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A taxonomic revision of the New World genus *Agamopus* Bates, 1887 (Coleoptera: Scarabaeinae: Ateuchini)

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Abstract. Differential diagnoses, updates on distribution ranges, and an illustrated identification key are given for all species of *Agamopus*. The first record for *A. castaneus* from Brazil is given. Type specimens of all valid species-group names are studied and illustrated. Notes on the natural history of *Agamopus* species, as well as brief phylogenetic comments, are presented. The new species *Agamopus joker* sp. nov. is described based on a male from Paraná, southern Brazil. Lectotypes are designated for *Canthon unguicularis* Harold, 1883 and *Agamopus lampros* Bates, 1887. We also propose the transfer of *Agamopus convexus* Balthasar, 1965 to the *Ateuchus ovalis* species group (*Ateuchus convexus* comb. nov.) based on morphological features of the protibiae, clypeal teeth, and the posterior margin of the pronotum and pygidium.

Keywords. Dung beetles, Neotropical region, Scarabaeoidea, new combination, *Ateuchus*.

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Introduction

Agamopus Bates, 1887 is a New World genus distributed from western Mexico to southern Brazil. To date, five species are recognised from the following places: *A. castaneus* Balthasar, 1938, from French Guiana and Suriname; *A. convexus* Balthasar, 1965, from Brazil; *A. lampros* Bates, 1887, from western

Mexico to northern South America; *A. unguicularis* (Harold, 1883), from Bolivia (Santa Cruz) and Brazil (Minas Gerais, São Paulo and Santa Catarina); and *A. viridis* Boucomont, 1928, from central (Goiás) and southeastern (Bahia and São Paulo) Brazil (Halffter & Martínez 1968; Howden & Young 1981).

A previous, and hitherto the only, taxonomic revision of the genus was conducted by Halffter & Martínez (1968). According to Halffter & Martínez (1968) and subsequent authors (e.g., Howden & Young 1981; Medina & Lopera-Toro 2000; Vaz-de-Mello *et al.* 2011; Boilly & Vaz-de-Mello 2013), species of *Agamopus* are easily recognizable by the presence of a transverse sulcus on the pygidium (as in Figs 4D and 9E). For a comprehensive description of the genus, see Halffter & Martínez (1968) and Howden & Young (1981).

Harold (1883) was the first author to mention the sulcus on the pygidium in a species description. Even so, he apparently did not consider this character to be sufficient to delimit a new genus, as he placed his newly described species in the genus *Canthon* (*Canthon unguicularis* Harold, 1883). Four years later, Bates (1887) described the genus, with *Agamopus lampros* as the type species by original monotypy. However, Bates did not mention the sulcus on the pygidium in the genus or the species description. Boucomont (1928), Balthasar (1938) and Pereira (1947) all did mention this sulcus on the pygidium in the descriptions of, respectively, *A. viridis*, *A. castaneus* and *A. martinezi*, although it had not yet been stated as a diagnostic character of the genus.

After an examination of the type specimens, Halffter & Martínez (1968) observed the presence of the sulcus in *C. unguicularis*, transferring this species to the genus *Agamopus* and proposing that *A. martinezi* Pereira, 1947 was a junior synonym of *A. unguicularis.* These authors also suggested that *Agamopus convexus* Balthasar, 1965 does not belong to the genus *Agamopus*, considering the absence of the transverse sulcus on the pygidium in this species (for details, see Halffter & Martínez 1968). However, despite this observation, they refrained from transferring this species to another genus, and it has so far remained listed as *Agamopus convexus* in catalogues (e.g., Schoolmeesters 2021; Vaz-de-Mello 2021).

Since the last revision of *Agamopus*, a large number of specimens have been deposited in South American collections, but no one has paid special attention to the group during the last 50 years. After examination and comparative morphological analyses of specimens of this genus from various collections, we discovered a species of *Agamopus* that is still unknown to science.

Apart from presenting this new species, the present work aims to update the diagnoses of the *Agamopus* species, propose taxonomic changes and expand the known geographical range of all species in the genus. Images of type specimens of all taxa and their respective labels are presented, as well as an identification key to the species. We also propose the transfer of *Agamopus convexus* to the genus *Ateuchus* Weber, 1801 based on morphological features of the protibiae, clypeal teeth, posterior margin of the pronotum and shape of pygidium. Lectotypes of *Canthon unguicularis* (currently *Agamopus unguicularis*) and *Agamopus lampros* are designated, following Article 74.1 of the ICZN (1999), in order to fix each of the names to a single specimen.

Material and methods

Material

The type specimens of all available species-group names were personally examined. Each type specimen was traced based on the collections of the respective author (following the specialized literature [i.e., Horn *et al.* 1990; Evenhuis 1997]) and recognized by the author's handwriting and/or characteristic signature on the labels. Apart from the type material, a total of 594 additional specimens housed in the

institutions cited below was also personally examined. The names of the respective curators are given in brackets.

Repositories

BMNH = The Natural History Museum (formerly British Museum, Natural History), London, United Kingdom (Maxwell Barclay)
CEAH = Coleção Entomológica Adolph Hempel, Instituto Biológico de São Paulo, São Paulo, Brazil (Sérgio Ide)
CEMT = Setor de Entomologia da Coleção Zoológica da Universidade Federal de Mato Grosso (UFMT), Cuiabá, Mato Grosso, Brazil (Fernando Z. Vaz-de-Mello)
CMN = Canadian Museum of Nature, Ottawa, Ontario, Canada (François Génier)
DZUP = Coleção Entomológica Padre Jesus Santiago Moure, Universidade Federal do Paraná (UFPR), Curitiba, Paraná, Brazil (Lúcia Almeida)
MNHN = Muséum national d'Histoire naturelle, Paris, France (Olivier Montreuil and Antoine Mantilleri)
MZSP = Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (Sônia Casari and Carlos Campaner)
NMPC = National Museum (Natural History), Prague, Czech Republic (Jiří Hájek)
PKLC = Paul K. Lago Private collection, Biology Department, University of Mississippi, Oxford, Mississippi, USA (Paul K. Lago)

Methods

Dissected male specimens were placed in warm water for cleaning and to facilitate the extraction of the aedeagus (for details of the procedure, see Costa-Silva & Diéguez 2020; Cristóvão & Vaz-de-Mello 2020). For all dissected specimens, the aedeagus and abdomen were placed in a microvial with glycerine and pinned below the respective specimen. For description and analyses of specimens, a Leica stereo microscope model S8AP0 was used.

Photographs were prepared using a Leica model m205C (7.8×–160.0×) stereo microscope with image capture system MC190 HD. The set of images was subsequently edited using Adobe Photoshop. Scale bars and body measurements (in mm) were made using Leica software. Photographs not prepared by the authors are indicated in the figure captions with their respective copyrights. Distribution maps of species were prepared using ArcGIS ver. 10.8 software.

Treatment of type and non-type labels

Data of type labels were transcribed ipsis litteris in quotation marks (“”). A forward slash (/) was used to indicate a new line on the same label. Any additional or explanatory information was given in square brackets ([]). Non-type material was interpreted from each label and organized in the following manner: country (including French Guiana – e.g., **BRAZIL**; **FRENCH GUIANA**); State, Province or Department (e.g., **Rio de Janeiro**); number of males (♂ or ♂♂), female (♀ or ♀♀) and/or gender not determined (e.g., 1 spec. or 2 specs); city and/or specific locality (when cited); date and collector (when cited); collection method (when cited); and collection (e.g., CEMT). The countries and first-order political subdivisions are given in a north-south sequence. Cities or specific localities are given in alphabetical order.

Morphology nomenclature

For the holotype description, the terminology of Harris (1979) was followed for the microsculpture of the integument. The general morphological terminology proposed by Edmonds (1972) for Scarabaeinae was used, with modifications in the nomenclature for pleural and ventral sclerites as employed by

Lawrence *et al.* (2010). Finally, Cristóvão & Vaz-de-Mello (2020) were followed for the names of the structures of the aedeagus.

Results

Systematics

Class Insecta Linnaeus, 1758
Superfamily Scarabaeoidea Latreille, 1802
Family Scarabaeidae Latreille, 1802
Subfamily Scarabaeinae Latreille, 1802
Tribe Ateuchini Perty, 1830

Genus ***Agamopus*** Bates, 1887

Agamopus Bates, 1887: 42 (original description).

Agamopus – Gillet 1911: 49 (catalogue). — Blackwelder 1944: 203 (catalogue); 1973: 6 (catalogue). — Pereira 1947: 4 (key to species); 1954: 56 (key to the genera of American Dichotomiina). — Halffter & Martínez 1968: 226 (taxonomic revision). — Howden & Young 1981: 40 (diagnosis). — Medina & Lopera-Toro 2000: 301, 306 (key to the Scarabaeinae of Colombia). — Medina *et al.* 2001: 133 (dung beetle species from Colombia). — Halffter 2003: 24 (redescription). — Vaz-de-Mello *et al.* 2011: 4, 8, 15, 23, 30, 38, 44 (key to the genera of Scarabaeinae). — Boilly & Vaz-de-Mello 2013: 106 (key to the Scarabaeinae of Guiana). — Cupello & Vaz-de-Mello 2018: 13, 17 (list of genus-group names proposed for '*Canthon* sensu lato').

Type species

Agamopus lampros Bates, 1887, by original monotypy.

Diagnosis

Agamopus belongs to the tribe Ateuchini, which is recognized by the transverse clypeal process; hypomeron with a transverse carina and deep anterior excavation; apex of protibiae truncated in a straight angle (see Vaz-de-Mello 2008); metatibiae of males with an elongate apical process (Figs 4C – black arrow; 6A, C); and by the transverse sulcus on the pygidium (as in Figs 4D and 9E). The latter two characters can be used to separate *Agamopus* from all other genera in the tribe (Halffter & Martínez 1968; Howden & Young 1981; Vaz-de-Mello *et al.* 2011; Boilly & Vaz-de-Mello 2013). For a comprehensive description of the genus *Agamopus*, see Halffter & Martínez (1968) and Howden & Young (1981).

Agamopus castaneus Balthasar, 1938
Figs 1, 2B, 3

Agamopus castaneus Balthasar, 1938: 218 (original description).

Agamopus castaneus — Blackwelder 1944: 203 (catalogue). — Pereira 1947: 4 (key to the species of *Agamopus*). — Balthasar 1965: 19 (comparison with other species). — Vulcano & Pereira 1967: 582 (key to the Amazonian dung beetles). — Halffter & Martínez 1968: 237 (diagnosis and key to the species of *Agamopus*). — Bezděk & Hájek 2011: 360 (catalogue of type specimens housed in NMPC). — Larsen 2013: 95 (list of dung beetle species from Suriname). — Boilly & Vaz-de-Mello 2013: 104 (key to the Scarabaeinae from Guiana). — Feer 2013: 766 (dung beetles from French Guiana).

Differential diagnosis

Agamopus castaneus resembles *A. unguicularis* in its light brown colour and head completely covered by dense punctation, but the former can be distinguished by the presence of one row with two or three yellow setae on the pygidium (Fig. 2B). *Agamopus unguicularis* has a row of yellow setae disposed parallel to the anterior margin of the sulcus (Fig. 2A). Also, the completely unconnected geographical distribution of the two species can be used to separate them: *A. unguicularis* occurs in the centre of South America and *A. castaneus* occurs in the north of the continent.

Type material examined

Holotype (by original designation) (Fig. 1A)

FRENCH GUIANA • ♀; first label [white, typeset]: "CAYENNE / Kourou Fl. / Le Moult"; second label [green with black border, Balthasar's handwriting]: "*castaneus* / m."; third label [aged white, partly in Balthasar's handwriting, partly typeset]: *Agamopus* / *castaneus* / Dr. V. Balthasar det."; fourth label [red with black border]: "TYPUS"; fifth label [aged white, Ohaus' handwriting]: "Ohaus determ / *Uroxys* / sp."; sixth label [red, FZVM's handwriting]: "HOLOTYPE ♀"; NMPC (Fig. 1B).

Additional material examined (7 specimens)

FRENCH GUIANA – St. Laurent du Maroni • 1 ♂; Apr. 1976; P. Arnaud leg.; CEMT. – **Cayenne** • 1 ♂; Bénitier, La Trinité National Nature Reserve; 8 Oct. 2010; SEAG leg.; CEMT.

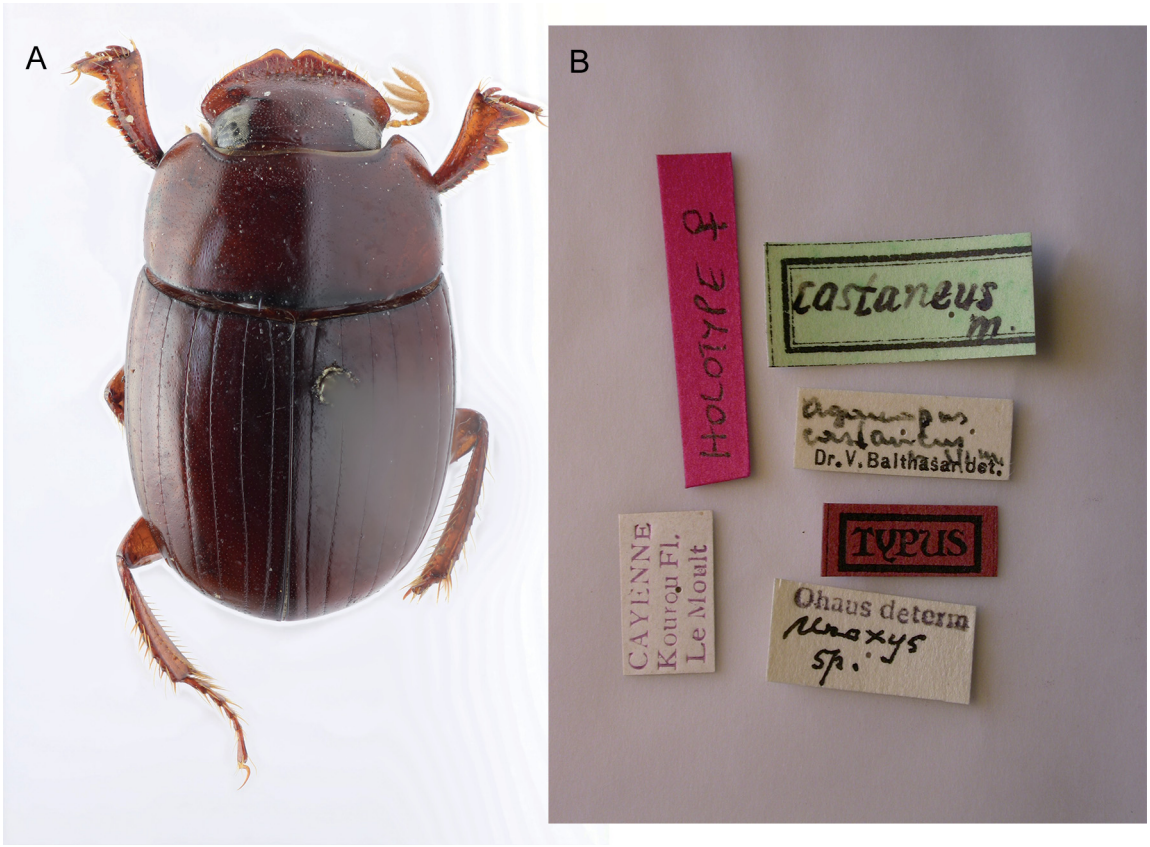

Fig. 1. *Agamopus castaneus* Balthasar, 1938. Holotype, ♀ (NMPC). **A**. Habitus, dorsal view. **B**. Labels. Length of specimen: 6.5 mm. Photographs: Jiří Hájek, NMPC.

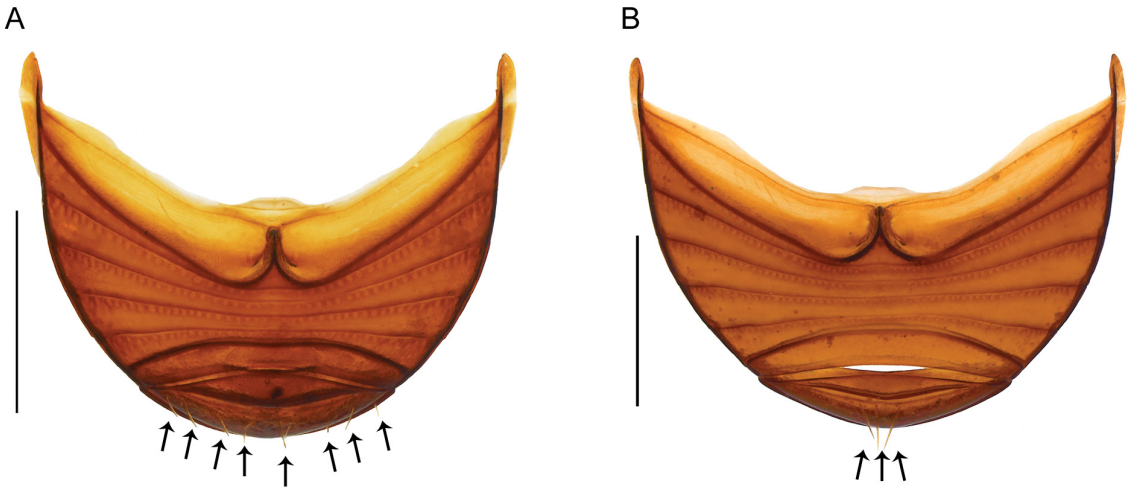

Fig. 2. Ventral view of the abdomen. **A**. *Agamopus unguicularis* (Harold, 1883), dissected specimen (CEMT), with one row of several yellow setae along the anterior edge of the pygidial sulcus (black arrows). **B**. *Agamopus castaneus* Balthasar, 1938, dissected specimen (CEMT) with three (sometimes two) yellow setae in the centre of the pygidial disc (black arrows). Scale bars = 1 mm.

BRAZIL – **Roraima** • 1 ♂, 1 ♀; Cantá, Serra Negra; Sep. 1996; Ribeiro and Vaz-de-Mello leg.; CEMT. – **Amapá** • 3 ♂♂; Serra do Navio; 0°53′6″ N, 51°52′53″ W; Sep. 2000; R. Ribon leg.; CEMT.

Geographic distribution

Agamopus castaneus is known from French Guiana and Suriname. Here we present the first record of this species from Brazil (Roraima and Amapá states) (Fig. 3).

Agamopus joker sp. nov.
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Figs 3–4, 5B

Differential diagnosis

Agamopus joker sp. nov. shares with *A. viridis* the presence of two small tubercles on the head (Fig. 5B – white arrows). However, the two species can easily be distinguished by the shape of the pygidial sulcus, which is arched in *A. viridis* (and other *Agamopus* species – as in Fig. 9E), but sinuous in *A. joker* (Fig. 4D). Furthermore, the inner edge of the metatibia is noticeably curved and strongly crenulate in *A. joker*, being unique among representatives of the genus (Fig. 4C). Also, *A. joker* has the apex of the parameres abruptly curved downwards and flattened dorso-ventrally (Fig. 4E), differing from other species of *Agamopus*.

Etymology

The specific name '*joker*', an English proper noun in the nominative case used in apposition, is an eponym after the homonymous supervillain from the DC Comics Universe. It is a reference to the sinuous pygidial sulcus of this species, which resembles the shape of a smiley clown's mouth.

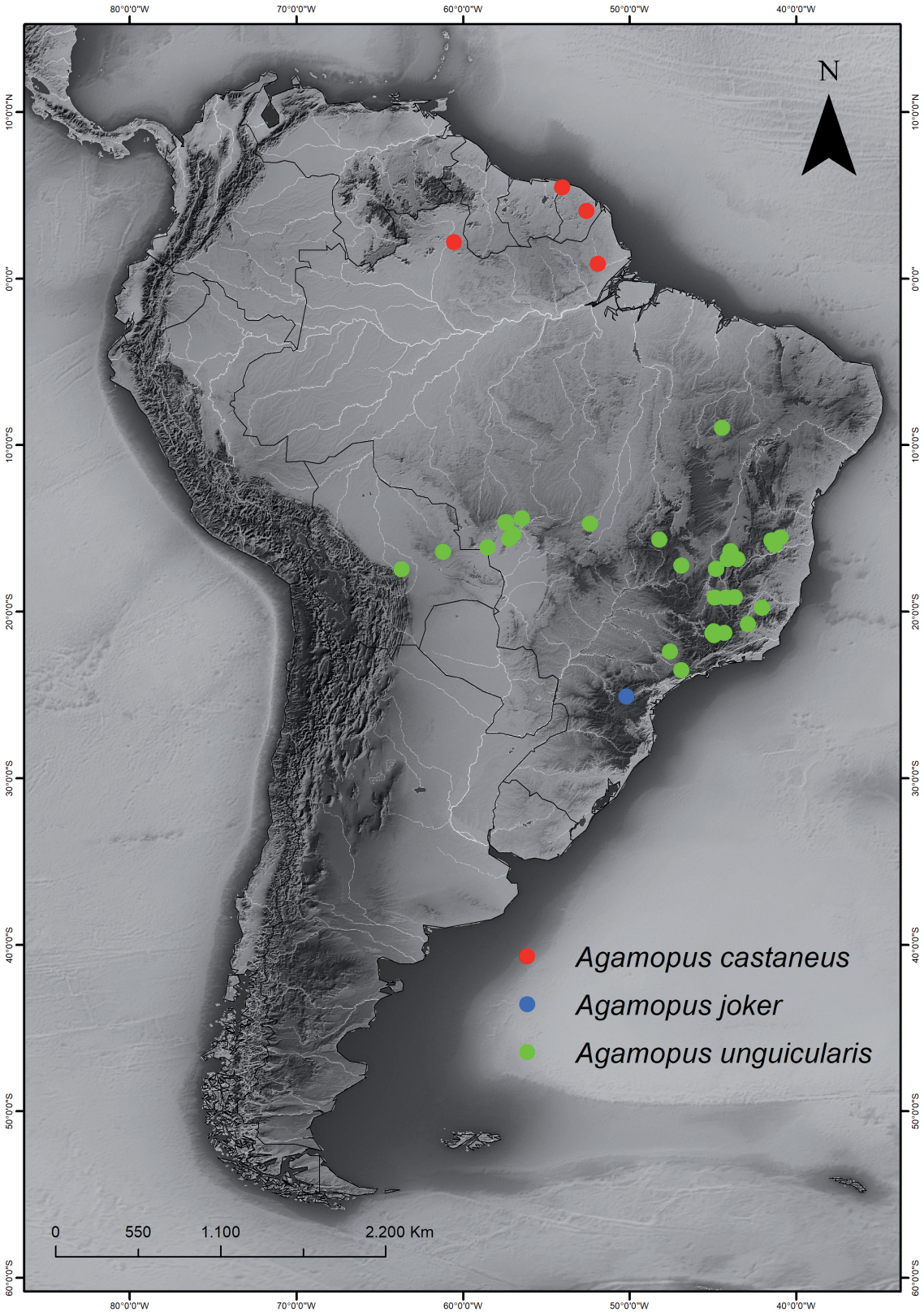

Fig. 3. Geographical distribution map of *Agamopus joker* sp. nov. (blue circle); *A. unguicularis* (Harold, 1883) (green circles); and *A. castaneus* Balthasar, 1938 (red circles).

Type material

Holotype

BRAZIL • ♂; first label [aged white, unknown handwriting]: "2 – 49 [vertical] / P. Grossa / Lageado."; second label [aged white, unknown handwriting]: "5211 [vertical] / *Agamopus* / *viridis* / Bouc."; third label [aged white, Pereira's handwriting]: "*Agamopus* / *viridis* 5211 / Bouc. / P. Pereira det. [typeset] 99 [Pereira's handwriting]"; fourth label [red with black border, printed]: *Agamopus joker* ♂ / Costa-Silva et al., 2022 / HOLOTYPE"; CEMT (Fig. 4G).

Holotype description

Habitus as in Figs 4A–B. Colour: dark brown, metallic. Oblong body. Length: 5.6 mm (excluding head). Width: 3.8 mm.

Head. Hemispheric. Surface with dense punctation; anterior half foveolate-puncticulate and with erect yellow setae. Clypeal margin and lateral margin of head with yellow setae projecting from underneath. Two triangular clypeal teeth, separation between teeth V-shaped. Lateral clypeal carina well-defined and

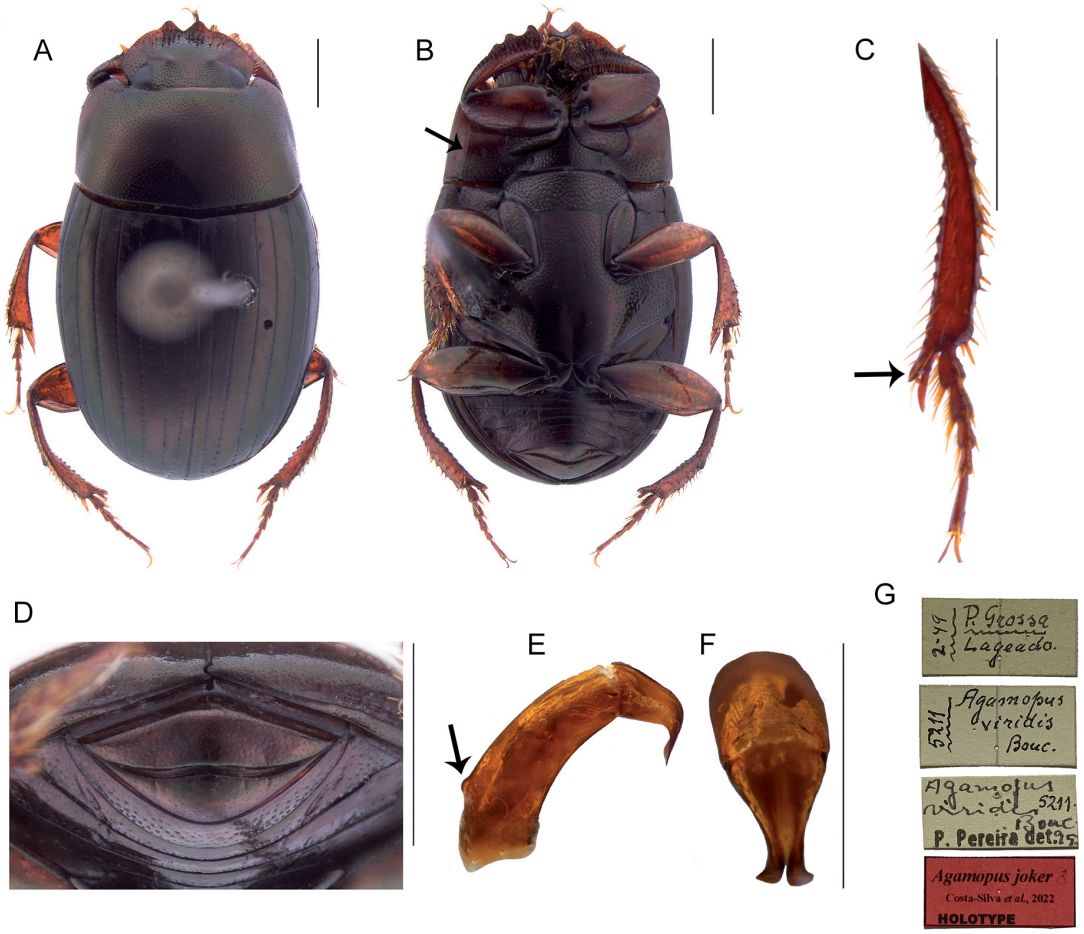

Fig. 4. *Agamopus joker* sp. nov. Holotype, ♂ (CEMT). **A**. Habitus, dorsal view. **B**. Habitus, ventral view (black arrow indicating the longitudinal keel slightly marked). **C**. Hind tibia (black arrow indicating the elongate apical process in the metatibia). **D**. Sulcus in the pygidium. **E**. Aedeagus, lateral view (black arrow indicating the gibbosity near base). **F**. Aedeagus, dorsal view. **G**. Labels. Scale bars = 1 mm.

oblique (as in Fig. 5B – red arrows), ending in small tubercle on each side. Antennae yellow; antennal club covered by small golden bristles.

Pronotum. Dark brown, metallic, shiny. Wider (3.18 mm) than long (1.7 mm); delimited by carina around. Surface covered by dense and homogeneous punctation (Figs 4A and 5B). Anterior angles rounded, pointed forward. Lateral margin smooth; rounded. Hypomeron with surface subtly rugose and densely punctate; anterior half deeply excavated, separated from posterior half by well-defined carina; posterior half with a longitudinal keel slightly marked, parallel with lateral margin (Fig. 4B – black arrow).

Mesoventrite. Trapezoidal; anterior margin wider than posterior. Surface fully punctated. Mesometasternal suture straight.

Metaventrite. Fully punctated. Punctures larger and well-marked between mesocoxae; punctures slightly smaller in the posteromedial region (Fig. 4B).

Elytra. Suboval. Lateral margins slightly angled. Seven striae well-defined; punctation equidistant on each stria. Surface of interstriae covered by micropunctation.

Legs. All fully covered by punctation. Protibiae slightly curved; three main teeth on outer edge and subtly crenulated to the base; inner apical angle of protibiae ~ 90°; ventral surface with longitudinal carina from base to apex. Meso- and metafemora with posterior edge smooth. Mesotibiae gradually widened apically; apical width approximately 1/4 of total length. Metatibiae visibly arched; inner edge crenulate with yellow setae (Fig. 4C); parallel margins in the anterior half, expanding slightly in the posterior half. Inner margin with a projection beyond apex, near to the spur. First to fourth protarsomeres almost rounded; 5th tarsomere elongate, longer than first three tarsomeres culminated; apex truncate. Meso- and metatarsomeres equal in shape and length; first to third tarsomeres with dense ventral yellow setae. Tarsal claws falciform; longer than first tarsomere (Fig. 4A–C).

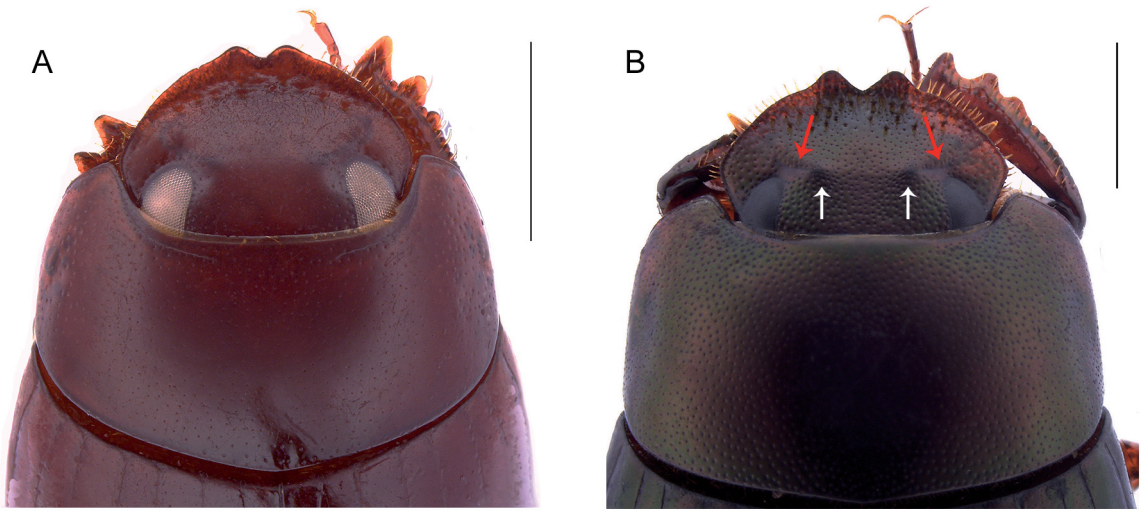

Fig. 5. Cephalic integument of species of *Agamopus* Bates, 1887. **A**. *A. lampros* Bates, 1887 (CEMT): smooth and lacking tubercles. **B**. *A. joker* sp. nov., holotype, ♂ (CEMT), with dense punctuation and two small tubercles. White arrows indicating the small cephalic tubercles. Red arrows indicating the lateral clypeal carina. Scale bars = 1 mm.

Abdomen. Six ventrites; each ventrite with row of punctation in the anterior margin; sides with sparse punctation. Lateral part of each ventrite longer than in the middle. Sixth ventrite completely covered by well-marked punctation.

Pygidium. Wider than long; glabrous, covered by micropunctation. Deep transverse and sinuous sulcus in centre of disc (Fig. 4D).

Male genitalia. Lateral view: parameres symmetrical; phallobase with dorsal gibbosity near base (Fig. 4E – black arrow); distal portion of parameres abruptly curved downwards (Fig. 4E). Dorsal view: tips of parameres trapezoidal, expanded laterally, pointed (Fig. 4F).

Female

Unknown.

Geographic distribution

The species is only known from type locality, Ponta Grossa, Paraná, Brazil (Fig. 3).

Agamopus lampros Bates, 1887
Figs 5A, 6–7

Agamopus lampros Bates, 1887 (original description).

Agamopus lampros — Gillet 1911: 49 (catalogue). — Boucomont 1928: 187 (diagnosis). — Balthasar 1938: 218 (diagnosis). — Blackwelder 1944: 203 (catalogue); 1973: 6 (catalogue). — Pereira 1947: 4 (key). — Halffter & Martínez 1968: 236 (female description and new data records). — Howden & Young 1981: 41 (redescription and distribution data). — Morón *et al.* 1988 (record from Mexico). — Thomas 1993: 395 (record from Mexico). — Schoolmeesters 1996: 20 (record from Nicaragua). — Medina & Lopera-Toro 2000: 310 (as "*lamprus*" – drawing of the sulcus on the pygidium). — Medina *et al.* 2001: 135 (checklist of dung beetles for Colombia). — Halffter 2003: 24 (redescription). — Solís & Kohlmann 2012: 4 (checklist from Costa Rica). — Arellano *et al.* 2013: 655 (citation). — Kohlmann & Wilkinson 2003: 221-222 (species cited from Costa Rica). — Noriega *et al.* 2013: 470 (checklist of beetles from Colombian Caribbean). — Cupello & Vaz-de-Mello 2018: 17 (list of genus-group names proposed for '*Canthon* sensu lato'). — Sánchez-Hernández *et al.* 2020: 226 (species list from Mexico).

Differential diagnosis

Unlike its congeneric species, *Agamopus lampros* is easily recognizable by its remarkably smooth head, without punctation (see Fig. 5A). All other *Agamopus* species are fully punctate on the head (as in Fig. 5B). Males of *A. lampros* have the posterior edge of the metafemora crenulate, while it is smooth in males of other species of *Agamopus*. For details, see Halffter & Martinez (1968).

Type material examined

Lectotype (here designated) (Fig. 6A)

PANAMA • ♂; first label [aged white, typeset]: "David / Panama / Champion"; second label [rounded with red border, typeset]: "Type"; third label [white, typeset]: "Sp. figured"; fourth label [aged white, typeset]: "B.C.A / 42.1."; fifth label [aged white, Bates' handwriting]: "*Agamopus* / *lampros* / Bates"; sixth label [red with black border, partly typeset, partly FZVM's handwriting]: "LECTOTYPE ♂ / *Agamopus* / *lampros* Bates / des. F.Z. Vaz-de-Mello, 2014"; BMNH (Fig. 6B).

Paralectotypes

PANAMA • 1 ♀; first label [aged white, typeset]: "David / Panama / Champion"; second label [rounded with red border, typeset]: "Type"; third label [white, typeset]: "Sp. figured"; fourth label [aged white,

typeset]: "B.C.A / 42.1."; fifth label [aged white, Bates' handwriting]: "*Agamopus* / *lampros* / Bates"; sixth label [yellow with black border, partly typeset, partly FZVM's handwriting]: "PARALECTOTYPE / *Agamopus* ♀ / *lampros* / Bates / des. F.Z. Vaz-de-Mello, 2014"; seventh label [white, typeset]: "2 specimens / separated / MVLB [M.V.L. Barclay] 2014"; BMNH • 1 ♀; first label [aged white, typeset]: "V. de Chiriqui, / 25-4000 ft. [feet] / Champion."; second label [aged white, typeset]: "B.C.A / 42.1."; third label [aged white, Bates' handwriting]: "*Agamopus* / *lampros* / Bates"; fourth label [white, unknown handwriting]: "*Agamopus lampros* / (Bates) / 614:45."; fifth label [yellow with black border, partly typeset, partly FZVM's handwriting]: "PARALECTOTYPE / *Agamopus* ♀ / *lampros* / Bates / des. F.Z. Vaz-de-Mello, 2014"; BMNH • 1 ♀; first label [aged white, typeset]: "V. de Chiriqui, / 25-4000 ft. [feet] / Champion."; second label [aged white, typeset]: "B.C.A / 42.1."; third label [white aged, Bates' handwriting]: "*Agamopus* / *lampros* / Bates"; fourth label [white, unknown handwriting]: "*Agamopus lampros* / (Bates) / 614:45."; fifth label [yellow with black border, partly typeset, partly FZVM's handwriting]: "PARALECTOTYPE / *Agamopus* ♀ / *lampros* / Bates / des. F.Z. Vaz-de-Mello, 2014"; sixth label [white, typeset]: "2 specimens / separated / MVLB 2014"; BMNH.

Note

The fixation of the name-bearing type of *Agamopus lampros* was previously indicated with a label (Fig. 6B) by one of the authors (FZVM). This designation is here formalized according to Art. 11.1 (ICZN 1999).

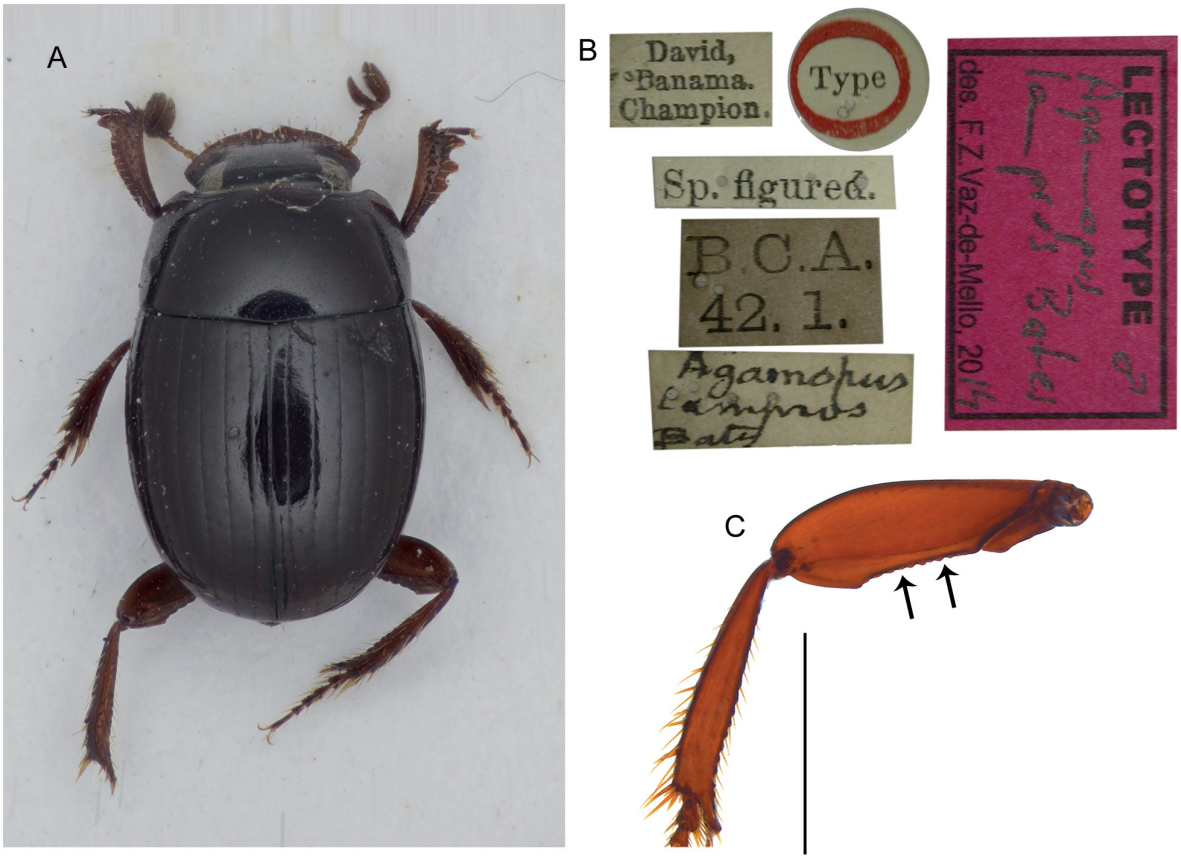

Fig. 6. *Agamopus lampros* Bates, 1887. **A–B**. Lectotype, ♂ (BMNH). **A**. Habitus, dorsal view. **B**. Labels. **C**. Hind leg of a non-type specimen (CEMT) showing the posterior femoral edge crenulate (black arrows). Length of specimen: 4.5 mm. Scale bar = 1 mm.

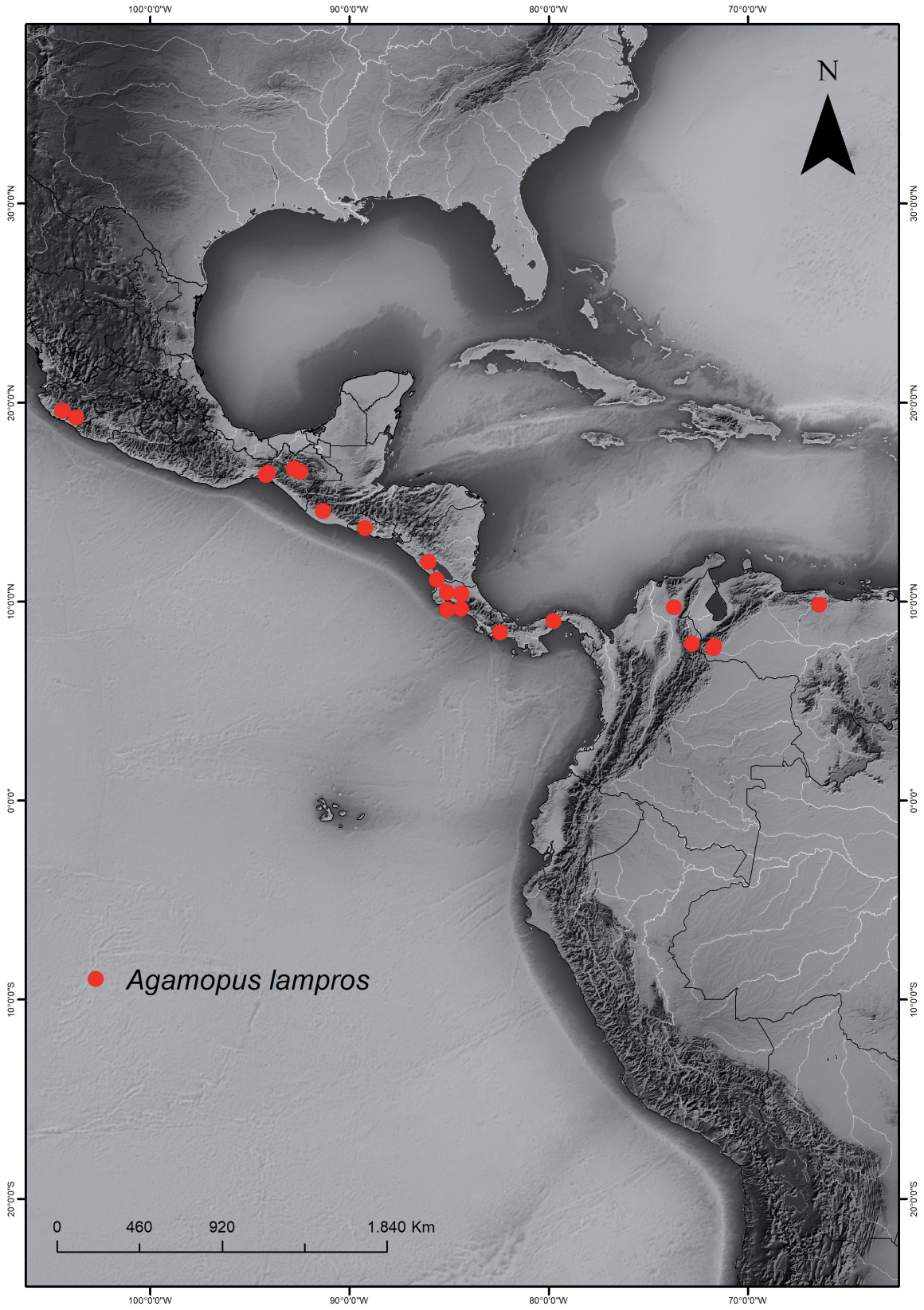

Fig. 7. Geographical distribution map of *Agamopus lampros* Bates, 1887.

Additional material examined (29 specimens)

MEXICO – Jalisco • 6 ♂♂, 1 ♀; Casimiro Castillo, way to the Ejido Barranca de la Naranjera parotal; 19°35′10″ N, 104°24′43″ W; alt. 550 m; 29 Jul. 2004; Nicolalde, Carrillo and Vaz-de-Mello leg.; CEMT. – **Oaxaca** • 1 ♂; SE San Pedro Tapanatepec; 26 Aug. 1971; A. Newton leg.; CEMT. – **Chiapas** • 1 ♂, 2 ♀♀; 6 km E of Rizo de Oro; alt. 890 m; 18–21 Jun. 1990; W.B. Warner leg.; CEMT • 1 ♀; Cintalapa, Cinco Cerros; alt. 860 m; 31 May 1990; H. and A. Howden leg.; CEMT • 1 ♂; Cintalapa, Cinco Cerros, Km 30 on Hwy 190; alt. 1500 m; 8 Jun. 1989; H. Howden leg.; at light; CEMT • 1 ♂; Teopisca, Ruta 24; 3–4 Jun. 1969; H. Howden leg.; CEMT.

GUATEMALA – Suchitepéquez • 1 ♂; Chicacao, San Julián; 9 Nov. 1988; C. Mendez leg.; CEMT.

EL SALVADOR – San Salvador • 1 ♀; San Salvador; 23 May 1958; O.L. Cartwright leg.; CEMT • 1 ♀; San Salvador; 7 Jun. 1958; O.L. Cartwright leg.; CEMT.

NICARAGUA – Masaya • 1 ♀; Las Flores; 1 Jun. 1994; CEMT.

COSTA RICA – Guanacaste • 1 ♂; 3km N of Cañas, Hacienda La Pacifica; alt. 90 m; 5–6 Jun. 1979; H. and A. Howden leg.; CEMT. **– Puntarenas** • 1 ♂; Cóbano, Reserva Natural Absoluta de Cabo Blanco, San Miguel Biological Station; alt. 200–300 m; 18–27 May 2001; W. Porras leg.; flight interception trap; CEMT.

PANAMA – Chiriqui • 1 ♂; 10 km North of Santa Clara; alt. 1600 m; 26 Jul. 1998; M. Hardy leg.; CEMT • 1 ♀; Dolequita; 25 Jul. 1964; A. Broce leg.; CEMT.

COLOMBIA – Cesar • 1 ♂; Sierra de Perijá; Jul. 1968; B. Malkin leg.; in a horse carcass; CEMT. – **Norte de Santander** • 1 ♀; 2 km E of Gramalote; alt. 1300 m; 11 May 1974; H. and A. Howden leg.; CEMT.

VENEZUELA – Guárico • 2 specs; Altagracia de Orituco; 23 Aug. 2006; curso NM2006 leg.; CEMT. – **Táchira** • 1 ♂; Libertador, San Joaquín de Navay; 7°39′44″ N, 71°42′37″ W; alt. 200 m; Aug. 2006; T. Good leg.; CEMT • 2 ♂♂; Libertador, San Joaquín de Navay; 7°46′27″ N, 71°40′03″ W; alt. 550 m; Aug. 2006; T. Good leg.; CEMT.

Geographic distribution

Agamopus lampros is recorded from western Mexico to Colombia and Venezuela (Fig. 7).

Agamopus unguicularis (Harold, 1883)
Figs 2A, 3, 8

Canthon unguicularis Harold, 1883: 430 (original description).

Agamopus martinezi Pereira, 1947: 1 (original description). Considered junior synonym for Halffter & Martínez 1968: 237.

Canthon unguicularis — Gillet 1911: 34 (catalogue). — Schmidt 1922: 72, 81 (catalogue). — Balthasar 1939: 225 (redescription). — Blackwelder 1944: 202 (catalogue). — Vulcano & Pereira 1964: 633-634 (catalogue).

Agamopus unguicularis — Halffter & Martínez 1968: 237 (new combination). — Louzada & Carvalho-Silva 2009: 48 (dung beetles from pastures). — Vaz-de-Mello *et al.* 2017: 2 (list of dung beetles from Mato Grosso do Sul). — Tissiani *et al.* 2017: 405 (species list and key to dung beetles from Brazilian pastures).

Differential diagnosis

Agamopus unguicularis is distinguished from *A. viridis* and *A. joker* sp. nov. by the absence of small tubercles on the head, which are present in the last two species. In its brown colour, *A. unguicularis* is more similar to *A. lampros* and *A. castaneus*, but can be easily separated from *A. lampros* by the head fully covered by micropunctation (smooth in the latter), and from *A. castaneus* by a presence of a one row of several yellow setae along the anterior edge of the sulcus (Fig. 2A). *Agamopus castaneus* has just two or three setae in the centre of anterior edge of sulcus.

After examination of the type-specimens of *Agamopus martinezi*, we agree with Halffter & Martínez's arguments (1968) and maintain this species as a junior synonym of *A. unguicularis*.

Type material examined

Lectotype of *Canthon unguicularis* Harold, 1883 (here designated) (Fig. 8A–C)
BRAZIL • ♀; first label [green, typeset]: "S^{n} Joao d'el Rey."; second label [white, typeset]: "Coll. Camille / Van Volxem"; third label [white, typeset]: "M.R. Belg"; fourth label [aged white, Harold's handwriting]: "*Canthon* / *unguicularis* / typ. Hrld"; fifth label [aged white with black border, typeset]: "Ex. Musæo / E. Harold"; sixth label [white, typeset]: Muséum Paris / 1952 / Coll. R. Oberthur"; seventh label [aged white, partly typeset, partly in Halffter's handwriting]: "*Agamopus* ♀ / *unguicularis* / G. Halffter y (Har.) / A. Martinez det 1968"; eighth label [red, typeset]: "TYPE"; ninth label [red, typeset]: "SYNTYPE"; tenth label [white, typeset] "SYNTYPE / *Agamopus* / *unguicularis* (Harold, 1883)"; eleventh label [white with black border]: "MNHN / EC10858" (Fig. 8D); MNHN.

Paralectotype of *Canthon unguicularis* Harold, 1883
BRAZIL • 1 ♂; first label [green, typeset]: "S^{n} Joao d'el Rey."; second label [white, typeset]: "Coll. Camille / Van Volxem"; third label [red, typeset]: "SYNTYPE"; fourth label [white, typeset] "SYNTYPE / *Agamopus* / *unguicularis* (Harold, 1883)"; fifth label [white with black border, typeset]: "MNHN / EC10859"; MNHN.

Holotype of *Agamopus martinezi* Pereira, 1947 (by original designation)
BRAZIL • ♂; first label [aged white with black border, partly typeset, partly in unknown handwriting]: "Rio Claro (S.P.) / XI-XII.942 / Coll. Claretiano"; second label [red with black border, printed]: "HOLOTYPYS"; third label [aged white with black border, partly typeset, partly in Pe. Pereira's handwriting]: "*Agamopus* / *martinezi* / F. Pereira / P. Pereira det. 945"; fourth label [aged white, partly typeset, partly in A. Martínez's handwriting]: "*Agamopus* ♀ / *unguicularis* / (Har.) / Det. A. Martínez 1972"; MZSP.

Paratype of *Agamopus martinezi* Pereira, 1947
BRAZIL • 1 ♀; first label [aged white with black border, partly typeset, partly in unknown's handwriting]: "Rio Claro (S.P.) / XII.942 / Coll. Claretiano"; second label [white with black border, printed]: "H. & A. Howden / COLLECTION / ex. A. Martínez coll."; third label [red with black border, printed]: "PARATYPUS"; fourth label [aged white with black border, partly typeset, partly in Pe. Pereira's handwriting]: "*Agamopus* / *martinezi* / F. Pereira / P. Pereira det. 945"; fifth label [aged white, partly typeset, partly in A. Martínez's handwriting]: "*Agamopus* ♀ / *unguicularis* / (Har.) / Det. A. Martínez 1972"; CNM.

Additional material examined (153 specimens)

BRAZIL – Piauí • 1 ♀; Currais, Agropecuária Rotilli; 8°57′22″ S, 44°25′49″ W; 28 Jan. 2014; R. Maciel leg.; human feces; CEMT. **– Mato Grosso** • 9 ♂♂, 3 ♀♀; Cáceres; Fazenda Santa Fé; 16°8′13″ S, 58°29′44″ W; 26–28 Nov. 2013; F. Coletti leg.; CEMT • 2 specs; Diamantino, Upper Rio Arinos; Jan. 2001; E. Furtado leg.; CEMT • 1 spec.; Nova Xavantina, Parque Natural Municipal do Bacaba;

14°42′26″ S, 52°21′06″ W; alt. 327 m; 13–15 Feb. 2019; R.J. Silva and R.S.A. Silva leg.; pitfall with human feces; Cerrado; CEMT • 4 ♂♂, 9 ♀♀; Porto Estrela, Serra das Araras Ecological Station, Boca do José; 15°37′47″ S, 57°11′39″ W; Nov. 2017; T.F. Conceição leg.; pitfall; CEMT • 1 ♂; Porto Estrela, Serra das Araras Ecological Station; Sep. 2011; M. Souza leg.; CEMT • 1 ♂; Porto Estrela, Serra das Araras Ecological Station, trilha do Heliporto; 15°21′49″ S, 56°57′32″ W; 12 Oct. 2011; F.Z. Vaz-de-Mello leg.; CEMT • 14 ♂♂, 8 ♀♀; Tangará da Serra, Fazenda Bahia; 14°37′14″ S, 57°25′15″ W; alt. 419 m; 12–14 Jan. 2011; R.J. Silva leg.; pitfall with a mixture of human and pig dung; CEMT • 8 ♂♂, 3 ♀♀; Tangará da Serra, Fazenda Bahia; 14°37′13″ S, 57°24′50″ W; alt. 428 m; 26–28 Jan. 2012; R.J. Silva leg.; pitfall with a mixture of human and pig dung; semi-deciduous forest; CEMT • 2 ♂♂, 4 ♀♀; Tangará da Serra, Filé do Boi Farm; 14°38′07″ S, 57°24′41″ W; alt. 439 m; 25–27 Jan. 2011; R.J. Silva leg.; pitfall with a mixture of human and pig dung; CEMT • 1 ♂; Tangará da Serra, Sítio Mauá; 14°39′42″ S, 57°24′18″ W; alt. 462 m; 19–21 Jan. 2011; R.J. Silva leg.; pitfall with a mixture of human and pig dung; semi-deciduous forest; CEMT. – **Bahia** • 1 ♀; Encruzilhada; alt. 980 m; Nov. 1972; M. Alvarenga leg.; CEAH • 1 spec.; Encruzilhada; Dec. 1997; A. Bello and F. Vaz-de-Mello leg.; CEMT • 4 ♂♂, 4 ♀♀; Encruzilhada; Nov. 1974; M. Alvarenga and A. Martínez leg.; light; CMN. – **Distrito Federal** • 1 ♂; Brasília, Brazlândia; Jan. 1994; E. Grossi leg.; CEMT. – **Minas Gerais** • 1 ♂; Águas Vermelhas; 15°45′ S, 41°27′ W; Dec. 1997; A. Bello and F. Vaz-de-Mello leg.; CEMT • 1 ♂; Cordisburgo, Fazenda Pontinha; Dec. 1993; F.Z. Vaz-de-Mello leg.; CEMT • 3 ♂♂; Cordisburgo; Jan. 1994; F.Z. Vaz-de-Mello leg.; CEMT • 1 ♂; Cordisburgo; Jan. 1998; F.Z. Vaz-de-Mello leg.; CEMT • 1 ♂; Felixlândia, EPAMIG Farm; 19°09′14″ S, 44°51′09″ W; alt. 480 m; 25 Jan. 2012; R. Macedo leg.; human dung; pasture; CEMT • 22 specs; Ijaci, Fazenda FAEPE [Fundação de Apoio ao Ensino, Pesquisa e Extensão]; Nov.

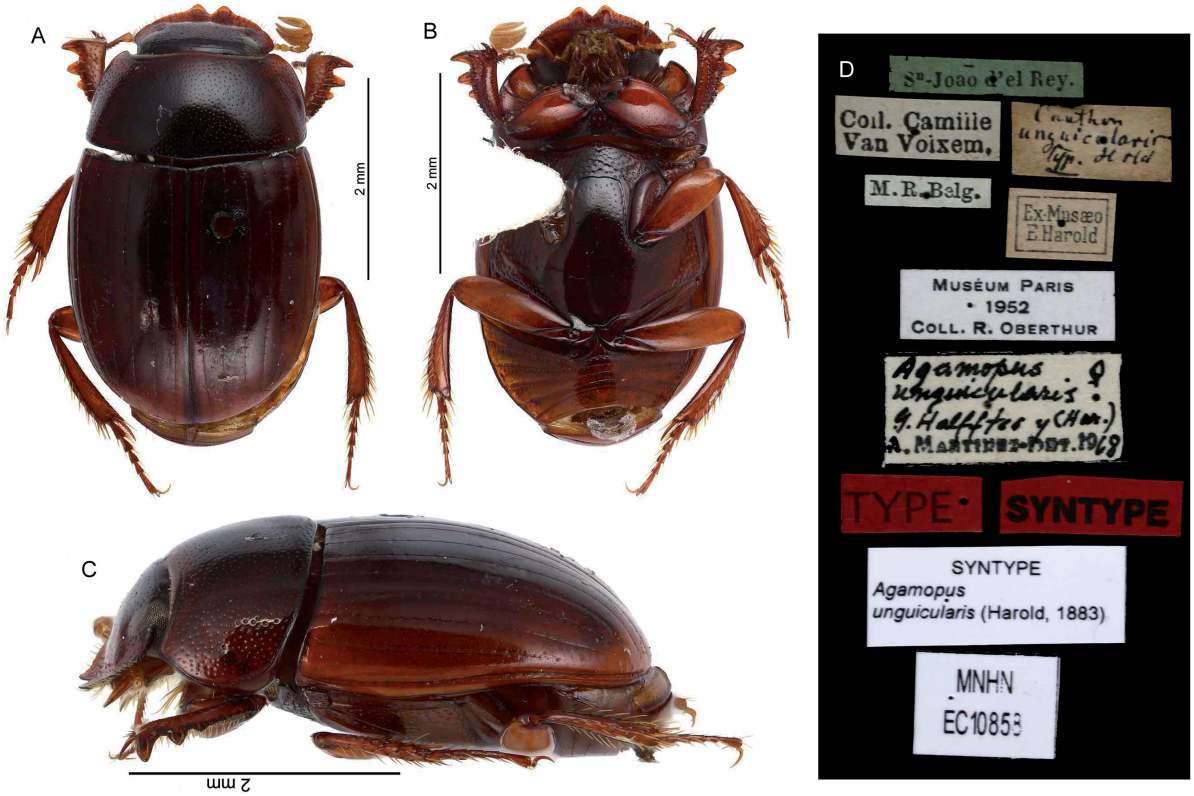

Fig. 8. *Canthon unguicularis* Harold, 1883 [now *Agamopus unguicularis*]. Lectotype, ♀ (MNHN). **A**. Habitus, dorsal view. **B**. Habitus, ventral view. **C**. Habitus, lateral view. **D**. Labels. Photographs: Christophe Rivier, MNHN.

2002; J. Louzada leg.; CEMT • 1 ♂; Ingaí, Boqueirão; 21°20′ S, 44°59′ W; 11 Nov. 2012; CEMT • 1 ♂, 1 ♀; Juramento; Jan. 2003; L.C. Rocha leg.; CEMT • 2 ♂; Lavras; 19 Jan. 1999; J. Louzada leg.; CEMT • 1 ♀; Lavras; 21°18′09″ S, 44°59′26″ W; 20 Jan. 2008; M.S. Rocha and D.I.H. Takahashi leg.; CEMT • 1 ♂; Lavras; 21°18′11″ S, 44°59′24″ W; 20 Jan. 2008; M.S. Rocha and D.I.H. Takahashi leg.; CEMT • 1 ♂; Lavras; 21°18′19″ S, 44°59′37″ W; 20 Jan. 2008; M.S. Rocha and D.I.H. Takahashi leg.; CEMT • 2 ♂♂; Lavras, Campus UFLA [= Federal University of Lavras]; Nov.–Dec. 2001; F.Z. Vaz-de-Mello leg.; CEMT • 1 ♂; Lavras, Mata do Capivari; 21°16′25″ S, 44°16′57″ W; Dec. 2001; G. Schiffler leg.; CEMT • 1 spec.; near to Lavras, Poço Bonito; 21°19′ S, 44°58′ W; Nov. 2002; J. Louzada leg.; CEMT • 2 specs; Lavras, near to Poço Bonito; 21°19′ S, 44°58′ W; Dec. 2002; J. Louzada leg.; CEMT • 4 ♂♂, 1 ♀; Montes Claros; Jan. 2000; Louzada and Louzada leg.; Cerrado; CEMT • 2 ♂♂; Montes Claros, Morro Agudo; 16°21′25″ S, 43°55′28″ W; alt. 816 m; 2 Feb. 2012; R. Macedo leg.; human feces; pasture; CEMT • 1 ♂; Montes Claros, Morro Agudo; 16°50′35″ S, 44°05′19″ W; alt. 879 m; 12 Feb. 2012; R. Macedo leg.; human dung; pasture; CEMT • 3 ♂♂; Montes Claros; Dec. 1994; J. Louzada leg. CEMT • 1 ♀; Nova Era; Oct. 1987; CEMT • 6 ♂♂; Paracatu; Dec. 1997; S. Lourenço leg.; CEMT • 1 ♀; Pedra Azul; alt. 700 m; Nov. 1972; Seabra and Oliveira leg.; CEAH • 1 ♀; Pirapora, Sérgio's Farm; 17°26′33″ S, 44°46′56″ W; alt. 457 m; 27 Jan. 2012; R. Macedo leg.; human feces; cerrado; CEMT • 1 ♀; Pirapora, Sérgio's Farm; 17°26′07″ S, 44°46′09″ W; alt. 512 m; 27 Jan. 2012; R. Macedo leg.; human dung; pasture; CEMT • 1 ♂; Santana do Riacho, Lapinha da Serra; Nov. 1981; Celso Jr leg.; CEMT • 1 ♀; Viçosa; 30 Dec. 1993; Louzada and Silva leg.; CEMT. **– São Paulo** • 1 spec.; Barueri; 23 Mar. 1957; K. Lenko leg.; DZUP.

BOLIVIA – Santa Cruz • 1 ♂; Ichilo, Buena Vista; Feb. 1950; Martínez coll.; CMN • 3 ♂♂; José Miguel de Velasco, San Ignácio de Velasco; 16°24′ S, 61°11′ W; alt. 430 m; 16 Jan. 2010; Vidaurre leg.; CEMT.

Geographic distribution

Agamopus unguicularis shows a wide distribution in non-Amazonian Brazil. The species is also recorded in Bolivia (Fig. 3).

Agamopus viridis Boucomont, 1928
Figs 9–10

Agamopus viridis Boucomont, 1928: 187 (original description).

Agamopus viridis — Balthasar 1938: 218 (diagnosis). — Blackwelder 1944: 203 (catalogue) — Pereira 1947: 4 (distribution records). — Halffter & Martínez 1968: 235 (diagnosis and key to species). — Marchiori *et al.* 2003: 175 (species of dung beetles from Goiás). — Mendes & Linhares 2006: 717, 719 (list of Coleoptera in pastures). — Nunes *et al.* 2012: 127 (list of species from Distrito Federal, Brazil). — Chaves *et al.* 2017: 187 (record from Planaltina, Brazil). — Tissiani *et al.* 2017: 405 (species list and key to dung beetles from Brazilian pastures). — Vaz-de-Mello *et al.* 2017: 2 (species list from Mato Grosso do Sul). — Uchoa & Rodrigues 2019: 21 (list of dung beetles from Midwest of Brazil).

Differential diagnosis

Agamopus viridis and *A. joker* sp. nov. are easily separated from other *Agamopus* species by the presence of two small tubercles on the frons, which are absent in all other species of the genus. The latter two species can be separated by the presence, in *A. viridis*, of an arched pygidial sulcus (Fig. 9E), which is sinuous in *A. joker* (Fig. 4D). For additional details, see description of *A. joker***.**

Type material examined

Holotype (by monotypy) (Fig. 9A–C)

BRAZIL • ♀; first label [green, printed]: "Jatahy / Prov. Goyas. Brésil"; second label [white, partly printed, partly in Boucomont's handwriting]: "Boucomont det 1927 / *Agamopus* / *viridis* n. sp."; third label [white with black border, partly printed, partly handwritten]: "Museum Paris / Boucomont"; fourth label [red with black border, printed]: "Typus"; fifth label [white with red border, Gonzalo Halffter's handwriting]: "TIPO / *AGAMOPUS* / *VIRIDIS* / BOUCOMONT / G.H.y A.M. DET. 76"; sixth label [red, printed]: "HOLOTYPE"; seventh label [white with black border, printed]: "MNHN / EC10857" (Fig. 9D); MNHN.

Additional material examined (404 specimens)

BRAZIL – **Bahia** • 1 ♀; Boa Nova; 14°19′ S, 40°13′ W; 28 Feb. 2015; J. Maciel leg.; human feces; CEMT • 1 ♂, 1 ♀; Caetité, Uranium Concentration Unit, INB [Nuclear Industries of Brazil]; 8–16 Jan. 2000; Nessimian and Baptista leg.; light; CEMT • 4 ♂♂, 4 ♀♀; Encruzilhada; Nov. 1974; M. Alvarenga and A. Martínez leg.; light; CMN • 2 ♂♂; Encruzilhada; Dec. 1980; A. Martínez and M. Alvarenga leg.; CEMT • 7 ♂♂, 8 ♀♀; same collection data as for preceding; CMN • 2 ♂♂, 1 ♀; Encruzilhada; 15°31′24″ S, 40°57′52″ W; alt. 780 m; 16 Dec. 2012; J.A. Rafael and E.J. Grossi leg.; light; CEMT • 1 ♂; Encruzilhada; 15°34′35″ S, 40°56′51″ W; alt. 850 m; 15 Dec. 2012; J.A. Rafael and E.J. Grossi leg.; light trap; CEMT • 1 ♀; Encruzilhada; alt. 980 m; Nov. 1972; M. Alvarenga leg.; CEAH • 3 ♂♂,

Fig. 9. A–D. *Agamopus viridis* Boucomont, 1928. Holotype, ♀ (MNHN). **A**. Habitus, dorsal view. **B**. Habitus, ventral view. **C**. Habitus, lateral view. **D**. Labels. **E**. Sulcus of the pygidium in an ordinary specimen (CEMT). Photographs A–D: Christophe Rivier, MNHN.

1 ♀; same collection data as for preceding; CEMT • 59 specs; Encruzilhada, Fazenda Veredão; Dec. 1997; A. Bello and F. Vaz-de-Mello leg.; CEMT • 2 ♂♂, 3 ♀♀; Maracás; Nov. 1965; W. Bokermann and F.M. Oliveira leg.; CEMT; • 13 specs; same collection data as for preceding; MZSP. – **Goiás** • 2 specs; Aragarças; Nov. 1965; M. Alvarenga leg.; DZUP • 1 ♂; Chapada dos Veadeiros; 14°06′33″ S, 47°42′52″ W; 6 Dec. 2015; M.V.C. Rocha leg.; CEMT • 1 ♀; Goiânia, Federal University of Goiás; 16°36′10″ S, 49°16′19″ W; alt. 55 m; 30 Jan. 2016; M.B. Pessoa leg.; CEMT • 1 ♀; Goiânia Km 4.5 UFG [Federal University of Goiás]; 16°34′59″ S, 49°15′03″ W; alt. 763 m; 31 Feb. 2016; M.B. Pessoa leg.; CEMT • 1 spec.; Goiânia Km 581; 16°32′20″ S, 49°13′43″ W; alt. 844; 31 Feb. 2016; M.B. Pessoa leg.; pasture; CEMT • 4 specs; Rio Verde, Escola Agrotecnica Federal de Rio Verde; 7 Apr. 2001; O.C. Sousa leg.; pasture; CEMT. – **Distrito Federal** • 1 ♂, 2 ♀♀; Brasília; Nov. 2000; N. Degallier leg.; CEMT • 1 ♂, 1 ♀; Brasília; Dec. 2000; N. Degallier leg.; CEMT • 2 ♂♂, 3 ♀♀, 14 specs; Brasília; alt. 1100 m; Jan. 2001; N. Degallier leg.; light; CEMT • 14 specs; same collection data as for preceding; Mar. 2001; light; CEMT • 6 ♂♂, 3 ♀♀; same collection data as for preceding; Nov. 2000; CEMT • 8 specs; Brasília; 15–30 Sep. 1999; N. Degallier leg.; CEMT • 1 ♂, 1 ♀; Brasília, Brasília National Park; 15°44′09″ S, 48°00′05″ W; 29 Nov. 2018; W.L. Cunha leg.; pitfall with faeces; CEMT • 15 specs; Brasília, Região Administrativa Plano Piloto; Dec. 1998; N. Degallier leg.; CEMT • 1 ♀, 1 spec.; Planaltina, Águas Emendadas Ecological Station; 15°32′31″ S, 47°36′49″ W; 1–15 Nov. 2009; M.R. Frizzas leg.; pitfall trap; CEMT • 3 ♂♂, 6 ♀♀; Planaltina, Sem Três Pinheiros Farm; 15°36′38″ S, 47°30′16″ W; 9 Dec. 2017; Y. Ferreira leg.; CEMT. – **Minas Gerais** • 2 ♂♂, 2 ♀♀; Águas Vermelhas; 15°45′ S, 41°27′ W; Dec. 1998; A. Bello and F. Vaz-de-Mello leg.; CEMT • 1 ♂, 3 ♀♀, 118 specs; same collection data as for preceding; CEMT • 1 ♂, 1 ♀; same collection data as for preceding; PKLC • 10 specs; Buritizeiro; 17°01′08″ S, 45°06′19″ W; alt. 460 m; 28 Jan. 2012; R. Macedo leg.; CEMT • 1 ♂; Cordisburgo, Fazenda Pontinha; Mar. 1992; F.Z. Vaz-de-Mello leg.; CEMT • 1 ♀ Cordisburgo, Fazenda Pontinha; 19°08′S, 44°12′W; Dec. 1997; CEMT • 1 ♂; Cordisburgo, Fazenda Pontinha; Dec. 1998; F.Z. Vaz-de-Mello leg.; CEMT • 1 ♀; Cordisburgo, Fazenda Pontinha; 19°8′53″ S, 44°12′01″ W; alt. 700 m; 6 Jan. 2001; F.Z. Vaz-de-Mello leg. CEMT • 2 specs; Jaíba, Mocambinho; 15°08′08″ S, 43°58′53″ W; alt. 450 m; 27 Mar. 2012; A. Fialho leg.; human feces; CEMT • 2 ♂♂, 1 ♀; Montes Claros; Jan. 2000; J. Louzada leg.; CEMT • 18 specs; Paracatu; Nov. 1997; S.L. Assis Jr leg.; CEMT • 1 ♀; Pedra Azul; alt. 700 m; Nov. 1972; Seabra and Oliveira leg.; CEAH • 2 specs; Pompéu, Pedro's Farm; alt. 458 m; 22 Jan. 2012; R. Macedo leg.; CEMT • 1 ♀; Três Marias; Sep. 1999; J.C. Zanúncio leg.; CEMT • 1 ♀; Três Marias; Oct. 1989; J.C. Zanúncio leg.; CEMT. – **Mato Grosso do Sul** • 1 spec.; Bataguassu, Rio Caraguatá; Mar. 1953; DZUP • 1 spec.; Campo Grande; 7 Jan. 1953; M. Alvarenga leg.; DZUP • 1 ♀; Campo Grande, National Beef Cattle Research Center; 13 Jun. 1993; W.W. Koller leg.; baited with cattle dung (Nelore bovine); *Brachiaria decumbens* pasture; CEMT • 2 ♀♀; Dourados; 22 Oct. 2005; M. Miloca leg.; CEMT. – **São Paulo** • 1 spec.; Botucatu; 22 Feb. 1955; Werner leg.; DZUP • 1 spec.; same collection data as for preceding; MZSP • 1 ♀; Cajuru; 9 Feb. 1964; H.M. Canter leg.; CEMT • 1 ♀; Pereira Barreto, Vale do Paraíso Farm; 2 Jun. 1993; M.F. Aio leg.; baited with cattle dung; *Brachiaria crizantha* pasture; CEMT • 1 ♂; Pereira Barreto, Vale do Paraíso Farm; 26 May 1993; M.F. Aio leg.; baited with cattle dung; *Brachiaria crizantha* pasture; CEMT • 17 specs; Rio Claro; Dec. 1942; Coll. Claretiano; MZSP • 1 ♀; São Carlos; 11 Nov. 1993; J. Mendes leg. CEMT.

Comments

As noted earlier by Halffter & Martínez (1968), *Agamopus viridis* is the only species of the genus with a green metallic colour. After the examination of a series of *A. viridis* specimens from several Brazilian states, we observed a colour variation between populations from Bahia (Boa Nova, Caetité, Encruzilhada and Maracás) and Minas Gerais states (Águas Vermelhas) (Fig. 10). Specimens from these localities have a pronotum with a reddish-brown metallic colour, while the elytra are metallic-green like individuals from other localities. Moreover, the punctation in the metaventrite and pronotum seems to be variable in form (weakly or strongly marked) and scattering of punctures (sparse or dense), and different punctation patterns are found in combination with the colour phases. Male specimens of the two colours

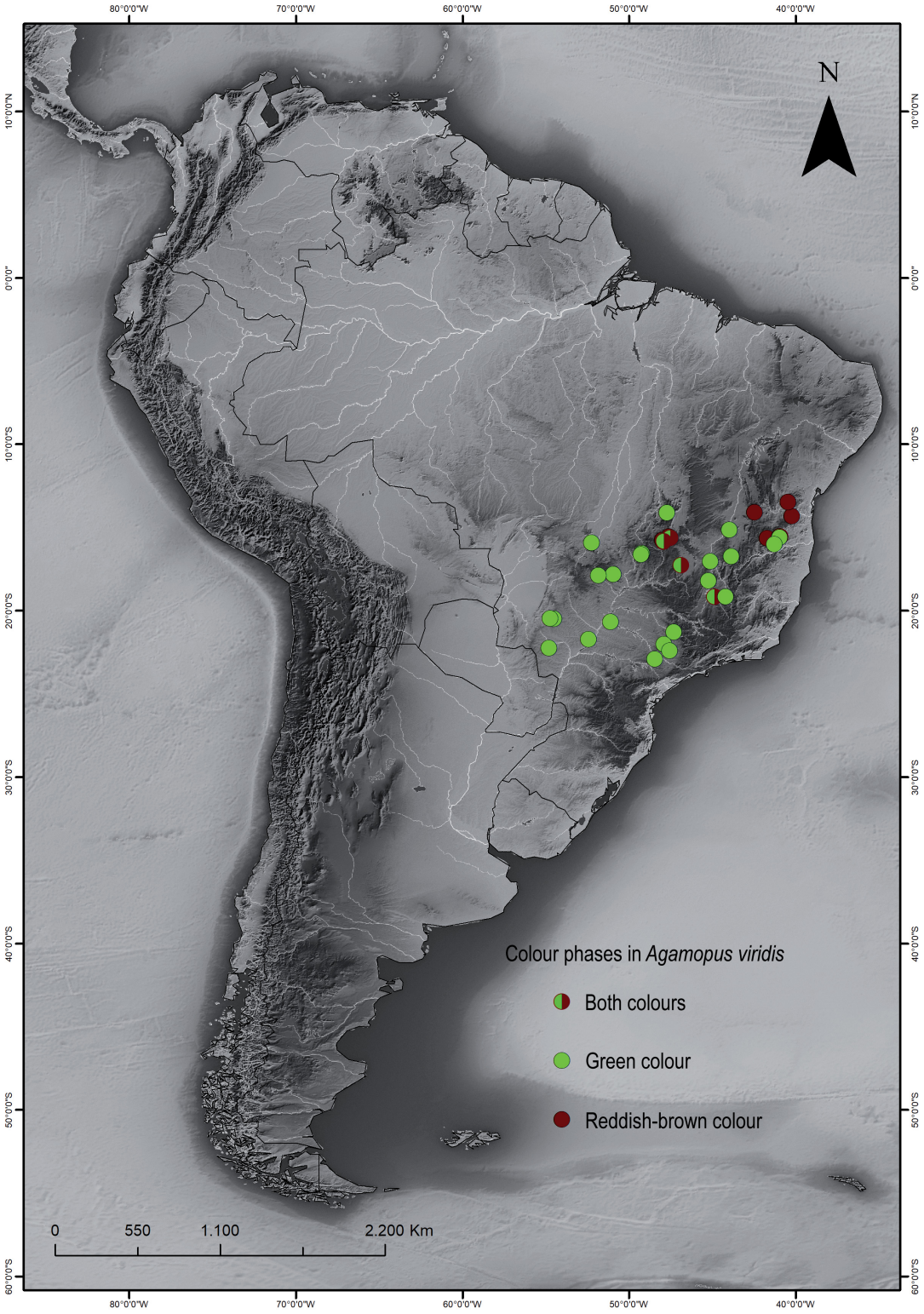

Fig. 10. Geographical distribution map of two colour phases of the pronotum of *Agamopus viridis* Boucomont, 1928. Green circles represent the specimens with the pronotum green metallic; the reddish-brown circles represent the specimens with a reddish-brown pronotum; the green/reddish-brown divided circles represent the sites where both colour phases were found.

phases were dissected and exhaustively examined, but no morphological differences were found in the tegmen (parameres and phallobase) or in the structures of endophallus between the populations. For these reasons, we interpret these distinct colour phases and punctation patterns as intraspecific variations within a single species.

Geographic distribution

Agamopus viridis is common in collections. Its distribution seems to be sympatric with that of *A. unguicularis*, occurring in the central region of Brazil (Fig. 10).

Identification key to the Agamopus species (adapted from Halffter & Martínez 1968)

1. Frons with two small tubercles near to fronto-clypeal sulcus (Fig. 5B, white setae). Pygidium without yellow setae 2
– Frons without tubercles (Fig. 5A). Pygidium bearing yellow setae (Fig. 2A–B) 3

2. Pygidium with arched sulcus (Fig. 9E). Anterior half of metatibiae with outer and inner edges gradually widened apically; inner edge smooth. Central Brazil .... ***Agamopus viridis*** Boucomont, 1928
– Pygidium with sinuous sulcus (Fig. 4D). Anterior half of metatibiae with outer and inner edges parallel (Fig. 4C); inner edge crenulated. Southern Brazil (Paraná) ..... ***Agamopus joker*** sp. nov.

3. Head fully covered by micropunctation (as in Fig 5B, but without tubercles); male with posterior margin of metafemora smooth 4
– Head with central part smooth or with sparse micropunctation (Fig. 5A); male with posterior edge of metafemora crenulated (Fig. 6C). From Mexico to northern South America (Colombia and Venezuela) ..... ***Agamopus lampros*** Bates, 1887

4. Pygidium with a single row of several yellow setae arranged along anterior edge of sulcus (Fig. 2A); Brazil and Bolivia ..... ***Agamopus unguicularis*** (Harold, 1883)
– Pygidium with a row of two or three yellow setae along centre of anterior edge of sulcus (Fig. 2B). Suriname, French Guiana, and northern Brazil ..... ***Agamopus castaneus*** Balthasar, 1938

Discussion

Remarks on *Agamopus convexus* Balthasar, 1965 (incertae sedis)

Agamopus is a morphologically well-defined genus (Halffter & Martínez 1968; Howden & Young 1981). *Agamopus convexus* was described by Balthasar (1965) based on a single specimen from Espírito Santo, Brazil (Fig. 11). Halffter & Martínez (1968) mentioned that Balthasar's specimen does not have any sulcus on the pygidium. Therefore, it does not match the diagnosis of *Agamopus*. We confirmed Halffter & Martínez's (1968) statement after reading Balthasar's original description and examining the holotype housed in the NMPC (Fig. 11). Albeit Halffter & Martínez (1968) knew that the species described by Balthasar (1965) was potentially assigned to the wrong genus, they never formally transferred the species to another genus. The original description provided by Balthasar (1965) and the comments made by Halffter & Martínez (1968) highlight some interesting features that, in our opinion, strongly suggest that this species could be potentially part of the *Ateuchus ovalis* species group as defined by Martínez & Martínez (1987) or another clade related to *Ateuchus*. Mario Cupello (pers. com. to the authors, 1st August 2021), who is currently revising *Ateuchus*, agrees with this.

As mentioned above, *A. convexus* lacks the transverse sulcus of the pygidium that is diagnostic – and presumably synapomorphic – of *Agamopus*. Its anterior legs also lack trochantofemoral pits, a hypothesised synapomorphy of Ateuchini (Tarasov & Génier 2015) and a character which is present in

the other *Agamopus*. A particular branch of the Ateuchini, however, the Ateuchina Perty, 1830, have lost the trochantofemoral pits and, as a result, all of its species are similar to *A. convexus* in lacking them altogether. This suggests that the absence of trochantofemoral pits in *A. convexus* may be secondary and, if so, that the species may be an Ateuchina instead of an *Agamopus*. More specifically, *A. convexus* shows many of the diagnostic features of the *Ateuchus ovalis* species group. According to Martínez & Martínez (1987), these include protibiae with two small teeth (sometimes with an additional smallest teeth) limited to the anterior half of the outer edge, with the rest of the outer edge crenulate until the base; two clypeal teeth poorly indicated; posterior edge of pronotum with a row of punctation; and the first metatarsomere longer than the second to fourth combined. This was later confirmed by Vaz-de-Mello (2007: 162), who suggested a new genus would have to be established to accommodate *Ateuchus confusus* Martínez & Martínez, 1987 and *Canthidium ovale* Boucomont, 1928 (both currently in the *Ateuchus ovalis* group); *Choeridium cernyi* Balthasar, 1938; and *Agamopus convexus* Balthasar, 1965. According to Vaz-de-Mello (2007: 162), *Choeridium contractum* Balthasar, 1938 and *Choeridium vigilans* Van Lansberge, 1874 should also be included in this genus. However, this potential new genus as suggested by Vaz-de-Mello (2007) and Bezděk & Hájek (2011) has never been formally named according to the ICZN (1999).

Considering the absence in *A. convexus* of the diagnostic characters of *Agamopus* (mainly the absence of a deep transverse sulcus in the pygidium), and, at the same time, the morphological similarity of this species with those composing the *Ateuchus ovalis* species group, we propose its transfer from *Agamopus* to the *ovalis* group of *Ateuchus*. It is, therefore, now named *Ateuchus convexus* (Balthasar, 1965) comb. nov., and should be treated as such until a detailed revision of *Ateuchus* is published and a more precise placement for the species is found.

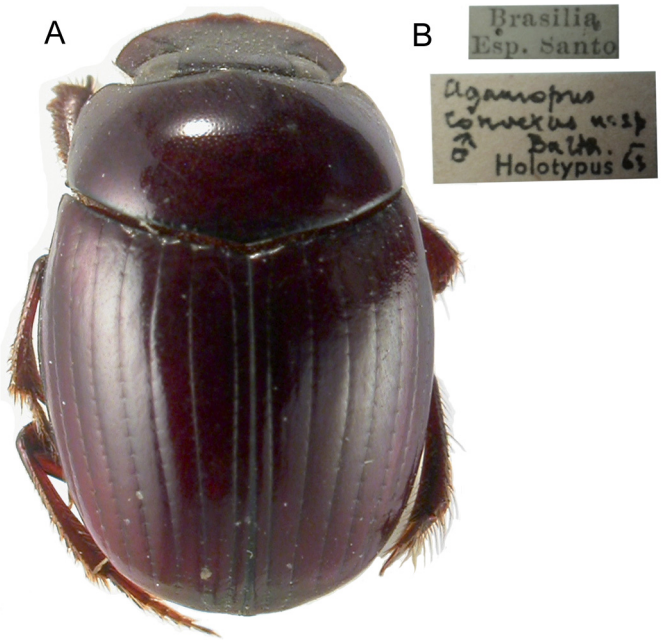

Fig. 11. *Agamopus convexus* Balthasar, 1965 (now *Ateuchus convexus* comb. nov.). Holotype (NMPC). **A**. Habitus, dorsal view. **B**. Labels. Length of specimen: 6.5 mm. Photograph: Jiří Hájek, NMPC.

A brief comment about the natural history and phylogenetic position of *Agamopus*

According to label records, species of *Agamopus* are associated with open vegetation or patchy forested areas, being frequently collected in pastures (Tissiani *et al.* 2017) between 200 and 1600 meters above sea level. The feeding behaviour of *Agamopus* is still unknown, but the high number of specimens collected with pitfall traps baited with excrement suggests coprophagous habits. Being more active at night (Howden & Young 1981), the species can be collected mainly with light traps, pitfalls baited with excrement (human, pig, cow, and horse) or, less successfully, with flight interception traps (FIT). Moreover, Vaz-de-Mello (2007) suggested that *Agamopus* species are kleptocoprids, laying their eggs in the nests (brood masses and balls) of other dung beetles. This activity was observed in nests of members of the genera *Dichotomius* Hope, 1838, *Isocopris* Pereira & Martínez, 1960 and *Ontherus* Erichson, 1847 (F.Z. Vaz-de-Mello, pers. com.).

In contrast to its mysterious biology, the phylogenetic relationship of *Agamopus* with the other scarabaeine lineages is better understood (Vaz-de-Mello 2007; Tarasov & Génier 2015). Bates (1887), in the description of *A. lampros*, related *Agamopus* to *Uroxys* Westwood, 1842, *Aphengium* Harold, 1868 and *Ateuchus* Weber, 1801 (cited as *Choeridium*) on morphological grounds. Even though not numerous, the few phylogenetic analyses including *Agamopus* species that have so far been published have supported the hypothesis suggested by Bates (1887) and placed the genus within Ateuchini, being apparently more closely related to the Ateuchina than to Scatimina Vaz-de-Mello, 2008 (Vaz-de-Mello 2007; Tarasov & Génier 2015). In spite of this close affinity to the Ateuchina, however, Vaz-de-Mello's (2008) phylogenetic circumscription of the subtribe does not include *Agamopus*; the latter is currently considered instead an incertae sedis genus in Ateuchini, with no formal subtribal assignment. It is likely that a new subtribe name will eventually be formally established for *Agamopus* (Vaz-de-Mello 2007). While the phylogenetic placement of *Agamopus* within Scarabaeinae is relatively well established, the relationships between its species are still unknown.

Conclusion

This work provides an updated taxonomic review of the genus *Agamopus*, which now includes five species: *Agamopus castaneus*, *A. joker* sp. nov., *A. lampros*, *A. unguicularis* and *A. viridis*. *Agamopus* is easily recognized by the presence of a transverse sulcus on the pygidium, which is likely a synapomorphy of the clade. All species of *Agamopus* are restricted to the Neotropical Region, with its geographical distribution being much wider than previously known to Halffter & Martínez (1968). The remarkable diagnostic characteristics of the species allied with their geographical distribution make their delimitation and identification easy. *Agamopus lampros* is the northernmost species, with records ranging from western Mexico to northern South America; *A. castaneus* also occurs in northern South America (Guiana and Suriname Shield), including the new records from Brazil; *Agamopus unguicularis* is widespread in Brazil and some parts of Bolivia; *Agamopus viridis* is also widespread in Brazil, while *A. joker* is known from a single specimen collected in Paraná, southern Brazil.

The present study contributes to the knowledge and discovery of the South American fauna, emphasizing the importance of scientific collections and taxonomic studies for public decision-making policies on biodiversity conservation. Also, we hope that future studies will address the evolutionary history of *Agamopus* species from a phylogenetic and biogeographic perspective.

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