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Original Article

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Underestimated diversity and range size of diving beetles in tank bromeliads—Coleoptera of 'hygrofloric' lifestyle (Dytiscidae)

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ABSTRACT

Tank bromeliads provide a vast amount of stagnant water high up in the Neotropical forest canopy. However, the aquatic macroinvertebrate diversity in this specialized habitat remains poorly explored. Here, we study obligatorily bromeliadicolous species of the diving beetle genus *Copelatus* Erichson, 1832. We review the known species *Copelatus bromeliarum* Scott, 1912 (Trinidad and Venezuela) and *Copelatus bimaculatus* Resende & Vanin, 1991 (Brazil). We describe three new species: ***Copelatus espinhasso* sp. nov.** (Brazil), ***Copelatus florae* sp. nov.** (Brazil, Colombia, Costa Rica, Ecuador and Panama) including its larva, and ***Copelatus panguana* sp. nov.** (Peru). Based on their male genital morphology, these species form a distinct clade within the genus. Other shared characters such as compact drop-shaped habitus, shortened appendages, and reduction of natatory setae on legs are interpreted as adaptations for what we call the 'hygrofloric' lifestyle. We document the thin water layer between leaf axils as the preferred habitat of both *Copelatus* adults and larvae, and not necessarily the central tank.

Keywords: Neotropical forest canopy; tank bromeliads; specialized Coleoptera; diving beetles; new species

INTRODUCTION

With more than 450 described species, the circumtropical genus *Copelatus* Erichson, 1832 represents the most speciose genus of the family Dytiscidae (Coleoptera: Adephaga) (Nilsson and Hájek 2023). These diving beetles generally inhabit a large variety of forested lentic and lotic habitats, typically temporary puddles and small stagnant pools and side pools of streams and rivers. One species from Brazil was described from a cave (Caetano *et al.* 2013). A highly specialized habitat of *Copelatus* is the water filled space between leaf bases (axils), and central tanks of *Pandanus* and bromeliad plants (Scott 1912a, b, Balfour-Browne 1938, Resende and Vanin 1991, Balke 2003, Balke *et al.* 2008). The bromeliads (*Bromeliaceae*) are a family of monocot flowering plants of about 80 genera and 3700 known species, native mainly to the tropical Americas (Gouda *et al.* 2023). About half of the species (known as 'tank bromeliads') show tightly

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interlocking leaves that collect rainwater and form actual tanks, a central tank being formed by the youngest leaves. Balke *et al.* (2008) reported three clades in which *Copelatus* species were found in bromeliad waters. Among these, two are monotypic and are not seen as obligatory bromeliadicolous. The fact that these two species do not differ morphologically from other terrestrial species of *Copelatus*, added to the fact that only a few specimens were collected, suggests that they were accidentally found in this type of environment potentially in reaction to drought conditions. The third lineage, however, was composed of two morphologically distinct species [*Copelatus bromeliarum* Scott, 1912 and *Copelatus bimaculatus* Resende & Vanin, 1991], whose origin (12–23 million years ago) coincides with that of the tank habitat where they were collected, suggesting some form of plant-insect co-evolution. Our recent collecting efforts in Latin America revealed that this lineage of *Copelatus* is more widespread and speciose than expected. Indeed, three new species were discovered in Brazil and Peru, as well as Colombia, Ecuador, Costa Rica, and Panama, respectively. The main objective of this article therefore is to describe these new species including the larva of the newly described *C. florae* and to compare them with two other known bromeliad *Copelatus* species. As an underlying objective, we intend to discuss what appears to us to be elements of adaptation to a way of life in the bromeliads.

MATERIAL AND METHODS

Adult morphology

The material was examined using an Olympus SZX12 stereomicroscope. Some of the habitus images were taken using a Canon EOS 550D digital camera with an attached Canon MP-E65 macro lens as numerous separate images set by hand at different focal planes and afterwards combined using Helicon Focus 6.3.0 software (at Prague Museum). In Munich, habitus images were taken with a Canon EOS 5 DS camera also fitted with a Canon MP-E65, and genital images with a 10 × ELWD Mitutoyo (Kawasaki, Japan) Plan Apo objective attached to a Carl Zeiss (Jena, Germany) Sonnar 3.5/ 135 MC as a focus lens. The camera was attached to a Stackmaster macrorail (Stonemaster: www.stonemaster-onlineshop.de, Linkenheim-Hochstetten, Germany) for image stacking. Illumination was with 3 Stonemaster LED-Segments SN-1.

Measurements were taken with an ocular graticule. The following abbreviations were used in the descriptions: TL—total length of body, a single measurement of length from front of head to apex of elytra; TL-h—total length without head length, length of body from anterior margin of pronotum to apex of elytra; MW—maximum width of body. The terminology to denote the orientation of the genitalia follows Miller and Nilsson (2003).

Larval morphology

Larvae were disarticulated and mounted on standard glass slides in Hoyer's medium. Microscopic examination at magnifications of 80–800 × was done using an Olympus BX50 compound microscope equipped with Nomarsky differential interference optics. Figures were prepared through use of a drawing tube attached to the microscope. Drawings were scanned and digitally inked using an Intuos 4 professional pen tablet (Wacom Co., Ltd. Kazo, Saitama, Japan).

The methods and terms used herein follow those employed in Alarie *et al.* (2022). All measurements were made with a compound microscope equipped with a micrometer eyepiece. Each part to be measured were adjusted so that it was, as nearly as possible, parallel to the plane of the objectives. The following measurements were taken (with abbreviations shown in parentheses): Head length (HL): total head length including the frontoclypeus, measured medially along epicranial stem. Head width (HW): maximum head width. Length of frontoclypeus (FRL): from apex of nasale to posterior margin of ecdysial suture. Occipital foramen width (OCW): maximum width measured along dorsal margin of occipital foramen. Coronal line length (COL). Length of mandible (MN): measured from laterobasal angle to apex. Width of MN: maximum width measured at base. Length of antenna (A), maxillary (MP) and labial (LP) palpi were derived by adding the lengths of the individual segments; each segments is denoted by the corresponding letter(s) followed by a number (e.g. A1: antennomere 1; MP1: maxillary palpomere 1; LP1: labial palpomere 1). A3' is used as an abbreviation for the apical lateroventral process of third antennomere. Palpifer length (PPF). Galea length (GA) measure along the midline. Length of leg (L1–L3), including the longest claw (CL), was derived by adding the lengths of the individual segments; each leg is denoted by the letter L followed by a number (e.g. L1: prothoracic leg). The length of trochanter includes only the proximal portion, and the length of distal portion is included in the femoral length. Dorsal length of last abdominal segment (LAS): measured along the midline from anterior to posterior margin. Length of urogomphus (U) total length from base to apex. These measurements were used to calculate several ratios that characterize the body shape.

Primary (present in first-instar larvae) and secondary (added in later instars) setae and pores were distinguished on the head capsule, head appendages, legs, last abdominal segment, and urogomphi. Whereas represented by instars II and III only, primary sensilla of *C. florae* were tentatively identified by comparison with the Copelatinae ground plan recently described (Alarie *et al.* 2022). As no instar I was available for this study, we could not determine exactly the number of additional setae present on femora of *C. florae* and therefore additional setae are deemed to be included in the count of secondary setae. Sensilla were coded by two capital letters and a number (setae) or a lowercase letter (pores). The following abbreviations were used: AN, antenna; CO, coxa; FE, femur; FR, frontoclypeus; LA, labium; MN, mandible; MX, maxilla; PA, parietale; PT, pretarsus; TA, tarsus; TI, tibia; TR, trochanter; UR, urogomphus.

Material examined

Exact label data are cited and given in quotation marks for the type material. Authors' additional remarks are provided in square brackets; [p]–preceding data are printed. Separate label lines are indicated by a slash (/), separate labels by a double slash (//).

The specimens included in this study are deposited in the following collections: INABIO (Instituto Nacional de Biodiversidad, Quito, Ecuador); INPA (Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil); LHCM [Lars Hendrich

Collection, Munich, Germany (property of Naturhistorisches Museum Wien, Vienna, Austria)]; MUSM (Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru); NMPC (National Museum, Prague, Czech Republic); UCR (University of Costa Rica, San Jose, Costa Rica); UNAL (Universidad Nacional de Colombia UNAL, Bogota, Colombia); YALC (Larval Collection of Y. Alarie, School of Natural Sciences, Laurentian University, Sudbury, Canada); ZSMG (SNSB-Zoologische Staatssammlung München, Munich, Germany).

The distribution map was created based on a map available from Wikimedia Commons (https://commons.wikimedia.org/wiki/File:South_America_laea_relief_location_map.jpg), created by Wikimedia Commons user Uwe Dedering, and licensed under the Creative Commons Attribution-ShareAlike 3.0 Unported license.

RESULTS

Taxonomy

Copelatus bimaculatus Resende & Vanin, 1991

(Figs 1A–B, 2A–B)

Aglymbus bimaculatus Resende & Vanin, 1991: 124 (Brazil: São Paulo Province: Salesópolis: Guaratuba).

Copelatus bimaculatus: Balke *et al.* 2008: 6357.

Material examined: Brazil: 1♂ 1♀, Nova Friburga, Macaé de Cima, 1200 m, viii.1997, (LHCM); 2♀♀, Florianopolis, Santo Amaro da Imperatriz, 300 m, x.2004 (ZSMG). 7♂♂ 5♀♀, same locality, but: in *Nidularium innocentii*, 15.ii.2005, Zillikens leg. (NMPC, ZSMG).

Diagnosis: Habitus drop-shaped, more strongly attenuated posteriorly than anteriorly, broadest at 1/3 of elytral length, slightly convex. Body black, clypeus, margins of pronotum and scutellar shield somewhat reddish translucent, appendages testaceous; elytra completely black in specimens from Nova Friburgo (Fig. 1B), but with small oval basal orange spot between striae 4–8 in specimens from St. Amaro (Fig. 1A). Dorsal surface submatt due to well impressed reticulation and presence of fine longitudinal striolae. Head moderately broad, *c.* 0.57 × width of pronotum, trapezoidal. Antennae with antennomeres rather broad, thus of stouter appearance. Pronotum transverse, broadest at posterior angles; sides strongly and evenly curved, lateral beading distinct except for anterior corners. Elytral striation consisting of 11 superficially impressed discal + a submarginal stria: odd striae, especially striae 5, 7, 9 often incomplete and badly perceptible due to striolation, in some specimens almost absent. Protibia modified, slightly angled near base, distinctly broadened anteriorly, club shaped. Pro- and mesotarsomeres 1–3 distinctly broadened, ventrally with adhesive setae. Natatorial setae present only on dorsal side of metatarsomeres. Median lobe of aedeagus in lateral aspect 'C'-shaped, apex obtusely pointed; in ventral aspect median lobe evenly attenuating to straight, pointed apex (Fig. 2A–B). Parameres broad, 'D' -shaped. Female somewhat smaller than male: TL♂♂: 6.1–6.4 mm; TL♀♀: 5.9–6.3 mm.

Distribution: The species is distributed in the Atlantic forests, along the coast from Rio de Janeiro to Santa Catarina provinces, south-eastern Brazil (Fig. 3).

Copelatus bromeliarum (Scott, 1912)

(Figs 1C, 2C–D)

Aglymbus bromeliarum Scott, 1912a: 433 (Trinidad: El Tucuche).

Copelatus bromeliarum: Balke *et al.* 2008: 6357.

Material examined: Trinidad: 3♂♂ 5♀♀, northern range, summit of Mount El Tucuche, 10°44′22.8″S, 61°24′29″W, 893 m, A.L. Viloria & A.D. Rincon leg. (NMPC, ZSMG). Venezuela: 1♂, Aragua, Henry Pittier NP, La Cumbre, 1500 m, 5.viii.2001, Hornburg leg. (LHCM); 4♀♀, Aragua, Henri Pittier NP, 1100 m, (*Guzmania* sp., 40 m above floor on *Gyr. curibensis*), 4.v.2004, Escalona, Villareal & Arias leg. (ZSMG); 1♂ 2♀♀, Caracas, IVIC, 1700 m, 27.i.2004, Balke & Garcia leg. (ZSMG); 6♂♂ 11♀♀, Maracay, Rancho Grande, 1200 m, 22.i.2004, Balke, Garcia & Escalona leg. (NMPC, ZSMG).

Diagnosis: Habitus drop-shaped, more strongly attenuated posteriorly than anteriorly, broadest at 1/3 of elytral length, slightly convex. Body black, appendages testaceous (Fig. 1C). Dorsal surface submatt due to well impressed reticulation and presence of fine longitudinal striolae. Head moderately broad, *c.* 0.60 × width of pronotum, trapezoidal. Antennae with antennomeres rather broad, thus of stouter appearance. Pronotum transverse, broadest at posterior angles; sides strongly and evenly curved, lateral beading distinct except for anterior corners. Elytral striation consisting of six superficially impressed discal striae: odd striae often incomplete and badly perceptible due to striolation. Protibia modified, slightly angled near base, distinctly broadened anteriorly, club shaped. Pro- and mesotarsomeres 1–3 distinctly broadened, ventrally with adhesive setae. Natatorial setae present only on dorsal side of metatarsomeres. Median lobe of aedeagus in lateral aspect 'C'-shaped, apex obtusely pointed; in ventral aspect median lobe attenuated in apical fourth, apex turned left (Fig. 2C–D). Parameres broad, 'D'-shaped. Female smaller than male: TL♂♂: 5.9–6.5 mm; TL♀♀: 5.1–6.1 mm.

Distribution: The species is so far known from Trinidad Island and from the Cordillera de la Costa in northern Venezuela (Fig. 3).

Copelatus espinhasso Hájek, Benetti, Hamada, Hendrich & Balke, sp. nov.

(Figs 1D, 2E)

Zoobank registration: urn:lsid:zoobank.org:act:5AC0F5A9-4B92-4F09-A5E8-C3064780940E.

Type material: Holotype ♂ (INPA), labelled: 'MB 8945 [p, green typing]// SNSB-Zoologische/ Staatssammlung München/ Digital imaging/ ZSM-COL-00181 [p]// Brazil: Minas Gerais, Serro/ Cachoeira Moinho de/ Esteira, afluente do rio Jequitinhonha [p]// 18°34'18'S, 043°29'31"W,/ 31.iii.2020 1040 m., G./ Jorge (MB8945) [p]// HOLOTYPE/ *COPELATUS*/ *espinhasso* sp. nov./ J. Hájek *et al.* det. 2022 [red

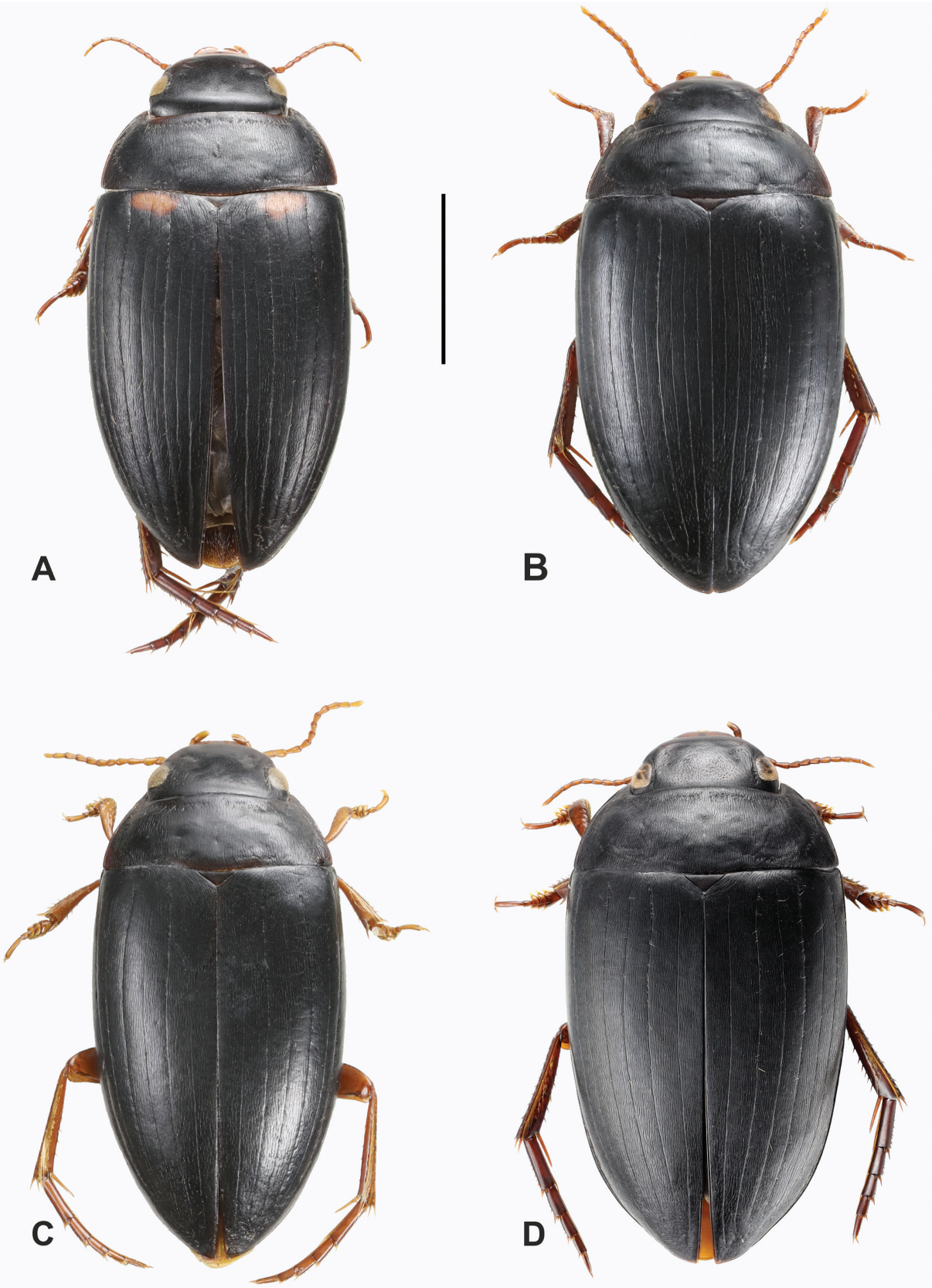

Figure 1. Habitus of bromeliadicolous *Copelatus*. A, *C. bimaculatus* (Santo Amaro da Imperatriz). B, *C. bimaculatus* (Nova Friburgo). C, *C. bromeliarum* (Henri Pittier). D, *C. espinhasso* (holotype). Scale bar = 2.0 mm.

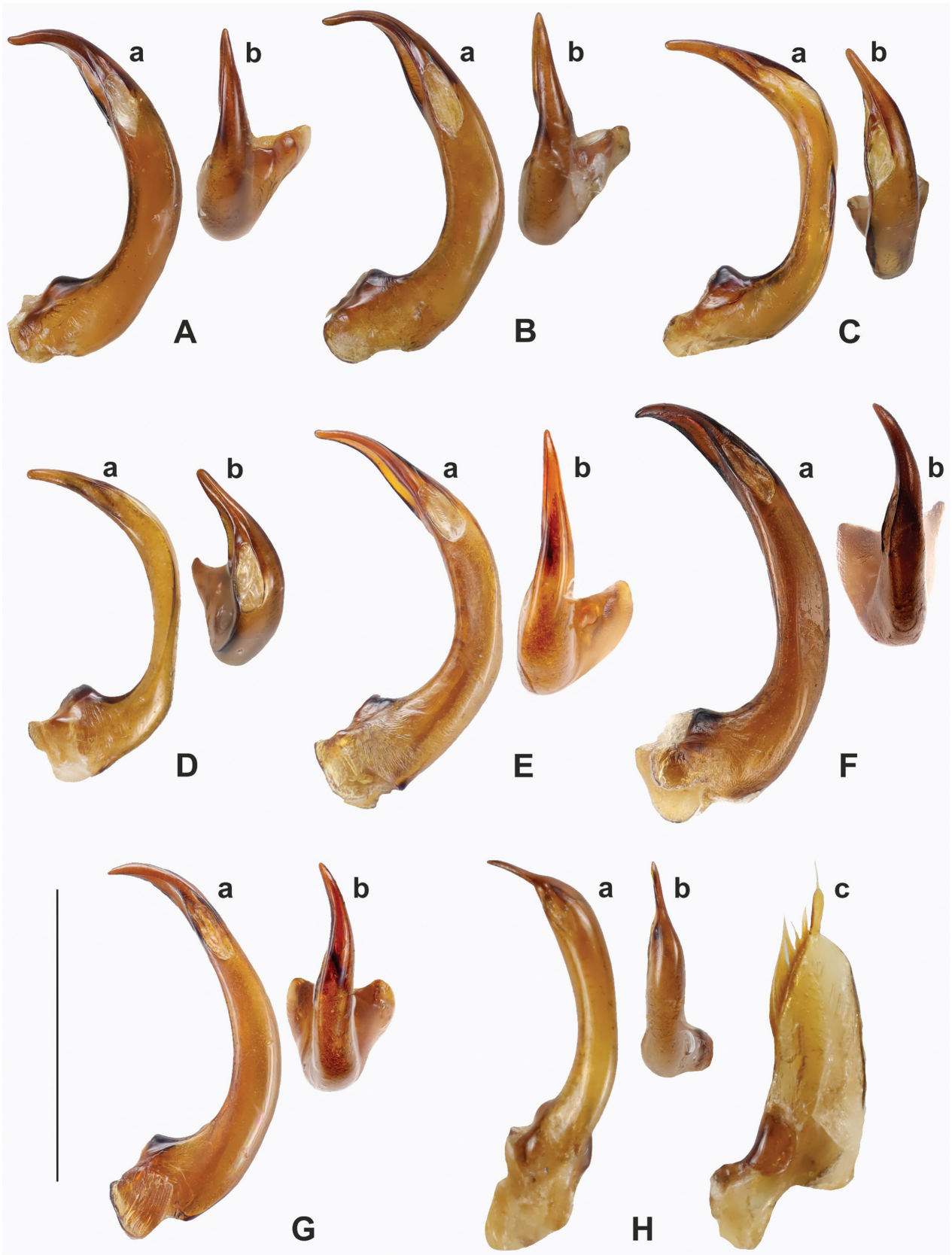

Figure 2. Male genitalia of *Copelatus*. A, *C. bimaculatus* (Santo Amaro da Imperatriz). B, *C. bimaculatus* (Nova Friburgo). C, *C. bromeliarum* (El Tucuche). D, *C. bromeliarum* (Henri Pittier). E, *C. espinhasso* (holotype). F, *C. florae* (Alto de Piedra). G, *C. florae* (Manaus). H, *C. panguana* (holotype). a, median lobe in lateral view. b, median lobe in ventral view. c, paramere. Scale bar = 1.0 mm.

Figure 3. Distributional map of bromeliadicolous *Copelatus* species.

label, p]'. Paratype: 1♀, same locality data as holotype and the respective red printed paratype label (ZSMG).

Description of male holotype: Habitus (Fig. 1D) broadly oblong oval, slightly attenuated posteriorly, broadest at 1/4 of elytral length, slightly convex. Dorsal surface submatt.

Coloration: Body black; base of pronotum and scutellar shield somewhat reddish translucent; ventral part of head, prosternum, abdomen, and appendages reddish brown.

Head: Small, *c.* 0.58 × width of pronotum, semi-elliptical. Anterior margin of clypeus convex. Antennae with antennomeres rather broad (antennomeres II–X *c.* 1.4 × longer than width), thus of stouter appearance. Reticulation consisting of fine, well impressed isodiametric polygonal meshes. Numerous short, shallow and isolated strioles present between eyes. Punctation double; several large setigerous punctures present in fronto-clypeal depressions, frontal depressions at level of anterior margin of eyes, and in depressions along inner margin of eyes; very fine and sparsely distributed punctures placed among meshes of reticulation.

Pronotum: Transverse, broadest at posterior angles. Anterior angles acute, posterior angles rectangular. Sides strongly and evenly curved, lateral beading distinct except for anterior corners. Anterior margin straight, posterior margin nearly straight with only indistinct sinuation medially. Reticulation similar to that of head, meshes somewhat more elongate. Surface of pronotum with numerous long shallow strioles; centre of disc with shallow longitudinal scratch. Punctation double; row of coarse setigerous punctures presents along anterior margin, laterally close to sides, and in basolateral depressions along basal margin; fine punctures placed among meshes of reticulation.

Elytra: Elytral striation consisting of six superficially impressed discal striae and a submarginal stria: all discal striae complete, except for stria 5 which is absent at base; submarginal stria long, but somewhat faint, starting at 1/3 of elytral length. Whole surface of elytra covered with fine, shallow long longitudinal striolae; striolae somewhat sparser and shorter and transverse in apical part of elytra. Surface reticulation consisting of very fine, superficially impressed polygonal meshes; meshes elongate in basal half, but isodiametric or transverse in apical half of elytra. Punctation double; large setigerous punctures present along lateral margin of elytra; badly perceptible, very fine punctures sparsely distributed among meshes of reticulation.

Legs: Protibia modified, slightly angled near base, distinctly broadened distally, club shaped. Pro- and mesotarsomeres 1–3 distinctly broadened, ventrally with adhesive setae. Natatorial setae present on dorsal side of all tibiae and on both sides of metatarsomeres.

Ventral side: Prosternum sinuate anteriorly, obtusely keeled medially. Prosternal process shortly lanceolate, in cross-section convex, apex obtuse; process distinctly bordered; reticulation consisting of well impressed polygonal meshes; punctation consisting of setigerous punctures along margin. Metaventrite with microsculpture consisting of polygonal meshes, meshes distinctly transverse laterally; lateral parts of metaventrite ('metasternal wings') tongue-shaped, slender. Metacoxal lines well impressed, abbreviated (absent in basal third). Metacoxal plates covered with long longitudinal strioles; reticulation consisting of extremely elongated, longitudinal polygonal meshes. Metacoxal processes rounded and incised at posterior margin. Abdominal ventrites I–II with longitudinal strioles; ventrites III–IV with oblique strioles laterally. Abdominal reticulation consisting of elongate polygonal meshes, longitudinal on ventrites I–II, oblique on ventrite III and transverse on ventrites IV–VI. Punctation double; coarse setigerous punctures present medially and medio-laterally on ventrites III–VI; fine punctures sparsely distributed on surface of ventrites, clusters of somewhat coarser punctures present laterally on ventrite V and basolaterally on ventrite VI.

Male genitalia: Median lobe in lateral aspect 'C'-shaped; broad in basal two-thirds, in apical third sinuous and narrowing to obtusely pointed apex; in ventral aspect median lobe attenuated continuously to pointed apex (Fig. 2E). Parameres broad, 'D'-shaped.

Female: Female does not differ in external morphology from male except for nearly straight, apically less broadened protibia, slender pro- and mesotarsi without adhesive setae, and sparser and shorter striolation of pronotum and elytra. The single female available is smaller than the male—see measurements.

Variability: A slight variability in dorsal coloration can be seen between the male holotype and the female paratype: anterior

margin and sides of pronotum are reddish translucent, and indistinct basal transverse reddish spot is perceptible on elytra between striae 2 and 4 in female.

Measurements (N = 2): TL♂: 6.3 mm; Tl-h♂: 5.7 mm; MW♂: 3.4 mm. TL♀: 5.4 mm; Tl-h♀: 4.9 mm; MW♀: 2.8 mm.

Identification: In habitus, this new species is the most similar to another Brazilian species *C. bimaculatus*; however, it can be easily recognized from the latter by the presence of only six dorsal striae on each elytron (Fig. 1D). Compared with the other bromeliadicolous *Copelatus*, *C. espinhasso* sp. nov. can be recognized with certainty by the characteristic shape of the median lobe of the aedeagus—in lateral view, the median lobe is in apical third sinuous on dorsal side, gradually attenuating to obtusely pointed, dorsally slightly curved apex (Fig. 2E).

Etymology: The new species is named after its area of occurrence—Serra do Espinhaço; the name is a noun in the nominative singular.

Collecting circumstances: The specimens were collected at 1040 m altitude in the water layer between leaf axils of bromeliads, growing on trees on the narrow vegetation margin of a stream, in the 'Cerrado' biome.

Distribution: So far known only from the type locality in Serra do Espinhaço, Minas Gerais State, Brazil (Fig. 3).

Copelatus florae Hájek, Alarie, Benetti, Basantes, Hendrich & Balke, sp. nov.

(Figs 4A–C, 2F–G, 5)

Zoobank registration: urn:lsid:zoobank.org:act:6CE5DC86-AD85-4478-95EF-8448C80A356C.

Type material: Holotype ♂ (NMPC), labelled: 'PANAMA: Veraguas 12.-13.ix.2017/ Santa Fé env., below Alto de Piedra/ 08°31.451′N, 81°7.650′W, 670 m/ pasture with solitary trees; in bromeliads; Fikáček, Hájek, Seidel & Sekerka lgt. [p]// HOLOTYPE/ *COPELATUS/ florae* sp. nov./ J. Hájek *et al.* det. 2022 [red label, p]'. Paratypes: PANAMA 7♂♂, 6♀♀, same label data as holotype (NMPC, ZSMG); 3♀♀, labelled: 'PANAMA: Panamá 13.ix.2017/ PN Altos de Campana: Cerro Campana/ 08°41.1′N, 79°56.0′W, 800–900 m/ lower montane forest; in bromeliads/ Fikáček, Hájek, Seidel & Sekerka lgt. [p]' (NMPC, ZSMG). COSTA RICA 17 exs, labelled: 'Costa Rica: Alajuela,/ NNW San Ramon,/ 810 m, 13.iii.2022, [p]// 10.2253° -84.5553°,/ Springer & Balke/ (CR_MB_2022_06) [p]', two males with additional labels 'MB 8902 [p, green typing]' and 'MB8903 [p, green typing]', respectively (UCR, ZSMG). BRAZIL 2♂♂, 1♀, labelled: 'SNSB-Zoologische, Staatssammlung München, Digital imaging, ZSM-COL-00182'/ 'Brazil: Amazonas, Manaus; Reserva Ducke, proximo ao Igarapé Acará, 02°56'06"S/ 59°57'12"W, 17.iv.2017, 72 m, G. Jorge', two males with additional labels 'MB 8946 [p, green typing]' and 'MB8948 [p, green typing]' (INPA, ZSMG); 2 exs, labelled; 'Brazil: Amazonas, Manaus, Reserva da Campina, BR 174, 02°35'52"S, 60°02'05"W, Jorge G., 06.i.2022, in bromelia' (INPA, ZSMG). COLOMBIA 4 exs: 'Colombia: Boya., Sta Maria, 1200 m, 29.x.2022, 4,8807° -73,2533°, Balke *et al.* (COL_MB_2022_10)'; 2 exs: 'Colombia: Boya., Sta Maria, 880 m, 29.x.2022, 4,8818° -73,2434°, Balke *et al.* (COL_MB_2022_11)'; 19 exs: 'Colombia: Boya., Sta Maria, 740 m, 30.x.2022, 4,8271° -73,2582°, Balke *et al.* (COL_MB_2022_12)' (UNAL, ZSMG). ECUADOR 2 exs: 'Ecuador: Napo, Road side to Archidona, Bromelia, 770 m, 13.xii.2022, -0,840° -77,7792°, Basantes (ECU_MB_2022_13)' (INABIO, ZSMG); 2 exs: 'Ecuador: Napo, Tena, Amazon Park La Isla, Bromelia, 502, 15.xii.2022, -0,994° -77,8174°, Basantes (ECU_MB_2022_15)' (INABIO, ZSMG). Each paratype provided with the respective red printed label.

Description of male holotype: Habitus (Fig. 4A) drop-shaped, strongly attenuated posteriorly, broadest at base of elytra, slightly convex. Dorsal surface submatt.

Coloration: Body black; sides of pronotum and abdomen somewhat reddish translucent; ventral part of head, prosternum, and appendages testaceous; elytra with oblong transverse orange spot on base between striae 1–5.

Head: Small, *c.* 0.54 × width of pronotum, trapezoidal. Anterior margin of clypeus slightly concave. Antennae with antennomeres rather broad (antennomeres II–X *c.* 1.5 × longer than width), club-shaped. Reticulation consisting of fine, well impressed isodiametric polygonal meshes. Numerous short, shallow, and isolated strioles present between eyes. Punctation double; several large setigerous punctures present in fronto-clypeal depressions, frontal depressions at level of anterior margin of eyes, and in depressions along inner margin of eyes; very fine and sparsely distributed punctures placed among meshes of reticulation.

Pronotum: Transverse, broadest at posterior angles. Anterior angles acute, posterior angles rectangular. Sides strongly and evenly curved, lateral beading distinct except for anterior corners. Anterior margin straight, posterior margin nearly straight with only indistinct sinuation medially. Reticulation similar to that of head, meshes longitudinally elongate. Surface of pronotum with numerous long shallow strioles; centre of disc with shallow longitudinal scratch. Punctation double; row of coarse setigerous punctures present along anterior margin, laterally close to sides, and in basolateral depressions along basal margin; fine punctures placed among meshes of reticulation.

Elytra: Elytral striation consisting of six superficially impressed discal striae and a submarginal stria: all discal striae complete, except for stria 5 which is absent at base; submarginal stria long, starting at 1/3 of elytral length. Whole surface of elytra covered with fine, shallow long longitudinal striolae; striolae somewhat sparser and shorter and transverse in apical part of elytra. Surface reticulation consisting of very fine, superficially impressed polygonal meshes; meshes longitudinally elongate in basal half, but isodiametric or transverse in apical half of elytra. Punctation double; large setigerous punctures present along lateral margin of elytra; badly perceptible, very fine punctures sparsely distributed among meshes of reticulation.

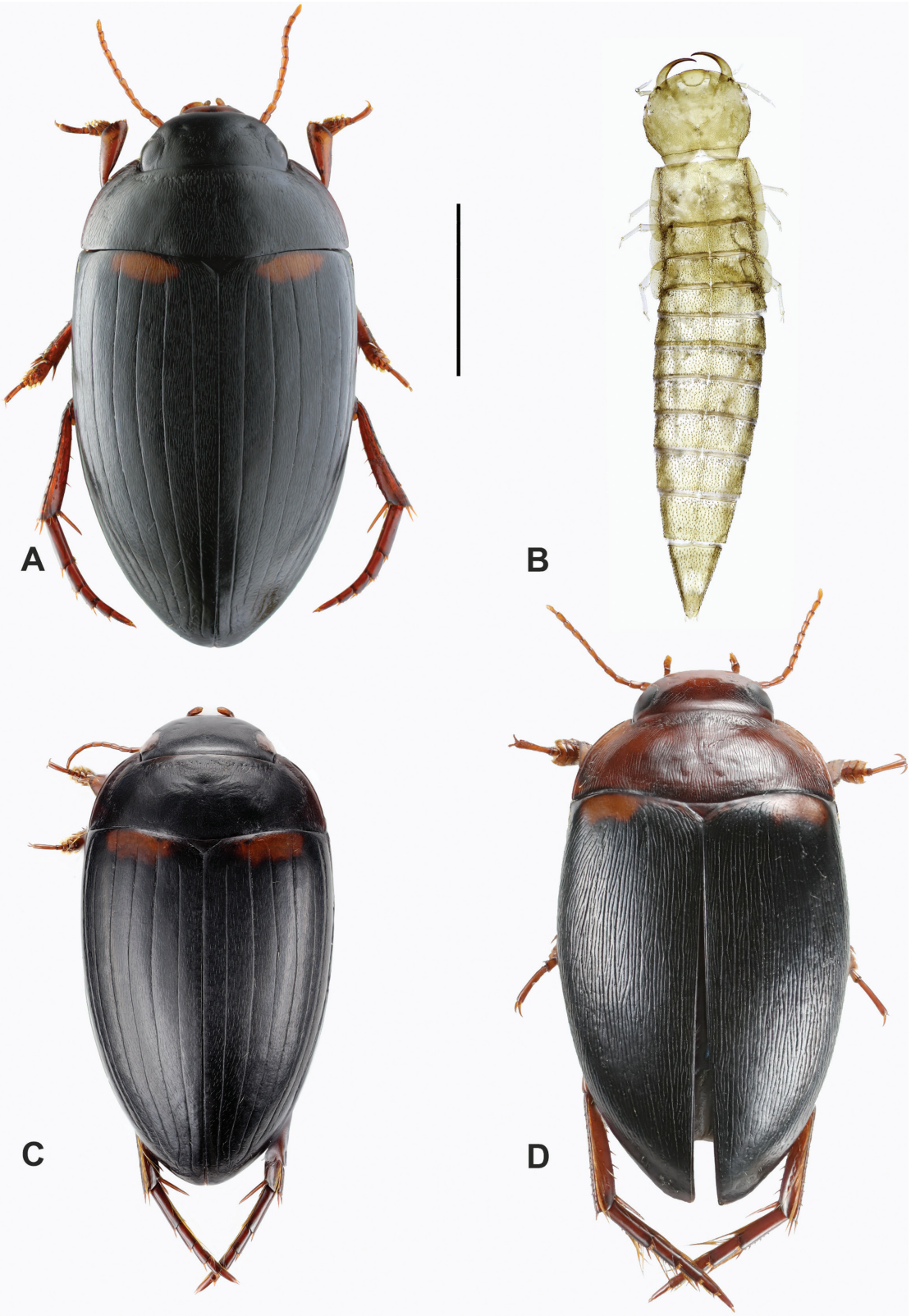

Figure 4. Habitus of bromeliadicolous *Copelatus*. A, *C. florae* (holotype). B, instar III larva of *C. florae* (Alto de Piedra). C, *C. florae* (Manaus). D, *C. panguana* (holotype). Scale bar = 2.0 mm.

Legs: Protibia modified, slightly angled near base, distinctly broadened distally, club shaped. Pro- and mesotarsomeres 1–3 distinctly broadened, ventrally with adhesive setae. Natatorial setae present only on dorsal side of metatarsomeres.

Ventral side: Prosternum sinuate anteriorly, obtusely keeled medially. Prosternal process shortly lanceolate, in cross-section convex, apex obtuse; process distinctly bordered; reticulation consisting of well impressed polygonal meshes; punctation

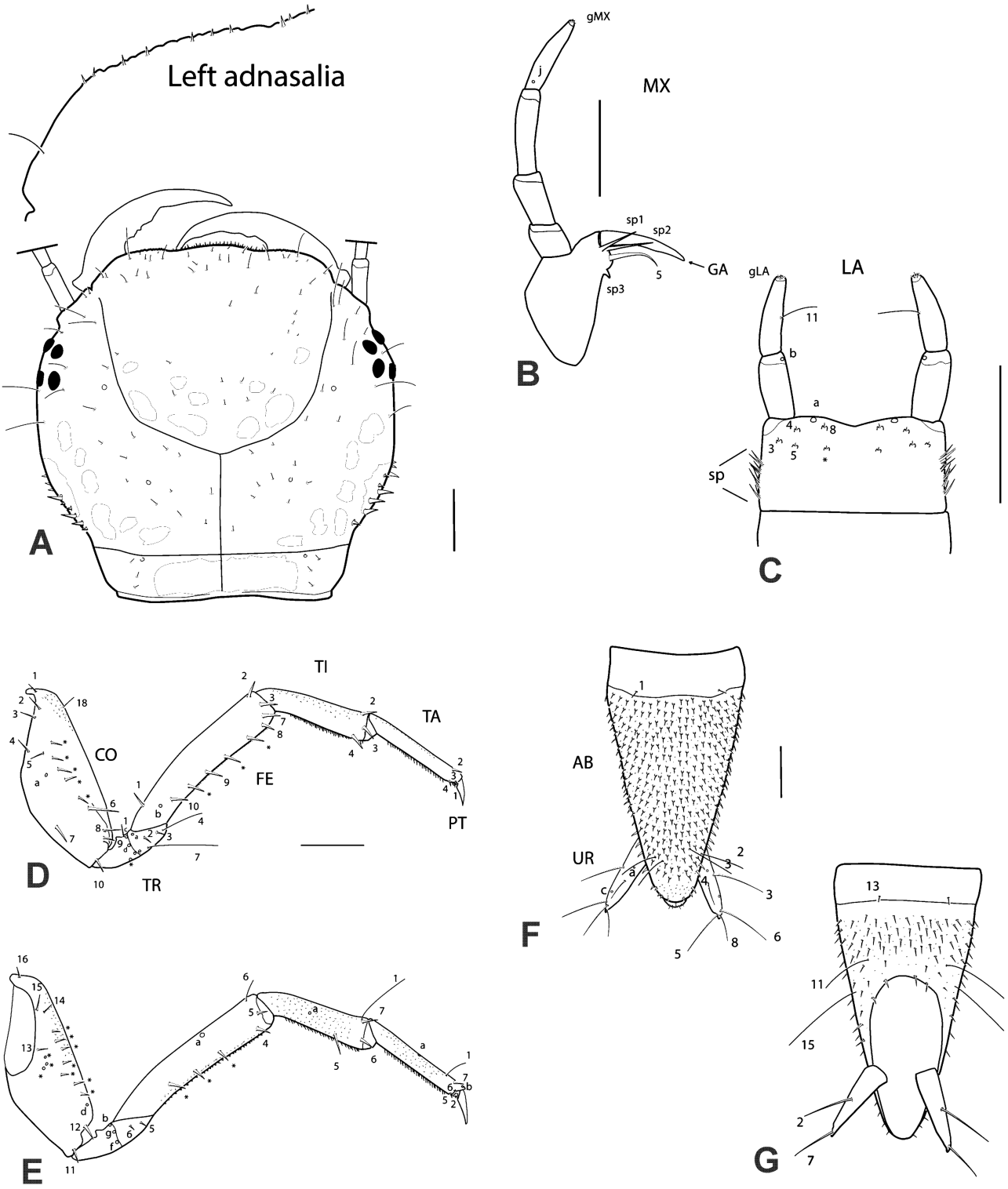

Figure 5. Details of instar III larva of *C. florae*. A, head capsule, dorsal aspect (scale-like microsculptures not represented). B, maxilla, dorsal aspect. C, labium, dorsal aspect. D, metathoracic leg, anterior surface. E, same, posterior surface. F, last abdominal segment, dorsal aspect. G, same, ventral aspect. Numbers and lowercase letters refer to primary setae and pores, respectively; asterisks refer to secondary seta (including additional setae) or pores. AB, abdominal segment VIII (= LAS). CO, coxa. FE, femur. GA, galea. LA, labium. MX, maxilla. PT, pretarsus. TA, tarsus. TI, tibia. TR, trochanter. UR, urogomphus. sp, spinulae. Pores TAc, TAd, Tae, and TAf not represented. Scale bars = 0.2 mm.

consisting of setigerous punctures along margin. Metaventrite with microsculpture consisting of polygonal meshes, meshes distinctly transverse laterally; lateral parts of metaventrite ('metasternal wings') tongue-shaped, slender. Metacoxal lines well impressed, abbreviated (absent in basal fourth). Metacoxal plates covered with long longitudinal strioles; reticulation consisting of extremely elongated, longitudinal polygonal meshes. Metacoxal processes rounded and incised at posterior margin. Abdominal ventrites I–II with longitudinal strioles; ventrites III–IV with oblique strioles laterally. Abdominal reticulation

consisting of elongate polygonal meshes, longitudinal on ventrites I–II, oblique on ventrite III and transverse on ventrites IV–VI. Punctation double; coarse setigerous punctures present medially and medio-laterally on ventrites III–VI; fine punctures sparsely distributed on surface of ventrites, clusters of somewhat coarser punctures present laterally on ventrite V and basolaterally on ventrite VI.

Male genitalia: Median lobe in lateral aspect 'C'-shaped, apex pointed; in ventral aspect median lobe attenuated in apical fourth, apex twisted left (as in Fig. 2F). Parameres broad, 'D'-shaped.

Female: Females do not differ in external morphology from males except for nearly straight, apically less broadened protibia, slender pro- and mesotarsi without adhesive setae, and sparser and shorter striolation of pronotum and elytra. Females are generally smaller than males.

Variability: This species displays allometric variability—larger specimens are more attenuated posteriorly (more drop-shaped), whereas the smaller specimens are more regularly oval (cf. Fig. 4A, C). In addition, the specimens vary in size and shape of orange spot at the base of elytra, and in the density of strioles on pronotum and elytra. The median lobe of aedeagus could appear more of less stout even within the same population (cf. Fig. 2F–G).

Measurements (N = 8♂♂ 9♀♀): TL♂♂: 6.2–6.5 mm (holotype: 6.5 mm); TL-h♂♂: 5.6–5.9 mm (holotype: 5.9 mm); MW♂♂: 3.1–3.4 mm (holotype: 3.4 mm). TL♀♀: 5.6–6.1 mm; TL-h♀♀: 5.0–5.5 mm; MW♀♀: 2.8–3.1 mm.

Identification: Compared with the other bromeliadicolous *Copelatus*, this new species can be easily recognized based on strongly drop-shaped habitus, elytra with transverse basal orange spot, well impressed six discal and a submarginal stria on each elytron, pronotum and elytra densely covered with fine longitudinal striolae (Fig. 4A, C), and by the characteristic shape of the median lobe of the aedeagus—in lateral view, the median lobe is in apical half slightly attenuating to pointed, dorsally distinctly curved apex (Fig. 2F–G).

Etymology: The new species is dedicated to the partner of the senior author 'Květa' which is the Slavic form of the Latin name 'Flora'; the name is a noun in the genitive case, standing in apposition.

Collecting circumstances: The specimens from Panama were collected at two medium altitude localities (670–900 m a.s.l.) in the thin water layer between leaf axils of a bromeliad species tentatively identified as *Werauhia gladioliflora* (H.Wendl.) J.R. Grant, growing on solitary trees on pasture, close to forest (Alto de Piedra, Fig. 6), and on trees along a forest road (Cerro Campana). The specimens from Brazil were collected at 100 m a.s.l. altitude, in the water layer between leaf axils of bromeliads, growing on trees on the banks of stream, inside the Ducke Forest Reserve. In Colombia, the beetles were collected from bromeliads which were tentatively identified as a *Werauhia* J.R. Grant species as well as others but without inflorescences that would aid identification. The latter is also true for the samples from Costa Rica.

Distribution: The species has apparently a very wide distribution, covering the area from central Costa Rica through Panama, eastern Colombia and Ecuador to Manaus in the heart of Brazilian Amazonia, more than 2600 km apart (Fig. 3). It inhabits places from lowlands to medium altitude (*c.* 70–1200 m a.s.l.).

Copelatus panguana Hájek, Hendrich & Balke, sp. nov.

(Figs 4D, 2H)

Zoobank registration: urn:lsid:zoobank.org:act:39B7EEED-0D74-4B97-A99F-BF6B86BA7D64.

Type material: Holotype ♂ (MUSM), labelled: 'PERU Dep. Huanuco/ Panguana ACP Rio Yuyapichis/ 3.XII.2017, fogging "tree Renako"/ Nr. 34 ZSM-HYM-FOG 171234/ 09°37′S 74°56′W leg. A. Floren [p]// HOLOTYPE/ *COPELATUS*/ *panguana* sp. nov./ J. Hájek *et al.* det. 2020 [red label, p]'. Paratypes: 1♂, 1♀, same label data as holotype (ZSMG). Each paratype provided with the respective red printed label.

Description of male holotype: Habitus (Fig. 4D) broadly oblong oval, strongly attenuated posteriorly, broadest at 1/3 of elytral length, strongly convex. Dorsal surface submatt.

Coloration: Body testaceous; elytra blackish with small transverse testaceous spot on the base, reaching neither suture nor lateral side.

Head: Small, *c.* 0.53 × width of pronotum, trapezoidal. Anterior margin of clypeus slightly concave. Antennae with antennomeres rather broad (antennomeres II–X *c.* 1.5 × longer than width), thus of stouter appearance. Reticulation consisting of fine, shallowly impressed isodiametric polygonal meshes. Numerous long, oblique, shallow strioles present posterolaterally from eyes. Punctation double; several large setigerous punctures present in fronto-clypeal depressions, frontal depressions at level of anterior margin of eyes, and in depressions along inner margin of eyes; fine, sparsely and irregularly distributed punctures placed among meshes of reticulation.

Pronotum: Transverse, broadest at posterior angles. Anterior angles acute, posterior angles rectangular. Sides strongly and evenly curved, lateral beading distinct except for anterior corners. Anterior margin straight, posterior margin nearly straight with only indistinct sinuation medially. Reticulation consisting of badly perceptible elongate polygonal meshes. Surface of pronotum with numerous long shallow longitudinal strioles; centre of disc with shallow longitudinal scratch. Punctation double; row of coarse setigerous punctures presents along anterior margin, laterally close to sides, and in basolateral depressions along basal margin; very fine punctures placed irregularly among meshes of reticulation.

Elytra: Elytral striation consisting of 11 superficially impressed discal striae, which are difficult to recognize due to strong striolation of elytra; striolae very long and dense, covering

Figure 6. Habitat of *C. florae* in Alto de Piedra, Panama. A, general view of the pasture with solitary trees. B, large cf. *Werauhia* bromeliad. C, collecting of beetles from leaf axils. D, specimen of *C. florae* crawling on the leaf.

whole surface of elytra except for apex. Surface reticulation consisting of very fine, badly perceptible polygonal meshes; meshes elongate in basal half, but isodiametric or transverse in apical third of elytra. Punctation double; large setigerous punctures present along lateral margin of elytra; badly perceptible, very fine punctures sparsely distributed among meshes of reticulation.

Legs: Protibia modified, slightly angled near base, distinctly broadened distally, club shaped. Pro- and mesotarsomeres 1–3 distinctly broadened, ventrally with adhesive setae. Natatorial setae developed on dorsal side of tibiae and both sides of metatarsomeres.

Ventral side: Prosternum sinuate anteriorly, obtusely keeled medially. Prosternal process shortly lanceolate, in cross-section convex, apex obtuse; process distinctly bordered; reticulation consisting of well impressed polygonal meshes; punctation consisting of setigerous punctures along margin. Metaventrite with microsculpture consisting of polygonal meshes, meshes elongate laterally; lateral parts of metaventrite ('metasternal wings') tongue-shaped, slender. Metacoxal lines well impressed, nearly complete—absent only close to metaventrite. Metacoxal plates covered with long longitudinal strioles; reticulation consisting of extremely elongated, longitudinal polygonal meshes. Metacoxal processes rounded and incised at posterior margin. Abdominal ventrites I–II with longitudinal strioles; ventrites III–IV with oblique strioles laterally. Abdominal reticulation consisting of elongate polygonal meshes, longitudinal on ventrites I–II, oblique on ventrite III and transverse on ventrites IV–VI. Punctation double; coarse setigerous punctures present medially and medio-laterally on ventrites III–VI; fine punctures sparsely distributed on surface of ventrites, clusters of somewhat coarser punctures present laterally on ventrite V and basolaterally on ventrite VI.

Male genitalia: Median lobe in lateral aspect 'C'-shaped, broad throughout most of its length, then abruptly attenuated to thin pointed apex; in ventral aspect median lobe attenuated in apical fourth, thin apical part straight. Parameres moderately broad, subparallel-sided (Fig. 2H).

Female: In habitus similar to males, but sides of pronotum less curved. Protibia nearly straight, apically less broadened; pro- and mesotarsi slender, without adhesive setae. Transverse testaceous spot on elytra extended, covering base of elytra from suture to lateral margin. Striolation of pronotum and elytra finer and sparser, thus 11 elytral striae easily perceptible. The single female available is smaller than males—see measurements.

Variability: No variability can be seen between two males of the type series.

Measurements (N = 3): TL♂♂: 6.0–6.4 mm (holotype: 6.4 mm); TL-h♂♂: 5.5–5.9 mm (holotype: 5.9 mm); MW♂♂: 3.2–3.4 mm (holotype: 3.4 mm). TL♀: 5.2 mm; TL-h♀: 4.9 mm; MW♀: 2.9 mm.

Identification: Compared with the other bromeliadicolous *Copelatus*, this new species can be easily recognized based on strongly convex, broadly oval oblong habitus, head and pronotum testaceous, male with imperceptible striae and female with 11 dorsal striae on elytra (Fig. 4D), and by the characteristic shape of the median lobe of the aedeagus—in lateral view, the median lobe is subequally broad in basal 5/6 of its length, apical 1/6 is very thin and almost straight; apex is sharply pointed (Fig. 2H).

Etymology: The new species is named after its type locality, 'Área de Conservación Privada Panguana'. The name is a noun in the nominative singular standing in apposition.

Collecting circumstances: Fogged from a renaco tree (*Ficus trigona* L.f.). We suggest that this species actually stems from epiphytic bromeliads observed on that tree, as no beetles were collected in forest floor puddles in spite of intensive sampling efforts.

Distribution: The species is so far known only from the type locality at the Panguana Research Station, Peruvian Amazonia (Fig. 3).

Description of larva

Copelatus florae Hájek, Alarie, Benetti, *et al.*, sp. nov.

(Figs 4B, 5)

Material studied: One larva of instar II, three larvae of instar III, same data as holotype (YALC, ZSMG); one larva of instar III, Brazil: Amazonas, Manaus, Reserva Ducke, collected together with adults (INPA).

Description of instar III: Body subcylindrical, narrowing towards abdominal apex (Fig. 4B). Measurements and ratios that characterize the body shape are shown in Table 1.

Colour: Body predominantly testaceous; head capsule yellow, pale yellow maculae posteriorly on frontoclypeus, laterally on parietale and over most of the occiput (Fig. 5A); head appendages, legs, and urogomphi pale yellow.

Head: Cephalic capsule (Fig. 5A) rounded, about as broad as long; dorsal surface covered with much impressed scale-like microsculptures; maximum width at about level of stemmata; neck constriction well marked; occipital suture present; ecdysial line well marked, coronal line short; occipital foramen broadly emarginate ventrally; frontoclypeus subtriangular, anterior margin rounded medially, with about 34–38 short spine-like spinulae [= lamellae clypeales of Bertrand (1972)]; slightly extending medially beyond level of lateral lobes [= adnasalia of Beutel (1994)]; lateral lobes almost indistinct, bluntly serrated along outer margin; gular suture visible; ocularium present, with six stemmata visible ventrally and subdivided into two vertical series; tentorial pits visible ventrally on each side of middle at about midlength. Antenna short, slender, shorter than HW, composed of four antennomeres; A4 shortest, A2 longest, A1 and A3 subequal in length; A3 with a ventroapical spinula; lateral elongation of antennomere 3 (A3') finger-like, short. Mandible (Fig. 5A) prominent, falciform, longer than broad, distal half projected inwards, apex sharp; mandibular channel absent, internal margin with bluntly rounded denticles. Maxilla (Fig. 5B) with cardo well developed; stipes trapezoidal with minute surface spinulae and three robust spinulae along inner margin proximad to galea; galea strongly developed, spiniform; palpifer well developed, palpomere like; palpus short, 3-segmented, shorter than antenna; MP2 and MP3 subequal in length, longer than MP1. Labium (Fig. 5C) with prementum well developed, subrectangular, broader than long, dorsal surface

with small rounded tuberculi bearing primary spiniform setae, lateral margin with elongate and spine-like spinulae; palpus short, 2-segmented, about half as long as maxillary palpus; LP2 subequal in length to LP1.

Thorax: Pronotum trapezoidal dorsally, ovate laterally, shorter than meso- and metanotum combined (Fig. 4B); meso- and metanotum subequal, with anterotransverse carina; sagittal line visible on the three tergites; thoracic terga densely tuberculate; meso- and metatergite tuberculi bearing a short hair-like seta; thoracic sterna membranous; spiracles present on mesothorax.

Legs (Fig. 5D–E) short, robust, composed of six articles (including pretarsus), L1 and L2 subequal in length, L3 the longest, slightly longer than L1 and L2; CO robust, elongate, TR divided into two parts by annulus, FE, TI and TA slender, subcylindrical; PT with two short and slightly curved claws, posterior claw shorter than anterior claw on L1 and L2, posterior claw longer than anterior one on L3; ventral margin of pro- and mesotibiae, and pro- and mesotarsi with elongate spine-like spinulae; marginal spinulae more faintly developed on metatibia and metatarsus; minute spine-like microsculptures broadly developed over posterior surface of tibiae and tarsi and, to a lesser extent, along the dorsal margin of metacoxae and posteroventral margin of femora.

Abdomen (Figs 4B, 5F–G) eight-segmented; segments I–VI sclerotized dorsally, membranous ventrally, segments VII and VIII (= LAS [last abdominal segment; i.e. abdominal segment VIII]) completely sclerotized; all tergites with an anterotransverse carina and densely tuberculate, tuberculi bearing a short spiniform seta; sagittal line visible on segments I–VII; spiracles present on segments I–VII; LAS the longest, subconical, extended posteriorly, lacking constriction at level of insertion of urogomphi, with a pair of spiracular openings extending apically, ventral surface much less sclerotized than dorsally and densely covered with spiniform setae. Urogomphus (Fig. 5F–G) one-segmented, very short.

Chaetotaxy: Similar to that of generalized Copelatinae larva (Alarie *et al.* 2022); cephalic capsule with numerous minute and hair-like secondary setae, 10–12 spine-like setae on lateral margin of parietale (Fig. 5A); mandible with several tiny secondary setae along external margin; stipes with two minute secondary setae on ventral surface; prementum with secondary pores on ventral surface; thoracic and abdominal tergites with numerous short either hair-like (thorax) or spine-like (abdomen) secondary setae inserted on the apices of rounded tuberculi; ventral surface of LAS with several spiniform secondary setae; secondary leg setation detailed in Figure 5D–E; coxae with three secondary pores on posterior surface; trochantera with one secondary pore on proximal portion; urogomphi lacking secondary setae (Fig. 5F–G).

Description of instar II: As instar III except for the following features:

Body: Measurements and ratios that characterize the body shape are shown in Table 1.

Head: Apical margin of frontoclypeus with 28 lamellae clypeales. Antenna with A2 and A3 longest, subequal in length; A1 shorter than A3. Maxilla with MP3 longer than MP2. Labium with LP2 distinctly longer than LP1.

Table 1. Measurements and ratios for the larvae of *C. florae*.

Measurement	Instar II (*N* = 1)	Instar III (*N* = 2)	Measure	Instar II (*N* = 1)	Instar III (*N* = 2)
HL (mm)	0.86	1.15	PPF/MP1	0.71	0.66–0.78
HW (mm)	0.89	1.20	MP/LP	1.83	1.86–2.26
FRL (mm)	0.55	0.70–0.71	LP2/LP1	1.54	0.83–1.18
OCW (mm)	0.56	0.70–0.72	L1 (mm)	1.39	1.89–1.93
HL/HW	0.96	0.96	L2 (mm)	1.34	1.93–1.98
HW/OCW	1.58	1.66–1.71	L3 (mm)	1.47	2.10–2.17
COL/HL	0.36	0.38–0.39	L2/L1	0.97	1.02–1.03
A/HW	0.50	0.47–0.48	L3/L1	1.06	1.11–1.13
A3/A1	1.48	1.04–1.11	L3/L2	1.10	1.09–1.10
A3/A2	1.00	0.76–0.82	L3/HW	1.65	1.75–1.81
A4/A1	0.84	0.53–0.56	L3(CO/FE)	0.99	1.00
A4/A3	0.57	0.48–0.54	L3(TI/FE)	0.61	0.62–0.63
A3'/A4	0.23	0.24–0.27	L3(TA/FE)	0.66	0.59–0.61
MNL/MNW	2.81	2.79–2.93	L3(CL/TA)	0.39	0.31–0.32
MNL/HL	0.49	0.51–0.54	LAS (mm)	0.69	0.97–0.98
A/MP	1.42	1.37–1.40	LAS/HW	0.78	0.81–0.82
MP2/MP1	1.74	1.49–1.66	U (mm)	0.33	0.33–0.36
MP3/MP2	1.10	0.97–1.03	U/HW	0.37	0.28–0.30
GA/MP1	1.74	1.53–1.54	U/LAS	0.47	0.34–0.37

l, length. w, width.

Chaetotaxy: Cephalic capsule with seven spiniform secondary setae along the lateral margin of parietale; secondary leg setation detailed in Table 2.

Comments: Until very recently, our knowledge of the larval morphology of the Copelatinae was scanty, while the larvae of a limited number of species were most often described very superficially (Williams 1936, Spangler 1962, Watts 1963, Bertrand 1972, De Marzo 1976, Mashke *et al.* 2001, Michat and Torres 2009, Watanabe *et al.* 2017, Watanabe and Hayashi 2019). All of these species and several others have recently been described in a detailed study of Copelatinae larval morphology including a provisional phylogenetic analysis (Alarie *et al.* 2022). This theoretical platform represents a useful tool for comparing the morphological particularities of *C. florae*.

Larvae of *C. florae* share with all previously described Copelatinae species: (1) the presence of two rows of denticles albeit in a much more reduced form along the internal margin of the mandible (Fig. 5A); (2) the anterior margin of anterolateral lobes (= adanasalia) of frontoclypeus dentate (Fig. 5A); (3) the absence of a mandibular channel; (4) the presence of three robust spinulae along the internal margin of the stipes (Fig. 5B); (5) the galea spiniform, much longer than maxillary palpomere I in instar III (Fig. 5B); (6) the lateral margin of prementum with strong spine-like spinulae (Fig. 5C); (7) the mesothoracic legs subequal in length to prothoracic legs; (8) the metathoracic legs less than twice as long as head width; and, (9) the presence of setiferous tubercles on the dorsal surface of the thoracic and abdominal segments (Fig. 5F). All these character states make *C. florae* unambiguously diagnosed within the Copelatinae. Although the number of species involved in Alarie *et al.* (2022) (13 species) is relatively low considering the degree of diversity of the Copelatinae, it allows us to attempt a positioning among the three genera known from larva (i.e. *Copelatus*, *Liopterus* Dejean, 1833, and *Exocelina* Broun, 1886). Based on current knowledge, it seems reasonable to position *C. florae* within *Copelatus* although the presence of a large number of secondary setae on coxae and femora associated with a broadly convex frontoclypeus distinguishes it from most *Copelatus* species.

DISCUSSION

Host specificity and habitat preference

So far, bromeliadicolous *Copelatus* have been collected from the following seven bromeliad genera: *Aechmea* Ruiz & Pav., *Brocchinia* Schult. & Schult.f., *Guzmania* Ruiz & Pav., *Hohenbergia* Schult. & Schult.f., *Nidularium* Lem., *Tillandsia* L., and *Vriesea* Lindl. (Balke *et al.* 2008), as well as *Werauhia*, apparently several of these genera syntopically (see Resende and Vanin 1991). It is therefore apparent that these species are not host specific. We suggest that a determinative factor for their abundant presence among these plants is the structure of the bromeliad rosette along with its size, which would enable the accumulation of water and debris. In Panama, we did not find any *Copelatus* specimens in bromeliads with a rosette diameter less than 60 cm; in Colombia, Costa Rica, Brazil, and Venezuela, however, we did find a few specimens in smaller bromeliads closer to the forest floor. This suggests that further ecological analysis would be needed to determine if there is an optimal rosette size to support actual breeding and thus stable regional populations.

Although some *Copelatus* species were also previously recorded from bromeliad central tanks (e.g. Balfour-Browne 1938, Resende and Vanin 1991), most of the specimens collected in this study were found in the thin water layer between leaf axils at the bromeliad base, in accordance with previous studies (e.g. Scott 1912a). This particular habitat may be revealed to be more stable than the central tanks, which are frequently filled with debris; moreover, we believe that leaf axils might be better hideouts from predators than open central tanks.

Morphological adaptations to the 'hygrofloric' lifestyle

In this article we refer to the hygrofloric lifestyle as a lifestyle in the thin water layer between leaf axils. This is correlated with some putative morphological adaptations of the *Copelatus* species studied:

Habitus: Compared with the other species of the genus, obligatory bromeliadicolous *Copelatus* can easily be recognized based on their compact, dorsally strongly convex, drop-shaped habitus [see, e.g. photos of other Neotropical *Copelatus* in Manuel *et al.* (2018) for comparison]. Such a change from the generalized copelatine hydrodynamic oval shape likely suggests a transition to a more specialized habitat. Similar modification in the shape of the body has been observed in semiterrestrial or troglomorphic species, although in these beetles the habitus is usually not as compact but rather dorso-ventrally flattened (see, e.g. Caetano *et al.* 2013). Interestingly, the recently described species *Copelatus ignacioi* Hájek, Hendrich & Balke, 2022 which is deemed to inhabit various phytotelmata in the tropical rainforest (Hájek *et al.* 2022) and is hypothesized to be sister to the clade of bromeliadicolous *Copelatus*, based on our unpublished global molecular phylogenetic analysis of Copelatinae, is also characterized by a more compact although rather cylindrical habitus.

Appendages: The appendages of bromeliadicolous *Copelatus* are deemed to be significantly shorter than those of species from epigeic water bodies. For one, the antennae of these species are composed of broad, filiform antennomeres and their length represents about one-quarter of the length of the body (0.23 ± 0.01); in comparison the antennae of randomly selected

Table 2. Number and position of secondary setae on the legs of *Copelatus florae* sp. nov.

Segment	Position	Instar II (n = 1)	Instar III (n = 2)
Coxa	PD[a]	2/3/1	7/6–8/5–6
	A[b]	0/0/0	3/4/3–6
	Total[c]	2/3/1	10/10–12/9–11
Femur	AV[d]	2/3/3	2-3/3/3
	PV[e]	3/3/3	3/3/3
	Total	5/6/6	5–6/6/6

Numbers between slash marks refer to pro-, meso-, and metathoracic leg, respectively. [a]PD, posterodorsal. [b]A, anterior. [c]Total, total number of secondary setae on the segment (including additional setae, see Material and Methods). [d]AV, anteroventral. [e]PV, posteroventral.

South American *Copelatus* are generally filiform and reach one-third of the length of the body (0.33 ± 0.02). A similar trend can also be observed in the length of tarsi. We have indeed observed among the bromeliadicolous species that the metatarsi reach 1.3 times the length of the metatibia (1.30 ± 0.04), compared to 1.7 times in other *Copelatus*. Interestingly, a marked reduction in the number of elongate (natatorial) leg setation is also observed among the bromeliadicolous *Copelatus*. Such modification added to the relative shorter body appendages may be considered as adaptation for crawling in the cramped space in the leaf axils.

Larva: Compared with the known species of Copelatinae (Alarie *et al.* 2022), larvae of *C. florae* are distinguished by: (1) the bluntly toothed mandible and lateral lobes (Fig. 5A); (2) the spiniferous tuberculi (compared to setiform) on abdominal tergites (Fig. 5F); and (3) the conical shape of LAS compared to a subcylindrical LAS (Fig. 5F–G). All these characters make *C. florae* a completely unique species among the known species of Copelatinae. One may wonder if any of these morphological peculiarities could result from an adaptation for a hygrofloric lifestyle in leaf axils. It is certainly difficult to answer this question with the limited knowledge of the larval morphology of Copelatinae. What is interesting to underline, however, is that the larva of *C. florae*, like those of any other described species of Copelatinae (Alarie *et al.* 2022), is characterized by the presence of a short mesothoracic leg, about as long as the prothoracic leg as well as by a very short urogomphus. Both these features were suggested to reflect an adaptation to a crawling lifestyle (Alarie *et al.* 2022). It is also worth noting the presence of blunt denticles along the inner margin of the mandibles as well as the significant reduction of denticles along the margin of the adansalia (Fig. 5A), both of which being unusual among the Copelatinae. Some may wonder whether such modifications may reflect a different eating pattern, which could potentially result from an adaptation to a hygrofloric way of life.

Large distribution of species and genetic divergence between populations

Species of this clade in the Atlantic rainforest of southern Brazil and mountain ranges of northern Venezuela and Trinidad show marked phylogeographical structure with up to 8% mtDNA divergence, respectively (Balke *et al.* 2008), possibly indicating ongoing allopatric speciation. Based on morphological characters described above, *C. florae* has a range spanning 2600 km, from the Amazonian lowland forest around Manaus to montane forests of eastern Colombia and Ecuador to Central America.

CONCLUSION

Here, we show that hygrofloric diving beetles have utilized bromeliad water tanks across the Neotropical region including Central America, with an altitudinal range from lowland to mid-montane forest up to 1700 m a.s.l. altitude. The upper limit remains to be challenged, but research above *c.* 2500 m in Colombia did not reveal these beetles. Defined based on morphological level, we find surprisingly vast geographical ranges, for example from Amazonia across the northern Andes to Costa Rica. There is already some evidence that such species can show pronounced genetic variation. In this case, a much more comprehensive sampling and the use of genomic methods will be needed to understand species structure and delineation, and the processes underlying the observed patterns. Finally, our study underpins the urgent need to direct attention to hitherto undersampled habitats to fully understand global biodiversity patterns.

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CONFLICT OF INTEREST

There is no conflict of interest to declare.

DATA AVAILABILITY

The data underlying this article are all available in the article.

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