



New species and revalidations of scarab beetles (Coleoptera: Geotrupidae: Athyreini and Coleoptera: Scarabaeidae: Scarabaeinae) from Costa Rica and Panama

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Abstract

The following new species of geotrupids and scarabs from Costa Rica and Panama are described: *Athyreus gulesseriani* **new species**, *Ateuchus alutacius* **new species** (the first recorded brachypterous *Ateuchus* species), *Coprophanaeus gephyra* **new species**, *Deltochilum acanthus* **new species**, and *Onthophagus turgidus* **new species**. The following two species of *Coprophanaeus* are revalidated: *C. kohlmanni* Arnaud and *C. uhleri* Malý & Pokorný. Illustrations of the dorsal habitus of the new species are provided, as well as distribution maps for all species.

Key words: Coleoptera, Geotrupidae, Scarabaeidae, *Ateuchus*, *Athyreus*, *Coprophanaeus*, *Deltochilum*, *Onthophagus*, new species, revalidation, Costa Rica, Panama

Introduction

During the last 20 years, the National Biodiversity Institute (INBio) in Costa Rica has been conducting an extensive nationwide insect survey, as well as having participated in some limited collecting on the Panamanian side of the border. Collections from these surveys have yielded five new beetle species of a geotrupid belonging to the genus *Athyreus* MacLeay and scarabs belonging to the genera *Ateuchus* Weber, *Coprophanaeus* Olsoufieff, *Deltochilum* Eschscholtz, and *Onthophagus* Latreille. The two following species of *Coprophanaeus*, *C. kohlmanni* and *C. uhleri*, are also revalidated.

Measurements were made to the nearest 0.1 mm using an ocular micrometer. The holotypes, allotypes, and paratypes of *Athyreus gulesseriani* and *Deltochilum acanthus*, and the holotype of *Ateuchus alutacius* are deposited in the INBio collection in Santo Domingo de Heredia, Costa Rica. The holotype of *Onthophagus turgidus* and the Panamanian paratypes of *D. acanthus* are deposited at the Invertebrate Museum of the University of Panama (MIUP). The holotype, allotype, and paratypes of *Coprophanaeus gephyra* are deposited in the Canadian Museum of Nature, Ottawa.

Athyreus gulesseriani Kohlmann & Solís, new species

Figs. 1–3, 13

Diagnosis. This species is distinguished from other *Athyreus* species by the following combination of characters: body extremely pilose (Fig. 1–2); males have a central pronotal horn nearly vertical, tapering to a slender, slightly tricuspid apex (Figs. 1, 3a); anterior and posterior base of horn impunctate; posterior to horn a shallow depression is present, with a mid-line of sparse setae running from the pronotal base to the mid-depression. Clypeal horn nearly vertical, slender, and longer than pronotal horn, with distinct anterior and lateral carinae (Figs. 1, 3a), posterior carina running from base to horn mid-height. Females almost impossible to separate from related species: pronotum as in figure 2, with the carina beside the median swelling forming an inverted “U”; lateral margin posterior to median angle slightly arcuate, curving lightly inward anterior to elytral humerus.

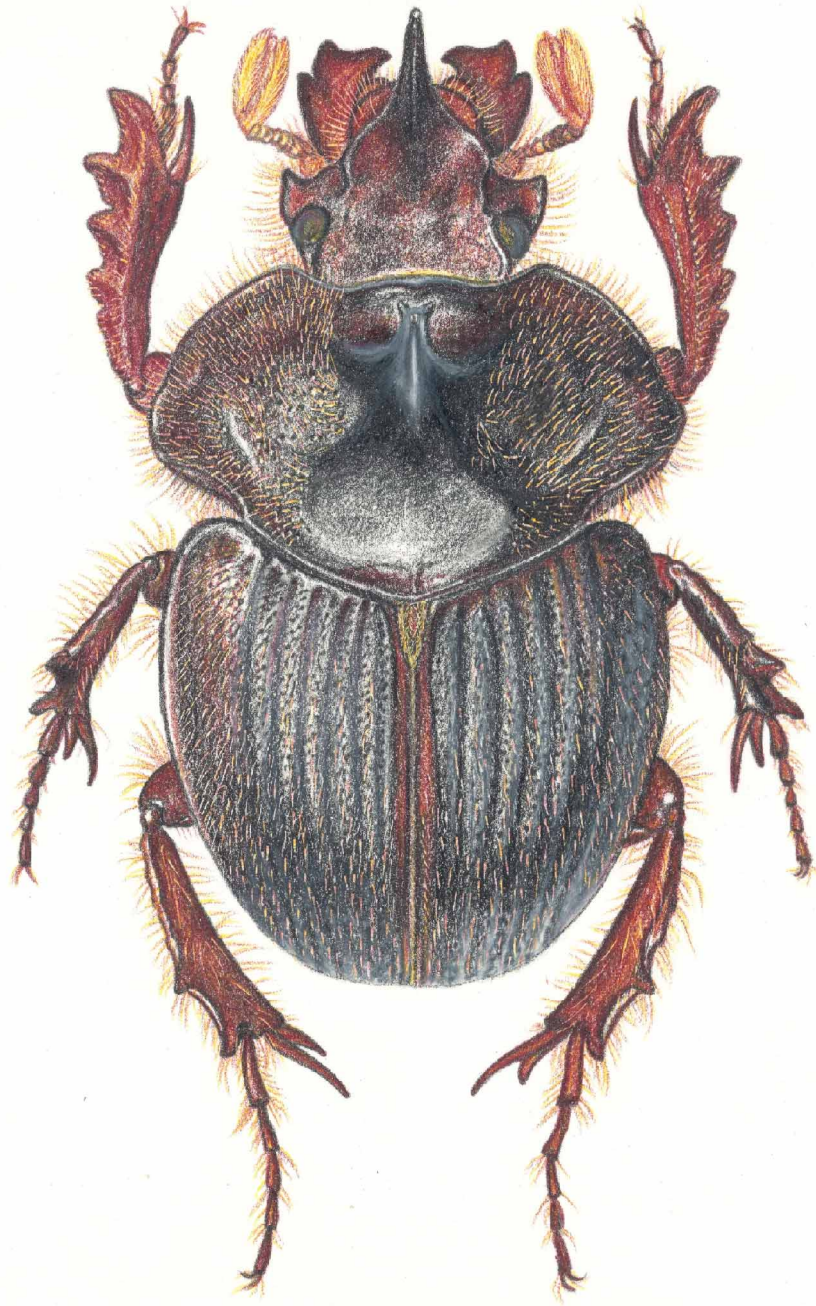


FIGURE 1. Dorsal habitus of the male holotype of *Athyreus gulesseriani* Kohlmann & Solís, new species.

Athyreus gulesseriani would key out to *A. championi* in Howden & Martínez's (1978) key. The males of *A. gulesseriani* can be easily separated from the males of *A. championi*, a very similar species, by the form of the pronotal horn (Fig. 3), which is very fine and slender in *A. gulesseriani* (Fig. 3a), whereas it is shorter and broader (Fig. 3b) in *A. championi*. Females of both species are indistinguishable.

Description. Holotype. Male (Figs. 1, 3a): Length 17.5 mm. Humeral width 10.2 mm. Body oblong and convex, color dorsally black, dorsal surface shagreened. Labrum and mandibles reddish brown.

Head with erect clypeal horn; anterior edge of horn arising from anterior clypeal margin; horn triangular in shape, sharp in front and bifurcating near anterior base into two carinae; carinae extending into proximate anterior angles. Posterior surface of clypeal horn flattened and faintly carinate from base to horn mid-height; basally, on each side of horn, a carina extending to gena (Figs. 1, 3a). Surface of frons concave, centrally impunctate with scattered punctures laterally. Vertex concave and impunctate.

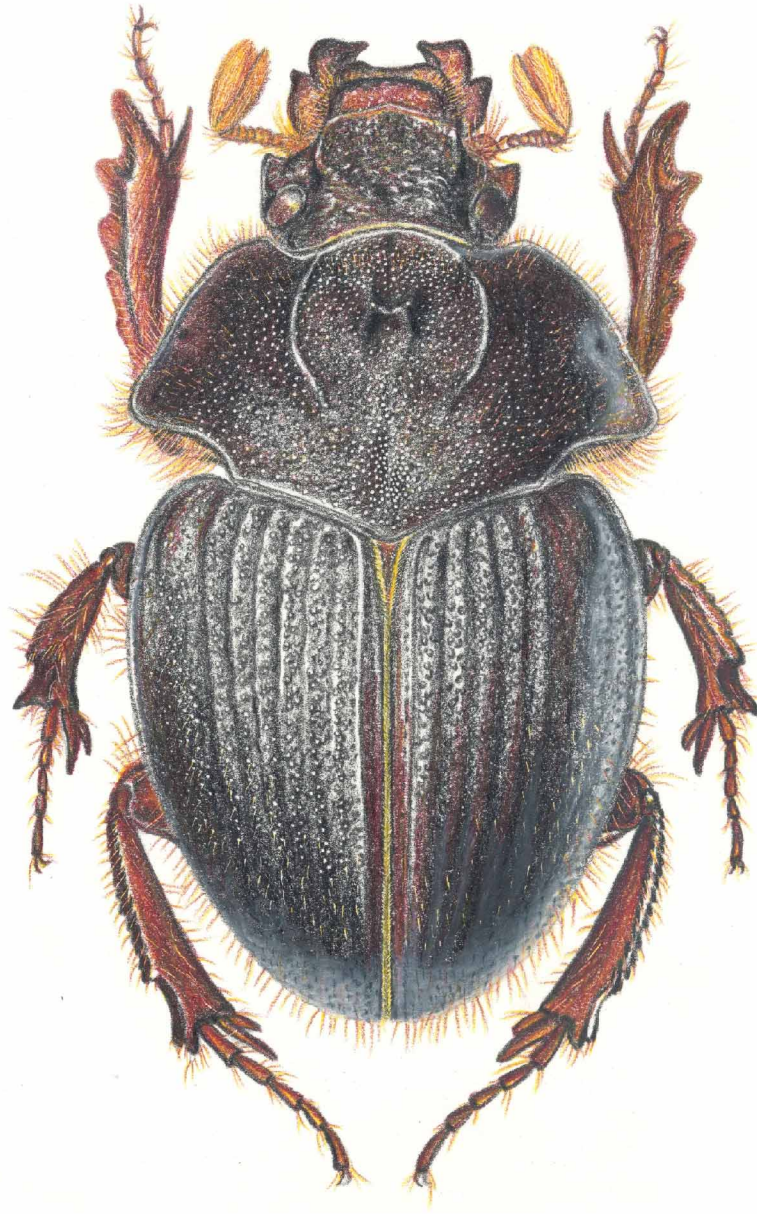


FIGURE 2. Dorsal habitus of the female allotype of *Athyreus gulesseriani* Kohlmann & Solís, new species.

Disc of pronotum with conspicuous, long, central, horn, tapering to a slender, almost trifurcate point; posterior projection of horn higher than two anterior projections (Figs. 1, 3a). Surface of pronotum concave, smooth, and impunctate in anterior and posterior area of horn; finely setose-granulate laterally. Carina on either side of central horn small but evident. Lateral pronotal margin in front of median angle slightly sinuate.

Elytra with striae indicated by seven shallow, biserially to quatriseserially punctate-setose longitudinal depressions; intervals between depressions glabrous, smooth, and weakly shiny; granular punctures only at elytral lateral borders; majority of setae arising from the strial punctures short and semierect, but occasionally long, erect setae (flying setae) intermixed.

Pygidium wider than long with a notch at its apex. Metasternum in front of mesocoxae forming a sharply pointed spine. Protibia with five teeth; ventrally rough and with distinct carina running down onto base of apical tooth.

Allotype. Female (Fig. 2). Length 16 mm. Humeral width 10.5 mm. Similar to male, but unarmed, clypeus with sharp, arcuately raised, transverse carina anteriorly, clypeal surface in front of carina with some large, setose punctures; surface behind carina distinctly, irregularly rugose or punctate. Clypeus transversally divided by tridentate carina; middle tubercle of carina more anterior than lateral ones, normally more elongate than lateral tubercles.

Posterior clypeal area distinctly punctate-serrate, punctures with small granules at anterior margins. Frons anteriorly setose-granulate and setose-punctate posteriorly. Pronotum with central, shiny, shallowly bifurcate protrusion (Fig. 2); on either side of central protrusion, and joining anterior pronotal margin, a distinct carina forms an inverted “U” around median projection; distinct oval depression present medially, just behind anterior margin; mid-line shallowly, distinctly depressed near posterior margin; on each side posteriorly, between U-shaped carina and posterior lateral pronotal margin, an indistinct, short, slightly elevated carina occupying the same position as in the male. Pronotum dull, except for shiny median swelling and carinae. Elytra similar to those described in the male. Pygidium broadly arcuate and much shorter than the male. Protibia as in male, except for additional very small sixth tooth evident basally.

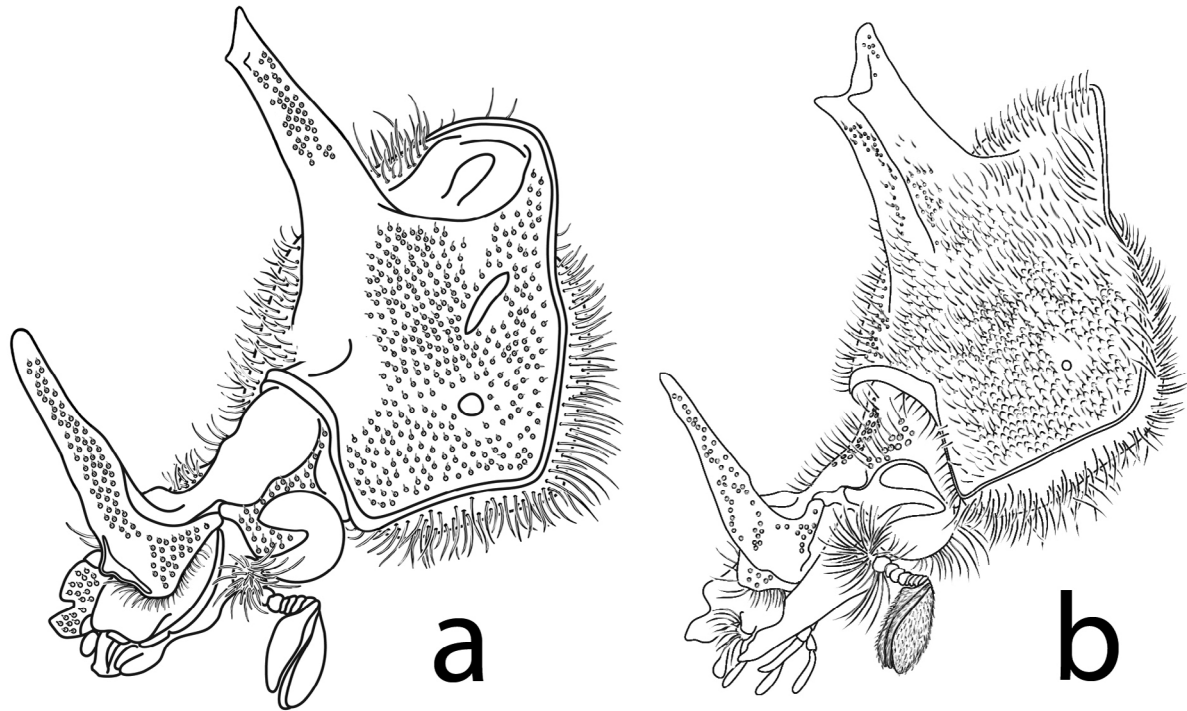


FIGURE 3. a. Side view of a male head and pronotum of *Athyreus gulesseriani* Kohlmann & Solís, new species; b. Side view of a male head and pronotum of *Athyreus championi* Bates.

Variation. Fifty-two specimens examined, 43 males and nine females. Length 14–19 mm. Humeral width 8.5–11 mm. Less developed males tend to have the central head area, as well as the anterior and posterior depressed pronotal horn area covered with setae, not smooth as in developed males, thus resembling females of the species in this characteristic. Size variation is evident by observing the differences in male horn length, going from individuals with just a slight bump, to individuals with very well developed horns (Fig. 3a). There is a wide variety of horn sizes, but preliminary analysis indicates no allometric horn size-body length variation exists.

Examined material (52 specimens). **Holotype**, male: COSTA RICA. Prov. Limón. R. B. Hitoy Cerere. Est. Hitoy Cerere, Send Espavel. 300 m. 21–30 JUN 2000. W. Arana. Intersección L_S_401500_570200 #57105. **Allotype**, female: COSTA RICA Prov. Limón. Valle de la Estrella. R.B. Hitoy Cerere, Sendero Espavel. 300 m. 24 MAY 2000. A. López. Intersección L_S_401500_570200 #57556. **Paratypes**. COSTA RICA. Same as allotype, 1–16 NOV 1999, W. Arana, #57439, 11 males, 1 female; Prov. Limón, R.B. Hitoy Cerere, Send. Espavel, 300m. 26 JUL-05 AGO 2000. W. Arana. Intersección. L_S_570200_401500 #58216, 2 females; 22 JUN–8 JUL 2003, B. Gamboa, E. Rojas, W. Arana, L_S_401200_569800 #74455, 1 female; 16 SEPT–03 OCT 2000, W. Arana, L_N_184100_643350 #63405, 1 male; 26 May 2000, A. López, L_N_184400_643300 #62659, 1 male; COSTA RICA, Prov. Limón, R.B. Hitoy Cerere. Sendero Espavel. 220m. JUL 1998. E. Rojas. Tp. Intersección. L_S_401558_570460 #51620, 1 male; COSTA RICA, Prov. Limón, Res Biol. Hitoy Cerere, Est. Hitoy Cerere, Send Espavel. 220m. 6–13 ABR 2000. W. Arana. Intersección L_S_401558_570460 #56362, 1 male; COSTA RICA, Prov. Limón, R. B. Hitoy Cerere, Est. Hitoy Cerere, Send Espavel. 300m. 21–30 JUN 2000. W. Arana. Intersección L_S_401500_570200 #57105, 1 male; COSTA RICA. Prov. Limón, R.B. Hitoy Cerere. Sendero

Espavel. 300m. 26 MAY 2000. A. López. Intersección. L_N_184400_643300 #62659, 1 male; COSTA RICA. Prov. Limón, R.B. Hitoy Cerere, Send. Espavel, 560m, 22 JUN – 8 JUL 2003, B. Gamboa, E. Rojas, W. Arana, Tp. Intersección, L_S_401200_569800 #74455, 4 males; COSTA RICA, Prov. Limón, Est. Hitoy Cerere, 100m. 20 MAR–7 ABR 1998. E. Rojas. Tp. Intersección. L_N_184600_643400 #49937, 1 male; Valle la Estrella, R.B. Hitoy Cerere, A. C. Amistad, Prov. Limón, COSTA RICA. 100 m. Jun 1994, G. Carballo, L N 184600_643400 # 3014, 1 female; COSTA RICA, Prov. Limón, Res Biol. Hitoy Cerere, Est. Hitoy Cerere, Send Bobócara. 300m. 16 ABR 2000. W. Arana. Intersección L_N_184250_641800 #56363, 1 male; Río Sardinias, R.N.F. S. Barra del Colorado, A.C.A.C. Tortuguero, Prov. Limón, 50m. Jun 1994, F. Araya L N 291900_565900 #2998, 5 males, 1 female, same collecting information as above, but with collecting date May 1994, #2916, 1 female; Sardinias, Barra del Colorado, Prov. Limón, COSTA RICA. 15 m. 29 JUL–20 AGO 1994, F. V. Araya, L N 291500_564700 # 3159, 1 male; 06–10 DIC 1994. F. Araya, L_N_291900_565900 #4363; Talamanca, Bratsi, Watsi (Volio), 80m. 29 AGO 2002. C. Cubillo. Manual, L_S_397500_587000 #79750, 1 male; Katsi, 2.3 Km. ESE de Amubri, Prov. Limón, COSTA RICA. 70m. 13 ABR 1995. G. Gallardo, L_S_384350_581400 #4813, 2 males; Amubri, Prov. Limón, COSTA RICA. 70m. 1–22 JUN 1995. G. Gallardo, L_S_385000_578100 #5333, 2 males, 1 female; Costa Rica. Prov. Cartago, Turrialba, P.N. Barbilla, 2Km después del Río Dantas. 400m. 17–28 NOV 2000. W. Arana. Intersección. L_N_596500_217700 #60959, 1 male; Prov. Alajuela. San Carlos. Pital. Boca Tapada. Finca Sergio Murillo. 50–400m. 24 JUL 2004. B. Hernández. Tp. Intersección L_N_293857_514072 #77924, 1 male; COSTA RICA, Prov. Alajuela, Sector Colonia Palmarena, 9 Km. SO. de Bajo Rodríguez. 700m. MAR 1997. G. Carballo. L_N_245900_475900 #45517, 1 male; COSTA RICA. Prov. Alajuela. P.N. Volcán Tenorio. Albergue Heliconias, Sendero Heliconias. 700m. 17 al 28 JUN 2001. A. López. Intersección. L_N_299100_422600 #63475, 2 males; COSTA RICA. Prov. Alajuela. Upala. P.N. Volcán Tenorio. Alb. Heliconias. Send. Puentes Colgantes. 800–900m. 6–9 JUN 2006. B. Gamboa, M. Moraga. Tp. Intersección. L_N_299800_423800 #86392, 1 male; Costa Rica. Prov. Alajuela, Upala, Alb Heliconias, Send Heliconias. 700m. 23 JUN–02 JUL 2000. A. López. Intersección. L_N_422600_299100 #58553, 1 male; COSTA RICA. Prov. Alajuela. Guatuso. Est. Pilón, Send. Atta, suampo. 600–700m. 27 JUL–2 AGO 2009. J. A. Azofeifa. Tp. Intersección. L_N_299670_428001 #97678, 1 male.

Habitat. The species has been collected with flight interception traps at night, inside primary tropical rain forest at altitudes varying from 15–900 m, from April to November.

Geographical distribution (Fig. 13). This species is known from the Caribbean slope of Costa Rica and probably also occurs under similar conditions in Nicaragua and Panama. *Athyreus gulessseriani* and *Athyreus championi* are the only two species in this genus known to occur in Central America, all other species occur in South America (Howden 1964).

Chorological affinities. *Athyreus gulessseriani* seems to show a geographic vicariant pattern in relation to the similar species *A. championi* Bates (Fig. 13); the former species being distributed along the Caribbean slope and the latter species along the Pacific slope of Costa Rica and Panama (Howden 1964).

Etymology. This species is dedicated to Haig Gulesserian, brother in law of one of the authors (B.K.), and a very genteel and supportive person. The name is a patronymic, a Latinized noun in the masculine genitive case, originating from his Armenian surname, derived from “gul” (rose) and “esser” (breeze).

Ateuchus alutacius Kohlmann & Solís, new species

Figs. 4, 5, 14

Diagnosis. This species is distinguished from other Costa Rican species by the following combination of characters: body slightly globose; head disc finely punctured with coarse punctures along clypeal margin; eyes viewed from above three times longer than wide; pronotum finely punctured with some coarse punctures at the base of the mid-line and anterior angles; surface of head and pronotum smooth; anterior pronotal margin incomplete; proepisternum shagreened and finely punctured; elytra, pygidium, and abdominal sternites strongly shagreened; profemur with a smooth surface; brachypterous.

Description. Holotype. Female (Fig. 4): Length 7.1 mm. Humeral width 4.0 mm. Body oblong and slightly globose. Head and pronotum black with cupreous red reflections, elytra black, shagreened, with faint cupreous red reflections; venter dark brown, legs less so, abdominal sternites black with faint cupreous red reflections.

Clypeal margin coarsely punctate, with a broad band of strong cupreous red reflections and broadly V-shaped; tooth on each side rounded; lateral margin arcuate; dorsal surface of head finely punctate, with faint cupreous red reflections; frons and vertex tumid; eyes appear small from above (three times longer than wide).

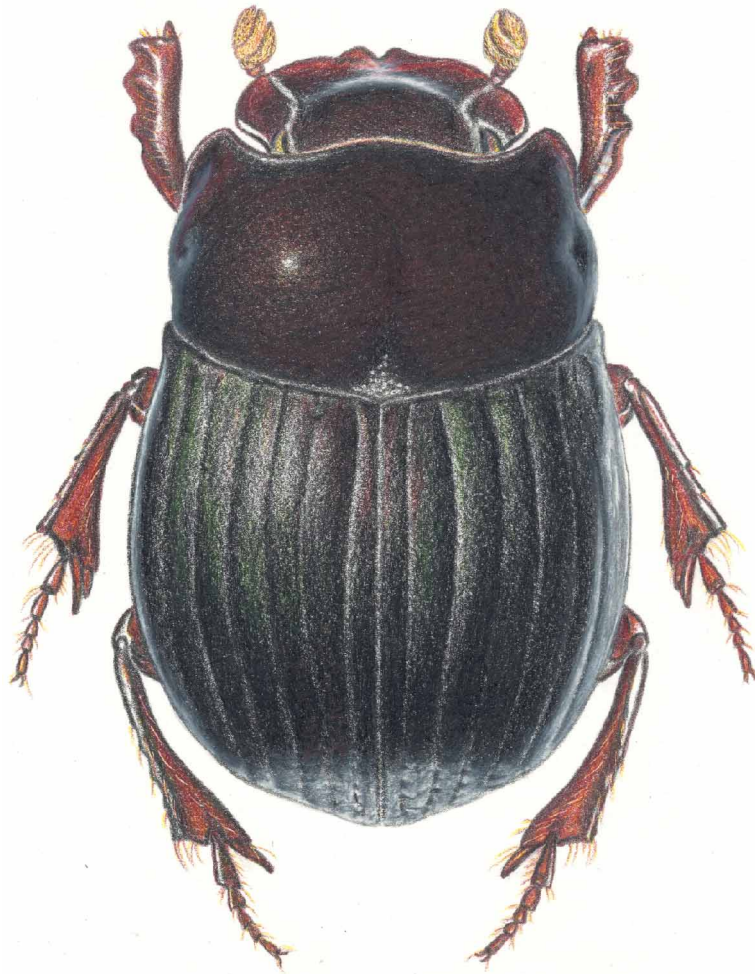


FIGURE 4. Dorsal habitus of the female holotype of *Ateuchus alutacius* Kohlmann & Solís, new species.

Disc of pronotum finely punctate with some coarse punctures at the base of mid-line and anterior angles; mid-line only impressed one-third the pronotal length; anterior pronotal margin incomplete. Proepisternum shagreened and finely punctured; proepimeron finely wrinkled.

Elytral surface strongly shagreened, with faint red cupreous reflections; striae slightly impressed and feebly punctate, more strongly impressed at the apex of the four inner striae; intervals slightly convex. Brachypterous, wing about half the size of an *A. candezei* wing (Fig. 5). Pygidium wider than long, very convex, and strongly shagreened with small reflective spots, completely grooved.

Protibia quadridentate, basal tooth small, protibial spur long and slender; profemora, mesofemora, and metafemora short, thick and with their ventral surface smooth. Abdominal sternites black, strongly shagreened; last one broad and with small reflective spots, the others with a line of coarse punctures at their base and a second incomplete line of coarse punctures near their centre.

Examined material (1 specimen). **Holotype**, female: COSTA RICA. Prov. Puntarenas. Golfito. Camino a Cerro Paraguas. Finca de Pito. 1100–1200 m. 8–10 AGO 2008. B. Hernández y M. Moraga. Tp. Foso. L_S_300700_569000 #95344. INB0004182326.

Habitat. The species has been collected with a pitfall trap at an altitude varying from 1100–1200 m, during the month of August. *Ateuchus alutacius* was collected in a cloud forest on the southern slope of the Fila Costeña, in an approximately 10 ha sized forest remnant, surrounded by cattle pasture and grasslands.

Geographical distribution (Fig. 14). This species is known from the Pacific slope of the Fila Costeña of Costa Rica.

Chorological affinities. *Ateuchus alutacius* is found at similar altitudes at the Fila Costeña as its ecological equivalents, small dung tunnellers living in cloud forests, in Guanacaste (*Ateuchus earthorum* Kohlmann & Solís, *A. fetteri* Kohlmann, and *A. hendrichsi* Kohlmann) and Central Cordillera (*A. ginae* Kohlmann) (Kohlmann 1997).

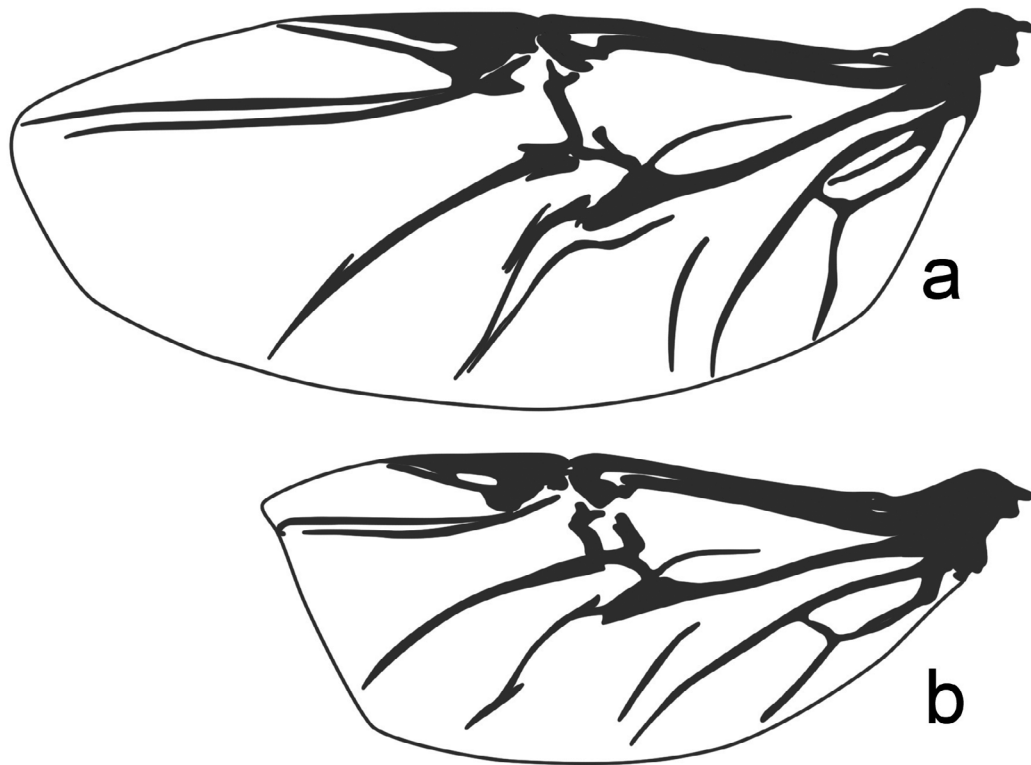


FIGURE 5. a. Dorsal view of left wing of *Ateuchus candezei*; b. Dorsal view of brachypterous left wing of the holotype of *Ateuchus alutacius* Kohlmann & Solís, new species.

This is the first brachypterous species described in the genus *Ateuchus*. It is also the fifth flightless species of Scarabaeinae recorded for Costa Rica. The other known species are: *Canthidium planovultum* Howden & Young, collected on the Pacific slopes of the Central and Talamanca Cordillera and also present in Panama (Solís & Kohlmann 2004); *Cryptocanthon lindemanae* Howden & Gill, collected on the Pacific slope of the Tilarán Cordillera in Monteverde (Cook 2002); and *Onthophagus inediapterus* Kohlmann & Solís and *Onthophagus micropterus* Zunino & Halffter, collected on the Pacific slope of the Talamanca Cordillera (Kohlmann & Solís 2001). All these species have in common that they live in mountain cloud forests, which apparently supports the theory that flightlessness increases with altitude in temperate forests in the tropics (Scholtz *et al.* 2009).

Regarding habitats, flightless dung beetles are not well represented in tropical forests (Scholtz *et al.* 2009). In Costa Rica, flightless dung beetles are associated with cloud forests in tropical mountains, not with tropical forests in the lowlands. It is argued that habitat stability is a key factor favouring the loss of flight (Roff 1990, Scholtz 2000). Following this train of thought, it would seem then that cloud forests represent such stable habitats and not the rain forests.

An analysis of species and endemism richness, reported by Kohlmann (2011), concluded that cloud forests are somewhat richer than lowland tropical rain forests in Costa Rica on both counts. This aspect contradicts Scholtz's (2000) hypothesis that flightless dung beetles occur at higher rates in temperate forests at high altitudes in the tropics, where these environments are relatively species-poor and thus lack complex biotic interactions. This is not the case for Costa Rican cloud forests, which are very species-rich.

Wagner & Lieberr (1992) present an analysis of flightlessness in insects, where it is calculated that around 10% of temperate Coleoptera species show this characteristic. Based on our current tally, 181 Scarabaeinae taxa have been listed for Costa Rica. It would seem then that the percentage of flightlessness of tropical dung beetle species in Costa Rica (2.7%) is below the percentage registered for temperate Coleoptera. This finding would seem to support the hypothesis that dung-beetle flightlessness increases with latitude (Scholtz *et al.* 2009).

Finally, Scholtz *et al.* (2009) indicate that flightless species of dung beetles tend to develop a rounded shoulder (humeral angle) and a globose body. Costa Rican flightless species are certainly globose in body shape, but they all have a sharply angled shoulder like their winged beetle counterparts. This could be probably explained by the fact that these species are of recent evolutionary origin.

Taxonomic relationships. More material is needed, especially males, and an actual phylogenetic analysis, in order to establish taxonomic relationships. Presently, and using the similar eye shape and the shagreened elytra and pygidium, the new species would seem to have a certain degree of affinity with *A. candezei* Harold. It is the only North and Central American species known so far to the authors that has shagreened abdominal sternites, as well as being the only brachypterous *Ateuchus* species described so far.

This species will key to *A. candezei* in Kohlmann's (1997) key. However, the two species are easily separated by the following combination of characters: In *A. alutacius*, both the pygidium and sternites are heavily shagreened and black in color; in *A. candezei*, only the upper part of the pygidium is shagreened, and the pygidium and the sternites are reddish brown. Additionally, the base of the thorax is not shagreened in *A. alutacius*, while the thorax base of *A. candezei* is shagreened. Finally, *A. alutacius* is brachypterous, the first recorded *Ateuchus* to show this characteristic.

With the description of this new species of *Ateuchus*, the total number of species reported from Costa Rica increases from 10 (Kohlmann & Solís 2009) to 11.

Etymology. *Alutacius*, Latin adjective in the genitive case, referring to the leathery appearance of this species.



FIGURE 6. Dorsal view of a male *Deltochilum acanthus* Kohlmann & Solís, new species.

Deltochilum acanthus Kohlmann & Solís, new species

Figs. 6, 7, 15

Diagnosis. This species is distinguished from other Costa Rican *Deltochilum* species by the following combination of characters: Pygidium with apex thickened, very acutely angled (90°) and outwardly produced (Fig. 7f). Apical half of metatibia bent inward.

Description. Holotype. Male (Fig. 6): Length 11.9 mm. Humeral width 8.0 mm. Body color black, head and pronotum distinctly punctate.

Head approximately as long as wide; clypeus with two distinct, narrowly separated, upwardly reflexed, pointed teeth, pointed anterior teeth; each clypeal-genal margin with low obtuse teeth; vertex closely punctate, nearly flat; dorsal eyes large.

Pronotum with lateral margin angulate at middle, otherwise straight to slightly sinuate before and behind; pronotal surface densely punctate, giving the appearance of a honeycomb.

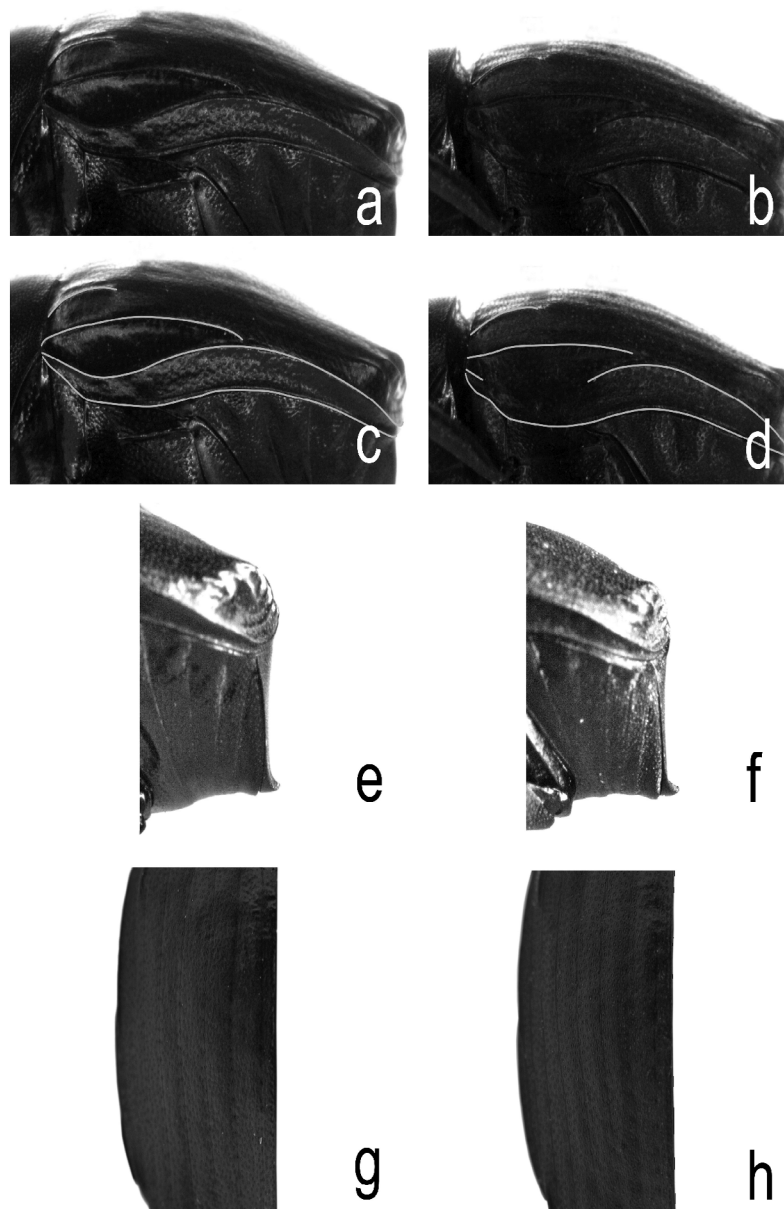


FIGURE 7. Side view of elytra (a, c) and pygidium (e) and dorsal view of left elytra (g) of *Deltochilum valgum acropyge*, and *Deltochilum acanthus* Kohlmann & Solís, new species (b, d, f, h). Carinae are delineated.

Elytral striae indicated by a double line, line expanded by widely separated, shallow strial punctures; disc intervals opaque, with numerous shallow, very close punctures (Fig. 7h); humeral umbone and apices of third to seventh intervals carinate; elytral surface shagreened. Epipleural upper carina interrupted (Figs. 7b, d).

Pygidium with apex thickened, very acutely angled and outwardly produced (Fig. 7f); disc nearly flat, shallowly and densely punctate, punctures umbilical. First abdominal sternite forms a rearward projection at the middle of the posterior border.

Profemur with margin unmodified; protibia with three apical teeth (the middle one smaller) and numerous serrations on outer margin. Apical half of metatibia bent inwardly.

Allotype. Female. Length 11.2 mm. Humeral width 7.6 mm. Similar to male, but the first abdominal sternite is evenly arched at the middle of the posterior border.

Variation. Fifty-eight specimens examined, 38 males and 20 females. Length 10.4–13.0 mm. Humeral width 7.3–8.0 mm.

Examined material (58 specimens). **Holotype**, male: COSTA RICA. Prov. Puntarenas. Res. Biol. Carara, Est., Quebrada Bonita. 50 m, jun 1993. J.C. Saborío. L-N-194500, 469850, CRI001185073. **Allotype**, female: COSTA RICA. Prov. Puntarenas. R.B. Carara, Est. Quebrada Bonita. 50 m, nov. 1993. J.C. Saborío. L S 194500_469850, #2470, CRI001969700. **Paratypes.** COSTA RICA. Prov. Puntarenas. Centro Juvenil Tropical. Alrededor de la Estación. 100m. 5–12 JUL 1997. M. Lobo. Colecta Nocturna. L_S_294700_517100 #47733, 1 female; Estación Esquinas, 0 m, Península de Osa, Abr 1993. M. Segura, L-S 301400_542200, 1 female; Estación Quebrada Bonita, 50 m, Res. Biol. Carara, 1 a 29 jul 1992, R. Guzmán, L- N 194500_469850, 1 male; Oct 1993. J. C. Saborío, L N 194500_469850 # 2396, 1 female; Set 1993. J. Saborío, L N 194500_469850 # 2354, 2 males; Nov 1993, R. Guzmán, L N 194500_469850 # 2447, 2 males; Jun 1993, R. Guzmán, L N 194500_469850 # 2202, 1 male; 2 a 23 set 1992, R. Guzmán, L-N 194500_469850, 3 males; agos 1993, R.M. Guzmán, L N 194500_469850 # 2297, 1 female; Ene 1994, R. M. Guzmán, L N 194500_469850 # 2572, 1 female; Feb 1994, R. M. Guzmán, L N 194500_469850 # 2613, 1 male; May 1994, R. M. Guzmán, L N 194500_469850 # 2914, 3 males, 1 female; Ago 1994, R. M. Guzmán, L N 194500_469850 # 3163, 1 female; Oct 1994. J.C. Saborío, Desconocido L_N_469850_194500 #3288, 1 female; Jun 1996. R. Guzmán. L_N_195250_469850 #7648, 1 male; Set 1994. R. M. Guzmán, L_N_194500,469850 #3214, 2 males, 1 female; May 1994. J. Saborío. L_N_470000_195200 #2849, 4 males, 1 female; Estación Sirena, 0–100m, P. N. Corcovado, Ago 1991, J. C. Saborío, L S 270500_508300, 1 female; G. Fonseca, Jun 1991, L- S 270500_508300, 1 male; Jun 1991, J. C. Saborío, L- S 270500_508300, 1 male; Oct 1993. G. Fonseca, L S 270500_508300 # 2380, 1 male; Jan 1990, G. Fonseca, L_S_270500_508300, 1 female; G. Fonseca, Abr 1991, L- S 270500_508300, 1 male, 1 female; G. Fonseca, Oct 1989, L- S 270500_508300, 1 female; F. Quesada, Jun 1990, L- S 270500_508300, 1 male; Refugio de Vida Silvestre Golfito, Estación Naranjales, 0 – 100m, 25 ABR 2004, W. Porras, Libre, L_S_289900_553450 #76842, 1 male; 22 – 27 ABR 2004, W. Porras, B. Gamboa, D. Briceño, M. Moraga, Amarilla, L_S_289900_553450 #76946, 2 males, 3 females; Rancho Quemado, 200 m, Península de Osa. 12 a 24 may 1993. A. Gutiérrez, L S 292500_511000, 1 male; Oct 1990. F. Quesada. L-S 292500,511000, 1 male; 11–28 Oct 1993, A. H. Gutiérrez, L S 292500_511000 # 2409, 2 males, 1 female; Río Agujas. Estación Agujas. Send. Ajo. 300m. 6–12 ENE 1998. M. Lobo. L_S_276750_526550 #49736, 1 male.

PANAMA. Canal Zone, Barro Colorado, Poscher's Peninsula, 6 jun 1986. H. Wolda, 1 male; 11 jun 1986. H. Wolda, 1 female; 18 jun 1986. H. Wolda, 1 male; 25 jun 1986, H. Wolda, 1 male; 11 sep 1987. H. Wolda, 1 male.

Habitat. The species has been collected with flight interception traps in tropical rain forest, ranging from 0–100 m altitude, during the months of April to November.

Geographical distribution (Fig. 15). This species is known so far from the Pacific rain forest of Costa Rica and the Canal Zone of Panama.

Chorological affinities. *Deltochilum acanthus* seems to show a geographic vicariant pattern in relation to the similar species *D. valgum acropyge*, which inhabits the Caribbean slope of Costa Rica.

Taxonomic relationships. It would appear that the new species originated from a vicariant event, when the Talamanca range rose up approximately 3 million years ago, isolating the rain forest on the Pacific coast from the rainforests on the Caribbean coast. This mechanism seems to account for the origin of a great number of other animal vicariant species, examined in Kohlmann & Wilkinson (2007). We believe that *D. valgum* needs to be studied, and that its different subspecies represent a species complex in need of hierarchical reevaluation. We therefore describe *D. acanthus* as a species and not as a subspecies, in anticipation of this process.

Deltochilum acanthus can be easily separated from *D. valgum* by its pygidium, which has the thickened apex, very acutely angled and outwardly produced (Fig. 7f), whereas *D. valgum* has a much less thickened and projected

pygidium (Fig. 7e). There are also differences in dorsal punctation: the pronotum in *D. acanthus* is very densely punctured, producing the effect of a honeycomb, whereas in *D. valgum* the punctures are more spaced, by at least the length of one puncture. The elytral punctures are also different, in *D. acanthus* punctation is dense and the elytral striae are broad (Fig. 7h), whereas *D. valgum* is less densely punctured and the striae are thin (Fig. 7g).

Etymology. *Acanthus* (ἀκανθοζ = acanthos), a Latinized Greek noun in apposition, meaning thorn, making reference to the spiny pygidial apex.

***Onthophagus turgidus* Kohlmann & Solís, new species**

Figs. 8, 14

Diagnosis. This species is distinguished from other species of the *O. dicranius* species group by the following combination of characters: body dark reddish brown (Fig. 8); clypeal horn upright, basal portion wide, forked in its apical third, apical portion nearly parallel-sided; pronotum broadly tumescent anteriorly (Fig. 8), apical portion of tumescence with well separated lateral tubercles; anterior pronotal apical bead angularly reflexed medially.

Description. Holotype. Male (Fig. 8): Length 10.3 mm. Humeral width 5.9 mm. Body oblong and dark brown. Vertex, pronotum, and elytral intervals closely punctate; vertex and pronotal punctures ocellate, surface between smooth; most elytral punctures with very minute setae.

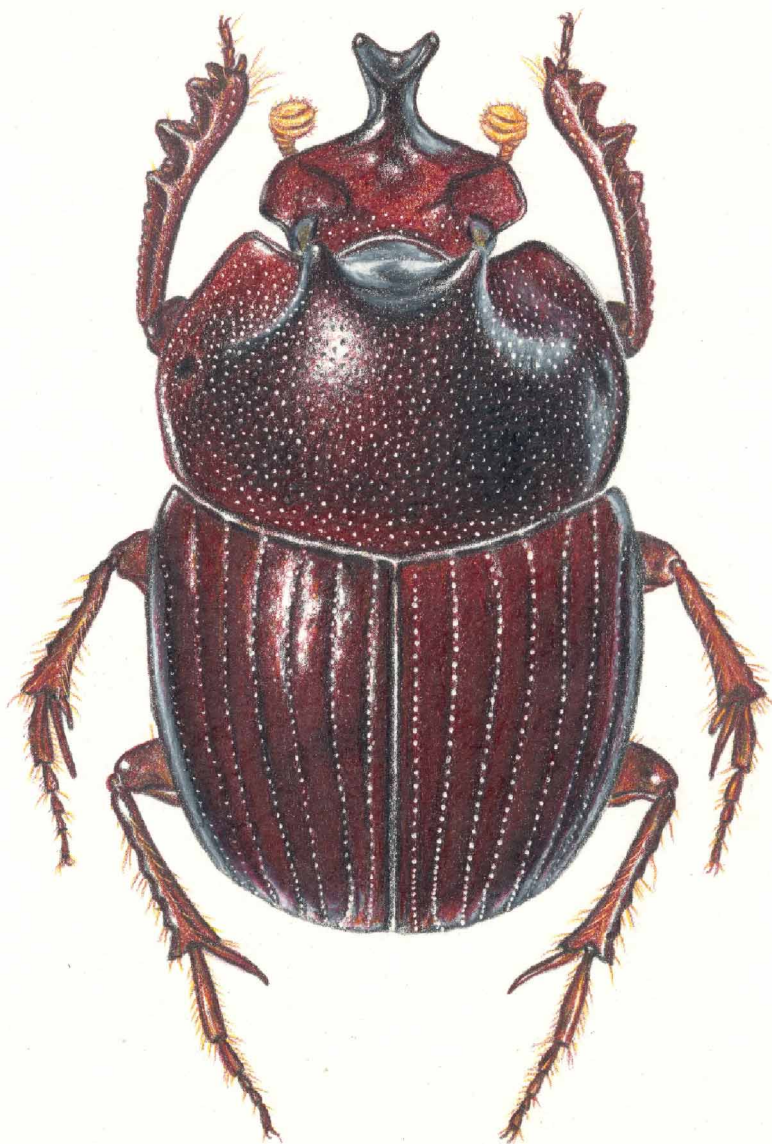


FIGURE 8. Dorsal habitus of the male holotype of *Onthophagus turgidus* Kohlmann & Solís, new species.

Clypeus at anterior median edge with an upright, slightly arched, and flattened horn (Fig. 8); horn in its apical third bifurcate, Y-shaped, apical portion nearly parallel-sided (Fig. 8). Side of clypeus from rounded edge of gena to base of horn almost straight. Clypeal surface behind the horn concave. Frons surface feebly convex medially and with scattered punctures. Vertex with very small tubercle on each side near anterior inner edge of each eye; surface anterior to and between tubercles punctate, punctures between eyes ocellate.

Pronotum with anterior margin raised medially; anterior median half with large transverse tumosity (Fig. 8), delimited on each side by a distinct conical tubercle, tubercles evidently separated; anterior face of tumosity almost vertical with a small, slightly convex, tuberculated mid-line, tubercles very small. Pronotal surfaces near anterior lateral angles concave; marginal bead of posterior margin obsolete medially.

Elytron with striae distinctly impressed with ocellate punctures at regular intervals; intervals on disc with two or more irregular rows of punctures, surface between shiny. Pygidium closely ocellate-punctate, each puncture with a short stiff seta.

Metasternum with ocellate punctures, except along mid-line. Protibia elongate, with terminal tuft of setae; apical and subapical teeth distinctly closer to each other than second to third or third to fourth teeth. Ventral surface of all femora with regular, shallow punctures.

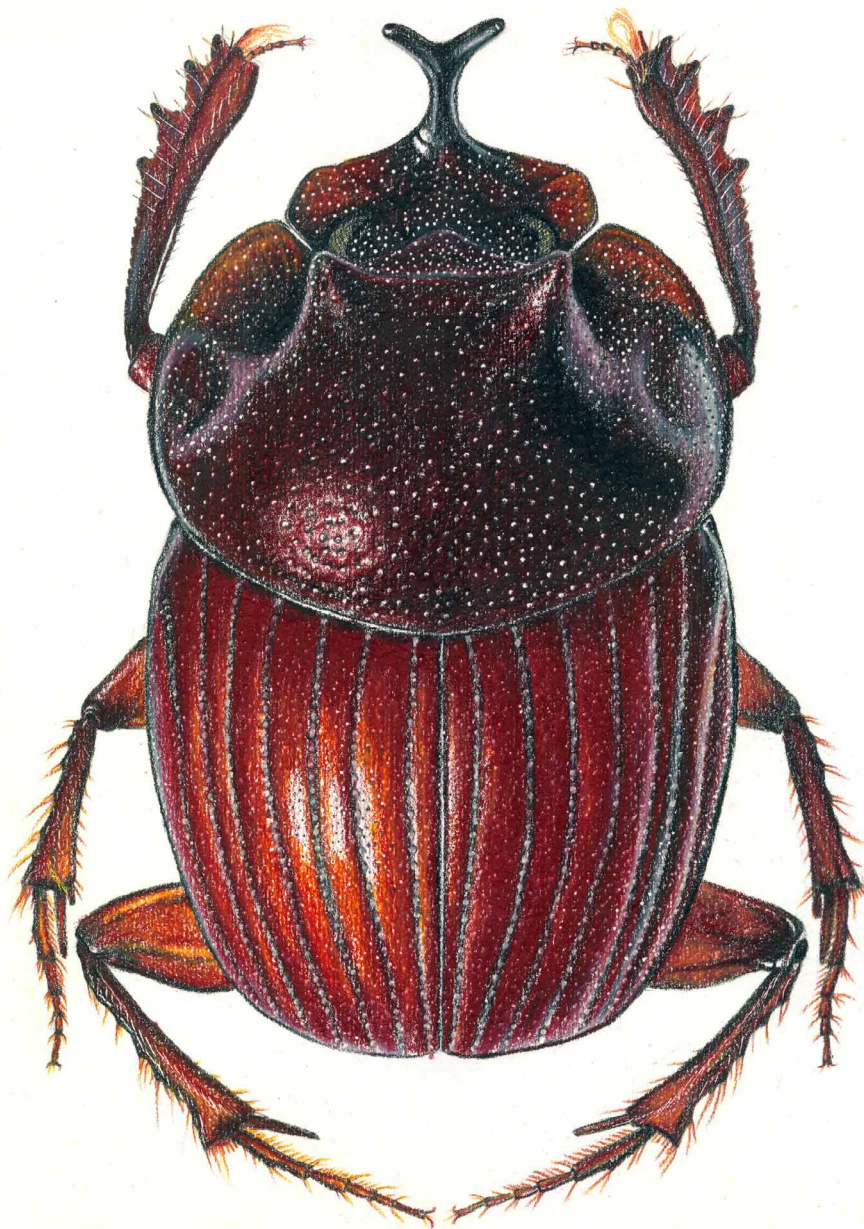


FIGURE 9. Dorsal habitus of a male *Onthophagus solisi* Howden & Gill.

Examined material (1 specimen). **Holotype**, male: PANAMA. Panamá, Bocas del Toro. Fila a 1.5 km este de río Tskui, 800 m. 9.4453° N -82.8471° W. Col: A. Solís y M. Moraga. Trampa 11. Proyecto Darwin.

Habitat. The specimen was collected with a trap baited with pig manure at an altitude of 800 m inside a primary tropical rain forest, during the month of October.

Geographical distribution (Fig. 14). This species is known so far from the Caribbean slope on the Panamanian Central Cordillera.

Chorological affinities. *Onthophagus turgidus* is found at similar altitudes in the Chiriquí Cordillera as *O. solisi* (500–1250 m; Kohlmann & Solís 2001; Fig. 9), its ecological equivalent (a small dung tunneller), in the Guanacaste and Tilarán Cordilleras.

Taxonomic relationships. More material is needed, especially females, in order to establish taxonomic relationships. Presently, and using the similar clypeal horn, the anterior pronotal marginal bead, and the pronotal tumescence, the new species would seem to be closely related to *O. solisi* Howden & Gill, and it might actually be its sister species.

This species will key to *O. solisi* in Kohlmann & Solís' (2001) key. The male of the new species (Fig. 8) can be easily separated from the males of *O. solisi* (Fig. 9) by the form of the clypeal horn, which is thicker and more robust in the new species; as well as having a developed pronotal tumescence with more divergent lateral tubercles. With the description of these new species of *Onthophagus* in this paper, there are now 24 known from Panama.

Etymology. *Turgidus*, Latin adjective in the genitive case meaning swollen, in reference to the transverse pronotal tumosity.

Coprophanaeus gephyra Kohlmann & Solís, new species

Figs. 10, 11, 16

Diagnosis. This species is distinguished from other species of the *C. pluto* species group by the following combination of characters: Length of male frons more than twice that of clypeus (in females one-half times that of clypeus); posterior portion of paraocular area smooth; pronotal transverse ridge quadrilobate with lobes linked by thick carina (Figs. 10c, 11a); basal pronotal fossae effaced; elytral interstriae flat; pygidium with wide basal groove; parameres viewed dorsally with wide, flattened subapical teeth.

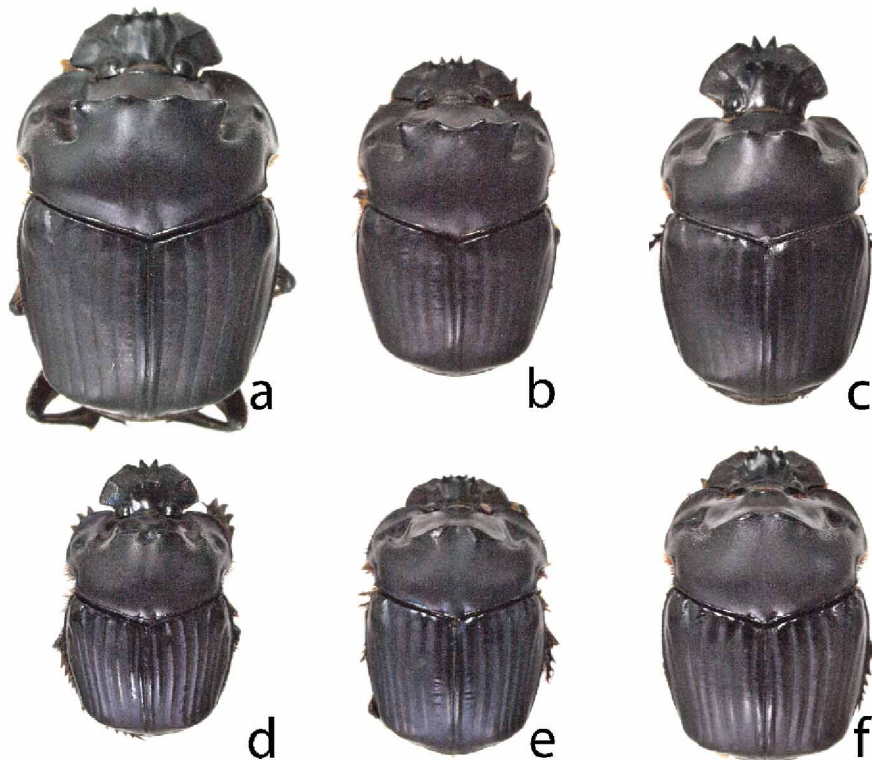


FIGURE 10. Dorsal habitus of males of six species of *Coprophanaeus*. a. *C. kohlmanni*; b. *C. morenoi*; c. *C. gephyra* Kohlmann & Solís, new species (holotype); d. *C. uhleri*; e. *C. chiriquensis*; f. *C. gilli*.

Description. Holotype. Male (Fig. 10c): Length 19 mm. Humeral width 13 mm. Completely black.

Transversal frontal carina low and trituberculate. Transverse protuberance on pronotum quadrilobate with lobes linked by thick carina (Fig. 10c); protuberance flanked by broad concavities; declivitous surface of pronotum beneath protuberance smooth, devoid of sculpturing. Tooth-like projection in the middle of the basal margin of the pygidium. The parameres of the aedeagus have their teeth backwards hooked.

Allotype. Female. Length 18 mm. Humeral width 12.5 mm. Similar to male, but allotype has a low and feeble frontal carina; transverse pronotal carina broadly obtuse, vaguely indented at anterior median edge; surface behind carina shallowly concave, transverse depression summit weakly bitumid.

Variation. Six specimens examined, four males and two females. Length 18–20 mm. Humeral width 12–13 mm. In smaller males the transverse pronotal protuberance is only evident as a thickening.

Examined material (6 specimens). **Holotype**, male: PANAMA. Panama, Cerro Campana (Capira), 08°44'N, 79°57'W, 5 June 1995, 790 m, J. Ashe, R. Brooks, #129, ex: flight intercept trap. **Allotype**, female: PANAMA. Panamá. Chepo Carti Rd., B. Gill, 400 m, 24 VI – 30 VII 82, Flt. intercept. **Paratypes**. PANAMA. Panamá. Chepo Carti Rd., 24 VI-30 VII 82, B. Gill, 400 m, Flt. Intercept, 1 male; 6-24 VI 1982, B. Gill, 400 m, Flt. Intercept, 1 male. Canal Zone. Madden Forest, 10-13.VI.77, S. Peck, carrion tps., 1 female. Colón. 270 m, 10 mi SE Colón, Santa Rita Ridge, 10-12.VI.77, S. Peck, carrion tps. Flt. Intercept, 1 male.

Habitat. Tropical moist forest, altitudinal distribution 120–790 m, collected from June to July, with flight interception and carrion traps.

Geographical distribution (Fig. 16). The new species is presently known from central Panama, distributed in the provinces of Colón, Panamá, and the Canal Zone.

Chorological affinities. *C. gephyra*, represents a geographical and morphological bridge, between *C. kohlmanni* to the north and *C. morenoi* to the south of its central Panamanian distribution. It is also found in tropical moist forest, as are the other two species.

Taxonomic relationships. This new species was originally, partly, and erroneously considered to be *C. ohausi* by Howden & Young (1981) and as a Panamanian variation of *C. morenoi* by Edmonds & Zidek (2010). In reality, a species complex exists (Fig. 16), where *C. kohlmanni* is distributed from Nicaragua to northwestern Panama (Bocas del Toro), *C. gephyra* is distributed in central Panama, and *C. morenoi* is distributed from southeastern Panama (Darién) to Ecuador. All three species are very similar in their morphological characters.

Etymology. A Greek word in apposition, *gephyra* (γέφυρα), meaning bridge, in reference to the fact that it acts like a bridge to the distribution of two similar species, *C. morenoi* in South America and *C. kohlmanni* in Central America.

Revalidation of Costa Rican *Coprophanaeus* Species

In a recent review of the genus *Coprophanaeus* by Edmonds & Zidek (2010), some taxonomical changes were made that concern Costa Rican taxa. Specifically, the authors synonymized two species. The established synonyms were: *Coprophanaeus kohlmanni* Arnaud = *Coprophanaeus morenoi* Arnaud and *Coprophanaeus uhleri* Malý & Pokorný = *Coprophanaeus chiriquensis* (Olsoufieff). We differ with these interpretations and consider these synonyms to be incorrect. We discuss below our points of view for revalidating these species.

Coprophanaeus kohlmanni Arnaud, 2002 versus *C. morenoi* Arnaud, 1982 *sensu* Edmonds & Zidek (2010) (Figs. 10, 11, 16)

In this section we undertake a detailed analysis and comparison of different characteristics between *C. kohlmanni* Arnaud and *C. morenoi* Arnaud in order to demonstrate the validity of the existence of *C. kohlmanni* as a good species.

We started the analysis by doing a body length statistical comparison between major males. There are notable specimen size differences that were already appreciated by Arnaud (2002) and Edmonds & Zidek (2010) themselves. In the case of *C. kohlmanni* (Costa Rica), we have recorded a mean size of 18.45 mm (SD = 0.45); for *C. morenoi* (Panama, Colombia, and Ecuador), we recorded a mean size of 16.01 mm (SD = 0.46); and for *C. geph-*

yra, from central Panama, a mean size of 16.30 mm (SD = 0.53). In order to avoid any variation in length size due to the angle of head position, measurements were made from the anterior border of the pronotal protuberance to the base of the pygidium. The following number of individuals was measured: *C. kohlmanni* = 9 specimens, *C. morenoi* = 9 specimens, and *C. gephyra* = 3 specimens. All specimens measured were major males. Body length means of *C. kohlmanni* with *C. morenoi* were contrasted using a t-test, a value of $t_{16} = 11.37$ was obtained, so the two sample means have a less than 99.9% probability of being from the same population of insects. In the same line a length mean comparison between *C. kohlmanni* and *C. gephyra* presented a value of $t_{10} = 6.24$, indicating again that the two sample means have a less than 99.9% probability of belonging to the same population. There is no statistical difference in mean length between *C. morenoi* and *C. gephyra*. Concluding, *C. kohlmanni* shows a statistically significant body size difference, it is distinctly larger than *C. morenoi* and *C. gephyra*. *Coprophanaeus kohlmanni* belongs size-wise to a different population of insects than *C. morenoi* and *C. gephyra*. This size difference becomes very apparent when comparing these species in Fig. 10.

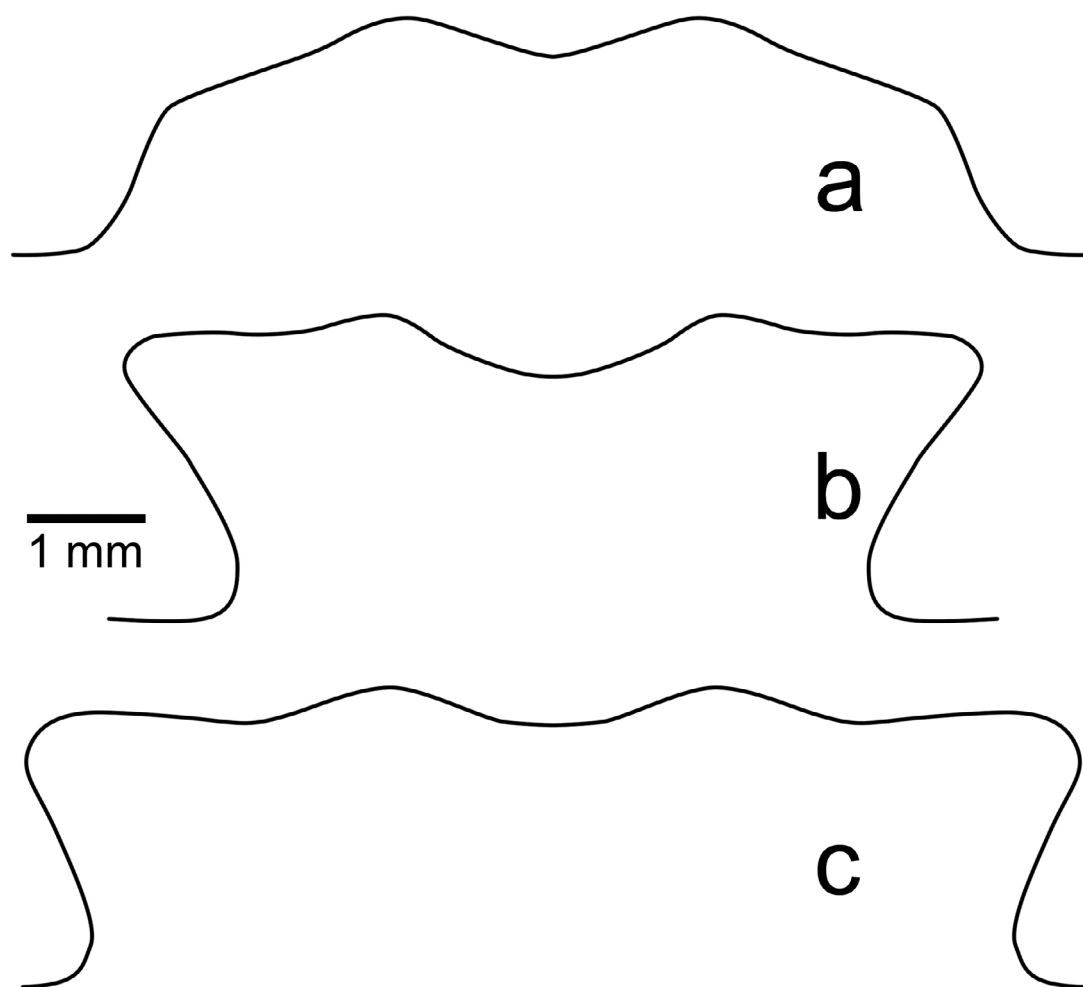


FIGURE 11. Shape of the male transversal pronotal protuberance in a. *Coprophanaeus gephyra* Kohlmann & Solís, new species; b. *C. morenoi*; c. *C. kohlmanni*.

We also studied the transversal pronotal protuberance in all three species (Fig. 11). Comparing the shape in major males, we found consistent differences in all three species (Fig. 11). *Coprophanaeus morenoi* has a smaller pronotal protuberance, more notched centrally and laterally (Fig. 11b), than the one in *C. kohlmanni* (Fig. 11c). Moreover, *C. kohlmanni* has no tooth-like indentation in the middle of the basal margin of the pygidium, whereas *C. morenoi* has a toothed condition. Edmonds & Zidek (2010) also mention this character and provide a very nice photographic comparison, indicating also that it was more frequent in Ecuadoran, Colombian, and eastern Panamanian populations, but becoming very rare beyond the Darién province. Actually, this character is also present in the new central Panamanian species described in this paper, but is completely absent westwards in all populations,

coinciding with the distribution range of *C. kohlmanni*. There is also a difference in pygidial shape; *C. kohlmanni* has a wide pygidium (width/length ratio=1.761), whereas in *C. morenoi* the pygidium is longer (width/length ratio=1.695) (see photographic comparison in Edmonds & Zidek 2010). Moreover, in *C. kohlmanni* the parameres of the aedeagus are backwardly hooked, whereas in *C. morenoi* they are rectangularly hooked (see drawings in Arnaud 2002). Finally, all three species have an allopatric distribution (Fig. 16); *C. morenoi* is found from Ecuador to eastern Panama (Darién), the new species is distributed in central Panama, and *C. kohlmanni* along the Caribbean coast from western Panama (Bocas del Toro) to Nicaragua. Edmonds & Zidek (2010) present a map indicating that the distribution reaches into Honduras, but no specimens have yet been recorded from that country.

On the basis of the above analysis, we reestablish *C. kohlmanni* Arnaud as *bona species*.

***Coprophanaeus kohlmanni* examined material** (844 specimens). COSTA RICA. Prov. Alajuela. Falda Este Volcán Tenorio, Colonia Río Celeste, Fca. Magil, 400–500m, A. Solís, Nov 1988, L- N 295000_432000, 1 specimen; Parque Nacional Volcán Tenorio, Sector El Pilón, Guatuso, Valle río Roble, 800 – 900m, 24 AGO-5 SEP 2004, J. Azofeifa, Intersección, L_N_297700_425800 #78108, 3 specimens; Parque Nacional Volcán Tenorio, Sector el Pilón, Send. La Catarata, 800m, 1 – 14 JUL 2004, J. Azofeifa, Tp. Intersección, L_N_297975_428089 #77654 1 specimen; Parque Nacional Volcán Tenorio. Estación El Pilón. 700–800m. 28–30 JUN 2006. J.A. Azofeifa. Tp. Intersección. L_N_298212_427913 #86633, 3 specimens; Parque Nacional Volcán Tenorio. Río Buenavista, Send. a Tenorio 1. 800–900m. 10–12 JUN 2007. J.A. Azofeifa. Tp. Intersección. L_N_296656_427876 #92161, 1 specimen; Puesto Quebradón. 300m. NOV 1997. G. Rodríguez. Trampa Intersección con agua sal también con Baykil y frutas en las tazas. L_N_291000_437000 #48758, 11 specimens; San Carlos, Boca Tapada, Bosque Ancianos, 50 – 100m, 14 SEP – 16 SEP 2004, B. Hernández, Tp. Foso, L_N_298721_516041 #78132, 2 specimens; 23 – 27 May 2004, B. Hernández, Tp. Intersección. L_N_298721_516041 #77254, 1 specimen; San Carlos, Finca del Dr. Murillo, Tajo, 70 – 150m, 25 – 27 ABR 2004, B. Hernández, Tp. Foso, L_N_295250_512725 #77258, 2 specimens; San Carlos, Laguna Lagarto Lodge, 0 – 100m, 23 – 27 FEB 2004, A. Solís, Tp. Foso, L_N_296095_516714 #76493, 2 specimens; 23 – 27 May 2004, B. Hernández, Tp. Intersección, L_N_296095_516714 #77253, 4 specimens; San Carlos, Pital, Boca Tapada, Laguna Lagarto Lodge, 50 – 100m, 22 – 24 JUL 2004, B. Hernández, Tp. Intersección, L_N_296095_516714 #77925, 2 specimens; San Ramón, Río San Lorencito, 800m, 27 ene 1987 Col: A. Solís Blanco, 1 specimen; Reserva Biológica San Ramón, 800 m. Nov 1994, G. Carballo, L N 244100_470100 # 3331, 1 specimen; Set 1994, G. Carballo, L N 245100_472100 # 3305, 1 specimen; 21 Oct–3 Nov 1994. G. Carballo, L_N_245100_472100 #3260, 2 specimens; Río San Lorencito, 900m, Reserva Forestal San Ramón, 5 km N de Colonia Palmareña. 13–18 Jun 1993. I Curso Scarabaeidae. L_N 244500_470700 #2125, 26 specimens; Mar 1990, Curso Carabidae, L- N 244500_470700, 1 specimen; Sector Colonia Palmarena, 9 Km SO. de Bajo Rodríguez. 700m. JUL 1997. G. Carballo. Intersección L_N_245900_475900 #46887, 5 specimens; ABR 1995. G. Carballo, L_N_245900_475900 #5455, 1 specimen; Bijagua, Parque Nacional Volcán Tenorio, Sendero Heliconias, 700m, 18 – 29 JUN 2002, A. López, Tp. Intersección, L_N_299100_422600 #70102, 2 specimens; Estación San Ramón Oeste, 620m. 3–19 Abr 1994, F. Quesada, L N 318100_381900 # 2817, 5 specimens; Parque Nacional Volcán Tenorio. Albergue Heliconias, Send. Mirador. 1000m. 09 al 20 JUL 2001. A. López. Intersección. L_N_298575_423400 #63477, 1 specimen; Sendero Heliconias. 700m. 27 JUL al 01 AGO 2000. A. López. Intersección. L_N_299100_422600 #62697, 1 specimen; Sector San Ramón de Dos Ríos, 1.5 Km NO. Hacienda Nueva Zelandia, 620m. 14–24 May 1996. D. Briceño, Intersección Excremento, L_N_318100_381900 #7566, 1 specimen; 8–28 JUN 1996. D. Briceño, Intersección L_N_318100_381900 #7562, 1 specimen; 12–21 JUL 1996. F. A. Quesada. L_N_318100_381900 #8342, 12 specimens; 13–30 AGO 1996. F. A. Quesada. Foso L_N_318100_381900 #44742, 1 specimen; 10–16 FEB 1996. F. A. Quesada, Intersección con Excremento. L_N_318100_381900 #7333, 1 specimen; 14–19 JUN 1995. F. A. Quesada, Intersección de Carne L_N_318100_381900 #5311, 10 specimens; 620m. 17–28 SET 1995. C. Cano, Intersección L_N_318100_381900 #6137, 1 specimen; 17–28 SET 1995. F. A. Quesada, Trampa de Vasos, L_N_318100_381900 #6135, 2 specimens; 26 JUN 1995. F. A. Quesada, L N 318100 381900 #5367, 5 specimens; OCT 1995. F. A. Quesada, L_N_318100_381900 #6418, 2 specimens; Sector San Ramón de Dos Ríos, Sendero Argentina, 620m. 17–28 SET 1995. C. Cano, Trampa de vasos, L_N_318100_381900 #6138, 2 specimens; Sector San Ramón, 620 m. 13–28 Mar 1994, K. Taylor, L N 318100_381900 # 2763, 3 specimens; 13–28 Mar 1994, D. García, L N 318100_381900 # 2766, 3 specimens; Upala, Bijagua, Parque Nacional Volcán Tenorio, Send. Heliconias 700m, 10 – 22 AGO 2001, A. López, Intersección. L_N_299100_422600 #64809, 2 specimens; Upala, Parque Nacional Volcán Tenorio, Send. Mirador, 1000m, 19 – 20 May 2002, A. López, Tp. de Intersección,

L_N_298575_423400 #69675, 2 specimens; 23 ABR 2002, A. López, Trampa de Intersección, L_N_298575_423400 #68921, 1 specimen; Monumento Nacional Guayabo, 1100 m, Turrialba, Abr 1993. G. Mora, L N 217200_570300, 23 specimens; Oct 1994, G. Fonseca, L N 217400_570000 # 3286, 1 specimen; Reserva Forestal Río Pacuare. Turrialba, Parque Nacional Barbilla, Send a Río Barbilla, 200 – 300m, 13 MAR 2001, W. Arana, Foso. L_N_217500_596893 #63600, 1 specimen; Turrialba, Parque Nacional Barbilla, Estación Barbilla, Sendero a Río Danta. 600m. 12 FEB 2001. W. Arana. Foso. L_N_596387_218279 #61579, 1 specimen; Turrialba. Monumento Nacional Guayabo, Los Cantarillos. 1100–1200m. 8–12 May 2007. Moraga, Azofeifa, González, Navarro. Intersección. L_N_217200_570300 #91209, 8 specimens; Tp. Foso. L_N_217200_570300 #91208, 2 specimens; Turrialba. Monumento Nacional Guayabo. Send. Montículos. 1100–1200m. 8–12 May 2007. Moraga, Azofeifa, González, Navarro. Intersección. L_N_217200_570300 #91254, 14 specimens; Tp. Foso. L_N_217200_570300 #91255, 1 specimen; Prov. Guanacaste. Estación Pitilla 9 km. S. de Santa Cecilia, 700m. FEB 1995. C. Moraga, L_N_329950_380450 #4355, 1 specimen; Estación Pitilla 9 km. S. de Santa Cecilia. 700m. SET 1996. C. Moraga. L_N_329950_380450 #8398, 1 specimen; Set 1991, L- N 330200_380200, 8 specimens; Set 1991, L- N 330200_380200, 7 specimens; P. Ríos, Set 1991, L- N 330200_380200, 1 specimen; 1 a 15 jul 1992, C. Moraga L- N 330200_380200, 1 specimen; Jan 1990, P. Ríos, L_N_330200_380200 #170, 5 specimens; Feb 1990, P. Ríos, C. Moraga & R. Blanco, L N 330200_380200, 1 specimen; Mar 1990, P. Ríos, C. Moraga & R. Blanco, L- N 330200_380200, 5 specimens; C. Moraga, 4–13 Dic 1991, L- N 330200_380200, 1 specimen; K. Taylor, 31 mar – 29 abr 1992, L- N 330200_380200, 1 specimen; C. Moraga, P. Ríos & M. Zumbado May 1990, L N 330200_380200, 1 specimen; Jun 1994, C. Moraga, L N 330200_380200 # 3002, 2 specimens; Ene 1994, C. Moraga, L N 330200_380200 # 2563, 1 specimen; May 1994, C. Moraga, L N 330200_380200 # 2898, 19 specimens; 18–23 Jul 1993. C. Moraga, L N 330200_380200 # 2269, 1 specimen; Estación Cacao, 1000–1400m, Lado suroeste del Volcán Cacao, II curso Parataxon., Jun 1990, L- N 323300_375700, 2 specimens; Estación Cacao, 2 Km SW del Cerro Cacao, 1100m. 12–14 SET 1995. C. Scarabaeidae, Carroña L_N_323100_375800 #6293, 3 specimens; Foso L_N_323100_375800 #6291, 1 specimen; Hacienda Santa Maria. 750m. SET 1996. D. Briceño, F. A. Quesada, A. Solís, E. Araya, C. Moraga. L_N_304700_393300 #8347, 4 specimens; Sector Las Pailas, Parque Nacional Rincón de la Vieja, 800 m. 21–28 Jun 1994, D. García, L N 307300_388600 # 3043, 1 specimen; Sector Santa María, 25 Km al NE. de Liberia. 790m. 11–28 NOV 1996. D. Briceño. L_N_304700_393450 #45440, 4 specimens; 12–28 SET 1996. D. Briceño. Foso L_N_304700_393450 #44749, 9 specimens; 9–27 OCT 1996. D. Briceño. Foso L_N_304700_393450 #44748, 5 specimens; 10–15 MAR 1996. F. A. Quesada, D. Briceño, A. Masís, L_N_304800_393700 #7335, 1 specimen; Río San Lorenzo, 1050 M, Tierras Morenas, Zona Protectora Tenorio, C. Alvarado, Ene 1992, L- N 287800_427600, 1 specimen; Dic 1992. G. Rodríguez, L N 287800_427600 #1764, 9 specimens; Mar 1993, G. Rodríguez, L N 287800_427600, 1 specimen; Abr 1991, C. Alvarado, L N 287800_427600, 1 specimen; Ene 1993. G. Rodríguez, L N 287800_427600, 16 specimens; Nov 1992 G. Rodríguez L N 287800_427600, 1 specimen; Oct 1992, G. Rodríguez, L- N 287800_427600, 3 specimens; SET 1995. G. Rodríguez, L_N_287800_427600 #5892, 19 specimens; Nov 1995. G. Rodríguez, L_N_287800_427600 #6449, 14 specimens; Abr 1994, G. Rodríguez, L N 287800_427600 # 2827, 13 specimens; Ene 1994, G. Rodríguez, L N 287800_427600 # 2574, 1 specimen; Tierras Morenas, Bajo Los Cartagos, R Sn Lorenzo, 1050m, Zona Prot. Tenorio, A. C. Arenal, C. Alvarado, Feb 1991, L- N 287800_427600, 1 specimen; C. Alvarado, Mar 1991, L- N 287800_427600, 1 specimen; Zona Protectora Tenorio, Tierras Morenas, Río San Lorenzo, 1050m, MAY 1991, C. Alvarado, Palanganas amarillas L_N_287800_427600 #1204, 4 specimens; Estación Biológica La Selva, 50–150m 10 26 N 84 01 W Jan 1996, INBio-OET, 8 specimens; Nov 1992, INBio-OET, 18 specimens; MAY 1994. INBio-OET, 1 specimen; Estación El Ceibo, Braulio Carrillo N. P. 400–600m, Apr 1990, C. Chaves, L- N 527700-256500, 5 specimens; Oct 1989. R. Aguilar & M. Zumbado, L N 527700,256500, 1 specimen; Nov 1989. R. Aguilar & M. Zumbado, L N 527700,256500, 16 specimens; Estación Magsasay, 200 m, Parque Nacional Braulio Carrillo, Jun 1991, A. Fernández, L- N 264600_531000, 4 specimens; May 1991. A. Fernández, L- N 264600_531000, 1 specimen; M. Barrelier, Ene 1991, L- N 264600_531100, 1 specimen; A. Fernández, Ene 1991, L- N 264600_531100, 1 specimen; Sarapiquí. Estación Biológica La Selva, Send. Canta Rana. 250–350m. 16 FEB 2003. A. Solís. Tp. Foso. 03/TF/01. L_N_260000_529500 #85772, 4 specimens; Sarapiquí. Zona Protectora La Selva. Send. Canta Rana. 250–350m. 12 MAR 2004. A. Solís. Tp. Foso. 03/TF/04. L_N_260000_529500 #85836, 1 specimen; Estación Hitoy Cerere, 100 m, R. Cerere, Res. Biológica Hitoy Cerere, E. López, 12 – 28 Abr 1992. L_N_184600_643400 #1138, 1 specimen; G. Carballo, 13 – 27 Abr 1992. L_N_184600_643400 #1136, 1 specimen; R. Guzmán. 12 – 28 Abr 1992. L_N_184600_643400 #1137, 1 specimen; Reserva Biológica Hitoy Cerere,

Send. Espavel, 560m, 18 SEP–5 OCT 2003, B.Gamboa, W.Arana, E.Rojas, Tp. Intersección, L_S_401200_569800 #75485, 1 specimen; 22 JUN – 8 JUL 2003, B. Gamboa, E. Rojas, W. Arana, Tp. Intersección, L_S_401200_569800 #74442, 6 specimens; 22 JUN – 8 JUL 2003, B. Gamboa, E. Rojas, W. Arana, Tp. Intersección, L_S_401200_569800 #74455, 3 specimens; Sendero Espavel, 170m. 24 ABR 2002. W. Arana, Trampa de Intersección. L_N_183792_643751 #68776, 2 specimens; Send. Espavel, 560m, 18 SEP–4 OCT 2003, B.Gamboa, W.Arana, E.Rojas, Tp. Intersección, L_S_401200_569800 #75515, 2 specimens; Send Espavel . 300m. 26 JUL–05 AGO 2000. W. Arana. Intersección. L_S_570200_401500 #58216, 2 specimens; Sendero Espavel. 220m. JUL 1998. E. Rojas. Tp. Intersección. L_S_401558_570460 #51620, 1 specimen; Sendero Espavel. 220m. 1 AGO–12 SET 1999. W. Arana. Intersección L_S_401558_570460 #57299, 1 specimen; Sendero Espavel. 300m. 1–16 NOV 1999. W. Arana. Intersección L_S_401500_570200 #57439, 5 specimens; Valle La Estrella, Reserva Biológica Hitoy Cerere, A. C. Amistad, 100–200 m. 5 Dic 1993–7 Ene 1994, G. Carballo, L N 184600_643400 # 2576, 2 specimens; Ene 1994, G. Carballo, L N 184600_643400 # 2575, 4 specimens; Base del Cerro Tortuguero, Parque Nacional Tortuguero, R. Delgado, Mar 1992, L N 285200_588050, 1 specimen; Cerro Tortuguero, 0–120 m, Parque Nacional Tortuguero, R. Delgado, Ene 1992, L- N 285000_588000, 2 specimens; Mar 1993, R. Delgado. L N 285000_588000, 5 specimens; R. Delgado, Feb 1992, L- N 285000_588000, 2 specimens; Oct 1991. L N 285000_588000, 3 specimens; Estación Aguas Frías. 10–20m. 14–19 AGO 1997. E. Rojas. Intersección L_N_264700_580300 #47713, 1 specimen; SET 1997. E. Rojas. Intersección L_N_264700_580300 #47716, 2 specimens; Río Sardinas, 10 m, R.N.F.S. Barra del Colorado, Set 1992, F. Araya, L N 291500_564700, 2 specimens; Sardinas, Barra del Colorado, 4 Km NO del Cerro Cocori, 15m. 23 ABR 1996. F. Araya, L_N_291900_565900 #7196, 1 specimen; 28 ENE 1996. F. Araya, Trampa de Carne. L_N_291900_565900 #7192, 11 specimens; 29 ENE 1996. F. Araya, Trampa Fecal. L_N_291900_565900 #71911, 1 specimen; 31 DIC 1995. F. Araya, L_N_291900_565900 #7189, 1 specimen; 25 AGO 1996. F. Araya. L_N_291900_565900 #8460, 2 specimens; Sardinas, Barra del Colorado, 50 m. 1–11 SET 1994. F. V. Araya, L N 221500_564700 #3200, 1 specimen; Sector Cedrales de la Rita, 3 Km N. del Puente Río Suerte, Ruta Puerto Lindo. 10m. JUN 1996. E. Rojas. Intersección L_N_278600_566500 #44873, 1 specimen; JUL 1996. E. Rojas. Intersección L_N_278600_566500 #46788, 1 specimen; Sector Cerro Cocori, Fca. de E. Rojas, 150 m, Mar 1993. E. Rojas, L N 286000_567500, 6 specimens; 10 a 30 set 1992, E. Rojas, L- N 286000_567500, 5 specimens; 12 a 31 ago 1992, E. Rojas, L- N 286000_567500, 1 specimen; 26 jul a 2 ago 1992, E. Rojas, L-N 286000_567500, 1 specimen; 26 jun a 16 jul 1992, E. Rojas, L- N 286000_567500, 1 specimen; 5 jun a 5 jul 1992, Tp Malaise, L N 286000_567500, 1 specimen; E. Rojas, Abr 1992, L- N 286000_567500, 6 specimens; Ene 1992, L- N 286000_567500, 9 specimens; Jul 1991, L- N 286000_567500, 23 specimens; Jun 1991, L- N 286000_567500, 57 specimens; Mar 1992, L N 286000_567500, 12 specimens; May 1991, L- N 286000_567500, 46 specimens; F. A. Quesada, 26 mar a 24 abr 1992, L- N 286000_567500, 11 specimens; E. Rojas, Nov 1991, L- N 286000_567500, 55 specimens; Dic 1992, E. Rojas, L N 286000_567500, 2 specimens; E. Rojas, Ago 1991, L- N 286000_567500, 10 specimens; May 1991, L N 286000_567500, 6 specimens; Oct 1991, L- N 286000_567500, 25 specimens; May 1993, E. Rojas, L- N 286000_567500 #2101, 3 specimens; Abr 1991, L- N 286000_567500, 13 specimens; Dic 1990, L- N 286000_567500, 15 specimens; Mar 1991, L- N 286000_567500, 9 specimens; Nov 1990, L- N 286000_567500, 9 specimens; Oct. 1992, E. Rojas, L-N 286000, 567500, 1 specimen; 31 ene a 21 feb 1992, E. Rojas, L N 286000_567500, 3 specimens; Set 1993. E. Rojas, L N 286000_567500 # 2347, 5 specimens; Oct 1993. E. Rojas, L N 286000_567500 # 2395, 1 specimen; Jun 1993, E. Rojas, L N 286000_567500 # 2179, 2 specimens; Manzanillo, 0–100m, RNFS Gandoca y Manzanillo, 22 oct a 11 nov 1992, K. Taylor, L S 398100_610600, 2 specimens; 24 set a 13 oct 1992, F. A. Quesada, L -S 398100_610600, 2 specimens; 4 a 12 dic 1992, F. Quesada, L S 398100_610600, 3 specimens; 5 a 13 dic 1992, K. Taylor, L S 398100_610600, 1 specimen; 9 set a 13 oct 1992, K. Taylor, L- S 398100_610600, 1 specimen; 7 a 14 ago 1992, F. A. Quesada, L S 398100_610600, 1 specimen; Talamanca. Parque Nacional La Amistad. Entre Laguna Dabagri y Laguna Sacabico. 980m. 23–25 JUL 2007. A. Solís, M. Moraga. Tp. de Foso. L_S_396600_542000 #92017, 1 specimen; Parque nacional Braulio Carrillo, Estación Carrillo Lat.10 09'75" Long. 84 57'15" 14-XII-1988 Col: J. F. Corrales, 33 specimens.

PANAMA. Prov. Bocas del Toro. Río Changena, 61–15, 2400', C.Z., IX-1961, C.E. Yunker; 61-1, IX.17.1961, 2 specimens.

***Coprophanaeus morenoi* examined material** (18 specimens). PANAMA. Darién. Cana Station, Pirre trail, 1200 m, 7°45'N, 77°41'W, 4-7.VI.1996, J. Ashe & R. Brooks, # 105, ex f.i.t., 1 specimen; Estación Ambiental Cana, 7°45.32'N 77°41.07'W, 600–750 m, 6.VI.1996, R.S. Anderson, 96-108, human dung traps, PM, 2 specimens.

COLOMBIA. Valle. 1200', Anchicaya Dam, 70 km E Buenaventura, VII.21.1970, H. & A. Howden, 1 specimen.

ECUADOR. Esmeraldas. 11 km SE San Lorenzo, La Chiquita Sta., 5 m, 6-11.VI.1975, S. Peck, forest dung traps, 1 specimen, forest carrion traps, 1 specimen; Yalare, Ex. Pitfall heces humanas, 11/17/00, J. Cell, 15309, 1 specimen; Punta Venado, Ex. Pitfall carroña, 11/23/00, J. Cell, 1 specimen; Playa de Oro, Ex Pitfall heces humanas, Marzo 2001, M. Kellog, 17825, 2 specimens; 11 km SE San Lorenzo, La Chiquita For. Sta. 6-11.VI.75, S. Peck, for. carrion traps, 1 specimen. Pichincha. 47 km S Sto. Domingo, Río Palenque, 5.V-25.VII.85, S&J Peck, 250 m, Falaise-FIT, rainforest, 2 specimens, 17-25.II.1979, L. Ling, on V slope, dung 2 cup traps Line 1, 1 specimen, 20-31.VII.1976, dung traps, 1 specimen; 16 km E Sto. Domingo, Tinalandia, 4.V-25.VII.85, S&J Peck, 680 m, Malaise-FIT. Rainforest, 1 specimen. Los Ríos. Quevedo Pichilingue, Abr. 1976, Coll. Martínez, 1 specimen. Guayas. Los Ceibos, XII-19-1982, Gary V. Marley, 1 specimen.

Coprophanaeus uhleri Malý & Pokorný, 2008 vs. *C. chiriquensis* (Olsoufieff, 1924) *sensu* Edmonds & Zidek (2010) (Figs. 10, 12, 17)

In this section we undertake a detailed analysis and comparison between *C. uhleri* Malý & Pokorný (Fig. 10d) and *C. chiriquensis* (Olsoufieff) (Fig. 10e) in order to demonstrate the validity of both species.

Malý & Pokorný (2008) indicated several characteristics in their study that differentiate *C. uhleri* from *C. chiriquensis*; however, they only had a study sample of seven *C. uhleri* specimens. Edmonds & Zidek (2010) synonymize *C. uhleri* with *C. chiriquensis* without much explanation, save that the original description is based on small specimens that fall within the variation of *C. chiriquensis*.

The most obvious and constant difference is the male pronotal carina (Fig. 12). This carina in *C. uhleri* is almost straight, weakly swollen laterally, and with a small mid-central depression (Fig. 12a). Males and females of this species have the elytral interstriae clearly keeled. The male pronotal carina in *C. chiriquensis* is very openly U-arched backwards, strongly swollen laterally, and with a strong and obvious mid-central depression (Fig. 12b). Males and females have the elytral interstriae not as strongly keeled. Finally, *C. gilli* (Fig. 10f) that is similar to both species has an almost V-shaped carina, with a mid-central depression (Fig. 12c). There is also the very clear geographical distribution (Fig. 17); *C. uhleri* is distributed from the Guanacaste to the Central Cordillera, whereas *C. chiriquensis* is found in the Talamanca Cordillera. This vicariant pattern has been reported for many dung beetle species-pairs previously (Solís & Kohlmann 2004).

On the basis of the above analysis, we reestablish *C. uhleri* Malý & Pokorný as *bona species*.

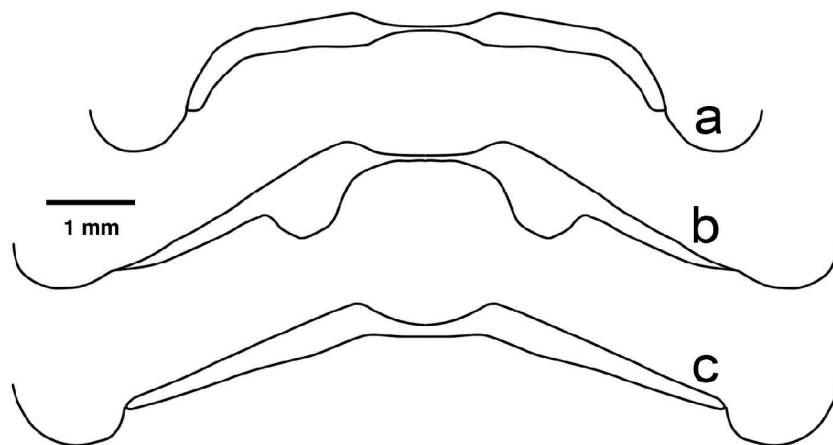


FIGURE 12. Shape of the male transversal pronotal protuberance in a. *Coprophanaeus uhleri*; b. *C. chiriquensis*; c. *C. gilli*.

***Coprophanaeus uhleri* examined material** (147 specimens). Prov. Alajuela. P.N. Volcán Tenorio, Sector el Pilón, Send. La Catarata, 800m, 1 – 14 JUL 2004, J. Azofeifa, Tp. Intersección, L_N_297975_428089 #77654, 1 specimen; R. San Lorencito, 900m, R. F. San Ramón, 5 km N de Colonia Palmarena, 13-18 Jun 1993. I Curso Scarabeidae. L_N 244500_470700 #2125, 5 specimens; Sector Colonia Palmarena, 9 Km SO. de Bajo Rodríguez.

700m. JUL 1997. G. Carballo. Intersección L_N_245900_475900 #46887, 1 specimen; Bijagua, P.N. Volcán Tenorio, Estac. Heliconias, Sect Mirador, 1000m, 10 – 22 SEP 2001, A. López, Intersección. L_N_298575_423400 #65067, 1 specimen; P.N. Volcán Tenorio, Upala, Alb. Heliconias, Send. Mirador, 1000m, 18 – 29 OCT 2000, A. López, Intersección. L_N_298575_423400 #63339, 1 specimen; P.N. Volcán Tenorio. Estación Heliconias, Sendero Heliconias. 700m. 27 JUL al 01 AGO 2000. A. López. Intersección. L_N_299100_422600 #62697, 1 specimen; Sect. San Ramón de Dos Ríos, 1.5 Km NO. Hda. Nueva Zelandia, 620m. 14–22 MAY 1996. F. A. Quesada, Intersección con Estiércol L_N_318100_381900 #7532, 1 specimen; 8–28 JUN 1996. D. Briceño, Intersección L_N_318100_381900 #7562, 1 specimen; 12–21 JUL 1996. F. A. Quesada. L_N_318100_381900 #8342, 3 specimens; 13–30 AGO 1996. D. Briceño. Intersección con Excremento L_N_318100_381900 #44745, 1 specimen; 10–16 FEB 1996. F. A. Quesada, Intersección con Excremento. L_N_318100_381900 #7333, 1 specimen; 17–28 SET 1995. C. Cano, Intersección L_N_318100_381900 #6137, 1 specimen; 17–28 SET 1995. F. A. Quesada, Intersección de Excremento, L_N_318100_381900 #6136, 1 specimen; Upala, Albergue Heliconias, Send Mirador 1000m. 20–31 AGO 2000. A. López. Intersección. L_N_298575_422400 #58478, 1 specimen; 09 al 20 JUL 2001. A. López. Intersección. L_N_298575_423400 #63477, 2 specimens; 18 JUL 2002, A. López, Tp. Foso, L_N_298575_423400, #70563, 1 specimen; Upala, Bijagua, P.N. Volcán Tenorio, Alb. Heliconias, Send. Heliconias, 700m, 18 – 29 MAY, A. López, Intersección, L_N_299100_422600 #63088, 1 specimen; 10 – 22 AGO 2001, A. López, Intersección. L_N_299100_422600 #64809, 1 specimen; 17 al 28 JUN 2001. A. López. Intersección. L_N_299100_422600 #63475, 2 specimens; Prov. Cartago. Quebrada Segunda, P. N. Tapantí, 1250 m, Feb 1993. G. Mora. L-N 194000_560000, 1 specimen; Monumento Nacional Guayabo, 1100M, Turrialba, Abr 1993. G. Mora, L N 217200_570300, 1 specimen; Prov. Guanacaste. Macizo Miravalles, Estac. Cabro Muco, 1100m, 23 SEP–5 OCT 2003, J. D. Gutiérrez, Tp. de Intersección, L_N_299769_411243 #75700, 5 specimens; Estación Pitilla 9 km. S. de Santa Cecilia, 700m. FEB 1995. C. Moraga, L_N_329950_380450 #4355, 2 specimens; JUL 1995. C. Moraga, L_N_329950_380450 #5352, 1 specimen; SET 1995. C. Moraga, Intersección L_N_329950_380450 #7322, 2 specimens; OCT 1996. C. Moraga. L_N_329950_380450 #45343, 10 specimens; SET 1996. C. Moraga. L_N_329950_380450 #8398, 5 specimens; P. Ríos, Set 1991, L- N 330200_380200, 1 specimen; Estac. Cacao, 1000–1400m, SW side Volcán Cacao, Nov-Dic. 1989. URCG R. Blanco & C. Cháves, L N 323300_375700, 1 specimen; C. Cano, 21 a 29 may 1992 L- N 323300_375700, 1 specimen; C. Cháves, Ago 1991, L- N 323300_375700, 1 specimen; II curso Parataxon., Jun 1990, L- N 323300_375700, 3 specimens; 12–14 SET 1995. C. Scarabaeidae, Carroña L_N_323100_375800 #6293, 3 specimens; 12–14 SET 1995. C. Scarabaeidae, Foso L_N_323100_375800 #6291, 5 specimens; Estación Las Pailas, 800m, P. N. Rincón de la Vieja, 24 ago a 14 set 1992 C. Cano L N 306300_388600, 1 specimen; Hda. Santa María. 750m. SET 1996. D. Briceño, F. A. Quesada, A. Solís, E. Araya, C. Moraga. L_N_304700_393300 #8347, 1 specimen; Sector Las Pailas, 4.5 Km. SW del volcán Rincón de la Vieja, 800m. 12 ABR–4 May 1995. K. Taylor, L_N_306300_388600 #6194, 1 specimen; Sector Santa María, 25 Km al NE. de Liberia. 790m. 11–28 NOV 1996. D. Briceño. L_N_304700_393450 #45440, 18 specimens; 12–28 SET 1996. D. Briceño. Foso L_N_304700_393450 #44749, 7 specimens; 9–27 OCT 1996. D. Briceño. Foso L_N_304700_393450 #44748, 3 specimens; Río San Lorenzo, 1050 m, Tierras Morenas, Z. P. Tenorio, C. Alvarado 10–20 feb 1992, L- N 287800_427600, 1 specimen; Río San Lorenzo, 1050 m, Tierras Morenas, Z. P. Tenorio, Feb 1993. G. Rodríguez, L N 287800_427600, 1 specimen; Dic 1992. G. Rodríguez, L N 287800_427600 #1764, 1 specimen; Nov 1992 G. Rodríguez L N 287800_427600, 3 specimens; Oct 1992, G. Rodríguez, L- N 287800_427600, 1 specimen; NOV 1995. G. Rodríguez, L_N_287800_427600 #6449, 1 specimen; Tierras Morenas, 700 m, Mar 1993, G. Rodríguez, L-N 283950_424500, 1 specimen; Prov. Heredia. Estación El Ceibo, Braulio Carrillo, N. P., 400 – 600 m. Nov 1989. R. Aguilar & M. Zumbado, L N 527700,256500, 1 specimen; P. N. Braulio Carrillo, Transecto entre La Selva y V. Barva, Refugio, 1070m. 15–20 FEB 2001, A. Solís, T. Foso . L_N_527281_249761 #61535, 1 specimen; Prov. Limón. Sector Cerro Cocori, Finca de E. Rojas, 150m, E. Rojas, May 1991, L N 286000_567500, 1 specimen; Prov. Puntarenas. Buen Amigo, San Luis Monteverde, 1000–1350m. ABR 1995. Z. Fuentes, L_N_250850_449250 #4801, 1 specimen; Estación La Casona, 1520m, Res. Biol. Monteverde, N. Obando, Set 1991, L- N 253250_449700, 1 specimen; 24 FEB–7 MAR 1995. K. Martínez, L_N_253900_449300 #4426, 1 specimen; 27 MAR–24 ABR 1995. K. Martínez, Amarilla L_N_253900_449300 #4428, 5 specimens; 3–24 ABR 1995. A. Azofeifa, Foso L_N_253900_449300 #5290, 3 specimens; Estación La Casona, Monteverde, 1520m. 9–25 JUN 1996. K. Martínez, Foso L_N_253900_449300 #7571, 6 specimens; 5–12 Jul 1994, K. Martínez, L N 253200_449700 # 3080, 1 specimen; 3–24 ABR 1995. A. Azofeifa, L_N_253900_449300 #5288, 1 specimen; Finca Los Leiton, 1200m, San Luis de Monteverde, N. Obando, Set

1991, L- N 215800_446700, 1 specimen; San Luis, 1040m, R. B. Monteverde, 24 ago a 15 set 1992, F. A. Quesada, L N 250850_449250, 3 specimens; Jul 1992, Z. Fuentes, L- N 250850_449250, 1 specimen; San Luis, 1040m, R. B. Monteverde, Set 1992. Z. Fuentes L- N 250850_449250, 4 specimens; San Luis, Monteverde. Buen Amigo. 1200 m. 15–30 Set 1994. Z. Fuentes. Malaise. L N 250850_449250 # 3361, 1 specimen; Prov. San José. Carrillo Lat.10 09'75" Long. 84 57'15" 14-XII-1988 Col: J. F. Corrales, 6 specimens.

***Coprophanaeus chiriquensis* examined material** (112 specimens). COSTA RICA. Prov. Cartago. Quebrada Segunda, Tapantí 1300m. 15 JUL–15 AGO 1995. R. Delgado, Intersección L_N_194000_559800 #6228, 1 specimen; OCT 1995. G. Mora. Intersección L_N_194000_559800 #7728, 1 specimen; Río Grande de Orosi, desde Administración hasta Sendero La Pava, 1150–1600m. DIC 1995. G. Mora, Intersección L_N_192500_560400 #648, 2 specimens; AGO 1996. R. Guzmán. L_N_192500_560400 #44640, 1 specimen; JUN 1996. G. Mora. Intersección L_N_192500_560400 #7684, 2 specimens; P.N. Barquilla, Turrialba, Tayutic, Campamento 2, 1200m, 5 – 8 MAY 2005, Y. Cardenas, Tp. de Foso, L_N_213371_600782 #80281, 1 specimen; Prov. Limón. Talamanca. P.N. La Amistad. Entre Laguna Dabagri y Laguna Sacabico. 980m. 23–25 JUL 2007. A. Solís, M. Moraga. Tp. de Foso. L_S_396600_542000 #92017, 4 specimens; Prov. Puntarenas. 1Km S.O. del Cerro Billey, Sector Altamira, Buenos Aires, A. C. Amistad, 1400 m. Oct 1994, M. Segura, L S 331500_571700 # 3297, 1 specimen; Buenos Aires, La Amistad, Sector Altamira, Nov 1993. R. Delgado, L S 572100_331700 # 2455, 1 specimen; May 1994, R. Delgado, L S 572100_331700 # 2905, 1 specimen; Nov 1994, M. Segura, L S 331700_572100 # 3298, 13 specimens; Estación Altamira, ACLA, PILA, 1450m. 1–28 ENE 1996. R. Villalobos, Foso L_S_331700_572100 #6881, 1 specimen; 26 SET–16 OCT 1995. R. Villalobos, Foso L_S_331700_572100 #6345, 1 specimen; 23 AGO–23 SET 1995. R. Villalobos, Foso. L_S_331700_572100 #6181, 1 specimen; 28 JUL–7 AGO 1995. R. Villalobos. Foso L_S_331700_572100 #7908, 8 specimens; Avenida El Pizote, 1.4 KM. NE. de la Tigra. 1300m. 10–29 JUL 1996. E. Navarro. Carroña. L_S_318500_597100 #8335, 3 specimens; Foso L_S_318500_597100 #8336, 5 specimens; Coto Brus, Estación Pittier. 1680m. 04 al 16 AGO 2000. R. González. Intersección. L_S_578645_330030 #58855, 1 specimen; Estación Biol. Las Alturas 1500m, Coto Brus, M. Ramírez, Oct 1991, L S 322500_591300, 3 specimens; Ago 1992, M. Ramírez y E. Sancho L-S 322500_591300, 1 specimen; Oct 1992, M. Ramírez, L- S 322500_591300, 4 specimens; 31 MAY–3 JUN 2004. J. Ashe, Z. Falin, I. Hinojosa. Ex: flight intercept trap. L_S_321241_591615 #85665, 1 specimen; Estación Pittier, 1670m. 21–28 JUN 1995. A. M. Maroto, L_S_330900_577400 #5441, 1 specimen; E. Navarro, L_S_330900_577400 #5386, 2 specimens; 21–28 JUN 1995. M. Moraga, L_S_330900_577400 #5398, 1 specimen; 22–28 JUN 1995. A. Azofeifa, L_S_330900_577400 #5298, 1 specimen; A. Picado, L_S_330900_577400 #5898, 1 specimen; Estación Pittier, Send. a Río Canasta, 1670m. 22–28 JUN 1995. R. Villalobos, L_S_330900_577400 #5936, 1 specimen; Estación Pittier, Send. Altamira, 4.2 Km SO. del Cerro Gemelo. 1670m. 21 JUN–29 JUL 1995. E. Fletes. L_S_330900_577400 #8316, 1 specimen; 10–20 MAY 1996. A. M. Maroto. Intersección con Carroña L_S_331500_576800 #8493, 5 specimens; Finca Cafrosa, 1300 m, Estación Las Mellizas, P. Internac. La Amistad, M. Ramírez, May 1991, L- S 316100_596100, 2 specimens; Jun 1991, L- S 316100_596100, 1 specimen; J. C. Saborío, Jun – Jul 1990, L- S 316100_596100, 1 specimen; M. Ramírez & G. Mora, May 1990. L- S 316100_596100, 3 specimens; R. Delgado 19 Jun – 26 Jul 1990. L- S 316100_596100, 1 specimen; Apr 1990, M. Ramírez & G. Mora, L- S 316100_596100, 1 specimen; Mar 1990 M. Ramírez & G. Mora, L S 316100_596100, 4 specimens; NOV 1989. M. Ramírez & G. Mora. L_S_316100_596100 #156, 3 specimens; Las Tablas, 1.4 Km SO del Cerro Gemelos. 1670m. 28 JUL–7 AGO 1995. E. Navarro, L S 330900 577400 #5385, 2 specimens; San Vito, Las Cruces 20 nov 1988 Col: A. Solís, 6 specimens; Send ac. Pittier, 1800m. 21 MAY–4 JUN 1995. E. Fletes, L_S_331800_577400 #7180, 2 specimens; Zona Protectora Las Tablas, 1 Km NE de Sitio Portones, 1530m. 23 AGO–6 SET 1995. M. Chinchilla, Foso L_S_320100_596800 #5867, 3 specimens; 30–31 AGO 1995. M. Segura, L_S_320100_596800 #6219, 1 specimen; MAY 1995. M. Segura, L_S_320100_596800 #7342, 5 specimens.

PANAMA. Chiriquí. : Chiriquí: La Fortuna, jul 1982, B. Gill, 2 specimens; Santa Clara, ago 1982, B. Gill, 4 specimens.

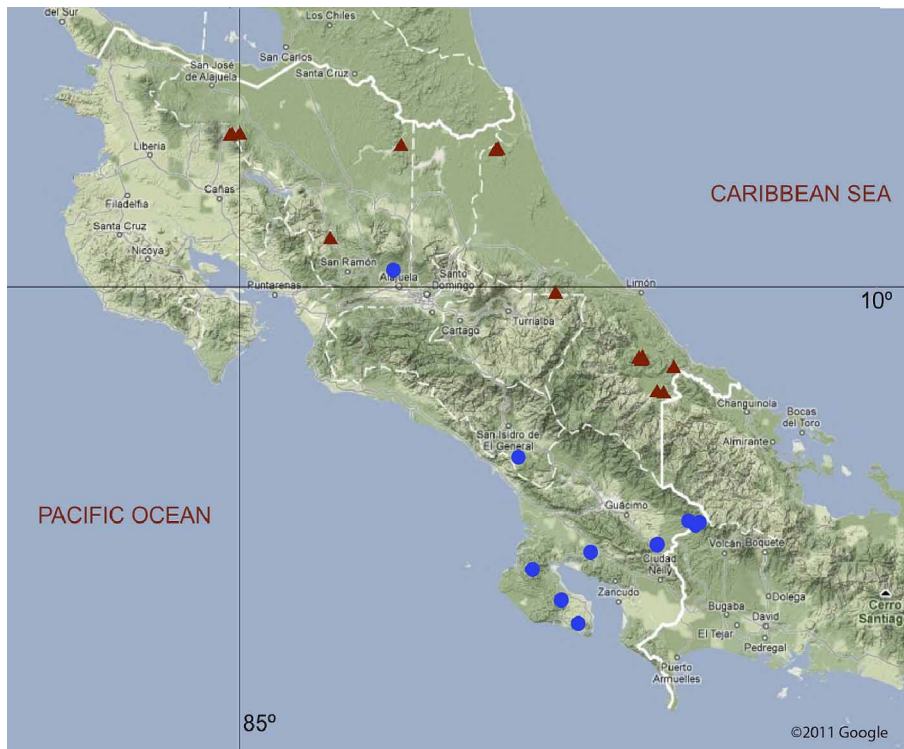


FIGURE 13. Known distribution of *Athyreus* in Costa Rica: *A. gulesseriani* (triangles) and *A. championi* (circles). Base map from Google Maps.



FIGURE 14. Known distribution of *Ateuchus alutacius* Kohlmann & Solís, new species (circle) and *Onthophagus turgidus* Kohlmann & Solís, new species (triangle). Base map from Google Maps.



FIGURE 15. Known distribution of *Deltochilum acanthus* Kohlmann & Solís, new species (triangles) and *Deltochilum valgum acropyge* (circles). Base map from Google Maps.

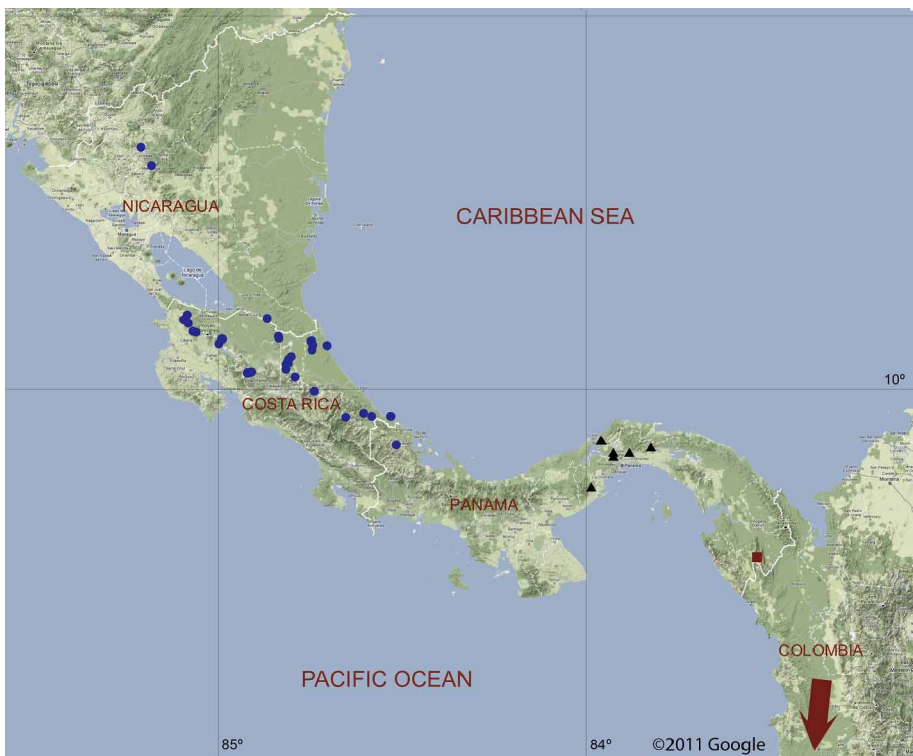


FIGURE 16. Known distribution of *Coprophanaeus kohlmanni* (circles), *C. gephyra* Kohlmann & Solís, new species (triangles), and *C. morenoi* in Central America (square, arrow indicates more records of this species in Colombia and Ecuador). Base map from Google Maps.

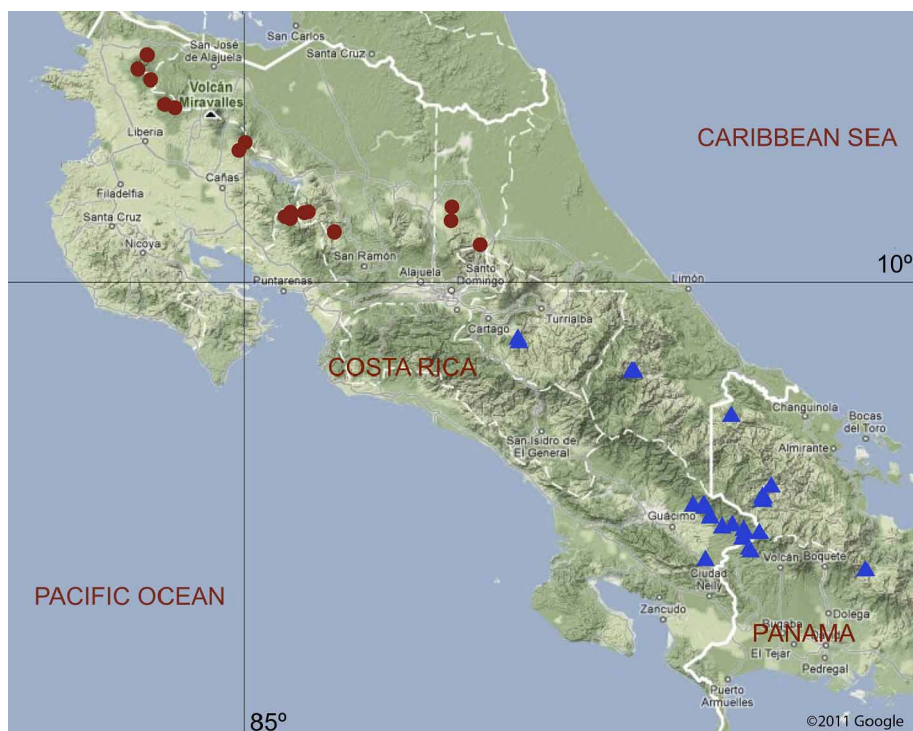


FIGURE 17. Known distribution of *Coprophanaeus uhleri* (circles) and *C. chiriquensis* (triangles). Base map from Google Maps.

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