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The return of the Duke—locality data for *Megadytes ducalis* Sharp, 1882, the world's largest diving beetle, with notes on related species (Coleoptera: Dytiscidae)

LARS HENDRICH¹, MICHAEL MANUEL² & MICHAEL BALKE¹

¹SNSB-Zoologische Staatssammlung, Münchhausenstraße 21, D-81247 München, Germany.

E-mail: hendrich@snsb.de, balke.m@snsb.de

²Sorbonne Université, Institut de Systématique, Evolution, Biodiversité (ISYEB UMR7205 CNRS MNHN), Case courrier 05, 7 quai St Bernard, 75 005 Paris, France. E-mail: michael.manuel@upmc.fr

Abstract

Megadytes (Bifurcitus) ducalis Sharp, 1882 is the largest diving beetle in the world and has been considered a candidate for the world's rarest insect (Jones 2010). It was described from "Brazil", is only known from the male holotype in the Natural History Museum (London), and typically thought to be extinct. Here we report the finding of 10 additional specimens, all collected at the end of the 19th century, which were discovered incidentally in different historical collections, including drawers with unsorted diving beetle accessions of the Muséum National d'Histoire Naturelle (Paris). These specimens, whilst old, reveal exact locality data for the first time, enabling focused field campaigns to attempt to rediscover this giant alive. Locality labels all indicate Santo Antônio da Barra (present name Condeúba), in the southern part of Bahia, Brazil, suggesting that the species may have a restricted distribution in wetter parts of the Brazilian savanna or cerrado. We also describe the female of *M. ducalis* for the first time and present new records of the putatively closely related species *Megadytes magnus* Trémouilles & Bachmann, 1980 and *M. lherminieri* (Guérin-Méneville, 1829), the latter being recorded for the first time from Ecuador. These three morphologically similar species together form the subgenus *Bifurcitus* Brinck, 1945 and we provide photographs of their habitus, median lobes and other morphological details.

Key words: Dytiscidae, *Megadytes ducalis*, Brazil, cerrado, historical collections, Paris Museum

Introduction

The genus *Megadytes* Sharp, 1882 is widely distributed throughout the Neotropical region, reaching the Nearctic in southern Florida (Miller & Bergsten 2016). *Megadytes* includes 21 species in four subgenera. Fourteen species are currently reported from Brazil (Blackwelder 1944; Mouchamps 1957; Trémouilles & Bachmann, 1980; Trémouilles 1989a, 1989b; Ferreira (Jr.) *et al.* 2006), including *Megadytes ducalis* Sharp, 1882. With a total length of around 47 mm, this is the largest species of diving beetle in the world, the second one being the Palearctic *Dytiscus latissimus* Linnaeus, 1758 with a length of up to 44 mm. *Megadytes ducalis* belongs to the subgenus *Bifurcitus* Brinck, 1945, together with *M. lherminieri* (Guérin-Méneville, 1829) and *M. magnus* Trémouilles & Bachmann, 1980.

It seems that most *Megadytes* species are associated with lentic habitats and can be found in heavily vegetated permanent and temporary water bodies, but detailed habitat requirements for each species remain unknown. Many species are attracted to light (Miller & Bergsten 2016), and the immature stages of several species have been described (Cekalovic 1974, 2000; Crespo 1982; Ferreira (Jr.) 1993, 1995; Ferreira (Jr.) *et al.* 2006; Michat 2006). Adults and larvae are capable of eating large prey items and attacks on swamp turtles and large frogs have been reported (Caputo *et al.* 2006; Oliveira *et al.* 2013; Zina *et al.* 2012).

Of all *Megadytes* species, by far the most mysterious one remains the largest, *M. ducalis*. Only the male holotype was known to date, collected before 1882 in "Brazil" and deposited in the Natural History Museum in London (Trémouilles 1989b; Jones 2010). With no exact locality data and no additional specimens ever sighted,

this "giant of the Dytiscidae" (Sharp 1882: 714) was listed as "extinct" in the IUCN Red data book (IUCN 2018). Its huge size, coupled with the lack of other specimens, led Jones (2010) to consider it a candidate for the world's rarest insect.

Here, we report the discovery of 10 additional specimens with more precise locality data, from historical collections as well as amongst unsorted historical material in the Muséum National d'Histoire Naturelle, Paris. This creates for the first time the possibility of a geographically focused research mission to hopefully rediscover the species alive. We also describe the unknown female of *M. ducalis*, discuss possible habitat requirements of the species in light of the locality data, and present additional records of the two other species of *Bifurcitus*.

Material and methods

A few specimens were cleaned with xylene and examined under a Leica M205C stereomicroscope at magnifications up to 60×. For examination of the male copulatory apparatus, specimens were relaxed in hot water for 30 minutes and the genital capsule extracted with strong, pointed forceps with curved tips. The median lobe of the aedeagus and the parameres were disarticulated and mounted together with the specimen.

Images were taken with a Canon EOS 550D camera fitted with either a 65 mm or MPE65 macro lens, attached to a Stackshot Macrorail controlled with Zerene Stacker software. Illumination was with two Canon Speedlite 430EX III-RT flashlights and translucent paper diffusers. Images were assembled using Helicon Focus software and cleaned using Adobe Photoshop CS6 software. The following abbreviations are used in the text: TL (total length), TL-H (total length without head), and TW (maximum width). Measurements were taken with a digital calliper "TACKLIFE". Exact label data are cited in quotation marks for all material. Our additional remarks are provided in square brackets.

Specimen depositories are as follows:

BMNH	British Museum Natural History, London
CLH	Collection of Lars Hendrich, Munich, Germany, property of NMW
CMM	Collection of Michaël Manuel, Paris, France
MNHN-Magasin	Muséum National d'Histoire Naturelle (indet. inserenda in boxes of unknown individual collection association)
MNHN-CG	Muséum National d'Histoire Naturelle, Coll. Legros, Paris, France
MNHN-CG	Muséum National d'Histoire Naturelle, Coll. Guignot, Paris, France
MNHN-CW	Muséum National d'Histoire Naturelle, Coll. Wehncke, Paris, France
MNHN-CR	Muséum National d'Histoire Naturelle, Coll. Régimbart, Paris, France
ZSM	SNSB-Zoologische Staatssammlung München, Germany

Taxonomy

Genus *Megadytes* Sharp, 1882

Subgenus *Bifurcitus* Brinck, 1945

Type species of *Megadytes*: *Dytiscus latus* Fabricius, 1801; of *Bifurcitus*: *Cybister giganteus* Laporte, 1835.

Diagnosis of subgenus *Bifurcitus*: Posterior metatibial spur (the narrower one) apically bifid.

Megadytes (Bifurcitus) ducalis Sharp, 1882

Megadytes ducalis Sharp, 1882: 713 (orig. descr.); Zimmermann 1920: 256; Blackwelder 1944: 80.

Megadytes (Bifurcitus) ducalis Sharp, 1882; Brinck 1945: 8; Trémouilles 1989b: 153; Miller & Bergsten 2016: 108; Nilsson & Hájek 2019: 80.

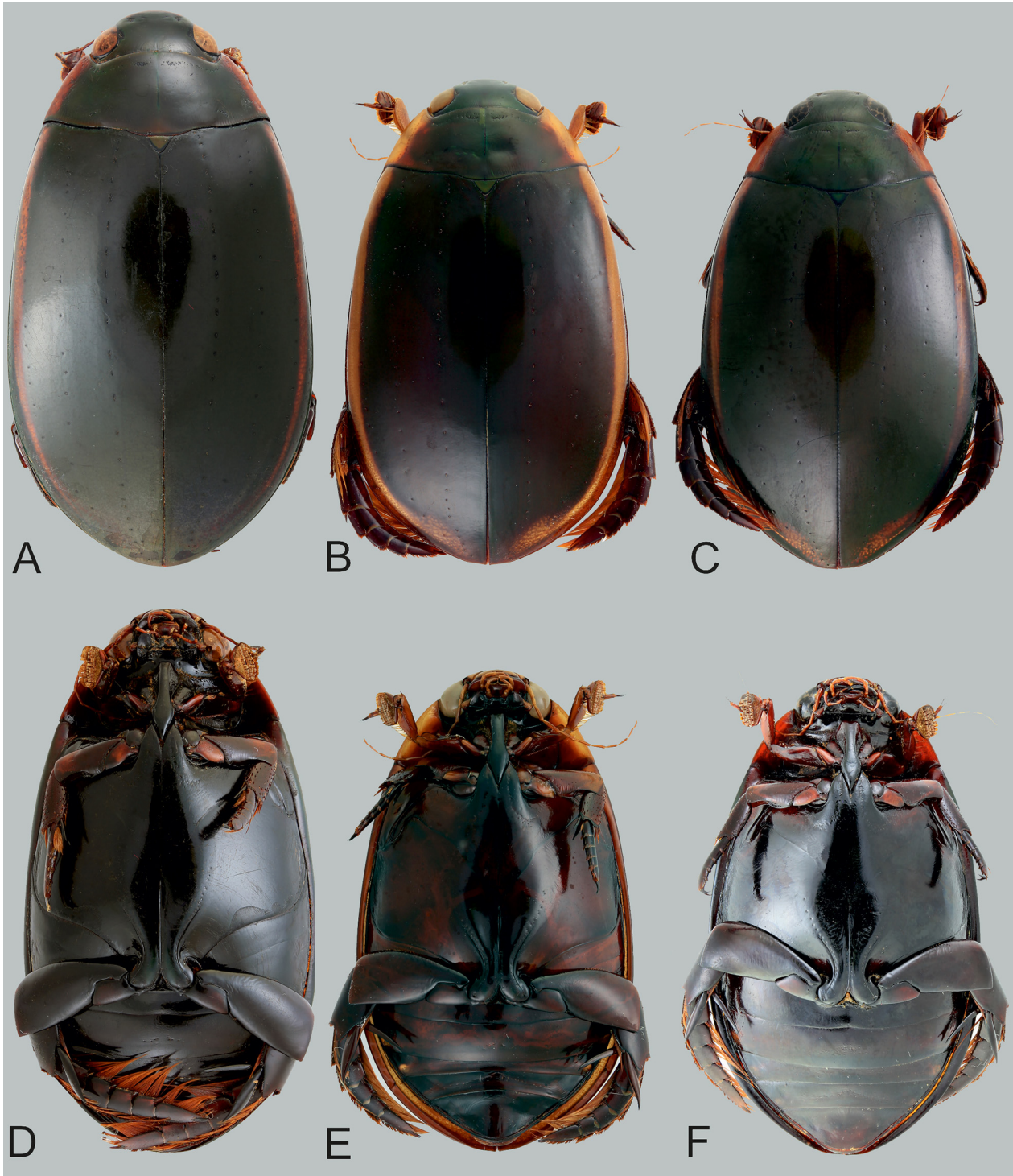


FIGURE 1. Habitus in dorsal view of: A) *M. ducalis*, B) *M. lherminieri*, C) *M. magnus*; habitus in ventral view of: D) *M. ducalis*, E) *M. lherminieri* (Ecuador, Esmeraldas), F) *M. magnus* (Paraguay, Cerro Lambaré).

Type locality. Brazil.

Type material examined. Holotype, male (BMNH): "Brazil, Saunders", "Type", "Megadytes ducalis Sharp".

Other material examined. Brazil: 1 male, 1 female, "San Antônio da Barra [= Condeúba, City Center is at -14.899° -41.968°, 660 m], Prov. de Bahia, Brésil"; 1 female, "S. Antonia da Barra pr. de Bahia Gounelle 11.12.1888" [printed label]; 1 female, "S. Antonia da Barra pr. De Bahia CH Pujol 1890" [printed label] (MNHN-CR, drawer 60); 1 female, "Bahia Brésil"; 1 male, "S. Antonia da Barra Pr. de Bahia Gounelle 11.12.1888" [printed label] (MNHN-CG, drawer 92); 1 male, "Museum Paris Brésil Coll. E. Gounelle 1915" [green printed label]

[among indet. material in separate drawer]; 1 female, "Brésil Bahia intr" [printed label], "ducalis Sharp" [handwritten label] (MNHN-CW); 1 female "Cybister giganteus Brésil" [handwritten label]; 1 female, "Museum Paris Brésil Coll. E. Gounelle 1915" [green printed label], "Megadytes ducalis Shp. San Antonio da Barra" [handwritten label] (MNHN-Magasin).

Descriptive notes. Large beetle (TL > 42.9 mm) of very robust and "thick" appearance (Fig. 2A). Descriptions of this species, based on the male holotype, were provided by Sharp (1882) and Trémouilles (1989). Here we provide photos of the habitus (Figs 1A, D, 2A, 3) and focus on morphological characters of the male in different views (Figs 7A–E).

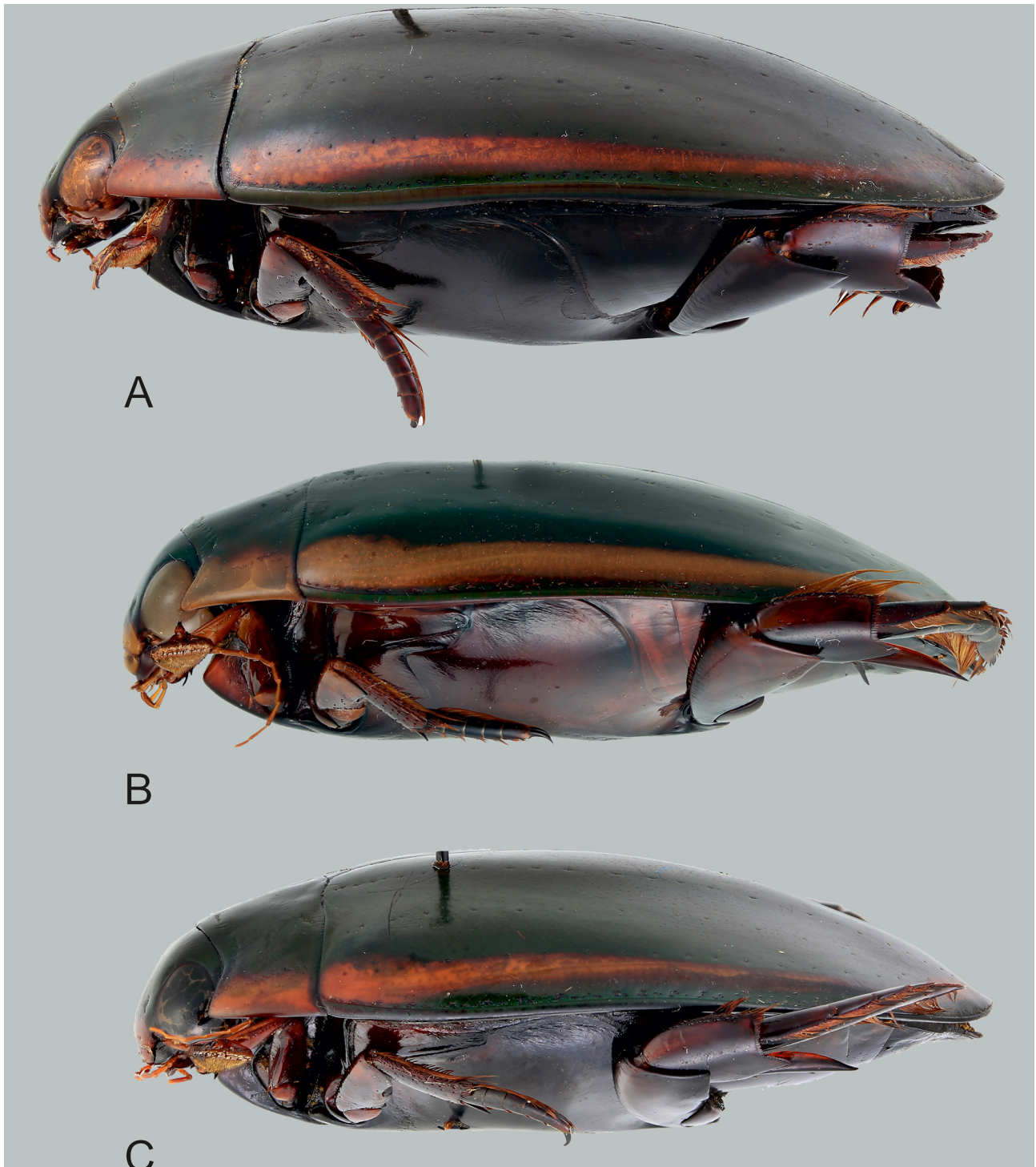


FIGURE 2. Habitus in lateral view of: A) *M. ducalis*, B) *M. lherminieri*, C) *M. magnus*.



FIGURE 3. Female of *M. ducalis* from collection Régimbart in MNHN [TL = 47.4 mm], the largest known diving beetle specimen in the world: "San Antônio da Barra, Prov. de Bahia, Brésil".



FIGURE 4. *Megadytes ducalis*, male specimen from collection Guignot: A) median lobe with parameres in ventral view, B) tip of median lobe in lateral view, C) anterior half median lobe in ventro-apical view; *Megadytes ducalis*, holotype: D) median lobe in ventral view (Foto: R. Angus). Scale bars = 1.5 mm.

The median lobe, with both parameres, of a male from Coll. Guignot is figured in ventral view (Fig. 4A), the anterior half of the median lobe in lateral view (Fig. 4B) and the tip of the median lobe in dorsal view (Fig. 4C). The median lobe of the holotype is presented in Fig. 4D. It appears much broader than in the other specimens we studied. This is apparently due to manipulation by previous researchers, perhaps J. Balfour-Browne, whereby cardboard wedges were inserted in between the main lobe and the ventral sclerite to expose the latter. This is actually seen in several other *Megadytes* specimens in the BMNH collection, and can lead to significant changes to the shape of the median lobe.

Female. No traces of elytral striae or any other kind of sexual sculpture on pronotum or elytra. Without protarsal disks and yellow setae on ventral surface of mesotarsomere I; otherwise no external difference with male. Broadest part of femur in hind legs 5.3 mm (Figs 1A, 7E).

Measurements, holotype: TL = 47.2 mm; TL-H = 44.1 mm; TW = 26.4 mm. **Additional specimens, males:** TL = 42.9–47.0 mm; TL-H = 41.3–43.8 mm; TW = 25.1–25.9 mm. **Females.** TL = 43.5–47.4 mm; TL-H = 40.7–44.1 mm; TW = 24.0–26.1 mm.

Note. The largest known specimen of *M. ducalis* (female, TL = 47.4 mm) is deposited in the collection of Maurice Régimbart in the Muséum National d'Histoire Naturelle in Paris (Fig. 3).

Distribution. Only known from Condeúba, Bahia, Brazil (Fig. 11).

Habitat. Unknown.

Megadytes (Bifurcitus) lherminieri (Guérin-Méneville, 1829)

Dytiscus lherminieri Guérin-Méneville, 1829: pl. 8.

Megadytes giganteus (Laporte, 1835); Sharp 1882: 713 (synonymy); Zimmermann 1920: 256; Blackwelder 1944: 80.

Megadytes (Bifurcitus) giganteus (Laporte, 1835); Brinck 1945: 8; Trémouilles & Bachmann, 1980: 118; Trémouilles 1989b: 160; Nilsson 2001: 94.

Trogus olivieri Crotch, 1872: 205, by indication to *Dytiscus costalis* Fabricius sensu Olivier 1795: 9; Wilke 1920: 246 (synonymy).

Megadytes (Bifurcitus) lherminieri (Guérin-Méneville, 1829); Nilsson & Fery 2006: 55; Miller & Bergsten 2016: 107; Nilsson & Hájek 2019: 81.

Type localities of *Dytiscus lherminieri*: Guadeloupe (by indication); of *Cybister giganteus*: Brazil; of *Trogus olivieri*: French Guyana (Cayenne), Surinam.

Type material. Location of the holotype of *D. lherminieri* and syntypes of *C. giganteus* and *T. olivieri* unknown.

Material examined. **Mexico:** 1 female, "Mexiko", "Megadytes giganteus det. Zimmermann" (ZSM); 1 female, "Mexique Salina Cruz" [Oaxaca Provinz], "Samml. A. Zimmermann" (ZSM); 1 female, "Mex. Behrens", "R. Mouchamps 1956 Megadytes giganteus Cast."; 1 male, "Mexiko – Jalisco Puerto Vallarta 03.02.20009 K. Renner", "Yelapa Wasserfall-Tümpel" (CLH); 1 female, "Mexico Yukatan/Tulum 1.3.-15.3.2000 leg. O. Blochwitz" (CLH); 1 female: "Mexico Sinaloa 8 mi S. Mazatlan, VII-27-73" (CLH); **Barbados:** 1 male, "Barbados: W.I., St. Philipp, pool on Stewarts Hill, 19.xii.1964" (BMNH); **Cayman Islands:** 49 exs., "17.iv-26.viii.1938. Oxf. Un. CAYMAN IS. Biol. Exped. Coll. By C.B. Lewis, G.H. Thompson", "28 vii.1938. Grand Cayman, East end of interior Wintersland Cistern."; "Pres. Hope Dept. Oxford B.M. 1967-147", "Megadytes gigantea Laporte det PJSpangler" (BMNH); **French Guyana:** 1 male, "French Guyana, Awala-Yalimapo, Marais de Panato, pond, N5°44'01" W53°55'48", VII 2003, Manuel & Alié leg. (hand net, by night)" (CMM), 1 female, "French Guyana, Awala-Yalimapo, Marais de Panato, Station de lagunage, N5°44'31.4" W53°55'48.8", 31 VII 2004, Manuel & Timarcha leg. (hand net)" (CMM); 1 male, 1 female, "French Guyana, Awala-Yalimapo, marais de Panato, Station de lagunage, N5°44'32" W53°55'55", 5 VIII 2004, Manuel & Timarcha leg. (trap)" (CMM); **Guadeloupe:** 1 female, "Guadeloupe, Basse-Terre, Sainte-Rose, Etang du Vieux Fort, N16°21'02.4" W61°45'17.7", 15 V 2012, Manuel leg. (hand net)" (CMM), 3 males, "Guadeloupe, Grande-Terre, Le Moule, Etang Fromager, N16°19'18" W61°24'04", 18 V 2012, Manuel leg. (hand net)" (CMM); 4 males, 4 females, Guadeloupe, Grande-Terre, Sainte Anne, in dense belt of *Eleocharis* surrounding a pond, N16°14'19" W61°21'03.6", 18 VIII 2013, Manuel, Chaillé & Sabroux leg. (traps); 3 males, 3 females, "Guadeloupe, Basse-Terre, Sainte Rose, Etang du Vieux Fort, N16°21'02-04" W61°45'17-20", 21 VIII 2013, Manuel, Chaillé &

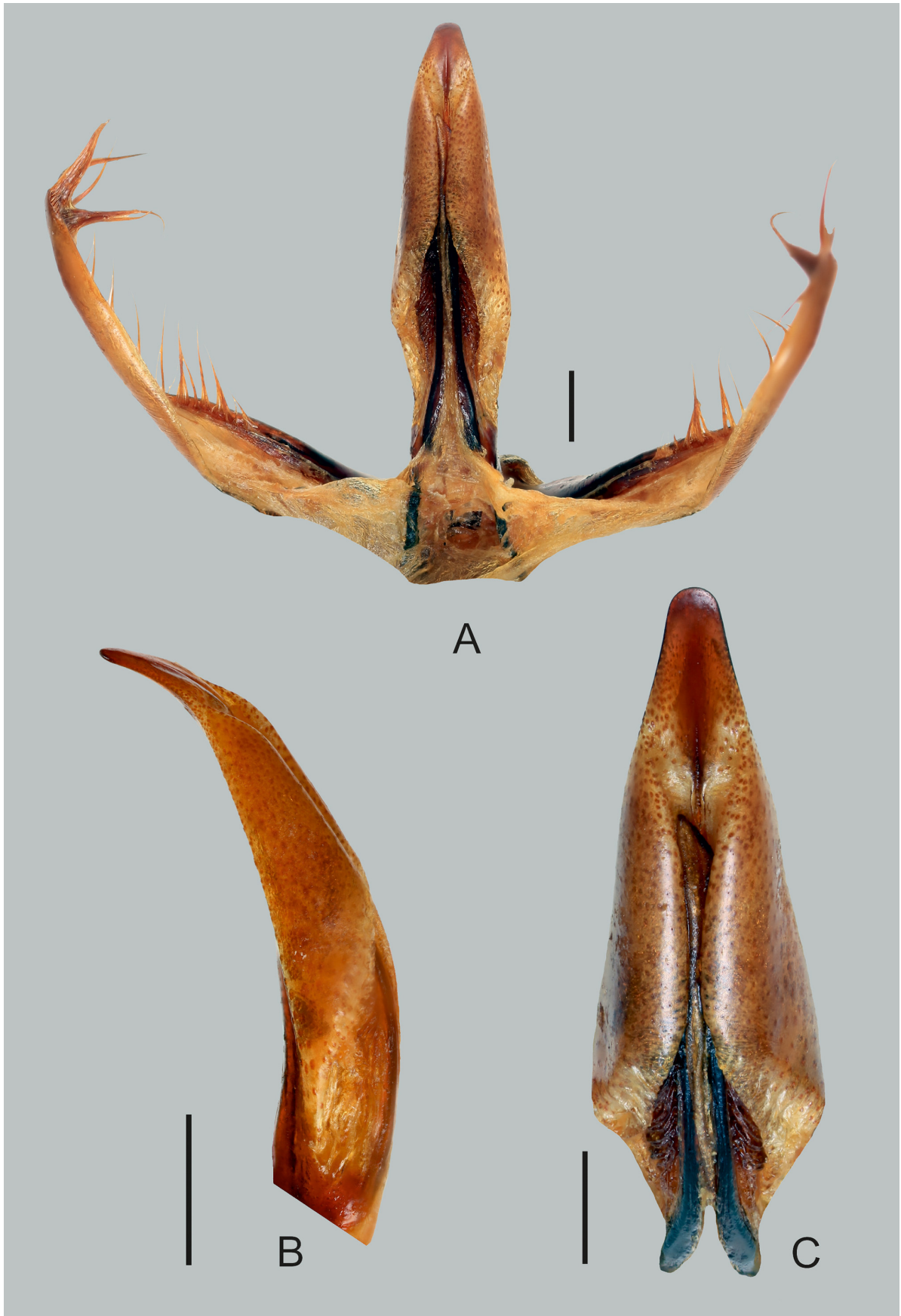


FIGURE 5. *Megadytes lherminieri*: A) median lobe with parameres in ventral view, B) tip of median lobe in lateral view, C) median lobe in ventro-apical view to show the flat tongue-like tip. Scale bars = 1.5 mm.

Sabroux leg. (traps)" (CMM); 1 male, 6 females, Guadeloupe, Grande-Terre, Anse Bertrand, savane Desrosière, pond, N16°30'09" W61°28'25", 27 VIII 2013, Manuel, Chaillé & Sabroux leg. (trap); **Puerto Rico**: 1 female: "S. Juan 1.6.34" (CLH); **Panama**: 1 male, "Panama, Chiriqui Prov., David, 5.8.1991, leg. S. Lehmann" (CLH); **Guatemala**: 1 male, "Guatemala", "Sammlung Cl. Müller" (ZSM); **Costa Rica**: 1 male, "C. Am. Costa Rica, Santa Rosa NP, Guanacaste, III.1993 leg. K.-G. Bernhardt" (CLH); **Surinam**: 1 female, "Surinam 4-5", "alte Sammlung" (ZSM); **Guyana**: 1 female, "B. Guinea Bartlett Coll. B.M. 1943-60." (BMNH); **Ecuador**: 1 male, "Same Esmeraldas Ecuador; 05.05.1997 leg. B. Hermann" (CLH); **Peru**: 1 female, "Peru" (BMNH); **Brazil**: 1 female, "Brasilia" (BMNH); **Venezuela**: 1 female: "Venezuela (Guàrico) Cabruta nr. Caicara del Orinoco, 30m 07°38'N 66°15'W 20.VIII.2001, S. Gottwald leg." (CLH); 1 male: "Venezuela (Apure) ca. 50 km nördlich San Fernando d'Apure 20.VIII.2001 leg. O. Hillert" (CLH); 1 male, "Venezuela/Bejuma-Carabobo (10.11N-68.16W), 800m, Via Palmichal/Finca Guarapito, 8.VII.1994, Casa Maria, R. Ehrmann leg." (CLH); **Bolivia**: 1 male, "Fertin Esteros Bolivia III.26 D. Chaco-Exped.", "Megadytes giganteus Zim." (ZSM).

Descriptive notes. A description of this species was given by Sharp (1882) (as *M. giganteus*). Here we provide photos of the habitus (Figs 1B, E, 2B) and focus on morphological characters of the male in different views (Figs 8A–C). The median lobe with both parameres is figured in ventral view (Fig. 5A), the tip of the median lobe in lateral view (Fig. 5B), and the median lobe in ventro-apical view (Fig. 5C).

Variability. Specimens from Venezuela and French Guyana differ from those of the type locality in Guadeloupe by: 1) habitus slightly broader and more convex; in lateral view maximum height situated a little more posteriorly; 2) in male, sexual pubescence on first mesotarsomere even more reduced, only present on proximal half of ventral midline (Guadeloupe: along entire ventral midline); distal half with only large punctures but no setae; 3) protarsal disk slightly smaller; 4) base of prosternal process antero-ventrally a bit broader and more angulate (Guadeloupe: more rounded); 5) parameres with transverse rugae more deeply impressed; apical region of median lobe in ventral view with lateral margins slightly less convergent and apex slightly broader. Further studies, including molecular work, will reveal whether *Megadytes lherminieri* is a species complex or not.

Distribution. The species is known from southern Mexico, Central America, Cuba, Puerto Rico, Caribbean, Venezuela, Bolivia, Peru, French Guyana, Surinam and the southern part of Brazil (Blackwelder 1944; Trémouilles & Bachmann 1980; Ferreira-Jr. 1993; Blanco 2016). This is the **first record** of the species for **Ecuador** (Fig. 11).

Habitat. All kinds of well-vegetated and permanent lentic sites such as larger swamps, ponds and oxbow lakes, farm dams and reservoirs. Ferreira (1993) collected the larvae in a sand dune swamp and several temporary ponds located in Maricá, Rio de Janeiro State, Brazil. Most records are from open and exposed sites and not in forested areas. Many specimens were collected at light. This species was sampled by one of us (MM) at 7 different localities in French Guyana and Guadeloupe (Figs 9, 10A). All were permanent lentic water bodies of moderate to large size, with neutral to basic water, in open or semi-shaded situations. The bottom was moderately to heavily covered with organic substrata (decaying plant material) and the mineral substratum consisted of clay (3 sites) or was entirely composed of organic material (4 sites). The water was clear in three of the collecting sites and moderately to very turbid in the remaining ones. All places where *M. lherminieri* was found were characterised by rich vegetation, with hygrophytes in the surroundings of the water bodies and a more or less continuous belt of helophytes (Cyperaceae and/or Poaceae; Figs 9, 10A); in addition, angiosperms with floating leaves (such as *Nymphaea*) were observed in 3/7 sites and all sites but one were densely colonised by submerged aquatic angiosperms. Four of the collecting sites clearly received substantial nutrients loads resulting from human activities and in one site the presence of *Azolla* was observed, indicating that *M. lherminieri* can tolerate some degree of anthropogenic eutrophication. From our field experience, the optimal micro-habitat for *M. lherminieri* is within dense belts of helophytes (e.g. *Eleocharis* and other large Cyperaceae, large Poaceae, etc.) at a moderate depth (e.g. 30 to 50 cm).

Biology. A female specimen (adult at the time of collecting) was kept alive in an aquarium for 3 years 9 months (Fig. 10C). As far as we know, this is the first record of a lifespan in *Megadytes*.

***Megadytes (Bifurcitus) magnus* Trémouilles & Bachmann, 1980**

Megadytes (Bifurcitus) magnus Trémouilles & Bachmann, 1980: 118 (orig. descr.); Trémouilles 1989b: 161; Miller & Bergsten 2016: 108; Nilsson & Hájek 2019: 81.

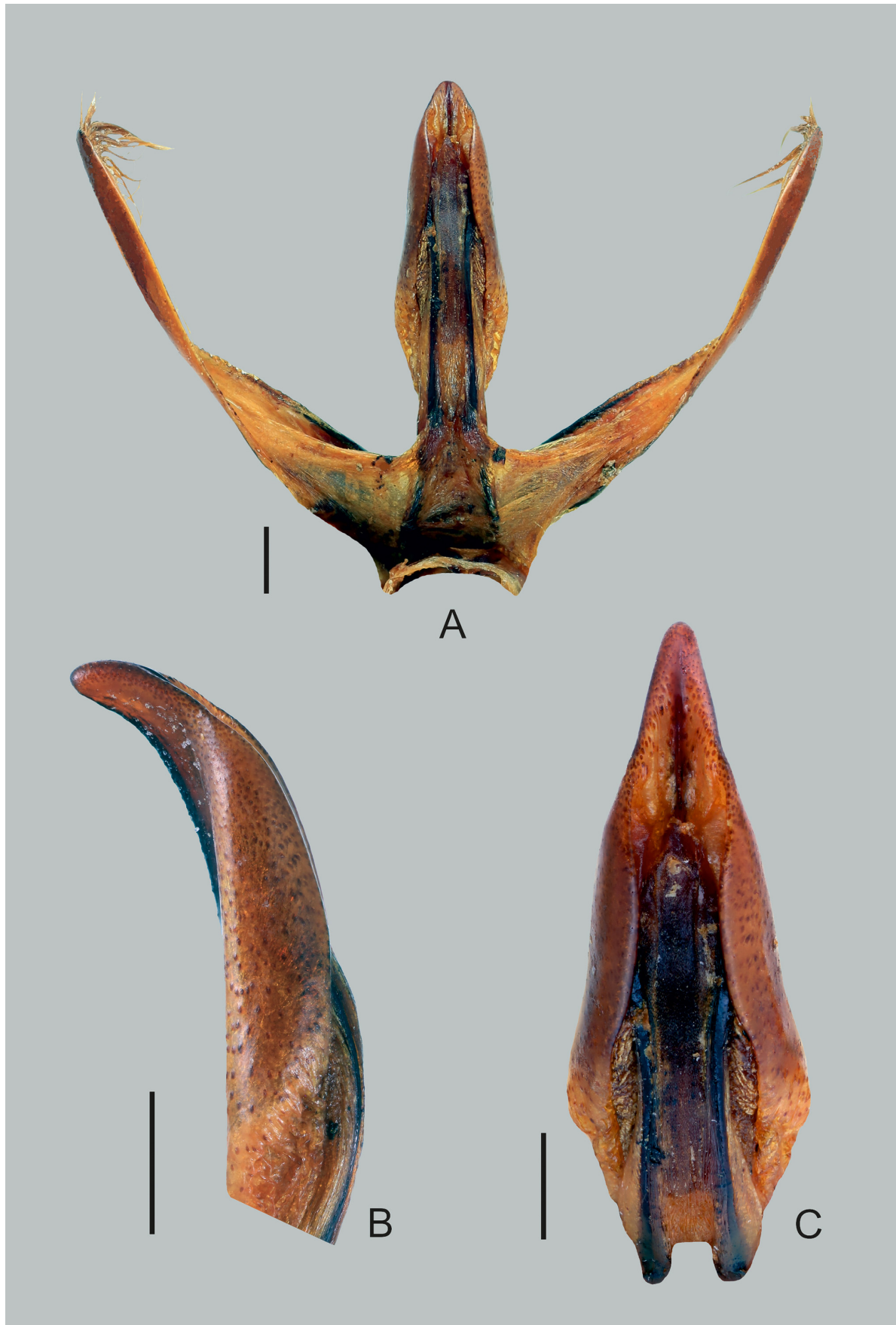


FIGURE 6. *Megadytes magnus*: A) median lobe with parameres in ventral view, B) tip of median lobe in lateral view, C) median lobe in ventro-apical view to show the long nose-like tip. Scale bars = 1.5 mm.



FIGURE 7. *Megadytes ducalis*, male from collection Guignot: A) frontal view, B) ventral view of head and protarsus, C) left middle leg, D) dorso-lateral view of left side of head, pronotum and elytral base, E) ventro-lateral view of left hind leg. Scale bars = 5 mm.

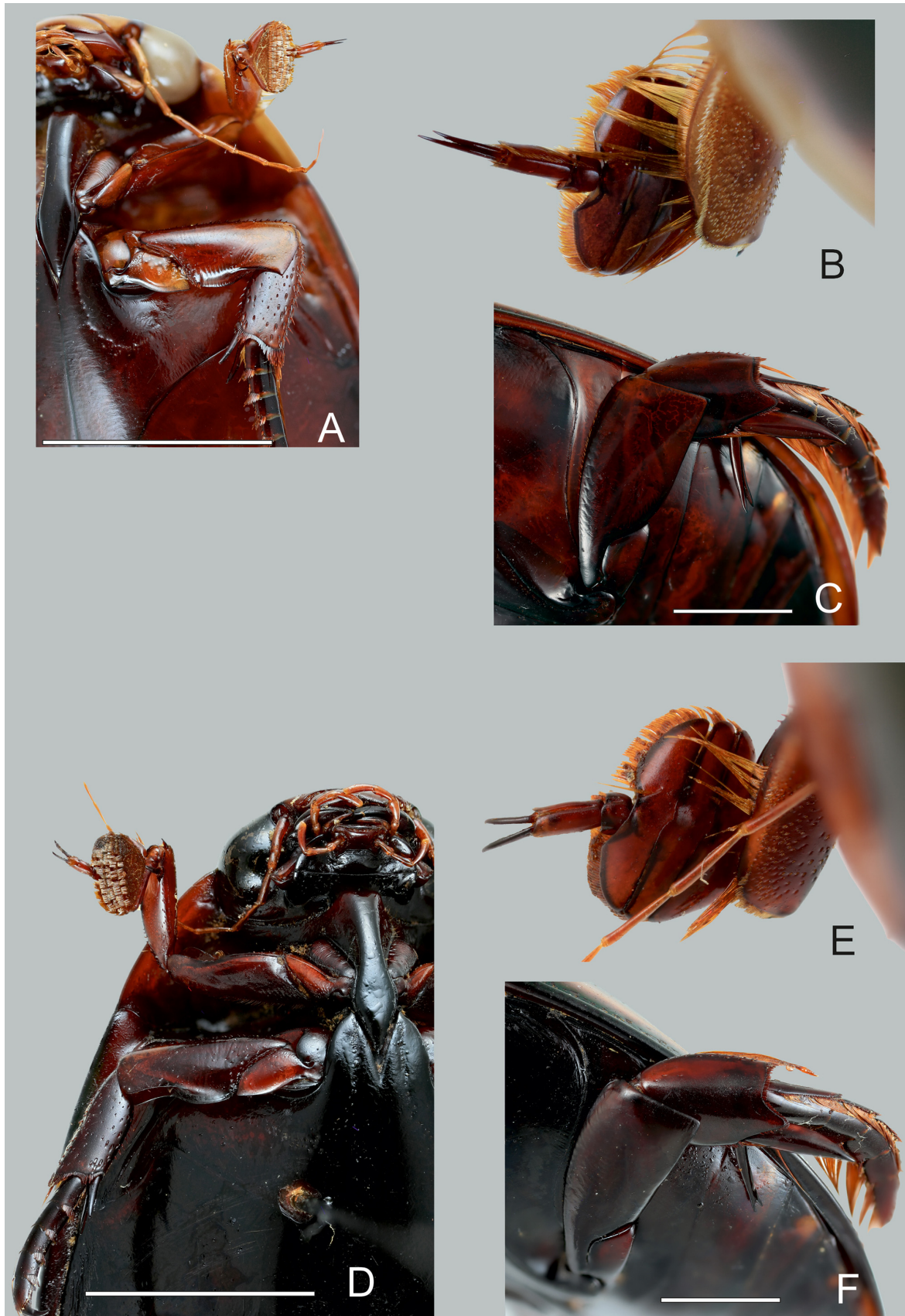


FIGURE 8. *Megadytes lherminieri*, male, Ecuador, Esmeraldas: A) ventral view of head, left protarsus and left middle leg, B) dorsal view of left protarsus, C) ventro-lateral view of left hind leg; *M. magnus*, male, Paraguay, cerro Lambaré: D) ventral view of head, right protarsus and right middle leg, E) dorsal view of left protarsus, F) ventro-lateral view of left hind leg. Scale bars = 5 mm.

Type locality. Argentina, Santa Fe.

Type material examined. Paratype: 1 male, "Argentina: S. Fe Ceres III.1943 leg. Polmer" [handwritten label], "PARATYPUS" [red printed label], "Brit. Mus. 1989-185" [printed label], "Col. A.O. Bachmann" [printed label], "Megadytes (Bifurcitus) magnus E.R. Trémouilles y A.O. Bachmann ano 1979" [red handwritten label] (BMNH).

Other material examined. Paraguay: 1 male, 2 females, "Paraguay/Chaco Dep. Boquéron 10 km SE Mariscal Estigarribia, 2.2.1990, leg. U. Drechsel" (CLH); 4 males, 6 females, "Paraguay/Chaco Dep. Boquéron 10 km SE Mariscal Estigarribia, 10.2.1990, leg. U. Drechsel" (CLH, ZSM); 1 male, "Paraguay/Cerro Lambaré, 5.6.1992, leg. U. Drechsel/Coll. Hendrich" (CLH); 1 male, "Paraguay/Dep. Central, Asunción, 31.10.1991, 5.6.1992, leg. U. Drechsel/Coll. Hendrich" (CLH); **Brazil:** 1 female, "Brasilien, Sao Paulo, 10.12.1984, in swimming pool, Gottwald leg." (CLH).

Descriptive notes. A description of this species was given by Trémouilles & Bachmann (1980). Here we provide photos of the habitus (Figs 1C, F, 2C) and focus on morphological characters of the male in different views (Figs 8D–F). The median lobe with both parameres of a specimen from Mariscal Estigarribia in Paraguay, is figured in ventral view (Fig. 6A), the tip of the median lobe in lateral view (Fig. 6B), and the tip of median lobe in ventro-apical view (Fig. 6C). Note that Figs 6A and C show the median lobe of the same individual, tilted at different angles.

Distribution. Southern part of tropical and subtropical South America. The species was described from Argentina, Paraguay and Uruguay, and later recorded from Brazil (Trémouilles 1989b) (Fig. 11).

Habitat. Unknown, probably similar to *M. lherminieri*. Most of the specimens in Paraguay were collected at light in a savannah region with temporary swamps and permanent farm dams. The swimming pool in Sao Paulo, where the single female has been collected, was not far away from a big reservoir or dam, overgrown with water lilies and water hyacinths (S. Gottwald pers. com.).

Differential diagnosis of the species in the subgenus *Bifurcitus*

Megadytes ducalis can be distinguished from *M. lherminieri* and *M. magnus* by the shape of the median lobe (Figs 4–6) and body size and shape (Figs 1, 2). Even the smallest *M. ducalis* (42.9 mm) is somewhat larger than the largest examined *M. lherminieri* (42.5 mm) and *M. magnus* (42.0 mm), the latter two appearing more broadly-oval in dorsal view. In lateral view, *M. magnus* and *M. lherminieri* differ from *M. ducalis* by their more flattened bodies (Fig. 2). The latter appears more robust and thicker. The sexual pubescence on the ventral surface of the first mesotarsomere of the male is much more developed in *M. ducalis* (Fig. 7C) than in *M. lherminieri* (Fig. 8A) and *M. magnus* (Fig. 8D). The broadest part of the hind femora is 5.1–5.3 mm in *M. ducalis* and 4.8–5.0 mm in *M. magnus* and *M. lherminieri*. Females of all three species are shiny without any signs of striae on the dorsal surface.

The observation of differences in length of setation on the dorsal side of protarsomere V between *M. magnus* (long setae) and *M. lherminieri* (short setae) (Trémouilles & Bachmann, 1980: 123) seems to be an artifact. They can be of the same length, longer or shorter (Figs 8A, E) or even missing, likely due to wear during life.

Megadytes lherminieri is distributed from Mexico, the Caribbean, over northern tropical South America to southern Brazil, whereas *M. magnus* is restricted to south-eastern tropical and subtropical America. According to our present knowledge, it seems that *Megadytes ducalis* has a restricted distribution in the cerrado of Western Brazil and might be sympatric if not syntopic with *M. lherminieri* (Fig. 11).

Discussion

At the end of the 19th Century, Santo Antônio da Barra [= Condeúba] in Bahia was a major locality for insect trading in the cerrado biome of Brazil. It has been documented that local people sold their catches on a weekly market in the small town (Schenkling 1906). The area around the village was especially famous as a habitat for the mole beetle (*Hypocephalus armatus* Desmarest, 1832) (YouTube video: <https://www.youtube.com/watch?v=IFozCrcLnHM>), at that time a highly prized ground-dwelling longhorn beetle (Vesperiidae), which has a restricted distribution in north-eastern Brazil.

From 1884 to 1914, the French entomologist and naturalist Pierre-Émile Gounelle (Paris, 9 June 1850–2 October 1914, Paris) made seven self-financed scientific expeditions to eastern and north-eastern Brazil. He is chiefly remembered for his studies on the Cerambycidae he found (Gounelle 1911) and was at least once for a longer period in Condeúba where he studied the behavior of *H. armatus* in detail (Gounelle 1905). Furthermore, he collected many other insects, spiders and plants that later became part of the collections at the Muséum National d'Histoire Naturelle.

Based on label data (Museum Paris Brésil Coll. E. Gounelle 1915) associated with several specimens, we believe that Gounelle brought a part, if not all, of the historical specimens of *M. ducalis* to Paris, where the series was distributed amongst famous collections of the time (Régimbart, Wehncke / Oberthür). Nevertheless, the French specimens were unknown to the scientific community until now and even Trémouilles & Bachmann (1980) and Trémouilles (1989a, 1989b) overlooked them when revising the genus.

Given the unique climatic and environmental parameters of the Brazilian cerrado, with a distinct wet (with temporary swamps in wet savannah) and dry season (dry savannah habitats with residual lakes and pools), and the rarity of *M. ducalis* in collections, which might indicate a restricted distribution as for *Hypocephalus*, the rumours that the holotype of *M. ducalis* was found in the bottom of a canoe in the Amazon region (Jones 2010) seem very doubtful.

During the last 25 years the cerrado has been increasingly threatened by industrial scale monoculture farming, particularly of soybeans. The unregulated intensification of industrial agriculture, the burning of vegetation for charcoal and the development of dams to provide irrigation have already been identified as potential threats to several rivers in the region (e.g. Jepson 2005). To determine whether *M. ducalis* is really extinct in the wild (IUCN 2018), it will be necessary to intensify water beetle research in Brazil, especially in the under-collected cerrado biome of Bahia and adjacent states (Pinheiro *et al.* 2002; Brasileiro *et al.* 2005).

Since large *Megadytes* species prefer densely vegetated habitats (Figs 9A, B, 10A), where it is very difficult or often almost impossible to use a sweep net, and because *Megadytes* are highly efficient swimmers, they are sampled more effectively by using trapping techniques rather than hand-netting (as is the general rule for species of Cybistrinae). We routinely obtain good success with traps made from 5 litre plastic bottles, to which we add an entrance funnel consisting of an aluminium can, with both extremities removed (Fig. 10B). The diameter of the entrance funnel can be adjusted easily to allow beetles to enter the trap, whilst lowering their chances of finding the exit. We bait these traps with fresh beef, pork or chicken liver, preferentially frozen prior to use for better efficiency, but other kinds of bait (e.g. fish flesh) are also attractive (e.g. Aiken & Roughley 1985; Hilsenhoff 1987; Volkova *et al.* 2013).

For trapping to be effective one needs to position the entrance within a dense clump of vegetation (helophytes or aquatic plants), without any volume of free water between the vegetation and the trap. The position of the trap in the water column can be adjusted by fastening it to the vegetation and/or anchoring it to the bottom, e.g. using a stone. These traps are effective during daytime as well as overnight. In densely populated habitats, large numbers of moderate to large diving beetles (e.g. in Neotropical lentic waters, species of *Hydaticus*, *Thermonectus* and *Megadytes*) often enter the trap in just a few hours.

As an example, in Guadeloupe on 27 August 2013, in the dense mat of Poaceae visible in Fig. 9A, a single trap left for only 2 hours during the day attracted 7 specimens of *M. lherminieri*, 15 specimens of *Megadytes* (*Megadytes*) *fraternus* Sharp, 1882, 13 specimens of *Thermonectus basillaris* (Harris, 1829) and 19 specimens of *T. circumscriptus* (Latreille, 1809). As a consequence, even with the trap only partially filled with water, to allow beetles to surface, they often rapidly die of asphyxia, particularly when there is a high ambient temperature. To avoid significant population damage during surveys using this kind of trap, we strongly advocate using traps with bases pierced with small several holes, in order to permit air renewal. For these holes to remain above the water surface, and to ensure that a sufficient volume of air is maintained inside the trap, it is necessary to attach a floating device, at an appropriate height, against the external surface of the trap (e.g., a 25 ml closed perspex tube fixed with tape as can be seen in the lower part of Fig. 10B).

Future fieldwork should be concentrated around suitable habitats in the surroundings of Condeúba and elsewhere in the remaining cerrado of the region. Furthermore, it seems important to check all scientific collections in Brazil, where macroinvertebrates from wetland surveys are stored and not yet identified to species level.



FIGURE 9. Habitat of *M. lherminieri* in Guadeloupe: (A) Pond in Savane Desrosière, Anse Bertrand, Grande-Terre, Guadeloupe, 27.VIII. 2013, N16°30'09" W61°28'25"; (B) Pond near Sainte Anne, Grande-Terre, Guadeloupe, 17.VIII. 2013, N16°14'19"/W61°21'03.6" (Photos: M. Manuel).



FIGURE 10. Collecting method for *M. lherminieri* in Guadeloupe: (A) Close up view at Etang Fromager, Le Moule, Grande-Terre, Guadeloupe, 18 V 2012, N16°19'18"/W61°24'04"; (B) Example of a trap with *Megadytes* and other diving beetles inside (trapping session in the pond shown in Fig. 9A); (C) Female of *M. lherminieri* from Guadeloupe (Photos: M. Manuel).



FIGURE 11. Distribution of the subgenus *Bifurcitus* in Central and South America: White line: distribution of *M. lherminieri*; black line: distribution of *M. magnus*; red spot: only known locality for *M. ducalis*.

Conclusions

For the first time we reveal precise locality data for the World's largest diving beetle, *Megadytes ducalis* Sharp, 1882—currently thought to be extinct. This provides the opportunity for a focused search effort to determine the conservation status of this highly emblematic animal, the distribution and habitat preference of which have remained shrouded in mystery for more than a century. Our findings highlight the importance of existing collections in biodiversity conservation, including that often considered the World's most extensive archive of biodiversity: the holdings of the Muséum National d'Histoire Naturelle in Paris.

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