype (designated here)
COLOMBIA • ♂; (green rectangle label) "*Phrenapates* / *Latreillei* Dj / Columbia [N J Les] // (green circle label) [unintelligible] / *Latreillei* Dej / Columb / [unintelligible]"; MNHN.

Other material examined

BRAZIL • 1 spec.; Roraima; Whiteley; 6000 m a.s.l.; Teneb_base 23279; MNHN.

COLOMBIA • 1 spec; s. loc.; Teneb_base 23278; MNHN • 2 specs; s. loc.; Teneb_base 23276 to 23277; repository unknown.

PANAMA • 36 specs; Darien Prov. Cana, Pirre Trail; 1560 m a.s.l.; 5 Jun. 1996; A.R Gillogly leg.; Teneb_base 23246, 22740 to 22746, 22764 to 22780, 22798 to 22808; AAAG • 10 specs; Darien Prov. Cana, Pirre Ridge; 1650 m a.s.l.; 7°45.825' N, 77° 43.325' W; 5 May 2008; A.R Gillogly and M. Seid leg.; Teneb_base 23247, 22730 to 22738; AAAG • 1 spec.; Bocas d. Toro Prov., 3 km N of Cont. Div. Trail, Fortuna Hwy; 950 m a.s.l.; 13 Jul. 1996; A.R. Gillogly leg..; Teneb_base 22739; AAAG.

PERU • 1 spec.; Satipo, Jauja Prov.; Nov. 1945; Teneb_base 23211; AMNH.

UNKNOWN LOCATION • 7 specs; s. loc; Teneb_base 23203 to 23207, 23209 to 23210; FMNH • 1 spec.; s. loc.; Teneb_base 23208; MCZ.

Fig. 17. *Phrenapates latreillei* Lacordaire 1859, lectotype, ♂ (MNHN), lateral view (top), ventral view (middle), and dorsal view (bottom).

Redescription

MEASUREMENTS. Length 18–28 mm, width 6–9 mm, specimens measured (n = 20).

HEAD. Medial edge of mandibles with additional tooth, inner margin without crenulation. Galea with cluster of bristles situated near midpoint. Mentum strongly sculptured, apex with medial notch; lateral apices produced. Clypeal apex not dilated. Supraorbital tubercles absent. Clypeal horn strongly arced (in lateral view); gradually tapering to sharp point.

Status

The name *Phrenapates latreillei* was made available by Lacordaire (1859). A specimen matching his provided locality and description was found in the MNHN. As Lacordaire (1859) did not specify the number of studied specimens, only indicating their plural form, a lectotype designation is needed to stabilize the concept of this species. A specimen of the presumed syntype series from MNHN is here designated as a lectotype (see label data above).

Investigation of the type material and available descriptions revealed that the morphology of Gebien's (1910) *Phrenapates mandibularis* is fully in line with the concept of *P. latreillei*. As such, *P. mandibularis* is hereby treated as a junior synonym of *P. latreillei*.

Distribution

Central America: Panama; South America: Brazil, Colombia, Peru (Fig. 7).

Phrenapates ohausi Gebien, 1910
Figs 2H, 3A, 4I–J, 6, 8A–B, 9H, 10B, 18

Phrenapates ohausi Gebien, 1910: 503.

Diagnosis

Phrenapates ohausi can be separated from all other known congeners based on the following characters: large (28–39 mm), generally not overlapping in size with the smaller species *P. latreillei, P. educator, P. erratus* Rincon, Lumen & Kamiński nom. nov. (18–28 mm). In *P. ohausi* the clypeal horn is thick and arced to an abrupt point (Fig. 3A), the horn of *P. latreillei* is thinner and tapers gradually from the base. Mandible without crenulation, unlike *P. bennettii* and *P. fortunaensis* Rincon & Smith sp. nov. Supraocular tubercles present, taller than wide (Fig. 8A–B), unlike in *P. bennettii* and *P. fortunaensis* (Fig. 8C–D), though not as tall as in *P. gilloglyi* Rincon & Smith sp. nov. (Fig. 8E–F). Mentum with apical notch that is deeper (Fig. 2F) than that of *P. bennettii* (Fig 2A).

Type material

Lectotype (designated here)
ECUADOR • ♂; (green label) "W. Ecuador / Pucay 300m / (Ohaus) / 7.II.1908 // 1 // *Phrenapates* / *Ohausi* / X Geb // (red label) Cotype! / No. 162 // (on circle yellow border) Paratype // *Phrenapates* / *ohausi* Geb / Det.H.Kulzer 1960 // Sammlung / H Gebien // Brit. Mus. / 1961–329 // (blue label) Tenebrionid Base / Aaron D. Smith / Catalog # 22810"; Teneb_base 22810"; BMNH.

Other material examined

ECUADOR • 2 specs; S. Domingo DLC; Mar. 1983; Teneb_base 23212 to 23213; CASC • 1 spec.; Balzapampa Route de Quita, Prov. de Bolivar; Sep.–Oct. 1893; M. de Mathan leg.; Teneb_base 23280; MNHN • 1 spec.; Chimbo; 1892; M. de Mathan leg.; Teneb_base 23284; MNHN • 3 specs; Quito Cap

D'Espinay; 1922; Teneb_base 23281 to 23283; MNHN • 1 spec.; [Bucay]; [1] Nov. 1905; F. Ohs leg.; Teneb_base 23182; NHMB • 3 specs; [Bucay]; 300 m a.s.l.; 31 Oct. 1905; Ohaus leg.; Teneb_base 23165, 23176, 23181; NHMB.

Redescription

Measurements. Length 28–39 mm, width 11–12 mm, specimens measured (n = 6).

Head. Medial edge of mandibles without tooth, inner margin without crenulation. Galea with cluster of bristles situated near midpoint. Mentum weakly sculptured, apex with medial notch; lateral apices rounded. Clypeal apex not dilated. Supraorbital tubercles present; height subequal to width. Clypeal horn arced (in lateral view); thick, tapering to abrupt point.

Status

While the original description does not provide a specific number of specimens examined; it does indicate that there were multiple individuals by providing a size range. Therefore, we designate here a lectotype from the presumed syntype series.

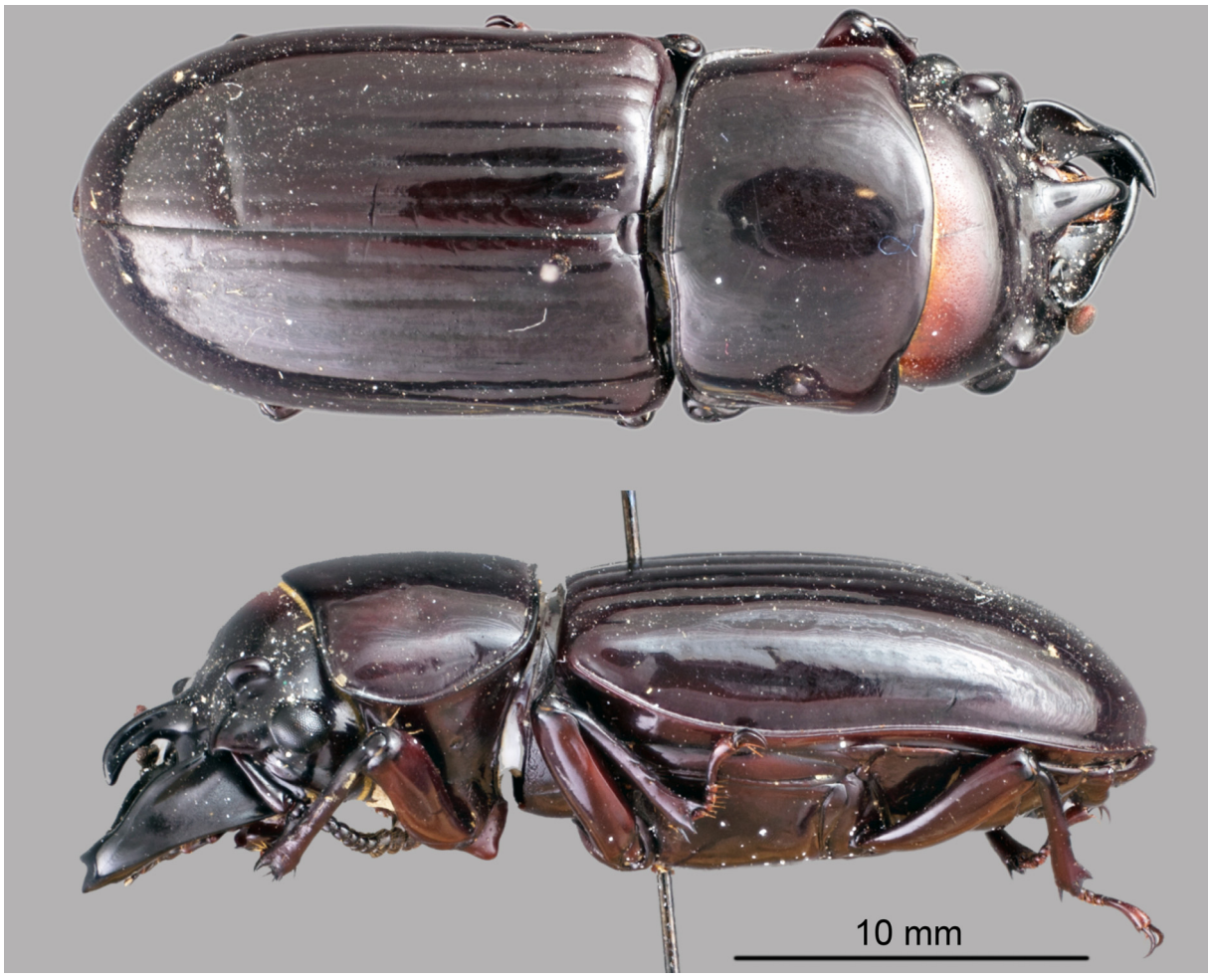

Fig. 18. *Phrenapates ohausi* Gebien 1910, lectotype, ♂ (Teneb_base 22810, BMNH), dorsal (top), lateral (bottom) views, and head (right).

Distribution

South America: Ecuador (Fig. 6).

Discussion

As of this revision, the current species of the genus *Phrenapates* are as follows: *P. bennettii* Gray, 1832, *P. dux* Gebien, 1910, *P. educator* Gebien, 1910, *P. erratus* Rincon, Lumen & Kaminski nom. nov., *P. fortunaensis* Rincon & Smith sp. nov., *P. gilloglyi* Rincon & Smith sp. nov., *P. latreillei* Lacordaire, 1859, *P. ohausi* Gebien, 1910.

All morphological differences found in this revision of *Phrenapates* are concentrated on the head (Figs 2–3, 8). In particular, the armature of the head (supraorbital tubercles and clypeal horns) differed between most species (presence / absence of supraorbital tubercles and shape of clypeal horns). The wide diversity of armature morphology may be related to ecological or ethological factors (e.g., resource defense / acquisition), and may therefore be subject to other selection pressures resulting in variation between species. For example, passalids (which occupy similar niches and exhibit similar behavior) are known for fighting behavior towards intruders of their galleries (Watt 1974; Nguyen *et al.* 2006; Wicknick & Miskelly 2009). The thorax and abdomen appear to be adapted for subcortical living, and characters such as the spines on the tibiae vary widely within species. Though Gebien (1911) illustrated the aedeagi for *Phrenapates bennettii*, *P. dux*, *P. educator* and *P. ohausi*, the only character he mentioned for the delineation of species was the median lobe in *P. ohausi* (does not extend past the parameres); however, even in the illustration he provides (Gebien 1911; Fig. 18), the median lobe protrudes slightly past the parameres.

Additionally, female terminalia of *Phrenapates* did not have any diagnostic characters at the species level. All species have a simplified reproductive tract with a rudimentary, partly sclerotized ovipositor (Fig. 5). Ovipositor reduction could be related to life history; subsocial beetles living within galleries may not need to inject eggs into substrate and may exhibit behavior to accommodate laying eggs freely within galleries. For instance, passalid beetles are known to lay eggs throughout the gallery for a time before gathering them up into a chamber with nests made of frass (Matthews & Seeman 2019). Study of male terminalia also failed to produce any phylogenetically informative characters for a determination of the species. The genus has long, terminally rounded, untapered parameres (basal portion subequal in length) with an often apically exposed median lobe. Gebien (1911) outlined subtle differences in his hand drawings of the type material; however, characters such as setae on the ends of the parameres are variable, and they are extremely prone to wear, making it difficult to establish presence or absence.

Phrenapates is distributed in Central and South America (Figs 6–7); *Phrenapates bennettii* has the largest range of species, from Guatemala to Bolivia. Interestingly, there are some species (*P. ohausi*, *P. educator)* seemingly limited to Ecuador (Fig. 6). It is possible these Ecuadorian taxa may have speciated in the various cloud forests of the area, known for being areas of endemism and refuges (Still *et al.* 1990; Bubb 2004). Some species have overlapping ranges within cloud forests in Ecuador such as the Bellavista Cloud Forest Reserve; however, their morphological differences are relatively coarse (e.g., clypeal horn shape, presence / absence of supraorbital tubercles). The new species *P. gilloglyi* Rincon & Smith sp. nov. and *P. fortunaensis* Rincon & Smith sp. nov. are both limited to Panama based on current records (Fig. 7). Very little material gathered in this revision was from eastern South America (e.g., Brazil), the potential for undiscovered species is high.

Taxonomic status of *Phrenapates latreillei* Lacordaire, 1859

Phrenapates latreillei was attributed to Dejean by both Lacordaire (1859) and Gebien (1911). However, confusingly, Gebien (1910) also provided a diagnosis for *P. latreillei* as a new species. Clarifying the

authorship of the species is important, as subsequent publications including the genus (e.g., Ascuntar-Osnas *et al.* 2023) may attribute names to Gebien (1911), compounding errors and making a delineation of species dubious or difficult. Upon closer examination of specimens, and a review of the literature, the attribution of this name to Dejean is not valid. Further, attributions to Gebien (1910, 1911) are also problematic, as Gebien's 1910 publication specifically provides diagnoses for new species (*P. ohausi*, *P. latreillei*, *P. mandibularis*, *P. educator*) in preparation for a treatment in a later publication (i.e., Gebien 1911). Though Gebien (1911) provides additional details (e.g., illustrations and geographical information) and lists the new species as sp. nov., his 1910 publication claims the authorship for the taxa. Lacordaire, in his 1859 publication, provides enough detail to qualify as a description for *P. latreillei*, which makes the name available under his authorship before either of Gebien's treatments (1910, 1911). Finally, Gebien's material for *P. mandibularis* matches the Lacordaire concept for *P. latreillei* which, therefore, leaves Gebien's concept for *P. latreillei* represented by a single specimen with no name. Though just a singleton, the specimen is diagnoseable from its most morphologically similar species (*P. educator*). As such, we provided a name for this specimen (*P. erratus* Rincon, Lumen & Kaminski nom. nov.).

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References

Ascuntar-Osnas O., López Bedoya P., Smith A. & Girón Duque J. 2023. State of knowledge of the Tenebrionidae (Insecta: Coleoptera) in Colombia based on bibliographic revision. *Caldasia*. 45. https://doi.org/10.15446/caldasia.v45n3.104445

Bouchard P. 2019. Descriptions of pupae of the darkling beetle subfamily phrenapatinae (Coleoptera: Tenebrionidae), *Annales Zoologici* 69 (1): 173–189. https://doi.org/10.3161/00034541ANZ2019.69.1.013

Bouchard P., Bousquet Y., Aalbu R.L., Alonso-Zarazaga M.A., Merkl O. & Davies A.E. 2021. Review of genus-group names in the family Tenebrionidae (Insecta, Coleoptera). *ZooKeys* 1050: 1–633. https://doi.org/10.3897/zookeys.1050.64217

Bubb P., May I., Miles L. & Sayer J. 2004. *Cloud Forest Agenda*. United Nations Environment Programme (UNEP) World Conservation Monitoring Centre, Cambridge, UK. Available from https://digitallibrary.un.org/record/515058?v=pdf [accessed 30 Jul. 2025].

Doyen J.T. 1966. *The Skeletal Anatomy of Tenebrio molitor (Coleoptera: Tenebrionidae)*. Entomological Society of America. https://doi.org/10.4182/SJQB3340.5-3.103

Doyen J.T. & Lawrence J.F. 1979. Relationships and higher classification of some Tenebrionidae and Zopheridae. *Systematic Entomology* 4: 333–377. https://doi.org/10.1111/j.1365-3113.1979.tb00619.x

Gebien H. 1910. Diagnosen neuer Arten von *Phrenapates*. *Deutsche Entomologische Zeitschrift* 5: 503–504. https://www.biodiversitylibrary.org/page/35571828

Gebien H. 1911. Die Gattung *Phrenapates* Kirby (Col.). *Deutsche Entomologische Zeitschrift* 2: 149–161. https://www.biodiversitylibrary.org/page/33104809

Gemminger M. & Harold E. 1870. *Catalogus Coleopterorum Hucusque Descriptorum Synonymicus et Systematicus. Tom. VII. Tenebrionidae, Nilionidae, Pythidae, Melandryidae, Lagriidae, Pedilidae, Anthicidae, Pyrochroidae, Mordellidae, Rhipidophoridae, Cantharidae, Oedemeridae*: 1801–2179. E.H. Gummi, Monachium [= München].

Griffith E. & Pidgeon E. 1832. *The Class Insecta Arranged by the Baron Cuvier, With Supplementary Additions to Each Order. And Notices of New Genera and Species by George Gray, Esq. Volume the second*. Whittaker, Treacher, and Co., London, UK.

Iwan D. & Kamiński M.J. 2016. Toward a natural classification of opatrine darkling beetles: comparative study of female terminalia. *Zoomorphology* 135 (4): 453–485. https://doi.org/10.1007/s00435-016-0328-5

Iwan D. & Raś M. 2020. Description of new Archaeoglenini Watt, 1974 Taxa (Tenebrionidae: Phrenapatinae), with application of non-destructive Micro-CT techniques. *Annales Zoologici* 70 (4): 775–792. https://doi.org/10.3161/00034541ANZ2020.70.4.018

Iwan D., Kamiński M.J. & Raś M. 2015. Amphi-Indian Ocean disjunction in the Trans-Pacific genus *Archaeoglenes* Brown (Coleoptera: Tenebrionidae: Phrenapatinae): new taxonomic and distributional data. *The Coleopterists Bulletin* 69 (mo14): 152–166. https://doi.org/10.1649/0010-065X-69.mo4.152

Iwan D., Schawaller W. & Kamiński M.J. 2023. Taxonomy of the *Archaeoglenes biroi* species-group (Tenebrionidae: Phrenapatinae: Archaeoglenini) with a description of the new species from the Moluccas. *Annales Zoologici* 73 (3): 529–534. https://doi.org/10.3161/00034541ANZ2023.73.3.015

Jiang R.X, Wang J.S., & Wang S. 2020. Discovery of the genus *Dioedus* LeConte, 1862 from China, with description of a new species (Coleoptera: Tenebrionidae). *Zootaxa* 4860 (1): 129–134. https://doi.org/10.11646/zootaxa.4860.1.7

Kirby W. 1837. *Fauna Boreali-Americana; or the Zoology of the Northern Parts of British America: Containing Descriptions of the Objects of Natural History Collected on the Late Northern Land Expeditions, Under Command of Captain Sir John Franklin, R.N. By John Richardson, assisted by William Swainson, and the Reverend William Kirby. Illustrated by Several Coloured Engravings. Published Under the Authority of the Right Honourable the Secretary of State for Colonial Affairs*. Josiah Fletcher, Norwich, UK.

Lacordaire T. 1859. *Histoire Naturelle des Insectes. Genera des Coléoptères, ou Exposé Méthodique et Critique de Tous les Genres Proposés Jusqu'ici Dans cet Ordre d'Insectes. Tome Cinquiéme, Premiére Partie*. Librairie Encyclopédique de Roret, Paris, France. https://doi.org/10.5962/bhl.title.8864

Matthews E.G. & Seeman O.D. 2019. 24. Passalidae Leach 1815. *In*: Slipinski A. & Lawrence J.F. (eds) *Australian Beetles. Volume 2. Archostemata, Myxophaga, Adephaga, Polyphaga (Part)*: 377–386. CSIRO publishing, Clayton South VIC, Australia.

Matthews E.G., Lawrence J.F., Bouchard P., Steiner W.E. & Ślipiński S.A. 2010. Tenebrionidae Latreille, 1802. *In*: Leschen R.A.B., Beutel R.G. & Lawrence J.F. (eds) *Handbook of Zoology. Volume IV, Arthropoda: Insecta. Part 39. Coleoptera, Beetles. Volume 2: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)*: 574–659. Walter de Gruyter, Berlin, Germany. https://doi.org/10.1515/9783110911213.574

Nguyen N.H., Suh S.O., Marshall C.J. & Blackwell M. 2006. Morphological and ecological similarities: wood-boring beetles associated with novel xylose-fermenting yeasts, *Spathaspora passalidarum* gen. sp. nov. and *Candida jeffriesii* sp. nov. *Mycological Research* 110: 1232–1241. https://doi.org/10.1016/j.mycres.2006.07.002

Ohaus F. 1909. Bericht über eine entomologische Studienreise in Südamerika. Entomologischer Verein in Stettin. *Entomologische Zeitung* 70 (1): 73–74. https://www.biodiversitylibrary.org/bibliography/8641

Rosas-Ramos N., Mas-Peinado P., Gil-Tapetado D., Recuero E., Ruiz J.L. & García-París M. 2020. Catalogue, distribution, taxonomic notes, and conservation of the Western Palearctic endemic hunchback beetles (Tenebrionidae, Misolampus). *ZooKeys* 963: 81–129. https://doi.org/10.3897/zookeys.963.53500

Schawaller W. & Bouchard P. 2019. New taxa of Phrenapatinae (Coleoptera: Tenebrionidae) from Southern Africa, with new distributional data and a checklist of the Afrotropical fauna. *Annales Zoologici* 69 (1): 191–200. https://doi.org/10.3161/00034541ANZ2019.69.1.014

Schuster J. & Schuster L. 1985. Social behavior in passalid beetles (Coleoptera: Passalidae): cooperative brood care. *Florida Entomologist* 68: 266–272. https://doi.org/10.2307/3494359

Schuster J. & Schuster L. 1997. The evolution of social behavior in Passalidae (Coleoptera). *In*: Choe J.C. & Crespi B. (eds) *The Evolution of Social Behavior in Insects and Arachnids*: 260–269. Cambridge University Press, Cambridge, USA. https://doi.org/10.1017/CBO9780511721953.013

Solier A.J. 1834. Essai d'une division des Coléoptères Hétéromères, et d'une monographie de la famille des Collaptèrides. *Annales de la Société entomologique de France* 3: 479–636.

Still C.J., Foster P.N. & Schneider S.H. 1999. Simulating the effects of climate change on tropical montane cloud forests. *Nature* 398: 608–610. https://doi.org/10.1038/19293

Tschinkel W.R. & Doyen J.T. 1980. Comparative anatomy of the defensive glands, ovipositors and female genital tubes of tenebrionid beetles (Coleoptera). *International Journal of Insect Morphology and Embryology* 9 (5–6): 321–368. https://doi.org/10.1016/0020-7322(80)90009-4

Watt J.C. 1974. A revised subfamily classification of Tenebrionidae (Coleoptera*). New Zealand Journal of Zoology* 1 (4): 381–452. https://doi.org/10.1080/03014223.1974.9517846

Wicknick J.A & Miskelly S.A. 2009. Behavioral interactions between non-cohabiting bess beetles, *Odontotaenius disjunctus* (Illiger) (Coleoptera: Passalidae). *The Coleopterists Bulletin* 63 (1): 108–116. https://doi.org/10.1649/0010-065X-63.1.108

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