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Digitonthophagus Balthasar, 1959: taxonomy, systematics, and morphological phylogeny of the genus revealing an African species complex (Coleoptera: Scarabaeidae: Scarabaeinae)

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***Digitonthophagus* Balthasar, 1959: taxonomy, systematics, and morphological phylogeny of the genus revealing an African species complex (Coleoptera: Scarabaeidae: Scarabaeinae)**

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Abstract

The taxonomy and systematics of the genus *Digitonthophagus* Balthasar (Coleoptera: Scarabaeidae: Scarabaeinae: Onthophagini) is revised. A detailed study of the male genitalia combined with external morphology suggests that the variability, previously recognized, for *D. gazella* is hiding a species complex within the Afrotropical region and the Arabian Peninsula. The current study recognizes 16 species; 13 from the Afrotropical region and Arabian Peninsula and three from the eastern portion of the Saharo-Arabian region and the continental Indomalayan region. Species are organized into six species groups based on the results of the morphology-based phylogenetic analysis. The following 12 species are described as new: *D. aksumensis* Génier **new species**; *D. biflagellatus* Génier **new species**; *D. dilatatus* Génier **new species**; *D. eucatta* Génier **new species**; *D. falciger* Génier **new species**; *D. fimator* Génier **new species**; *D. namaquensis* Génier **new species**; *D. petilus* Génier **new species**; *D. sahelicus* Moretto **new species**; *D. uk*s Génier **new species**; *D. ulcerosus* Génier **new species**; and *D. viridicollis* Génier **new species**. In order to stabilize nomenclature, lectotypes are designated for *Scarabaeus bonasus* Fabricius, 1775; *Scarabaeus catta* Fabricius, 1787, and *Onthophagus gazella lusinganus* d'Orbigny. A neotype is designated for *Scarabaeus dorcas* Olivier, 1789 whose status and synonymy need to be altered in order to clarify the status of *Scarabaeus gazella* auctorum, the widely introduced species with economic importance. A naming scheme is presented for the sclerites of the internal sac. External and male genitalia are illustrated and distribution maps are provided for each species.

Key words: Scarabaeidae, Scarabaeinae, *Digitonthophagus*, *Onthophagus*, *Digitonthophagus gazella*, Nomenclature, taxonomy, distribution, Afrotropical region, Indomalayan region, biological control of dung, pasture improvement

Résumé

La taxonomie et la systématique du genre *Digitonthophagus* Balthasar (Coleoptera: Scarabaeidae: Scarabaeinae: Onthophagini) sont révisées. Une étude détaillée des génitalias des mâles, combinée à celle de la morphologie externe, suggère que la variabilité qui était jusque-là admise pour le *D. gazella* des auteurs cachait un complexe d'espèces dans la région afro-tropicale et la Péninsule Arabique. La présente étude reconnaît seize espèces : treize pour la région afro-tropicale et la Péninsule Arabique et trois pour la partie orientale du Moyen Orient et la région indo-malaise. Une analyse phylogénétique utilisant les caractères de la morphologie répartit ces seize espèces en six groupes. Les 12 espèces suivantes sont décrites : *D. aksumensis* Génier **espèce nouvelle**, *D. biflagellatus* Génier **espèce nouvelle**, *D. dilatatus* Génier **espèce nouvelle**, *D. eucatta* Génier **espèce nouvelle**, *D. falciger* Génier **espèce nouvelle**, *D. fimator* Génier **espèce nouvelle**, *D. namaquensis* Génier **espèce nouvelle**, *D. petilus* Génier **espèce nouvelle**, *D. sahelicus* Moretto **espèce nouvelle**, *D. uks* Génier **espèce nouvelle**, *D. ulcerosus* Génier **espèce nouvelle**, *D. viridicollis* Génier **espèce nouvelle**. Afin de stabiliser la nomenclature, des lectotypes sont désignés pour *Scarabaeus bonasus* Fabricius, 1775, *Scarabaeus catta* Fabricius, 1787 et *Onthophagus gazella lusinganus* d'Orbigny. Un néotype est désigné pour *Scarabaeus dorcas* Olivier, 1789 dont le statut et la synonymie doivent être modifiés, afin de clarifier le statut du *Scarabaeus gazella* des auteurs, qui se trouve être l'espèce la plus largement introduite et la plus importante du point de vue économique. Des schémas légendés sont présentés pour les sclérites du sac interne. Les parties externes et internes des génitalias sont illustrées et des cartes de distribution produites pour chaque espèce.

Introduction

Prior to this study the genus *Digitonthophagus* Balthasar (Coleoptera: Scarabaeidae: Scarabaeinae: Onthophagini) as defined by Zunino (1981) was composed of two species. The Asian *D. bonasus* Fabricius easily separated from the "Afro-Asian" *D. gazella* Fabricius by its larger average size and the presence of a median horn on the vertex in both sexes. *D. gazella* was considered widespread and morphologically highly variable (d'Orbigny 1900b; Müller 1942). Despite this variability, a single form has been named *Onthophagus (O.) gazella lusinganus* by d'Orbigny for specimens originating from Rusinga Island and a few localities in Kenya. This form was later elevated to species rank by Müller (1942) but some modern authors still considered the taxon as infraspecific (Balthasar 1963). All other names associated with the genus *Digitonthophagus* were considered synonyms of *D. gazella*, with the *D. catta* Fabricius being considered valid or not depending of the authors.

While studying material collected in Burkina Faso it became apparent that large males and females could be separated into up to four morphotypes within single collecting events with a proportional number of individuals of each morphotype varying in each sample, especially with samples coming from northern compared to samples from southern localities. One morphotype in which males display obliquely divergent cephalic horns and females display shorter cephalic horns instead of a simple transverse carina could easily be separated with external characters (now *D. sahelicus* Moretto). The other three morphotypes were more similar externally and differences were ambiguous in smaller individuals. To test if this variation was intraspecific the aedeagus internal sac of a large sample of males were extracted and compared. Although the parameres were similar, the sclerites of the internal sac, especially the frontolateral peripheral sclerite (FLP) were varying in shape. This variation was not continuous but showed three distinct morphological patterns. These three distinct pattern were congruous with the external morphology of each of the three morphotypes (now *D. eucatta* Génier, *D. falciger* Génier, and *D. fimator* Génier). We hypothesized that each of these morphotypes could not represent intraspecific variation as there were no morphological intermediate or possible subspecific variation as the individuals were collected in the same trapping event. Furthermore, the traps set in the northern part of Burkina Faso (Toulfé) had more individuals of *D. eucatta* and traps set in the south (Nazinga Forest) were dominated by *D. fimator* and *D. falciger* suggesting that each species had different ecological preferences. Interestingly, *D. sahelicus*, which is associated with desert and grassland was also collected once in the much wetter Nazinga Forest but only at a light trap set in a football field covered with grass. None of the traps set around in the native vegetation caught a single individual of *D. sahelicus*; suggesting that each of the *Digitonthophagus* species avoids competition by specializing in a single microhabitat within a mosaic. While dissecting male genitalia, individuals not matching one of the four isolated morphotype were discovered. Only small individuals were first available for study, but when larger males became available,

secondary sexual characters of these specimens were also morphologically different. This morphotype is here considered the fifth species present in West Africa and is here described as *D. dilatatus* Génier. This species is much scarcer than the other four West African species. After disentangling the five West African species, it was decided to look at the rest of the African and Asian fauna. The final results of this study are presented here and is revealing a complex of 12 African species, excluding the easily recognizable *D. sahelicus*, which is closely related to the oriental *D. bonasus* and *D. uks* Génier. All species recognized here show discrete and definite differences in the internal sac sclerite morphology and all of these differences are constant, relate to external characters and distribution of each species matches recognized biogeographic divisions. The lack of intermediate forms strongly supports postzygotic incompatibility, and similar cases have been studied for cryptic *Onthophagus* species in Europe (Roy *et al.* 2015). In our opinion, the status quo, recognizing a single polymorphic Afro-Asian species can no longer be justifiable based on the presented evidence.

Digitonthophagus gazella is perhaps the most widely known dung beetle species of economic importance and has been introduced worldwide for pasture improvement and biocontrol of pest flies. The reader is referred to Génier & Davis, 2017 for detailed information on the history of the introduction worldwide and an overview of the taxonomic problem relating to the name "*D. gazella*".

Material and methods

Morphology. External morphology. Terminology for the overall skeletal morphology is primarily based on Edmonds (1972) with some exceptions. We here refer to the pronotal lower folded portion as the hypomeron instead of the propleuron. In Scarabaeinae, and the rest of Polyphaga, the remnant of the propleuron is embedded in the membranous portion attaching the head to the pronotum and referred as cryptopleuron. Figure 1 summarizes the terminology used for the anterior hypomeral region. Note that the anterior hypomeral depression is only slightly concave in *Digitonthophagus* species.

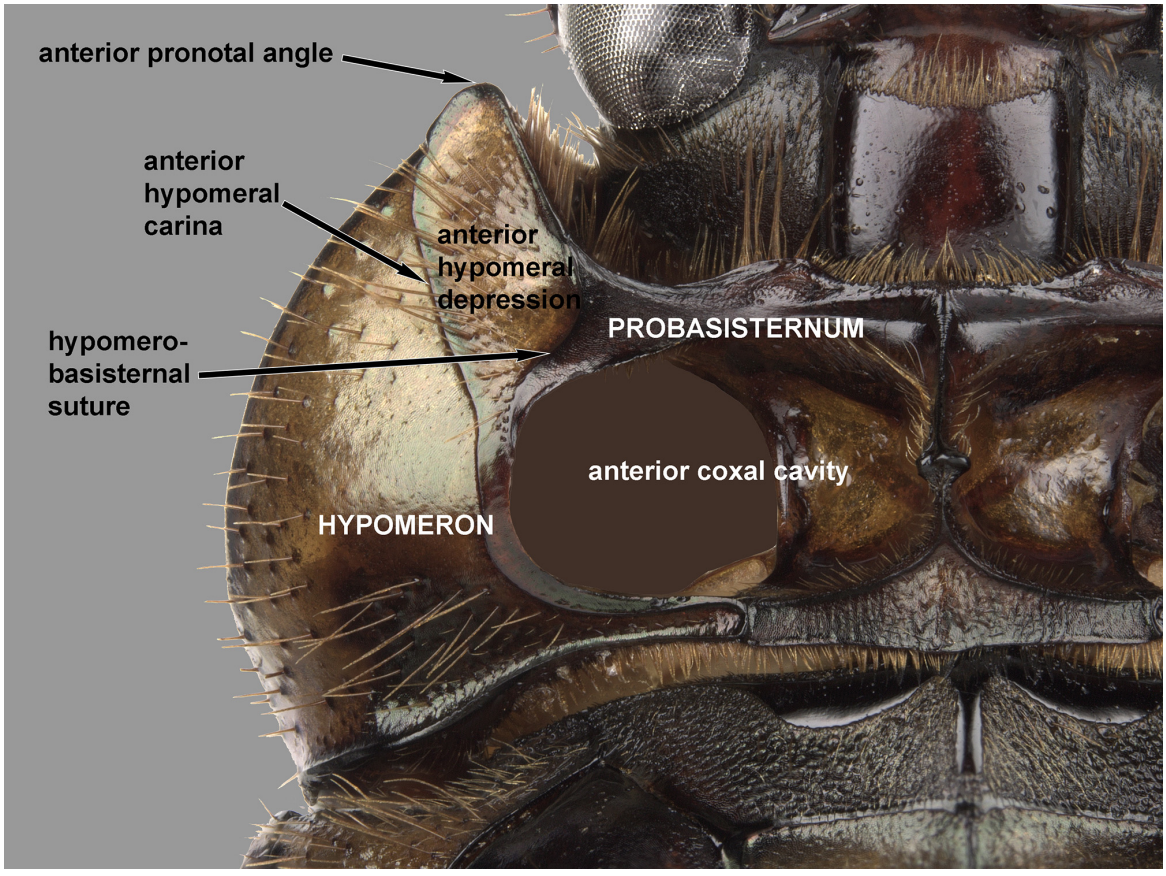


FIGURE 1. Detailed terminology for the anterior hypomeral region (procoxae removed).

Male genitalia. The overall morphology and homologies are based on Tarasov & Solodovnikov (2011) and Tarasov & Génier (2015). The anatomy of the internal sac differs substantially from other Onthophagini whose functioning has been studied in detail by Werner & Simmons (2008) for *Onthophagus taurus* (Schreber). In species of the *Phalops* Erichson complex of genera the internal sac is missing the lamella copulatrix (LC) and the superior right peripheral sclerite (SRP) is reduced in size. After several trials we managed to evert the internal sac of a few *Digitonthophagus* specimens. The frontolateral peripheral sclerite (FLP) is positioned at the internal sac apex and the membrane (Fig. 2, colored red) attached to the basal portion of FLP (Fig. 2). Because A + SA sclerites complex are more or less fused, it is not clear if more than two sclerites are present. Tarasov and Solodovnikov (2011) suggested that this complex might be composed of A + SA1 + SA2 + SA3. However, to simplify descriptions in this work, we consider that only two sclerites (A + SA) are present and more or less fused basally. The axial sclerite (A) that is ventral and more-or-less pointed apically and the subaxial sclerite (SA) that is dorsal and villous apically. In addition to those, two small sclerites, seemingly unique to the *Phalops* complex of genera, are present between the basal portion of A + SA and FLP. The apices of these sclerites, here named parafrontolateral sclerite 1 (PFLP1) for the more dorsal and parafrontolateral sclerite 2 (PFLP2) for the more ventral, are protruding along the opening of the ejaculatory duct. The SRP is set in the membrane on the right side of FLP and border an enlargement of the internal sac. The basal portion of FLP is strongly sclerotized and approximately hemispherical ventrally and the wall presents a fulcrum along the basal portion of the basoventral apophysis. The distal portion of FLP is complex (Figs. 2-5) and a new and detailed terminology for the different structures is introduced here to describe and use this complex morphology whose overall shape is unique to the *Phalops* complex of genera. The ground plan for the apical portion of FLP in *Digitonthophagus* is a lamellate projection with additional structures dorsally, both laterally, and ventrally. The apex of FLP is terminated by the always villous apical lobe. The dorsal surface possesses a membranous lobe (subapicodorsal lobe) in the same plane as the apical lobe, the subapicodorsal lobe is heavily sclerotized and folded in *D. catta* and *D. eucatta*. The right lateral edge is produced into a complex fold whose apical portion is produced into a convoluted and more or less concave structure (right lateral fold), except in *D. catta* and *D. eucatta* where it is simply foliate. The left edge is comparatively less intricate, but possesses either a more-or-less sclerotized lobate projection (left lateral lobe) or a large dentate process (left lateral apophysis) in *D. catta* and *D. eucatta*. The ventral surface always possesses a longitudinal lobate structure (subapicoventral lobe) set perpendicular to the plane of the apical lobe and in some species one or two additional more or less transverse or angulate carinae (medioventral carinae). Figures 3 and 4 show the terminology in *D. gazella*, which is characteristic of most *Digitonthophagus* species. Figure 5 shows the same terminology in *D. eucatta*, which differs from the general ground plan by its enlarged and sclerotized subapicodorsal lobe of FLP obscuring the apical lobe and the presence of a large left lateral apophysis. It is interesting to note that even in very teneral specimens, the internal sac sclerites are always perfectly formed and strongly sclerotized, suggesting that the final shape of this structure is crucial for the reproductive mechanisms.

Although beyond the scope of this work, we tried to infer a possible biomechanical integration of the FLP, A, SA, PFLP1, PFLP2 sclerites complex while dissecting the internal sac. The anatomy of the internal sac differs substantially from the remaining Onthophagini. We hypothesize here that the sperm transfer process occurring in the *Phalops* genera complex substantially differs from the process involved in other Onthophagini. This process has been shown to involve several sclerites to form a "spermatophore tube die" (Werner & Simmons 2008) in the rest of Onthophagini. The rather complex, and homogenous within the genus, apical portion of the parameres also suggest a different coupling mechanism with the female pygidium and last abdominal ventrite in *Digitonthophagus* compared to that of *Onthophagus taurus*. A number of muscles are present in the basal portion of FLP. These muscles are attached to the basal rim portion of the FLP as well as the base of A + SA sclerites. When dissections are performed, the A + SA sclerites are easily rotated in the same axis as FLP, in such a way that the apical portion moves laterally. It is unclear if a basoapical movement of the apex of A + SA is also possible. Additionally, the fulcrum along the base suggests that a dorsoventral movement is also possible for the apical portion of FLP. The basoventral apophysis of FLP suggests an anchoring mechanism for the FLP. We are unable to speculate on the function of PFLP1, PFLP2, but their presence adjacent to the opening of the ejaculatory duct suggest a function in sperm discharge. The presence of villi on the internal side of A + AS and setae on the left lateral surface of FLP could possibly help in funneling sperm into the spermathecal duct opening, but this is speculative at the moment. The SRP is reduced in size and set on a short distance from the base of FLP. It is bordering a protrusion of the internal and probably an additional anchoring device.

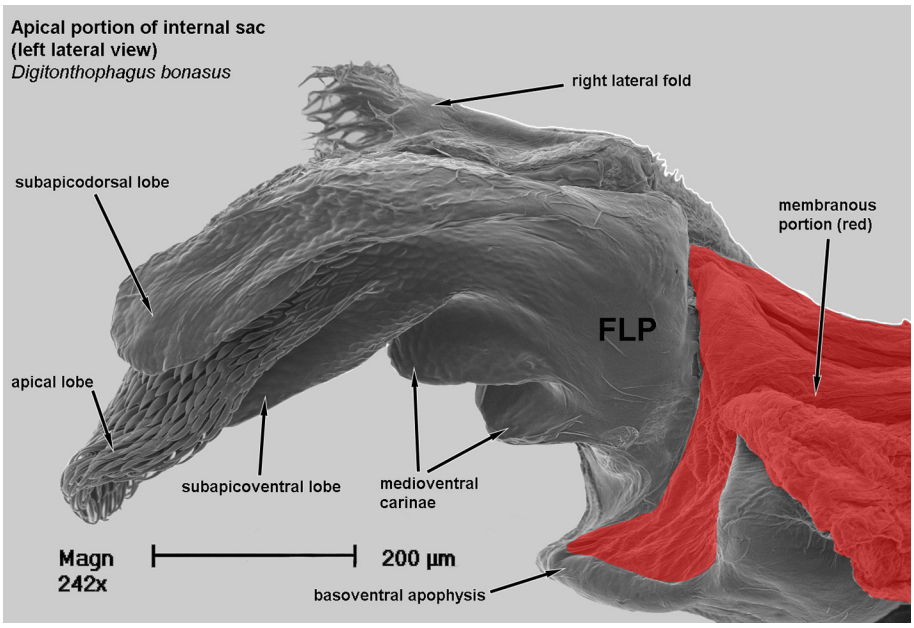


FIGURE 2. Apical portion of internal sac of *Digitonthophagus bonasus* (membranous portion colored red).

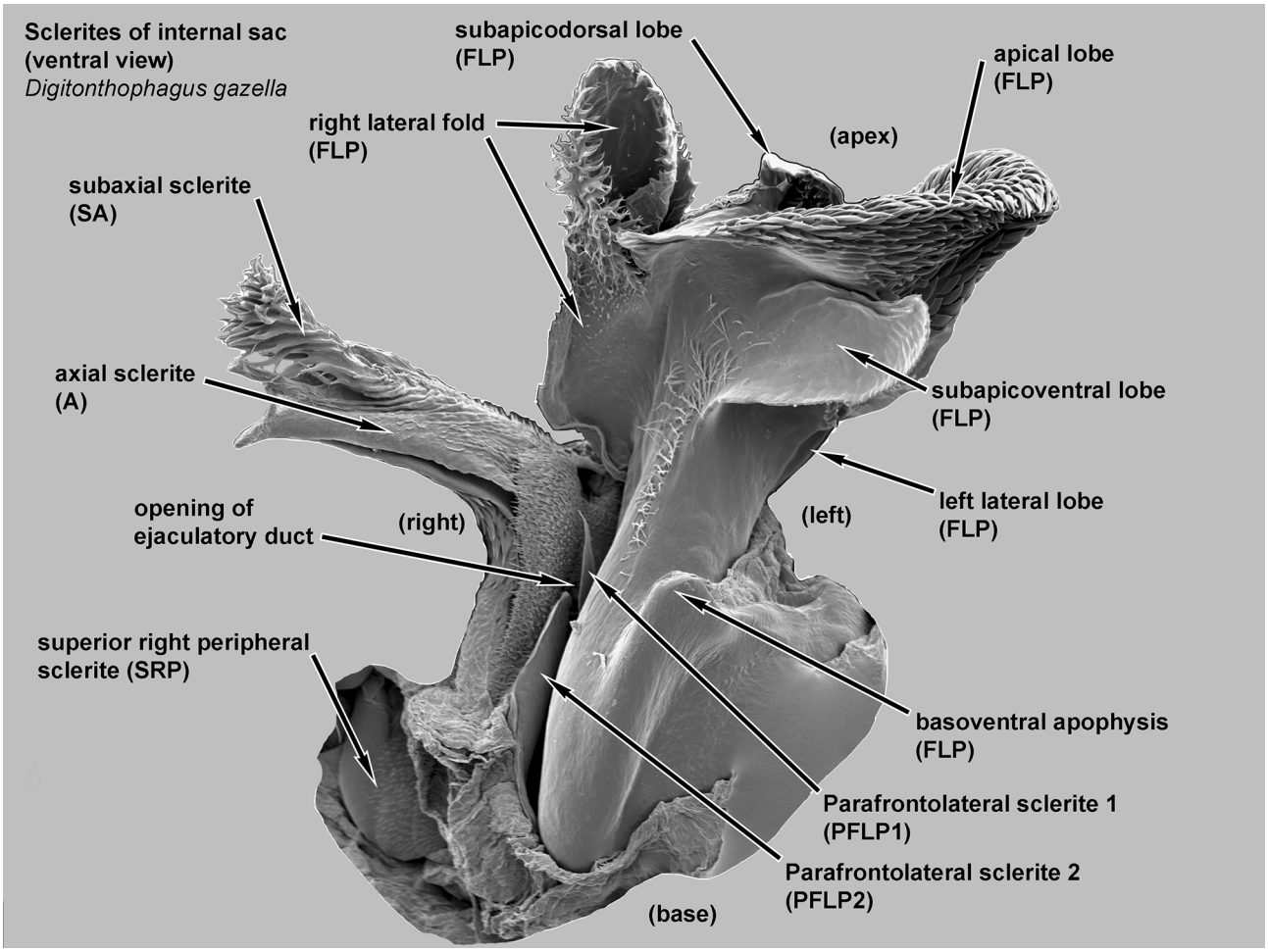


FIGURE 3. Detailed terminology of the frontolateral peripheral and associated sclerites of *Digitonthophagus gazella*.

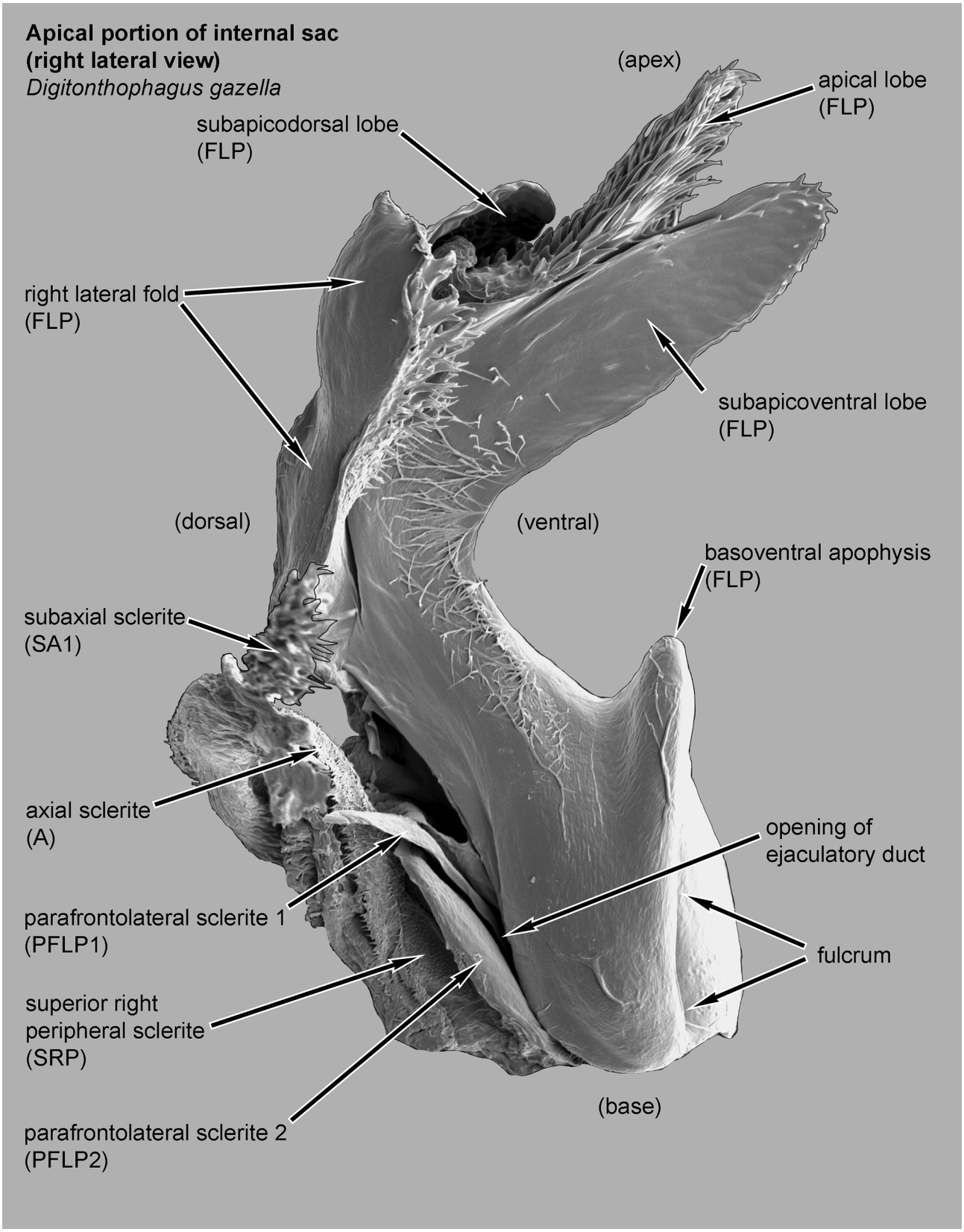


FIGURE 4. Detailed terminology of the frontolateral peripheral and associated sclerites of *Digitonthophagus gazella*, right lateral view.

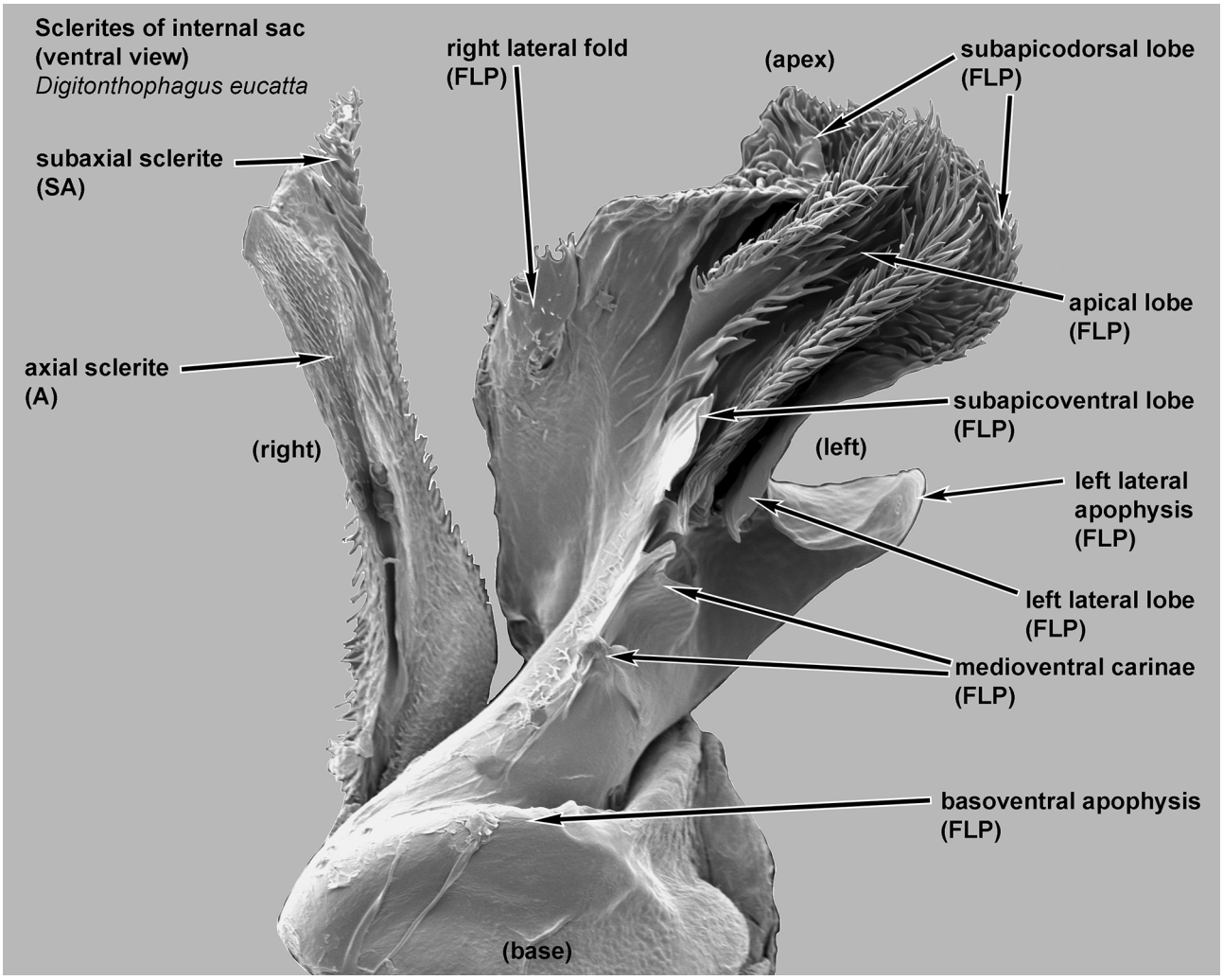


FIGURE 5. Detailed terminology of the frontolateral peripheral and associated sclerites of *Digitonthophagus eucatta*, ventral view.

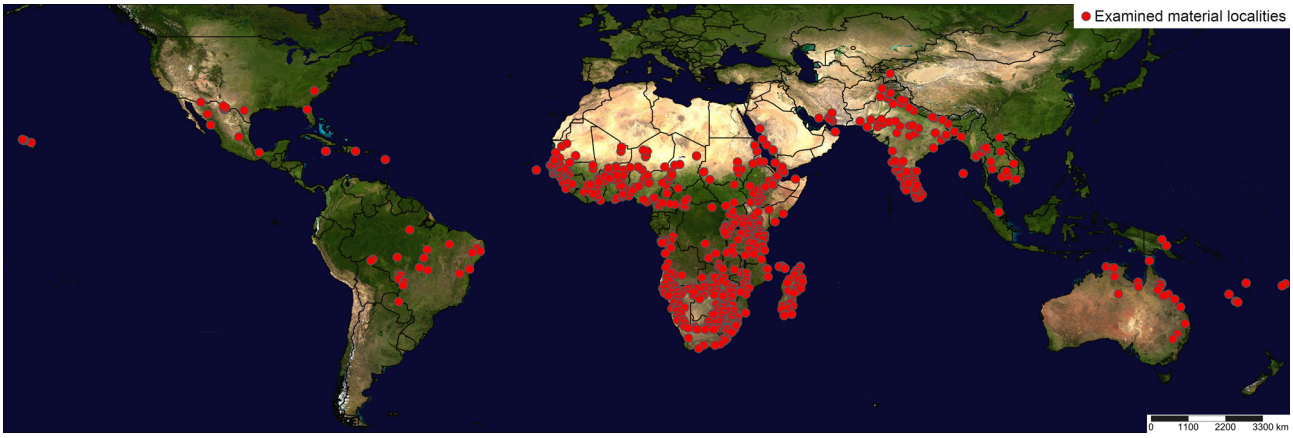
Female genitalia. The female genital tract is relatively simple and similar within the Onthophagini (Rogerro *et al.* 2016a), it was not thoroughly investigated here.

Specimens and their deposition. More than 11,000 specimens were examined. Informative data of 7,870 specimens (Map 1) were recorded using the Mantis Database version 2.1 (Naskrecki 2008). When long series (approximately 10 or more individuals) of previously described species (*D. bonasus*, *D. catta*, and *D. gazella*) with identical data were studied, data of only one or two pairs were recorded. Identification labels were affixed to all specimens studied.

The acronyms used in the text were taken from Evenhuis (2007) or were generated if missing from The Insects and Spider Collections of the World Website.

BDGC	Bruce D. Gill personal collection, Woodlawn, Ontario, Canada.
BMNH	The Natural History Museum, London, United Kingdom; Max Barkley, Malcolm Kerley.
CAC	Alain Coache personal collection, La Brillanne, France.
CADB	Alain Drumont personal collection, Brussels, Belgium.
CBR	Bernard Rainon personal collection, Chassagny, France.
CEMT	Seção de Entomologia da Coleção Zoológica da Universidade Federal de Mato Grosso, Cuiabá, Mato Grosso, Brazil; Fernando Vaz-de-Mello.
CMD	Michaël Dierkens personal collection, Lyon, France.
CMNC	Canadian Museum of Nature, Gatineau, Quebec, Canada.

CNC Canadian National Collection of Insects and Arachnids, Agriculture and Agri-Food Canada, Ottawa, Ontario, Canada; Pat Bouchard, Serge Laplante.
CTT Thomas Thery personal collection, Fleury-les-Aubrais, France.
CVM Vladislav Malý personal collection, Prague, Czech Republic.
FETC †Federico Tagliaferri, Roncaglia, Italia.
FGIC François Génier personal collection, Gatineau, Quebec, Canada.
GWPC Georg Werner personal collection, Peiting, Germany.
HMIM Hayk Mirzayans Insect Museum, Teheran, Iran; Sayed Serri.
IRSNB Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; Alain Drumont, Pol Limbour.
JFJC Jean-François Josso personal collection, Muzillac, France.
MHNL Musée des Confluences [formerly Muséum d'Histoire naturelle de Lyon], Lyon, France.
MMUE The University, Manchester Museum, Manchester, United Kingdom; Dmitri Logunov.
MNHN Muséum national d'Histoire naturelle, Paris, France; Olivier Montreuil, Antoine Mantilleri.
NMPC Natural History Museum, Prague, Czech Republic: Jiří Hájek.
OMOC Olivier Montreuil personal collection, Fleury-les-Aubrais, France.
OUMNH Oxford University Museum of Natural History, Oxford, United Kingdom; Darren J. Mann.
PCSR Sebastien Rojkoff personal collection, Lyon, France.
PHWC Philippe Walter personal collection, Montségur, France.
PMOC Philippe Moretto personal collection, Toulon, France.
PSCW Peter Schäfer personal collection, Mainz, Germany.
RMNH Naturalis Biodiversity Centre [formerly Rijksmuseum van Natuurlijke Historie], Leiden, Netherlands; Hans Huijbregts.
SMF Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt-am-Main, Germany; Damir Kovac.
SMNS Staatliches Museum für Naturkunde, Stuttgart, Germany; Wolfgang Schawaller.
ZMUC University of Copenhagen, Zoological Museum, Copenhagen, Denmark; Alexey Solodovnikov.
ZMUK Christian-Albrechts-Universität zu Kiel, Zoologische Museum Kiel, Kiel, Germany; Michael Kuhlmann.



MAP 1. Plotted localities of examined material (adventive range for *D. gazella* not studied in detail).

Terminology, material preparation, and format. In this paper, the term edge refers to the outermost portion of a structure (*e.g.*, clypeal edge, pronotal edge). The term margin refers to the internally delimited portion along the edge.

All measurements were rounded to the nearest 0.5 mm. More precise measurements were deemed unnecessary as specimens have the head and/or pronotum more-or-less tilted down consequently slightly changing the overall length measurement. The length was taken in dorsal view from the apex of clypeal teeth to the posterior most portion of the pygidium and width is the maximum width, which in some species is at the pronotal level and in other species at the elytral level.

All primary type label data are transcribed verbatim. Each label text is in brackets ([]) and each text line is

separated by a slash (/), this is followed by the sex and deposition of the specimen. If not indicated otherwise, the label text is printed on white card or paper.

Internal sacs of more than 1100 specimens, representing at least one male per collecting event, were extracted from the basal opening of the phallobase, after the specimen was rehydrated in warm tap water for approximately one hour. Muscles, fat, and tracheal remains were removed with fine dissecting forceps. All dissected internal sacs were cleared in room temperature 30–40% potassium hydroxide for half an hour to two hours depending on the preservation state. Because the internal sac is not everted when removed from the phallobase basal opening, sclerites are in repose position and the FLP and accessory sclerites are embedded in the membranous portion of the internal sac. To uncover these structures a small incision, made with fine dissecting forceps, was performed in line with the dorsal portion of the FLP. The FLP was then pulled out and left attached to the rest of the internal sac and treated again in a bath potassium hydroxide for few more minutes. The lateral portions of the internal sac were then further detached with fine forceps as to leave only a narrow band of membrane holding to the base of FLP to ensure that the FLP would remain freely moveable. The internal sac was then rinsed in warm water and in 70% ethanol before the structure was mounted in a small drop of alcohol and water-soluble Dimethylhydantoin Formaldehyde Resin (DMHF), on a piece of white card (Fig. 6). To show a maximum of characteristics from the dorsal view, the axial and subaxial sclerites (A + SA), which form a compact structure and is collapsed along the right lateral portion of FLP, were pulled toward the right and set as much as possible in the same plane as the dorsal surface of FLP. The aedeagus was glued with water soluble glue (Weldbond™) to the apex of the cardboard piece for easy examination in all directions along with the internal sac. To facilitate comparison, all preparations were set with the FLP dorsal portion facing up. Over a thousand specimens were dissected, representing at least one male per collecting event for species that could not be reliably identified with external characters only. In some instances longer series from the same collecting even were prepared to assess variability within local populations.

FIGURE 6. Card attached to specimen showing the dissected male genitalia preparation.

All photographs were taken with a Leica Z16 APOA system and images stacked with the LAS software. Preference was given to primary types for illustrations of the external and internal morphology. An unabraded and well-developed specimen was used when primary types were unsuitable for a high-quality image. The dorsal and frontal images of the head were taken with the head set flat and the horns set flat respectively, to ensure proper cephalic and horns shape outline comparison. The flat positioning of the horns is important to show the actual length and shape of the horns as they are more or less sloping backward depending on the species. Parameres were photographed in frontal view to better illustrate the angle and shape of the apical carinae and the shape of the basolateral paramerites. Because internal sac sclerites are in part slightly sclerotized, the membranous portions, such as the subapicodorsal lobe of most species, are difficult to observe when embedded in DMHF resin. These structures were imaged immersed in a translucent alcohol-based hand disinfectant (Purell advanced™) topped with a glass cover. The thickness of this media allows precise positioning and ensure that the structure does not move when multiple images are taken for stacking. Images were edited and assembled into plates with Photoshop CS6 extended software.

Bibliography, measurements, and list of material examined were generated with the Mantis Database version 2.1 (Naskrecki 2008), with some modifications. In the bibliographic sections of genus and species, the generic and species names are reported verbatim from the original publication. In the "Nomenclature and taxonomy" sections, the second epithet is valid. Distribution maps were prepared with SimpleMappr (Shorthouse, 2010).

For *D. bonasus* and *D. catta* a male alloreferent specimen (Dechambre 2002) was selected and used for the species descriptions, which are based on the male. For both of these Fabrician species all of the syntypes are females. The utility of an alloreferent is discussed by Dechambre (2002), such designation is practical and not regulated by the International Commission on Zoological Nomenclature (1999).

Taxonomy

Historical account. Historically, two species belonging to genus *Digitonthophagus* were recognized: *D. bonasus* and *D. gazella*, with the currently valid species *D. catta* historically considered a synonym of *D. gazella*. *Scarabaeus bonasus* Fabricius, 1775, was the first *Digitonthophagus* species described. Goeze (1777) gave a brief diagnosis in his *Entomologische Beyträges.* Fabricius (1781) diagnosed this species in the first volume of the *Species Insectorum* and in Pallas (1781). Pallas (1781) indicates that the illustration of *S. vacca* in Schröter (1776) is of *S. bonasus*. The available online version of Schröter (1776) lacks the plate so this makes the illustration in Pallas (Plate A, Fig. 5) the first confirmed illustration for *D. bonasus*. Herbst (1786) provided additional characters to diagnose the species. In the following year, Fabricius (1787a) repeated his laconic diagnosis. Olivier (1789) presented a diagnosis and illustration of a male specimen, which poorly matched his species description. Illiger (1800) redescribed *S. bonasus* and interestingly argues that *S. gazella* is simply a "variety" of *S. bonasus* with smaller cephalic horns and smaller body. Illiger was apparently unaware of the type locality Fabricius (1792) added in his treatment of the species *S. gazella*. Fabricius (1801) later transferred the species in the genus *Copris* Geoffroy. The species was subsequently transferred to the genus *Onthophagus* Latreille by Sturm (1826). Motchulsky (1860) considered the female of *Copris bonasus* to be a synonym of *Copris metallica* (Fabricius) and indicated that both taxa were synonyms of *Onthophagus catta* (Fabricius). The first comprehensive treatment of *D. bonasus* is by d'Orbigny (1900a) in his "Synopsis des *Onthophagus* paléarctiques". D'Orbigny (1900a) placed the species in the subgenus *Onthophagus*, and provided an identification key and distribution data. His description clearly refers to *D. uks* Génier new species as he stated that the anterior portion of the pronotum has either two large tubercles (*D. uks*) or sometimes only two large calluses (*D. bonasus*), but he considered the character variation to be intraspecific. *Digitonthophagus bonasus* was treated in Boucomont (1921), which included a key and distribution data. Arrow (1931), in his treatment of the Fauna of British India presented a detailed description with additional distribution data, reflecting the collection effort made in the region. Unlike d'Orbigny, Arrow did not discuss the two pronotal morphologies and only described *D. bonasus* in the current sense. Paulian (1945), in his monograph of the Indochinese scarabs maintained *D. bonasus* in the subgenus *Onthophagus*. Balthasar (1959) described the subgenus *Digitonthophagus* for an unspecified number of species possessing "long, bent, and rather slim" anterior tibiae in males, also indicating that this subgenus possesses characters that are also present in the subgenera *Proagoderus* van Lansberge and *Serrophorus* Balthasar. Shortly after, Balthasar (1963), in his

"Monographie der Scarabaeidae und Aphodiidae der palearktischen und orientalischen Region", listed 20 species for his subgenus *Digitonthophagus*. All of them, except for *D. bonasus* and *D. gazella*, have since been transferred to other subgenera. The illustration of *D. bonasus* male presented by Balthasar featured a specimen of *D. uks*. Recently, *D. bonasus* has been included in phylogenetic analyses (Barbero *et al.* 2003; Tarasov & Solodovnikov 2011) and the chromosomal formula has been described by Cabral-de-Mello *et al.* (2008).

Scarabaeus gazella is the second species of *Digitonthophagus* historically recognized, which has also gone under the names *Scarabaeus catta*, *Scarabaeus dorcas*, and *Onthophagus gazella lusinganus*. Fabricius (1787a) published the diagnosis of *Scarabaeus catta* (p. 12, number 115) from specimens collected in Coromandel Coast, India. Later the same year, the description of *S. gazella* appeared in the appendix of the second volume of *Mantissa Insectorum* (p. 377, numbers 125–126) based on specimens of an unknown origin (Fabricius 1787b). Both descriptions were published 12 years after the description of *S. bonasus* Fabricius (1775).

Olivier (1789) described *S. dorcas* from Madagascar and redescribes *S. catta*. Both species are illustrated using females (plate 4, fig. 29 and plate 23, fig. 201). The illustrations provided by Olivier are life-size and did not provide additional diagnostic characters. In his treatise, Illiger (1800) considers *S. gazella* to be a variety of *S. bonasus* with shorter horns and a smaller body size. *Scarabaeus catta* was compared to *S. vacca* (Linnaeus) and treated as a different species than *S. gazella*. Fabricius (1801) transfered *S. catta* and *S. gazella* to the genus *Copris*. Illiger (1804), in his comments on Fabrician species, noted that *Copris metallica* is a "variation" of *C. gazella* therefore establishing the synonymy. Illiger (1804) also stated that *C. metallica* and *C. catta* are females and are different from *C. gazella*. Schönherr (1806) treated *Copris metallica* as a "female variety" of *Copris gazella*. In addition, Schönherr (1806) considered the treatment of *S. bonasus* by Herbst (1786) as a misidentification of a female *C. gazella*. Dejean (1821) in his catalog, transfers *S. gazella* and *S. catta* to the genus *Onthophagus* and treated the names as synymyms with *O. gazella* as the male and *O. catta* as the female. Sturm (1826) followed Dejean (1821) and cited *O. gazella* as an *Onthophagus*. Dejean (1836), introduced the name "Var. *Intermedius* Dupont" from Senegal as a variety of *O. gazella*. The name "*O. gazella* var. *intermedius* Dupont" is a nomen nudum, since there was never a formal description of this name. Latreille (1827), in his descriptions of the insects collected by M. Cailliaud in northern Africa, noted that *Copris catta* was the female or a variety of *O. bonasus*. Klug (1833) listed *S. dorcas* Olivier, described from Madagascar, as a synonym of *O. gazella* and therefore established the synonymy. Hope (1837) lists the two Fabrician species, *O. catta* and *O. gazella*, in the genus *Onthophagus*. Laporte (1840) follows Dejean (1836) and considered *O. gazella* as the male and *O. catta* as the female of the same species, with *O. gazella* as the valid name. Reiche (1840) created the name *O. intermedius* and classified it as a synonym of *O. gazella*. The International Commission on Zoological Nomenclature (1999) stated that when a name is first introduced as a synonym, it is unavailable (Article 11.6). Therefore, the name *O. intermedius* is unavailable for nomenclatural purposes. Sturm (1843) listed *O. catta* as a synonym of *O. gazella*. Motschulsky (1860) in a footnote, stated that *C. metallica* "equals" the *C. bonasus* female, and that both names are synonyms of *S. catta*. Harold (1869), in his catalog, listed *Copris antilope* (Fabricius) as a synonym of *O. gazella* for the first time, establishing the synonymy. Harold (1869) also cited *O. catta* (Fabricius) and *O. dorcas* (Olivier) as synonyms of *O. gazella* and indicated that they are both based on females. Harold (1869) also listed "var. *intermedius* Dupont" and "*metallicus* Fabricius" as varieties of *O. gazella*. D'Orbigny (1905) described *Onthophagus gazella lusinganus* for what he considered a variety. D'Orbigny (1914), cited *O. catta* as dubious; listed *O. dorcas*, *O. metallicus*, *O. antilope*, and *O. intermedius* as synonyms of *O. gazella*; and listed *O. lusinganus* as a variety of *O. gazella*. With d'Orbigny (1914), the synonymy of *O. gazella* is established in its modern sense and was almost universally accepted until now. Gillet & Boucomont (1927), repeated d'Orbigny (1914) in the second part of the *Coleopterorum Catalogus*. Arrow (1931), in the Fauna of British India, correctly established *O. catta* as the valid name based on the principle of priority. Arrow (1937) stated that "Males were named by Fabricius *gazella* and *antilope* and females *catta* and *metallicus*." Müller (1942) changed the status of *O. lusinganus* d'Orbigny to the species level. Balthasar (1963) described *Digitonthophagus*, a subgenus of *Onthophagus*, with *O. bonasus* as the type species. His concept of the subgenus included *Onthophagus* (*Digitonthophagus*) *gazella*, but is paraphyletic. Balthasar (1963) followed d'Orbigny (1914) and Gillet & Boucomont (1927) for the synonymy of *O. gazella*. Zunino (1981) cited *Digitonthophagus gazella*, with *Digitonthophagus* used as a genus for the first time. Zunino (1981) gave characters of male and female genitalia to justify the genus-level rank. *Digitonthophagus* sensu Zunino was restricted to *D. bonasus* and *D. gazella*, which "con … algunas otras especies, todas indoafricanas … forman un grupo de nivel genérico." (Zunino & Halffter 1988). In this paper, we recognize *D. gazella* and *D. catta* as separate, valid species.

Generic placement. All recent works dealing with morphological and molecular phylogeny of Scarabaeinae, which include representatives of the genus *Digitonthophagus*, suggest a very close relationship between *Phalops* and *Digitonthophagus* (Monaghan *et al*. 2007; Wirta *et al*. 2008; Mlambo *et al*. 2015; Breeschoten *et al.* 2016). All of these phylogenies present the genera *Digitonthophagus* and *Phalops* as a well a supported group basal to the rest of the Onthophagini. Although externally very similar to the Onthophagini, the genera *Digitonthophagus* and *Phalops* are unique in lacking the lamella copulatrix present in all other Onthophagini and Oniticellini. Recently, the molecular phylogeny presented by Breeschoten *et al*. (2016), which support the placement of the genera *Phalops* and *Digitonthophagus* basal to the rest of the Onthophagini, suggested that Oniticellini is paraphyletic within the Onthophagini. In addition, Roggero *et al*. (2016a) place their newly defined genus *Kurtops* Roggero *et al*. in their morphological analysis sister to the genus *Digitonthophagus*. The inclusion of *Hamonthophagus bituberculatus* (Olivier) and *Hamonthophagus depressus* (Harold) (Roggero *et al*. 2016b) in their analysis also suggest a close relationship of these two species with *Digitonthophagus*, *Phalops*, and *Kurtops*. The Roggero *et al*. (2016a) analysis is based on a relatively small taxa sample (18 species) compared to the rest of the Onthophagini diversity and was aiming at isolating *Kurtops* from other closely related genera. Based on current evidence, the placement of the genus *Digitonthophagus* should be in a new tribe or subtribe along with *Phalops*, *Kurtops*, *Hamonthophagus* Roggero *et al*., and *Morettius* Roggero *et al*. This group is currently known as the "*Phalops* genera complex". It is beyond the scope of this work to address this issue, which will be treated in a forthcoming review of the "*Phalops* genera complex".

Digitonthophagus Balthasar, 1959

Digitonthophagus Balthasar, 1959: 464 (original description)
Digitonthophagus—Balthasar 1963: 159 (monograph)
Digitonthophagus—Ferreira 1968: 593 (monograph)
Digitonthophagus—Ferreira 1972: 779 (diagnosis)
Digitonthophagus—Kabakov 1979: 94 (diagnosis)
Digitonthophagus—Zunino 1981: 413 (new combination, comment taxonomy)
Digitonthophagus—Zunino & Halffter 1988: 17 (comment taxonomy)
Digitonthophagus—Ochi 2003: 260 (diagnosis, comment)
Digitonthophagus—Monaghan *et al.* 2007: 678 (phylogeny)
Digitonthophagus—Tarasov & Kabakov 2010: 24 (comment)
Digitonthophagus—Tarasov & Solodovnikov 2011: 2 (phylogeny)
Digitonthophagus—Génier 2013: 2 (comment taxonomy)
Digitonthophagus—Mlambo *et al.* 2015: 318 (phylogeny)
Digitonthophagus—Breeschoten *et al*, 2016: 87 (phylogeny)
Digitonthophagus—Roggero *et al*. 2016a: [1] (phylogeny)
Digitonthophagus—Roggero *et al*. 2016b: 2 (phylogeny)

Type species. *Scarabaeus bonasus* Fabricius, 1775 (original designation)

Diagnosis. Externally, the genus *Digitonthophagus* is almost indistinguishable from the rest of the Onthophagini. However, all *Digitonthophagus* species have the anterior portion of the hypomeron produced anteriorly and visible from above; therefore, setae that would be located along the anterior edge in ventral portion are moved to a dorsal position. The only other external characters found separating the genus *Digitonthophagus* and the other closely related genera, is the presence of a distinctly shaped internoapical tooth of the male protibia (Figs. 7–22). This tooth is usually elongate, ventrally flat, and obliquely oriented downward. This character must be combined with females completely lacking this protibial internoapical tooth. In *Onthophagus* species where a similar tooth is present, the shape of this tooth is spiniform and forwardly directed in males and present in females as well but reduced in size (in African species examined). Internally, the parameres are rather short and the basolateral paramerites always present with the apex of the later adjacent to the lateral portion of the apical carinae. The internal sac of the aedeagus is lacking the lamella copulatrix and associated small sclerites and bristle pads. The frontolateral peripheral sclerite (Figs. 2–5) is located at the apex of the internal sac and a subapicoventral lobe oriented perpendicularly to the main plan of FLP is present.

Description. **Size**. Small to moderately large (6.5–17.0 mm). **Color**. Overall color fulvous to light brown with structure edges and sutures more-or-less darker; pronotal disc and head darker and with distinct metallic sheen;

elytral margins brown to green, disc with a more-or-less distinct darker irregular macula; metasternum and femoral ventral surface usually with much darker maculae. **Head**. With a sharply defined clypeofrontal carina in both sexes; antenna with 9 antennomeres, with deep pits on distal surface of antennomeres 7–8. **Pronotum**. With distinct squamiform granules anteriorly posterior to the anterior declivity that is always simply punctate, granules larger anteriorly and extending more-or-less posteriorly; anterior discal punctures weakly-defined and becoming well-defined posteriorly, when present. **Elytra**. Juxtasutural interval with strong metallic sheen along sutures; usually with a dark oval macula on the apical declivity on intervals 4–5. **Pygidium**. Surface with scattered, fine granulate punctures; each puncture with an erect, yellow seta. **Ventrites**. Hypomeron slightly convex; anterior hypomeral carina well-defined throughout; mesosternum with a bisinuate, glossy surface anteriorly and a more-or-less developed longitudinal glossy, keel-shaped structure medially; posterior portion completely rugopunctate and setose; metasternal median lobe usually with a distinct longitudinal ridge behind the anterior suture. **Aedeagus**. Parameres rather short and basolateral paramerites always present, with the apex of the later adjacent to the lateral portion of the apical carinae. **Female genitalia**. Infundibulum thin, simple with a median portion reduced; receptaculum seminis elongate, simple, lacking annulate ridges internally (female genitalia characters from Zunino 1981).

Remarks. Balthasar's (1959) original description was restricted to external morphology and included a number of unrelated species (*O. actaeon* Balthasar, *O. anguliceps* Boucomont, *O. avocetta* Arrow, *O. blumei* van Lansberge, *O. bonasus* Fabricius, *O. cameloides* d'Orbigny, *O. curvicarinatus* Boucomont, *O. diabolicus* Harold, *O. digitatus* Arrow, *O. diversiformis* Boucomont, *O. fossor* Arrow, *O. gazella* Fabricius, *O. kuluensis* Bates, *O. manipurensis* Arrow, *O. ohbayashii* Nomura, *O. ribbei* Boucomont, *O. rubricollis* Hope, *O. solivagus* Harold, *O. troniceki* Balthasar, and *O. wallacei* Harold). The main characteristic used by Balthasar to define his subgenus was the elongate and thin protibia of the male. This character state is highly homoplasious in Scarabaeinae and evolved many times in the Onthophagini. The subgenus, as originally defined, was clearly paraphyletic (Zunino 1981).

Remarks for species descriptions and identification key. Diagnoses based on external morphology refer to well-developed individuals. As in many scarabaeine species, strong allometric variation in the development of external secondary sexual characters is present. Smallest males will show completely feminized head and thoracic ornamentation, while largest males present two horns on the vertex. Pronotal and elytral granulations and punctation are usually diagnostic but variable, and extremes of one species can be similar to individuals of another species, which makes identification difficult with external characters for some specimens. Examination of the FLP sclerite shape will always provide a definite identification for males. Diagnoses for species groups must be used in conjunction with species diagnoses.

Species are arranged into six groups based on the current phylogeny in order to facilitate comparison of closely-related species. Species are listed in alphabetical order within each group except for the *Digitonthophagus bonasus* group, where *D. uks* is treated next to *D. bonasus* since it is the most closely related species from the same biogeographical region.

Digitonthophagus bonasus species group

Diagnosis. Male cephalic horns long, obliquely divergent in frontal view (Figs. 24, 26, 28); females with horns on vertex (Figs. 71–73).

Digitonthophagus bonasus (Fabricius, 1775)

(Figs. 7, 23–24, 55, 71, 87–88, 119, 135–137, 183; Map 2)

Scarabaeus Bonasus Fabricius, 1775: 23 (original description)
Scarabaeus Bonasus—Goeze 1777: 69 (diagnosis)
Scarabaeus Bonasus—Fabricius 1781: 26 (redescription)
Scarabaeus bonasus—Pallas 1781: 5 (redescription)
Scarabæus Bonasus—Herbst 1786: 153 (diagnosis, distribution)
Scarabaeus Bonasus—Fabricius 1787a: 14 (diagnosis)

Scarabæus Bonasus—Olivier 1789: 121 (redescription)
Scarabæus Bonasus—Herbst 1789 *2*: 180 (monograph)
Scarabaeus Bonasus—Gmelin 1790: 1541 (diagnosis)
Scarabaeus Bonasus—Fabricius 1792: 50 (diagnosis)
Scarabaeus Bonasus—Illiger 1800: 228 (monograph)
Copris Bonasus—Fabricius 1801: 40 (diagnosis)
Copris Bonasus—Illiger 1804: 149 (comment taxonomy)
Copris Bonasus—Schönherr 1806: 42 (catalog)
Ontophagus Bonasus—Sturm 1826: 177 (catalog)
Onthophagus bonasus—Latreille 1827: 282 (misidentification)
Onthophagus bonasus—LePeletier & Audinet-Serville 1828: 353 (identification key, comment)
Onthophagus Bonasus—Hope 1837: 32 (catalog)
Ontophagus bonasus—Laporte 1840: 85 (diagnosis, distribution)
Onthophagus Bonasus—Sturm 1843: 107 (catalog)
Onthophagus bonasus—Motschulsky 1860: 154 (comment taxonomy)
Onthophagus bonasus—Motschulsky 1863: 457 (checklist)
Onthophagus bonasus—Harold 1869: 1026 (catalog)
Onthophagus (*O.*) *bonasus*—d'Orbigny 1900a: 218 (monograph)
Onthophagus bonasus—Boucomont 1914: 241 (distribution)
Onthophagus bonasus—Boucomont 1921: 29 (identification key, distribution)
Onthophagus bonasus—Gillet & Boucomont 1927: 133 (catalog)
Onthophagus bonasus—Arrow 1931: 231 (monograph)
Onthophagus (*O.*) *bonasus*—Paulian 1945: 101 (monograph)
Onthophagus bonasus—Petrovitz 1955: 277 (distribution)
Onthophagus bonasus—Balthasar 1956: 435 (distribution)
Onthophagus (*Digitonthophagus*) *bonasus*—Balthasar 1959: 464 (genotype designation)
Onthophagus (*Digitonthophagus*) *bonasus*—Balthasar 1963: 296 (monograph)
Digitonthophagus bonasus—Zunino 1981: 413 (new combination)
Onthophagus (*Matashia*) *bonasus*—Masumoto 1988: 140 (distribution)
Digitonthophagus bonasus—Zunino & Halffter 1988: 20 (comment taxonomy)
Digitonthophagus bonasus—Barbero & Palestrini 2003: 333 (phylogeny)
Digitonthophagus bonasus—Cabral-de-Mello *et al*. 2008: 1248 (chromosomal formula)
Digitonthophagus bonasus—Tarasov & Solodovnikov 2011: 4 (phylogeny)
Digitonthophagus bonasus—Génier 2013: 2 (comment taxonomy)
Digitonthophagus bonasus—Roggero *et al*. 2016a: [2] (phylogeny)
Digitonthophagus bonasus—Roggero *et al*. 2016b: 2 (phylogeny)
Digitonthophagus bonasus—Breeschoten *et al*. 2016: 90 (phylogeny)

Type locality. Tranquebariae [=Tharangambadi, Tamil Nadu State, India].

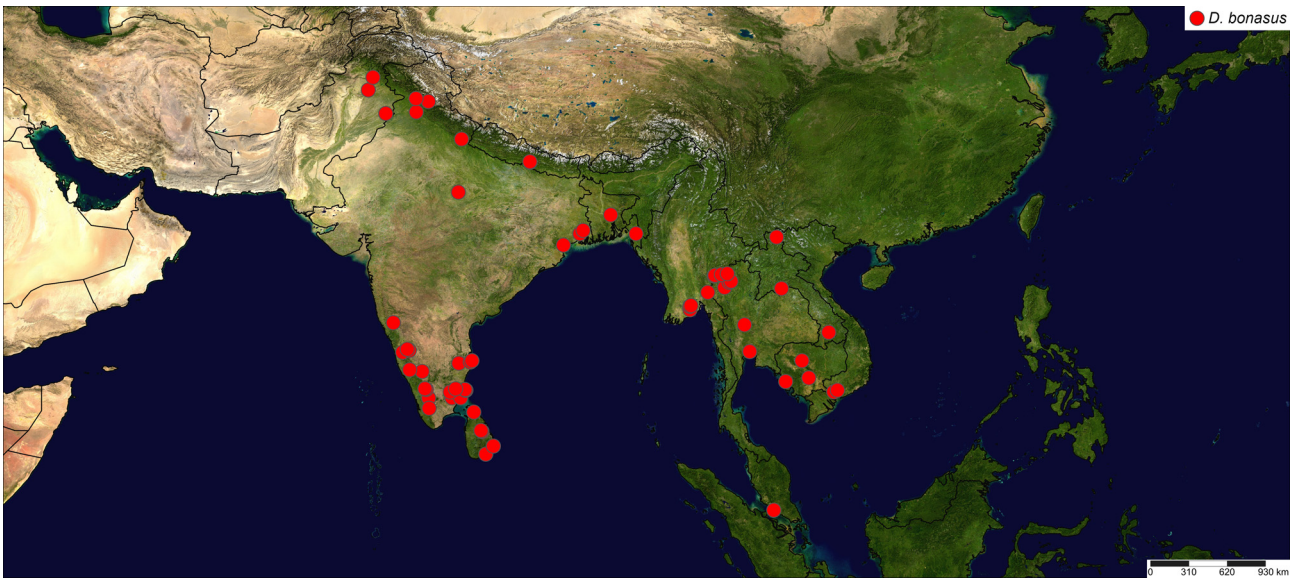
Diagnosis. Male and female pronotal anteromedian tubercle similar, well developed, forming an angular projection in lateral view (Fig. 88); pronotal anterior median longitudinal sulcus wide and deep (Figs. 55, 87).

Description. Alloreferent ♂ (Fig. 7). **Measurements**. Length 14.5 mm, width 9.0 mm. **Head** (Figs. 23–24). Anterior clypeal edge slightly sinuous on median seventh in dorsal view; clypeofrontal carina broadly arcuate and interrupted at gena; vertex with an acute median conical process higher than wide basally, surface with dense irregular granules. Horns long, obliquely divergent in frontal view, gradually tapering from base to apex, posterointernal edge unmodified basally, internal surface coarsely and densely granulated; genal edge slightly upturned and arcuate on anterior third, forming a broad angle with clypeal edge. **Pronotum** (Fig. 55). Surface with granules restricted to median third, lacking distinct umbilicate punctures, punctures weaker but distinct posterolaterally with distinct, minute punctures throughout. Anteromedian tubercle well developed, forming an angular projection in lateral view and forming two short blunt longitudinal carinae in dorsal view; median longitudinal sulcus wide and deep; surface behind the eyes with a small round depression; surface of anterior angles sloping laterally; anterior half of lateral edge strongly sinuous in dorsal and lateral view; posterior angles produced into a obliquely-oriented tooth in dorsal view. Anterior hypomeral ridge broadly arcuate anteriorly with anterior most portion crenulate, anterior hypomeral depression surface slightly darker in color. **Elytra** (Fig. 7). Intervals 2 and 4 with few fine granules on apical fourth. **Legs**. Protibial apicointernal tooth enlarged, with dorsal ridge extending to apex. **Aedeagus** (Fig. 119). Parameres with dorsal and ventral edges diverging toward apex in lateral view. **Internal sac sclerites** (Figs. 135–137)**.** Axial sclerite strongly sclerotized, crescent shaped. Subaxial sclerite extending straight approximately in line with apex right lateral fold apical portion, with fine villi.

Frontolateral peripheral sclerite basoventral apophysis moderately developed; two medioventral carinae present; right lateral fold produced into a rather large everted and open apically conical process with extremely irregular apical edge; left lateral lobe absent; subapicodorsal lobe membranous, narrow, not reaching anterior edge, apex set medially in dorsal view; apical lobe round and directed obliquely on left side, apical villi regular in shape; subapicoventral lobe short not reaching apical edge of apical lobe, oriented obliquely.

Variation. Measurements (111 ♂♂, 103 ♀♀). Length: male 11.0–16.5 mm (13.9 ± 1.3 mm), female 10.0–16.0 mm (13.4 ± 1.2 mm). Female lectotype. Cephalic outline in dorsal view similar to Fig. 71; vertex with horns wide basally and regularly tapering to apex, posterointernal edge with an acute tooth basally; anterior pronotal configuration (Figs. 87–88) similar to males. Protibia short, with external teeth more robust. A number of females from various localities in Asia east of India present much shorter cephalic horns. The horns in these females (Fig. 183) are wide and taper abruptly just before the apex, which is internally diverging in frontal view. Males collected with these females are identical to typical male *D. bonasus* and we consider this variation as intraspecific.

Primary type data. Lectotype ♀ (ZMUK) **present designation**: [ZMUC / 00021685]; WORLD / SCARAB. / DATABASE / WSD00032218] barcode label; [LECTOTYPE ♀ / *Scarabaeus* / *bonasus* / Fabricius, 1775 / dés. F. Génier, 2016] red card.



MAP 2. Distribution of *Digitonthophagus bonasus*.

Material examined (169 ♂♂, 164 ♀♀, 377 sex not recorded), distribution (Map 2): **BANGLADESH**: CHITTAGONG, Chittagong Hill Tracts (22°20'N, 92°13'E), 1883, H.M. Parish—1 ♀, 1 ♂ (BMNH); DHAKA, Dacca [=Dhaka] (23°42'N, 90°22'30"E), 5.v.1945, D. Leston—1 ♀ (BMNH); **CAMBODIA**: KOH KONG, 20 km SE Koh Kong, Tatai river, 50–300 m (11°34'N, 103°7'E), 17.x–15.xi.2011, Z. Linek—2 ♀♀, 2 ♂♂ (FGIC); PHNOM PENH, Kompong Luong (11°50'N, 104°48'E), [no date], [anonymous]—1 ♀ (MNHN); SIEM REAP, Kompong Chikreng (13°5'N, 104°18'E), 1912, G. Thomas—1 ♂ (MNHN); **INDIA**: Côte de Malabar, 1900, T. Deschamps—4 ♀♀, 6 ♂♂ (MNHN); HIMACHAL PRADESH, Near Kullu, Pirpandzhal range, 1500 m (31°57'30"N, 77°6'30"E), 21.vii.2003, A. Gorodinski—1 ♂ (CMD); Yol, Kangra Valley, 1300 m (32°10'N, 76°12'E), viii–ix.1943, C. Lomi—1 ♀, 1 ♂ (CMNC); KARNATAKA, Kanara [=Coastal Karnataka], [no date], [anonymous]—2 ♂♂ (BMNH); Belgaum District, Belgaum (15°51'N, 74°33'0"E), [no date], [anonymous]—1 ♀, 3 ♂♂ (BMNH); Kodagu District, Mercara [= Madikeri] (12°25'14"N, 75°44'23"E), v.1973, T.R.S. Nathan—1 ♂ (RMNH); Mysore District, Mysore (12°18'N, 76°39'E), [no date], [anonymous]—1 ♀, 1 ♂ (BMNH); Shimoga District, Bhadravati (13°50'24"N, 75°42'7.2"E), vii.1938, [anonymous]—1 ♀ (FETC); Shimoga District, Bhadravati (13°50'24"N, 75°42'7.2"E), 13.v.1935, [anonymous]—1 ♀ (CMNC); Shimoga (13°55'N, 75°34'E), vi.1897, [anonymous]—1 ♀, 1 ♂ (MNHN); Shimoga (13°55'N, 75°34'E), [no date], [anonymous]—1 ♂ (NMPC); Thirthahalli, 700 m (13°42'N, 75°13'48"E), 14.xii.1989, A. Kumar—2 ♀♀ (OUMNH); KERALA, Kumily (9°37'6"N, 77°9'29"E), v.1986, T.R.S. Nathan—1 ♀, 1 ♂ (CMNC); Kumily (9°37'6"N, 77°9'29"E), vi.1986, T.R.S.

Nathan—1 ♂ (CMNC); KERALA/ TAMIL NADU, Anaimalai Hills, 1067 m (10°22'N, 77°7.5'E), iv.1963, P.S. Nathan—3 ♀♀, 3 ♂♂ (CNC); ORISSA, Balasore District, Balasore (21°30'N, 86°56'E), [no date], R.P. Gengler—1 ♀, 2 ♂♂ (MNHN); PONDICHERRY, Karaikal District, Karaikal (10°56'N, 79°50'E), iii.1963, P.S. Nathan—91 specimens, 1 ♀ (BDGC, CNC); PONDICHERRY, Karaikal District, Karaikal (10°56'N, 79°50'E), iv.1963, P.S. Nathan—20 specimens, 1 ♀ (BDGC, CNC); Karaikal (10°56'N, 79°50'E), ix.1969, P.S. Nathan—1 ♀ (CMNC); Karaikal (10°56'N, 79°50'E), iii.1968, T.R.S. Nathan—1 ♀ (CMNC); Karaikal (10°56'N, 79°50'E), v.1988, T.R.S. Nathan—1 ♀ (CMNC); Karaikal (10°56'N, 79°50'E), viii.1991, T.R.S. Nathan—1 ♀, 1 ♂ (CMNC); Karaikal (10°56'N, 79°50'E), xii.1961, P.S. Nathan—3 ♀♀, 2 ♂♂ (CNC); Karaikal (10°56'N, 79°50'E), i.1962, P.S. Nathan—5 ♀♀, 5 ♂♂ (CNC); Karaikal (10°56'N, 79°50'E), ii.1962, P.S. Nathan—5 ♀♀, 5 ♂♂ (CNC); Karaikal (10°56'N, 79°50'E), iii.1962, P.S. Nathan—5 ♀♀, 5 ♂♂ (CNC); Karaikal (10°56'N, 79°50'E), vi.1962, P.S. Nathan—1 ♀ (CNC); Karaikal (10°56'N, 79°50'E), iv.1962, P.S. Nathan—14 specimens (CNC); Karaikal (10°56'N, 79°50'E), v.1962, P.S. Nathan—2 specimens (CNC); Karaikal (10°56'N, 79°50'E), vii.1962, P.S. Nathan—45 specimens (CNC); Karaikal (10°56'N, 79°50'E), viii.1962, P.S. Nathan—21 specimens (CNC); Karaikal (10°56'N, 79°50'E), ix.1962, P.S. Nathan—63 specimens (CNC); Karaikal (10°56'N, 79°50'E), x.1962, P.S. Nathan—42 specimens (CNC); Karaikal (10°56'N, 79°50'E), xii.1962, P.S. Nathan—5 specimens (CNC); Karaikal (10°56'N, 79°50'E), i.1963, P.S. Nathan—36 specimens (CNC); Karaikal (10°56'N, 79°50'E), ii.1963, P.S. Nathan—18 specimens (CNC); Karaikal (10°56'N, 79°50'E), vi.1963, P.S. Nathan—8 specimens (CNC); Karaikal (10°56'N, 79°50'E), x.1963, P.S. Nathan—4 specimens (CNC); Karaikal (10°56'N, 79°50'E), x.1966, P.S. Nathan—4 specimens (CNC); Karaikal (10°56'N, 79°50'E), iii.1967, P.S. Nathan—4 specimens (CNC); Karaikal (10°56'N, 79°50'E), [no date], [anonymous]—1 ♀, 2 ♂♂ (FETC); Karaikal (10°56'N, 79°50'E), i–ii.1964, T.R.S. Nathan—4 ♀♀, 1 ♂ (MMUE); Karaikal (10°56'N, 79°50'E), viii.1963, T.R.S. Nathan—1 ♂ (MMUE); Karaikal (10°56'N, 79°50'E), v.2005, Nathan—1 ♀, 1 ♂ (PMOC); Karaikal (10°56'N, 79°50'E), v.1973, T.R.S. Nathan—1 ♂ (RMNH); Kurumbagaram (10°59'N, 79°46'E), xii.1950, P.S. Nathan—1 ♂ (CMNC); Nedungadu (10°58'N, 79°46'E), v.1938, [anonymous]—1 ♂ (FETC); Nedungadu (10°58'N, 79°46'E), [no date], [anonymous]—1 ♂ (FETC); Nedungadu (10°58'N, 79°46'E), 1936, P.S. Nathan—14 ♀♀, 10 ♂♂ (MNHN); Nedungadu (10°58'N, 79°46'E), 1.vi.1931, P.S. Nathan—1 ♂ (BMNH); PUNJAB, Rormazara, Hoshiarpur (31°11'50.7"N, 76°12'58"E), 6–9.vii.2004, M. Uhler—2 ♀♀ (CVM); TAMIL NADU, Arcot (12°54'N, 79°19'E), ix.2012, [anonymous]—1 ♀ (CMD); Coimbatore, 427 m (11°0'N, 76°57'E), iv.1962, P.S. Nathan—10 ♀♀, 12 ♂♂ (BDGC, CNC); Coimbatore, 427 m (11°0'N, 76°57'E), ix.1962, P.S. Nathan—1 ♀ (CNC); Coimbatore, 427 m (11°0'N, 76°57'E), x.1962, P.S. Nathan—1 ♀, 4 ♂♂ (CNC); Coimbatore, 427 m (11°0'N, 76°57'E), xi.1962, P.S. Nathan—1 ♀, 2 ♂♂ (CNC); Coimbatore, 427 m (11°0'N, 76°57'E), xii.1962, P.S. Nathan—1 ♀, 3 ♂♂ (CNC); Coimbatore, 427 m (11°0'N, 76°57'E), i.1963, P.S. Nathan—1 ♀, 1 ♂ (CNC); Coimbatore, 427 m (11°0'N, 76°57'E), iv.1963, P.S. Nathan—10 ♀♀, 10 ♂♂ (CNC); Coimbatore, 427 m (11°0'N, 76°57'E), viii.1963, T.R.S. Nathan—1 ♀, 3 ♂♂ (MMUE); Coimbatore, 427 m (11°0'N, 76°57'E), ix.1964, T.R.S. Nathan—4 ♀♀, 2 ♂♂ (MMUE); Coimbatore, 427 m (11°0'N, 76°57'E), x–xi.1964, T.R.S. Nathan—1 ♀ (MMUE); Pudukkottai (10°23'N, 78°49'E), x.1984, T.R.S. Nathan—1 ♀ (CMNC); Thambikkottai (10°23'N, 79°27'E), vi.1962, P.S. Nathan—1 ♀ (CNC); Tranquebar [=Tharangambadi] (11°2'N, 79°5'E), [no date], [anonymous]—3 ♀♀, 1 ♂ (lectotype, paralectotypes, alloreferent) (ZMUC, ZMUK); Chennai District, Madras [=Chennai] (13°5'2"N, 80°16'12"E), xi.1907, Tomlin—1 ♀ (BMNH); Madras Airport [=Chennai Airport] (12°59'38"N, 80°9'28"E), x.1962, P.S. Nathan—3 ♀♀, 2 ♂♂ (CNC); Coimbatore District, Coimbatore (11°0'N, 76°57'E), iii.1962, P.S. Nathan—3 ♀♀ (CNC); Coimbatore District, Coimbatore (11°0'N, 76°57'E), vii.1939, [anonymous]—1 ♂ (FETC); Coimbatore District, Coimbatore (11°0'N, 76°57'E), [no date], P.S. Nathan—1 ♀, 2 ♂♂ (MNHN); Coimbatore District, Coimbatore (11°0'N, 76°57'E), xii.1971, T.R.S. Nathan—1 ♂ (RMNH); Coimbatore District, Coimbatore (11°0'N, 76°57'E), 15.ix.1947, P.S. Nathan—2 ♂♂ (CMNC); Marudamalai Hills (11°2'46"N, 76°51'7"E), xi.2004, Nathan—1 ♂ (PMOC); Tiruchirappalli District, Trichinopoly [=Tiruchirappalli] (10°48'18"N, 78°41'8"E), iii.1907, [anonymous]—1 ♀ (BMNH); Tiruchirappalli District, Trichinopoly [=Tiruchirappalli] (10°48'18"N, 78°41'8"E), x.1919, C. Leigh—1 ♂ (BMNH); Tiruchirappalli District, Trichinopoly [=Tiruchirappalli] (10°48'18"N, 78°41'8"E), [no date], R.P. Castets—1 ♀, 1 ♂ (MNHN); UTTAR PRADESH, Kheri Reserved Forest (25°21'11"N, 79°17'9"E), ii.1916, H.G. Champion—1 ♂ (BMNH); UTTARAKHAND, Haldwani District, Kumaon [=Haldwani] (29°13'N, 79°31'E), [no date], H.G. Champion—2 ♀♀ (BMNH); WEST BENGAL, Howrah District, Sarda (22°20'N, 88°8'E), [no date], F.W. Champion—2 ♂♂ (BMNH); Kalkata District, Calcutta [=Kolkata] (22°34'N, 88°22'E), [no date], [anonymous]—1 ♂ (BMNH); Kalkata District, Calcutta [=Kolkata] (22°34'N, 88°22'E), [no date], Waagen—1 ♀

(SMF); **LAOS**: CHAMPASAK, Ban Sepian (15°9'N, 106°15'E), 1–7.iv.2003, R. N.—1 ♂ (CEMT); PHONGSALY, Gnot-Ou District, Mount Phu Nam Khé (22°5'N, 102°27'E), 15–20.vi.2006, Local collectors—12 ♀♀, 7 ♂♂ (FGIC, OUMNH); VIENTIANE, Phou Khao Khouay National Bio-Biversity Conservation Area, 700–800 m (18°20.369'N, 102°48.523'E), 25–30.v.2008, A. Solodovnikov & J. Pedersen—6 ♀♀, 7 ♂♂ (FGIC, ZMUC); **MALAYSIA**: MALACCA, Malacca (2°12'N, 102°15'E), [no date], [anonymous]—1 ♂ (SMF); **MYANMAR**: KAYIN, Hpapun (18°3'30"N, 97°26'30"E), 1932, R.P. Loizeau—1 ♂ (MNHN); YANGON, Hlegu-Goygon (17°5'43"N, 96°13'16"E), iii.1997, M. Klicha—2 ♂♂ (OUMNH); Htauk Kyant (17°2'40"N, 96°8'12"E), ii.1997, M. Klicha—1 ♀, 1 ♂ (OUMNH); Rangoon [=Yangon] (16°48'N, 96°9'E), v.1934, F.J. Meggitt—3 ♀♀, 2 ♂♂ (BMNH); Rangoon [=Yangon] (16°48'N, 96°9'E), 1933–1934, F.J. Meggitt—5 ♀♀, 4 ♂♂ (BMNH); **NEPAL**: CENTRAL, Chitwan District, Sauraha, Chitwan National Park, 213 m (27°31'57"N, 84°30'20"E), 4.vi.1983, M.J.D. Brendell—1 ♂ (BMNH); Chitwan District, Sauraha, Chitwan National Park, 213 m (27°31'57"N, 84°30'20"E), 1–4.vi.1999, M. Pejcha—1 ♀ (FETC); Chitwan District, Sauraha, Chitwan National Park, 213 m (27°31'57"N, 84°30'20"E), 4–6.vi.1999, A. Kudrna—1 ♂ (FETC); **PAKISTAN**: ISLAMABAD CAPITAL TERRITORY, Islamabad (33°43'N, 73°4'E), 6.vi.1991, S. Prepsl—1 ♀ (CMD); PENJAB, Changa Manga Forest, 70 km S Lahore (31°5'N, 74°0'E), 19–21.viii.1998, L. Cerný—3 ♀♀ (CVM); Kallar Kahar (32°47'32"N, 72°43'34"E), 26.vi.2008, A. Zubair—1 ♂ (PMOC); **SRI LANKA**: EASTERN, Pottuvil (6°52'N, 81°50'E), 1–12.vii.1983, O. Mehl—1 ♂ (ZMUC); NORTH CENTRAL, Girithale (8°0'N, 80°56'E), 16.viii.1979, G. de Rougemont—1 ♀ (OUMNH); Polonnaruwa (7°56'N, 81°0'E), 24.vii.1982, P. Moretto—2 ♂♂ (PMOC); NORTHERN, Jaffa (9°20.5'N, 80°24.3'E), 1.iii.2010, Kuduvidanage *et al*.—1 ♂ (OUMNH); SOUTHERN, Hambantota District, Tissamaharama (6°17'N, 81°17'E), 1.viii.1982, P. Moretto—2 ♀♀, 2 ♂♂ (PMOC); **THAILAND**: BANGKOK, Bangkok (13°45'N, 100°30'E), [no date], S.S. Flower—1 ♀ (BMNH); CHIANG MAI, Chiang Dao (19°25'N, 98°52'E), 17–24.v.1991, V. Kubáň—1 ♀, 1 ♂ (CVM); Chiang Mai (18°48'N, 99°0'E), v.1986, N. Koyama—2 ♂♂ (CEMT); Chiang Mai (18°48'N, 99°0'E), 28.vi.1990, R. Minetti—1 ♀ (FETC); Chom Thong (18°25'N, 98°40'E), 24–27.iv.1991, J. Horák—1 ♀, 1 ♂ (BDGC); Doi Saket District, [unspecified locality] (18°52'N, 99°8'E), 1.vii.1959, B. Degerbol—1 ♂ (ZMUC); MAE HONG SON, Ban Huai Suea Thao (19°15'35"N, 97°54'15"E), 11–12.v.1992, J. Strnad—1 ♀ (CVM); Mae Hong Son (19°18'N, 97°58'E), 6–9.v.1991, J. Horák—1 ♀, 1 ♂ (BDGC); Pai (19°21'32"N, 98°26'12"E), 1–14.v.2001, J. Hromádka—1 ♀, 3 ♂♂ (OUMNH); NAKHON SAWAN, Nakhon Sawan (15°42'N, 100°7'E), 25.v.1980, A. Chaminade—1 ♀ (PMOC); Nakhon Sawan (15°42'N, 100°7'E), 22.v.1982, A. Chaminade—1 ♂ (PMOC); **VIETNAM**: DONG NAI, Long Binh R.V.N., Bien Hoa Province (10°56'N, 106°53'E), 12.v.1970, W.H. Tyson—1 ♂ (BDGC); HO CHI MINH, Saigon [=Ho Chi Minh City] (10°49'N, 106°37'E), x.1982, S. Pokorný—2 ♀♀, 4 ♂♂ (CVM).

Natural history. A single specimen collected in arid scrub forest in Sri Lanka and 13 specimens collected near strongly disturbed primary forest in Laos. A few specimens were collected in cow dung, pitfall traps baited with human dung, and at light.

Remarks. The redescription is based on a male alloreferent (ZMUK) from the type locality and matching the female lectotype of *S. bonasus*.

Nomenclature and taxonomy. *Digitonthophagus bonasus* was the first species described included in the genus *Digitonthophagus*. The type series consist of three females. The larger and less abraded specimen has been chosen as lectotype (**present designation**). A lectotype is designated in order to choose a single specimen as name bearing type in the event that the other specimens of the syntype series could belong to a different cryptic species in this genus. This single specimen also shows better diagnostic characters as it is relatively undamaged and the original cephalic outline is clearly delimited. It is important to mention that these specimens together with the other Fabrician types were borrowed from the ZMUC but will eventually be deposited in the ZMUK collection.

Digitonthophagus uks Génier, new species

http://zoobank.org/urn:lsid:zoobank.org:act:E305B328-472B-418B-9737-C24249F6E1D8
(Figs. 8, 25–26, 56, 72, 89–90, 120, 138–140; Map 3)

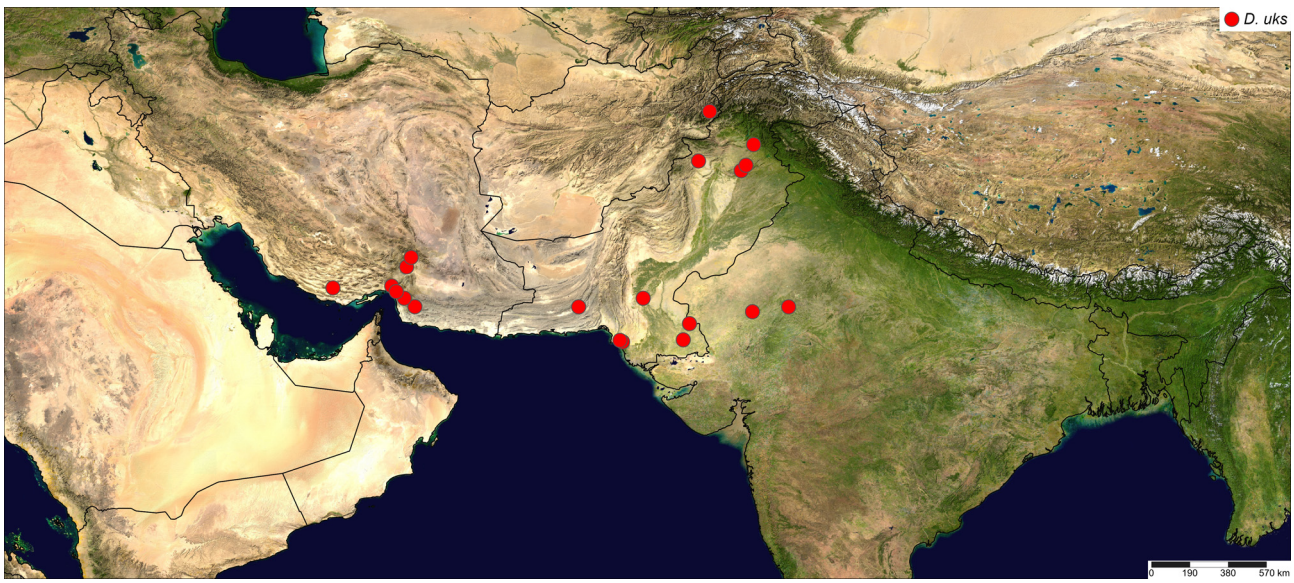
Type locality. Awaran, Khuzdar District, Pakistan.

Diagnosis. Male and female pronotal anteromedian tubercle similar, well developed, simply round in lateral view (Fig. 90); pronotal anterior median longitudinal sulcus wide and deep (Figs. 56, 89).

Description. Holotype ♂ (Fig. 8). **Measurements**. Length 15.5 mm, width 9.0 mm. **Head** (Figs. 25–26). Anterior clypeal edge straight on median fifth in dorsal view; clypeofrontal carina broadly arcuate and interrupted at gena; vertex with a median acute conical process approximately as high as wide, surface with rather dense, irregular granules. Horns long, strongly divergent on basal half in frontal view, gradually tapering from base to apex, posterointernal edge unmodified basally, internal surface with a few small, scattered granules. Genal edge slightly upturned and arcuate on anterior third, forming a broad angle with clypeal edge. **Pronotum** (Fig. 56). Surface with granulate punctures extending slightly beyond posterior half, lacking simply umbilicate punctures; punctures smaller posterolaterally, with distinct minute punctures throughout. Anteromedian tubercle well developed, forming a simply convex projection in lateral view; surface of tubercles covered with rather regular and fine scabrous granules; median longitudinal sulcus very wide and deep. Surface behind the eyes with a small and shallow round depression, surface of anterior angles sloping laterally; anterior half of lateral edge sinuous in dorsal and lateral view; posterior angles produced into a obliquely oriented tooth in dorsal view; anterior hypomeral ridge broadly arcuate anteriorly with anterior most portion crenulate, anterior hypomeral depression surface darker in color. **Elytra** (Fig. 8). Intervals 2 and 4 with irregularly scattered, fine granules from base to apex. **Legs**. Protibial apicointernal tooth enlarged, with dorsal ridge extending to apex. **Aedeagus** (Fig. 120). Parameres with dorsal and ventral edges diverging toward apex in lateral view. **Internal sac sclerites** (Figs. 138–140)**.** Axial sclerite strongly sclerotized, abruptly bent ventrally on apical third. Subaxial sclerite, extending straight past apex of right lateral fold apical portion, with villi on apical half. Frontolateral peripheral sclerite basoventral apophysis moderately developed; two medioventral carinae present; right lateral fold produced into a rather large everted and open apically conical process with extremely irregular apical edge; left lateral lobe absent; subapicodorsal lobe membranous, narrow, not reaching anterior edge, apex set medially in dorsal view; apical lobe round and directed obliquely on left side, apical villi regular in shape; subapicoventral lobe short not reaching apical edge of apical lobe, oriented obliquely and in line with ventrally folded left edge of apical lobe.

Variation. Measurements (14 ♂♂, 36 ♀♀). Length: male 11.5–16.5 mm (14.5 ± 1.5 mm), female 11.5–17.0 mm (14.7 ± 1.1 mm). Female allotype. Cephalic outline in dorsal view as in Fig. 72; vertex with horns wide basally and regularly tapering to apex, posterointernal edge lacking acute tooth basally; anterior pronotal configuration (Figs. 89–90) similar to male. Protibia short, with external teeth more robust.

Primary type data. Holotype ♂ (MNHN): [PAKISTAN / Khuzdar Distr. / Awaran / 5-VII-1993 / Leg. S. Becvar] white card with one orange edge; [WORLD / SCARAB. / DATABASE / WSD00020553] barcode label; [HOLOTYPE ♂ / *Digitonthophagus* / *uks n.sp.* / des. F. Génier, 2016] red card.



MAP 3. Distribution of *Digitonthophagus uks*.

Material examined (24♂♂, 51 ♀♀), distribution (Map 3): **AFGHANISTAN**: Torkham – Hindukus, viii.1974, J. Smielowski—1 ♀ (paratype) (CVM); NOURESTAN, Bashgultal [Bashgal Valley], 1200 m (35°12'N,

71°6'E), 3.v.1953, J. Klapperich—2 ♀♀, 2 ♂♂ (4 paratypes) (CMNC, NMPC); Bashgultal [Bashgal Valley], 1200 m (35°12'N, 71°6'E), 7.v.1953, J. Klapperich—5 ♀♀ (5 paratypes) (NMPC); Bashgultal [Bashgal Valley], 1200 m (35°12'N, 71°6'E), 13.v.1953, J. Klapperich—2 ♀♀, 2 ♂♂ (4 paratypes) (FGIC, NMPC); Bashgultal [Bashgal Valley], 1200 m (35°12'N, 71°6'E), 23.v.1953, J. Klapperich—1 ♀ (paratype) (FGIC); **INDIA**: RAJASTHAN, Ajmer (26°27'N, 74°38'E), [no date], [anonymous]—3 ♀♀ (3 paratypes) (IRSNB); Jodhpur (26°14'N, 73°1'E), 18.viii.1987, A. Riedel—1 ♀ (paratype) (FETC); **IRAN**: HORMOZGAN, 62 km E Bandare Abbas (27°23'N, 56°52'E), 26.iv.2002, S. Kadlec—1 ♂ (paratype) (NMPC); Bashagerd, Gru (26°27'30"N, 57°54'7"E), 30.iv.1996, [anonymous]—1 ♂ (paratype) (HMIM); Issin, 130 m (27°18'N, 54°14'E), 1–6.v.1977, [anonymous]—2 ♀♀, 2 ♂♂ (4 paratypes) (HMIM); Minab, Ostan-Saheli (27°8'N, 57°4'E), 18–22.v.1973, [anonymous]—1 ♂ (paratype) (HMIM); Senderk, Bashagerd, 220 m (26°50'15"N, 57°25'38"E), 12.v.1977, [anonymous]—1 ♀ (paratype) (HMIM); KERMAN, Boluk (28°14'20"N, 57°31'50"E), 27.v.2008, O. Montreuil—5 ♀♀, 2 ♂♂ (7 paratypes) (FGIC, OMOC); Jiroft, 43 km N Kohnuj, 540 m (28°40'N, 57°44'E), 16.v.1977, [anonymous]—2 ♀♀, 2 ♂♂ (4 paratypes) (HMIM); **PAKISTAN**: Thar, 12.vii.2007, M.A. Akhter—1 ♀ (paratype) (CMD); BALOUTCHISTAN, Awaran (26°27'N, 65°14'E), 5.vii.1993, S. Becvar—8 ♀♀, 3 ♂♂ (holotype, allotype, 9 paratypes) (FETC, MNHN); ISLAMABAD CAPITAL TERRITORY, Islamabad area, 1981 m (33°43'N, 73°4'E), 8.vii.2006, A. Zubair—1 ♀ (paratype) (BDGC); KHYBER PAKHTUNKHWA, Bannu (32°59'N, 70°36'E), [no date], T.L. Pennell—1 ♀ (paratype) (BMNH); PENJAB, Chakwal (32°33'N, 72°30'36"E), 19.v.1990, Naeem—1 ♀ (paratype) (CNC); Kallar Kahar (32°47'32"N, 72°43'34"E), 26.vi.2008, A. Zubair—4 ♀♀, 2 ♂♂ (6 paratypes) (FGIC, PMOC); SINDH, Chelhar (24°58'30"N, 69°55'0"E), 19.viii.2007, A. Zubair & M.A. Akhter—1 ♀, 2 ♂♂ (3 paratypes) (BDGC, PMOC); Karachi (24°57'N, 67°5'E), [no date], T.R. Bell—5 ♀♀, 2 ♂♂ (7 paratypes) (BMNH, OUMNH); Karachi (24°57'N, 67°5'E), viii–ix, Maindron—1 ♀ (paratype) (BMNH); Karachi (24°57'N, 67°5'E), [no date], [anonymous]—1 ♀ (paratype) (BMNH); Karachi (24°57'N, 67°5'E), 26.i.2007, Hareem & Atige—1 ♀ (paratype) (CEMT); Khokhropar (25°42'1"N, 70°11'42"E), 3.v.2006, Hareem—1 ♂ (paratype) (PMOC); Malir Cantonment (24°53'N, 67°12'E), 9.vi.2006, Zubair—1 ♀ (paratype) (PMOC); Nausharo Feroze (26°50'15"N, 68°7'21"E), 3.v.2006, A. Zubair & M.A. Akhter—1 ♂ (paratype) (PMOC).

Etymology. *Uks* (ox) is a Sanskrit noun in apposition for bull, pertaining to the aspect of the cephalic horns in this species.

Natural history. The specimens collected in Iran are from pastures, no other data.

Remarks. In addition to the characters given in the description, the pronotal color pattern slightly differs by having the pale edging posterior portion less sharply defined medially, with the dark discal coloration extending further posteriorly compared to *D. bonasus*.

Digitonthophagus sahelicus Moretto, new species

http://zoobank.org/urn:lsid:zoobank.org:act:659D2617-892E-4CA3-803B-A727B64D643C
(Figs. 9, 27–28, 57, 73, 91–92, 121, 141–143; Map 4)

Type locality. Toulfé (13°53'43"N 01°52'25"W), 300 m, Lorum, Burkina Faso.

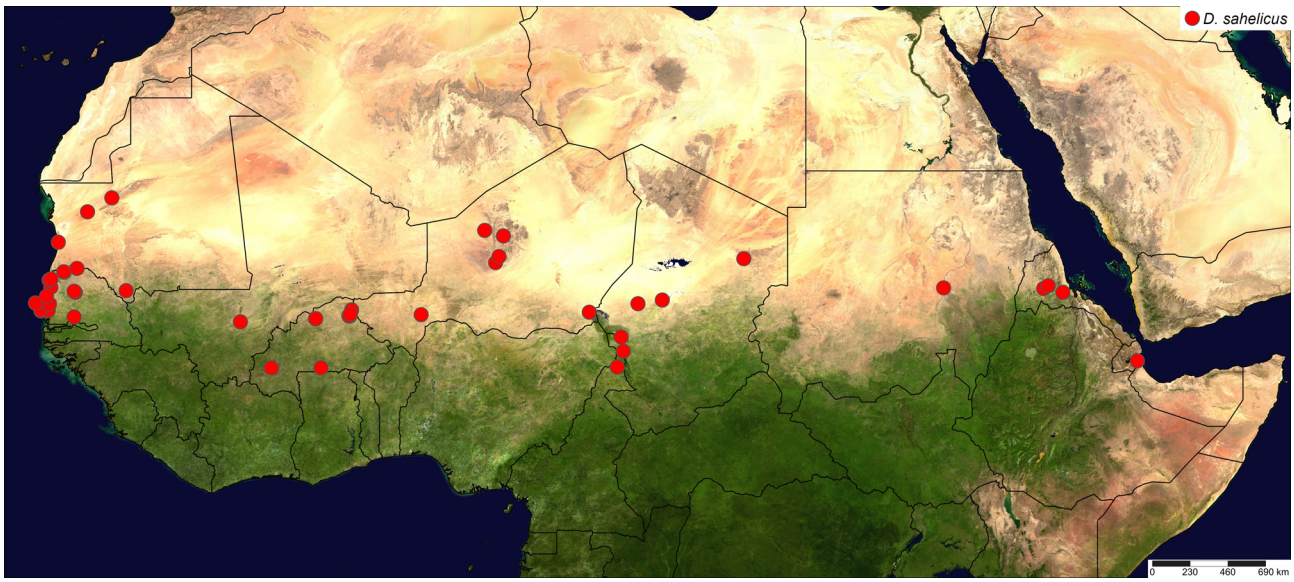
Diagnosis. Africa species; Male pronotal anterior angles surface sloping laterally and usually with a dark spot (Figs. 57); female vertex with horns (Fig. 73).

Description. Holotype ♂ (Fig. 9). **Measurements**. Length 9.5 mm, width 5.5 mm. **Head** (Figs. 27–28). Anterior clypeal edge emarginate on median fifth in dorsal view; clypeofrontal carina nearly straight and extending to clypeal edge; vertex convex medially, surface with scabrous punctures. Horns long, divergent in frontal view, gradually tapering from base to apex, posterointernal edge unmodified basally, internal surface with numerous coarse granules. Genal edge slightly upturned and arcuate on anterior third, forming a broad angle with clypeal edge. **Pronotum** (Fig. 57). Surface with granulate punctures extending slightly beyond posterior half, with a few scattered simple punctures on posterior portion of disc, larger punctures absent posterolaterally, with distinct, minute punctures throughout. Anteromedian tubercle atrophied, forming a simply convex projection in lateral view, surface of tubercles covered with rather regular and fine squamiform granules; median longitudinal sulcus absent; surface behind the eyes with a small and shallow oval depression, surface of anterior angles irregularly sloping laterally; anterior half of lateral edge slightly sinuous in dorsal and lateral view; posterior angles simply arcuate in dorsal view. Anterior hypomeral ridge nearly straight posteriorly and abruptly arcuate anteriorly with

anterior most portion crenulate, anterior hypomeral depression surface light in color. **Elytra** (Fig. 9). Interval 2 and 4 lacking fine granules from base to apex. **Legs**. Protibial apicointernal tooth enlarged, with dorsal ridge interrupted before apex. **Aedeagus** (Fig. 121). Parameres with dorsal and ventral edges slightly diverging toward apex in lateral view. **Internal sac sclerites** (Figs. 141–143)**.** Axial sclerite strongly sclerotized, abruptly bent ventrally on apical third. Subaxial sclerite, extending straight past apex of right lateral fold apical portion, with villi on apical half. Frontolateral peripheral sclerite basoventral apophysis moderately developed; a single medioventral carinae present; right lateral fold short, produced into a rather large everted and open apically conical process with extremely irregular apical edge; left lateral lobe absent; subapicodorsal lobe membranous, narrow, not reaching anterior edge, apex set on left side in dorsal view; apical lobe elongate and round apically, directed obliquely on left side, apical villi regular in shape; subapicoventral lobe short not reaching apical edge of apical lobe, oriented obliquely and in line with ventrally folded left edge of apical lobe.

Variation. Measurements (103 ♂♂, 111 ♀♀). Length: male 6.5–11.0 mm (9.5 ± 0.8 mm), female 7.5–11.0 mm (9.4 ± 0.7 mm). Female lectotype. Cephalic outline in dorsal view as in Fig. 73; vertex with horns low, very wide basally and tapering to apex, posterointernal edge lacking tooth basally; anterior pronotal surface (Figs. 91–92) with a single callus approximately half interocular distance in width, dorsal edge of callus weakly defined. Protibia short, with external teeth more robust.

Primary type data. Holotype ♂ (CMNC): [BURKINA FASO: LORUM / Toulfé, 300m / 13°53’43”N 01°52’25”O / 18.VII.2006, zone sahélienne / steppe arborée, collecte géné- / rale, F. & S. Génier, 2006-43]; [COLÉOPTÈRES / DU / BURKINA FASO / BF008585] barcode label; [HOLOTYPE ♂ / *Digitonthophagus* / *sahelicus n.sp.* / des. P. Moretto, 2016] red card.



Map 4. Distribution of *Digitonthophagus sahelicus*.

Material examined (266 ♂♂, 193 ♀♀, 496 sex not recorded), distribution (Map 4): **BURKINA FASO**: HAUTS-BASSINS, Bobo-Dioulasso (11°12'N, 4°18'W), viii.2002, [anonymous]—1 ♀ (paratype) (PMOC); SAHEL, après le pont, route Essakane-Dori, Gorum-Gorum, 271 m (14°9'32.8"N, 0°1'20.4"E), 7.viii.2012, P. Moretto—1 ♀, 1 ♂ (paratypes) (PMOC); Conseil régional, Dori, 283 m (14°2'4.5"N, 0°3'10.5"W), 23–25.viii.2013, P. Moretto (2013-50)—9 ♀♀, 9 ♂♂ (18 paratypes) (PMOC); Conseil régional, Dori, 283 m (14°2'4.5"N, 0°3'10.5"W), 30.viii.2013, P. Moretto—1 ♀ (paratype) (PMOC); Dori (14°2'N, 0°1'W), iv.2007, [anonymous]—8 ♀♀, 3 ♂♂ (11 paratypes) (JFJC); Essakane, Gorum-Gorum, 264 m (14°22'40.2"N, 0°5'47.7"E), 13–15.viii.2012, P. Moretto—1 ♀, 1 ♂ (paratypes) (PMOC); N’djomga, Dori (14°3'55.7"N, 0°3'3.4"W), 24–27.viii.2013, P. Moretto—3 ♂♂ (3 paratypes) (PMOC); LOROUM, Toulfé, 300 m (13°53'43"N, 1°52'25"W), 16.vii.2006, F. & S. Génier (2006-38)—24 ♀♀, 28 ♂♂ (52 paratypes) (FGIC); Toulfé, 300 m (13°53'43"N, 1°52'25"W), 16.vii.2006, F. & S. Génier (2006-40)—2 ♀♀, 13 ♂♂ (15 paratypes) (FGIC); Toulfé, 300 m (13°53'43"N, 1°52'25"W), 17.vii.2006, F. & S. Génier (2006-41)—2 ♀♀, 7 ♂♂ (9 paratypes) (FGIC); Toulfé, 300

m (13°53'43"N, 1°52'25"W), 18.vii.2006, F. & S. Génier (2006-43)—23 ♀♀, 24 ♂♂ (holotype, allotype, 45 paratypes) (CMNC, FGIC); Toulfé, 300 m (13°53'43"N, 1°52'25"W), 18.vii.2006, F. & S. Génier (2006-42)—4 ♂♂ (4 paratypes) (FGIC); NAHOURI, Forêt de Nazinga, Boulieselo, 310 m (11°11'50"N, 1°35'9"W), 27.vii.2006, F. & S. Génier (2006-82)—2 ♂♂ (2 paratypes) (FGIC); **CAMEROON**: EXTREME NORTH, Waza National Park (11°15'N, 14°39'E), 18.viii.2006, C. Vanderbergh—1 ♂ (paratype) (PMOC); **CHAD**: ENNEDI, Fada (17°11'N, 21°35'E), 9/4/1935, [anonymous]—1 ♂ (paratype) (MNHN); HADJER-LAMIS, Sitje, rive sud Lac Tchad (12°53'N, 14°52'E), 11.viii.2006, C. Vanderbergh—1 ♀, 2 ♂♂ (3 paratypes) (PMOC); KANEM, Zigueï (14°43'N, 15°47'E), 19–21.vii.1935, [anonymous]—1 ♀ (paratype) (MNHN); N'DJAMENA, Farcha (12°7'N, 14°59'E), vi.1968, [anonymous]—1 ♀, 1 ♂ (paratypes) (MNHN); **DJIBOUTI**: DJIBOUTI, Djibouti (11°35'N, 43°9'E), [no date], [anonymous]—4 ♀♀, 3 ♂♂ (7 paratypes) (IRSNB); **ERITREA**: ANSEBA, Hagaz (15°42'N, 38°16'E), vii.2003, M. Forti—1 ♂ (paratype) (PMOC); GASH-BARKA, 18 km E Akordat (15°33'N, 38°1'E), vii.2003, M. Forti—2 ♀♀, 3 ♂♂ (5 paratypes) (FGIC, PMOC); NORTHERN RED SEA, Nefasit (15°20'N, 39°4'E), vii.2002, Czeppel & Forti—3 ♀♀, 3 ♂♂ (6 paratypes) (FETC); **MALI**: SEGOU, Sansanding (13°43'18"N, 6°0'11"W), [no date], R. Demange—1 ♀ (paratype) (MNHN); **MAURITANIA**: Trarza Desert, [no date], [anonymous]—2 ♀♀, 2 ♂♂ (4 paratypes) (IRSNB); ADRAR, Atar (20°31'N, 13°3'W), 24.ix.1968, P. Tauzin—1 ♂ (paratype) (PMOC); INCHIRI, Oued Akjoujt (19°45'N, 14°23'W), x.1937, P. Malzy—1 ♂ (paratype) (MNHN); NOUAKCHOOT, Nouakchoot (18°5'N, 15°59'W), 15.viii–30.ix.2006, Famille Stalmanns—5 ♀♀, 1 ♂ (paratypes) (PMOC); SÉLIBABY, Tachoot [=Tassota Barene] (15°26'N, 12°16'W), 20.x.1941, [anonymous]—1 ♂ (paratype) (OMOC); **NIGER**: AGADEZ, Agadez (16°58'N, 7°59'E), 1909, Cortier—2 ♂♂ (2 paratypes) (MNHN); Agadez (16°58'N, 7°59'E), 2.viii.1947, L. Chopard & A. Villiers—1 ♀ (paratype) (MNHN); Agadez (16°58'N, 7°59'E), 20.viii.1947, L. Chopard & A. Villiers—1 ♂ (paratype) (MNHN); Agadez (16°58'N, 7°59'E), 25.viii.1947, L. Chopard & A. Villiers—1 ♀ (paratype) (MNHN); Agadez (16°58'N, 7°59'E), 20.viii.1989, [anonymous]—3 ♀♀, 1 ♂ (paratypes) (OMOC); Arlit (18°44'N, 7°23'E), 15.ix.1977, P. Tauzin—1 ♀ (paratype) (PMOC); Dabaga, Aïr sud, 600 m (17°18'N, 8°10'E), 13–16.viii.1947, L. Chopard & A. Villiers—2 ♂♂ (2 paratypes) (MNHN); Taquei, Aïr Massif (18°25'48"N, 8°24'36"E), 26.viii.1983, P.C. Matteson—1 ♂ (paratype) (BMNH); DIFFA, N'Guigmi (14°15'N, 13°7'E), viii.1919, Dr. Noel—7 ♀♀, 5 ♂♂ (12 paratypes) (MNHN); N'Guigmi (14°15'N, 13°7'E), ix.1919, Dr. Noel—12 ♀♀, 13 ♂♂ (25 paratypes) (MNHN); N'Guigmi (14°15'N, 13°7'E), vi–vii.1919, Dr. Noel—1 ♂ (paratype) (MNHN); N'Guigmi (14°15'N, 13°7'E), x.1919, Dr. Noel—1 ♂ (paratype) (MNHN); DOSSO, Toudou (14°7'N, 3°54'E), 10.viii.1989, [anonymous]—1 ♀ (paratype) (OMOC); Toudou (14°7'N, 3°54'E), 13.viii.1989, [anonymous]—2 ♀♀, 1 ♂ (paratypes) (OMOC); **SENEGAL**: [unspecified locality], [no date], [anonymous]—1 ♂ (paratype) (BMNH); DAKAR, Keur Ndiaye Lô (14°45'25"N, 17°14'11"W), 20.viii.2013, I. de Dinechin—1 ♂ (paratype) (CMD); DIOURBEL, Bambey (14°42'N, 16°28'W), viii.1939, J. Risbec—2 ♂♂ (2 paratypes) (BMNH); Bambey (14°42'N, 16°28'W), 1945, J. Risbec—1 ♂ (paratype) (BMNH); FATICK, Diouroup (14°21'N, 16°32'W), 14–18.viii.2007, P. Moretto—4 ♀♀, 9 ♂♂ (13 paratypes) (FGIC, PMOC); KAOLAK, Missirah, 45 m (13°59'26"N, 15°7'4"W), 16.vii.2007, F. Génier (2007-01)—12 ♀♀, 9 ♂♂ (21 paratypes) (FGIC); LOUGA, Linguère (15°24'N, 15°7'W), ix.1967, A. Descarpentries, T. Leye & A. Villiers—496 specimens (paratype) (MNHN); Ndam-Dam (15°36'22"N, 16°23'35"W), xi.1967, A. Descarpentries, T. Leye & A. Villiers—2 ♀♀, 7 ♂♂ (9 paratypes) (MNHN); Ndilla (15°20'N, 15°3'W), ix.1967, A. Descarpentries, T. Leye & A. Villiers—1 ♂ (paratype) (MNHN); SAINT-LOUIS, Commune de Saint-Louis, 7 m (16°4'34"N, 16°22'40"W), 27.viii.2009, F. Génier (2009-33)—1 ♀ (paratype) (FGIC); Commune de Saint-Louis, 7 m (16°4'34"N, 16°22'40"W), 27.viii.2009, P. Moretto—2 ♀♀, 2 ♂♂ (4 paratypes) (PMOC); Podor (16°39'N, 14°57'30"W), viii–ix.1911, R. Chudeau—1 ♀ (paratype) (MNHN); Richard-Toll (16°28'N, 15°41'W), 7–10.viii.2008, P. Moretto—1 ♀ (paratype) (PMOC); Richard-Toll (16°28'N, 15°41'W), 28–31.viii.2009, F. Génier (2009-38)—8 ♀♀, 20 ♂♂ (28 paratypes) (FGIC); Richard-Toll (16°28'N, 15°41'W), 28–30.viii.2009, F. Génier (2009-40)—4 ♀♀, 1 ♂ (paratypes) (FGIC); Richard-Toll (16°28'N, 15°41'W), 28.viii.2009, F. Génier (2009-36)—1 ♂ (paratype) (FGIC); Richard-Toll (16°28'N, 15°41'W), 28.viii–1.ix.2009, P. Moretto & F. Génier—1 ♀, 2 ♂♂ (3 paratypes) (PMOC); Richard-Toll (16°28'N, 15°41'W), 30.viii.2009, F. Génier (2009-43)—2 ♀♀, 3 ♂♂ (5 paratypes) (FGIC); Richard-Toll (16°28'N, 15°41'W), 30.viii.2009, F. Génier (2009-44)—3 ♀♀, 17 ♂♂ (20 paratypes) (FGIC); Richard-Toll (16°28'N, 15°41'W), 31.viii.2009, F. Génier (2009-48)—6 ♂♂ (6 paratypes) (FGIC); Richard-Toll (16°28'N, 15°41'W), 1.ix.2009, F. Génier (2009-49)—1 ♀, 4 ♂♂ (5 paratypes) (FGIC); Richard-Toll (16°28'N, 15°41'W), 1.ix.2009, F. Génier (2009-50)—3 ♂♂ (3 paratypes) (FGIC); Richard-Toll (16°28'N, 15°41'W), 3.ix.2009, F. Génier (2009-52)—1 ♀, 1 ♂ (paratypes) (FGIC); Saint-Louis (16°0'30"N, 16°29'30"W), 1899, V. Planchat—13 ♀♀, 19 ♂♂ (32

paratypes) (MNHN); THIÈS, Kayar (14°55'N, 17°7'E), viii.1971, A. Villiers—1 ♀, 1 ♂ (paratypes) (OMOC); Mbour (14°25'N, 16°58'W), viii.1995, P. Moretto—13 ♀♀, 8 ♂♂ (21 paratypes) (PMOC); Meckhé (15°7'N, 16°38'W), [no date], [anonymous]—1 ♂ (paratype) (MNHN); Nianing, 8 m (14°19'N, 16°55'43"W), 23.vii.2006, A. Coache—1 ♀, 1 ♂ (paratypes) (JFJC); **SUDAN**: KHARTOUM, Environs de Khartoum (15°35'N, 32°32'E), [no date], [anonymous]—2 ♀♀, 1 ♂ (paratypes) (MNHN).

Etymology. *Sahelicus* is a Latin adjective pertaining to the distribution of this species.

Natural history. A mostly Sahelian species associated with grassland and wooded and acacia steppes habitats and grassland enclave within degraded sudanese vegetation and along dried sandy riverbeds, on deep sandy soils. Individuals are common at light traps and also collected from, donkey, cow, and human dung. Some individuals collected in pitfall traps baited with rumen content, recently killed toads and monitor lizards.

Digitonthophagus catta species group

Diagnosis. Pronotal punctures scattered and small on posterior half (Figs. 58, 93); surface behind anterior pronotal angles concave; male with two erected cephalic horns (Figs. 30, 32); females with anterior pronotal tubercles well developed and deeply obliquely concave (Figs. 94, 96); subapicodorsal lobe of FLP sclerite enlarged and sclerotized (Figs. 144, 147); FLP left surface with a conspicuous apophysis (Figs. 144, 147).

Digitonthophagus catta (Fabricius, 1787)

(Figs. 10, 29–30, 58, 74, 93–94, 122, 144–146; Map 5)

Scarabaeus Catta Fabricius, 1787a: 12 (original description)
Scarabæus Catta—Olivier 1789: 125 (redescription)
Scarabaeus Catta—Gmelin 1790: 1534 (diagnosis)
Scarabaeus Catta—Fabricius 1792: 44 (diagnosis)
Scarabaeus Catta—Illiger 1800: 232 (monograph)
Copris Catta—Fabricius 1801: 35 (diagnosis)
Copris Catta—Illiger 1804: 149 (comment taxonomy)
Copris Catta—Schönherr 1806: 49 (mentioned as synonym)
Onthophagus Catta—Dejean 1821: 53 (mentioned as synonym)
Copris Catta—LePeletier & Audinet-Serville 1828: 354 (comment taxonomy)
Copris Catta—Klug 1833: 163 (mentioned as synonym)
[*Onthophagus*] *Catta*—Dejean 1836: 157 (mentioned as synonym)
Onthophagus Catta—Hope 1837: 32 (catalog)
Ontophagus Catta—Reiche 1840: 243 (comment taxonomy)
[*Ontophagus*] *Catta*—Laporte 1840: 85 (mentioned as synonym)
Onthophagus Catta—Sturm 1843: 107 (mentioned as synonym)
Onthophagus catta—Motschulsky 1860: 154 (comment taxonomy)
Onthophagus catta—Harold 1869: 1029 (mentioned as synonym)
Onthophagus catta—Gerstaecker 1871: 50 (distribution)
Onthophagus catta—Gerstaecker 1873: 130 (monograph)
Onthophagus catta—Quedenfeldt 1884: 272 (distribution)
Onthophagus catta—Kolbe 1887: 246 (distribution)
Onthophagus catta—Kolbe 1897: 150 (mentioned as synonym)
Onthophagus catta—Péringuey 1901: 181 (mentioned as synonym)
Onthophagus catta—Gillet & Boucomont 1927: 138 (mentioned as synonym)
Onthophagus catta—Arrow 1931: 230 (monograph)
Onthophagus catta—Boucomont 1934: 26 (mentioned as valid species)
Onthophagus catta—Boucomont 1935: 284 (distribution)
Onthophagus catta—Paulian 1937: 12 (distribution)
Onthophagus catta—Paulian 1948: 151 (distribution)
Onthophagus catta—Janssens 1953: 1549 (distribution)
Onthophagus catta—Frey 1958: 73 (mentioned as synonym)
[*Scarabaeus*] *catta*—Balthasar 1963: 365 (mentioned as synonym)
Onthophagus catta—Ferreira 1967: 1169 (mentioned as synonym)
Onthophagus catta—Ferreira 1968: 593 (mentioned as synonym)

Onthophagus catta—Ferreira 1972: 780 (mentioned as synonym)
Onthophagus catta—Paulian 1986: 107 (catalog)
Onthophagus gazella—Veenakumari & Veeresh 1996: 252 (natural history)
Onthophagus catta—Gaikwad & Bhawane 2015: 1538 (natural history)
Digitonthophagus catta—Génier & Davis 2017: 497 (comment taxonomy, distribution)

Diagnosis. Species distributed from Pakistan eastward; left lateral apophysis of FLP sclerite moderately developed (Fig. 144).

Description. Alloreferent ♂ (Fig. 10): **Measurements**. Length 11.5 mm, width 6.5 mm. **Head** (Figs. 29–30). Anterior clypeal edge straight on median fifth in dorsal view; clypeofrontal carina broadly arcuate and interrupted at gena; vertex lacking median tubercle, surface with punctures fine to small, separated by one to four diameters. Horns moderately long, arcuate in frontal view, parallel sided on basal four-fifths; distinctly tapering externally before apex and narrower on apical sixth; posterointernal edge unmodified basally; apicointernal surface lacking granules. Genal edge upturned and distinctly angulate on anterior third, forming a broad angle with clypeal edge. **Pronotum** (Fig. 58). Surface with granulate punctures restricted to anterior half medially, with smaller, irregularly-scattered, simple punctures on posterior half of disc; punctures lacking posterolaterally, with more-or-less distinct, minute punctures throughout. Anteromedian tubercle atrophied, simply round in lateral view; median longitudinal sulcus well defined; surface behind the eyes slightly concave, surface of anterior angles concave, anterior angles unmodified; anterior half of lateral edge arcuate in dorsal and slightly sinuous anteriorly in lateral view; posterior angles simply arcuate in dorsal view. Anterior hypomeral ridge broadly arcuate, anterior hypomeral depression surface slightly darker in color medially. **Elytra** (Fig. 10). Interval 2 with few fine granules on apical declivity, interval 4 lacking granules from base to apex. **Legs**. Protibial apicointernal tooth enlarged, with dorsal ridge extending to apex. **Aedeagus** (Fig. 122). Parameres with dorsal and ventral edges slightly diverging toward apex in lateral view. **Internal sac sclerites** (Figs. 144–146)**.** Axial sclerite moderately sclerotized, shorter than subaxial sclerite, almost straight. Subaxial sclerite, larger basally and gradually tapering, extending straight and interrupted at apex of frontolateral peripheral sclerite apical portion, with villi on apical sixth. Frontolateral peripheral sclerite basoventral apophysis moderately developed, angular in lateral view; with a single acute medioventral carinae; right lateral fold produced into a uneven bifurcate process, lateral edge with few indentations; left lateral apophysis present, moderately developed; left lateral lobe absent; subapicodorsal lobe well sclerotized, reaching anterior edge, partly fused to apical lobe, with villi similar to apical lobe, right edge round before apex; apical lobe round apically, longitudinally folded and partly fused to subapicodorsal lobe, apical villi regular in shape; subapicoventral lobe atrophied, oriented ventrally.

Variation. Measurements (107 ♂♂, 106 ♀♀). Length: male 7.0–13.0 mm (10.6 ± 1.0 mm), female 7.5–12.5 mm (10.2 ± 1.0 mm). Female specimen. Cephalic outline in dorsal view similar to Fig. 74; vertex with a broadly arcuate transverse carina, dorsal edge broadly arcuate in frontal view, lateral portion gradually sloping down posteriorly; anterior pronotal tubercles well developed, external lateral edges approximately parallel in dorsal view (Fig. 93), anterolateral surface obliquely concave, anterosuperior edge slightly arcuate in dorsal view, lateral portion of anterosuperior edge slightly upturned (Fig. 94). Protibia short, with external teeth more robust.

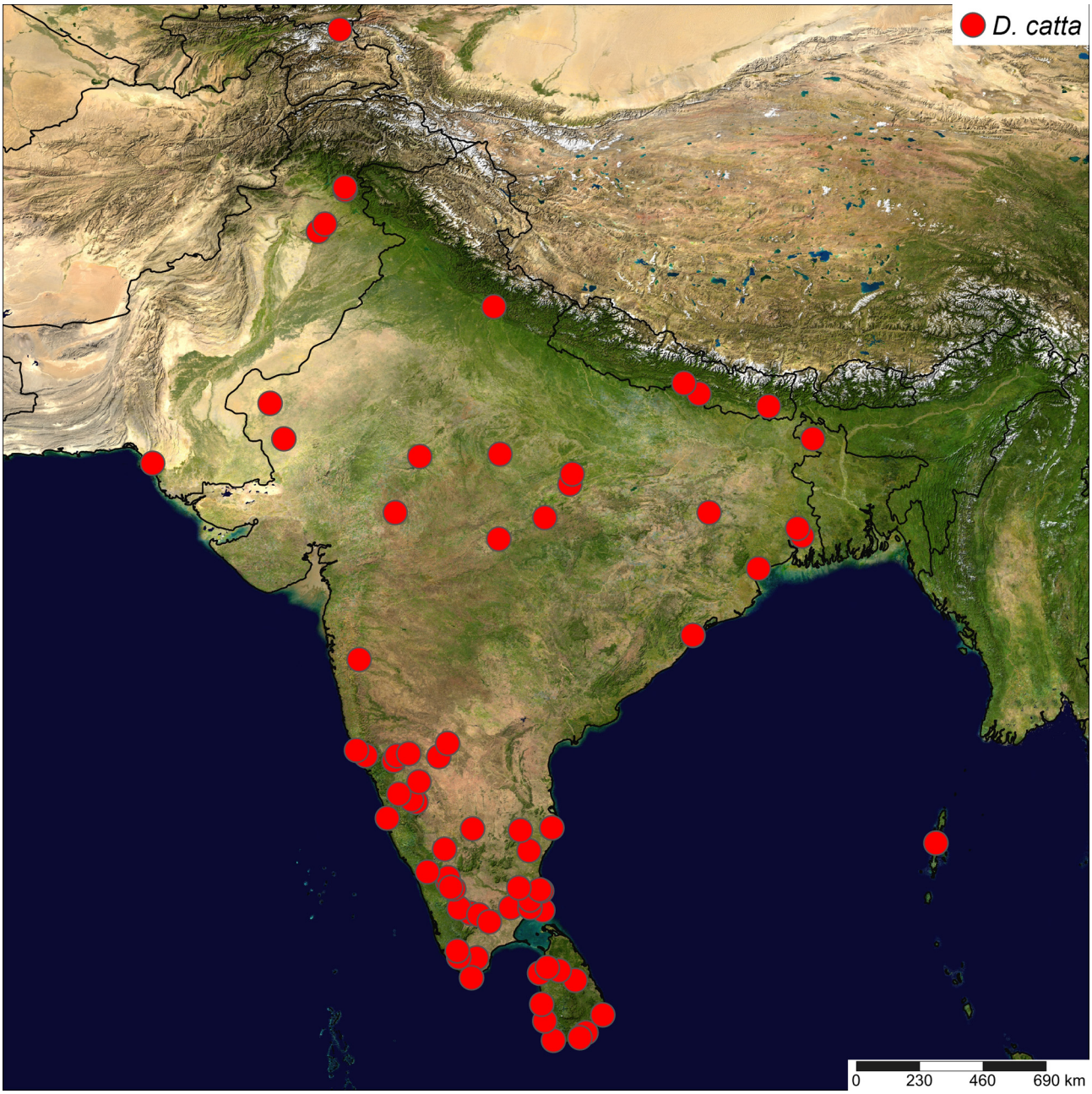
Primary type data. Lectotype ♀ (ZMUK) **present designation**: [WORLD / SCARAB. / DATABASE / WSD00032221] barcode label; [LECTOTYPE ♀ / *Scarabaeus* / *catta* / Fabricius, 1787 / des. F. Génier, 2016] red card.

Material examined (188 ♂♂, 199 ♀♀, 855 sex no recorded), distribution (Map 5): **AFGHANISTAN**: KHYBER PAKHTUNKHWA, Hazara, Abbottabad (39°10'N, 73°13'E), vi.2002, [anonymous]—2 ♀♀, 2 ♂♂ (CEMT); **BANGLADESH**: RANGPUR, Dinajpur (25°45'N, 88°43'E), iv.1970, Barbe—1 ♂ (CMNC); **INDIA**: Coromandel Coast, [no date], Zschuck—4 ♀♀ (lectotype, 3 paralectotypes) (ZMUC); ANDAMAN AND NICOBAR ISLANDS, [unspecified locality] (12°30'N, 92°45'E), [no date], Roepstorff—1 ♂ (ZMUC); GOA, Calangute (15°32'30"N, 73°45'45"E), 15.xii.1976, [anonymous]—4 ♀♀, 3 ♂♂ (OMOC); [unspecified locality] (15°22'N, 74°4'E), 22–23.x.1986, J.L. & A. Nicolas—1 ♀, 1 ♂ (CMD); JHARKHAND, Ranchi (23°20'N, 85°19'E), 1970, Dr. Soběslavský—1 ♀ (CVM); Ranchi (23°20'N, 85°19'E), [no date], R.P. Bretaudeau—1 ♀, 1 ♂ (MNHN); KARNATAKA, 15 km W Gadag, 670 m (15°25'48"N, 75°28'39"E), 13.viii.1984, B. Gill—1 ♀ (BDGC); 20 km SW Hubli, 650 m (15°12'3"N, 74°59'34"E), 11.vii.1984, B. Gill—3 ♀♀, 1 ♂ (BDGC); Bangalore, 970 m (12°58'N, 77°34'E), 17–19.vii.1984, B. Gill—7 ♀♀, 2 ♂♂ (BDGC); Chikkangalur, près de Bangalore [=Chickmagaluru] (13°18'53"N, 74°46'29"E), vii–ix.1899, R.P. Tabourel—1 ♀ (MNHN); Hampi (15°20'6"N,

76°27'36"E), 18.x.1986, J.L. Nicolas—2 ♀♀, 2 ♂♂ (CMD); Harihar, 750 m (14°30'30"N, 75°48'30"E), 15.vii.1984, B. Gill—2 ♀♀, 5 ♂♂ (BDGC); Hubli, 670 m (15°21'42"N, 75°5'6"E), 7–14.vii.1984, B. Gill—5 ♀♀, 8 ♂♂ (BDGC); Sindhanur (15°46'N, 76°45'E), 21.xii.1989, C. Mahalingappa—1 ♀, 2 ♂♂ (OUMNH); Mysore District, Mysore (12°18'N, 76°39'E), [no date], [anonymous]—1 ♀, 1 ♂ (MNHN); Shimoga District, Bhadravati (13°50'24"N, 75°42'7.2"E), 13.v.1935, [anonymous]—1 ♀, 1 ♂ (CMNC); Shimoga (13°55'N, 75°34'E), v.1897, [anonymous]—1 ♀, 1 ♂ (MNHN); Shimoga (13°55'N, 75°34'E), vi.1897, [anonymous]—1 ♀, 1 ♂ (MNHN); Shimoga (13°55'N, 75°34'E), iv.1936, [anonymous]—1 ♂ (PMOC); KERALA, Chembra Peak, 1067 m (11°33'12"N, 76°5'14"E), iv.1970, T.R.S. Nathan—1 ♂ (CMNC); Thenmala (8°58'N, 77°4'E), v.1988, T.R.S. Nathan—1 ♀, 1 ♂ (CMNC); Thiruvananthapuram District, Poonmudi Range, 914 m (8°45'27"N, 77°6'54"E), v.1989, T.R.S. Nathan—1 ♀, 1 ♂ (CMNC); KERALA/ TAMIL NADU, Anaimalai Hills, 1067 m (10°22'N, 77°7.5'E), v.1963, P.S. Nathan—1 ♀ (CNC); Anaimalai Hills, 1067 m (10°22'N, 77°7.5'E), v.1977, [anonymous]—4 ♀♀, 4 ♂♂ (CNC); Anaimalai Hills, 1067 m (10°22'N, 77°7.5'E), iv.1963, P.S. Nathan—2 ♂♂ (CNC); Anaimalai Hills, 1067 m (10°22'N, 77°7.5'E), x.1977, T.R.S. Nathan—1 ♂ (RMNH); Cinchona, Anaimalai Hills, 1067 m, iv.1964, P.S. Nathan—1 ♂ (CNC); MADHYA PRADESH, Jabalpur (23°10'N, 79°56'E), x.1957, Nathan—1 ♀, 1 ♂ (CMNC); Maihar (24°16'10"N, 80°45'24"E), x.1972, [anonymous]—1 ♀ (ZMUC); Pachmarhi, Satputa Hills, 1067 m (22°28'.12"N, 78°25'59.88"E), x.1970, T. Nathan—1 ♀, 1 ♂ (CNC); Ratlam (23°20'N, 75°2'E), [no date], [anonymous]—1 ♂ (MNHN); Satna (24°36'N, 80°50'E), [no date], Stloukal—1 ♂ (CMNC); MAHARASHTRA, Pune (18°31'N, 73°51'E), viii.1984, S. Pokorný—2 ♀♀, 2 ♂♂ (CVM); ODISHA, Brahmapur (19°19'N, 84°47'E), xi.1972, [anonymous]—1 ♂ (ZMUC); ORISSA, Berhampur (19°18'30"N, 84°47'26"E), [no date], Atkinson—1 ♂ (OUMNH); Balasore District, Balasore (21°30'N, 86°56'E), [no date], R.P. Gengler—1 ♀, 1 ♂ (MNHN); PONDICHERRY, Karaikal District, Karaikal (10°56'N, 79°50'E), viii.1991, T.R.S. Nathan—1 ♀ (CMNC); Karaikal District, Karaikal (10°56'N, 79°50'E), x.1991, T.R.S. Nathan—1 ♂ (CMNC); Karaikal District, Karaikal (10°56'N, 79°50'E), iv.1962, P.S. Nathan—1 ♀, 1 ♂ (CNC); Karaikal District, Karaikal (10°56'N, 79°50'E), x.1963, P.S. Nathan—1 ♀, 1 ♂ (CNC); Karaikal District, Karaikal (10°56'N, 79°50'E), ix.1952, P.S. Nathan—2 ♀♀ (CNC); Karaikal District, Karaikal (10°56'N, 79°50'E), vi.1962, P.S. Nathan—1 ♂ (CNC); Karaikal District, Karaikal (10°56'N, 79°50'E), vii.1963, P.S. Nathan—1 ♂ (CNC); Karaikal District, Karaikal (10°56'N, 79°50'E), i.1962, P.S. Nathan—11 specimens (CNC); Karaikal District, Karaikal (10°56'N, 79°50'E), ii.1962, P.S. Nathan—36 specimens (CNC); Karaikal District, Karaikal (10°56'N, 79°50'E), iii.1962, P.S. Nathan—34 specimens (CNC); Karaikal District, Karaikal (10°56'N, 79°50'E), vii.1962, P.S. Nathan—40 specimens (CNC); Karaikal District, Karaikal (10°56'N, 79°50'E), viii.1962, P.S. Nathan—74 specimens (CNC); Karaikal District, Karaikal (10°56'N, 79°50'E), ix.1962, P.S. Nathan—146 specimens (CNC); Karaikal District, Karaikal (10°56'N, 79°50'E), x.1962, P.S. Nathan—83 specimens (CNC); Karaikal District, Karaikal (10°56'N, 79°50'E), xi.1962, P.S. Nathan—39 specimens (CNC); Karaikal District, Karaikal (10°56'N, 79°50'E), xii.1962, P.S. Nathan—9 specimens (CNC); Karaikal District, Karaikal (10°56'N, 79°50'E), i.1963, P.S. Nathan—16 specimens (CNC); Karaikal District, Karaikal (10°56'N, 79°50'E), ii.1963, P.S. Nathan—12 specimens (CNC); Karaikal District, Karaikal (10°56'N, 79°50'E), iii.1963, P.S. Nathan—34 specimens (CNC); Karaikal District, Karaikal (10°56'N, 79°50'E), iv.1963, P.S. Nathan—12 specimens (CNC); Karaikal District, Karaikal (10°56'N, 79°50'E), vi.1963, P.S. Nathan—4 specimens (CNC); Karaikal District, Karaikal (10°56'N, 79°50'E), x.1966, P.S. Nathan—13 specimens (CNC); Karaikal District, Karaikal (10°56'N, 79°50'E), viii.1963, T.R.S. Nathan—2 ♀♀, 2 ♂♂ (MMUE); Karaikal District, Karaikal (10°56'N, 79°50'E), i–ii.1964, T.R.S. Nathan—4 ♀♀, 4 ♂♂ (MMUE); Karaikal District, Karaikal (10°56'N, 79°50'E), vii.1970, P. Susai Nathan—1 ♂ (RMNH); Nedungadu (10°58'N, 79°46'E), [no date], [anonymous]—1 ♂ (NMPC); RAJASTHAN, Barmer (25°45'N, 71°23'E), ix.1973, T.R.S. Nathan—1 ♀ (RMNH); Kota, 250 m (25°10'28"N, 75°50'14"E), x.1981, T.R.S. Nathan—2 ♀♀, 2 ♂♂ (OUMNH); Thar desert around Jaisalmer (26°55'N, 70°56'E), 2.viii.2007, I. Nádai—4 ♀♀, 7 ♂♂ (PMOC); TAMIL NADU, 20 km SE Sagar, 600 m (14°6.37'N, 75°8.93'E), 12.v.2005, M. Halada—1 ♀ (OUMNH); 20 km SW Karamadai, 450 m (11°12.6'N, 76°44.9'E), 27.iv.2005, M. Halada—1 ♂ (OUMNH); Cap Comorin [=Kanyakumari] (8°5'N, 77°32'E), 1888, R.P. Castets—16 specimens (MNHN); Coimbatore, 427 m (11°0'N, 76°57'E), xi.1969, P.S. Nathan—1 ♀, 3 ♂♂ (CMNC, CNC); Coimbatore, 427 m (11°0'N, 76°57'E), iv.1959, P.S. Nathan—1 ♀ (CNC); Coimbatore, 427 m (11°0'N, 76°57'E), iv.1962, P.S. Nathan—25 specimens (CNC); Coimbatore, 427 m (11°0'N, 76°57'E), v.1962, P.S. Nathan—19 specimens (CNC); Coimbatore, 427 m (11°0'N, 76°57'E), vii.1962, P.S. Nathan—18 specimens (CNC); Coimbatore, 427 m (11°0'N, 76°57'E), ix.1962, P.S. Nathan—14 specimens (CNC); Coimbatore, 427 m (11°0'N, 76°57'E), x.1962, P.S. Nathan—3 specimens (CNC); Coimbatore, 427 m (11°0'N, 76°57'E), xi.1962, P.S.

Nathan—20 specimens (CNC); Coimbatore, 427 m (11°0'N, 76°57'E), xii.1962, P.S. Nathan—5 specimens (CNC); Coimbatore, 427 m (11°0'N, 76°57'E), i.1963, P.S. Nathan—6 specimens (CNC); Coimbatore, 427 m (11°0'N, 76°57'E), iv.1963, P.S. Nathan—50 specimens (CNC); Coimbatore, 427 m (11°0'N, 76°57'E), xi.1966, P.S. Nathan—20 specimens, 2 ♂♂ (CNC, PMOC); Coimbatore, 427 m (11°0'N, 76°57'E), viii.1963, T.R.S. Nathan—6 ♀♀, 6 ♂♂ (MMUE); Coimbatore, 427 m (11°0'N, 76°57'E), ix.1964, T.R.S. Nathan—1 ♀, 5 ♂♂ (MMUE); Coimbatore, 427 m (11°0'N, 76°57'E), x–xi.1964, T.R.S. Nathan—4 ♂♂ (MMUE); Coimbatore, 427 m (11°0'N, 76°57'E), xi.1967, P.S. Nathan—1 ♀ (PMOC); Coimbatore, 427 m (11°0'N, 76°57'E), ix.1972, T.R.S. Nathan—2 ♀♀, 1 ♂ (PMOC, RMNH); Coimbatore, 427 m (11°0'N, 76°57'E), x.1972, T.R.S. Nathan—2 ♀♀, 2 ♂♂ (PMOC); Coimbatore, 427 m (11°0'N, 76°57'E), xii.1976, T.R.S. Nathan—1 ♂ (RMNH); Gingee (12°15'N, 79°25'E), [no date], M. André—1 ♂ (PMOC); Madurai (9°55'N, 78°7'E), x.1975, M. Coe—1 ♀, 4 ♂♂ (OUMNH); Maravakkadu (10°38'N, 79°27'E), v.1962, T.R.S. Nathan—2 ♀♀ (CNC); NE of Madurai, 200 m (10°8.7'N, 77°46.5'E), 6.v.2005, M. Halada—1 ♀ (OUMNH); Palni Hills (10°12'N, 77°30'E), 1898, R.P. Castets—1 ♀, 1 ♂ (MNHN); Point Calimere (10°17'35"N, 79°52'6"E), 1972, T.R.S. Nathan—1 ♀ (RMNH); Pudukkottai (10°23'N, 78°49'E), x.1984, T.R.S. Nathan—1 ♀, 1 ♂ (CMNC); Singara, Nilgiri Hills (11°22'N, 76°46'E), v.1963, T.R.S. Nathan—2 ♀♀, 2 ♂♂ (MMUE); Thambikkottai (10°23'N, 79°27'E), vi.1962, P.S. Nathan—3 ♀♀ (CNC); Tirunelveli (8°44'N, 77°42'E), x.1986, [anonymous]—1 ♀, 1 ♂ (OMOC); Tranquebar [=Tharangambadi] (11°2'N, 79°5'E), [no date], [anonymous]—1 ♂ (ZMUC); Vellore (12°55'N, 79°8'E), [no date], Löventhal—2 ♂♂ (ZMUC); Chennai District, Madras Airport [=Chennai Airport] (12°59'38"N, 80°9'28"E), v.1962, P.S. Nathan—64 ♀♀, 42 ♂♂ (CNC); Chennai District, Madras Airport [=Chennai Airport] (12°59'38"N, 80°9'28"E), viii.1962, P.S. Nathan—19 specimens (CNC); Chennai District, Madras Airport [=Chennai Airport] (12°59'38"N, 80°9'28"E), ix.1962, P.S. Nathan—9 specimens (CNC); Chennai District, Madras Airport [=Chennai Airport] (12°59'38"N, 80°9'28"E), x.1962, P.S. Nathan—14 specimens (CNC); Coimbatore District, Coimbatore (11°0'N, 76°57'E), x.1958, P.S. Nathan—1 ♀ (CNC); Coimbatore District, Coimbatore (11°0'N, 76°57'E), vi.1962, P.S. Nathan—1 ♀ (CNC); Coimbatore District, Coimbatore (11°0'N, 76°57'E), x.1976, [anonymous]—1 ♀, 1 ♂ (CNC); Coimbatore District, Coimbatore (11°0'N, 76°57'E), xi.1976, [anonymous]—1 ♂ (CNC); Coimbatore District, Coimbatore (11°0'N, 76°57'E), iv.1976, [anonymous]—1 ♂ (CNC); Coimbatore District, Coimbatore (11°0'N, 76°57'E), xi.1957, P.S. Nathan—3 specimens (CNC); Coimbatore District, Coimbatore (11°0'N, 76°57'E), xi.1962, P.S. Nathan—12 specimens (CNC); Coimbatore District, Coimbatore (11°0'N, 76°57'E), xi.1965, P.S. Nathan—10 specimens (CNC); Marudamalai Hills (11°2'46"N, 76°51'7"E), xi.1969, P.S. Nathan—29 specimens, 1 ♀, 1 ♂ (CMNC, CNC); Marudamalai Hills (11°2'46"N, 76°51'7"E), x.1969, P.S. Nathan—2 ♀♀ (CNC); Kancheepuram District, Manapakkam (13°0'N, 80°10'E), 20.ix.2002, S. Saluk—1 ♂ (PMOC); UTTAR PRADESH, Babina, 300 m (25°15'N, 78°28'E), viii.1984, T.R.S. Nathan—1 ♀, 2 ♂♂ (CMNC); Babina, 300 m (25°15'N, 78°28'E), viii.1987, T.R.S. Nathan—3 ♀♀, 3 ♂♂ (CMNC, FETC); UTTARAKHAND, Rishikesh (30°5'N, 78°16'E), 7.x.1981, F. Tagliaferri—1 ♀ (FETC); WEST BENGAL, Burasanti, Singur (22°49'N, 88°13'E), 14.vi.1971, Oppenheimer—1 ♂ (CMNC); Burasanti, Singur (22°49'N, 88°13'E), 27.vi.1971, Oppenheimer—2 ♀♀ (CMNC); Kalkata District, Calcutta [=Kolkata] (22°34'N, 88°22'E), [no date], [anonymous]—1 ♀ (NMPC); **NEPAL**: CENTRAL, Adhabar, near Simra, 183 m (27°13'49"N, 84°59'14"E), 23.viii.1967, Canadian Nepal Expedition—1 ♂ (CNC); Adhabar, near Simra, 183 m (27°13'49"N, 84°59'14"E), 25.viii.1967, Canadian Nepal Expedition—1 ♀ (CNC); Adhabar, near Simra, 183 m (27°13'49"N, 84°59'14"E), 27.viii.1967, Canadian Nepal Expedition—1 ♀ (CNC); Adhabar, near Simra, 183 m (27°13'49"N, 84°59'14"E), 28.viii.1967, Canadian Nepal Expedition—1 ♂ (CNC); Chitwan District, Sauraha, Chitwan National Park, 300 m (27°34'29"N, 84°29'37"E), 1–4.vi.1999, M. Pejcha—1 ♀ (FETC); EASTERN, Dharan (26°49'N, 87°16'E), 4.iv.1959, K. Becker Larsen—1 ♀ (ZMUC); Dharan (26°49'N, 87°16'E), 8.vii.1959, K. Becker Larsen—1 ♀ (ZMUC); **PAKISTAN**: Thar, 18.ix.2007, Zubair & Atique—2 ♂♂ (BDGC); KHYBER PAKHTUNKHWA, Changla Gali, Murree, Islamabad area, 1981 m (33°59'42"N, 73°23'2"E), 5.vii.2006, Z. Ahmed—1 ♀ (BDGC); PENJAB, Chakwal (32°33'N, 72°30'36"E), 19.v.1990, Naeem—1 ♀ (CNC); Kallar Kahar (32°47'32"N, 72°43'34"E), 26.vi.2008, A. Zubair—2 ♂♂ (PMOC); Murree, Islamabad area, 1981 m (33°54'27"N, 73°23'29"E), vii.2006, Z. Ahmed—2 ♀♀, 2 ♂♂ (BDGC); SINDH, Karachi (24°57'N, 67°5'E), viii–ix, Maindron—1 ♀, 1 ♂ (MNHN); Karachi (24°57'N, 67°5'E), 26.i.2007, Hareem & Atige—2 ♀♀, 2 ♂♂ (CEMT); **SRI LANKA**: Wilpattu National Park (8°25'N, 80°1'E), 18.vii.1979, G. de Rougemont—1 ♀ (OUMNH); EASTERN, Pottuvil (6°52'N, 81°50'E), 1–12.vii.1983, O. Mehl—1 ♀ (ZMUC); NORTH CENTRAL, Anuradhapura (8°19'N, 80°24'E), 9.vii.1977, O. Mehl—1 ♀ (ZMUC); Girithale (8°0'N, 80°56'E), 16.viii.1979, G. de Rougemont—1 ♀ (OUMNH); NORTH WESTERN, Kalpitiya (8°14'N, 79°45.8'E), 12.xi.2009, Kuduvidanage

et al.—2 ♂♂ (OUMNH); SOUTHERN, Galle (6°2'N, 80°13'E), 30.vii.1982, P. Moretto—2 ♀♀, 2 ♂♂ (PMOC); Hambantota District, Hambantota (6°7'2"N, 81°5'9"E), 10.xii.1979, V. Mahler—1 ♀ (ZMUC); Tissamaharama (6°17'N, 81°17'E), 12.xii.1979, [anonymous]—1 ♂ (ZMUC); Tissamaharama (6°17'N, 81°17'E), 1.viii.1982, P. Moretto—2 ♀♀, 1 ♂ (PMOC); W of Tissamaharama (6°16'N, 81°14'E), 20.ii.1986, R.W. Lekkerkerk—1 ♂ (RMNH); WESTERN, Negombo (7°13'N, 79°50'E), 17–20.vi.1985, O. Mehl—1 ♀ (ZMUC); Negombo (7°13'N, 79°50'E), 21.viii.1986, C. Lestrade—1 ♀ (PMOC); Negombo (7°13'N, 79°50'E), 23.viii.1986, C. Lestrade—2 ♂♂ (PMOC); Wadduwa (6°40'N, 79°56'E), [no date], v. de Poll—1 ♂ (PMOC).



MAP 5. Distribution of *Digitonthophagus catta*.

Natural history. Grassy plot in West Bengal (India) and arid scrub forest in Sri Lanka. A few specimens collected in buffalo, cow, goat, northern plains gray langur (*Semnopithecus entellus*), and human dung. The nesting behavior and some aspects of larval natural history are described by Veenakumari & Veeresh (1996) and Gaikwad & Bhawane (2015).

Nomenclature and taxonomy. *Scarabaeus catta* Fabricius was described in the first volume of *Mantissa Insectorum*. This work, which contained the Coleoptera, was published in June 1787 (Evenhuis 1997; Bousquet

2016). There is a misspelling of the type locality (Ceromandel) in the original description, but there is no doubt that it pertains to Coromandel Coast, which historically was covering the coastal area of the current states of Tamil Nadu and Andhra Pradesh. These specimens are most likely from the area of Tranquebar, a former Danish colony from 1620–1845. However, there is no biographical information on Zschuck the stated collector of the specimens (see Zimsen 1964). The four specimens forming the type series are unlabeled females from Kiel collection. Based on the pins used, these four specimens are unquestionably from Fabricius time. The three different types of pins used also suggest that these specimens are from more than a single collecting event. In order to stabilize nomenclature, we designate here the clean and unabraded specimen as the lectotype (**present designation**). A lectotype is designated in order to choose a single specimen as name bearing type in the event that the other specimens of the syntype series could belong to a different cryptic species in this genus. The lectotype has a steel pin similar to those used to pin the syntypes of *D. bonasus*, which were collected from the same area in India. This female specimen, with the distinctly concave ventral surface of the median pronotal tubercle combined with the distinctly arcuate anterior hypomeral carina, matches the taxon present in India. One of the female syntypes is pinned with a *Crataegus* thorn and appears to have the same origin as the four male specimens from Kiel collection which have been prepared in the same way. This pinning method suggests that this fourth female specimen was from the same collecting event as the four males *S. gazella* from the Kiel collection. All of these specimens do also lack the typical small green label used to identify Fabrician types. This gives support to the hypothesis that Fabricius considered females as *S. catta* and males as *S. gazella*.

***Digitonthophagus eucatta* Génier, new species**
http://zoobank.org/urn:lsid:zoobank.org:act:D66876EF-FA95-493B-B87B-1D88858C8406
(Figs. 11, 31–32, 59, 75, 95–96, 123, 147–149, 187; Map 6)

Type locality. Toulfé (13°53’33”N 01°53’39”W), 325 m, Loroum, Burkina Faso.

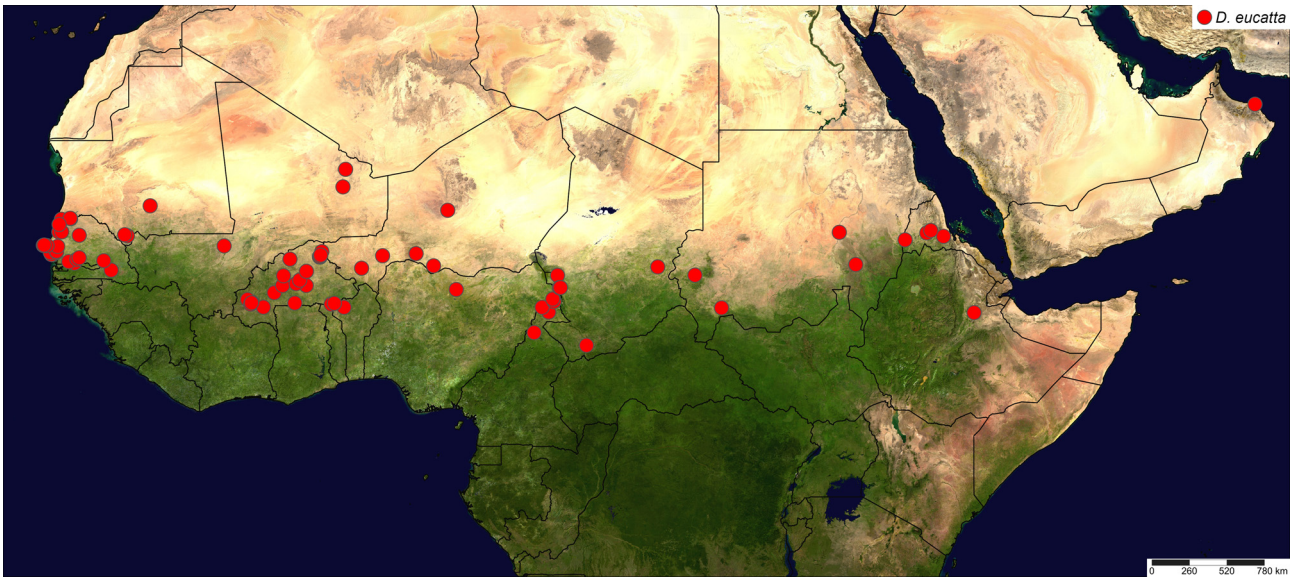
Diagnosis. Species distributed from Oman westward; left lateral apophysis of FLP sclerite large (Fig. 147).

Description. Holotype ♂ (Fig. 11). **Measurements**. Length 11.5 mm, width 6.5 mm. **Head** (Figs. 31–32). Anterior clypeal edge straight on median fourth in dorsal view; clypeofrontal carina broadly arcuate and interrupted at gena. Vertex lacking median tubercle; surface with punctures moderate, scabrous anteriorly, separated by less than a diameter. Horns moderately long, parallel on apical half in frontal view, parallel sided on basal four-fifths, slightly tapering externally before apex; posterointernal edge produced into a low, angular projection; apicointernal surface lacking granules, with a few small scabrous punctures; genal edge upturned and distinctly angulate on anterior third, forming a broad angle with clypeal edge. **Pronotum** (Fig. 59). Surface with granulate punctures restricted to anterior half medially, with smaller, irregularly-scattered, simple punctures on posterior half of disc; punctures lacking posterolaterally, with more-or-less distinct minute punctures throughout; anteromedian tubercle atrophied, simply round in lateral view, median longitudinal sulcus well defined; surface behind the eyes slightly concave, surface of anterior angles concave, anterior angles unmodified; anterior half of lateral edge arcuate in dorsal and slightly sinuous anteriorly in lateral view; posterior angles simply arcuate in dorsal view. Anterior hypomeral ridge straight, abruptly curved before anterior angle, anterior hypomeral depression surface light in color medially. **Elytra** (Fig. 11). Intervals 2 and 4 with few fine granules on apical declivity only. **Legs**. Protibial apicointernal tooth enlarged, with dorsal ridge extending to apex. **Aedeagus** (Fig. 123). Parameres with dorsal and ventral edges slightly diverging toward apex in lateral view. **Internal sac sclerites** (Figs. 147–149)**.** Axial sclerite moderately sclerotized, shorter than subaxial sclerite and almost straight. Subaxial sclerite, larger basally and abruptly tapering in line with apex of axial sclerite, extending straight and interrupted approximately at apex of frontolateral peripheral sclerite apical portion, with fine villi on apical sixth. Frontolateral peripheral sclerite basoventral apophysis moderately developed, angular in lateral view; with a single acute medioventral carinae; right lateral fold produced into a uneven bifurcate process, lateral edge straight; left lateral apophysis present, large; left lateral lobe absent; subapicodorsal lobe well sclerotized, entirely covering apical lobe, with villi much shorter than apical lobe villi, right edge obliquely truncated before apex; apical lobe truncated apically, apical villi regular in shape; subapicoventral lobe atrophied, oriented ventrally

Variation. Measurements (107 ♂♂, 118 ♀♀). Length: male 7.0–12.5 mm (10.4 ± 1.0 mm), female 8.0–12.5 mm (10.6 ± 1.0 mm). Female allotype. Cephalic outline in dorsal view as in Fig. 75; vertex with a broadly arcuate

transverse carina, dorsal edge straight in frontal view, lateral portion subangular and sloping down posteriorly; anterior pronotal tubercles well developed, external lateral edges rather strongly widening in dorsal view (Fig. 95), anterolateral surface deeply, obliquely concave, anterosuperior edge slightly arcuate in dorsal view, lateral portion of anterosuperior edge slightly upturned (Fig. 96). Protibia short, with external teeth more robust.

Primary type data. Holotype ♂ (CMNC): [BURKINA FASO: LORUM / Toulfé, 325m / 13°53'33"N 001°53'39"O / 17.VII.2006, zone sahélienne / steppe arborée, piège lumineux / F. & S. Génier, 2006-41]; [COLÉOPTÈRES / DU / BURKINA FASO / BF015417] barcode label; [HOLOTYPE ♂ / *Digitonthophagus* / *eucatta n.sp.* / des. F. Génier, 2016] red card.



MAP 6. Distribution of *Digitonthophagus eucatta*

Material examined (403 ♂♂, 237 ♀♀), distribution (Map 6): **BENIN**: ATAKORA, Batia (10°53'N, 1°29'E), 24.vii.2009, B. Rainon—1 ♂ (paratype) (CMD); **BURKINA FASO**: CENTRE, Ouagadougou (12°22'N, 1°31'W), viii.1977, P. Ardoin—2 ♀♀, 7 ♂♂ (9 paratypes) (FETC); CENTRE-NORD, 19 km N Kaya, 314 m (13°8'46.2"N, 0°52'42.1"W), 16.viii.2012, P. Moretto—1 ♂ (paratype) (PMOC); CENTRE-OUEST, Forêt de Sorobouli [=Forêt Classée de Baporo], 270 m (11°47'44"N, 2°53'25"W), 10–15.viii.2005, P. Moretto—31 ♀♀, 41 ♂♂ (72 paratypes) (FETC, PMOC); Koudougou (12°15'N, 2°22'W), vii.1998, J.B. Yaméogo—1 ♂ (paratype) (PMOC); CENTRE-SUD, Réserve de Nazinga (11°9'N, 1°36'W), 9–12.vi.2005, S. Rojkoff—2 ♀♀, 1 ♂ (paratypes) (PCSR); EST, 25 km SE Pama (11°7'49"N, 0°52'38"E), 3–24.ix.1988, F. Génier & M. Sanborne—2 ♀♀, 6 ♂♂ (8 paratypes) (CMNC); Kompienga, 20 km S Pama (11°4'37"N, 0°40'50"E), 1–16.vi.1988, Sanborne, Landry & Tou—2 ♂♂ (2 paratypes) (CMNC); Kompienga, 20 km S Pama (11°4'37"N, 0°40'50"E), 3–24.ix.1988, F. Génier & M. Sanborne—2 ♀♀, 4 ♂♂ (6 paratypes) (CMNC); HAUTS-BASSINS, Aéroport, Bobo-Dioulasso (11°9'47"N, 4°19'12"W), 27.ix.2012, P. Moretto—1 ♀, 2 ♂♂ (3 paratypes) (PMOC); Bobo-Dioulasso (11°12'N, 4°18'W), 29.iv.1953, Hamon—7 ♀♀, 7 ♂♂ (14 paratypes) (MNHN); Bobo-Dioulasso (11°12'N, 4°18'W), 7.v.1953, Hamon—1 ♀, 2 ♂♂ (3 paratypes) (MNHN); Matourkou (11°5'N, 4°22'W), 15.vi.2005, S. Rojkoff—3 ♂♂ (3 paratypes) (CMD, PCSR); site de Samandéni, Bama, 330 m (11°22'24.5"N, 4°33'57"W), vii.2012, F. Rousset—1 ♂ (paratype) (PMOC); NORD, 8 km SW Yako, Passoré, 320 m (12°51'44"N, 2°18'35"W), 7.viii.2005, P. Moretto—1 ♀, 1 ♂ (paratypes) (PMOC); Toulfé, Lorum, 330 m (13°54'13"N, 1°54'19"W), 9.viii.2005, P. Moretto—5 ♀♀, 6 ♂♂ (11 paratypes) (PMOC); PLATEAU-CENTRAL, Piste de Bomboré (12°15'N, 0°53'W), 11.viii.2012, P. Moretto—1 ♂ (paratype) (PMOC); Ziniare (12°35'N, 1°18'W), 19.vi.2005, S. Rojkoff—1 ♀, 4 ♂♂ (5 paratypes) (PCSR, PMOC); SAHEL, 3,7 km NW piste vers Essakane, N'djomga, Dori, 287 m (14°5'20.9"N, 0°1'36.3"W), 1–5.ix.2013, P. Moretto—2 ♂♂ (2 paratypes) (PMOC); après le pont, route Essakane-Dori, Gorum-Gorum, 271 m (14°9'32.8"N, 0°1'20.4"E), 7.viii.2012, P. Moretto—2 ♂♂ (2 paratypes) (PMOC); Conseil régional, Dori, 283 m (14°2'4.5"N, 0°3'10.5"W), 30.viii.2013, P. Moretto—1 ♂ (paratype) (PMOC); Dori (14°2'N, 0°1'W), iv.2007, [anonymous]—1 ♂ (paratype) (JFJC); Dori (14°2'N, 0°1'W), 24.viii.2012, P. Moretto—1 ♂ (paratype) (PMOC);

Essakane, Gorum-Gorum, 264 m (14°22'40.2"N, 0°5'47.7"E), 13–15.viii.2012, P. Moretto—1 ♂ (paratype) (PMOC); Essakane, Gorum-Gorum, 264 m (14°22'40.2"N, 0°5'47.7"E), 22–24.viii.2012, P. Moretto—2 ♀♀, 2 ♂♂ (4 paratypes) (PMOC); Essakane, Gorum-Gorum, 264 m (14°22'40.2"N, 0°5'47.7"E), 10–13.ix.2012, P. Moretto—1 ♀, 2 ♂♂ (3 paratypes) (PMOC); Essakane, Gorum-Gorum, 264 m (14°22'40.2"N, 0°5'47.7"E), 2–4.x.2012, P. Moretto—1 ♀, 1 ♂ (paratypes) (PMOC); N'djomga, Dori (14°3'55.7"N, 0°3'3.4"W), 24–27.viii.2013, P. Moretto—4 ♂♂ (4 paratypes) (PMOC); SUD-OUEST, Bondigui, 324 m (10°53'56.5"N, 3°34'15"W), v.2012, F. Rousset—1 ♀, 1 ♂ (paratypes) (PMOC); BALÉ, Boromo, 250 m (11°45'6"N, 2°51'58"W), 10.viii.2005, F. Génier (2005-10)—1 ♀, 4 ♂♂ (5 paratypes) (FGIC); GOURMA, Fada N'Gourma, 300 m (12°3'5"N, 0°21'27"E), 14.vii.2006, F. & S. Génier (2006-35)—1 ♂ (paratype) (FGIC); KOMPIENGA, 15 km E Nadiagou, 155 m (11°4'31"N, 0°56'8"E), 22.viii.2005, F. Génier (2005-40)—1 ♂ (paratype) (FGIC); Kompienga, 160 m (11°5'5"N, 0°42'42"E), 21.viii.2005, F. Génier (2005-39)—2 ♂♂ (2 paratypes) (FGIC); Pama, 230 m (11°17'N, 0°42'59"E), 24.viii.2005, F. Génier (2005-44)—2 ♂♂ (2 paratypes) (FGIC); Pama, 230 m (11°17'N, 0°42'59"E), 25.viii.2005, F. Génier (2005-45)—1 ♂ (paratype) (FGIC); Pama, 230 m (11°17'N, 0°42'59"E), 26–27.viii.2005, F. Génier (2005-49)—2 ♂♂ (2 paratypes) (FGIC); LOROUM, Toulfé, 330 m (13°54'16"N, 1°54'19"W), 9.viii.2005, F. Génier (2005-08)—1 ♀, 2 ♂♂ (3 paratypes) (FGIC); Toulfé, 330 m (13°54'16"N, 1°54'19"W), 16.vii.2006, F. & S. Génier (2006-38)—1 ♀, 3 ♂♂ (4 paratypes) (FGIC); Toulfé, 330 m (13°54'16"N, 1°54'19"W), 16.vii.2006, F. & S. Génier (2006-40)—1 ♀, 1 ♂ (paratypes) (FGIC); Toulfé, 330 m (13°54'16"N, 1°54'19"W), 17.vii.2006, F. & S. Génier (2006-41)—22 ♀♀, 21 ♂♂ (holotype, allotype, 41 paratypes) (CMNC, FGIC); Toulfé, 330 m (13°54'16"N, 1°54'19"W), 18.vii.2006, F. & S. Génier (2006-42)—2 ♂♂ (2 paratypes) (FGIC); Toulfé, 330 m (13°54'16"N, 1°54'19"W), 18.vii.2006, F. & S. Génier (2006-43)—2 ♂♂ (2 paratypes) (FGIC); NAHOURI, Forêt de Nazinga, 275 m (11°9'24"N, 1°36'44"W), 20.vii.2006, F. & S. Génier (2006-46)—1 ♂ (paratype) (FGIC); Forêt de Nazinga, Akwazena, 275 m (11°9'24"N, 1°36'44"W), 26.vii.2006, F. & S. Génier (2006-76)—3 ♂♂ (3 paratypes) (FGIC); Forêt de Nazinga, Boulieselo, 310 m (11°11'50"N, 1°35'9"W), 27.vii.2006, F. & S. Génier (2006-82)—2 ♂♂ (2 paratypes) (FGIC); Forêt de Nazinga, Kouzougou, 285 m (11°9'17"N, 1°32'10"W), 21.vii.2006, F. & S. Génier (2006-47)—1 ♀, 4 ♂♂ (5 paratypes) (FGIC); Forêt de Nazinga, Naguio, 270 m (11°7'52"N, 1°34'38"W), 24.vii.2006, F. & S. Génier (2006-66)—1 ♂ (paratype) (FGIC); Tiakané, 320 m (11°11'37"N, 1°14'10"W), 20.viii.2005, F. Génier (2005-29)—2 ♀♀ (2 paratypes) (FGIC); PASSORÉ, 8 km SW Yako, 320 m (12°51'44"N, 2°18'35"W), 7.viii.2005, F. Génier (2005-03)—4 ♀♀, 2 ♂♂ (6 paratypes) (FGIC); 8 km S.O. Yako, 320 m (12°51'44"N, 2°18'35"W), 7.viii.2005, F. Génier (2005-04)—1 ♀ (paratype) (FGIC); 8 km S.O. Yako, 320 m (12°51'44"N, 2°18'35"W), 7.viii.2005, F. Génier (2005-02)—7 ♂♂ (7 paratypes) (FGIC); SANGUIÉ, Forêt de Sorobouli, 270 m (11°47'44"N, 2°53'25"W), 13.viii.2005, F. Génier (2005-14)—1 ♀, 1 ♂ (paratypes) (FGIC); Forêt de Sorobouli, 270 m (11°47'44"N, 2°53'25"W), 14.viii.2005, F. Génier (2005-18)—2 ♂♂ (2 paratypes) (FGIC); Forêt de Sorobouli, 270 m (11°47'44"N, 2°53'25"W), 15.viii.2005, F. Génier (2005-19)—2 ♀♀, 2 ♂♂ (4 paratypes) (FGIC); **CAMEROON**: EXTREME NORTH, Guétalé, Koza (10°53'N, 13°54'E), 13.vi.1967, [anonymous]—1 ♀ (paratype) (MNHN); Maroua (10°35'N, 14°19'E), vii.1989, D. Bernaud—3 ♀♀, 5 ♂♂ (8 paratypes) (CMD); Maroua (10°35'N, 14°19'E), vii.1979, G. Onore—2 ♀♀, 2 ♂♂ (4 paratypes) (PHWC); Maroua (10°35'N, 14°19'E), 5.vii.1978, [anonymous]—1 ♂ (paratype) (MNHN); Waza (11°24'N, 14°34'E), 18.viii.2006, C. Vanderbergh—4 ♀♀, 2 ♂♂ (6 paratypes) (PMOC); Waza National Park (11°15'N, 14°39'E), 18.viii.2006, C. Vanderbergh—3 ♀♀, 4 ♂♂ (7 paratypes) (PMOC); NORTH, Garoua (9°18'N, 13°24'E), x.1973, B. de Miré—1 ♀ (paratype) (MNHN); **CHAD**: HADJER-LAMIS, Sitje, rive sud Lac Tchad (12°53'N, 14°52'E), 11.viii.2006, C. Vanderbergh—1 ♂ (paratype) (PMOC); LOGONE ORIENTAL, Komé, 80 km Moundou (8°30'N, 16°41'E), vii.2002, T. Garnier—2 ♂♂ (2 paratypes) (PMOC); N'DJAMENA, Farcha (12°7'N, 14°59'E), 28.vi.1967, [anonymous]—4 ♀♀, 8 ♂♂ (12 paratypes) (MNHN); Fort Lamy [=N'Djamena_] (12°7'N, 15°3'E), [no date], M. André—3 ♀♀, 5 ♂♂ (8 paratypes) (PMOC); OUADAI, Massif de Kabla (13°25'N, 21°9'W), 5.viii.1949, P. de Miré—1 ♂ (paratype) (MNHN); **ERITREA**: ANSEBA, Hagaz (15°42'N, 38°16'E), vii.2003, M. Forti—1 ♀, 1 ♂ (paratypes) (PMOC); GASH-BARKA, 18 km E Akordat (15°33'N, 38°1'E), vii.2003, M. Forti—1 ♀, 1 ♂ (paratypes) (PMOC); Tesseney, 1200 m (15°6'36"N, 36°39'27"E), 30.viii.2001, L. & M. Stalmans—2 ♀♀, 4 ♂♂ (6 paratypes) (CADB, PMOC); NORTHERN RED SEA, Nefasit (15°20'N, 39°4'E), vii.2002, Czeppel & Forti—2 ♀♀, 5 ♂♂ (7 paratypes) (FETC); **ETHIOPIA**: AFAR, Yangudi Rassa National Park (10°33'N, 40°59'E), 9/2/2006, S. Rojkoff—1 ♀, 1 ♂ (paratypes) (CMD); **GAMBIA**: CENTRAL RIVER, Lower Saloum District, Ballangharr (13°39'N, 15°25'W), 23.viii.1997, D.J. Mann—2 ♀♀, 5 ♂♂ (7 paratypes) (OUMNH); **MALI**: KIDAL, Adrar des Ifoghas (19°32'N, 1°35'E), viii.1941, Volkonsky—2 ♂♂ (2 paratypes) (MNHN); Etambar, Kidal (18°26'N,

1°25'E), ix.1941, M. Volkoneky—1 ♀ (paratype) (MNHN); SEGOU, [Station centrale de] Kogoni (14°44'N, 6°2'W), 19.ix.1955, J.-G. Pointel—2 ♀♀, 1 ♂ (paratypes) (MNHN); [Station centrale de] Kogoni (14°44'N, 6°2'W), 7.x.1955, J.-G. Pointel—2 ♀♀ (2 paratypes) (MNHN); [Station centrale de] Kogoni (14°44'N, 6°2'W), 11.x.1955, J.-G. Pointel—1 ♂ (paratype) (MNHN); [Station centrale de] Kogoni (14°44'N, 6°2'W), 24.x.1955, J.-G. Pointel—1 ♀, 1 ♂ (paratypes) (MNHN); [Station centrale de] Kogoni (14°44'N, 6°2'W), 27.x.1955, J.-G. Pointel—1 ♂ (paratype) (MNHN); [Station centrale de] Kogoni (14°44'N, 6°2'W), 2.xi.1955, J.-G. Pointel—1 ♀, 2 ♂♂ (3 paratypes) (MNHN); [Station centrale de] Kogoni (14°44'N, 6°2'W), 21.ix.1959, J.-G. Pointel—1 ♂ (paratype) (MNHN); **MAURITANIA**: GUIDIMAKA, [unspecified locality] (15°22'N, 12°6'W), 1908, G. Audan—4 ♀♀, 7 ♂♂ (11 paratypes) (FGIC, MNHN); HODH EL GHARBI, Tamchekett (17°14'44"N, 10°40'11"W), x.1947, B. de Miré—1 ♂ (paratype) (MNHN); SÉLIBABY, Tachoot [=Tassota Barene] (15°26'N, 12°16'W), 20.x.1941, [anonymous]—1 ♀ (paratype) (OMOC); **NIGER**: AGADEZ, Agadez (16°58'N, 7°59'E), 20.viii.1989, [anonymous]—1 ♀, 1 ♂ (paratypes) (OMOC); DOSSO, Toudou (14°7'N, 3°54'E), 10.viii.1989, [anonymous]—1 ♀, 1 ♂ (paratypes) (OMOC); MARADI, Maradi (13°29'N, 7°6'E), [no date], J. Roggeman—2 ♂♂ (2 paratypes) (BMNH); TAHOUA, Entre Madaoua et Bouza (14°15'N, 6°0'E), 3.vii.1980, P. Leblanc—2 ♂♂ (2 paratypes) (FETC); TILLABERI, Koure (13°20'N, 2°35'E), 19–21.ix.2003, Josso, Juhel & Monfort—1 ♂ (paratype) (JFJC); **NIGERIA**: KANO, [unspecified locality] (11°59'47"N, 8°31'0"E), v.1952, W.E.S. Merrett—4 ♂♂ (4 paratypes) (BMNH); [unspecified locality] (11°59'47"N, 8°31'0"E), vii.1954, W.E.S. Merrett—2 ♂♂ (2 paratypes) (BMNH); [unspecified locality] (11°59'47"N, 8°31'0"E), v.1953, W.E.S. Merrett—4 ♂♂ (4 paratypes) (BMNH); [unspecified locality] (11°59'47"N, 8°31'0"E), vi.1953, W.E.S. Merrett—5 ♂♂ (5 paratypes) (BMNH); [unspecified locality] (11°59'47"N, 8°31'0"E), vi.1954, W.E.S. Merrett—1 ♂ (paratype) (BMNH); **OMAN**: MINTAQAT MASQAT, Mascat (23°36'48"N, 58°35'36"E), ix–x, Maindron—2 ♂♂ (2 paratypes) (BMNH); **SENEGAL**: DAKAR, Cité Gendarmerie, Keur Massar (14°45'51"N, 17°16'45"W), 29.viii.2012, I. de Dinechin—1 ♂ (paratype) (CMD); Dakar (14°46'N, 17°22'W), 1914, Chissadon—3 ♀♀, 4 ♂♂ (7 paratypes) (MNHN); Dakar (14°46'N, 17°22'W), 1902, Waterlot—1 ♂ (paratype) (MNHN); Entrée du parc Marine, Keur Massar, Dakar (14°47'11"N, 17°18'43"W), viii.2015, I. de Dinechin—1 ♀, 1 ♂ (paratypes) (CMD); Keur Ndiaye Lô (14°45'25"N, 17°14'11"W), ix.2013, Local collectors—1 ♂ (paratype) (CMD); Keur Ndiaye Lô (14°45'25"N, 17°14'11"W), 18.viii.2013, I. de Dinechin—1 ♂ (paratype) (CMD); Sebikotane (14°45'N, 17°8'W), viii.1971, A. Villiers—1 ♂ (paratype) (OMOC); DIOURBEL, Bambey (14°42'N, 16°28'W), 1945, J. Risbec—4 ♀♀, 5 ♂♂ (9 paratypes) (BMNH); Bambey (14°42'N, 16°28'W), viii.1939, J. Risbec—3 ♂♂ (3 paratypes) (BMNH); FATICK, Diouroup (14°21'N, 16°32'W), viii.2008, [anonymous]—1 ♀, 1 ♂ (paratypes) (OMOC); Diouroup (14°21'N, 16°32'W), 14–18.viii.2007, P. Moretto—11 ♀♀, 17 ♂♂ (28 paratypes) (FGIC, PMOC); Diouroup (14°21'N, 16°32'W), 19–20.xi.2009, P. Moretto—1 ♀, 1 ♂ (paratypes) (PMOC); KAFFRINE, Tamba (13°53'49"N, 15°15'33"W), 2.vii.1948, [anonymous]—1 ♀, 1 ♂ (paratypes) (CNC); KAOLAK, Missirah, 45 m (13°59'26"N, 15°7'4"W), 16.vii.2007, F. Génier (2007-01)—3 ♀♀, 9 ♂♂ (12 paratypes) (FGIC); Missirah, 45 m (13°59'26"N, 15°7'4"W), 17.vii.2007, F. Génier (2007-02)—2 ♂♂ (2 paratypes) (FGIC); Nioro du Rip (13°44'43"N, 15°46'23"W), 10–11.viii.2009, P. Moretto—1 ♀, 1 ♂ (paratypes) (PMOC); LOUGA, Linguère (15°24'N, 15°7'W), ix.1967, A. Descarpentries, T. Leye & A. Villiers—14 ♀♀, 9 ♂♂ (23 paratypes) (MNHN); Linguère (15°24'N, 15°7'W), 5–15.ix.1967, A. Descarpentries, T. Leye & A. Villiers—1 ♀, 1 ♂ (paratypes) (MNHN); Louga (15°37'N, 16°13'W), 1945, Risbec—1 ♂ (paratype) (MNHN); Ndam-Dam (15°36'22"N, 16°23'35"W), xi.1967, A. Descarpentries, T. Leye & A. Villiers—2 ♀♀, 5 ♂♂ (7 paratypes) (MNHN); SAINT-LOUIS, Commune de Saint-Louis, 7 m (16°4'34"N, 16°22'40"W), 27.viii.2009, F. Génier (2009-33)—1 ♀ (paratype) (FGIC); Commune de Saint-Louis, 7 m (16°4'34"N, 16°22'40"W), 27.viii.2009, P. Moretto—1 ♀ (paratype) (PMOC); Parc National des Oiseaux du Djoudj (16°24'N, 16°14'W), x.1996, [anonymous]—1 ♂ (paratype) (PSCW); Richard-Toll (16°28'N, 15°41'W), xi.1967, A. Descarpentries, T. Leye & A. Villiers—8 ♀♀, 10 ♂♂ (18 paratypes) (MNHN); Richard-Toll (16°28'N, 15°41'W), 28–31.viii.2009, F. Génier (2009-38)—4 ♀♀, 5 ♂♂ (9 paratypes) (FGIC); Richard-Toll (16°28'N, 15°41'W), 28–30.viii.2009, F. Génier (2009-40)—2 ♀♀, 2 ♂♂ (4 paratypes) (FGIC); Richard-Toll (16°28'N, 15°41'W), 28.viii.2009, F. Génier (2009-36)—1 ♂ (paratype) (FGIC); Richard-Toll (16°28'N, 15°41'W), 28.viii–1.ix.2009, P. Moretto—15 ♀♀, 15 ♂♂ (30 paratypes) (PMOC); Richard-Toll (16°28'N, 15°41'W), 30.viii.2009, F. Génier (2009-43)—1 ♀, 2 ♂♂ (3 paratypes) (FGIC); Richard-Toll (16°28'N, 15°41'W), 30.viii.2009, F. Génier (2009-44)—2 ♀♀, 5 ♂♂ (7 paratypes) (FGIC); Richard-Toll (16°28'N, 15°41'W), 31.viii.2009, F. Génier (2009-48)—2 ♀♀, 4 ♂♂ (6 paratypes) (FGIC); Richard-Toll (16°28'N, 15°41'W), 1.ix.2009, F. Génier (2009-49)—1 ♀, 2 ♂♂ (3 paratypes) (FGIC); Richard-Toll (16°28'N, 15°41'W), 1.ix.2009, F. Génier (2009-50)—2 ♀♀, 1 ♂

(paratypes) (FGIC, GWPC); TAMBACOUNDA, Botou, 52 m (13°48'16"N, 13°34'47"W), 11.vii.2008, P. Moretto—1 ♂ (paratype) (PMOC); Dienoun Diala (13°12'47"N, 13°6'44"W), 29.vii.1995, P. Moretto—1 ♂ (paratype) (PMOC); THIÈS, 4.5 km E Joal-Fadiouth, piste de Samba Dia, 11 m (14°11'3"N, 16°48'28"W), 9.viii.2007, F. Génier (2007-65)—2 ♂♂ (2 paratypes) (FGIC); 4.5 km E Joal-Fadiouth, piste de Samba Dia, 11 m (14°11'3"N, 16°48'28"W), 10.viii.2007, F. Génier & P. Moretto (2007-67)—6 ♀♀ (6 paratypes) (FGIC); 4.5 km E Joal-Fadiouth, piste de Samba Dia, 11 m (14°11'3"N, 16°48'28"W), 10.viii.2007, F. Génier (2007-68)—1 ♀, 1 ♂ (paratypes) (FGIC); Ngazobil (14°12'N, 16°52'W), viii.1971, A. Villiers—1 ♂ (paratype) (OMOC); Nianing, 8 m (14°19'N, 16°55'43"W), 8.viii.2007, F. Génier (2007-63)—2 ♀♀, 3 ♂♂ (5 paratypes) (FGIC); Nianing, 8 m (14°19'N, 16°55'43"W), 8–9.vii.2008, P. Moretto—2 ♂♂ (2 paratypes) (PMOC); **SUDAN**: GHARB DARFUR, Zalingei, 1021 m (12°54'N, 23°29'E), vii.1984, P. Ruse—1 ♀, 1 ♂ (paratypes) (BMNH); JANUB DARFUR, Buram (10°51'N, 25°9'E), viii.1984, P. Ruse—2 ♀♀, 1 ♂ (paratypes) (BMNH); KHARTOUM, Environs de Khartoum (15°35'N, 32°32'E), [no date], [anonymous]—1 ♀, 5 ♂♂ (6 paratypes) (MNHN); Khartoum (15°35'N, 32°32'E), [no date], [anonymous]—1 ♀, 2 ♂♂ (3 paratypes) (MNHN); SENNAR, Sennar (13°34'N, 33°34'E), [no date], Parreys—1 ♂ (paratype) (SMF).

Etymology. *Eucatta* is a noun indicative of the close relationship of this African species with the Oriental *D. catta*.

Natural history. Specimens with data mostly collected in disturbed area and pastures from southern Sahelian and Sudanese zone. This species is common at light traps (mercury vapor and ultraviolet light). Some specimens were collected in cow, donkey, elephant, and zebu (*Bos indices*) dung and pitfall traps baited with human dung, toad carcasses, and rumen content.

Digitonthophagus falciger species group

Diagnosis. A single species with FLP sclerite right preapical edge deeply notched, basal edge of emargination produced into a sickle-shape projection (Fig. 150); axial sclerite apical portion thong shape, longer than subaxial sclerite.

Digitonthophagus falciger Génier, new species

http://zoobank.org/urn:lsid:zoobank.org:act:84E0D6CA-8B72-407C-8012-024F76BCCBE0
(Figs. 12, 33–34, 60, 76, 97–98, 124, 150–152; Map 7)

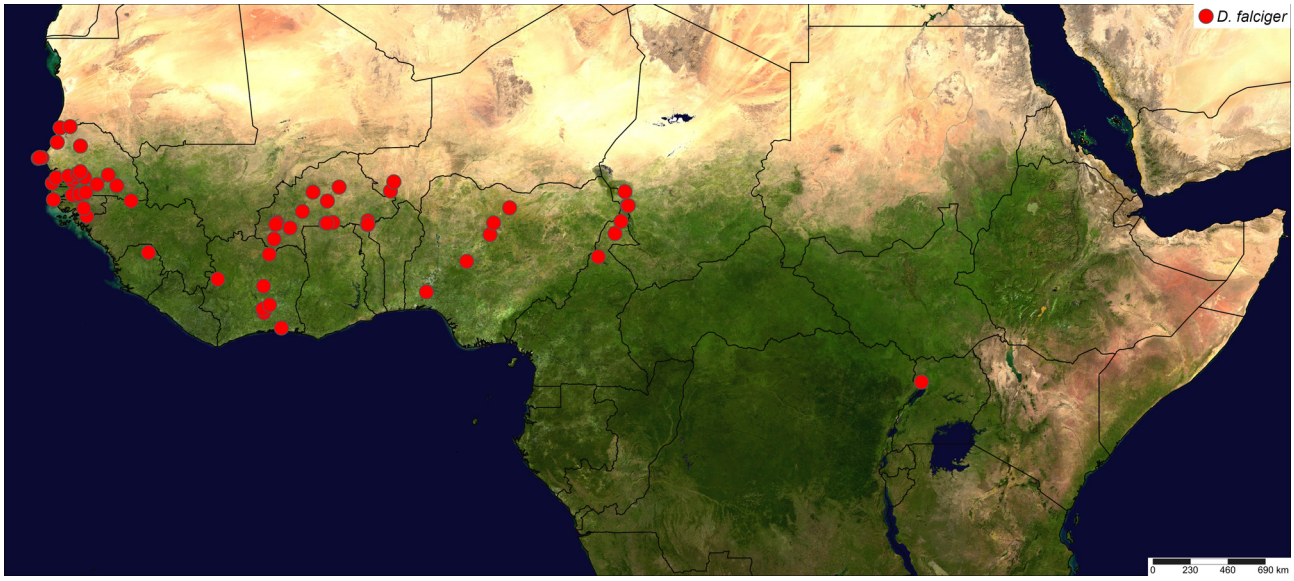
Type locality. Forêt de Boulon (10°16’27”N 04°27’15”W), 270 m, Comoé, Burkina Faso.

Description. Holotype ♂ (Fig. 12). **Measurements**. Length 11.0 mm, width 7.0 mm. **Head** (Figs. 33–34). Anterior clypeal edge straight on median fourth in dorsal view; clypeofrontal carina broadly arcuate and interrupted at gena. Vertex lacking median tubercle, surface with punctures fine to small, scabrous anteriorly, separated by one to four diameters. Horns moderately long, parallel on apical half in frontal view, gradually tapering from base to apex; posterointernal edge unmodified basally, apicointernal surface lacking granules; genal edge upturned and distinctly angulate on anterior third, forming a very broad angle with clypeal edge. **Pronotum** (Fig. 60). Surface with granulate punctures restricted to anterior half medially, with distinct, scattered, umbilicate punctures on posterior half of disc; punctures weaker but distinct posterolaterally, with more-or-less distinct, minute punctures throughout. Anteromedian tubercle atrophied, simply round in lateral view, median longitudinal sulcus well defined; surface behind the eyes with a simple, round depression, surface of anterior angles flat; anterior half of lateral edge arcuate in dorsal and lateral view; posterior angles simply arcuate in dorsal view. Anterior hypomeral ridge arcuate anteriorly, nearly straight posteriorly, anterior hypomeral depression surface slightly darker in color medially. **Elytra**. (Fig. 12). Intervals 2 and 4 with few scattered fine granules from base to apex. **Legs**. Protibial apicointernal tooth enlarged, with dorsal ridge extending to apex. **Aedeagus** (Fig. 124). Parameres with dorsal and ventral edges slightly diverging toward apex in lateral view. **Internal sac sclerites** (Figs. 150–152). Axial sclerite weekly sclerotized, as long as subaxial sclerite and almost straight. Subaxial sclerite, more-or-less even in width, extending straight and interrupted before apex of frontolateral peripheral sclerite apical portion, with short to long villi on apical sixth. Frontolateral peripheral sclerite basoventral apophysis moderately developed; with a spiniform medioventral carina; right lateral fold produced into a bifurcate

process apically; left lateral lobe moderately sclerotized and developed; subapicodorsal lobe membranous, small, not reaching anterior edge, apex set on right side in dorsal view; right preapical edge deeply notched, basal edge of emargination produced into a sickle-shape projection; apex of apical lobe round apically, narrow and directed at right angle on the left side, apical villi regular in shape; subapicoventral lobe large, round, and interrupted in line with apical lobe.

Variation. Measurements (117 ♂♂, 123 ♀♀). Length: male 7.5–11.5 mm (9.9 ± 1.0 mm), female 7.5–12.0 mm (10.0 ± 0.8 mm). Female allotype. Cephalic outline in dorsal view as in Fig. 76; vertex with a broadly arcuate and slightly sinuous medially transverse carina, dorsal edge slightly sinuous in frontal view (Fig. 97), lateral portion subangular and sloping down posteriorly; anterior pronotal tubercles well developed, external lateral edges nearly straight and slightly widening toward apex in dorsal view (Fig. 98), anterolateral surface obliquely concave, anterosuperior edge slightly arcuate in dorsal view, lateral portion of anterosuperior edge slightly upturned. Protibia short, with external teeth robust.

Primary type data. Holotype ♂ (CMNC): [BURKINA FASO: LORUM / Forêt de Boulon, 270m / 10°16'27"N 004°27'15"O / 6.VII.2006, zone soudanienne / savane boisée, piège lumineux / F. & S. Génier, 2006-05]; [COLÉOPTÈRES / DU / BURKINA FASO / BF015489] barcode label; [HOLOTYPE ♂ / *Digitonthophagus* / *falciger n.sp.* / des. F. Génier, 2016] red card.



MAP 7. Distribution of *Digitonthophagus falciger*.

Material examined (292 ♂♂, 159 ♀♀), distribution (Map 7): **BENIN**: MONO, Agoué (6°15'N, 1°41'E), vii–ix.1878, Abbé Ménager—2 ♀♀, 2 ♂♂ (4 paratypes) (FGIC, MNHN); Agoué (6°15'N, 1°41'E), 1879, Abbé Ménager—4 ♀♀, 18 ♂♂ (22 paratypes) (FGIC, MNHN); **BURKINA FASO**: CENTRE, Ouagadougou (12°22'N, 1°31'W), viii.1977, P. Ardoin—1 ♂ (paratype) (FETC); Ouagadougou (12°22'N, 1°31'W), 1977, J. Remy—1 ♂ (paratype) (PMOC); CENTRE-NORD, 19 km N Kaya, 314 m (13°8'46.2"N, 0°52'42.1"W), 16.viii.2012, P. Moretto—1 ♂ (paratype) (PMOC); CENTRE-OUEST, Forêt de Sorobouli [=Forêt Classée de Baporo], 270 m (11°47'44"N, 2°53'25"W), 10–15.viii.2005, P. Moretto—6 ♀♀, 3 ♂♂ (9 paratypes) (PMOC); CENTRE-SUD, Réserve de Nazinga (11°9'N, 1°36'W), 9–12.vi.2005, S. Rojkoff—1 ♂ (paratype) (PCSR); EST, Kompienga (11°4'26"N, 0°42'8"E), 3–24.ix.1988, F. Génier & M. Sanborne—19 ♀♀, 47 ♂♂ (66 paratypes) (CMNC); Kompienga, 20 km S Pama (11°4'37"N, 0°40'50"E), 1–16.vi.1988, Sanborne, Landry & Tou—2 ♀♀ (2 paratypes) (CMNC); Kompienga, 20 km S Pama (11°4'37"N, 0°40'50"E), 3–24.ix.1988, F. Génier & M. Sanborne—2 ♀♀, 2 ♂♂ (4 paratypes) (BDGC); HAUTS-BASSINS, Bobo-Dioulasso (11°12'N, 4°18'W), 11.i.1975, H. Pollitzar—1 ♂ (paratype) (BMNH); Bobo-Dioulasso (11°12'N, 4°18'W), 14.xi.1976, R.H. Gooding—3 ♂♂ (3 paratypes) (CMNC); Matourkou (11°5'N, 4°22'W), 15.vi.2005, S. Rojkoff—1 ♂ (paratype) (PMOC); NORD, 8 km SW Yako, Passoré, 320 m (12°51'44"N, 2°18'35"W), 7.viii.2005, P. Moretto—1 ♂ (paratype) (PMOC); SUD-OUEST, Bondigui, 324 m (10°53'56.5"N, 3°34'15"W), v.2012, F. Rousset—1 ♂ (paratype) (PMOC); Bondigui, 324 m (10°53'56.5"N, 3°34'15"W), 20.viii.2012, P. Moretto—2 ♀♀, 1 ♂ (paratypes) (PMOC); Gaoua (10°19'N, 3°10'W),

1924, H. Labouret—1 ♂ (paratype) (MNHN); COMOÉ, Forêt de Boulon (savane boisée), 270 m (10°16'27"N, 4°27'15"W), 6.vii.2006, F. & S. Génier (2006-05)—1 ♀, 1 ♂ (holotype, allotype) (CMNC); Forêt de Boulon (savane boisée), 270 m (10°16'27"N, 4°27'15"W), 9.vii.2006, F. & S. Génier (2006-17)—2 ♂♂ (2 paratypes) (FGIC); Forêt de Boulon (savane boisée), 270 m (10°16'27"N, 4°27'15"W), 10.vii.2006, F. & S. Génier (2006-24)—1 ♂ (paratype) (FGIC); KOMPIENGA, Kompienga, 160 m (11°5'5"N, 0°42'42"E), 21.viii.2005, F. Génier (2005-39)—2 ♀♀, 5 ♂♂ (7 paratypes) (FGIC); Pama, 230 m (11°17'N, 0°42'59"E), 24.viii.2005, F. Génier (2005-44)—1 ♂ (paratype) (FGIC); NAHOURI, Forêt de Nazinga, Kouzougou, 285 m (11°9'17"N, 1°32'10"W), 21.vii.2006, F. & S. Génier (2006-47)—1 ♂ (paratype) (FGIC); Forêt de Nazinga, Kouzougou, 285 m (11°9'17"N, 1°32'10"W), 25.vii.2006, F. & S. Génier (2006-70)—1 ♂ (paratype) (FGIC); Tiakané, 340 m (11°11'3"N, 1°12'28"W), 18.viii.2005, F. Génier (2005-23)—1 ♀, 3 ♂♂ (4 paratypes) (FGIC); Tiakané, 340 m (11°11'3"N, 1°12'28"W), 20.viii.2005, F. Génier (2005-34)—1 ♂ (paratype) (FGIC); Tiakané, 340 m (11°11'3"N, 1°12'28"W), 24.vii.2006, F. & S. Génier (2006-64)—1 ♂ (paratype) (FGIC); **CAMEROON**: EXTREME NORTH, Maroua (10°35'N, 14°19'E), vii.1979, G. Onore—1 ♀, 2 ♂♂ (3 paratypes) (PHWC); Waza National Park (11°15'N, 14°39'E), 18.viii.2006, C. Vanderbergh—2 ♂♂ (2 paratypes) (PMOC); NORTH, Garoua (9°18'N, 13°24'E), x.1973, B. de Miré—1 ♀, 2 ♂♂ (3 paratypes) (MNHN); Garoua (9°18'N, 13°24'E), [no date], [anonymous]—1 ♀, 1 ♂ (paratypes) (OMOC); **CHAD**: HADJER-LAMIS, Sitje, rive sud Lac Tchad (12°53'N, 14°52'E), 11.viii.2006, C. Vanderbergh—1 ♀, 1 ♂ (paratypes) (PMOC); N'DJAMENA, Farcha (12°7'N, 14°59'E), vi.1968, [anonymous]—1 ♀, 2 ♂♂ (3 paratypes) (MNHN); Farcha (12°7'N, 14°59'E), 28.vi.1967, [anonymous]—1 ♀, 1 ♂ (paratypes) (MNHN); Fort Lamy [=N'Djamena_] (12°7'N, 15°3'E), [no date], M. André—1 ♀ (paratype) (PMOC); Fort Lamy [=N'Djamena_] (12°7'N, 15°3'E), 17.vii.1958, J. Mateu—2 ♂♂ (2 paratypes) (FETC); **CÔTE D'IVOIRE**: BAFING, Ranch de Dolla, Biémasso (8°4'N, 7°33'W), 1–5.vi.2000, P. Moretto—2 ♀♀, 14 ♂♂ (16 paratypes) (PMOC); LACS, Bringakro near (6°25'53"N, 5°4'32"W), 12.vi.2003–13.vi.2006, Newman *et al*.—2 ♀♀, 3 ♂♂ (5 paratypes) (BMNH); Bringakro near (6°25'53"N, 5°4'32"W), 13.vi.2003, Newman *et al*.—2 ♀♀, 4 ♂♂ (6 paratypes) (BMNH); Bringakro near (6°25'53"N, 5°4'32"W), 17.vi.2003, Newman *et al*.—1 ♂ (paratype) (BMNH); LAGUNES, 5 km Lamto (6°13'N, 5°1'W), viii.1968, C. Girard—2 ♀♀, 3 ♂♂ (5 paratypes) (MNHN); Forêt du Banco (5°23'N, 4°3'W), ii.1989, [anonymous]—1 ♂ (paratype) (CEMT); NZI-COMOE, Dimbroko (6°39'N, 4°42'W), [no date], [anonymous]—1 ♂ (paratype) (IRSNB); SAVANES, Koko, Korhogo (9°26'1"N, 4°43'9"W), 24–25.vi.2000, P. Moretto—1 ♂ (paratype) (PMOC); VALLÉE DU BANDAMA, Bouaké (7°41'N, 5°2'W), iii.1976, R. Couilloud—2 ♀♀, 1 ♂ (paratypes) (PMOC); Bouaké (7°41'N, 5°2'W), iv.1976, R. Couilloud—2 ♀♀, 7 ♂♂ (9 paratypes) (PMOC); Bouaké (7°41'N, 5°2'W), 13.vii.1977, [anonymous]—1 ♀ (paratype) (PMOC); **GAMBIA**: CENTRAL RIVER, Lower Saloum District, Ballangharr (13°39'N, 15°25'W), 23.viii.1997, D.J. Mann—7 ♀♀, 7 ♂♂ (14 paratypes) (OUMNH); Naini District, Kuntaur Agricultural Station (13°40'N, 14°53'W), 9.ix.1997, D.J. Mann—1 ♂ (paratype) (OUMNH); LOWER RIVER, Jarra West District, Jenoi DEC (13°28'51"N, 15°33'43"W), 29.viii.1997, Mann & Woodcock—2 ♀♀, 2 ♂♂ (4 paratypes) (OUMNH); UPPER RIVER, Bassa Government Rest Home, Mansanjang Kunda (13°16'53"N, 14°12'13"W), 26.viii.1997, D.J. Mann & B. Woodcock—1 ♂ (paratype) (OUMNH); WEST COAST, Kombo District, Yundum Agricultural Station (13°21'43"N, 16°39'43"W), vii.1997, D.J. Mann—1 ♂ (paratype) (OUMNH); Kombo District, Yundum Agricultural Station (13°21'43"N, 16°39'43"W), 19.viii.1997, D.J. Mann & B.A. Woodcock—2 ♂♂ (2 paratypes) (OUMNH); **GHANA**: "Danish Guinea", [no date], P. E. Isert—1 ♀, 1 ♂ (paratypes) (ZMUC); **GUINEA**: BOFFA, Rio Pongo (10°10'N, 14°2'W), 1883–1884, P. Lutz—1 ♂ (paratype) (MNHN); **GUINEA-BISSAU**: BAFATÁ, Chime [= Xime], Rio Géba (11°58'N, 14°56'W), 1906, G. Favarel—2 ♀♀, 2 ♂♂ (4 paratypes) (MNHN); TOMBALI, Quebo (11°32'N, 14°46'W), 25.vi–17.vii.1995, A. Serrano—1 ♂ (paratype) (CEMT); **MAURITANIA**: GUIDIMAKA, [unspecified locality] (15°22'N, 12°6'W), 1908, G. Audan—1 ♀, 8 ♂♂ (9 paratypes) (FGIC, MNHN); **NIGER**: NIAMEY, Gorou Kirey (13°25'34"N, 2°8'32"E), 22.i.1976, [anonymous]—1 ♂ (paratype) (PHWC); TILLABERI, Kolo (12°55'22"N, 1°57'24"E), 15.iii.1972, D. Rougon—1 ♂ (paratype) (PHWC); **NIGERIA**: KADUNA, Kaduna (10°31'23"N, 7°26'25"E), 4.v.1962, D.C. Eidt—1 ♂ (paratype) (CNC); Samaru (11°10'N, 7°38'E), 18–25.v.1970, P.H. Ward—1 ♀, 3 ♂♂ (4 paratypes) (BMNH); Samaru (11°10'N, 7°38'E), 15–22.vi.1970, P.H. Ward—1 ♂ (paratype) (BMNH); KANO, [unspecified locality] (11°59'47"N, 8°31'0"E), v.1952, W.E.S. Merrett—1 ♂ (paratype) (BMNH); [unspecified locality] (11°59'47"N, 8°31'0"E), xi.1951, W.E.S. Merrett—1 ♂ (paratype) (BMNH); [unspecified locality] (11°59'47"N, 8°31'0"E), v.1953, W.E.S. Merrett—1 ♂ (paratype) (BMNH); [unspecified locality] (11°59'47"N, 8°31'0"E), vi.1954, W.E.S. Merrett—1 ♂ (paratype) (BMNH); NIGER, Badeggi (9°3'N, 6°9'E), 19.iii.1972, E.W. Classey—1 ♂ (paratype) (BMNH); OYO,

Ibadan (7°22'N, 3°56'E), 2.iv.1957, J.L. Gregory—1 ♀, 1 ♂ (paratypes) (BMNH); **SENEGAL**: DAKAR, Dakar (14°46'N, 17°22'W), 1939, P. Lepesme, R. Paulian, & A. Villiers—1 ♂ (paratype) (MNHN); Hann (14°43'14"N, 17°26'12"W), 1939, P. Lepesme, R. Paulian, & A. Villiers—15 ♀♀, 15 ♂♂ (30 paratypes) (MNHN); Keur Ndiaye Lô (14°45'25"N, 17°14'11"W), 18.viii.2013, I. de Dinechin—1 ♂ (paratype) (CMD); FATICK, Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 22.vi.2009, A. Coache—1 ♀, 3 ♂♂ (4 paratypes) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 23.vi.2009, A. Coache—2 ♀♀, 3 ♂♂ (5 paratypes) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 24.vi.2009, A. Coache—3 ♂♂ (3 paratypes) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 16.x.2009, A. Coache—1 ♂ (paratype) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 28.xi.2009, A. Coache—1 ♀ (paratype) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 20.iv.2010, A. Coache—1 ♂ (paratype) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 15.vii.2010, A. Coache—1 ♀, 1 ♂ (paratypes) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 22.vii.2010, A. Coache—1 ♂ (paratype) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 13.viii.2010, A. Coache—1 ♀, 1 ♂ (paratypes) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 14.viii.2010, A. Coache—2 ♀♀ (2 paratypes) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 15.viii.2010, A. Coache—1 ♂ (paratype) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 16.viii.2010, A. Coache—1 ♂ (paratype) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 17.viii.2010, A. Coache—2 ♂♂ (2 paratypes) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 21.ix.2010, A. Coache—1 ♀, 3 ♂♂ (4 paratypes) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 22.ix.2010, A. Coache—1 ♀ (paratype) (CAC); KAFFRINE, Tamba (13°53'49"N, 15°15'33"W), 2.vii.1948, [anonymous]—2 ♂♂ (2 paratypes) (CMNC, CNC); KAOLAK, Missirah, 45 m (13°59'26"N, 15°7'4"W), 16.vii.2007, F. Génier (2007-01)—2 ♂♂ (2 paratypes) (FGIC); Missirah, 45 m (13°59'26"N, 15°7'4"W), 17.vii.2007, F. Génier (2007-03)—1 ♂ (paratype) (FGIC); Nioro du Rip (13°44'43"N, 15°46'23"W), 3.viii.2008, P. Moretto—1 ♂ (paratype) (PMOC); Nioro du Rip (13°44'43"N, 15°46'23"W), 10–11.viii.2009, P. Moretto—1 ♀, 1 ♂ (paratypes) (PMOC); KÉDOUGOU, Dinndefelou (12°22'43"N, 12°19'30"W), 13–14.vii.2008, P. Moretto—1 ♂ (paratype) (PMOC); KOLDA, Forêt de Bakor, Mahon (12°51'N, 14°49'W), 31.vii–2.viii.2008, P. Moretto—1 ♂ (paratype) (PMOC); Mahon (12°51'22"N, 14°48'42"W), 22–23.xi.2009, P. Moretto—2 ♀♀, 3 ♂♂ (5 paratypes) (PMOC); Sare Gnako, 31 m (12°44'16"N, 15°9'56"W), 31.vii.2007, F. Génier & P. Moretto (2007-49)—2 ♂♂ (2 paratypes) (FGIC); Sothoto, 23 m (12°39'55"N, 15°24'3"W), 31.vii.2007, Génier & Moretto (2007-47)—2 ♂♂ (2 paratypes) (FGIC); LOUGA, Linguère (15°24'N, 15°7'W), ix.1967, A. Descarpentries, T. Leye, & A. Villiers—10 ♀♀, 6 ♂♂ (16 paratypes) (MNHN); Ndam-Dam (15°36'22"N, 16°23'35"W), xi.1967, A. Descarpentries, T. Leye, & A. Villiers—4 ♀♀, 1 ♂ (paratypes) (MNHN); SAINT-LOUIS, Parc National des Oiseaux du Djoudj (16°24'N, 16°14'W), x.1996, [anonymous]—1 ♀, 3 ♂♂ (4 paratypes) (PSCW); Richard-Toll (16°28'N, 15°41'W), xi.1967, A. Descarpentries, T. Leye & A. Villiers—30 ♀♀, 23 ♂♂ (53 paratypes) (MNHN); SEDHIOU, Sedhiou (12°42'N, 15°34'W), [no date], [anonymous]—1 ♂ (paratype) (MNHN); Sedhiou (12°42'N, 15°34'W), 14.vii.1947, [anonymous]—1 ♂ (paratype) (MNHN); TAMBACOUNDA, Boutou, 52 m (13°48'16"N, 13°34'47"W), 20.vii.2007, F. Génier (2007-06)—1 ♂ (paratype) (FGIC); Dienoun Diala (13°12'47"N, 13°6'44"W), 29.vii.1995, P. Moretto—8 ♀♀, 4 ♂♂ (12 paratypes) (PMOC); ZIGUINCHOR, Boukitimgo, 18 m (12°26'41"N, 16°35'53"W), 4.viii.2007, F. Génier (2007-56)—1 ♂ (paratype) (FGIC); Boukitimgo, 18 m (12°26'41"N, 16°35'53"W), 4.viii.2007, P. Moretto & F. Génier (2007-58)—1 ♂ (paratype) (FGIC); **SIERRA LEONE**: NORTHERN, Koinadugu (9°32'9"N, 11°22'6"W), 23.v.1963, Mission ENS-IFAN aux Monts Loma—1 ♀, 4 ♂♂ (5 paratypes) (MNHN); **UGANDA**: Nebbi District, Pamora, Padyere subcounty (2°24'25"N, 31°11'40"E), v.2006, Local collectors—1 ♀, 1 ♂ (paratypes) (PMOC).

Etymology. *Falciger* (sickle + bear) is a Latin adjective in apposition referring to the distinctive configuration of the left edge of the frontolateral peripheral sclerite of this species.

Natural history. The few specimens with data were collected from savanna, disturbed areas, and pastures in soudanian zone and from degraded Guinean Forest. Attracted to mercury vapor and ultraviolet light, some specimens were collected using pitfall traps baited with human or western red colobus (*Procolobus badius*) dung, some specimens retrieved from cow, donkey, elephant, rhinoceros, zebra, and zebu dung.

Remarks. The Ugandan record based on two specimens need confirmation.

Digitonthophagus gazella species group

Diagnosis. Subapicoventral lobe of FLP sclerite round apically (Figs. 155, 158, 161, 164); right lateral fold of FLP sclerite apical portion more-or-less spoon shape (Figs. 153, 156, 159, 162).

Digitonthophagus biflagellatus Génier, new species

http://zoobank.org/urn:lsid:zoobank.org:act:C93B1EB9-87CE-4E82-9017-F6D5D946DDFB
(Figs. 13, 35–36, 61, 77, 99–100, 125, 153–155; Map 6)

Type locality. Lake Ndutu area (02°59'S 35°01'E), Serengeti National Park, Shinyanga, Tanzania.

Diagnosis. Axial sclerite as long as or longer than subaxial sclerite (Fig. 153).

Description. Holotype ♂ (Fig. 13). **Measurements**. Length 11.0 mm, width 6.5 mm. **Head** (Figs. 35–36). Anterior clypeal edge straight on median fifth in dorsal view; clypeofrontal carina broadly arcuate and interrupted at gena. Vertex lacking median tubercle, surface with punctures fine to small, separated by one to four diameters. Horns rather short, slightly divergent in frontal view, gradually tapering from base to apex; posterointernal edge unmodified basally, apicointernal surface lacking granules; genal edge upturned and distinctly angulate on anterior third, forming a broad angle with clypeal edge. **Pronotum** (Fig. 61). Surface with granulate punctures restricted to anterior half medially, with distinct scattered umbilicate punctures on posterior half of disc; punctures weaker but distinct posterolaterally, with more-or-less distinct, minute punctures throughout. Anteromedian tubercle atrophied, simply round in lateral view, median longitudinal sulcus well defined; surface behind the eyes with a simple, round depression, surface of anterior angles convex; anterior half of lateral edge arcuate in dorsal and lateral view; posterior angles simply arcuate in dorsal view. Anterior hypomeral ridge arcuate, anterior hypomeral depression surface slightly darker in color medially. **Elytra** (Fig. 13). Intervals 2 and 4 lacking fine granules from base to apex. **Legs**. Protibial apicointernal tooth enlarged, with dorsal ridge extending to apex. **Aedeagus** (Fig. 125). Parameres with dorsal and ventral edges slightly diverging toward apex in lateral view. **Internal sac sclerites** (Figs. 153–155)**.** Axial sclerite weekly sclerotized, longer than subaxial sclerite, and almost straight. Subaxial sclerite, large basally, and abruptly reduced, extending straight and interrupted before apex of frontolateral peripheral sclerite apical portion, with fine and scattered villi on apical 10th. Frontolateral peripheral sclerite basoventral apophysis moderately developed; lacking medioventral carinae; right lateral fold produced into a rather large everted and open apically conical process, apical edge deeply emarginate externally and open internally, appearing tong shaped; left lateral lobe absent; subapicodorsal lobe membranous, not reaching anterior edge, apex set on right side in dorsal view; apical lobe round apically, narrow and directed obliquely on left side, apical villi regular in shape; subapicoventral lobe large, round and interrupted in line with apical lobe apically.

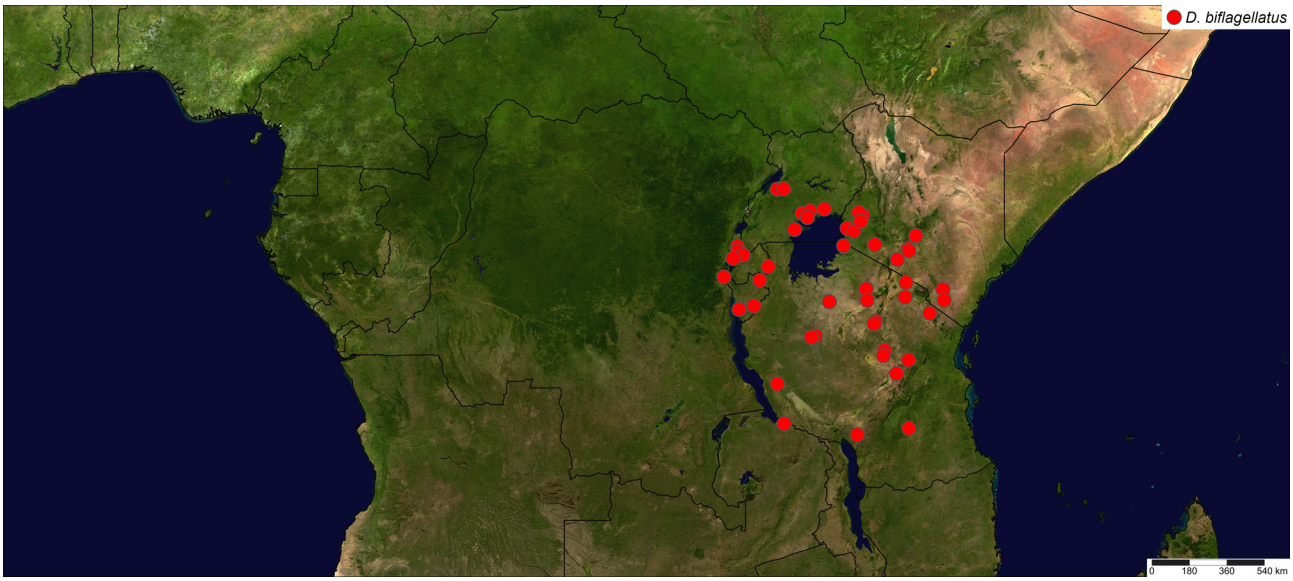
Variation. Measurements (94 ♂♂, 69 ♀♀). Length: male 7.5–11.5 mm (9.8 ± 0.9 mm), female 8.0–12.0 mm (9.8 ± 0.7 mm). Female allotype. Cephalic outline in dorsal view as in Fig. 77; vertex with a slightly sinuate, transverse carina, dorsal edge broadly arcuate in frontal view, lateral portion gradually sloping down posteriorly; anterior pronotal tubercles moderately developed, external lateral edges widening toward apex, anterolateral surface simply convex, anterosuperior edge slightly arcuate in dorsal view (Fig. 99), lateral portion of anterosuperior edge distinctly upturned (Fig. 100). Protibia short, with external teeth more robust.

Primary type data. Holotype ♂ (OUMNH): [18 /05 /91 / L. Ndutu area, / Serengeti National Park / Tanzania, 35°1'E 2°59'S / dung-baited pitfall trap / R. Foster O.U.M. 2-1993] partly handwritten; [WORLD / SCARAB. / DATABASE / WSD00030055] barcode label; HOLOTYPE ♂ / *Digitonthophagus* / *biflagellatus n.sp.* / des. F. Génier, 2016] red card.

Material examined (135 ♂♂, 82 ♀♀), distribution (Map 8): **BURUNDI**: [unspecified locality], [no date], R.P. Giraudin—1 ♀, 4 ♂♂ (5 paratypes) (MNHN); BURURI, Bururi (3°54'S, 29°31'E), [no date], R.P. Giraudin—1 ♀, 1 ♂ (paratypes) (MNHN); Muyinga, Colline Kobero (2°38'59"S, 30°24'48"E), 10.ix.1940, H.-J. Brédo—1 ♂ (paratype) (IRSNB); RUTANA, 03°45'S 30°10'E, 2000 m (3°45'S, 30°10'E), iii.1968, R.P. Giraudin—1 ♀, 1 ♂ (paratypes) (OMOC); Mpinga (3°45'S, 30°10'E), [no date], R.P. Giraudin—1 ♂ (paratype) (MNHN); **DEMOCRATIC REPUBLIC OF THE CONGO**: NORTH-KIVU, Parc National Rwindi [=SE Parc National Virunga] (1°23'S, 29°28'E), 26.iii.1979, [anonymous]—1 ♂ (paratype) (PHWC); Rutshuru (1°11'S, 29°27'E), 1927, G. Babault—2 ♀♀, 1 ♂ (paratypes) (MNHN); SOUTH-KIVU, Bukavu (2°30'S, 28°52'E), 30.i.1952, C.

Verbeke—3 ♂♂ (3 paratypes) (IRSNB); **KENYA**: HOMA BAY, Baie de Kavirondo, Lac Victoria (0°31'S, 34°29'E), ix–x.1903, C. Alluaud—2 ♂♂ (2 paratypes) (MNHN); Baie de Kavirondo, Lac Victoria (0°31'S, 34°29'E), xii.1911, Alluaud & Jeannel—1 ♂ (paratype) (MNHN); Ile de Lusinga [= Rusinga], Victoria-Nyanza N.-E. (0°24'S, 34°11'E), x.1903, C. Alluaud—1 ♂ (paratype) (IRSNB); KAJIADO, 60 km SW Nairobi, 1200 m (1°45'S, 36°21'E), 23.xii.1990, B.D. Gill—2 ♀♀, 1 ♂ (paratypes) (BDGC); KAKAMEGA, Ilala, 14 mi. E Mumias, 1372 m (0°17'N, 34°41'E), 18–21.vi.1911, S.A. Neave—1 ♂ (paratype) (BMNH); KISUMU, Kisumu (0°6'S, 34°46'E), [no date], P.S. Corbet—2 ♀♀, 4 ♂♂ (6 paratypes) (BMNH); MURANG'A, Fort Hall [=Muranga Town] (0°43'S, 37°9'E), i.1912, Alluaud & Jeannel—1 ♂ (paratype) (MNHN); NAIROBI, Nairobi (1°17'S, 36°49'E), 24.iv.1957, [anonymous]—2 ♀♀, 2 ♂♂ (4 paratypes) (BMNH); Nairobi National Park (1°22'S, 36°51'E), iv.1993, W. Hoek—1 ♂ (paratype) (CEMT); NANDI, Kamililo, vi.1903, F.J. Jackson—1 ♂ (paratype) (BMNH); NAROK, Lemek Valey (1°6'S, 35°23'E), ii.1913, G.B.—6 ♀♀, 8 ♂♂ (14 paratypes) (FGIC, MNHN); TAITA TAVETA, Bura (3°2'S, 38°19'E), i–iv.1904, C. Alluaud—5 ♂♂ (5 paratypes) (IRSNB, MNHN); Mwatate (3°30'S, 38°22'E), i–iv.1904, C. Alluaud—1 ♀, 3 ♂♂ (4 paratypes) (IRSNB, MNHN); Mwatate, 25 km SW Voi (3°30'S, 38°22'E), 26.xii.1990, B.D. Gill—2 ♀♀, 2 ♂♂ (4 paratypes) (BDGC); VIHIGA, Forêt de Kakamegoes [=Kakamega], Environs de Kaimosi, Mont-Elgon, 2000 m (0°10'N, 34°52'E), 1913, G. Babault—6 ♂♂ (6 paratypes) (FGIC, MNHN); **RWANDA**: EASTERN, Ranch Mpanga (2°3'13"S, 30°47'0"E), iii.1987, [anonymous]—2 ♀♀, 3 ♂♂ (5 paratypes) (PSCW); NORTHERN, Bugarula District, [unspecified locality] (1°33'S, 29°42'E), 21.viii.1941, H.-J. Brédo—2 ♀♀, 3 ♂♂ (5 paratypes) (IRSNB); WESTERN, Rwaza (1°42'S, 29°16'E), 1927, G. Babault—2 ♂♂ (2 paratypes) (MNHN); **TANZANIA**: Lake Rukwa, iv.1945, H.-J. Brédo—1 ♀, 2 ♂♂ (3 paratypes) (FGIC, IRSNB); Lake Rukwa, xii.1948, H.-J. Brédo—1 ♀, 3 ♂♂ (4 paratypes) (IRSNB); ARUSHA, Arusha environs (3°22'S, 36°41'E), 3–4.iv.1997, M. Kuboň—5 ♀♀, 1 ♂ (paratypes) (PMOC); Karatu Ndutu Safari Lodge, Serengeti (3°1'S, 35°0'E), 15.xi.1990, R. Foster—1 ♂ (paratype) (BDGC); Mumba Hills (3°30'S, 35°3'E), 8.iii.1938, Dr. S.G. Kohl-Larsen—1 ♀ (paratype) (SMF); Mumba Hills (3°30'S, 35°3'E), 23.iii.1938, Dr. S.G. Kohl-Larsen—1 ♂ (paratype) (SMF); Mumba Hills (3°30'S, 35°3'E), 24.iii.1938, Dr. S.G. Kohl-Larsen—1 ♂ (paratype) (SMF); Orekeryan, Mount Longido (2°43'47"S, 36°43'26"E), 8.vi–9.viii.2012, Smith, Takano & Garner—1 ♂ (paratype) (BMNH); DODOMA, 40 km N Dodoma, 1100 m (5°54'S, 35°45'E), 15.xii.2007, F. Kantner—5 ♀♀, 3 ♂♂ (8 paratypes) (SMNS); 70 km N Dodoma, 1330 m (5°40'S, 35°48'E), 17.xii.2006, F. Kantner—1 ♂ (paratype) (SMNS); Lulanguru, 17 mi. W Tabora, 1148 m (5°6'S, 32°38'E), x–xii.1917, G.D.H. Carpenter—1 ♀, 1 ♂ (paratypes) (BMNH); Tosamaganga, near Iringa (6°40'S, 36°19'E), [no date], W. Ruddock—1 ♂ (paratype) (BMNH); IRINGA, Magema, Ulembwe Village, 2048 m (9°18.389'S, 34°37.213'E), 7.i.2011, P. Darge—1 ♂ (paratype) (MHNL); KILIMANDJARO, Same (4°4'S, 37°45'E), v.1962, [anonymous]—2 ♂♂ (2 paratypes) (CNC); Zone inférieure, Kilimandjaro, i–iv.1904, C. Alluaud—1 ♀, 3 ♂♂ (4 paratypes) (MNHN); MANYARA, 100 km NNE Singida, 1650 m (4°31'S, 35°21'E), 20.xii.2006, F. Kantner—5 ♀♀, 2 ♂♂ (7 paratypes) (SMNS); Giting, Mount Hanang, 1964 m (4°24'14"S, 35°24'56"E), 22–26.xi.2011, R. Smith & H. Takano—8 ♀♀, 2 ♂♂ (10 paratypes) (BMNH); MARA, Shirati (1°9'S, 34°2'E), 1909, [anonymous]—5 ♀♀, 1 ♂ (paratypes) (SMF); MOROGORO, Llonga (9°2'S, 36°51'E), 21.x.1966, Robertson—1 ♀, 2 ♂♂ (3 paratypes) (FETC); Majawanga, 1400 m (6°5'S, 36°50'E), 14–18.iii.2004, S. Tind Nielsen—1 ♀, 3 ♂♂ (4 paratypes) (ZMUC); RUKWA, Tumba (7°7'S, 31°10'E), 15.xii.1950, H.-J. Brédo—1 ♀, 2 ♂♂ (3 paratypes) (FGIC, IRSNB); SHINYANGA, Lake Ndutu area, Serengeti National Park (2°59'S, 35°1'E), 15.xi.1990, R. Foster—3 ♀♀, 2 ♂♂ (allotype, 4 paratypes) (OUMNH); Lake Ndutu area, Serengeti National Park (2°59'S, 35°1'E), 17.xii.1990, R. Foster—3 ♀♀, 1 ♂ (paratypes) (OUMNH); Lake Ndutu area, Serengeti National Park (2°59'S, 35°1'E), 18.xii.1990, R. Foster—1 ♂ (paratype) (OUMNH); Lake Ndutu area, Serengeti National Park (2°59'S, 35°1'E), 22.xii.1990, R. Foster—1 ♂ (paratype) (OUMNH); Lake Ndutu area, Serengeti National Park (2°59'S, 35°1'E), 26.xii.1990, R. Foster—1 ♂ (paratype) (OUMNH); Lake Ndutu area, Serengeti National Park (2°59'S, 35°1'E), 18.v.1991, R. Foster—2 ♂♂ (holotype, 1 paratype) (OUMNH); Old Shinyanga (3°34'S, 33°25'E), 1.xii.1935, E. Burtt—1 ♂ (paratype) (BMNH); Old Shinyanga (3°34'S, 33°25'E), 26.i.1936, E. Burtt—1 ♂ (paratype) (BMNH); Old Shinyanga (3°34'S, 33°25'E), 10.iv.1936, E. Burtt—1 ♀ (paratype) (BMNH); TABORA, Tabore (5°2'S, 32°49'E), 1886, Révoil—1 ♂ (paratype) (MNHN); **UGANDA**: CENTRAL, Entebbe (0°4'N, 32°28'E), ii–vii.1972, H. Falke—10 ♀♀, 9 ♂♂ (19 paratypes) (CNC, FGIC); Entebbe (0°4'N, 32°28'E), ii.1972, H. Falke—2 ♂♂ (2 paratypes) (CNC); Entebbe (0°4'N, 32°28'E), 22.vi.1912, C.A. Wiggins—1 ♀ (paratype) (OUMNH); Entebbe (0°4'N, 32°28'E), 15.viii.1912, C.A. Wiggins—1 ♂ (paratype) (OUMNH); Entebbe (0°4'N, 32°28'E), 9.ii.1914, [anonymous]—1 ♂ (paratype) (BMNH); Entebbe (0°4'N, 32°28'E), 11.ii.1914, [anonymous]—1 ♀ (paratype) (BMNH); Entebbe (0°4'N, 32°28'E), 20–28.v.1914,

C.C. Gowdey—2 ♂♂ (2 paratypes) (BMNH); Kampala (0°21'N, 32°35'E), 1–10.i.1918, C.C. Gowdey—1 ♀, 5 ♂♂ (6 paratypes) (BMNH); Kampala (0°21'N, 32°35'E), 11.ii.1918, [anonymous]—1 ♀, 1 ♂ (paratypes) (BMNH); Région du Bouganda (0°27'S, 31°55'E), 1906, [anonymous]—1 ♂ (paratype) (IRSNB); [unspecified locality] (0°15'N, 32°15'E), i–ii.1909, C. Alluaud—1 ♀, 3 ♂♂ (4 paratypes) (MNHN); EASTERN, Jinja, 1151 m (0°26'N, 33°12'E), 14.ii.1906, C.A. Wiggins—1 ♂ (paratype) (OUMNH); WESTERN, Kafu River near Hoima, Kampala Road (1°18'N, 31°27'E), 29–31.xii.1911, S.A. Neave—1 ♂ (paratype) (BMNH); Province d'Unyoro, Région de l'Albert-Nyanza (1°17'N, 31°10'E), ii.1909, C. Alluaud—1 ♂ (paratype) (MNHN); **ZAMBIA**: NORTHERN PROVINCE, Mbala (8°50'S, 31°28'E), 15.xii.1943, H.-J. Brédo—2 ♂♂ (2 paratypes) (IRSNB).



MAP 8. Distribution of *Digitonthophagus biflagellatus*.

Etymology. *Biflagellatus* is a Latin adjective referring to the configuration of the axial and subaxial sclerites of the internal sac.

Natural history. The single specimen with habitat data was collected in woodland in Eastern Province, Uganda. The few specimens with collecting data indicate light and dung traps.

Digitonthophagus gazella **(Fabricius, 1787), conservation of name in prevailing usage**

(Figs. 14, 37–38, 62, 78, 101–102, 126, 156–158, 185, 188, 190; Map 9)

Scarabaeus Gazella Fabricius, 1787b: 377 (original description)
Scarabæus Dorcas Olivier, 1789: 121 (original description) **proposed new synonymy**
Scarabaeus Gazella—Gmelin 1790: 1537 (diagnosis)
Scarabaeus gazella—Fabricius 1792: 56 (diagnosis)
Copris Dorcas—Fabricius 1798: 31 (diagnosis)
Scarabaeus Dorcas—Illiger 1800: 228 (monograph)
Scarabaeus Gazella—Illiger 1800: 228 (mentioned as synonym)
Copris Dorcas—Fabricius 1801: 44 (diagnosis)
Copris Gazella—Fabricius 1801: 47 (diagnosis)
Copris Gazella—Illiger 1804: 149 (mentioned as synonym)
Copris Gazella—Schönherr 1806: 48 (catalog)
Onthophagus Gazella—Dejean 1821: 53 (catalog)
Onthophagus Gazella—Sturm 1826: 178 (catalog)
Onthophagus bonasus—Latreille 1827: 282 (diagnosis, distribution, comment)
Onthophagus Gazella—LePeletier & Audinet-Serville 1828: 354 (comment taxonomy)
Onthopagus [*sic*] *Gazella*—Klug 1833: 163 (diagnosis)
Scarabaeus Dorcas—Klug 1833: 163 (synonymy)
Onthophagus Gazella—Klug 1835: 33 (distribution)

Onthophagus Gazella—Dejean 1836: 157 (catalog)
Onthophagus Gazella—Hope 1837: 33 (catalog)
Ontophagus gazella—Reiche 1840: 243 (comment)
Ontophagus gazella—Laporte 1840: 85 (diagnosis, distribution)
Onthophagus Gazella—Sturm 1843: 107 (catalog)
Ontophagus gazella—Erichson 1843: 208 (mention)
Onthophagus Gazella—Bertoloni 1849: 415 (diagnosis, distribution)
Onthophagus gazella—Fåhraeus 1857: 275 (redescription)
Onthophagus gazella—Motschulsky 1860: 153 (mention)
Onthophagus gazella—Klug 1862: 232 (comment, distribution)
Onthophagus gazella—Harold 1867: 49 (comment)
Onthophagus gazella—Harold 1869: 1029 (catalog)
[*Scarabaeus*] *dorcas*—Harold 1869: 1029 (mentioned as synonym)
Copris gazella—Gerstaecker 1871: 50 (synonymy)
Onthophagus gazella—Harold 1871: 119 (comment)
Scarabaeus Dorcas—Gerstaecker 1873: 130 (mentioned as synonym)
Scarabaeus gazella—Gerstaecker 1873: 130 (mentioned as synonym)
Onthophagus gazella—Wallengren 1881: 21 (comment)
Onthophagus gazella—Lansberge 1882: XXII (mention)
Onthophagus gazella—Reitter 1892: 183 (identification key, distribution)
Onthophagus gazella—Péringuey 1892: 29 (distribution)
Onthophagus gazella—Fairmaire 1893: 10 (distribution)
Onthophagus gazella—Brancsik 1893: 223 (distribution)
Onthophagus gazella—Reitter 1893: 62 (identification key, distribution)
Onthophagus gazella—Kolbe 1897a: 150 (distribution)
Onthophagus gazella—Kolbe 1897b: 83 (distribution)
Onthophagus gazella—Gahan & Arrow 1900: 24 (distribution)
Onthophagus (*O.*) *gazella*—d'Orbigny 1900a: 218 (monograph)
Onthophagus gazella—d'Orbigny 1900b: 299 (comment, distribution)
Onthophagus gazella—Péringuey 1901: 181 (monograph)
Onthophagus (*O.*) *gazella*—d'Orbigny 1904: 304 (distribution)
Onthophagus (*O.*) *gazella*—d'Orbigny 1905a: 494 (diagnosis, distribution)
Onthophagus gazella—d'Orbigny 1905b: 445 (distribution)
Onthophagus gazella—Kolbe 1908: 128 (distribution)
Onthophagus gazella—d'Orbigny 1909: 525 (distribution)
Onthophagus gazella—d'Orbigny 1911: 20 (distribution)
Onthophagus (*O.*) *gazella*—d'Orbigny 1913a: 249 (monograph)
Onthophagus (*O.*) *gazella*—d'Orbigny 1913b: 96 (comment, distribution)
Onthophagus (*O.*) *gazella*—Kolbe 1914: 297 (distribution)
Onthophagus (*O.*) *gazella*—d'Orbigny 1914: 654 (catalog)
Onthophagus (*O.*) *gazella*—d'Orbigny 1916: 11 (distribution)
Onthophagus gazella—Boucomont 1923: 96 (distribution)
Onthophagus gazella—Gillet & Boucomont 1927: 138 (catalog)
[*Scarabaeus*] *dorcas*—Gillet & Boucomont 1927: 138 (mentioned as synonym)
Scarabæus gazella—Arrow 1931: 230 (mentioned as synonym)
Onthophagus gazella—Boucomont 1934: 26 (mentioned as synonym)
Onthophagus gazella—Paulian 1936: 132 (identification key)
Onthophagus gazella—Boucomont 1937: 131 (distribution)
Onthophagus gazella—Balthasar 1941: 110 (distribution)
Onthophagus gazella—Müller 1942: 96 (comment, distribution)
Onthophagus gazella—Gomes Alves 1944: 3 (distribution)
Onthophagus gazella—Paulian 1948: 151 (mentioned as synonym)
Onthophagus (*O.*) *gazella*—Gomes Alves 1956: 94 (distribution)
Onthophagus gazella—Frey 1956: 654 (distribution)
Onthophagus gazella—Ferreira 1958: 512 (faunistic)
Onthophagus gazella—Frey 1958: 73 (distribution)
Onthophagus gazella—Ferreira 1959: 84 (distribution)
Onthophagus gazella—Frey 1961: 90 (distribution, ecology)
Onthophagus gazella—Petrovitz 1961: 102 (distribution)
Onthophagus gazella—Ferreira 1962: 153 (faunistic)
Onthophagus (*Digitonthophagus*) *gazella*—Balthasar 1963: 365 (monograph)

[Scarabaeus] dorcas—Balthasar 1963: 365 (mentioned as synonym)
Onthophagus gazella—Ferreira 1967: 1169 (catalog)
Onthophagus dorcas—Ferreira 1968: 593 (mentioned as synonym)
Onthophagus gazella—Ferreira 1968: 593 (monograph)
Onthophagus (*Digitonthophagus*) *gazella*—Balthasar 1969: 68 (faunistic)
Onthophagus gazella—Bornemissza 1970: 31 (natural history)
Onthophagus (*O.*) *gazella*—Endrödi 1971: 294 (faunistic)
Onthophagus (*Digitonthophagus*) *gazella*—Cambefort 1972: 246 (distribution, ecology)
Onthophagus (*Digitonthophagus*) *gazella*—Ferreira 1972: 780 (catalog)
Onthophagus dorcas—Ferreira 1972: 780 (mentioned as synonym)
Onthophagus gazella—Balthasar 1972: 22 (faunistic)
Onthophagus gazella—Endrödi 1973a: 125 (faunistic)
Onthophagus (*O.*) *gazella*—Endrödi 1973b: 198 (distribution)
Onthophagus gazella—Endrödi 1974: 3 (faunistic)
Onthophagus gazella—Blume & Aga 1975: 735 (natural history)
Onthophagus gazella—Endrödi 1976: 156 (distribution)
Onthophagus gazella—Alfieri 1976: 205 (faunistic)
Onthophagus gazella—Bornemissza 1976: 7 (natural history)
Onthophagus gazella—Blume & Aga 1978: 190 (distribution, ecology)
Onthophagus gazella—Rougon & Rougon 1980: 381 (natural history, description of larvae)
Digitonthophagus gazella—Zunino 1981: 414 (new combination, faunistic)
Onthophagus gazella—Rougon & Rougon 1981: 6 (description of larvae)
Onthophagus gazella—Rougon & Rougon 1983: 499 (natural history)
Onthophagus gazella—Fincher *et al*. 1986: 2 (natural history)
Onthophagus gazella—Paulian 1986: 107 (mentioned as synonym)
Onthophagus gazella—Gutierrez *et al* 1988: 39 (natural history)
Digitonthophagus gazella—Zunino & Halffter 1988: 17 (distribution)
Digitonthophagus gazella—Kohlmann 1994: 35 (distribution)
Onthophagus gazella—Ripa *et al*. 1995: 438 (distribution)
Digitonthophagus gazella—Barbero *et al*. 1998: 242 (distribution)
Onthophagus (*Digitonthophagus*) *gazella*—Kim & Lumaret, 1989: 336 (description of larvae)
Digitonthophagus gazella—Deloya 2000: 125 (faunistic)
Onthophagus gazella—MacRae & Penn 2001: 49 (distribution)
Digitonthophagus gazella—Noriega 2002: 213 (distribution)
Digitonthophagus gazella—Barbero & Palestrini 2003: 316 (distribution)
Digitonthophagus gazella—Barbero *et al*. 2003: 333 (phylogeny)
Digitonthophagus gazella—Cambefort & Bordat 2003: 560 (distribution, ecology)
Digitonthophagus gazella—Noriega *et al*. 2006: 379 (distribution)
Digitonthophagus gazella—Moretto & Bordat 2007: 122 (distribution, ecology)
Digitonthophagus gazella—Monaghan *et al.* 2007: 678 (phylogeny)
Digitonthophagus gazella—Ivie & Philips 2008: 10 (distribution)
Digitonthophagus gazella—Cabral-de-Mello *et al*. 2008: 1244 (karyotype)
Onthophagus gazella—Wirta *et al.* 2008: 1079 (phylogeny)
Digitonthophagus gazella—Noriega *et al*. 2010: 451 (distribution)
Digitonthophagus gazella—Noriega *et al*. 2011: 35 (distribution)
Digitonthophagus gazella—Tarasov & Solodovnikov 2011: 9 (phylogeny)
Digitonthophagus gazella—Whipple *et al*. 2012: 45 (DNA analysis)
Digitonthophagus gazella—Mlambo *et al.* 2015: 318 (phylogeny)
Digitonthophagus gazella—Roggero *et al*. 2016a: [2] (phylogeny)
Digitonthophagus gazella—Breeschoten *et al*. 2016: 90 (phylogeny)
Digitonthophagus gazella—Génier & Davis 2017: 497 (comment taxonomy, distribution)
Scarabaeus dorcas—Génier & Davis 2017: 498 (comment taxonomy)

Type locality. Unspecified.

Diagnosis. Pronotum rather glossy (Fig. 62); FLP sclerite subapicodorsal lobe short anteriorly (Figs. 156–157); right lateral fold produced into a longitudinal spoon-shape process with apical portion open ventrally, ventral edge bordered with a conspicuous brush of villi (Fig. 185A), lacking well-sclerotized projection on apicoventral edge (Fig. 185B); axial sclerite shorter than subaxial sclerite, acute apically (Fig. 156); subaxial sclerite moderately long and robust (Fig. 153).

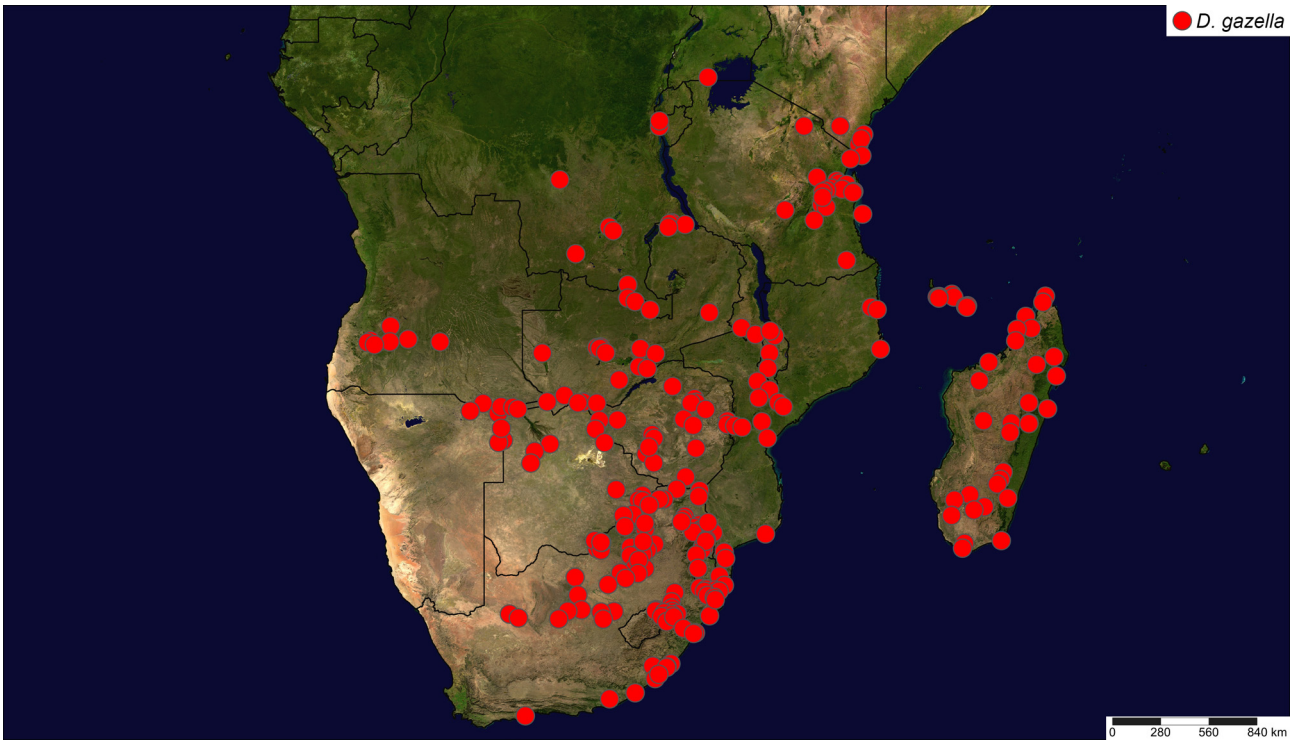
Description. Male specimen from Central Province, Zambia (Fig. 14). **Measurements**. Length 12.5 mm, width 7.0 mm. **Head** (Figs. 37–38). Anterior clypeal edge straight on median fifth in dorsal view; clypeofrontal carina broadly arcuate and interrupted at gena; vertex lacking median tubercle, surface with punctures fine to small, separated by one to four diameters. Horns rather short, slightly divergent in frontal view, parallel sided on basal four-fifths and abruptly tapering externally and narrower on apical sixth, posterointernal edge produced into low, angular projection basally, apicointernal surface lacking granules, with few scabrous punctures; genal edge slightly upturned and feebly angulate on anterior third, forming a broad angle with clypeal edge. **Pronotum** (Fig. 62). Surface with granulate punctures extending on posterior half, with distinct umbilicate punctures on posterior half of disc; punctures smaller posterolaterally, with distinct, minute punctures throughout. Anteromedian tubercle atrophied, simply round in lateral view, median longitudinal sulcus narrow and moderately deep; surface behind the eyes with a simple, round, shallow depression, surface of anterior angles flat; anterior half of lateral edge arcuate in dorsal and lateral view; posterior angles slightly upturned and simply arcuate in dorsal view; anterior hypomeral ridge arcuate anteriorly, anterior hypomeral depression surface slightly darker in color medially. **Elytra** (Fig. 14). Interval 2 with few scattered fine granules on apical declivity, interval 4 lacking fine granules from base to apex. **Legs**. Protibial apicointernal tooth enlarged, with dorsal ridge extending to apex. **Aedeagus** (Fig. 126). Parameres with dorsal and ventral edges slightly diverging toward apex in lateral view. **Internal sac sclerites** (Figs. 156–158). Axial sclerite broadly arcuate, with apex acute. Subaxial sclerite, gradually tapering from base to apex, slightly angled on apical third, extending straight approximately in line with apex of frontolateral peripheral sclerite apical portion, with a thick brush of villi on apical fifth. Frontolateral peripheral sclerite basoventral apophysis well developed; lacking medioventral carinae; right lateral fold produced into longitudinal spoon-shape process with apical portion open ventrally, ventral edge bordered with a brush of villi; left lateral lobe membranous, slightly developed; subapicodorsal lobe membranous, not reaching anterior edge, apex set medially in dorsal view; apical lobe round and directed obliquely on left side, left edge emarginate, apical villi irregular in shape; subapicoventral lobe round and interrupted in line with apical lobe, with few villi along apical edge only.

Variation. Measurements (237 ♂♂, 169 ♀♀). Length: male 7.0–13.0 mm (10.6 ± 1.1), female 7.5–13.0 mm (10.5 ± 1.0 mm). Female specimen. Cephalic outline in dorsal view as in Fig. 78; vertex with a slightly sinuate transverse carina, dorsal edge slightly sinuous in frontal view, lateral portion abruptly sloping down; anterior pronotal tubercles well developed, external lateral edges slightly widening toward apex in dorsal view, anterolateral surface obliquely concave, anterosuperior edge slightly arcuate in dorsal view (Fig. 101), lateral portion of anterosuperior edge slightly upturned (Fig. 102). Protibia short, with external teeth more robust.

Primary type data. ***Scarabaeus gazella*** **Fabricius**: Syntype (ZMUK): [ ] small green square; [ZMUC / 00508509]; [TYPE] red card; [WORLD / SCARAB. / DATABASE / WSD00029479] barcode label; [SYNTYPE ♂ / *Scarabaeus* / *gazella* / Fabricius, 1787 / vid. F. Génier, 2016] red card; [Guinea / Isert / Mus. T. Lund / Copris / gazella / ♂ / F.] handwritten [in error] see Nomenclature and taxonomy below for more details.

Note. The first label, a small green square without inscription, confirms this specimen as a Fabrician type (Zimsen 1964). The last label was added after Fabricius's time and is erroneously cited as African. See nomenclature and taxonomy below section for more details.

Scarabaeus dorcas **Olivier**: Neotype ♂ (MNHN) **present designation**: [Madagascar / Diego-Suarez 7 / Ch. Alluaud, 1893] partly handwritten; [MUSEUM PARIS / MADAGASCAR / COLL. CH. ALLUAUD 1904] green card; [WORLD / SCARAB. / DATABASE / WSD00030025] barcode label; [NEOTYPE / *Scarabaeus* / *dorcas* / Olivier, 1789 / des. F. Génier, 2016] red card. **Note**. This neotype designation is made with the express purpose of clarifying the taxonomic status and the type locality of *Scarabaeus dorcas* Olivier. The specimen designated agrees in morphology to the description presented above. The original type material used for Olivier's description is lost or destroyed (Olivier Montreuil, MNHN, personal communication). The neotype has been selected to match Olivier's description and type locality, in addition to possessing the best diagnostic character for the species. The neotype is deposited in the collection of the Museum national d'Histoire naturelle de Paris along with the remains of Olivier's collection.



MAP 9. Distribution of *Digitonthophagus gazella* (native range in continental Africa only).

Material examined (715 ♂♂, 407 ♀♀), distribution (Map 9): **ANGOLA**: CUANDO CUBANGO, Menongue (14°39'S, 17°41'E), iii.1914, Mission Rohan-Chabot—1 ♂ (MNHN); HUILA, 10 km S Caconda (13°50'S, 15°6'E), 5.xi.2011, G. Werner—2 ♀♀, 2 ♂♂ (FGIC, GWPC); 10 km S Cacula (14°35'S, 14°3'E), 4.xi.2011, G. Werner—1 ♂ (GWPC); 30 km W Quipungo (14°48.02'S, 14°15.32'E), 26.xi.2013, G. Werner—3 ♀♀, 2 ♂♂ (FGIC, GWPC); 33 km S Cacula (14°41'S, 13°54'E), 13.xi.2011, G. Werner—1 ♀, 1 ♂ (GWPC); Capelongo près Luceque (14°39'S, 15°4'E), xii.1914, Mission Rohan-Chabot—1 ♂ (MNHN); Capelongo-Dongo (14°31'S, 16°1'E), 1914, Mission Rohan-Chabot—1 ♀ (MNHN); Capelongo-Dongo (14°31'S, 16°1'E), xii.1914, Mission Rohan-Chabot—2 ♂♂ (MNHN); **AUSTRALIA**: NEW SOUTH WALES, Camp Blackman, Warrumbungle National Park (31°16'37"S, 148°59'51"E), 5–6.xii.1988, H. & A. Howden—1 ♀, 1 ♂ (CMNC); Gilgandra (31°43'S, 148°40'E), 12.iv.1988, H. & A. Howden—1 ♂ (CMNC); Narrabri (30°20'S, 149°47'E), 5.xii.1977, G.G. Burns—2 ♀♀ (CMNC); NORTHERN TERRITORY, CSIRO McMillans Road, Darwin (12°24'42"S, 130°55'19"E), 1–10.xii.1993, S. & J. Peck (93-85)—1 ♀, 1 ♂ (CMNC); CSIRO McMillans Road, Darwin (12°24'42"S, 130°55'19"E), 5.i.1994, S. & J. Peck (93-166)—1 ♀, 1 ♂ (CMNC); CSIRO McMillans Road, Darwin (12°24'42"S, 130°55'19"E), 9.i.1994, S. & J. Peck (93-167)—1 ♂ (CMNC); Elsey National Park, Mataranka (14°58'S, 133°11'E), 9.xii.1993, S. & J. Peck (93-115)—1 ♀, 1 ♂ (CMNC); Elsey National Park, Mataranka (14°58'S, 133°11'E), 9.xii.1993, S. & J. Peck (93-116)—1 ♀, 1 ♂ (CMNC); Gungaree Rainforest, South Alligator River, Kakadu National Park (12°40'46"S, 132°29'9"E), 22.xii.1993, S. & J. Peck (93-133)—1 ♂ (CMNC); Magela Creek (12°40'S, 133°1'E), 4.xi.1989, C.W. & L.B. O'Brien—1 ♂ (CMNC); Tenat Creek (19°39'S, 134°11'E), 22.ix.1988, H. & A. Howden—1 ♀, 1 ♂ (CMNC); QUEENSLAND, 12 mi. S Ayr (19°44'S, 147°28'E), 26.ii.1975, H. & A. Howden—1 ♂ (CMNC); 16 km W Ravenshoe (17°39'S, 145°21'E), 2.i.1975, M.S. & B.J. Moulds—1 ♂ (CMNC); 4–8 km S Atherton (17°20'S, 145°30'E), 26.xii.1988, H. & A. Howden—1 ♂ (CMNC); 40 km N Lynd (18°36'S, 144°43'E), ii.1993, H. Demarz—1 ♂ (CEMT); 8 km N Mareeba (16°55'S, 145°25'E), 28.i.1997, H. & A. Howden—1 ♀ (CMNC); 9 km NE Julatten (16°33'S, 145°23'E), 13.xii.1986, H. & A. Howden—1 ♀, 1 ♂ (CMNC); Atherton (17°16'S, 145°29'E), 7.ii.1975, H. & A. Howden—1 ♀ (CMNC); Atherton (17°16'S, 145°29'E), 10.ii.1975, H. & A. Howden—1 ♀, 1 ♂ (CMNC); Black Beach Reserve, near Mackay (21°4'39"S, 149°11'44"E), 28.i.1975, H. & A. Howden—2 ♂♂ (CMNC); Burketown (17°44'S, 139°33'E), 20.ix.1975, Walford-Huggins—1 ♀, 1 ♂ (CMNC); Cairns (16°55'S, 145°46'E), 10.v.1971, A. & M. Walford-Huggins—1 ♀, 1 ♂ (CMNC); Cairns (16°55'S, 145°46'E), 24.viii.1971, A. & M. Walford-Huggins—1 ♀, 1 ♂ (CMNC); Cairns (16°55'S, 145°46'E), 30.i.1975, H.

& A. Howden—2 ♂♂ (CMNC); Cairns (16°55'S, 145°46'E), 3.ii.1975, H. & A. Howden—1 ♂ (CMNC); Cairns (16°55'S, 145°46'E), 5.ii.1975, H. & A. Howden—1 ♀ (CMNC); Charters Towers (20°5'S, 146°16'E), 16–23.xii.1988, C. Lockett—1 ♂ (CMNC); Granite Gorge Nature Park, 12 km SW Mareeba (17°2'32"S, 145°21'4"E), 8.i.1989, H. & A. Howden—1 ♂ (CMNC); Holloways Beach (16°50'40"S, 145°44'20"E), 30.ix.1973, R.E. Parrott—2 ♂♂ (CNC); Lockerbie, Cape York Peninsula (10°47'19"S, 142°27'33"E), 11.iv.1975, M. Walford-Huggins—1 ♀, 1 ♂ (CMNC); Mareeba (16°59'S, 145°25'E), 19–28.xii.1988, H. & A. Howden—1 ♀ (CMNC); Mornington Island (16°31'S, 139°24'E), 21.ix.1975, A. & M. Walford-Huggins—1 ♂ (CMNC); Petford (17°20'34"S, 144°55'45"E), 5.ii.1989, H. & A. Howden—1 ♂ (CMNC); Station Creek, 10 mi. S Mount Carbine (16°37'S, 145°13'E), 11.vi.1974, A. & M. Walford-Huggins—1 ♂ (CMNC); Toowoomba (27°34'S, 151°57'E), 26–27.ii.1983, Munroe & Common—1 ♀, 1 ♂ (CMNC); Yeppoon (23°7'40"S, 150°44'43"E), 25.i.1975, H. & A. Howden—1 ♀ (CMNC); Yeppoon (23°7'40"S, 150°44'43"E), 26.i.1975, H. & A. Howden—1 ♂ (CMNC); Yeppoon (23°7'40"S, 150°44'43"E), 27.i.1975, H. & A. Howden—1 ♂ (CMNC); **BOTSWANA**: CENTRAL, 120 km N Nata (19°12'58"S, 25°47'38"E), 29.xi.2003, Werner & Smrz—1 ♂ (CMD); 35 km N Nata (19°55'S, 26°16'E), 26.xi.2001, B.D. Gill—2 ♀♀, 2 ♂♂ (BDGC); 5 km SE Serowe (22°22'30"S, 26°52'30"E), 22.i.1985, Johnson—1 ♂ (BMNH); Stevensford Game Reserve, 13 km E Sherwood (22°54.56'S, 28°2.36'E), 27–29.xi.2001, B. & J. Gill—2 ♀♀, 2 ♂♂ (BDGC); NORTH-WEST, 20 km SW Sehitwa (20°22'30"S, 22°37'30"E), 22.i.1978, Holm, Jacobs, Kirsten, Scholtz—1 ♂ (BMNH); Chobe River, 5 km E Kasane (17°48'S, 25°9'E), 18.i.2002, Holm, Marais, Nel, Saieva—1 ♀, 3 ♂♂ (BMNH); Chobe, 20 km WSW Kasane, 938 m (17°50.2'S, 24°52.93'E), 25–26.xi.2001, B. & J. Gill—1 ♀, 2 ♂♂ (BDGC); Kasane (17°47'S, 25°10'E), 2.xii.2012, M. Boulétreau—2 ♀♀, 1 ♂ (CMD); Kuke Pan (20°59'S, 22°25'E), 15.iv.1972, Southern Africa Expedition—1 ♀, 1 ♂ (BMNH); Maun (19°59'S, 23°25'E), ii.1973, [anonymous]—1 ♂ (OMOC); SOUTH-EAST, Otse (25°2'S, 25°45'E), 16.i.1980, D. Levin—1 ♂ (CMNC); **BRAZIL**: BAHIA, Cruz das Almas (12°40'27"S, 39°6'8"W), ii.1995, J.D.B. Macedo—1 ♂ (CEMT); Mercado, Brumado (14°12'44"S, 41°40'18"W), 20.i.2012, B.N. de Souza—1 ♂ (CEMT); Nazaré das Farinhas (13°2'17"S, 39°0'10"W), iii.2005, C. Ribeiro & A. Fonseca—1 ♂ (CEMT); GOIÁS, Fazenda Piratininga, São Miguel do Araguaia (13°16'23"S, 50°9'49"W), 6–9.i.2000, V. Canhedo—1 ♂ (CEMT); MARANHÃO, Sitio Melancia, Zona Rural, Mirador (6°22'21"S, 44°21'55"W), 19–20.xii.2006, F. Limeira-de-Oliveira—1 ♂ (CEMT); MATO GROSSO, Base UFMT, Poconé (16°29'58"S, 56°24'49"W), iii.2012, M. Rossini—1 ♂ (CEMT); Cáceres, Curvelândia (15°36'43"S, 57°55'19"W), ii–iii.2010, L.S. Silva—1 ♂ (CEMT); Fazenda Conceição, Poconé (16°19'39"S, 56°30'14"W), 20.v.2012, M.B. Pessoa—1 ♂ (CEMT); Fazenda Curitiba, Tangará da Serra, 320 m (14°21'48"S, 57°29'29"W), 31.iii.2012, R.J. Silva—1 ♂ (CEMT); Fazenda São Luiz, Querêcia (12°38.611'S, 52°22.637'W), ii.2009, R. Andrade—1 ♂ (CEMT); Fazenda São Nicolau, Cotriguaçu (9°51'23"S, 58°14'57"W), 14.x.2007, F. Vaz de Mello—1 ♂ (CEMT); Fazenda São Nicolau, Cotriguaçu (9°51'23"S, 58°14'57"W), 31.x.2007, O. Peres Filho—1 ♂ (CEMT); Fazenda São Nicolau, Cotriguaçu (9°51'23"S, 58°14'57"W), 14.xi.2007, O. Peres Filho—2 ♂♂ (CEMT); Fazenda São Nicolau, Cotriguaçu (9°51'23"S, 58°14'57"W), 15.xii.2007, O. Peres Filho—1 ♂ (CEMT); UNEMAT, Tangará da Serra, 442 m (14°39'58"S, 57°25'58"W), 26.vii.2008, R.J. Silva—1 ♂ (CEMT); Vila Rica (10°1'S, 51°7'W), ii.2000, D.C. Souza—1 ♀, 1 ♂ (CEMT); MATO GROSSO DO SUL, Fazenda São Bento, Proximo Porto Jofre, Corumbá (17°21'S, 56°44'W), 6.xii.2010, F.R. Tortato—1 ♂ (CEMT); Pôrto Murtinho (21°42'53"S, 57°53'3"W), 26.i.2008, F.R. Fernandes—1 ♀, 1 ♂ (CEMT); PARÁ, Alter do Chão (2°31'S, 54°57'W), 5.viii.2003, R.A. Matavelli—1 ♂ (CEMT); Fazenda Marajoara, Pau d'Arco (7°50'S, 50°16'W), 16.x.1998, P.Y. Scheffler—1 ♂ (CEMT); PARAÍBA, Fazenda Almas, São José dos Cordeiros, 650 m (7°28'S, 36°53'W), iii.2003, M.I.M. Hernández—1 ♂ (CEMT); PERNAMBUCO, Floresta (8°35'S, 38°14'W), vii.2012, R.V. Nunes—1 ♂ (CEMT); Japecanga (8°14'S, 36°8'W), 1.iv.2007, C.E.B. Nobre—1 ♂ (CEMT); RONDÔNIA, Guajará-Mirim (10°22'16"S, 64°44'47"W), 25–27.i.2010, F. Coletti—1 ♂ (CEMT); Guajará-Mirim (10°22'16"S, 64°44'47"W), 27.i.2010, F. Coletti—1 ♂ (CEMT); Guajará-Mirim (10°22'16"S, 64°44'47"W), 15–18.ii.2010, F. Coletti—1 ♀, 1 ♂ (CEMT); **COMOROS**: MWALI, Bandamalé, 420 m, ix.1958, Raharizonina—4 ♀♀, 3 ♂♂ (MNHN); Fomboni, 10 m (12°17'2"S, 43°44'34"E), ix.1958, Raharizonina—4 ♀♀, 3 ♂♂ (MNHN); Miringoni, 40 m (12°18'10"S, 43°38'11"E), ix.1958, Raharizonina—4 ♀♀, 4 ♂♂ (MNHN); Mohéli Island (12°19'S, 43°43'E), 21.viii.1973, R. Mourglia—1 ♀, 1 ♂ (FETC); Nioumachoua (12°22'S, 43°43'E), [no date], Pupier—1 ♂ (MNHN); NZWANI, M'Remani, Anjouan (12°18'47"S, 44°29'51"E), ix.1958, Raharizonina—1 ♀, 6 ♂♂ (MNHN); Mutsamudu, Anjouan, 50 m (12°10'S, 44°24'E), x.1958, Raharizonina—1 ♀, 1 ♂ (MNHN); **DEMOCRATIC REPUBLIC OF THE CONGO**: KASAI ORIENTAL, Pastorale Lomami (6°11'S, 23°56'E), 12.iv.1941, H.-J. Brédo—1 ♀, 2 ♂♂ (FGIC, IRSNB); KATANGA, Kaswabilenga, Parc National de l'Upemba, 700 m (8°51'S, 26°43'12"E), 11–

16.x.1947, G.F. de Witte (817a)—1 ♂ (IRSNB); Kaswabilenga, Parc National de l'Upemba, 700 m (8°51'S, 26°43'12"E), 29–30.x.1947, G.F. de Witte (889a)—2 ♀♀, 2 ♂♂ (IRSNB); Kaswabilenga, Parc National de l'Upemba, 700 m (8°51'S, 26°43'12"E), 30.x.1947, G.F. de Witte (902bis a)—2 ♀♀, 2 ♂♂ (IRSNB); Kaswabilenga, Parc National de l'Upemba, 700 m (8°51'S, 26°43'12"E), 3–8.xi.1947, G.F. de Witte (915a)—2 ♀♀, 2 ♂♂ (IRSNB); Kazofu (10°3'S, 24°46'E), xii.2004, T. Garnier—1 ♀, 1 ♂ (PMOC); Lubumbashi (11°40'S, 27°29'E), 19.ii.1941, H.-J. Brédo—1 ♂ (IRSNB); Mabwe, Parc National de l'Upemba, 585 m (8°39'12"S, 26°30'38"E), 17–22.xi.1948, G.F. de Witte (1970a)—2 ♀♀, 2 ♂♂ (IRSNB); SOUTH-KIVU, Kabunambo (3°6'36"S, 29°8'18"E), 1956–1957, [anonymous]—2 ♀♀, 2 ♂♂ (MNHN); Uvira (3°24'S, 29°8'E), [no date], [anonymous]—2 ♀♀, 2 ♂♂ (MNHN); Uvira (3°24'S, 29°8'E), 1927, G. Babault—1 ♂ (MNHN); **DOMINICAN REPUBLIC**: SAN PEDRO DE MACORÍS, Juan Dolio (18°26'37"N, 69°24'51"W), 26.x.2000, D. Prunier—2 ♀♀, 2 ♂♂ (OMOC); **FIJI**: NORTHERN DIVISION, Nadi (16°55'55"S, 178°46'7"E), 27.viii.2004, H. & A. Howden—1 ♂ (CMNC); WESTERN DIVISION, Tavua (17°26'30"S, 177°51'48"E), 20–23.viii.1978, S. & J. Peck—1 ♀, 1 ♂ (CMNC); **FRANCE**: MAYOTTE, Chingoni, 70 m (12°48'S, 45°7'E), x.1958, Raharizonina—1 ♂ (MNHN); Dembeni (12°50'40"S, 45°11'5"E), 1971, Brunhes—1 ♀, 1 ♂ (MNHN); [unspecified locality] (12°46'S, 45°13'E), [no date], [anonymous]—2 ♂♂ (BMNH, IRSNB); **GUADELOUPE**: GRANDE-TERRE, Le Gosier (16°13'N, 61°29'W), ii.1992, O. Montreuil—1 ♂ (OMOC); **JAMAICA**: ST. ANN PARISH, Discovery Bay (18°27'30"N, 77°23'55"W), 25.v.1990, G. Haghebaert—1 ♂ (IRSNB); Priory (18°26'27"N, 77°13'26"W), 4.vi.1990, G. Haghebaert—1 ♂ (IRSNB); **KENYA**: KILIFI, Kikambala (3°49'S, 39°48'E), v.1993, [anonymous]—5 ♀♀, 6 ♂♂ (JFJC); KWALE, de Tiwi à Gazi (4°20'S, 39°33'E), xi.1911, Alluaud & Jeannel—2 ♀♀, 1 ♂ (MNHN); MOMBASSA, Mombassa (4°3'S, 39°40'E), xi.1985, [anonymous]—2 ♀♀, 2 ♂♂ (CMD); Mombassa (4°3'S, 39°40'E), [no date], C. Alluaud—1 ♂ (MNHN); Mombassa (4°3'S, 39°40'E), 10.i.1939, A.H.N.—1 ♂ (BMNH); Mombassa (4°3'S, 39°40'E), 10.iii.1939, A.H.N.—3 ♀♀, 3 ♂♂ (BMNH); TAITA TAVETA, Voi (3°23'S, 38°34'E), xi.1997, M. Snižek—1 ♂ (CEMT); **MADAGASCAR**: ANTANANARIVO, Ambatolampy (19°23'S, 47°26'E), 1931, Lasère—1 ♀, 1 ♂ (MNHN); Antananarivo (18°53'S, 47°30'E), 1931, Lasère—1 ♀, 1 ♂ (MNHN); DIEGO-SUAREZ, Amber Gebirge [=Montagne d'Ambre] (12°35'S, 49°9'E), [no date], H. Rolle—2 ♂♂ (IRSNB); Diego-Suarez [=Antisiranana] (12°16'S, 49°17'E), 1893, C. Alluaud—2 ♀♀, 3 ♂♂ (IRSNB, MNHN); Diego-Suarez [=Antisiranana] (12°16'S, 49°17'E), 1939–1941, [anonymous]—1 ♀ (MNHN); Marovato, 30 km E Ambanja (13°56'51"S, 48°33'19"E), 1.xii.2001, I. Pljushtch—1 ♂ (OUMNH); Nosy Be (13°19'24"S, 48°15'34"E), 1885, Stumpff—3 ♀♀, 3 ♂♂ (SMF); Nosy Be (13°19'24"S, 48°15'34"E), 23.xi.1898, P. Frey—2 ♀♀ (SMF); Nosy Be (13°19'24"S, 48°15'34"E), 30.xii.1998, G. Ferrer—3 ♂♂ (OMOC); FIANARANTSOA, Ambalavao (21°50'S, 46°56'E), [no date], [anonymous]—1 ♀, 1 ♂ (MNHN); Camp Catta, 40 km S Ambalavao (22°4'48"S, 46°46'29"E), 26.xi–2.xii.2003, S. Murzin & A. Shamaev—1 ♀ (CMD); Fianarantsoa (21°27'S, 47°5'E), [no date], [anonymous]—1 ♀, 2 ♂♂ (BMNH); km. P. 713, Isalo, 1000 m (22°38'S, 45°20'E), 18.iii.1968, K.M.G. & P.D.—1 ♂ (BMNH); Vondrozo (22°49'S, 47°19'E), 1921, [anonymous]—1 ♀, 1 ♂ (MNHN); MAHAJANGA, Ananalava (14°36'S, 47°44'E), 13.v.1973, P. Calabri—1 ♂ (CMNC); Environs Ambodimanga (16°41'S, 45°50'E), 14–16.xi.1995, J. Stolarczyk—2 ♂♂ (OUMNH); Mandritsara (15°50'S, 48°49'E), [no date], [anonymous]—1 ♀, 1 ♂ (MNHN); Nosy Béraphia (14°0'S, 47°48'E), 1934, [anonymous]—1 ♂ (MNHN); MAJUNGA, Majunga (15°43'S, 46°20'E), v.1968, S. Key—2 ♂♂ (BMNH); Majunga (15°43'S, 46°20'E), 14.v.1968, K.M. Guichard—1 ♂ (BMNH); TAMATAVE, Ambatondrazaka (17°50'S, 48°25'E), xi.1983, P. Arnaud—1 ♂ (BDGC); Andasibe-Mantadia National Park, Périnet (18°53'3"S, 48°25'44"E), 21.iv.1993, J.P. & S. Lignon—1 ♀, 1 ♂ (CMD); Antanambe (16°26'S, 49°51'E), x.1972, [anonymous]—2 ♂♂ (CEMT); Antanambe (16°26'S, 49°51'E), x.1970, [anonymous]—1 ♂ (CEMT); Antanambe (16°26'S, 49°51'E), x.1971, [anonymous]—1 ♂ (CEMT); Périnet (18°55'24"S, 48°25'11"E), xi.2003, [anonymous]—1 ♀, 1 ♂ (CMD); Tamatave [=Toamasina] (18°8'50"S, 49°23'43"E), [no date], [anonymous]—1 ♂ (IRSNB); TANARIVE, Tsiroanomandidy (18°46'11"S, 46°2'58"E), xi.1983, P. Arnaud—1 ♀, 1 ♂ (BDGC); TOAMASINA, Maroantsetra (15°26'S, 49°44'E), 7.i.1999, J. Moravec—1 ♂ (FETC); Station agronomique du lac Alaotra (17°48'S, 48°24'E), 18.ii.1988, Donskoff—1 ♀, 1 ♂ (MNHN); TOLIARA, Ankilimary (23°26'S, 45°33'E), 25.v.1948, [anonymous]—2 ♂♂ (CMNC); Beloha (25°10'26"S, 45°3'36"E), [no date], [anonymous]—1 ♀, 1 ♂ (MNHN); Betioky, 275 m (23°43'S, 44°23'E), 4.iv.1968, K.M.G. & P.D.—1 ♀, 2 ♂♂ (BMNH); Betroka (23°16'2"S, 46°5'50"E), [no date], [anonymous]—2 ♀♀, 2 ♂♂ (IRSNB); Fort Dauphin [=Taolagnaro] (25°2'S, 46°59'E), x.2006, Bouletreau—1 ♀, 1 ♂ (CMD); Lavanono (25°25'47"S, 44°57'16"E), 20.x.2009, G. Prelle—5 ♀♀, 5 ♂♂ (PMOC); Sakaraha (22°54'41"S, 44°31'55"E), [no date], [anonymous]—3 ♀♀, 3 ♂♂ (SMF); Sakaraha (22°54'41"S, 44°31'55"E), 2.iii.1963, R. Vieu—2 ♂♂ (PMOC);

MALAWI: CENTRAL REGION, 20 km NW Dedza (14°16'S, 34°9'E), 28.xi.1983, [anonymous]—1 ♂ (BMNH); Lilongwe, Sani (13°55'S, 33°25'E), 5.xii.1983, [anonymous]—1 ♂ (BMNH); SOUTHERN REGION, Chikwawa (16°2'14"S, 34°47'55"E), 14.xii.1993, C.R. Owen—1 ♀, 1 ♂ (PMOC); Monkey Bay (14°5'S, 34°55'E), iii.1989, C.R. Owen—1 ♀, 1 ♂ (PMOC); Balaka, near Phalula (15°14'S, 34°53'E), 27.i.2001, J.-F. Josso—1 ♀, 1 ♂ (JFJC); Mangochi, Nkopola Forest Reserve (14°19'39"S, 35°8'57"E), 20–21.i.1985, A.V. Evans & C.H. Scholtz—1 ♀, 1 ♂ (BMNH); **MEXICO**: SAN LUIS POTOSÍ, San Nicolás Tolentino (22°15'N, 100°33'W), viii.1996, S. Boucher—2 ♀♀, 2 ♂♂ (PMOC); SINALOA, Guamúchil (25°27'31"N, 108°4'40"W), 1.viii.2002, [anonymous]—1 ♀ (CMD); SONORA, Yécora (28°22'N, 108°55'W), 5.ix.2012, [anonymous]—1 ♀, 1 ♂ (CMD); VERACRUZ, Corral Nuevo (18°6'46"N, 95°6'54"W), 17.viii.2002, S. Prepsl—1 ♂ (CMD); **MOZAMBIQUE**: CABO DELGADO, Mareja (site 1), Parque Nacional Quirimbas, 100 m (12°50'56"S, 40°10'53"E), 22.xii.2012, F. & S. Génier & M. Denja (2012-02)—1 ♀ (FGIC); Parque Nacional Quirimbas, 100 m (12°50'56"S, 40°10'53"E), 23.xii.2012, F. & S. Génier & M. Denja (2012-05)—2 ♀♀, 2 ♂♂ (FGIC); Pemba (12°58'S, 40°30'E), [no date], F.V. Beste—1 ♂ (BMNH); INHAMBANE, Zavala, Quissico (24°40'58"S, 34°40'7"E), 12.xi.1967, M.I. Russell—1 ♂ (BMNH); MANICA, Casa Msika Lodge/Camping, 20 km E Chimoio (19°2'25"S, 33°3'55"E), 24.xii.2005, P. Schüle—1 ♂ (SMNS); Chimoio (19°7'S, 33°27'E), ix.1928, P. Lesne—3 ♂♂ (FGIC, MNHN); Chimoio (19°7'S, 33°27'E), iii.1928, P. Lesne—1 ♀, 1 ♂ (MNHN); environs de Tambara (16°43'S, 34°15'E), iv.1926, J. Surcouf—1 ♂ (MNHN); MAPUTO, Lourenço Marques [= Maputo] (25°57'55"S, 32°35'21"E), 10.viii.1900, F. Muir—2 ♂♂ (BMNH); Mission Rikatla (25°38'S, 32°31'E), [no date], H.A. Junod—2 ♀♀, 2 ♂♂ (MNHN); NAMPULA, Lumbo (15°2'S, 40°40'E), ii.1983, F. Králík—1 ♀ (CVM); SOFALA, 10 mi. NW Beira (19°41'S, 34°46'E), 16.iv.1971, Bornemissza & Aschenborn—1 ♂ (CMNC); Caia (17°49'13"S, 35°20'39"E), xii.1926, J. Surcouf—1 ♂ (MNHN); Caia (17°49'13"S, 35°20'39"E), 23.x.1910, H. Swale—1 ♂ (BMNH); Caia (17°49'13"S, 35°20'39"E), 25.x.1910, H. Swale—1 ♀, 1 ♂ (BMNH); Caia (17°49'13"S, 35°20'39"E), 5.xii.1910, H. Swale—1 ♂ (BMNH); Caia (17°49'13"S, 35°20'39"E), 25.xii.1910, H. Swale—1 ♀, 2 ♂♂ (BMNH); Caia (17°49'13"S, 35°20'39"E), 23.ix.1911, H. Swale—1 ♂ (BMNH); Caia (17°49'13"S, 35°20'39"E), 29.ii.1912, H. Swale—1 ♂ (BMNH); Caia (17°49'13"S, 35°20'39"E), 18.iii.1912, H. Swale—1 ♂ (BMNH); Canxixe (17°35'S, 34°19'E), xii.1926, J. Surcouf—2 ♀♀ (MNHN); Chemba (17°10'S, 34°53'E), xi.1928, J. Surcouf—1 ♀, 1 ♂ (MNHN); Chemba (17°10'S, 34°53'E), xii.1928, J. Surcouf—1 ♀, 1 ♂ (MNHN); Chemba (17°10'S, 34°53'E), 1928, J. Surcouf—2 ♂♂ (MNHN); Gorongoza National Park (18°49'S, 34°29'E), 15.xii.1972, C. Besnard—1 ♀, 2 ♂♂ (PMOC); Nova Chupanda (18°2'S, 35°36'E), xii.1928–i.1929, J. Surcouf—2 ♀♀, 2 ♂♂ (FGIC, MNHN); **NAMIBIA**: CAPRIVI, 4 km W Immelman runway, West Caprivi game Park (17°46'56"S, 23°16'31"E), 14.xii.1999, Mann & Marais—1 ♀ (OUMNH); KAVANGO, 2 km W Xawasha Pan, Tsunkwe District (19°9'57"S, 20°52'55"E), 26.xii.1998, D.J. Mann & E. Marais—1 ♀ (OUMNH); 5 km N Nova, Caprivi Game Park (18°9'56"S, 21°44'31"E), 16.xii.1999, Mann & Marais—3 ♂♂ (OUMNH); 5 km N Nova, Caprivi Game Park (18°9'56"S, 21°44'31"E), 17.xii.1999, Mann, Marais, & Newman—4 ♀♀, 5 ♂♂ (OUMNH); 5 km N Nova, Caprivi Game Park (18°9'56"S, 21°44'31"E), 17.xii.1999, Mann & Marais—2 ♀♀, 2 ♂♂ (OUMNH); Divundu, West Caprivi Game Park (18°4'4"S, 21°28'51"E), 1.i.1999, D.J. Mann & E. Marais—1 ♀, 1 ♂ (OUMNH); Khaudom Game Reserve, 5 km N Cwiba (18°23'4"S, 20°43'1"E), 30.xii.1998, D.J. Mann & E. Marais—2 ♂♂ (OUMNH); Mayana Lodge, Rundu District (17°51'55"S, 19°55'48"E), 19.xii.1999, Mann & Marais—1 ♀ (OUMNH); Mile 46 Agricultural Station, Novo area (18°15'52"S, 19°15'18"E), 25.iii.2002, Mann, Marais, & Kasch—4 ♀♀, 5 ♂♂ (OUMNH); Shamvura Camp (18°2'3"S, 20°51'40"E), 30–31.xii.2006, R. Perissinoto & L. Clennell—1 ♀, 1 ♂ (PMOC); OTJOZONDJUPA, Aha Hills, Tsumkwe District (19°47'36"S, 20°59'51"E), 22.xii.1998, Mann & Marais—1 ♀ (OUMNH); Nama Pan area, Tsumkwe district (19°54'34"S, 20°44'8"E), 21.xii.1998, D.J. Mann & E. Marais—1 ♀ (OUMNH); **NEW CALEDONIA**: NORTH PROVINCE, Île Art (19°43'S, 163°40'E), 7–8.iii.1995, M. Boulard—1 ♂ (MNHN); SOUTH PROVINCE, La Foa (21°42'36"S, 165°49'40"E), 16.xi.2007, T. Thery—1 ♀, 1 ♂ (CTT); La Foa (21°42'36"S, 165°49'40"E), 3.xii.2007, T. Thery—1 ♀, 1 ♂ (CTT); Route des Nordistes, Bourail (21°35.706'S, 165°24.593'E), 21.ii.2015, M. Dierkens—1 ♀, 1 ♂ (CMD); Sentier du Pic de Ouitchambo, Bouloupari (21°52'S, 166°3'E), 15.iii.2013, M. Dierkens—1 ♀, 1 ♂ (CMD); **[NO DATA]**: , [no date], [anonymous]—1 ♂ (ZMUC); **PAPUA NEW GUINEA**: MADANG, Nagada Mission (5°9'24"S, 145°47'24"E), 6.v.1992, I. Lansbury—1 ♂ (OUMNH); Nagada Mission (5°9'24"S, 145°47'24"E), 18.v.1992, I. Lansbury—1 ♂ (OUMNH); MOROBE, Lae (6°44'S, 147°0'E), 3.iii.1973, K.W. Stroeder—1 ♂ (CNC); **SOUTH AFRICA**: EASTERN CAPE, Black Rock (32°1'S, 29°6'E), 15.ii.1997, C.R. Owen—1 ♀, 1 ♂ (CEMT); East London (32°59'S, 27°52'E), [no date], Dr. Martin—1 ♂ (MNHN); East London (32°59'S, 27°52'E), 13.i.1976, R.E. Parrott—1 ♂ (CNC); East London

(32°59'S, 27°52'E), 15.ii.1976, R.E. Parrott—2 ♀♀, 1 ♂ (CNC); Grahamstown (33°18'S, 26°32'E), [no date], A. Vogt—1 ♂ (IRSNB); Mbotyi Coast and Forest (31°27'47"S, 29°43'58"E), 29.xi–3.xii.2003, W. Schawaller—2 ♀♀, 2 ♂♂ (SMNS); Port St. John, Pondoland (31°38'S, 29°32'E), x.1923, R.E. Turner—1 ♂ (BMNH); Port St. John, Pondoland (31°38'S, 29°32'E), 6–25.ii.1924, R.E. Turner—1 ♂ (BMNH); Silaka Wildlife Reserve, Port St. John (31°39'15"S, 29°30'20"E), 8.i.2009, P. Schüle—1 ♂ (PMOC); The Haven Hotel, Dwesa-Cwebe Wildlife Reserve & Marine Sanctuary (32°14'26"S, 28°54'38"E), 4–6.xii.2003, P. Schüle—1 ♂ (SMNS); Umtata [=Mthatha] (31°35'S, 28°47'E), 18.ii–18.iii.1923, R.E. Turner—2 ♂♂ (BMNH); FREE STATE, 20 km W Boshof (28°39'S, 25°4'E), 12–14.xii.1984, H. & A. Howden—2 ♂♂ (CMNC); Bloemfontein (29°8'S, 26°12'E), [no date], E. Eckersley—1 ♂ (BMNH); Florisbad (28°46'S, 26°5'E), 9–12.xii.1984, H. & A. Howden—1 ♀, 1 ♂ (CMNC); Kimberley (28°44'S, 26°46'E), [no date], [anonymous]—1 ♀, 2 ♂♂ (BMNH); Kimberley (28°44'S, 26°46'E), [no date], Rombach—1 ♂ (IRSNB); Vredefort (27°0'27"S, 27°22'6"E), 17.xii.2009, Perissinoto & Clennell—1 ♀, 1 ♂ (PMOC); GAUTENG, 15 mi. SW Johannesburg (26°25'S, 27°52'E), 28.xii.1971, Southern Africa Expedition ((3))—1 ♂ (BMNH); Boekenhoutskloof, 30 km NE Pretoria (25°32'S, 28°30'E), 4.i.1977, G. Bernon—2 ♀♀, 2 ♂♂ (BDGC); Boekenhoutskloof, 30 km NE Pretoria (25°32'S, 28°30'E), 7.i.1977, G. Bernon—1 ♀, 2 ♂♂ (BDGC); Boekenhoutskloof, 30 km NE Pretoria (25°32'S, 28°30'E), 7.xii.1977, G. Bernon—1 ♂ (CMNC); Boekenhoutskloof, 30 km NE Pretoria (25°32'S, 28°30'E), 5.ii.1978, G. Bernon—2 ♂♂ (BDGC); Castel Gorge, 42 mi. W Pretoria (25°49'S, 27°37'E), 27.ii.1972, Bornemissza & Insley—1 ♂ (MNHN); Die Wilgers Silverton (25°37'30"S, 28°7'30"E), iii.1986, C.H. Scholtz—4 ♂♂ (BMNH); Heidelberg (26°29'30"S, 28°23'0"E), 25.xii.1978, P. Walter—1 ♀ (PHWC); Johannesburg (26°12'S, 28°2'E), 28.xii.1971, Southern Africa Expedition—2 ♀♀, 2 ♂♂ (BMNH); Magalieskruin, Pretoria (25°41'9"S, 28°14'2"E), 31.x.1977, J. Boomker—1 ♀, 1 ♂ (BMNH); Nagana Research Laboratory, Onderstepoort (25°39'S, 28°11'E), 1922, H.H. Curson—3 ♂♂ (BMNH); Nagana Research Laboratory, Onderstepoort (25°39'S, 28°11'E), xii.1922, H.H. Curson—1 ♂ (BMNH); Pretoria (25°42'25"S, 28°13'46"E), [no date], W.L. Distant—2 ♀♀, 2 ♂♂ (BMNH); Pretoria (25°42'25"S, 28°13'46"E), iv.1962, S.C. K.—1 ♂ (BMNH); Pretoria (25°42'25"S, 28°13'46"E), iii.1963, W. R.—1 ♂ (BMNH); Pretoria (25°42'25"S, 28°13'46"E), [no date], L.M. Bucknill—2 ♂♂ (BMNH); Pretoria (25°42'25"S, 28°13'46"E), 1893, E. Simon—1 ♂ (MNHN); Pretoria (25°42'25"S, 28°13'46"E), 24.x.1914, [anonymous]—1 ♂ (BMNH); Pumulani (25°37'30"S, 28°7'30"E), 9.x.1981, T.J.H. Bernaro—1 ♂ (BMNH); Rietondale Research Station, Pretoria (25°43'49"S, 28°14'7"E), 5.ii.1978, G. Bernon—1 ♂ (BDGC); Rivonia (26°3'S, 28°3'E), 28.x.1967, M.I. Russell—1 ♂ (BMNH); Soetvelde (26°45'S, 28°1'E), 27.xii.1989, L.G. Le Roux—1 ♂ (BMNH); Soutpan near Pretoria (25°36'S, 28°10'E), 10.iii.1992, J. Klimaszewski—1 ♂ (CMNC); University of Pretoria Experimental Farm (25°44'49"S, 28°15'31"E), 3.vi.1985, D. D'Hotman—1 ♂ (BMNH); KWAZULU-NATAL, 30 km NW Nongoma, 808 m (27°41'S, 31°29'E), 28.i.2008, P. Schüle—1 ♀, 1 ♂ (PMOC); 5 mi. S Bergville (28°48'S, 29°23'E), 4–5.xii.1971, A.A. Kirk—1 ♂ (CMNC); Boschberg Farm, Ladysmith (28°14'S, 29°46'E), 9–11.i.2001, A.L.V. Davis—2 ♀♀, 2 ♂♂ (BMNH); Busland's Halt (28°0'S, 32°0'E), 15.i.1986, H.H. Aschenborn—1 ♀, 1 ♂ (BMNH); Cathedral Peak State Forest, 75 km WSW Estcourt (29°0'S, 29°15'E), 7–31.xii.1979, S. & J. Peck—2 ♂♂ (CMNC); Colenso (28°44'S, 29°49'E), ii–iii.1900, H.B. Marley—2 ♂♂ (BMNH); Durban (29°51'S, 31°1'E), 1902, F. Muir—1 ♂ (BMNH); Enseleni [=Mseleni] (27°22'13"S, 32°31'32"E), 15.x.2005, Perissinoto & Clennell—2 ♂♂ (PMOC); Enseleni [=Mseleni] (27°22'13"S, 32°31'32"E), 19.xi.2009, Perissinoto & Clennell—1 ♀ (PMOC); Estcourt (29°1'S, 29°53'E), [no date], [anonymous]—1 ♂ (BMNH); Estcourt (29°1'S, 29°53'E), 24.x.2009, Perissinoto & Clennell—1 ♂ (PMOC); Frere, 1158 m (28°53'35"S, 29°46'24"E), x.1891, G.A.K. Marshall—1 ♀, 1 ♂ (BMNH); Giants Castle, Drakensberg (29°16'S, 29°31'E), 27.xii.1978, P. Walter—2 ♀♀, 2 ♂♂ (PHWC); Hluhluwe Game Reserve (28°0'S, 32°0'E), i.1986, Aschenborn—1 ♂ (BDGC); Hluhluwe Game Reserve (28°0'S, 32°0'E), 3.i.1978, J.C. & E. Willame—1 ♂ (PHWC); Hluhluwe Game Reserve (28°0'S, 32°0'E), 30.xii.1978, P. Walter—1 ♀, 4 ♂♂ (PHWC); Hluhluwe Game Reserve (28°0'S, 32°0'E), 2.x.1985, E. Jane Wright—3 ♂♂ (BMNH); Hluhluwe Game Reserve (28°0'S, 32°0'E), 16.xi.1985, H.H. Aschenborn—6 ♀♀, 3 ♂♂ (BMNH); Hluhluwe Game Reserve (28°0'S, 32°0'E), 19–22.ii.1986, DBRU [= Dung Beetle Research Unit]—2 ♀♀, 2 ♂♂ (BDGC); Ithala Game Reserve (27°30'S, 31°14'E), 13–14.i.1999, A.L.V. Davis—3 ♀♀, 1 ♂ (BMNH); Ladysmith (28°33'S, 29°47'E), [no date], [anonymous]—1 ♀, 1 ♂ (BMNH); Ladysmith (28°33'S, 29°47'E), [no date], Dr. Martin—1 ♂ (MNHN); Malvern (29°53'S, 30°55'E), iii.1896, G.A.K. Marshall—1 ♂ (BMNH); Maritzburg (29°37'S, 30°23'E), xi.1896, [anonymous]—1 ♀, 1 ♂ (BMNH); Maritzburg (29°37'S, 30°23'E), ii.1896, J. Cregoe—2 ♀♀, 2 ♂♂ (BMNH); Mkuze (27°37'S, 32°2'E), iii.1984, O. Schmitt—1 ♂ (PMOC); Mtunzini (28°57'35"S, 31°45'0"E), 28.ix.2007, Perissinoto & Clennell—1 ♂ (PMOC); Ndumu Game Reserve (26°53'S,

32°16'E), 5–7.xi.1984, H. & A. Howden—1 ♀, 1 ♂ (CMNC); Newcastle (27°45'S, 29°56'E), [no date], J.P. Cregoe—2 ♀♀, 2 ♂♂ (BMNH); Nongoma (27°53'40"S, 31°38'34"E), 28.i.2008, Perissinoto & Clennell—2 ♀♀, 2 ♂♂ (PMOC); Nongoma (27°53'40"S, 31°38'34"E), 28.i.2008, P. Schüle—1 ♀, 1 ♂ (PMOC); Port Natal [=Durban] (29°51'S, 31°1'E), [no date], [anonymous]—2 ♂♂ (BMNH); Port Natal [=Durban] (29°51'S, 31°1'E), [no date], V. van De Poll—1 ♀, 1 ♂ (ZMUC); Royal Natal Park (28°42'S, 28°56'E), 3.i.1978, J. & E. Willame—1 ♀, 2 ♂♂ (PHWC); SW Magudu (27°34'S, 31°35'E), 4–5.i.2009, P. Schüle—2 ♀♀, 2 ♂♂ (SMNS); The Caverns Drakensberg (28°38'8"S, 28°57'43"E), 26.xii.1978, P. Walter—1 ♀ (PHWC); Umfolozi Game Reserve (28°7'S, 32°3'E), 11.xi.1970, H. & M. Townes—1 ♂ (CMNC); Umfolozi Game Reserve (28°7'S, 32°3'E), 2.i.1978, J. & E. Willame—1 ♀ (PHWC); Umfolozi Game Reserve (28°7'S, 32°3'E), 30.xii.1978, P. Walter—2 ♂♂ (PHWC); Umfolozi Game Reserve (28°7'S, 32°3'E), 5.x.2000, W. Grosser—2 ♀♀, 2 ♂♂ (OUMNH); uMkhuze Game Reserve (27°40'S, 32°15'E), 22–24.iii.1984, P.B. Edwards & H.H. Aschenborn—1 ♀, 1 ♂ (CMD); Weenen (28°51'S, 30°4'E), 1925, H.P. Thomasset—1 ♀, 2 ♂♂ (BMNH); Weenen (28°51'S, 30°4'E), iii.1928, H.P. Thomasset—1 ♂ (BMNH); Weenen (28°51'S, 30°4'E), xi.1923, H.P. Thomasset—1 ♂ (BMNH); LIMPOPO, Anthrax camp, Pafuri, Kruger National Park (22°25'S, 31°14'E), 9–24.xi.1985, M. Brigham—1 ♀, 1 ♂ (CMNC); Ellisras [= Lephalale] (23°40'S, 27°45'E), iv.1909, R. H.—1 ♂ (BMNH); Farm Sericea, Nylsvaley (24°25'48"S, 28°23'24"E), 27.xi.1985, S.L. Chown—5 ♂♂ (BDGC); Farm Sericea, Nylsvaley (24°25'48"S, 28°23'24"E), 11–12.xii.1985, A.V. Evans—1 ♂ (BMNH); Guernsey Farm, 15 km E Klaserie, 500 m (24°33'S, 31°9'E), 19–31.xii.1985, H. & A. Howden—1 ♂ (CMNC); Guernsey Farm, 15 km NE Klaserie (24°33'S, 31°9'E), 18–30.xii.1985, S. & J. Peck—1 ♀, 1 ♂ (CMNC); Guernsey Farm, 15 km NE Klaserie (24°33'S, 31°9'E), 18–31.xii.1985, S. & J. Peck—2 ♀♀, 2 ♂♂ (CMNC); Kruger National Park North (22°44'S, 31°11'E), 25.xi.2012, P. Richoux—1 ♀, 2 ♂♂ (CMD); Langjan (22°57'S, 28°15'E), 27.ii.1988, M. Vogt—1 ♂ (BMNH); Langjan Nature Reserve (22°52'30"S, 29°7'30"E), 21.ii.1987, W.Z. Schultz—1 ♂ (BMNH); Makapan (23°11'S, 28°36'E), 1893, E. Simon—1 ♂ (MNHN); Mmabolela estate (22°40'S, 28°15'E), 20–24.xi.1991, F. Génier—2 ♀♀, 1 ♂ (CMNC); Musina (22°21'S, 30°2'E), 28.ii.1998, F.M. Brits—1 ♂ (BMNH); Nwanedzi (23°45'28"S, 30°27'17"E), 28.xii.2009, Perissinoto & Clennell—1 ♀, 2 ♂♂ (PMOC); Radium (25°5'S, 28°17'E), 3.iii.1989, P. Snyman—1 ♂ (BMNH); Sentrum (24°18'S, 27°20'E), 11.iii.1989, E. Swanepoel—1 ♂ (BMNH); Shiluvane (24°3'S, 30°17'E), [no date], H.A. Junod—7 ♂♂ (IRSNB, MNHN); Steenbokpan (23°43'S, 27°15'E), 4.v.1988, E. Swanepoel—1 ♂ (BMNH); Thornybush Lodge, Hoedspruit (24°21'S, 30°57'E), 7.xii.1992, Jansen & Klimaszewski—1 ♂ (CMNC); Vaalwater (24°7'30"S, 28°22'30"E), 2.iii.1980, T.L. Prinsloo—1 ♂ (BMNH); Waterpoort (22°52'30"S, 29°22'30"E), iv.1978, I. Bruner—1 ♂ (BMNH); Woodside, Letsitele (23°53'25"S, 30°23'10"E), 15.iii.1976, R.E. Parrott—2 ♀♀, 3 ♂♂ (CMNC, CNC); MPUMALANGA, 10 km S Skukuza, Kruger National Park (25°4'6"S, 31°32'56"E), 12–14.xii.1985, E.G. Monroe—2 ♂♂ (CMNC); Barberton (25°47'S, 31°3'E), xi–xii.1908, L.C. de Beer—1 ♀, 2 ♂♂ (MNHN); Berg-en-Dahl Camp, Kruger National Park (25°25'24"S, 31°27'0"E), 15.xii.1984, M. Davis—1 ♀, 4 ♂♂ (CNC); Kaapmuiden (25°32'S, 31°20'E), 4–7.xii.1984, H. & A. Howden—2 ♂♂ (CMNC); Klaserie Nature Reserve (24°12'20"S, 31°12'19"E), 28.xi.1998, J.-F. Josso—1 ♂ (JFJC); Klaserie Nature Reserve (24°12'20"S, 31°12'19"E), 25–27.xi.2002, P. Schüle—2 ♂♂ (SMNS); Leeuwfontein (25°13'S, 28°53'E), 8.iv.1998, Jiya—1 ♂ (BMNH); Mariepskop, Blyde River, 800–1000 m (24°35'32"S, 30°52'56"E), 23–26.xi.2008, W. Schawaller—1 ♀, 1 ♂ (SMNS); Near Satara, Kruger National Park (24°24'S, 31°47'E), 15–18.xii.1985, H. & A. Howden—1 ♀, 1 ♂ (CMNC); Satara, Kruger N. Pk. (24°23'S, 31°43'E), 15–18.xii.1985, S. & J. Peck—1 ♀, 1 ♂ (CMNC); SE 25 31 Ad (25°22'30"S, 31°22'30"E), 17.ii.1981, S. Mostert—1 ♂ (BMNH); Skukuza Camp (24°59'40"S, 31°35'14"E), i.1999, D. Inward—5 ♀♀, 5 ♂♂ (BMNH); Skukuza, Kruger National Park (24°59'40"S, 31°35'14"E), 12–15.xii.1985, S. & J. Peck—2 ♀♀, 1 ♂ (CMNC); Skukuza, Kruger National Park (24°59'40"S, 31°35'14"E), 12–14.xii.1985, S. & J. Peck—1 ♂ (CMNC); Skukuza, Kruger National Park (24°59'40"S, 31°35'14"E), 12–14.xii.1985, H. & A. Howden—1 ♂ (CMNC); Skukuza, Kruger National Park (24°59'40"S, 31°35'14"E), 12.xii.1986, M. Sanborne—1 ♂ (CNC); Timbavati Game Reserve (24°28'S, 31°17'E), 23.i.1996, P. Holter—1 ♀, 3 ♂♂ (ZMUC); Timbavati river, Kruger National Park (24°5'S, 31°40'E), i.1999, D. Inward—2 ♀♀, 3 ♂♂ (BMNH); Tshokwana-Nwanedzi Road, Kruger National Park (24°37'S, 31°57'E), i.1999, D. Inward—2 ♀♀, 2 ♂♂ (BMNH); NORTH WEST, 16 km NW Brits (25°22'30"S, 27°37'30"E), xii.1977, E.E. Zocke—1 ♂ (BMNH); 20 km W Bothaville (27°19'48"S, 26°27'12"E), 31.i.2001, M. Snižek—1 ♀, 1 ♂ (CEMT); Baberspan (25°7'S, 26°5'E), 14–21.xii.1993, T. Joffe—1 ♂ (BMNH); Dinokana (25°27'S, 25°52'E), [no date], [anonymous]—1 ♀, 2 ♂♂ (SMF); Nieverdiend (25°7'30"S, 26°7'30"E), 8.i.1978, Holm, Jacobs, Kirsten, Scholtz—1 ♀, 1 ♂ (BMNH); Potchefstroom (26°43'S, 27°6'E), 6.xii.1913, [anonymous]—1 ♀, 2 ♂♂ (BMNH); Vryburg (26°57'S, 24°44'E), 1893, E. Simon—

1 ♀, 1 ♂ (MNHN); Zeerust (25°32'S, 26°5'E), [no date], P. Born—1 ♂ (IRSNB); NORTHERN CAPE, Farm Klipkoppies, 957 m (28°52'16.93"S, 21°18'33.98"E), 12–14.iii.2004, A.L.V. Davis & C. Deschodt—1 ♂ (CMNC); J. Kempdorp (27°52'30"S, 24°52'30"E), 5.xi.1983, F. van Eeden—1 ♂ (BMNH); Koegrabie Farm (1) (29°4'33.6"S, 21°46'5.63"E), 6–8.iii.2004, A.L.V. Davis & C. Deschodt—2 ♂♂ (PMOC); Pneil Road, 35 km W Kimberley (28°43'S, 24°21'E), 12–13.xii.1984, H. & A. Howden—1 ♂ (CMNC); SE 29 23 Bb (29°7'30"S, 23°52'30"E), iv.1978, J.P. Krygsman—1 ♂ (BMNH); WESTERN CAPE, Mossel Bay (34°11'S, 22°8'E), xii.1921, [anonymous]—1 ♂ (BMNH); **SWAZILAND**: MANZINI, Mlilwane Wildlife Sanctuary (26°29'S, 31°9'E), 13.xii.1984, M. Davis—1 ♀, 7 ♂♂ (CNC, FGIC); **TANZANIA**: Zanzibar, [no date], Raffray—1 ♂ (IRSNB); ARUSHA, Arusha (3°23'S, 36°41'E), 11.iii.1995, [anonymous]—1 ♀, 1 ♂ (OMOC); DAR ES SALAAM, Dar-es-Salaam (6°48'S, 39°17'E), iv.1924, W.A. Cutler—1 ♂ (BMNH); Dar-es-Salaam (6°48'S, 39°17'E), [no date], R. v. Bennigsen—1 ♂ (SMF); Dar-es-Salaam (6°48'S, 39°17'E), 2.iii.1925, F.W.H. Migeod—1 ♂ (BMNH); Dar-es-Salaam (6°48'S, 39°17'E), 14.ix.1961, G. Heinrich—1 ♀, 3 ♂♂ (CNC); Yombo (6°51'S, 39°14'E), 28.x.1992, W.R.B. Hynd—2 ♂♂ (BMNH); IRINGA, Mkimbizi Mountain (7°46'12"S, 35°41'24"E), 28.i.2006, K. Angelus—1 ♀, 1 ♂ (PMOC); Mkimbizi-Bima Mountain, 20.ii.2006, K. Angelus—1 ♂ (PMOC); LINDI, Nachingwea, Mtokokuyana (10°23'51"S, 38°53'55"E), 21–24.xii.2009, Local collectors—1 ♀, 1 ♂ (PMOC); MOROGO, Morogoro area (6°49'20"S, 37°39'40"E), 21.xi.1989, P. Holter & C. Sommer—2 ♀♀, 1 ♂ (ZMUC); MOROGORO, Beho Beho Camp, Selous Game reserve (7°36'44"S, 37°50'23"E), 8–11.i.2001, T. Bouyer—2 ♀♀, 2 ♂♂ (PMOC); Kisaki (7°29'S, 37°36'E), i–v.2011, Local collectors—4 ♀♀, 5 ♂♂ (BMNH); Magubike, 787 m (8°18.049'S, 37°13.005'E), 20.ii.2010, P. Darge—5 ♀♀, 5 ♂♂ (MHNL, PMOC); Mhonda-Ouzingua [=Station du Sacré-Coeur de Mhonda] (6°3'36"S, 37°21'36"E), 1879–i–iii.1880, A. Hacquard—1 ♀, 1 ♂ (MNHN); Savane à l'O. de Mikesse, 525 m (6°43.752'S, 37°51.395'E), 29.iv.2005, R. Minetti—2 ♀♀, 2 ♂♂ (PMOC); Uluguru Mountains (7°6'S, 37°39'E), 27–29.xi.2005, [anonymous]—2 ♀♀, 2 ♂♂ (PMOC); PEMBA NORD, Ngezi Forest (4°55'35"S, 39°42'4"E), viii.1994, [anonymous]—1 ♀ (JFJC); PWANI, 70 km E Morogoro, 300 m (6°38'S, 38°8.2'E), 12.xii.2006, F. Kantner—2 ♀♀, 1 ♂ (SMNS); Bagamoyo (6°26'S, 38°54'E), [no date], H. Schaedle—2 ♀♀, 2 ♂♂ (BMNH, MNHN); Mandera, 166 m (6°14.3'S, 38°23.197'E), 7.xii.2008, P. Darge—2 ♀♀, 2 ♂♂ (MHNL); Mwetemo, 191 m (6°21.808'S, 38°30.852'E), 9.xii.2008, P. Darge—2 ♀♀, 1 ♂ (MHNL); Route Dar-es-Salam-Chalinze, 40 m (6°40.739'S, 38°40.188'E), 1.v.2005, R. Minetti—2 ♀♀, 2 ♂♂ (PMOC); Utende Base Camp, Mafia Island, 15 m (7°58'46"S, 39°44'31"E), 3.xii.1992, [anonymous]—2 ♀♀, 3 ♂♂ (BMNH); TANGA, Tanga (5°5'30"S, 39°6'0"E), iv.1912, Alluaud & Jeannel—1 ♂ (MNHN); Tanga (5°5'30"S, 39°6'0"E), [no date], Gierra—2 ♂♂ (MNHN); Tanga (5°5'30"S, 39°6'0"E), iii.1916, Methner—1 ♂ (NMPC); **UGANDA**: CENTRAL, Tero Forest (0°50'S, 31°40'E), 26–30.ix.1911, S.A. Neave—1 ♂ (BMNH); **UNITED STATES OF AMERICA**: ARIZONA, Santa Cruz County, Harshaw Creek Road (31°30'53"N, 110°41'32"W), 10–18.viii.1990, L. Desaulniers—1 ♂ (CMNC); FLORIDA, Alachua County, Paynes Prairies Preserve State Park (29°34'8"N, 82°18'3"W), 25.iv.1996, R. Vigneault—1 ♀, 1 ♂ (PMOC); HAWAII, Honolulu County, Ewa, O'ahu (21°20'29"N, 158°2'14"W), 6.i.1961, D.F. Hardwick—1 ♂ (CNC); Honolulu County, Ewa, O'ahu (21°20'29"N, 158°2'14"W), 10.ii.1961, D.F. Hardwick—2 ♀♀, 3 ♂♂ (CNC); Honolulu (21°18'N, 157°51'W), 30.ix.1966, J.R. Vockeroth—1 ♂ (CNC); Honolulu (21°18'N, 157°51'W), 1.xii.1966, J.R. Vockeroth—2 ♀♀, 2 ♂♂ (CNC); Honolulu (21°18'N, 157°51'W), 27.xii.1966, J.R. Vockeroth—2 ♀♀, 2 ♂♂ (CNC); Honolulu (21°18'N, 157°51'W), 20.i.1967, J.R. Vockeroth—1 ♀, 1 ♂ (CNC); Ka'Ena Point, O'ahu (21°34'6"N, 158°14'53"W), 11.i.1960, [anonymous]—2 ♂♂ (CNC); Makapuu Point, O'ahu (21°18'30"N, 157°39'5"W), 16.i.1961, D.F. Hardwick—3 ♀♀ (CNC); Manoa, Honolulu (21°18'57"N, 157°48'12"W), 27.vii.1963, D.M. Tsuda & R.M. Young—1 ♂ (MNHN); South end Waianae Mountains, 244 m (21°28'19"N, 158°7'36"W), 18.i.1961, D.F. Hardwick—3 ♀♀, 3 ♂♂ (CNC); Wailupe Valley, 305 m (21°18'24"N, 157°45'12"W), 14.iii.1961, D.F. Hardwick—1 ♀, 1 ♂ (CNC); Waipio, O'ahu (21°24'52"N, 157°59'44"W), 11.i.1961, D.F. Hardwick—3 ♀♀ (CNC); Waipio, O'ahu (21°24'52"N, 157°59'44"W), 18.i.1961, D.F. Hardwick—2 ♂♂ (CNC); West side Ka'Ena Point (21°34'28"N, 158°16'37"W), 14.i.1961, D.F. Hardwick—1 ♀, 2 ♂♂ (CNC); West side Ka'Ena Point (21°34'28"N, 158°16'37"W), 21.i.1961, D.F. Hardwick—4 ♀♀, 2 ♂♂ (CNC); Maui County, Hana (20°45'27"N, 155°59'18"W), 22.ii.2004, B. & M. Holme—1 ♂ (CMNC); SOUTH CAROLINA, Chesterfield County, Hwy 151, approx. 10.7 mi. NW McBee (34°33'57"N, 80°22'1"W), 11.v.2002, J.P. Gruber—1 ♂ (CMD); TEXAS, Medina County, Hondo (29°20'49"N, 99°8'44"W), 26.x.1982, B.F. & J.L. Carr—1 ♂ (CNC); Presidio County, 10 km S Ruidosa, 800 m (29°45'45"N, 104°33'17"W), 16.viii.2007, Mann & Edmonds—1 ♂ (OUMNH); Humphrey Ranch, approximately 30 km SE Marfa (hwy 169), 1250 m (30°2'34"N, 104°1'18"W), 10.viii.2007, Mann & Edmonds—1 ♀ (OUMNH); Miller

Ranch, approximately 20 km W Valentine, 1390 m (30°32'50"N, 104°39'40"W), 13.viii.2007, Mann & Edmonds—1 ♀ (OUMNH); Presidio (29°34'N, 104°22'W), 2.x.1982, B.F. & J.L. Carr—1 ♂ (CNC); Ruidosa (29°59'37"N, 104°40'42"W), 16.viii.2007, Mann & Edmonds—1 ♂ (OUMNH); **VANUATU**: SHEFA, Epi (16°44'S, 168°16'E), 12.xii.2007, P. Moulin—2 ♀♀, 2 ♂♂ (PMOC); **ZAMBIA**: CENTRAL PROVINCE, 25 km NE Lilemone, 1250 m (15°13'14"S, 26°19'41"E), 11.xii.2009, S. Rojkoff—1 ♂ (PMOC); 6 km N Chunga, 1075 m (14°59'39"S, 26°1'11"E), 4.xii.2010, S. Rojkoff—1 ♀, 1 ♂ (OMOC); 6.2 km W Mukambi Lodge Junction on M9, 1100 m (14°57'2"S, 25°56'21"E), 18.xi.2010, F. Génier (2010-02)—10 ♀♀, 12 ♂♂ (FGIC); 6.2 km W Mukambi Lodge Junction on M9, 1100 m (14°57'2"S, 25°56'21"E), 4.xii.2010, F. Génier (2010-42)—1 ♀, 2 ♂♂ (FGIC); 6.5 km N Chunga, 1100 m (14°59'40"S, 26°1'11"E), 4.xii.2010, F. Génier (2010-43)—12 ♀♀, 12 ♂♂ (FGIC); Huntley Farm, Chisamba, 1122 m (15°0'33.57"S, 28°8'41.91"E), 26–27.xi.2005, S. Beynon & M. Jubb—1 ♂ (OUMNH); Mayukuyuku Camp (14°54'58"S, 26°3'55"E), 13.xii.2009, Josso, Juhel, & Minetti—1 ♀, 1 ♂ (JFJC); Mukambi Safari Lodge, 1250 m (14°58'32"S, 25°59'29"E), 8.xii.2010, F. Génier (2010-50)—10 ♀♀, 10 ♂♂ (FGIC); Mukambi Safari Lodge, 1250 m (14°58'32"S, 25°59'29"E), 9.xii.2010, F. Génier (2010-52)—14 ♀♀, 14 ♂♂ (FGIC); route principale, Kafue National Park (14°57'S, 25°52'E), 8.xii.2008, J.F. Josso & R. Minetti—1 ♀, 1 ♂ (JFJC); route principale, Kafue National Park (14°57'S, 25°52'E), 16–17.xii.2008, J.F. Josso & R. Minetti—1 ♂ (JFJC); Zambeef Farming Limited, 1122 m (15°0'33.57"S, 28°8'41.91"E), 25–26.xi.2005, S. Beynon & M. Jubb—1 ♂ (OUMNH); Zambeef Farming Limited, 1122 m (15°0'33.57"S, 28°8'41.91"E), 26–27.xi.2005, S. Beynon & M. Jubb—1 ♂ (OUMNH); Zambeef Farming Limited, 1122 m (15°0'33.57"S, 28°8'41.91"E), 28–29.xi.2005, S. Beynon & M. Jubb—1 ♀, 1 ♂ (OUMNH); Zambeef Farming Limited, 1122 m (15°0'33.57"S, 28°8'41.91"E), 29–30.xi.2005, S. Beynon & M. Jubb—1 ♀, 1 ♂ (OUMNH); COPPERBELT, Chingola (12°33'S, 27°52'E), 20.xi.1989, [anonymous]—1 ♀, 2 ♂♂ (CVM, OUMNH); Chingola (12°33'S, 27°52'E), 22.xi.1989, [anonymous]—1 ♂ (OUMNH); Kishikishi, Rural Ndola (12°59'S, 28°39'E), [no date], Samukole—1 ♂ (FETC); LUSAKA PROVINCE, 30 km E Lusaka (15°16'S, 28°56'E), 20.iii.1991, P. Schüle—1 ♂ (SMNS); Kafue City - Kafue River, 1200 m (16°3'S, 28°30'E), 22.xi–2.xii.1987, R. Mourglia—2 ♀♀, 2 ♂♂ (CVM); NORTH-WESTERN PROVINCE, Chimfunzi Nature Reserve, 1312 m (12°21.95'S, 27°28.93'E), 9–11.xi.2001, B. & J. Gill—1 ♂ (BDGC); NORTHERN PROVINCE, Chocha (8°26'S, 29°48'E), 21.i.1944, H.-J. Brédo—1 ♂ (IRSNB); Chocha (8°26'S, 29°48'E), 1.ii.1944, H.-J. Brédo—3 ♂♂ (FGIC, IRSNB); Kaputa (8°28'13"S, 29°40'4"E), 3.ii.1944, H.-J. Brédo—2 ♂♂ (IRSNB); Lake Mweru Mantipa (8°40'S, 29°36'E), [no date], H.-J. Brédo—1 ♂ (IRSNB); Sumbu (8°31'30"S, 30°28'30"E), [no date], J. Duvivier—1 ♂ (IRSNB); SOUTHERN PROVINCE, 12 km NE Choma (16°38'32"S, 27°1'47"E), 16.i.2010, P. Schüle—2 ♀♀, 2 ♂♂ (PMOC); Bruce-Miller Game Farm, 18 km NNW Choma, 1170 m (16°38.22'S, 27°1.51'E), 6–8.xi.2001, B. & J. Gill—4 ♀♀, 2 ♂♂ (BDGC); Bruce-Miller Game Farm, 18 km NNW Choma, 1170 m (16°38.22'S, 27°1.51'E), 22–24.xi.2001, B. & J. Gill—2 ♀♀, 2 ♂♂ (BDGC); Bruce-Miller Game Farm, 18 km NNW Choma, 1170 m (16°38.22'S, 27°1.51'E), 26.xi–7.xii.2013, Josso, Juhel, & Minetti—1 ♂ (FGIC); Livingstone, Zambesi River (17°51'S, 25°52'E), ii.1913, H.C. Dollman—1 ♂ (BMNH); Livingstone, Zambesi River (17°51'S, 25°52'E), i.1913, H.C. Dollman—1 ♂ (BMNH); Livingstone, Zambesi River (17°51'S, 25°52'E), 30.i.1913, H.C. Dollman—1 ♂ (BMNH); Namwazi (15°57'S, 28°4'E), 1.vi.1916, H.C. Dollman—1 ♀, 1 ♂ (BMNH); Namwazi (15°57'S, 28°4'E), 4.vi.1916, H.C. Dollman—3 ♂♂ (BMNH); Nkwali Camp, South Luangwa GMA (13°7'3"S, 31°44'16"E), 10–18.xi.2012, R. Smith & H. Takano—3 ♀♀, 2 ♂♂ (BMNH); WESTERN PROVINCE, 13 km W Sesheke, 1000 m (17°26'55"S, 24°10'15"E), 7.xii.2013, S. Rojkoff—1 ♂ (CMD); Lealui (15°14'S, 23°1'E), 1919, V. Ellenberger—3 ♀♀, 3 ♂♂ (MNHN); Lealui (15°14'S, 23°1'E), 1915, V. Ellenberger—2 ♂♂ (MNHN); **ZIMBABWE**: BULAWAYO, Bulawayo (20°9'S, 28°35'E), [no date], [anonymous]—1 ♀, 4 ♂♂ (BMNH, FGIC, IRSNB); HARARE, 15 km N Harare (17°37'8"S, 30°57'59"E), 24.xii.1995, A. Thilliez—1 ♂ (PMOC); Harare (17°49'4"S, 31°2'41"E), 1989, G. Nazaret—1 ♀, 1 ♂ (CMD); Salisbury, 1524 m (17°49'S, 31°3'E), xi.1898–i.1899, G.A.K. Marshall—3 ♀♀, 3 ♂♂ (OUMNH); Salisbury [=Harare] (17°49'4"S, 31°2'41"E), i.1906, G.A.K. Marshall—1 ♀, 1 ♂ (BMNH); Salisbury [=Harare] (17°49'4"S, 31°2'41"E), [no date], G.A.K. Marshall—1 ♀, 1 ♂ (BMNH); MANICALAND, 15 mi. N Umtali [=Mutare] (18°47'S, 32°41'E), 9.iv.1971, Bornemissza & Aschenborn—1 ♂ (CMNC); Umtali [=Mutare] (18°58'S, 32°40'E), xii.1901, G.A.K. Marshall—1 ♂ (BMNH); Umtali [=Mutare] (18°58'S, 32°40'E), iii.1957, N.L.H. Krauss—5 ♂♂ (neotype) (ZMUK); MASHONALAND EAST, Enkeldoorn [=Chivhu] (19°1'S, 30°54'E), [no date], E.S. Youngs—5 ♀♀, 6 ♂♂ (BMNH); Marandellas (18°11'S, 31°33'E), ii.1962, J.S. Weir—2 ♀♀, 2 ♂♂ (BMNH); Marandellas (18°11'S, 31°33'E), 8.iv.1971, Bornemissza & Aschenborn—1 ♂ (CMNC); MASHONALAND WEST, 20 km SE Karoi (16°58'39"S, 29°49'3"E), 10.xii.2005, S. Rojkoff & K. Werner—2 ♂♂ (CMD, PMOC); Atlantica, 16 mi. W

Harare (17°51'S, 30°47'E), i.1974, M.B. Fenton—1 ♀, 1 ♂ (CMNC); MASVINGO, Bubi River, 95 km NE Beitbridge (21°42'26"S, 30°30'0"E), 12–27.xii.2005, P. Schüle—1 ♀ (PMOC); Lake Kyle, Lake Mutirikwe (20°12'36"S, 31°2'29"E), 27.xi.2006, P. Schüle—1 ♂ (PMOC); MATEBELELAND NORTH, Hwange National Park, Main Camp near pan 5 (18°44'S, 26°57'E), 10.xi.1961, J.S. Weir—2 ♀♀, 3 ♂♂ (BMNH); Inyati (19°41'S, 28°51'E), i.1969, R. Nielson—1 ♂ (BMNH); Lonely Mine (19°30'S, 28°45'E), [no date], A. Swale—1 ♂ (BMNH); Lonely Mine (19°30'S, 28°45'E), 13.i.1913, H. Swale—1 ♂ (BMNH); Lonely Mine (19°30'S, 28°45'E), 15.i.1914, H. Swale—1 ♂ (BMNH); Lonely Mine (19°30'S, 28°45'E), 3.xii.1914, H. Swale—2 ♂♂ (BMNH); Wankie Nat. Park, Pan 0.8 (18°45'S, 26°0'E), xi.1961, J.S. Weir—1 ♂ (BMNH); MATEBELELAND SOUTH, 20 km W Gwanda, 120 km SE Bulawayo (20°58'19"S, 28°50'13"E), 6.xii.1999, Kantner—2 ♀♀, 2 ♂♂ (SMNS); Matopos, 35 km S Bulawayo (20°30'20"S, 28°26'11"E), 31.i.1996, F. Kantner—2 ♀♀, 2 ♂♂ (SMNS); MIDLANDS, Ngezi Recreational Park, 60 km E Kwekwe (18°41'S, 30°24'E), 1.xii.1998, F. Kantner—2 ♀♀, 1 ♂ (SMNS).

Natural history. In fact, very little is known about the natural history and ecology of *D. gazella* in the field within its native distribution. The main contributions were performed in controlled environments and were part of "The Australian dung beetle project" (Bornemissza 1976) initiated to introduce *D. gazella* in Australia. A second series of studies were done for a subsequent introduction in continental United States of America. For more information, Bornemissza (1970, 1976), Blume & Aga (1975, 1978), Fincher *et al*. (1986), Gutierrez *et al*. (1988) are among more than 200 applied entomology publications related to "*O. gazella*". The Rougon & Rougon (1980, 1983) studies on the nesting behavior and the morphology of the larvae applies to a different Sahelian species, presumably *D. eucatta*.

Nomenclature and taxonomy. An application was submitted to the International Commission of Zoological Nomenclature on 20 October 2016 (Génier & Krell 2017) and was assigned case number 3722. The application is made to maintain prevailing usage of the species name *D. gazella* for the widely introduced species through the process of setting aside all previous type fixations for the nominal species *Scarabaeus gazella* Fabricius and the designation of a neotype.

The circumstances with the type material of *Scarabaeus gazella* are more intricate. In this case we are in presence of three putative syntypes. Unlike the syntypes of *S. catta*, these three specimens all bear a small green square typical of Fabrician types (Zimsen 1964). There is a well-developed male (10.5 mm), a small male (8.0 mm) with secondary sexual characters resembling a female, and a moderately large female (10.0 mm). The large male and the female bear a handwritten label with the following information: "Guinea, Isert, Mus. T. Lund, *Copris gazella* F." These labels were added at least 14 years after the species was originally described, as the generic name used on these labels is *Copris*, a genus Fabricius used for the first time in Fabricius (1801). After a careful study of these three specimens, which include the dissection and examination of the internal sac sclerites of the two males, we conclude that this series is a mixture of two species. The large male is a representative of the oriental species *D. catta* and the small male and female are representative of the West African species *D. falciger*. At this point, there is no realistic possibility of finding out the true historical details about these specimens. The most likely chain of events is that Fabricius had only the large male specimen lacking geographic information when he described the species in the appendix of the second volume of *Mantissa Insectorum* published in December 1787 (Evenhuis 1997; Bousquet 2016). The original description is clear: "occipite cornubus duobus arcuatis", and can only apply to the specimen with two well-developed cephalic horns. We can only speculate on the number of specimens seen by Fabricius at the time of the description. Subsequently, Fabricius had received two additional specimens from Tønder Lund collected in Africa (Guinea), which he identified as his *S. gazella* and added the new information on the distribution five years later in the *Entomologia systematica* (Fabricius 1792).

The currently recognized synonymy for *D. gazella* was established by d'Orbigny (1913). The first species listed is *Scarabaeus catta* Fabricius, the entry is preceded by a question mark indicating that this synonymy is dubious. There is, however, no indication as to why d'Orbigny considered this synonymy dubious. This synonymy is here resolved on the principle of priority and the name *D. catta* is valid for an oriental species. The second synonym listed is *Scarabaeus dorcas* Olivier, described from Madagascar. This name is as a synonym of *D. gazella* assuming that the International Commission on Zoological Nomenclature rules on the conservation of the name *D. gazella* for the widely introduced species. The third species listed is *Copris metallicus* Fabricius, described from India. The holotype (by monotypy) of the species has been studied and despite the fact that it is missing the head and prothorax, it can be stated here that it does not belong to the genus *Digitonthophagus*. It is an *Onthophagus* of the *Onthophagus orientalis* species group and most likely belonging to the subgenus *Sinonthophagus* Kabakov.

The species is therefore here removed from synonymy with *D. gazella* and considered valid with the following combination *Onthophagus metallicus* (Fabricius). It should be noted here that a junior homonym, *Onthophagus metallicus* Fåhraeus, exists as a synonym of *Proagoderus bicallosus* (Klug). The fourth species listed is *Copris antilope* Fabricius, also described from India. Three syntypes are in ZMUC and an additional specimen in the ZMUK. The examination of the specimens revealed that they do not belong to the genus *Digitonthophagus* but rather belong to the genus *Onthophagus* and are similar to *Onthophagus* (*Colobonthophagus*) *dama* (Fabricius). The species is therefore here removed from synonymy with *D. gazella* and considered valid with the following combination *Onthophagus antilope* (Fabricius). Again, it should be noted here that a junior homonym, *Onthophagus antilope* Motschulsky exists, the latter is a synonym of *Onthophagus* (*Palaeonthophagus*) *vacca* Linnaeus. It is beyond the scope of this work to determine if *O. antilope* is synonymous with *O. dama*. The fifth name listed as synonyms is *Onthophagus intermedius* Reiche with a type locality "Sénégal." This name was first listed as "*O. gazella* var. *intermedius* Dupont" a variety of *Onthophagus gazella* in Dejean (1836) and is a ***nomen nudum***. A specimen of *D. sahelicus* with a small manuscript label stating "1395" and a second manuscript label stating, "*intermedius* Reiche. *gazella* ? Fab. Senegal" was found in the BMNH collection. It is not clear if this is a specimen acquired from Dupont's collection by The Natural History Museum of London. Reiche (1840) stated that Dupont, who was a prominent natural history specimen merchant in the 19th century (Cambefort 2006), was the first to use the name *O. intermedius* for specimens in his collection. The name *O. intermedius* Reiche is, however, unavailable as it was first published in an available work as a synonym of "*Onthophagus gazella*" (Article 11.6; International Commission on Zoological Nomenclature 1999).

Digitonthophagus petilus **Génier, new species**

http://zoobank.org/urn:lsid:zoobank.org:act:4B8CB6CC-46E9-49CC-9A3D-5C8C74A4F878

(Figs. 15, 39–40, 63, 79, 103–104, 127, 159–161; Map 10)

Type locality. El Wak, North Eastern Province, Kenya.

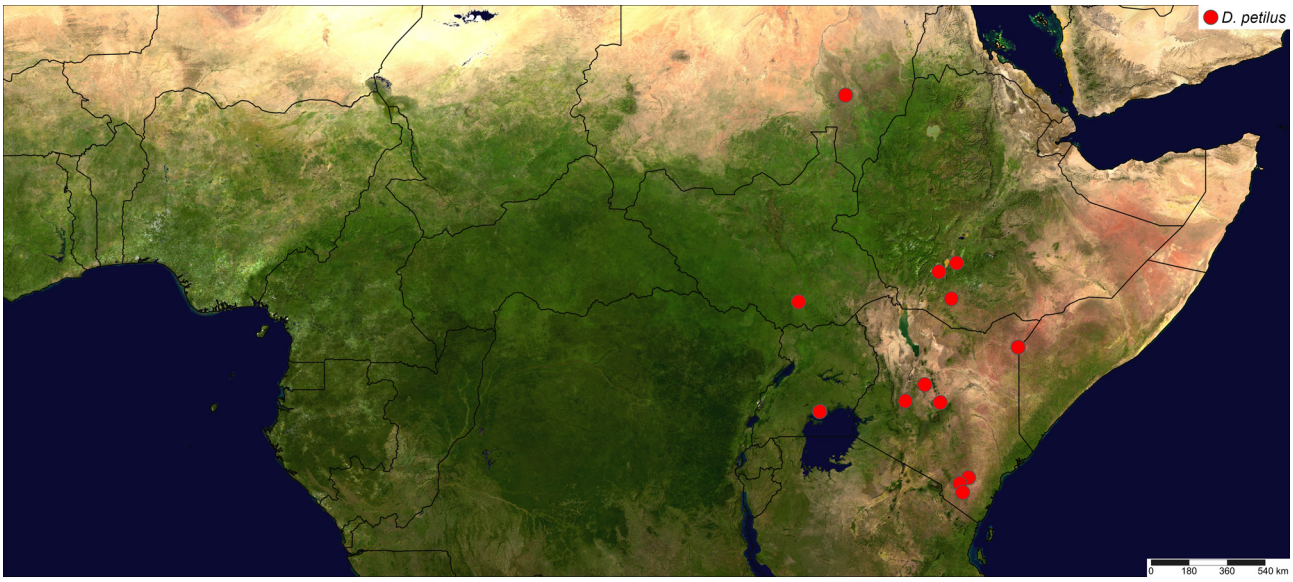
Diagnosis. Pronotum rather opaque (Fig. 63); FLP sclerite subapicodorsal lobe strongly produced anteriorly (Figs. 159–160); right lateral fold produced into a longitudinal spoon-shape process with apical portion open ventrally, ventral edge with a brush of minute villi, lacking well-sclerotized projection on apicoventral edge (Fig. 160); axial sclerite shorter than subaxial sclerite, acute apically (Figs. 159–160); subaxial sclerite long and thin (Fig. 160).

Description. Holotype ♂ (Fig. 15). **Measurements**. Length 11.5 mm, width 6.0 mm. **Head** (Figs. 39–40). Anterior clypeal edge straight on median fifth in dorsal view; clypeofrontal carina broadly arcuate and interrupted at gena; vertex lacking median tubercle, surface with punctures fine to small, separated by one to four diameters. Horns rather short, divergent from base to apex in frontal view, gradually tapering from base to apex; posterointernal edge with a low angular projection; apicointernal surface lacking granules, with few feebly scabrous punctures; genal edge slightly upturned and feebly angulate on anterior third, forming a broad angle with clypeal edge. **Pronotum** (Fig. 63). Surface with granulate punctures restricted to anterior half, with moderately large punctures on posterior half of disc; punctures smaller posterolaterally, with minute punctures distinct and rather dense throughout. Anteromedian tubercle atrophied, simply round in lateral view; median longitudinal sulcus narrow and shallow; surface behind the eyes with a simple round shallow depression, surface of anterior angles convex; anterior half of lateral edge arcuate in dorsal and lateral view; posterior angles slightly upturned and simply arcuate in dorsal view. Anterior hypomeral ridge broadly arcuate anteriorly, anterior hypomeral depression surface light in color. **Elytra** (Fig. 15). Intervals 2 and 4 with few scattered, fine granules on apical declivity. **Legs**. Protibial apicointernal tooth enlarged, with dorsal ridge extending to apex. **Aedeagus** (Fig. 127). Parameres with dorsal and ventral edges slightly diverging toward apex in lateral view. **Internal sac sclerites** (Figs. 159–161). Axial sclerite broadly arcuate, with apex acute. Subaxial sclerite, gradually tapering from base to mid-distance, fine and straight on apical half, extending straight beyond apex of right lateral fold of frontolateral peripheral sclerite apical portion, with villi on apical third. Frontolateral peripheral sclerite basoventral apophysis well developed; lacking medioventral carinae; right lateral fold produced into longitudinal spoon-shape process with apical portion open internally, ventral edge bordered with a brush of villi; left lateral lobe membranous, slightly developed; subapicodorsal lobe membranous, reaching anterior edge, apex set on right side in dorsal view; apical lobe round

and directed obliquely on left side and bent ventrally, left edge emarginate, apical villi similarly shaped throughout; subapicoventral lobe apical portion acute and in line with apical lobe apically, with distinct villi on apical third.

Variation. Measurements (50 ♂♂, 40 ♀♀). Length: male 8.0–12.0 mm (10.1 ± 1.0 mm), female 8.0–11.0 mm (9.7 ± 0.7 mm). Female allotype. Cephalic outline in dorsal view as in Fig. 79; vertex with a straight, transverse carina, dorsal edge broadly arcuate in frontal view, lateral portion gradually sloping down; anterior pronotal tubercles atrophied, external lateral edges parallel sided, anterolateral surface simply convex, anterosuperior edge slightly arcuate in dorsal view (Fig, 103), lateral portion of anterosuperior edge slightly upturned (Fig. 104). Protibia short, with external teeth more robust.

Primary type data. Holotype ♂ (CMNC): [KENYA: NE PROV. / El Wak / 1-3.V.2001 / Werner & Smrz leg.]; [WORLD / SCARAB. / DATABASE / WSD00029750] barcode label; [HOLOTYPE ♂ / *Digitonthophagus* / *petilus n.sp.* / des. F. Génier, 2016] red card.



MAP 10. Distribution of *Digitonthophagus petilus*.

Material examined (69 ♂♂, 63 ♀♀), distribution (Map 10): **ETHIOPIA**: OROMIA, Yabelo (4°53'N, 38°5'E), iv.1994, Werner—1 ♂ (paratype) (CMD); SOUTHERN NATIONS, NATIONALITIES, AND PEOPLE'S REGION, Arba Minch (6°2'N, 37°33'E), 11–17.ix.2000, P. Léonard—23 ♀♀, 22 ♂♂ (45 paratypes) (FGIC, PMOC); Dila (6°24'30"N, 38°18'30"E), ix.2000, P. Léonard—1 ♂ (paratype) (PMOC); **KENYA**: Tsavo National Park [=Tsavo East National Park] (2°45'S, 38°49'E), 18.x.1973, T.J. Kingston—1 ♀, 3 ♂♂ (4 paratypes) (OUMNH); Tsavo National Park [=Tsavo East National Park] (2°45'S, 38°49'E), 9.xi.1973, T.J. Kingston—1 ♀, 1 ♂ (paratypes) (OUMNH); Tsavo National Park [=Tsavo East National Park] (2°45'S, 38°49'E), 13.xi.1973, T.J. Kingston—1 ♀ (paratype) (OUMNH); Tsavo National Park [=Tsavo East National Park] (2°45'S, 38°49'E), 18.xi.1973, T.J. Kingston—1 ♀ (paratype) (OUMNH); Tsavo National Park [=Tsavo East National Park] (2°45'S, 38°49'E), 21.xi.1973, T.J. Kingston—3 ♀♀, 1 ♂ (paratypes) (OUMNH); Tsavo National Park [=Tsavo East National Park] (2°45'S, 38°49'E), 10.xii.1973, T.J. Kingston—1 ♀ (paratype) (OUMNH); Tsavo National Park [=Tsavo East National Park] (2°45'S, 38°49'E), 15.xii.1973, T.J. Kingston—1 ♂ (paratype) (OUMNH); BARINGO, Loiminange, 980 m (0°31'N, 36°7'E), 24.x.1988, M.N. Mungal & R.K. Butlin—6 ♀♀, 5 ♂♂ (11 paratypes) (OUMNH); ISIOLO, 10 km N Isiolo (0°27'14"N, 37°36'36"E), 16.xii.1990, B.D. Gill—7 ♀♀, 11 ♂♂ (18 paratypes) (BDGC); MANDERA, El Wak (2°49'N, 40°56'E), 1–3.v.2001, Werner & Smrz—10 ♀♀, 9 ♂♂ (holotype, allotype, 17 paratypes) (CMD, CMNC); RIFT VALLEY, Samburu National Reserve (1°13'N, 36°57'E), 4.xii.1989, Moreno-Mestre—1 ♀, 3 ♂♂ (4 paratypes) (PMOC); TAITA TAVETA, Tsavo, 50 km N Voi (3°0'S, 38°27'E), 25.xii.1990, B.D. Gill—1 ♀, 4 ♂♂ (5 paratypes) (BDGC); Voi, Tsavo East National Park (3°23'S, 38°34'E), 31.xii.1990, B.D. Gill—3 ♀♀, 2 ♂♂ (5 paratypes) (BDGC); **SOUTH SUDAN**: CENTRAL EQUATORIA, Rejaf (4°45'N, 31°34'E), 29.xii.1911, [anonymous]—4 ♀♀, 2 ♂♂ (6 paratypes) (MNHN); **SUDAN**: SENNAR, Sennar (13°34'N, 33°34'E), [no date], Tritsch—1 ♂ (paratype) (SMF); **UGANDA**: CENTRAL, Entebbe (0°4'N, 32°28'E), [no date], H. Rolle—2 ♂♂ (2 paratypes) (IRSNB).

Etymology. *Petilus* is a Latin adjective (frail, slight, puny) pertaining to the aspect of the apical portion of the internal sac subaxial sclerite (SA).

Natural history. Some specimens collected in buffalo, cow, and elephant dung.

Remarks. We first regarded *D. petilus* as a northern population of *D. gazella*. The very similar configuration of the right lateral fold and lacking the ventral sclerotized projection was nearly identical to typical *D. gazella*. But after careful observations of the FLP sclerite, several additional congruous characters were found; the much more developed subapicodorsal lobe and the much narrower subapicoventral lobe with its apex covered with distinct villi (Figs. 159–161) combined with the external characters such as the overall dorsum dull aspect and smaller average size are consistent. The possibility that *D. petilus* could be a subspecies of *D. gazella* needs to be tested. However, the fact that its distribution is parapatric with *D. gazella* seems to preclude this possibility.

Digitonthophagus viridicollis Génier, new species

http://zoobank.org/urn:lsid:zoobank.org:act:11622669-B240-4DF1-AF7B-0757A587DCEF
(Figs. 16, 41–42, 64, 80, 105–106, 128, 162–164, 186; Map 11)

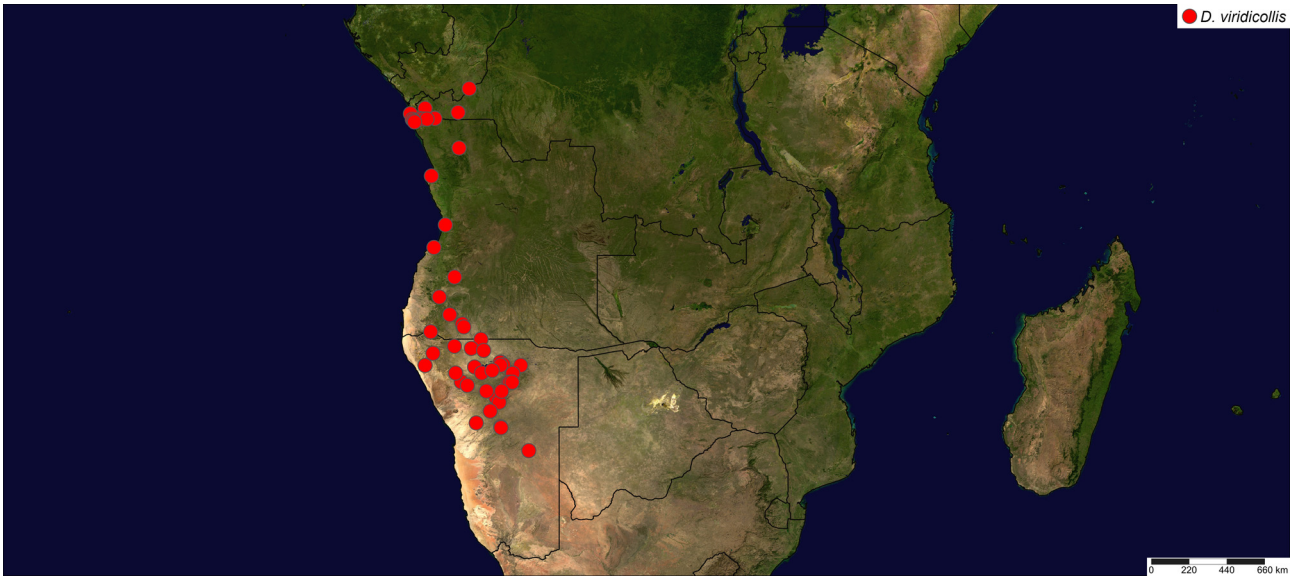
Type locality. Moanda, Zaïre [= Democratic Republic of the Congo].

Diagnosis. Pronotum rather glossy (Fig. 64); FLP sclerite subapicodorsal lobe short anteriorly (Figs. 162–163); right lateral fold produced into a longitudinal spoon-shape process with apical portion open ventrally, ventral edge with minute villi (Fig. 186A), with a well-sclerotized projection on apicoventral edge (Fig. 186B); axial sclerite shorter than subaxial sclerite, acute apically (Fig. 163); subaxial sclerite short and robust (Fig. 163).

Description. Holotype ♂ (Fig. 16). **Measurements**. Length 12.5 mm, width 7.0 mm. **Head** (Figs. 41–42). Anterior clypeal edge straight on median fourth in dorsal view; clypeofrontal carina broadly arcuate and interrupted at gena; vertex lacking median tubercle, surface with punctures fine to small, separated by one to four diameters. Horns rather short, slightly divergent in frontal view, parallel sided on basal three-fourth and abruptly tapering externally and narrower on apical fifth; posterointernal edge with a distinct low angular projection basally; apicointernal surface lacking granules, with few scabrous punctures; genal edge upturned and bluntly angulate on anterior third, forming a broad angle with clypeal edge. **Pronotum** (Fig. 64). Surface with granulate punctures extending on a short distance on posterior half with distinct, finely granulate, simple punctures on posterior half of disc; punctures scattered and smaller posterolaterally with distinct, minute punctures throughout. Anteromedian tubercle atrophied, simply round in lateral view; median longitudinal sulcus weakly-defined and shallow; surface behind the eyes with a simple, round, rather deep depression; surface of anterior angles slightly concave; anterior half of lateral edge arcuate in dorsal and lateral view; posterior angles unmodified and simply arcuate in dorsal view. Anterior hypomeral ridge arcuate anteriorly, anterior hypomeral depression surface slightly darker in color medially. **Elytra** (Fig. 16). Intervals 2 and 4 with the odd fine granules on apical declivity. **Legs**. Protibial apicointernal tooth enlarged, with dorsal ridge extending to apex. **Aedeagus** (Fig. 128). Parameres with dorsal and ventral edges slightly diverging toward apex in lateral view. **Internal sac sclerites** (Figs. 162–164). Axial sclerite broadly arcuate, with apex acute. Subaxial sclerite, gradually tapering from base to apex, extending straight approximately in line with apex of right lateral fold, with a brush of villi on apical fourth. Frontolateral peripheral sclerite basoventral apophysis moderately developed; lacking medioventral carinae; right lateral fold produced into a rather large everted and open internally conical process with irregular apical edge, always with a well-sclerotized projection on apicoventral edge, ventral edge bordered with minute villi; left lateral lobe membranous, slightly developed; subapicodorsal lobe membranous, not reaching anterior edge, apex set medially in dorsal view; apical lobe round and directed obliquely on left side, left edge emarginate, apical villi regular in shape; subapicoventral lobe round and interrupted in line with apical lobe, with few villi along apical edge only.

Variation. Measurements (170 ♂♂, 112 ♀♀). Length: male 7.0–13.0 mm (9.8 ± 1.0 mm), female 8.0–11.5 mm (9.7 ± 0.8 mm). Female allotype. Cephalic outline in dorsal view as in Fig. 80; vertex with a straight transverse carina, dorsal edge broadly arcuate in frontal view, lateral portion round and gradually sloping down posteriorly; anterior pronotal tubercles moderately developed, external lateral edges strongly divergent toward apex, anterolateral surface slightly concave, anterosuperior edge slightly arcuate in dorsal view (Fig. 105), lateral portion of anterosuperior edge strongly upturned (Fig. 106). Protibia short, with external teeth more robust.

Primary type data. Holotype ♂ (CMNC): [Moanda / (Zaïre) 30.iv.1979] partly handwritten; [WORLD / SCARAB. / DATABASE / WSD00032092] barcode label; [HOLOTYPE ♂ / *Digitonthophagus* / *viridicollis n.sp.* / des. F. Génier, 2016] red card.



MAP 11. Distribution of *Digitonthophagus viridicollis*.

Material examined (183 ♂♂, 115 ♀♀), distribution (Map 11): **ANGOLA**: [unspecified locality], [no date], [anonymous]—2 ♂♂ (2 paratypes) (BMNH); [unspecified locality], [no date], Monteiro—3 ♂♂ (3 paratypes) (BMNH); BENGUELA, Benguela (12°35'S, 13°25'E), iv.1981, L. Hilburger—2 ♀♀, 3 ♂♂ (5 paratypes) (OUMNH); CABINDA, Cabinda (5°34'S, 12°11'E), 1885, Hesse—1 ♂ (paratype) (SMF); CUANZA SUL, Cossoço [=Coçoço] (11°24'S, 14°1'E), iii.2005, [anonymous]—2 ♀♀, 3 ♂♂ (5 paratypes) (PMOC); Cossoço [=Coçoço] (11°24'S, 14°1'E), 3–13.iii.2005, M. Hansson & Th. Bouyer—1 ♂ (paratype) (PMOC); [unspecified locality], ii–iii.1999, T. Bouyer & M. Hasson—2 ♀♀, 1 ♂ (paratypes) (PMOC); CUNENE, 10 km N Humbe (16°35'49"S, 14°54'24"E), 3.xi.2011, G. Werner—2 ♀♀, 4 ♂♂ (6 paratypes) (FGIC, GWPC); Near Categuero (17°45.765'S, 14°29.411'E), 11.xii.2012, S. Rojkoff—1 ♂ (paratype) (CMD); Roçadas (16°45'S, 14°59'E), 19–22.ii.1972, Southern Africa Expedition—3 ♀♀, 3 ♂♂ (6 paratypes) (BMNH); HUILA, 26 km S Cahila (16°6'18.3"S, 14°14'7.6"E), 2.xii.2015, G. Werner—1 ♂ (paratype) (GWPC); 5 mi. NE Negola (14°8'S, 14°30'E), 25.iii.1972, Southern Africa Expedition—2 ♀♀, 1 ♂ (paratypes) (BMNH); João de Almeida [=Chibia] (15°11'S, 13°42'E), 29.iii.1972, [anonymous] (A41)—1 ♂ (paratype) (BMNH); LUANDA, Luanda (8°50'S, 13°17'E), [no date], Welwitch—1 ♀, 1 ♂ (paratypes) (BMNH); Luanda (8°50'S, 13°17'E), [no date], [anonymous]—1 ♂ (paratype) (IRSNB); UIGE, 3 mi. N Santa Clara (7°22'S, 14°44'E), 3.iii–1.iv.1972, Southern Africa Expedition—3 ♀♀, 2 ♂♂ (5 paratypes) (BMNH); **CONGO**: BRAZZAVILLE, Environs de Brazzaville (4°15'S, 15°16'E), 1907, E. Roubaud & A Weiss—1 ♂ (paratype) (MNHN); **DEMOCRATIC REPUBLIC OF THE CONGO**: BAS-CONGO, Banana (5°59'53"S, 12°23'56"E), [no date], F. Busschodts—2 ♂♂ (2 paratypes) (IRSNB); Banana (5°59'53"S, 12°23'56"E), iii.1885, Hesse—3 ♀♀, 8 ♂♂ (11 paratypes) (SMF); Banana (5°59'53"S, 12°23'56"E), v.1886, Hesse—4 ♂♂ (4 paratypes) (SMF); Banana-Boma (5°50'S, 12°43'E), 1891, M. Tschoffen—4 ♂♂ (4 paratypes) (IRSNB); Boma (5°51'S, 13°3'E), [no date], P. Rolin—1 ♀, 1 ♂ (paratypes) (IRSNB); Boma (5°51'S, 13°3'E), [no date], M. Tschoffen—4 ♂♂ (4 paratypes) (IRSNB); Boma (5°51'S, 13°3'E), 3.i.1977, P. Walter—8 ♀♀, 6 ♂♂ (14 paratypes) (PHWC); Boma (5°51'S, 13°3'E), 4.i.1977, P. Walter—16 ♀♀, 14 ♂♂ (30 paratypes) (PHWC); Environs de Kangu, Mayumbé (5°17'S, 12°57'E), 6.i.1977, Yimi-di-Phambu—18 ♀♀, 21 ♂♂ (39 paratypes) (PHWC); Kwilu (5°30'S, 14°41'E), iv.1885, Hesse—1 ♀, 1 ♂ (paratypes) (SMF); Matadi (5°49'S, 13°28'E), [no date], [anonymous]—1 ♂ (paratype) (IRSNB); Muanda (5°56'S, 12°21'E), 30.iv.1979, P. Walter—1 ♀, 4 ♂♂ (holotype, allotype, 3 paratypes) (CMNC, PHWC); Vista [=Nsiamfumu] (5°52'S, 12°17'E), [no date], V. Moerenhout—1 ♂ (paratype) (IRSNB); Vivi (5°48'S, 13°27'E), [no date], [anonymous]—1 ♂ (paratype) (IRSNB); Zambi (5°51'S, 12°52'E), [no date], M. Tschoffen—2 ♀♀, 6 ♂♂ (8 paratypes) (IRSNB); Zambi (5°51'S, 12°52'E), [no date], C. Haas—1 ♂ (paratype) (IRSNB); **NAMIBIA**: ERONGO, Ameib Farm, 19 km NW Karibib (21°47'S, 15°38'E), 31.i–2.ii.1972, Southern Africa Expedition—2 ♀♀ (2 paratypes) (BMNH); Otjikoko Süd Farm, 33 mi.

ENE Omaruru (21°10'S, 16°22'E), 10–13.ii.1972, Southern Africa Expedition—3 ♀♀, 3 ♂♂ (6 paratypes) (BMNH); KUNENE, Kamanjab (19°38'S, 14°51'E), 9.iv.2005, W. Schawaller—1 ♀, 1 ♂ (paratypes) (SMNS); Ongongo (18°8'S, 13°22'E), 17–18.iv.2005, W. Schawaller—1 ♂ (paratype) (SMNS); Otjitambi farm, 27 mi. ESE Kamanjab (19°49'S, 15°10'E), 13–15.ii.1972, Southern Africa Expedition—1 ♀, 2 ♂♂ (3 paratypes) (BMNH); Outjo (20°7'S, 16°10'E), i–ii.1998, Forti, Gzeppel & Giannatelli—1 ♂ (paratype) (FETC); Purros (Hoaruzsib Valley) (18°46'S, 12°57'E), 15–16.iv.2005, W. Schawaller—1 ♂ (paratype) (SMNS); OHANGWENA, Oshikango (17°24'S, 15°53'E), 19.ii.1972, Southern Africa Expedition—1 ♂ (paratype) (BMNH); OMAHEKE, Kuzikus Wildlife Reserve (23°14'17"S, 18°23'28"E), 30.iii–11.iv.2011, J. Constant—3 ♂♂ (3 paratypes) (IRSNB); Kuzikus Wildlife Reserve (23°14'17"S, 18°23'28"E), 3–10.iv.2011, J. Constant—1 ♂ (paratype) (IRSNB); OMUSATI, 2 km E Renostervlei (19°9'59"S, 14°33'12"E), 26.xii.1999, Mann & Marais—1 ♂ (paratype) (OUMNH); Narawandu road, Etosha National Park (18°51'4"S, 15°32'55"E), 24.xii.1999, Mann, Marais & Newman—2 ♀♀, 1 ♂ (paratypes) (OUMNH); Narawandu road, Etosha National Park (18°51'4"S, 15°32'55"E), 24–25.xii.1999, Mann & Marais—1 ♂ (paratype) (OUMNH); Narawandu road, Etosha National Park (18°51'4"S, 15°32'55"E), 24.xii.1999, Mann & Marais—1 ♂ (paratype) (OUMNH); Narawandu road, Etosha National Park (18°51'4"S, 15°32'55"E), 25–26.xii.1999, Mann & Marais—1 ♀, 1 ♂ (paratypes) (OUMNH); OSHANA, Oshakati (17°52'30"S, 15°22'30"E), 15.vii.1975, R. Venter—1 ♂ (paratype) (BMNH); OSHIKOTO, Andoni road (18°45'37"S, 16°54'24"E), 20.xii.1999, Mann & Marais—6 ♀♀, 6 ♂♂ (12 paratypes) (OUMNH); Etosha National Park (19°2'S, 16°28'E), i–ii.1998, Czeppel, Forti, & Giannatelli—1 ♀ (paratype) (FETC); Etosha National Park (19°2'S, 16°28'E), 13.ii.1998, Forti—1 ♂ (paratype) (SMNS); Mushara area, sandy road (18°36'24"S, 16°53'23"E), 21.xii.1999, Mann & Marais—5 ♀♀, 4 ♂♂ (9 paratypes) (OUMNH); Mushara Waterhole (18°35'19"S, 16°55'11"E), 22–23.xii.1999, Mann & Marais—2 ♂♂ (2 paratypes) (OUMNH); Mushara Waterhole (18°35'19"S, 16°55'11"E), 23.xii.1999, Mann & Marais—3 ♀♀, 2 ♂♂ (5 paratypes) (OUMNH); North Tsintsabis (18°46'S, 17°58'E), 1.i.2007, R. Perissinoto & L. Clennell—1 ♂ (paratype) (PMOC); Okaukuejo, Etosha National Park, 1113 m (19°10'S, 15°55'E), i.2007, M. Forti—1 ♂ (paratype) (SMNS); Oluconda (17°59'7"S, 16°1'24"E), 1901, Schinz—1 ♀, 1 ♂ (paratypes) (SMF); Onguma Farm, 55 mi. NW Tsumeb (18°44'S, 17°3'E), 17–19.ii.1972, Southern Africa Expedition—7 ♀♀, 4 ♂♂ (11 paratypes) (BMNH); Otjikata [= Otjikoto] Lake (19°11'S, 17°33'E), 16.xi.1933, K. Jordan—7 ♀♀, 4 ♂♂ (11 paratypes) (BMNH); OTJOZONDJUPA, 12 mi. E Otavi (19°39'S, 17°31'E), 17.ii.1972, Southern Africa Expedition—3 ♀♀, 5 ♂♂ (8 paratypes) (BMNH); Epupa Falls, 660 m (17°0'3"S, 13°14'36"E), 11–12.iv.2005, W. Schawaller—5 ♂♂ (5 paratypes) (SMNS); Hohenfels (20°41.928'S, 16°50.498'E), 7.i.2011, G. Werner—1 ♂ (paratype) (FGIC); Okahandja (21°59'S, 16°55'E), 11.xi.1909, G. Fock—2 ♀♀, 3 ♂♂ (5 paratypes) (IRSNB); Okahandja (21°59'S, 16°55'E), 2–18.iii.1922, R.E. Turner—2 ♂♂ (2 paratypes) (BMNH); Okahandja (21°59'S, 16°55'E), 1–12.i.1928, R.E. Turner—1 ♂ (paratype) (BMNH); Okahandja (21°59'S, 16°55'E), 3–9.ii.1928, R.E. Turner—2 ♂♂ (2 paratypes) (BMNH); Otavi (19°39'S, 17°20'E), 8.i.1934, J. Ogilvie—1 ♀ (paratype) (BMNH); Otavifontein (19°39'S, 17°24'E), 21.xi.1933, K. Jordan—1 ♂ (paratype) (BMNH); Otjawarongo (20°27'S, 16°40'E), 1909, Külz—1 ♀, 4 ♂♂ (5 paratypes) (SMF); Otjawarongo (20°27'S, 16°40'E), 13.i.1934, J. Ogilvie—1 ♀, 1 ♂ (paratypes) (BMNH); Otjawarongo (20°27'S, 16°40'E), 4.i.2004, R. Perissinoto & L. Clennell—1 ♂ (paratype) (PMOC); Swakop River, 3 mi. S Okahandja (22°2'S, 16°56'E), 7.iv.1972, Southern Africa Expedition—1 ♂ (paratype) (BMNH); Grootfontein District, Okaputa 334 at: campsite (20°7'26"S, 16°57'54"E), 12.xii.1999, Mann, Marais & Newman—1 ♂ (paratype) (OUMNH).

Etymology. *Viridicollis*, a Latin adjective pertaining to the metallic green coloration of the pronotum typical for this species.

Natural history. The material examined shows a Kalahari xeric savanna and Angolan scarp savanna and woodland centered distribution. The only specimens with habitat data were collected in pastures. Some specimens collected at light traps and cow, elephant, and zebra dung. A few specimens collected in pitfall traps baited with giraffe, zebra, or human dung.

Remarks. This species is very closely related to *D. gazella.* Despite the relative high number of individuals examined, no intermediates were found for the character of the shape of the right lateral fold (see diagnosis). Large females of *D. viridicollis* also have very characteristic strongly upturned anterosuperior edges of the anterior pronotal tubercles. The green metallic tinge of the dorsum is also characteristic of most specimens.

Digitonthophagus lusinganus species group

Diagnosis. FLP sclerite ventral portion with one or two medioventral carinae (Fig. 184A); right lateral fold produced into a rather large everted and open apically conical process with irregular apical edge (Figs. 165, 168, 171, 174, 177); FLP sclerite subapicoventral lobe acute apically (Figs. 167, 176); axial and subaxial sclerite rather short, with a distinct transverse uniting sclerotized area medially (Fig. 171, 174, 177).

Digitonthophagus aksumensis Génier, new species

http://zoobank.org/urn:lsid:zoobank.org:act:2316941C-3BDF-4900-9212-25C83F5AC88F
(Figs. 17, 43–44, 65, 81, 107–108, 129, 165–167, 184; Map 12)

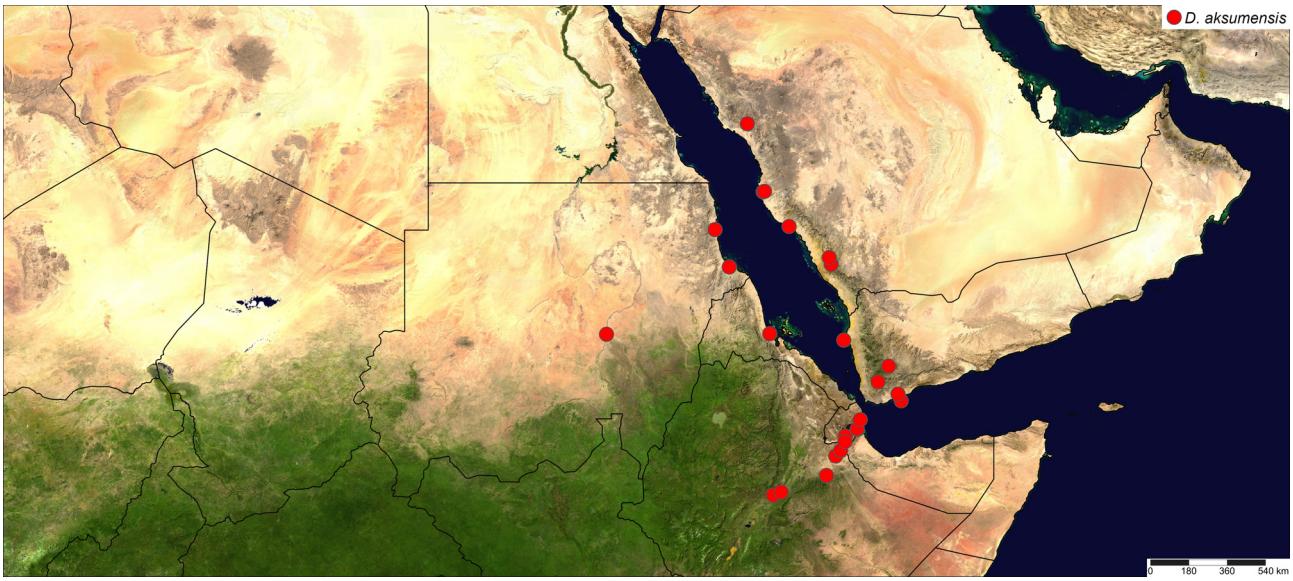
Type locality. Obock, Colonie française des Somalies [=Djibouti].

Diagnosis. Male cephalic horns lacking granules internally at apex (Fig. 44); FLP sclerite apical portion rather large, obliquely oriented and tapering to apex (Fig. 165–166); males with pronotal anterior angles surface convex, simply round anteriorly (Fig. 43); FLP sclerite ventral portion with two carinae (Fig. 167); SA sclerite apex approximately in line with apex of apical portion of FLP sclerite (Figs. 165–166).

Description. Holotype ♂ (Fig. 17). **Measurements**. Length 11.0 mm, width 6.5 mm. **Head** (Figs. 43–44). Anterior clypeal edge straight on median fifth in dorsal view; clypeofrontal carina broadly arcuate and interrupted at gena; vertex lacking median tubercle, surface with punctures fine to small, separated by one to four diameters. Horns rather short, slightly divergent in frontal view, gradually tapering from base to apex; posterointernal edge produced into an low, angular projection basally; apicointernal surface lacking granules; genal edge upturned and distinctly angulate on anterior third, forming a distinct angle with clypeal edge. **Pronotum** (Fig. 65). Surface with granulate punctures restricted to anterior half medially, with distinct umbilicate punctures on posterior half of disc; punctures weaker but distinct posterolaterally with distinct, minute punctures throughout. Anteromedian tubercle atrophied, forming an obtuse angle in lateral view, median longitudinal sulcus weakly-defined; surface behind the eyes with a simple round depression, surface of anterior angles convex; anterior half of lateral edge arcuate in dorsal and lateral view; posterior angles slightly upturned and simply arcuate in dorsal view. Anterior hypomeral ridge arcuate, anterior hypomeral depression slightly darker in color medially. **Elytra** (Fig. 17). Intervals 2 and 4 lacking fine granules from base to apex. **Legs**. Protibial apicointernal tooth enlarged, with dorsal ridge extending to apex. **Aedeagus** (Fig. 129). Parameres with dorsal and ventral edges slightly diverging toward apex in lateral view. **Internal sac sclerites** (Figs. 165–167). Axial sclerite weekly sclerotized, reduced in size and almost straight. Subaxial sclerite, large basally and abruptly reduced, extending straight approximately in line with apex of frontolateral peripheral sclerite apical portion, with fine and scattered villi. Frontolateral peripheral sclerite basoventral apophysis well developed; two medioventral carinae present; right lateral fold produced into a rather large everted and open apically conical process with irregular apical edge; left lateral lobe membranous, slightly developed; subapicodorsal lobe membranous not reaching anterior edge, apex set on left side in dorsal view; apical lobe tapering into a point and directed obliquely on left side, apical villi regular in shape; subapicoventral lobe acute and in line with apical lobe apically.

Variation. Measurements (86 ♂♂, 69 ♀♀). Length: male 6.5–11.5 mm (10.1 ± 1.0 mm), female 7.0–11.0 mm (9.6 ± 0.9 mm). Female allotype. Cephalic outline in dorsal view as in Fig. 81; vertex with a straight, transverse carina, dorsal edge broadly arcuate in frontal view, lateral portion gradually sloping down; anterior pronotal tubercles atrophied, external lateral edges parallel sided, anterolateral surface simply convex, anterosuperior edge slightly arcuate in dorsal view (Fig. 107), lateral portions of anterosuperior edge slightly upturned (Fig. 108). Protibia short, with external teeth more robust.

Primary type data. Holotype ♂ (MNHN): [C. FR. Des SOMALIES / Obock] handwritten; [MUSÉUM PARIS / 1918 / Dr. Yousseaume] partly handwritten on blue card; [WORLD / SCARAB. / DATABASE / WSD00029901]; [HOLOTYPE ♂ / *Digitonthophagus* / *aksumensis n.sp.* / des. F. Génier, 2016] red card.



MAP 12. Distribution of *Digitonthophagus aksumensis*.

Material examined (92 ♂♂, 74 ♀♀), distribution (Map 12): **DJIBOUTI**: ARTA, Grand Bara (11°16'N, 42°39'E), 22.xii.1989, [anonymous]—1 ♂ (paratype) (CMD); Grand Bara (11°16'N, 42°39'E), 24.v.1991, G. Nazaret—4 ♀♀, 2 ♂♂ (6 paratypes) (CMD); DJIBOUTI, Ambouli (11°33'13"N, 43°9'31"E), v.1990, G. Nazaret—3 ♀♀, 3 ♂♂ (6 paratypes) (CMD); Ambouli (11°33'13"N, 43°9'31"E), 9.xi.1972, Mission Balachowsky-Menier—1 ♀, 3 ♂♂ (4 paratypes) (MNHN); Ambouli (11°33'13"N, 43°9'31"E), 15.ii.1990, G. Nazaret—4 ♀♀, 4 ♂♂ (8 paratypes) (PMOC); Ambouli (11°33'13"N, 43°9'31"E), 21.ii.1990, G. Nazaret—2 ♀♀, 2 ♂♂ (4 paratypes) (CMD); Ambouli (11°33'13"N, 43°9'31"E), 12.i.1992, G. Nazaret—2 ♂♂ (2 paratypes) (CMD); Ambouli (11°33'13"N, 43°9'31"E), 12.i.1992, [anonymous]—1 ♂ (paratype) (PCSR); Djibouti (11°35'N, 43°9'E), vii.1897, Jousseaume—6 ♀♀, 7 ♂♂ (13 paratypes) (MNHN); Djibouti (11°35'N, 43°9'E), 1897, H. Coutière—2 ♀♀, 1 ♂ (paratypes) (MNHN); Djibouti (11°35'N, 43°9'E), [no date], [anonymous]—2 ♀♀, 1 ♂ (paratypes) (MNHN); OBOCK, Obock (11°58'N, 43°17'E), 1918, Dr. Yousseaume—3 ♀♀, 4 ♂♂ (holotype, allotype, 5 paratypes) (MNHN); Obock (11°58'N, 43°17'E), [no date], Faurot—1 ♀ (paratype) (MNHN); Obock (11°58'N, 43°17'E), 1893, Maindron—1 ♀, 1 ♂ (paratypes) (MNHN); **ERITREA**: SEMENAWI-KEYIH-BAHRI, Massawa (15°36'35"N, 39°27'0"E), [no date], [anonymous]—1 ♂ (paratype) (BMNH); **ETHIOPIA**: DIRE DAWA, Dire Dawa (9°36'N, 41°51'E), ix.1935, H. Ulenhuth—1 ♀, 2 ♂♂ (3 paratypes) (BMNH); Dire Dawa (9°36'N, 41°51'E), 1936, [anonymous]—1 ♀, 1 ♂ (paratypes) (MNHN); Dire Dawa (9°36'N, 41°51'E), 1935, [anonymous]—1 ♀ (paratype) (MNHN); OROMIA, 23 km NEE Welenchiti (8°46'N, 39°36'E), 29.iv.2013, [anonymous]—1 ♂ (paratype) (CMD); 30 km SW Awash (8°54'N, 39°56'E), 29–30.iv.2013, I. Martinu—1 ♂ (paratype) (JFJC); SOMALI, Adigala (10°25'35"N, 42°14'25"E), [no date], Dr. Martin—2 ♂♂ (2 paratypes) (MNHN); Dewele (11°2'5"N, 42°37'53"E), [no date], Dr. Martin—1 ♂ (paratype) (MNHN); Lassarat (10°39'52"N, 42°27'21"E), [no date], Dr. Martin—2 ♀♀, 7 ♂♂ (9 paratypes) (MNHN); **SAUDI ARABIA**: Hedjaz (24°30'N, 38°30'E), [no date], [anonymous]—1 ♀, 2 ♂♂ (3 paratypes) (MNHN); [unspecified locality], [no date], [anonymous]—1 ♀, 1 ♂ (paratypes) (MNHN); ASEER, 35 km N Mahayl [=Muhayil] (18°50'N, 41°58'E), 7.xi.1982, A.R. Pittaway—1 ♂ (paratype) (OUMNH); Muhayl [=Muhayil] (18°32'40"N, 42°3'3"E), 8.i.1983, A.R. Pittaway—1 ♀, 1 ♂ (paratypes) (OUMNH); MAKKAH, Lith, 10 mi. inland (20°9'N, 40°16'E), i.1945, B.P. Uvarov—1 ♂ (paratype) (BMNH); Wadi Jizan (21°37'N, 39°10'E), 18.iii.1978, Filipponi—1 ♂ (paratype) (FETC); Wadi Jizan (21°37'N, 39°10'E), 26.iii.1978, Filipponi—1 ♀, 1 ♂ (paratypes) (FETC); Wadi Jizan (21°37'N, 39°10'E), 6.viii.1978, Filipponi—1 ♂ (paratype) (FETC); Wadi Jizan (21°37'N, 39°10'E), 11.viii.1978, Filipponi—2 ♀♀, 6 ♂♂ (8 paratypes) (FETC); Wadi Jizan (21°37'N, 39°10'E), 14.viii.1978, Filipponi—7 ♀♀, 7 ♂♂ (14 paratypes) (FETC); Wadi Jizan (21°37'N, 39°10'E), 18.viii.1978, Filipponi—7 ♀♀, 2 ♂♂ (9 paratypes) (FETC); Wadi Jizan (21°37'N, 39°10'E), 24.viii.1978, Filipponi—1 ♂ (paratype) (FETC); Wadi Jizan (21°37'N, 39°10'E), 30.xi.1978, Filipponi—1 ♀, 2 ♂♂ (3 paratypes) (FETC); MINTAQAT MAKKAH, 12 mi. N Jidda [=Jeddah] (21°38'15"N, 39°13'35"E), 4.xii.1944, A.R. Waterston—1 ♂ (paratype) (BMNH); **SOMALIA**: Dolphin Bay , 22.iii.1903, M. Cameron—2

♀♀, 1 ♂ (paratypes) (BMNH); **SUDAN**: KHARTOUM, Environs de Khartoum (15°35'N, 32°32'E), [no date], [anonymous]—2 ♀♀, 1 ♂ (paratypes) (MNHN); Khartoum (15°35'N, 32°32'E), 18.i.1904, Zaphiro—1 ♀, 1 ♂ (paratypes) (BMNH); RED SEA, Khor Arbaat Delta (20°1'N, 37°8'E), iv–v.1926, H.B. Johnston—1 ♂ (paratype) (BMNH); Tokar (18°26'N, 37°44'E), 1914, H.W. Bedford—1 ♂ (paratype) (BMNH); **YEMEN**: [unspecified locality] (14°14'N, 44°29'E), [no date], Mellingen—3 ♀♀, 2 ♂♂ (5 paratypes) (BMNH); [unspecified locality] (14°14'N, 44°29'E), [no date], [anonymous]—2 ♀♀, 1 ♂ (paratypes) (MNHN); ADEN, Aden (12°45'56"N, 45°1'1"E), [no date], [anonymous]—2 ♀♀, 1 ♂ (paratypes) (BMNH); Aden (12°45'56"N, 45°1'1"E), [no date], C. Pérez—4 ♀♀, 4 ♂♂ (8 paratypes) (MNHN); AL HUDAYDAH, Kamaran Island (15°20'N, 42°35'E), 24.xii.1902, M. Cameron—1 ♀, 1 ♂ (paratypes) (BMNH); Lahij, Lahij (13°3'N, 44°53'E), [no date], Dodson—2 ♀♀, 1 ♂ (paratypes) (MNHN); TA'IZZ, Taizz (13°34'N, 44°2'E), xi.1975, N. Hadi—1 ♂ (paratype) (BMNH).

Etymology. Derived from Aksum, a historical kingdom approximately corresponding to the distribution of the species.

Natural history. Unknown except for two specimens collected from camel dung and five specimens collected at light.

Remarks. The Egyptian records for *D. gazella* from Quena in the Nil Valley (Alfieri 1976) presumably refer to this species.

Digitonthophagus dilatatus Génier, new species

http://zoobank.org/urn:lsid:zoobank.org:act:28F9FCFD-2012-4B76-B546-B444F54327D9
(Figs. 18, 45–46, 66, 82, 109–110, 130, 168–170; Map 13)

Type locality. Forêt de Sorobouli (11°47'44"N 02°53'25"W), 270 m, Sanguié, Burkina Faso.

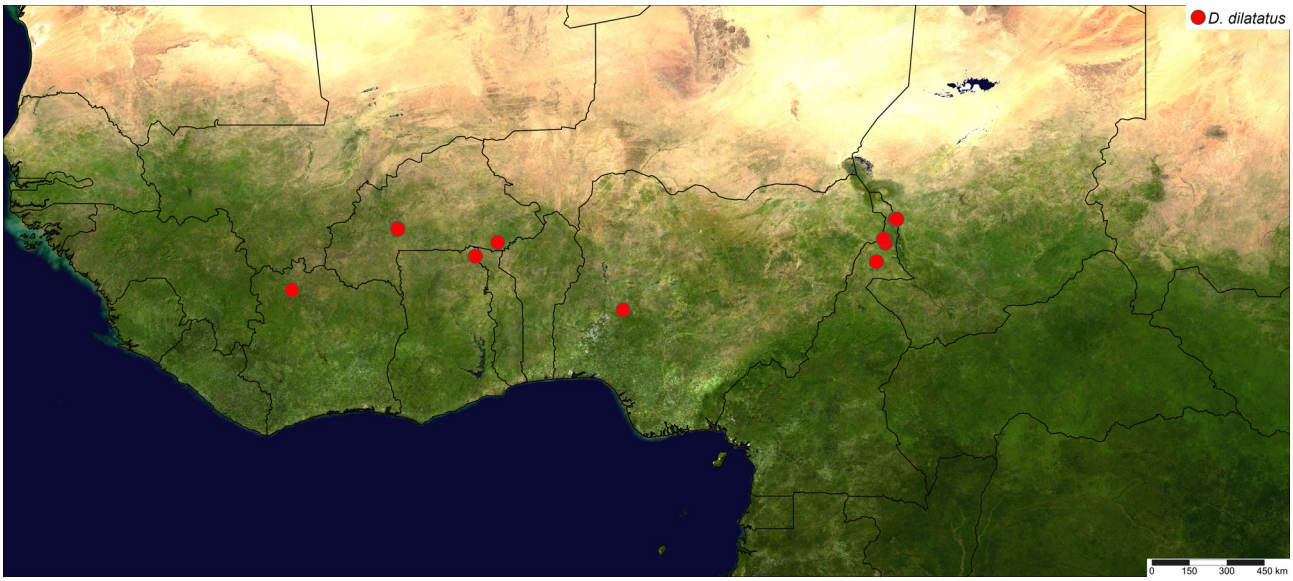
Diagnosis. Male cephalic horns granulate internally at apex (Fig. 46); males with pronotal anterior angles surface concave, produced anteriorly (Fig. 45); FLP sclerite ventral portion with a single carina (Fig. 170); SA sclerite apex interrupted much before apex of apical portion of FLP sclerite (Figs. 168–169).

Description. Holotype ♂ (Fig. 18). **Measurements**. Length 12.0 mm, width 7.0 mm. **Head** (Figs. 45–46). Anterior clypeal edge straight on median seventh and appearing semicircular in dorsal view; clypeofrontal carina broadly arcuate and interrupted at gena; vertex lacking median tubercle, surface with punctures fine to small, separated by one to four diameters. Horns rather long, distinctly arcuate and divergent in frontal view, parallel sided on basal four-fifths and abruptly tapering externally and narrower on apical sixth; posterointernal edge unmodified basally; apicointernal surface with few, coarse granules; genal edge slightly upturned and simply arcuate on anterior third, in line with clypeal edge. **Pronotum** (Fig. 66). Surface with granulate punctures restricted to anterior half medially, with distinct umbilicate punctures on posterior half of disc; punctures distinct posterolaterally, with distinct minute punctures throughout. Anteromedian tubercle atrophied, forming an obtuse angle in lateral view; median longitudinal sulcus well-defined but narrow; surface behind the eyes slightly concave, surface of anterior angles concave with anterior angles produced forwardly; anterior half of lateral edge sinuous in dorsal and lateral view; posterior angles unmodified and simply arcuate in dorsal view. Anterior hypomeral ridge straight on most of its length and abruptly arcuate on anterior third, anterior hypomeral depression surface darker in color. **Elytra** (Fig. 18). Intervals 2 and 4 lacking fine granules from base to apex. **Legs**. Protibial apicointernal tooth enlarged, with dorsal ridge extending to apex. **Aedeagus** (Fig. 130). Parameres with dorsal and ventral edges slightly diverging toward apex in lateral view. **Internal sac sclerites** (Figs. 168–170). Axial sclerite short, angular and extending into a point apically. Subaxial sclerite, large basally and abruptly reduced, extending straight and approximately in line with apex of right lateral fold of frontolateral peripheral sclerite, with fine and scattered villi. Frontolateral peripheral sclerite basoventral apophysis well developed; a single rather large medioventral carina present; right lateral fold produced into a rather small everted and open apically conical process with irregular apical edge located behind oblique right lateral edge of apical lobe; left lateral lobe membranous, slightly developed; subapicodorsal lobe membranous, not reaching anterior edge, apex set on left side in dorsal view; apical lobe truncate apically and directed obliquely on left side, apical villi regular in shape; subapicoventral lobe small, acute apically, short not reaching apical edge of apical lobe.

Variation. Measurements (42 ♂♂, 83 ♀♀). Length: male 8.5–12.0 mm (10.5 ± 0.9 mm), female 7.5–12.0 mm (10.1 ± 0.8 mm). Female allotype. Cephalic outline in dorsal view as in Fig. 82; vertex with a broadly arcuate

transverse carina, dorsal edge broadly arcuate in frontal view, lateral portion gradually sloping down posteriorly; anterior pronotal tubercles well developed, external lateral edges slightly widening toward apex in dorsal view, anterolateral surface simply convex, anterosuperior edge slightly arcuate in dorsal view (Fig. 109), lateral portion of anterosuperior edge slightly upturned (Fig. 110). Protibia short, with external teeth more robust.

Primary type data. Holotype ♂ (CMNC): [BURKINA FASO: SANGUIÉ / Forêt de Sorobouli, 270m / 11°47’44”N 002°53’25”O / 13.VIII.2005, F. Génier / zone soudanienne sud / piège excr. humain, 2005-14]; [COLÉOPTÈRES / DU / BURKINA FASO / BF015361] barcode label; [HOLOTYPE ♂ / *Digitonthophagus* / *dilatatus n.sp.* / des. F. Génier, 2016] red card.



MAP 13. Distribution of *Digitonthophagus dilatatus*.

Material examined (57 ♂♂, 93 ♀♀), distribution (Map 13): **BURKINA FASO**: CENTRE-OUEST, Forêt de Sorobouli [=Forêt Classée de Baporo], 270 m (11°47'44"N, 2°53'25"W), 10–15.viii.2005, P. Moretto—78 ♀♀, 30 ♂♂ (108 paratypes) (FGIC, PMOC); BALÉ, Boromo, 250 m (11°45'6"N, 2°51'58"W), 10.viii.2005, F. Génier (2005-10)—1 ♀, 1 ♂ (paratypes) (FGIC); KOMPIENGA, Pama, 230 m (11°17'N, 0°42'59"E), 24.viii.2005, F. Génier (2005-44)—3 ♂♂ (3 paratypes) (FGIC); SANGUIÉ, Forêt de Sorobouli, 270 m (11°47'44"N, 2°53'25"W), 13.viii.2005, F. Génier (2005-14)—1 ♀, 1 ♂ (holotype, allotype) (CMNC); Forêt de Sorobouli, 270 m (11°47'44"N, 2°53'25"W), 13.viii.2005, F. Génier (2005-15)—2 ♀♀, 1 ♂ (paratypes) (FGIC); Forêt de Sorobouli, 270 m (11°47'44"N, 2°53'25"W), 28.vii.2006, F. & S. Génier (2006-83)—1 ♂ (paratype) (FGIC).; **CAMEROON**: EXTREME NORTH, Maroua (10°35'N, 14°19'E), 4.vii.1978, [anonymous]—1 ♂ (paratype) (MNHN); Waza (11°24'N, 14°34'E), 18.viii.2006, C. Vanderbergh—2 ♂♂ (2 paratypes) (FGIC, PMOC); Waza National Park (11°15'N, 14°39'E), 18.viii.2006, C. Vanderbergh—5 ♀♀, 5 ♂♂ (10 paratypes) (FGIC, PMOC); **CHAD**: N’DJAMENA, Farcha (12°7'N, 14°59'E), vi.1968, [anonymous]—1 ♀, 1 ♂ (paratypes) (MNHN); Farcha (12°7'N, 14°59'E), 28.vi.1967, [anonymous]—1 ♀, 2 ♂♂ (3 paratypes) (MNHN); Fort Lamy [=N’Djamena] (12°7'N, 15°3'E), 17.vii.1958, J. Mateu—1 ♂ (paratype) (FETC); **CÔTE D’IVOIRE**: SAVANES, M’banto, Boundiali, 395 m (9°34'10.4"N, 6°40'56.5"W), 13–15.vii.2013, P. Moretto—2 ♀♀, 5 ♂♂ (7 paratypes) (FGIC, PMOC); **GHANA**: UPPER EAST, Bolgatanga (10°47'N, 0°5'W), 20.xi.2002, Bowku—2 ♀♀, 2 ♂♂ (4 paratypes) (OMOC); **NIGERIA**: KWARA, Bussa (8°51'24"N, 5°13'9"E), 4.v.1962, D.C. Eidt—1 ♂ (paratype) (CNC).

Etymology. *Dilatatus* is a Latin adjective pertaining to the development of the anterior pronotal angles of well-developed males of this species. This development is unique in the genus.

Natural history. The known distribution pattern of this species suggests that it is endemic to the Sudanese savanna. Interestingly, all specimens with data were collected at light or in pitfall traps baited with human dung, no specimens were collected in ruminant dung. Additional observations are required to confirm that it is a non-ruminant dung specialist.

Remarks. Externally, this species can be confused with *D. fimator* in West Africa. However, in addition to the characters given, the parameres are smaller and approximately parallel sided in lateral view as opposed to being wider and divergent in lateral view in *D. fimator*.

***Digitonthophagus fimator* Génier, new species**
http://zoobank.org/urn:lsid:zoobank.org:act:534A9261-6403-4272-93EA-24D061542886
(Figs. 19, 47–48, 67, 83, 111–112, 131, 171–173; Map 14)

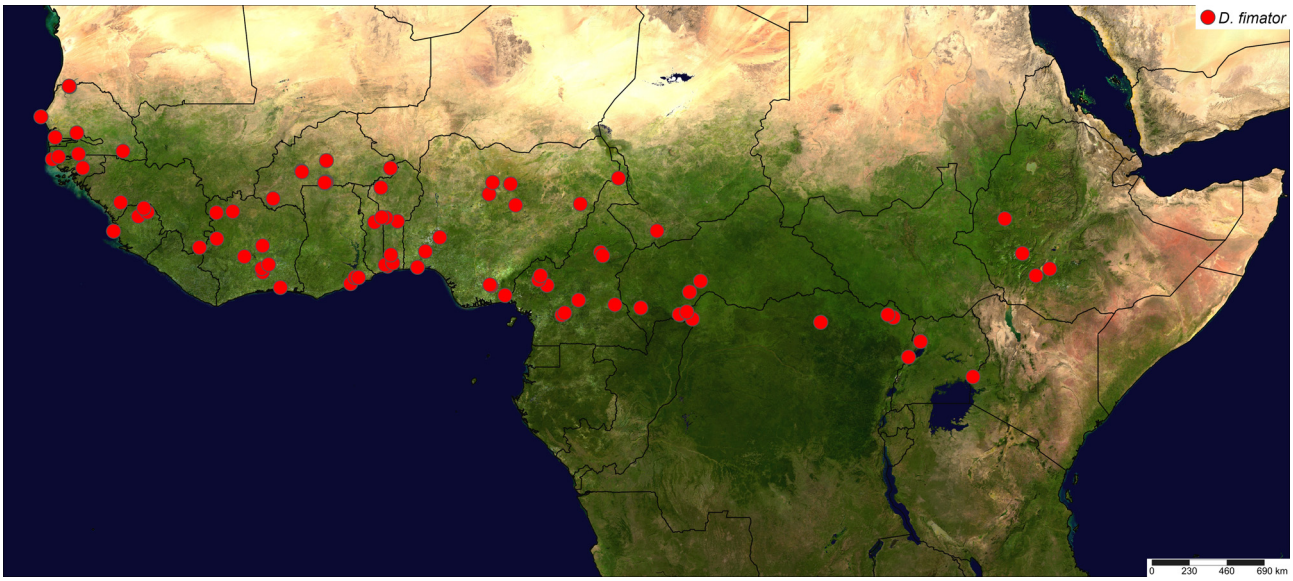
Type locality. Forêt de Sorobouli (11°47'44"N 02°53'25"W), 270 m, Sanguié, Burkina Faso.

Diagnosis. Male cephalic horns lacking granules internally at apex (Fig. 48); males with pronotal anterior angles surface flat, at most slightly produced anteriorly (Fig. 47); FLP sclerite ventral portion with a single carina (Fig. 173); SA sclerite apex interrupted much before apex of apical portion of FLP sclerite (Figs. 171–172).

Description. Holotype ♂ (Fig. 19). **Measurements**. Length 11.5 mm, width 6.5 mm. **Head** (Figs. 47–48). Anterior clypeal edge slightly sinuous on median fifth and appearing arcuate in dorsal view; clypeofrontal carina broadly arcuate and interrupted at gena; lacking median tubercle, surface with punctures fine to small, scabrous anteriorly, separated by one to four diameters. Horns rather long and thick, parallel on apical half in frontal view, parallel sided on apical two-thirds, posterointernal edge unmodified basally, apicointernal surface with few, fine, scabrous punctures; genal edge slightly upturned and simply arcuate on anterior third, forming a broad angle with clypeal edge. **Pronotum** (Fig. 67). Surface with coarse granulate punctures present on posterior half medially and laterally, with more-or-less distinct, minute punctures throughout. Anteromedian tubercle atrophied, round in lateral view; median longitudinal sulcus rather deep but narrow; surface behind the eyes slightly concave, surface of anterior angles flat with anterior angles unmodified; anterior half of lateral edge slightly sinuous in dorsal and lateral view; posterior angles unmodified and simply arcuate in dorsal view. Anterior hypomeral ridge regularly arcuate, anterior hypomeral depression surface completely dark. **Elytra** (Fig. 19). Intervals 2 and 4 with fine granules on disc and apical declivity. **Legs**. Protibial apicointernal tooth enlarged, with dorsal ridge extending to apex. **Aedeagus** (Fig. 131). Parameres with dorsal and ventral edges diverging toward apex in lateral view. **Internal sac sclerites** (Figs. 171–173). Axial sclerite short, angular and extending into a point apically. Subaxial sclerite, large basally and abruptly reduced, extending straight and approximately in line with apex of right lateral fold of frontolateral peripheral sclerite, with fine and scattered villi. Frontolateral peripheral sclerite basoventral apophysis moderately developed; a single large medioventral carina present, carina semicircular in ventral view; right lateral fold produced into a rather small everted and open apically conical process with irregular apical edge located behind oblique right lateral edge of apical lobe; left lateral lobe sclerotized, well developed; subapicodorsal lobe membranous, not reaching anterior edge, apex set on right side in dorsal view; apical lobe truncated apically and directed obliquely on left side, apical villi regular in shape, with a small additional fold ventrally in line with subapicoventral lobe; subapicoventral lobe small, acute apically and obliquely oriented ventrally, short not reaching apical edge of apical lobe.

Variation. Measurements (115 ♂♂, 106 ♀♀). Length: male 7.0–13.0 mm (10.8 ± 1.2 mm), female 9.0–12.0 mm (10.6 ± 0.7 mm). Female allotype. Cephalic outline in dorsal view as in Fig. 83; vertex with a broadly arcuate, transverse carina, dorsal edge broadly arcuate in frontal view, lateral portion obtusely angulated, sloping down posteriorly; anterior pronotal tubercles well developed, external lateral edges slightly widening toward apex in dorsal view, anterolateral surface simply convex, anterosuperior edge slightly arcuate in dorsal view (Fig. 111), lateral portion of anterosuperior edge slightly upturned (Fig. 112). Protibia short, with external teeth more robust.

Primary type data. Holotype ♂ (CMNC): [BURKINA FASO: SANGUIÉ / Forêt de Sorobouli, 270m / 11°47'44"N 002°53'25"W / 13.VIII.2005, F. Génier / zone soudanienne sud / piège excr. Humain, 2005-14]; [COLÉOPTÈRES / DU / BURKINA FASO / BF015498] barcode label; [HOLOTYPE ♂ / *Digitonthophagus* / *fimator n.sp.* / des. F. Génier, 2016] red card.



MAP 14. Distribution of *Digitonthophagus fimator*.

Material examined (415 ♂♂, 345 ♀♀, 279 sex no recorded), distribution (Map 14): **BENIN**: ATAKORA, Batia (10°53'N, 1°29'E), 27.vii.2009, B. Rainon—1 ♂ (paratype) (CMD); ATLANTIQUE, Forêt de Niaouli, Attogon, 117 m (6°44'7"N, 2°8'27"E), 1.v.2013, B. Rainon—3 ♀♀, 2 ♂♂ (5 paratypes) (CBR); BORGOU, Alafiarou, Forêt de Wari-Maro (WM2) (9°1'37"N, 2°24'13"E), 14.iv.2007, S. Tchibozo—1 ♂ (paratype) (PMOC); DONGA, Forêt de Pénélan, Pénéssoulou, 392 m (9°14'50"N, 1°31'45"E), 23.v.2013, B. Rainon—12 ♀♀, 9 ♂♂ (21 paratypes) (CBR); Saramanga, 390 m (9°13'9"N, 1°46'29"E), 24.v.2013, B. Rainon—1 ♂ (paratype) (CBR); MONO, Forêt de Houéyogbé, Houéyogbé, 82 m (6°33'43"N, 1°51'2"E), 8.v.2013, B. Rainon—2 ♀♀, 2 ♂♂ (4 paratypes) (CBR); Lokossa (6°38'N, 1°43'E), 24.iii.2006, B. Rainon—4 ♀♀, 8 ♂♂ (12 paratypes) (CBR); Lokossa (6°38'N, 1°43'E), 12.viii.2007, B. Rainon—1 ♀, 1 ♂ (paratypes) (CMD); OUÉMÉ, environs de Porto Novo (6°30'N, 3°30'E), 1912, Waterlot—1 ♀, 2 ♂♂ (3 paratypes) (MNHN); ZOU, Quartier Soglogon, Bohicon, 200 m (7°10'54"N, 2°1'54"E), 14.iv.2012, B. Rainon—3 ♀♀, 4 ♂♂ (7 paratypes) (CBR); Quartier Soglogon, Bohicon, 200 m (7°10'54"N, 2°1'54"E), 18.iv.2012, B. Rainon—2 ♀♀, 1 ♂ (paratypes) (CBR); **BURKINA FASO**: CENTRE, Ouagadougou (12°22'N, 1°31'W), viii.1977, P. Ardoin—2 ♀♀, 8 ♂♂ (10 paratypes) (FETC); CENTRE-OUEST, Forêt de Sorobouli [=Forêt Classée de Baporo], 270 m (11°47'44"N, 2°53'25"W), 10–15.viii.2005, P. Moretto—4 ♀♀, 2 ♂♂ (6 paratypes) (FETC, PMOC); CENTRE-SUD, Réserve de Nazinga (11°9'N, 1°36'W), 9–12.vi.2005, S. Rojkoff—17 ♀♀, 16 ♂♂ (33 paratypes) (PCSR, PMOC); BALÉ, Boromo, 250 m (11°45'6"N, 2°51'58"W), 10.viii.2005, F. Génier (2005-10)—1 ♂ (paratype) (FGIC); COMOÉ, Forêt de Boulon (savane boisée), 270 m (10°16'27"N, 4°27'15"W), 5.vii.2006, F. & S. Génier (2006-02)—1 ♂ (paratype) (FGIC); Forêt de Boulon (savane boisée), 270 m (10°16'27"N, 4°27'15"W), 6.vii.2006, F. & S. Génier (2006-05)—1 ♂ (paratype) (FGIC); Forêt de Boulon (savane boisée), 270 m (10°16'27"N, 4°27'15"W), 9.vii.2006, F. & S. Génier (2006-17)—3 ♂♂ (3 paratypes) (FGIC); Koflandé (Village), 290 m (10°14'42"N, 4°27'50"W), 4.vii.2006, F. & S. Génier (2006-01)—4 ♂♂ (4 paratypes) (FGIC); NAHOURI, Forêt de Nazinga, 275 m (11°9'24"N, 1°36'44"W), 20.vii.2006, F. & S. Génier (2006-46)—8 ♀♀, 9 ♂♂ (17 paratypes) (FGIC); Forêt de Nazinga, Akwazena, 275 m (11°9'24"N, 1°36'44"W), 21.vii.2006, F. & S. Génier (2006-53)—1 ♂ (paratype) (FGIC); Forêt de Nazinga, Akwazena, 275 m (11°9'24"N, 1°36'44"W), 26.vii.2006, F. & S. Génier (2006-73)—1 ♀, 2 ♂♂ (3 paratypes) (FGIC); Forêt de Nazinga, Akwazena, 275 m (11°9'24"N, 1°36'44"W), 26.vii.2006, F. & S. Génier (2006-75)—2 ♀♀, 3 ♂♂ (5 paratypes) (FGIC); Forêt de Nazinga, Barka, 265 m (11°8'30"N, 1°36'35"W), 22.vii.2006, F. & S. Génier (2006-57)—7 ♀♀, 10 ♂♂ (17 paratypes) (FGIC); Forêt de Nazinga, Barka, 265 m (11°8'30"N, 1°36'35"W), 24.vii.2006, F. & S. Génier (2006-62)—1 ♂ (paratype) (FGIC); Forêt de Nazinga, Boulieselo, 310 m (11°11'50"N, 1°35'9"W), 27.vii.2006, F. & S. Génier (2006-82)—2 ♂♂ (2 paratypes) (FGIC); Forêt de Nazinga, Kalie Boulou, 275 m (11°11'29"N, 1°30'26"W), 22.vii.2006, F. & S. Génier (2006-54)—1 ♂ (paratype) (FGIC); Forêt de Nazinga, Kalie Boulou, 275 m (11°11'29"N, 1°30'26"W), 25.vii.2006, F. & S. Génier (2006-67)—1 ♀ (paratype) (FGIC); Forêt de Nazinga, Kouzougou, 285 m (11°9'17"N, 1°32'10"W), 21.vii.2006, F. & S. Génier (2006-47)—8 ♀♀, 2 ♂♂ (10

paratypes) (FGIC); Forêt de Nazinga, Naguio, 270 m (11°7'52"N, 1°34'38"W), 24.vii.2006, F. & S. Génier (2006-66)—1 ♂ (paratype) (FGIC); SANGUIÉ, Forêt de Sorobouli, 270 m (11°47'44"N, 2°53'25"W), 13.viii.2005, F. Génier (2005-14)—1 ♀, 1 ♂ (holotype, allotype) (CMNC); Forêt de Sorobouli, 270 m (11°47'44"N, 2°53'25"W), 14.viii.2005, F. Génier (2005-18)—2 ♀♀, 1 ♂ (paratypes) (FGIC); TAPOA, Kaabougou, 280 m (11°57'22"N, 2°0'40"E), 12.vii.2006, F. & S. Génier (2006-30)—1 ♂ (paratype) (FGIC); Kaabougou, 280 m (11°57'22"N, 2°0'40"E), 12.vii.2006, F. & S. Génier (2006-31)—1 ♂ (paratype) (FGIC); **CAMEROON**: Yaoundé-Bertoua, v.2003, M. Ondoa—55 ♀♀, 60 ♂♂ (115 paratypes) (CMD, PMOC); ADAMAWA, Ngaoundéré (7°19'N, 13°35'E), iii–v.2003, M. Dongmo—1 ♂ (paratype) (CMD); Ranch de Ngaoundaba (7°8'N, 13°41'45"E), iv.1976, J.L. & A. Nicolas—2 ♀♀, 3 ♂♂ (5 paratypes) (CMD); CENTRAL, Nanga-Eboko (4°41'N, 12°22'E), 1960, Dr. Lenczy—1 ♀, 1 ♂ (paratypes) (CNC); Nkolbisson, Yaoundé (3°52'16"N, 11°27'14"E), 18.x.1973, B. de Miré—1 ♀, 2 ♂♂ (3 paratypes) (MNHN); Nkolbisson, Yaoundé (3°52'16"N, 11°27'14"E), 24.iv.1979, J. Carayon—1 ♂ (paratype) (MNHN); Soa (3°59'N, 11°36'E), i–iii.2003, M. Ondoa—1 ♀, 1 ♂ (paratypes) (CMD); EAST, Batouri (4°26'N, 14°22'E), 1939, P. Lepesme, R. Paulian, & A. Villiers—18 ♀♀, 8 ♂♂ (26 paratypes) (FGIC, MNHN); EXTREME NORTH, Waza (11°24'N, 14°34'E), v.2008, D. Moore—2 ♀♀, 2 ♂♂ (4 paratypes) (PMOC); NORTHWEST, Bankim (6°2'25.8"N, 10°16'25.32"E), 8–13.vi.2009, P. LeGall—11 ♀♀, 8 ♂♂ (19 paratypes) (PMOC); Santa, Monts Bamboutos (5°48'N, 10°10'E), 26.v.1967, [anonymous]—1 ♂ (paratype) (MNHN); WEST, Foumbot (5°30'N, 10°38'E), iv.1966, B. de Miré—1 ♂ (paratype) (MNHN); **CENTRAL AFRICAN REPUBLIC**: KEMO, Sibut (5°44'N, 19°5'E), [no date], [anonymous]—1 ♂ (paratype) (IRSNB); LOBAYE, Boukoko (3°54'N, 17°55'E), iv.1964, R. Pujol—142 specimens (paratype) (MNHN); Boukoko (3°54'N, 17°55'E), 5.vi.1965, M. Boulard—40 specimens (paratype) (MNHN); Kapou (4°2'28"N, 18°19'28"E), 2.v.1970, M. Boulard—1 ♀, 2 ♂♂ (3 paratypes) (MNHN); Station de La Maboké (3°53'N, 17°58'E), 20.vi.1965, [anonymous]—1 ♀ (paratype) (MNHN); Station de La Maboké (3°53'N, 17°58'E), 23.ix.1965, R. Pujol—1 ♀ (paratype) (MNHN); Station de La Maboké (3°53'N, 17°58'E), 24.ix.1965, R. Pujol—2 ♀♀, 2 ♂♂ (4 paratypes) (MNHN); Station de La Maboké (3°53'N, 17°58'E), 31.xii.1965, [anonymous]—2 ♀♀ (2 paratypes) (MNHN); Station de La Maboké (3°53'N, 17°58'E), 22.iii.1966, R. Pujol—1 ♂ (paratype) (MNHN); Station de La Maboké (3°53'N, 17°58'E), 27.iv.1968, R. Pujol—97 specimens (paratypes) (MNHN); Station de La Maboké (3°53'N, 17°58'E), 19.ii.1969, P. Teocchi—2 ♀♀, 2 ♂♂ (4 paratypes) (MNHN); MAMBERE-KADEI, Berbérati (4°15'41"N, 15°47'22"E), 10.iii.1996, Poirier & Ducrocq—2 ♀♀, 6 ♂♂ (8 paratypes) (PMOC); OMBELLA-M'POKO, Bozo (5°8'N, 18°29'E), ix.1975, L. Hervé—1 ♀, 3 ♂♂ (4 paratypes) (PMOC); **CHAD**: LOGONE ORIENTAL, Komé, 80 km Moundou (8°30'N, 16°41'E), vii.2002, T. Garnier—2 ♀♀, 2 ♂♂ (4 paratypes) (PMOC); **CÔTE D'IVOIRE**: BAFING, Ranch de Dolla, Biémasso, 450 m (8°4'N, 7°33'W), iii–iv.2002, P. Moretto—43 ♀♀, 36 ♂♂ (79 paratypes) (FGIC, PMOC); Ranch de Dolla, Biémasso, 450 m (8°4'N, 7°33'W), 1–5.vi.2000, P. Moretto—6 ♀♀, 6 ♂♂ (12 paratypes) (PMOC); DENGUELE, hotel des frontières, Odienné, 416 m (9°30'20.3"N, 7°34'23.6"W), 9–10.vii.2013, P. Moretto—2 ♂♂ (2 paratypes) (PMOC); LACS, Bringakro near (6°25'53"N, 5°4'32"W), 13.vi.2003, Newman *et al*.—1 ♂ (paratype) (BMNH); Bringakro near (6°25'53"N, 5°4'32"W), 16–17.vi.2003, Newman *et al*.—1 ♂ (paratype) (BMNH); Bringakro near (6°25'53"N, 5°4'32"W), 19.vi.2003, Newman *et al*.—1 ♂ (paratype) (BMNH); LAGUNES, Forêt du Banco (5°23'N, 4°3'W), ii.1989, [anonymous]—2 ♀♀, 1 ♂ (paratypes) (CEMT); Lamto (6°13'25"N, 5°1'36"W), 10.iv.1964, [anonymous]—2 ♂♂ (2 paratypes) (OMOC); Lamto (6°13'25"N, 5°1'36"W), 20.ii–28.iii.1968, C. Girard—1 ♀, 1 ♂ (paratypes) (MNHN); Lamto (6°13'25"N, 5°1'36"W), 20–21.iii.1968, C. Girard—1 ♀ (paratype) (MNHN); Lamto (6°13'25"N, 5°1'36"W), 20–24.iii.1968, C. Girard—1 ♀, 4 ♂♂ (5 paratypes) (MNHN); MARAHOUE, Parque National Marahoué (7°5'N, 6°2'W), 17.v.1975, G. & V. Halffter—1 ♀, 1 ♂ (paratypes) (CEMT); NZI-COMOE, Dimbokro (6°39'N, 4°42'W), [no date], [anonymous]—1 ♀, 4 ♂♂ (5 paratypes) (IRSNB); SAVANES, M'banto, Boundiali, 395 m (9°34'10.4"N, 6°40'56.5"W), 6–8.vii.2013, P. Moretto—1 ♂ (paratype) (PMOC); M'banto, Boundiali, 395 m (9°34'10.4"N, 6°40'56.5"W), 13–15.vii.2013, P. Moretto—1 ♀, 7 ♂♂ (8 paratypes) (PMOC); VALLÉE DU BANDAMA, Bouaké (7°41'N, 5°2'W), 5.iv.1974, E. & I. Munroe—1 ♀, 1 ♂ (paratypes) (CMNC); Bouaké (7°41'N, 5°2'W), 7–28.v.1980, O. Kukal—3 ♀♀, 2 ♂♂ (5 paratypes) (CMNC); Bouaké (7°41'N, 5°2'W), 8–17.v.1980, O. Kukal—1 ♀ (paratype) (CMNC); **DEMOCRATIC REPUBLIC OF THE CONGO**: EQUATEUR, Libenge (3°39'N, 18°38'E), 14.xi.1947, R. Cremer & M. Neuman—1 ♂ (paratype) (IRSNB); Savane Liki-Bembe, Libenge (3°39'N, 18°38'E), iii.1948, R. Cremer & M. Neuman—1 ♀, 1 ♂ (paratypes) (IRSNB); Savane Liki-Bembe, Libenge (3°39'N, 18°38'E), iii.1948, R. Cremer & M. Neuman—1 ♂ (paratype) (IRSNB); ORIENTALE, Bambesa (3°28'N, 25°42'E), 13.ii.1940, J. Vrydagh—1 ♂ (paratype) (IRSNB); Cellule II, Parc National de la Garamba (3°53'N, 29°24'E), 28.ii.1951, H. de Saeger (1391)—1 ♀, 2 ♂♂ (3

paratypes) (IRSNB); Cellule II, Parc National de la Garamba (3°53'N, 29°24'E), 5.iii.1951, H. de Saeger (1402)—2 ♀♀, 3 ♂♂ (5 paratypes) (IRSNB); Cellule II, Parc National de la Garamba (3°53'N, 29°24'E), 5.iii.1951, H. de Saeger (1405)—1 ♀, 2 ♂♂ (3 paratypes) (IRSNB); Cellule II, Parc National de la Garamba (3°53'N, 29°24'E), 20.iii.1951, H. de Saeger (1406)—1 ♂ (paratype) (IRSNB); Cellule II, Parc National de la Garamba (3°53'N, 29°24'E), 20.iii.1951, H. de Saeger (1499)—1 ♂ (paratype) (IRSNB); Cellule II, Parc National de la Garamba (3°53'N, 29°24'E), 7.iv.1952, H. de Saeger (3530)—2 ♀♀, 1 ♂ (paratypes) (IRSNB); Faradje (3°44'N, 29°42'E), 13.iv.1930, A. Collart—2 ♀♀, 3 ♂♂ (5 paratypes) (IRSNB); Forêt de Kawa (1°33'N, 30°32'E), 15.iv.1929, A. Collart—1 ♂ (paratype) (IRSNB); Forêt de Kawa (1°33'N, 30°32'E), 20.iv.1929, A. Collart—1 ♀, 3 ♂♂ (4 paratypes) (IRSNB); **ETHIOPIA**: OROMIA, 12 km N Ch'ida (7°15'25"N, 36°48'5"E), 15.v.2013, I. Martinu—1 ♀, 2 ♂♂ (3 paratypes) (JFJC); Gimbi (9°10'N, 35°50'E), 26.vii.2002, Werner—1 ♂ (paratype) (CMD); SOUTHERN NATIONS, NATIONALITIES, AND PEOPLE'S REGION, Arba Minch (6°2'N, 37°33'E), 11–17.ix.2000, P. Léonard—3 ♂♂ (3 paratypes) (FGIC, PMOC); Dila (6°24'30"N, 38°18'30"E), ix.2000, P. Léonard—1 ♂ (paratype) (PMOC); **GHANA**: EASTERN, Hwapa (5°56'N, 0°15'E), 3.iv.1930, [anonymous]—1 ♂ (paratype) (BMNH); GREATER ACCRA, Accra (5°36'N, 0°11'W), ii–iii.1989, Strada—2 ♂♂ (2 paratypes) (FETC); north end, Shai Hills, 125 m (5°56.376'N, 0°3.406'E), 23–25.vi.2006, Bell, Davis, Paemka & Philips—1 ♀, 2 ♂♂ (3 paratypes) (PMOC); **GUINEA**: KINDIA, Kindia (10°4'N, 12°51'W), 20.v.1983, S. Murzin—1 ♀, 1 ♂ (paratypes) (FETC); Kindia (10°4'N, 12°51'W), 23.vi.1983, [anonymous]—1 ♂ (paratype) (OUMNH); NZÉRÉKORÉ, Thio, Mont Nimba (7°35'10"N, 8°30'7"W), ii–vi.1942, M. Lamotte—2 ♀♀, 3 ♂♂ (5 paratypes) (IRSNB); **GUINEA-BISSAU**: BAFATÁ, Chime [= Xime], Rio Géba (11°58'N, 14°56'W), 1906, G. Favarel—1 ♀, 2 ♂♂ (3 paratypes) (IRSNB, MNHN); **NIGERIA**: ABIA, Umuahia (5°32'N, 7°29'E), 12.vii–2.ix.1960, J.L. Gregory—1 ♂ (paratype) (BMNH); Umudike (5°29'N, 7°33'E), 23–31.iii.1960, J.L. Gregory—8 ♀♀, 6 ♂♂ (14 paratypes) (BMNH); ADAMAWA, Zungera (9°59'N, 12°28'E), iv.1911, J.W. Scott-Macfie—1 ♀, 1 ♂ (paratypes) (BMNH); BAUCHI, Lame Burra Game Reserve, 630 m (11°4'57"N, 8°37'26"E), 21–25.vii.2006, P. Léonard & P. Vingerhoedt—3 ♀♀, 5 ♂♂ (8 paratypes) (PMOC); [unspecified locality], vi.1955, A.M. Robertson—2 ♀♀ (2 paratypes) (BMNH); CROSS RIVER, Calabar (4°57'N, 8°19'E), 11.v.1984, [anonymous]—1 ♀ (paratype) (BMNH); Calabar (4°57'N, 8°19'E), 2–3.vii.1984, [anonymous]—1 ♂ (paratype) (BMNH); KADUNA, Kaduna (10°31'23"N, 7°26'25"E), 9.vi.1970, P.H. Ward—2 ♂♂ (2 paratypes) (BMNH); Samaru (11°10'N, 7°38'E), 18–25.v.1970, P.H. Ward—5 ♀♀, 3 ♂♂ (8 paratypes) (BMNH); KWARA, Offa (8°8'25"N, 4°43'32"E), [no date], R.C. Hiscock—1 ♂ (paratype) (BMNH); OYO, Ibadan (7°22'N, 3°56'E), 2.v.1957, J.L. Gregory—1 ♀, 3 ♂♂ (4 paratypes) (BMNH); PLATEAU, Jos (9°55'N, 8°54'E), vi.1976, [anonymous]—2 ♀♀, 1 ♂ (paratypes) (PHWC); Jos (9°55'N, 8°54'E), v.1976, R. Raoux—1 ♂ (paratype) (PHWC); Jos (9°55'N, 8°54'E), 13.iii.1976, R. Raoux—3 ♀♀ (3 paratypes) (PHWC); **SENEGAL**: DAKAR, Sangalkam (14°47'N, 17°14'W), viii.1971, A. Villiers—2 ♂♂ (2 paratypes) (OMOC); FATICK, Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 25.iii.2009, A. Coache—1 ♀, 2 ♂♂ (3 paratypes) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 26.iii.2009, A. Coache—2 ♀♀, 1 ♂ (paratypes) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 27.iii.2009, A. Coache—1 ♂ (paratype) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 28.iv.2009, A. Coache—2 ♀♀, 1 ♂ (paratypes) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 22.vi.2009, A. Coache—4 ♀♀, 7 ♂♂ (11 paratypes) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 23.vi.2009, A. Coache—2 ♀♀, 4 ♂♂ (6 paratypes) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 24.vi.2009, A. Coache—7 ♀♀, 4 ♂♂ (11 paratypes) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 21.iv.2010, A. Coache—1 ♂ (paratype) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 12.vii.2010, A. Coache—4 ♀♀, 2 ♂♂ (6 paratypes) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 13.vii.2010, A. Coache—2 ♀♀ (2 paratypes) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 14.vii.2010, A. Coache—2 ♀♀, 1 ♂ (paratypes) (CAC); Réserve de Fathala, Parc national du delta du Saloum (13°39'N, 16°27'W), 15.vii.2010, A. Coache—2 ♂♂ (2 paratypes) (CAC); KAFFRINE, Tamba (13°53'49"N, 15°15'33"W), 2.vii.1948, [anonymous]—1 ♂ (paratype) (CNC); KOLDA, Sare Gnako, 31 m (12°44'16"N, 15°9'56"W), 31.vii.2007, F. Génier & P. Moretto (2007-49)—1 ♀ (paratype) (FGIC); SAINT-LOUIS, Richard-Toll (16°28'N, 15°41'W), xi.1967, A. Descarpentries, T. Leye & A. Villiers—8 ♀♀, 4 ♂♂ (12 paratypes) (MNHN); Richard-Toll (16°28'N, 15°41'W), 28.viii–1.ix.2009, P. Moretto & F. Génier—4 ♀♀, 4 ♂♂ (8 paratypes) (PMOC); Richard-Toll (16°28'N, 15°41'W), 1.ix.2009, F. Génier (2009-49)—1 ♂ (paratype) (FGIC); TAMBACOUNDA, Ancien Poste, Parc National Niokolo-Koba, 144 m (12°53'19"N, 12°43'10"W), 24–

26.vii.2007, F. Génier & P. Moretto (2007-27)—1 ♀, 2 ♂♂ (3 paratypes) (FGIC); Ancien Poste, Parc National Niokolo-Koba, 144 m (12°53'19"N, 12°43'10"W), 24.vii.2007, F. Génier & P. Moretto (2007-23)—3 ♂♂ (3 paratypes) (FGIC); Ancien Poste, Parc National Niokolo-Koba, 144 m (12°53'19"N, 12°43'10"W), 24–25.vii.2007, F. Génier & P. Moretto (2007-26)—1 ♂ (paratype) (FGIC); ZIGUINCHOR, Boukitimgo, 18 m (12°26'41"N, 16°35'53"W), 4.viii.2007, P. Moretto & F. Génier (2007-58)—1 ♂ (paratype) (FGIC); Ziguinchor (12°35'N, 16°16'W), 28–31.iii.1977, J.L. & A. Nicolas—2 ♀♀, 2 ♂♂ (4 paratypes) (CMD); **SIERRA LEONE**: NORTHERN, Kanike (9°18'N, 11°52'W), 22.v.1912, J.J. Simson—1 ♂ (paratype) (BMNH); Koinadugu (9°32'9"N, 11°22'6"W), 23.v.1963, Mission ENS-IFAN aux Monts Loma—7 ♀♀, 10 ♂♂ (17 paratypes) (MNHN); Musaia [=Musala] (9°45'N, 11°34'W), 26.v.1950, F.A.S.—1 ♀, 2 ♂♂ (3 paratypes) (BMNH); WESTERN, Freetown (8°29'N, 13°14'W), 1889, A. Mocquerys—1 ♀ (paratype) (MNHN); **TOGO**: CENTRALE, Sokode (8°59'N, 1°8'E), iii.1957, P. Jauffret—2 ♂♂ (2 paratypes) (PMOC); **UGANDA**: BUSIA, Busia (0°28'N, 34°5'E), i.1990, B. Wandera—2 ♀♀, 1 ♂ (paratypes) (FETC); Busia (0°28'N, 34°5'E), vii.1990, [anonymous]—1 ♂ (paratype) (FETC); NORTHERN, Nebbi District, Pamora, Padyere subcounty (2°24'25"N, 31°11'40"E), v.2006, Local collectors—2 ♀♀, 3 ♂♂ (5 paratypes) (PMOC).

Etymology. *Fimator* (from *fimus*) a Latin noun in apposition meaning dung remover. Pertaining to the natural history of this species.

Natural history. The distribution of this species in the soudanian zone and forest/savanna mosaic areas, with intrusions in the northern portion of the central forest block, suggests that it can colonize wetter environments when used as pastures. All Cameroonian and Central African records are from pastures in forest/savanna mosaic. Few individuals were collected from the Sahelian region. Specimens were collected from ruminants and non-ruminants such as cow, elephant, roan antelope (*Hippotragus equinus*), pig, rhinoceros, warthog, and zebra dung. This species is attracted to mercury vapor and ultraviolet light.

Digitonthophagus lusinganus (d'Orbigny, 1905)

(Figs. 20, 49–50, 68, 84, 113–114, 132, 174–176; Map 15)

Onthophagus (*O.*) *gazella* var. *lusinganus* d'Orbigny, 1905: 495 (original description)
Onthophagus (*O.*) *gazella* var. *lusinganus*—d'Orbigny 1913b: 249 (monograph)
Onthophagus (*O.*) *gazella* race *lusinganus*—Kolbe 1914: 297 (distribution)
Onthophagus gazella var. *lusinganus*—Gillet & Boucomont 1927: 138 (mentioned as synonym)
Onthophagus lusinganus—Müller 1942: 96 (new combination, distribution)
Onthophagus (*Digitonthophagus*) *gazella* var. *lusinganus*—Balthasar 1963: 365 (mentioned as synonym)
Onthophagus (*O.*) *lusinganus*—Ferreira 1972: 680 (catalog)
Onthophagus (*Digitonthophagus*) *lusinganus*—Kim & Lumaret, 1989: 336 (description of larvae)

Type locality. Ile de Lusinga (Victoria-Nyanza N.-E.), Afrique Orientale Anglaise [Kenya].

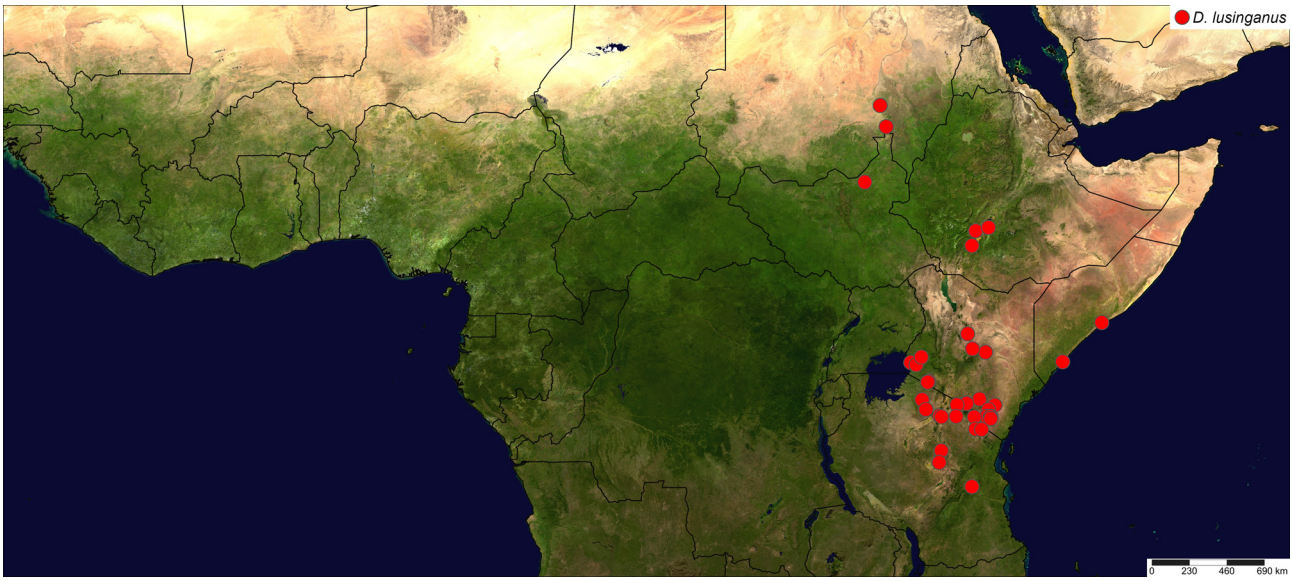
Diagnosis. Male cephalic horns lacking granules internally at apex (Fig. 50); males with pronotal anterior angles surface distinctly concave, simply round anteriorly (Fig. 49); pronotal surface with dense, small punctures throughout (Fig. 70); FLP sclerite ventral portion with a single carinae (Fig. 176); SA sclerite apex interrupted much before apex of apical portion of FLP sclerite (Figs. 174–175).

Description. Lectotype ♂ (Fig. 20). **Measurements**. Length 13.5 mm, width 8.0 mm. **Head** (Figs. 49–50). Anterior clypeal edge straight on median fifth in dorsal view; clypeofrontal carina broadly arcuate and interrupted at gena; vertex lacking median tubercle, surface with fine and minute punctures; fine punctures separated by one to three diameters. Horns rather long, arcuate, divergent in frontal view, gradually tapering from base to apex; posterointernal edge with a low, angular projection; apicointernal surface lacking granules. Punctures slightly scabrous; genal edge strongly upturned and distinctly angulate on anterior third, forming a broad angle with clypeal edge. **Pronotum** (Fig. 68). Surface with large, weakly-defined, strongly granulate punctures restricted to anterior half medially, with smaller scattered scabrous punctures on posterior half of disc; punctures weaker but distinct posterolaterally, with dense small punctures throughout; anteromedian tubercle well developed, produced into a small, transverse, sharp ridge on each side of midline, median longitudinal sulcus deep; surface behind the eyes slightly concave, surface of anterior angles concave, anterior angles unmodified; anterior half of lateral edge arcuate in dorsal and lateral view; posterior angles simply arcuate in dorsal view. Anterior hypomeral ridge arcuate

throughout, anterior hypomeral depression surface slightly darker in color medially. **Elytra** (Fig. 20). Intervals 2 and 4 lacking fine granules from base to apical declivity. **Legs**. Protibial apicointernal tooth enlarged, with dorsal ridge extending to apex. **Aedeagus** (Fig. 132). Parameres with dorsal and ventral edges diverging toward apex in lateral view. **Internal sac sclerites** (Figs. 174–176)**.** Axial sclerite weekly sclerotized, short, semicircular. Subaxial sclerite wide basally and abruptly narrowed at mid distance, apical half short, extending straight, interrupted before apex of frontolateral peripheral sclerite apical portion, with villi on apical half. Frontolateral peripheral sclerite basoventral apophysis well developed, forming an acute angle in lateral view; with a more-or-less rectangular medioventral carina; right lateral fold produced into a spoon-like process apically; left lateral lobe moderately sclerotized and well developed; subapicodorsal lobe membranous, small, extending in line with apex of right lateral fold, apex set on left side in dorsal view; right preapical edge entire; apex of apical lobe round apically, directed obliquely on left side, apical villi regular in shape, ventral portion with a small additional lobate projection above subapicoventral lobe; subapicoventral lobe rather small, round and interrupted before apex of apical lobe.

Variation. Measurements (64 ♂♂, 73 ♀♀). Length: male 9.5–15.0 mm (12.6 ± 1.2 mm), female 9.0–14.0 mm (12.1 ± 1.1 mm). Female paralectotype. Cephalic outline in dorsal view as in Fig. 84; vertex with a broadly arcuate, transverse carina, dorsal edge broadly arcuate in frontal view, lateral low and portion shortly gradually sloping down posteriorly; anterior pronotal tubercles well developed, external lateral edges rather short and slightly widening toward apex in dorsal view, anterolateral surface slightly obliquely concave, anterosuperior edge slightly arcuate in dorsal view (Fig. 113), lateral portion of anterosuperior edge slightly upturned (Fig. 114). Protibia short, with external teeth more robust.

Primary type data. Lectotype ♂ (MNHN) **present designation**: [AFRIQUE OR[le] ANGLAISE / Ile de LUSINGA / (VICTORIA-NYANZA N.-E) / CH. ALLUAUD X. 1903]; [MUSEUM PARIS / Coll. H. d' ORBIGNY / 1913] blue card; [WORLD / SCARAB. / DATABASE / WSD00030000] barcode label; [gazella Fabr. / v. lusinganus / var. nov. d'Orb.] handwritten on card; [LECTOTYPE ♂ / *Onthophagus* / *gazella v. lusinganus* / d'Orbigny, 1905 / dés. F. Génier, 2016] red card; [*Digitonthophagus* / *lusinganus* ♂ / (d'Orbigny, 1905) / dét. F. Génier, 2016].



MAP 15. Distribution of *Digitonthophagus lusinganus*.

Material examined (91 ♂♂, 116 ♀♀), distribution (Map 15): **ETHIOPIA**: SOUTHERN NATIONS, NATIONALITIES, AND PEOPLE'S REGION, Arba Minch (6°2'N, 37°33'E), iv.1993, Werner—1 ♂ (PMOC); Arba Minch (6°2'N, 37°33'E), 6.ii.1978, P.-C. Rougeot—1 ♀ (MNHN); Arba Minch (6°2'N, 37°33'E), 6.ii.1978, P.-C. Rougeot—1 ♀ (MNHN); Arba Minch (6°2'N, 37°33'E), 11–17.ix.2000, P. Léonard—19 ♀♀, 12 ♂♂ (FGIC, PMOC); Lac Awassa (7°2'N, 38°28'E), 10.xi.1973, P.C. Rougeot—1 ♀ (MNHN); Nanoropus, bord du Rodolphe, 565 m (4°51'N, 36°5'E), 1932–1933, C. Arambour, P.-A. Chapuis, & R. Jeannel—6 ♀♀, 6 ♂♂ (FGIC, MNHN); Soddu [=Sodo] (6°51'N, 37°45'30"E), 20.vii.1971, [anonymous]—1 ♂ (FETC); **KENYA**: Tsavo National Park [=Tsavo East National Park] (2°45'S, 38°49'E), 14.xi.1972, T.J. Kingston—1 ♀, 1 ♂ (OUMNH); Tsavo National

Park [=Tsavo East National Park] (2°45'S, 38°49'E), 18.x.1973, T.J. Kingston—8 ♀♀, 4 ♂♂ (OUMNH); Tsavo National Park [=Tsavo East National Park] (2°45'S, 38°49'E), 21.xi.1973, T.J. Kingston—4 ♀♀ (OUMNH); Tsavo National Park [=Tsavo East National Park] (2°45'S, 38°49'E), 29.xi.1973, T.J. Kingston—1 ♂ (OUMNH); HOMA BAY, Baie de Kavirondo, Lac Victoria (0°31'S, 34°29'E), ix–x.1903, C. Alluaud—1 ♂ (MNHN); Ile de Lusinga [= Rusinga], Victoria-Nyanza N.-E. (0°24'S, 34°11'E), x.1903, C. Alluaud—12 ♀♀, 11 ♂♂ (lectotype, 22 paralectotypes) (IRSNB, MNHN); ISIOLO, Isiola Samburni (0°21'23"N, 37°34'56"E), 18.xi.1975, H.A.—1 ♀ (BMNH); Meru National Park, Tana River near Post 96, 275 m (0°10'N, 38°18'E), 13.xi.1975, C.F. Dewhurst—1 ♂ (BMNH); KISUMU, 3 km SE Kisumu, 1120 m (0°9'S, 34°51'E), 17.iv.1975, Davis & Dewhurst—1 ♀ (MNHN); 6 km S Ahero, 1200 m (0°13'16"S, 34°57'24"E), 22.xi.1975, C.F. Dewhurst—1 ♂ (MNHN); Kisumu (0°6'S, 34°46'E), [no date], P.S. Corbet—1 ♀ (BMNH); MAKUENI, Kibwezi (2°24'38"S, 37°58'4"E), 20.xi.1989, P. Smerz—1 ♂ (JFJC); MERU, Leopard Rock Swamp - Post 12–33, Meru National Park, 600 m (0°12'N, 38°14'E), 14.xi.1975, C.F. Dewhurst—1 ♂ (MNHN); NAROK, Massai Mara National Reserve (1°29'S, 35°7'E), ii.1994, Czeppel—1 ♂ (FETC); Massai Mara National Reserve (1°29'S, 35°7'E), iii.1995, Cursi—1 ♂ (FETC); RIFT VALLEY, Amboseli National Park (2°38'S, 37°14'E), 22.i.1986, R. Minetti—2 ♀♀, 1 ♂ (PMOC); Headquarters area, Lake Amboseli basin, Amboseli National Park, 1050 m (2°39'14"S, 37°15'22"E), 5.v.1975, Davies & Dewhurst—1 ♀ (BMNH); Talek River, Massai Mara, 1300 m (1°26'S, 35°10'E), xii.1997, P. Bleuzen—1 ♀, 1 ♂ (JFJC); SAMBURU, approximately 35 km N Wamba, Mattews Range, Rift Valley, 1300–1400 m (1°10.707'N, 37°18.962'E), 7–12.xii.2002, C. Hauser, D. Bartsch, & A. Zahm—1 ♂ (SMNS); TAITA TAVETA, Entrance Gate Tsavo National Park, Voi (3°21'47"S, 38°35'46"E), 26.xii.1990, B.D. Gill—1 ♀ (BDGC); Sagala Hills (3°29'S, 38°35'E), xii.1993, Werner—1 ♀ (CMD); Taita (3°22'S, 38°22'E), [no date], [anonymous]—2 ♀♀, 1 ♂ (BMNH); Taveta (3°24'S, 37°41'E), i–iv.1904, C. Alluaud—1 ♂ (MNHN); Taveta (3°24'S, 37°41'E), iii.1912, Alluaud & Jeannel (St. 65)—1 ♂ (MNHN); Tsavo, 60 km N Voi (2°59'42"S, 38°27'41"E), 25.xii.1990, B.D. Gill—2 ♂♂ (BDGC); Voi (3°23'S, 38°34'E), xi.1997, M. Snižek—1 ♂ (CEMT); Voi (3°23'S, 38°34'E), vi/1997, O. Bužga—1 ♂ (PMOC); Voi (3°23'S, 38°34'E), 10.xii.1999, P. Smerz—1 ♀ (JFJC); Voi, Tsavo East National Park (3°23'S, 38°34'E), 31.xii.1990, B.D. Gill—20 ♀♀, 12 ♂♂ (BDGC); **SOMALIA**: JUBBADA HOOSE, Kismaayo, Mareri (0°21'37"S, 42°32'56"E), 29.x.1986, M.J.W. Cock—1 ♀, 1 ♂ (BMNH); SHABEELLAHA HOOSE, Genale (1°48'N, 44°42'0"E), v.1935, F. Bigi—1 ♀ (FETC); Genale (1°48'N, 44°42'0"E), [no date], [anonymous]—1 ♀ (NMPC); **SOUTH SUDAN**: UPPER NILE, Malakal (9°32'N, 31°39'E), 30.xi.1960, B. Hocking—1 ♀ (BMNH); **SUDAN**: KHARTOUM, Kawa, 157 mi. S Khartoum (13°45'N, 32°30'E), 2–3.xii.1961, J.L. Cloudsley-Thompson—2 ♀♀, 1 ♂ (BMNH); SENNAR, [unspecified locality], 1906, C. Alluaud—2 ♀♀, 2 ♂♂ (IRSNB); WHITE NIL, El Jebelain (12°35'N, 32°50'E), 3–4.xii.1961, J.L. Cloudsley-Thompson—1 ♀ (BMNH); **TANZANIA**: ARUSHA, Arusha environs (3°22'S, 36°41'E), 3–4.iv.1997, M. Kuboň—5 ♀♀, 1 ♂ (PMOC); Orekeryan, Mount Longido (2°43'47"S, 36°43'26"E), 8.xi.2011, R. Smith & H. Takano—1 ♂ (BMNH); DODOMA, 40 km N Dodoma, 1100 m (5°54'S, 35°45'E), 15.xii.2007, F. Kantner—1 ♂ (SMNS); Babati-Dodoma (5°15'S, 35°52'E), 6.xii.1997, Werner & Lizler—1 ♂ (CMD); KILIMANDJARO, Ibaya Camp, Mkomazi Game Reserve (4°5'11"S, 38°4'55"E), 13.iv.1995, J.G. Davies—1 ♀ (BMNH); Ibaya Camp, Mkomazi Game Reserve (4°5'11"S, 38°4'55"E), 29.iii.1996, G.C. McGavin—1 ♂ (OUMNH); Same (4°4'S, 37°45'E), 12–17.v.1999, O. Bužga—3 ♂♂ (PMOC); MANYARA, Kibaone, 1348 m (3°20'11"S, 35°46'36"E), 8–10.v.2012, R. Smith & H. Takano—1 ♂ (BMNH); Mto Wa MBu, Lake Manyara National Park, 963 m (3°23'12"S, 35°52'36"E), 21.xi.2011, R. Smith & H. Takano—14 ♀♀, 11 ♂♂ (BMNH); MARA, Seronera Wildlife Lodge (2°26'50"S, 34°48'24"E), 14–17.ii.1989, G. Bassi & Scaramozzino—1 ♂ (CMNC); MOROGO, Monts Uluguru (7°14'S, 37°33'E), 20.xi.2005, Local collectors—1 ♀ (PMOC); SHINYANGA, Lake Ndutu area, Serengeti National Park (2°59'S, 35°1'E), 20.i.1991, R. Foster—1 ♀ (OUMNH).

Natural history. No habitat data, some specimens collected in buffalo and elephant dung. This species is attracted to mercury vapor and ultraviolet light traps.

Nomenclature and taxonomy. *Digitonthophagus lusinganus* was first described as a variety of *Onthophagus gazella* by d'Orbigny (1905). In a note on the Coleoptera of Benadir (Somalia) Müller (1942) concluded that the coexistence of two forms of "*O. gazella"* and the "*O. gazella* form *lusinganus"* in several East African localities was not possible and considered this form as a good species. We concur with Müller (1942) and Ferreira (1972) that this revised status is correct. The original syntype series comprises 23 specimens deposited in the Muséum national d'Histoire naturelle (Paris) and Royal Belgian Institute of Natural Sciences (Brussels). In order to stabilize nomenclature a male specimen possessing the best diagnostic characters is selected as lectotype, (**present**

designation). This lectotype is designated in order to choose a single specimen as name bearing type in the event that the other specimens of the syntype series could belong to a different cryptic species in this genus.

***Digitonthophagus ulcerosus* Génier, new species**
http://zoobank.org/urn:lsid:zoobank.org:act:CEBB9AB5-F6F4-4BDF-A6C1-037C15BBBD24
(Figs. 21, 51–52, 69, 85, 115–116, 133, 177–179; Map 16)

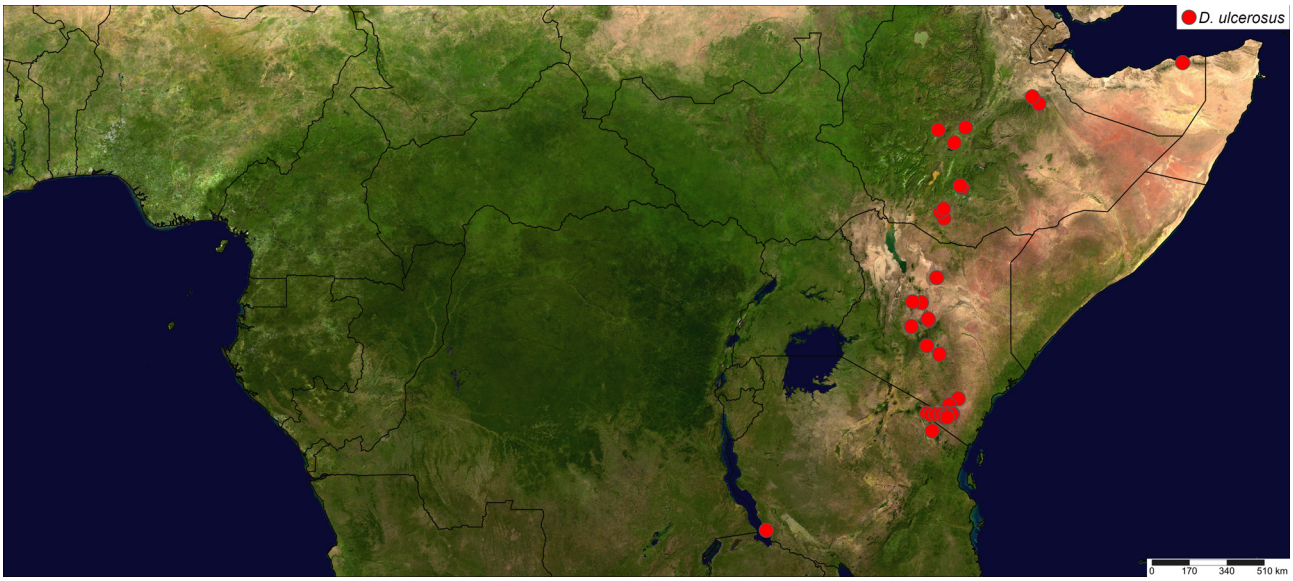
Type locality. Ouarsangueli [=Warsangeli Sultanate], Somalia.

Diagnosis. Male cephalic horns with coarse granules internally at apex (Fig. 52); males with pronotal anterior angles surface deeply concave, simply round anteriorly (Fig. 51); FLP sclerite ventral portion with a single carinae (Fig. 179); SA sclerite apex interrupted much before apex of apical portion of FLP sclerite (Figs. 177–178).

Description. Holotype ♂ (Fig. 21). **Measurements**. Length 13.5 mm, width 8.0 mm. **Head** (Figs. 51–52). Anterior clypeal edge sinuous on median seventh in dorsal view; clypeofrontal carina broadly arcuate and interrupted at gena; vertex lacking median tubercle, surface with fine and minute punctures; fine, simple punctures separated by one to three diameters. Horns rather long, arcuate and slightly divergent in frontal view apical third more abruptly curved internally, parallel sided on basal two-thirds, and tapering into a point on apical third; posterointernal edge unmodified, internal surface with numerous coarse granules; genal edge upturned and simply arcuate, almost in line with clypeal edge. **Pronotum** (Fig. 69). Surface with rather small, granulate punctures restricted to anterior half medially, with smaller scattered simple or slightly scabrous punctures on posterior half of disc; punctures scattered and obsolete posterolaterally, with minute punctures throughout. Anteromedian tubercle well developed, produced into small acute denticle on each side of midline; median longitudinal sulcus deep; surface behind the eyes concave, surface of anterior angles with a deeply concave, anterior angles unmodified; anterior half of lateral edge arcuate in dorsal view and slightly sinuous in lateral view; posterior angles slightly lobate in dorsal view. Anterior hypomeral ridge nearly straight posteriorly and strongly arcuate on anterior third, anterior hypomeral depression surface slightly darker in color medially. **Elytra** (Fig. 21). Intervals 2 and 4 with odd, fine granules on apical declivity only. **Legs**. Protibial apicointernal tooth enlarged, with dorsal ridge extending to apex. **Aedeagus** (Fig. 133). Parameres with dorsal and ventral edges diverging toward apex in lateral view. **Internal sac sclerites** (Figs. 177–179)**.** Axial sclerite strongly sclerotized, abruptly bent ventrally on apical third. Subaxial sclerite, extending straight and interrupted in line with right lateral fold apical portion, with villi on apical third. Frontolateral peripheral sclerite basoventral apophysis moderately developed; a single medioventral carina present, carina distinctly folded and angulate in ventral view; right lateral fold produced into a large everted and open apically conical process with sinuous apical edge located behind oblique right lateral edge of apical lobe; left lateral lobe well sclerotized; subapicodorsal lobe membranous, narrow, not reaching anterior edge, apex set medially in dorsal view; apical lobe truncate apically and approximately in line with the axis frontolateral peripheral sclerite, ventral portion produced into and additional fold separating two concavities, ventral portion of additional lobe more-or-less parallel to apex of ventral portion of apical lobe, apical villi regular in shape; subapicoventral lobe small, not reaching apical edge of apical lobe, oriented ventrally and in line with ventrally folded left edge of apical lobe.

Variation. Measurements (96 ♂♂, 92 ♀♀). Length: male 9.0–13.5 mm (11.7 ± 0.9 mm), female 8.0–13.0 mm (11.1 ± 1.0 mm). Female allotype. Cephalic outline in dorsal view as in Fig. 85; vertex with a broadly arcuate, transverse carina, dorsal edge broadly arcuate in frontal view, lateral portion gradually sloping down posteriorly; anterior pronotal tubercles well developed, external lateral edges parallel sided in dorsal view, anterolateral surface simply convex, anterosuperior edge arcuate in dorsal view (Fig. 115), lateral portion of anterosuperior edge slightly upturned (Fig. 116). Protibia short, with external teeth more robust.

Primary type data. Holotype ♂ (MNHN): [MUSEUM PARIS / SOMALI / OUARSANGUELI / REVOIL 1881] green card; [1648 / 81] blue disc verso; [WORLD / SCARAB. / DATABASE / WSD00029929] barcode label; [HOLOTYPE ♂ / *Digitonthophagus* / *ulcerosus n.sp.* / des. F. Génier, 2016] red card.



MAP 16. Distribution of *Digitonthophagus ulcerosus*.

Material examined (134 ♂♂, 111 ♀♀), distribution (Map 16): **ETHIOPIA**: Fourri, [no date], [anonymous]—1 ♀ (paratype) (MNHN); Hora Oitu, [no date], [anonymous]—2 ♀♀ (2 paratypes) (MNHN); DIRE DAWA, Dire Dawa (9°36'N, 41°51'E), ix.1935, H. Ulenhuth—1 ♂ (paratype) (BMNH); Dire Dawa (9°36'N, 41°51'E), 1919, A. Marchand—4 ♀♀, 5 ♂♂ (9 paratypes) (FGIC, MNHN); Dire Dawa (9°36'N, 41°51'E), iv, [anonymous]—3 ♀♀ (3 paratypes) (IRSNB); Dire Dawa (9°36'N, 41°51'E), [no date], [anonymous]—1 ♀, 5 ♂♂ (6 paratypes) (IRSNB); Dire Dawa (9°36'N, 41°51'E), 1912, G. Kristensen—2 ♂♂ (2 paratypes) (MNHN); Dire Dawa (9°36'N, 41°51'E), 1936, [anonymous]—1 ♂ (paratype) (MNHN); Dire Dawa (9°36'N, 41°51'E), iii, [anonymous]—1 ♂ (paratype) (MNHN); Dire Dawa (9°36'N, 41°51'E), 2.x.1903, [anonymous]—1 ♂ (paratype) (MNHN); HARARI, Harrar (9°19'N, 42°7'E), [no date], [anonymous]—6 ♀♀, 8 ♂♂ (14 paratypes) (MNHN); Harrar (9°19'N, 42°7'E), 1910, [anonymous]—4 ♀♀ (4 paratypes) (MNHN); Harrar (9°19'N, 42°7'E), 1911, [anonymous]—1 ♂ (paratype) (MNHN); OROMIA, 35 km S Yabello (4°38'N, 38°14'E), 10.v.2013, I. Martinu—1 ♂ (paratype) (JFJC); 76 km S Agere Maryam (5°1'N, 38°13'E), 8.v.2013, I. Martinu—2 ♂♂ (2 paratypes) (JFJC); Bulbulla (7°43'N, 38°39'E), [no date], [anonymous]—9 ♀♀, 9 ♂♂ (18 paratypes) (FGIC, MNHN); Environs de Kibre Mengis, 1800–2000 m (5°53'N, 38°59'E), 12–15.xi.1973, P.C. Rougeot—1 ♂ (paratype) (MNHN); Lake K'ok'a [= Lake Koka; Harairobi-see; Garairobisee] (8°21'N, 39°7'E), ii.1931, Huyn—15 ♀♀, 19 ♂♂ (34 paratypes) (FGIC, NMPC); Lake K'ok'a [= Lake Koka; Harairobi-see; Garairobisee] (8°21'N, 39°7'E), [no date], A. Hepp—2 ♀♀ (2 paratypes) (SMF); Maleka, 15 km W Kibre Mengist (5°58'N, 38°54'E), 14–16.iv.2002, Josso, Juhel & Legrand—1 ♂ (paratype) (JFJC); Yabelo (4°53'N, 38°5'E), iv.1994, Werner—1 ♀, 1 ♂ (paratypes) (CMD); SOUTHERN NATIONS, NATIONALITIES, AND PEOPLE'S REGION, Maraquo (8°15'N, 38°0'E), viii.1914, [anonymous]—4 ♀♀, 10 ♂♂ (14 paratypes) (FGIC, IRSNB); Maraquo (8°15'N, 38°0'E), [no date], [anonymous]—19 ♀♀, 21 ♂♂ (40 paratypes) (IRSNB, MNHN); **KENYA**: Tsavo National Park [=Tsavo East National Park] (2°45'S, 38°49'E), 18.x.1973, T.J. Kingston—2 ♀♀, 4 ♂♂ (6 paratypes) (OUMNH); Tsavo National Park [=Tsavo East National Park] (2°45'S, 38°49'E), 19.xi.1973, T.J. Kingston—1 ♂ (paratype) (OUMNH); Tsavo National Park [=Tsavo East National Park] (2°45'S, 38°49'E), 21.xi.1973, T.J. Kingston—1 ♂ (paratype) (OUMNH); Tsavo National Park [=Tsavo East National Park] (2°45'S, 38°49'E), 29.xi.1973, T.J. Kingston—1 ♂ (paratype) (OUMNH); ISIOLO, 10 km N Isiolo (0°27'14"N, 37°36'36"E), 16.xii.1990, B.D. Gill—2 ♀♀, 3 ♂♂ (5 paratypes) (BDGC); Buffalo Spring National Reserve, 900 m (0°31'N, 37°35'E), 15–16.xii.1990, B.D. Gill—1 ♀, 1 ♂ (paratypes) (BDGC); KITUI, S of Mwingi, Kavati Road. (0°56'S, 38°3'E), 27–28.xi.1999, P. Smerz—1 ♂ (paratype) (JFJC); LAIKIPIA, Karama [Hunting Camp], Tigania (0°12'25"N, 36°54'15"E), 23.x.1982, R. Mourglia—7 ♀♀, 6 ♂♂ (13 paratypes) (FETC); MARSABIT, near Gof Bongole Crater, Marsabit National Park & Reserve (2°12'N, 37°56'E), 18.v.1975, Davis & Dewhurst—1 ♀, 1 ♂ (paratypes) (BMNH); RIFT VALLEY, Samburu National Reserve (1°13'N, 36°57'E), 4.xii.1989, Moreno-Mestre—2 ♀♀, 2 ♂♂ (4 paratypes) (PMOC); SAMBURU, approximately 35 km N Wamba, Mattews Range, Rift Valley, 1300–1400 m (1°10.707'N, 37°18.962'E), 7–12.xii.2002, C. Hauser, D. Bartsch, & A.

Zahm—1 ♀ (paratype) (SMNS); Uaso Nyiro (0°35'S, 37°32'E), [no date], Machulka—1 ♀, 2 ♂♂ (3 paratypes) (NMPC); TAITA TAVETA, Entrance Gate Tsavo National Park, Voi (3°21'47"S, 38°35'46"E), 26.xii.1990, B.D. Gill—1 ♂ (paratype) (BDGC); Maktau, Pori, 1050 m (3°24'S, 38°7'E), iii.1912, Alluaud & Jeannel (St. 62)—1 ♀ (paratype) (MNHN); Mbuyuni, Pori, 1110 m (3°24'S, 37°54'E), iii.1912, Alluaud & Jeannel (St. 63)—1 ♀, 1 ♂ (paratypes) (MNHN); Mwatate, 25 km SW Voi (3°30'S, 38°22'E), 26.xii.1990, B.D. Gill—5 ♀♀, 3 ♂♂ (8 paratypes) (BDGC); Taita (3°22'S, 38°22'E), [no date], [anonymous]—3 ♀♀, 2 ♂♂ (5 paratypes) (BMNH, MNHN); Taita Hills (3°25'S, 38°20'E), 12.xii.1989, Moreno-Mestre—2 ♀♀, 3 ♂♂ (5 paratypes) (PMOC); Taita Hills Game Lodge (3°30'42"S, 38°15'5"E), 26.xii.1990, B.D. Gill—1 ♀ (paratype) (BDGC); Taveta, 750 m (3°24'S, 37°41'E), iii.1912, Alluaud & Jeannel (St. 65)—1 ♀ (paratype) (MNHN); Tsavo, 50 km N Voi (3°0'S, 38°27'E), 25.xii.1990, B.D. Gill—1 ♂ (paratype) (BDGC); Voi, Tsavo East National Park (3°23'S, 38°34'E), 31.xii.1990, B.D. Gill—4 ♀♀, 2 ♂♂ (6 paratypes) (BDGC); **SOMALIA**: [unspecified locality], [no date], [anonymous]—2 ♂♂ (2 paratypes) (MNHN); [unspecified locality], [no date], Révoil—3 ♂♂ (3 paratypes) (MNHN); SANAAG, Ouarsangueli [=Warsangeli Sultanate] (11°0'N, 48°0'E), 1881, Révoil—1 ♀, 2 ♂♂ (holotype, allotype, 1 paratype) (MNHN); **TANZANIA**: KILIMANDJARO, Rivière Himo, zone inférieure, versant sud-ouest, Kilimandjaro, 1000 m (3°20'41"S, 37°31'56"E), iii.1912, Alluaud & Jeannel (St. 66)—2 ♀♀ (2 paratypes) (MNHN); Same (4°4'S, 37°45'E), v.1962, [anonymous]—1 ♀ (paratype) (CNC); Same (4°4'S, 37°45'E), 12–17.v.1999, O. Bužga—1 ♂ (paratype) (PMOC); RUKWA, Near Kala, Tanganyika (8°8'S, 30°58'E), [no date], J.P. Lacroix—1 ♀ (paratype) (MNHN).

Etymology. *Ulcerosus* is a Latin adjective pertaining to the deeply concave surface of the male anterior pronotal angles of this species.

Natural history. No habitat data are known. Some specimens were collected in buffalo and elephant dung.

Digitonthophagus namaquensis species group

Diagnosis. A single species with subapicodorsal lobe of FLP sclerite set on left side (Fig. 180); right lateral fold of FLP sclerite apical portion atrophied, set behind oblique right lateral edge of apical lobe (Fig. 180); basoventral apophysis of FLP sclerite large (Fig. 182).

Digitonthophagus namaquensis Génier, new species

http://zoobank.org/urn:lsid:zoobank.org:act:48DC7E17-6D54-4345-9746-183D5D580AB8
(Figs. 22, 53–54, 70, 86, 117–118, 134, 180–182, 189; Map 17)

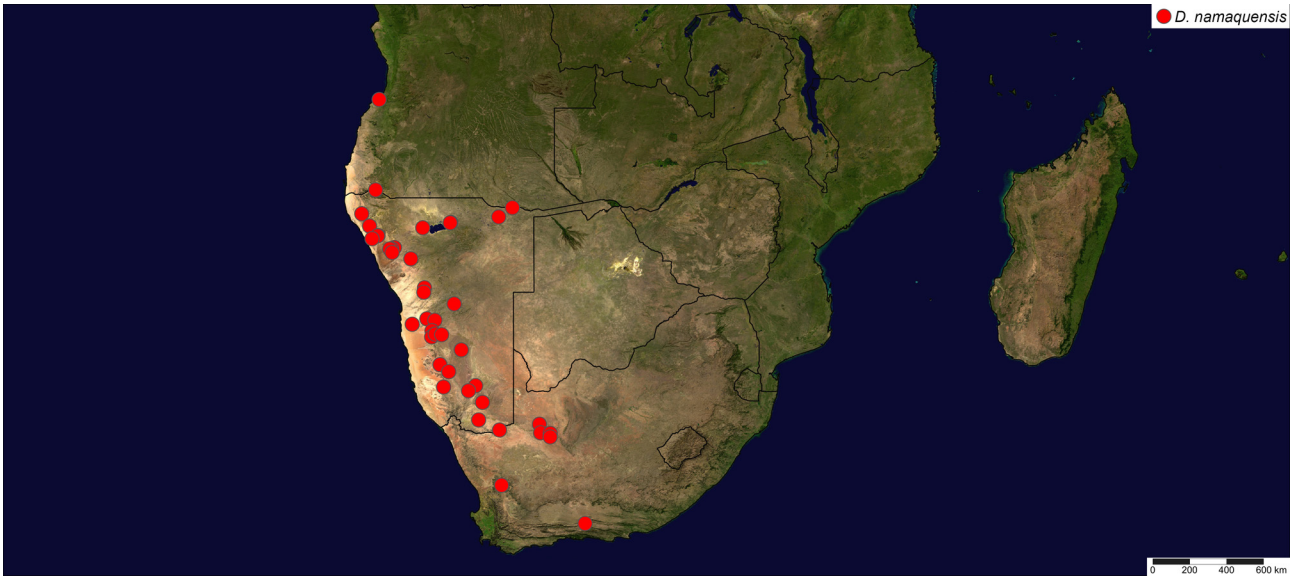
Type locality. Farm Klipkoppies (6) (28.87137 S 21.30944 E), 957 m, Northern Cape, South Africa.

Description. Holotype ♂ (Fig. 22). **Measurements**. Length 10.5 mm, width 6.0 mm. **Head** (Figs. 53–54). Anterior clypeal edge straight on median fifth in dorsal view; clypeofrontal carina broadly arcuate and interrupted at gena; vertex lacking median tubercle, surface with punctures fine to small, separated by one to four diameters, scabrous. Horns rather short, slightly arcuate in frontal view, gradually tapering from base to apex; posterointernal edge unmodified basally, apicointernal surface with few scabrous punctures; genal edge slightly upturned and broadly arcuate, forming a broad angle with clypeal edge. **Pronotum** (Fig. 70). Surface with weakly-defined granulate punctures on anterior half only, with scattered punctures on posterior half of disc; punctures scattered and small posterolaterally, with distinct minute punctures throughout; anteromedian tubercle atrophied, forming an obtuse angle in lateral view, median longitudinal sulcus rather wide and moderately deep; surface behind the eyes with a transverse oval and shallow depression, surface of anterior angles slightly concave; anterior half of lateral edge arcuate in dorsal and lateral view; posterior angles slightly upturned and simply arcuate in dorsal view; anterior hypomeral ridge broadly arcuate anteriorly, anterior hypomeral depression surface light in color. **Elytra** (Fig. 22). Interval 2 with one to three fine granules on apical declivity, interval 4 lacking fine granules from base to apex. **Legs**. Protibial apicointernal tooth enlarged, with dorsal ridge extending to apex. **Aedeagus** (Fig. 134). Parameres with dorsal and ventral edges slightly diverging toward apex in lateral view. **Internal sac sclerites** (Figs. 180–182). Axial sclerite arcuate, with apex acute. Subaxial sclerite, gradually tapering from base to apex, extending straight and interrupted before apex of frontolateral peripheral sclerite apical portion, with a brush of

villi on apical fourth. Frontolateral peripheral sclerite basoventral apophysis large; lacking medioventral carinae; right lateral fold produced into a rather small everted and open apically conical process with irregular apical edge located behind oblique right lateral edge of apical lobe; left lateral lobe membranous, slightly developed; subapicodorsal lobe membranous, small and obliquely projecting dorsally, interrupted well before anterior edge of apical lobe, apex set on left side in dorsal view; apical lobe truncate and slightly directed obliquely on left side, lateral edges folded ventrally, with a small additional longitudinal fold in line with subapicoventral lobe; apical villi becoming longer toward apex; subapicoventral lobe acute in lateral view, interrupted before apex of apical lobe.

Variation. Measurements (97 ♂♂, 74 ♀♀). Length: male 7.0–12.0 mm (10.0 ± 0.9 mm), female 8.0–11.5 mm (9.9 ± 0.8 mm). Females allotype. Cephalic outline in dorsal view as in Fig. 86; vertex with a high and broadly arcuate, transverse carina, dorsal edge subangular medially in frontal view, lateral portion gradually sloping down posteriorly; anterior pronotal tubercles well developed, external lateral edges distinctly widening toward apex in dorsal view, anterolateral surface obliquely excavated, anterosuperior edge slightly arcuate in dorsal view (Fig. 117), lateral portion of anterosuperior edge slightly upturned (Fig. 118). Anterior tibia short, with external teeth more robust.

Primary type data. Holotype ♂ (CMNC): [SOUTH AFRICA: N. CAPE / Farm Klipkoppies (6) / S28.87137° E21°30.944' [*sic*] / 957 m; 12–14 March 2004 / A.L.V. Davis & C. Deschodt]; [WORLD / SCARAB. / DATABASE / WSD00029107] barcode label; [HOLOTYPE ♂ / *Digitonthophagus* / *namaquensis n.sp.* / des. F. Génier, 2016] red card.



MAP 17. Distribution of *Digitonthophagus namaquensis*.

Material examined (100 ♂♂, 75 ♀♀), distribution (Map 17): **ANGOLA**: BENGUELA, Benguela (12°35'S, 13°25'E), [no date], [illegible]—1 ♀, 1 ♂ (paratypes) (IRSNB); **NAMIBIA**: ERONGO, Ameib Farm, 19 km NW Karibib (21°47'S, 15°38'E), 31.i–2.ii.1972, Southern Africa Expedition—1 ♂ (paratype) (BMNH); Gobabeb (23°34'S, 15°2'E), 10.ii.1978, O. Lomhodlt—1 ♂ (paratype) (ZMUC); Kahn River, 5 mi. N Usakos (22°0'S, 15°36'E), 30–31.i.1972, Southern Africa Expedition—1 ♀, 1 ♂ (paratypes) (BMNH); Kuiseb Canyon (23°18'S, 15°45'E), 22–23.i.1972, Southern Africa Expedition—1 ♀, 1 ♂ (paratypes) (BMNH); HARDAP, Farm Lovedale, N Tiras Mountains, 1600 m (25°32'24"S, 16°23'24"E), 16–17.ii.2010, W. Schawaller—1 ♀, 5 ♂♂ (6 paratypes) (SMNS); Sesriem Farm, Maltahoe District (24°11'S, 15°59'E), 19–20.i.1972, Southern Africa Expedition—1 ♀ (paratype) (BMNH); Voigtgrund (24°49'S, 17°26'E), [no date], K. Jordan—1 ♀, 2 ♂♂ (3 paratypes) (BMNH); Malthahöhe district, Zais 6 (24°2'58"S, 16°9'14"E), 16.i.2000, Mann & Marais—1 ♀ (paratype) (OUMNH); Rehoboth district, on road verge, Kambes 498 (24°4'32"S, 16°28'21"E), 17.i.2000, Mann & Marais—1 ♀, 3 ♂♂ (4 paratypes) (OUMNH); KARAS, Barby Farm, 25 mi. W Helmeringhausen (25°53'S, 16°49'E), 17–18.i.1972, Southern Africa Expedition—11 ♀♀, 16 ♂♂ (27 paratypes) (BMNH); Keetmannshoop (26°34'S, 18°8'E), 1913, S. Hardt & G. Lotz—3 ♀♀, 2 ♂♂ (5 paratypes) (SMF); Mesosaurus Fossil Farm, NE Keetmanshoop, 1100 m (28°14'24"S, 18°16'48"E), 18–19.ii.2010, W. Schawaller—1 ♂ (paratype) (SMNS); Noachabeb, 27 mi. NNE

Grunau (27°23'S, 18°28'E), 10–12.i.1972, Southern Africa Expedition—3 ♀♀, 5 ♂♂ (8 paratypes) (BMNH); near Onseepkans, Orange RIVER banks (28°44'S, 19°18'E), 8–10.i.1972, Southern Africa Expedition—1 ♂ (paratype) (BMNH); Plateau Farm, 22 mi. E Aus (26°38'S, 16°34'E), 14–17.i.1972, Southern Africa Expedition—1 ♀, 1 ♂ (paratypes) (BMNH); Seeheim (26°49'S, 17°47'E), 16.ii.1934, J. Ogilvie—1 ♀ (paratype) (BMNH); KAVANGO, Mayana Lodge, Rundu District (17°51'55"S, 19°55'48"E), 19.xii.1999, Mann & Marais—6 ♀♀, 7 ♂♂ (13 paratypes) (OUMNH); Mile 46 Agricultutal Station, Sovo area (18°19'14"S, 19°15'28"E), 23.iii.2002, Mann, Marais, & Kasch—1 ♀, 1 ♂ (paratypes) (OUMNH); KHOMAS, Farm Namibgrens, Spreetshoogte, 1800 m (23°22'12"S, 16°8'24"E), 3–6.ii.2010, W. Schawaller—1 ♀, 2 ♂♂ (3 paratypes) (SMNS); Solitaire (23°53'S, 16°0'E), 22.i.1972, Southern Africa Expedition—2 ♀♀, 8 ♂♂ (10 paratypes) (BMNH); Windhoek (22°34'12"S, 17°5'1"E), 1909, Külz—2 ♀♀ (2 paratypes) (SMF); KUNENE, 87 km W Kamanjab (19°49'S, 14°10'E), 2.iv.1977, J. Boomker—1 ♂ (paratype) (BMNH); Khorixas (20°22'S, 14°58'E), iii.2004, O. Aschenborn—3 ♀♀, 2 ♂♂ (5 paratypes) (CMD); Orupembe (18°10'S, 12°34'E), 14.iv.2005, W. Schawaller—1 ♀, 2 ♂♂ (3 paratypes) (SMNS); Palmwag Lodge (19°53'10"S, 13°56'13"E), 18.iv.2005, W. Schawaller—1 ♀, 2 ♂♂ (3 paratypes) (SMNS); Purros (Hoaruzsib Valley) (18°46'S, 12°57'E), 15–16.iv.2005, W. Schawaller—1 ♀ (paratype) (SMNS); Khorixas District, Ae-ams/Khoanib confluence (19°14'44"S, 13°20'34"E), 28.xii.1999, Mann, Marais, & Newman—1 ♀, 1 ♂ (paratypes) (OUMNH); Hoanib river near Dubis (19°13'36"S, 13°22'E), 28.xii.1999, Mann & Marais—1 ♂ (paratype) (OUMNH); Palm 708, adjacent to spring (19°52'6"S, 14°1'13"E), 4.i.2000, Mann & Marais—1 ♂ (paratype) (OUMNH); Spaarwater 711, near water hole (20°3'24"S, 14°2'55"E), 5.i.2000, Mann & Marais—3 ♀♀, 1 ♂ (paratypes) (OUMNH); Opuwo District, Lower Hoanib (19°23'7"S, 13°4'11"E), 30.xii.1999, Mann & Marais—1 ♀, 1 ♂ (paratypes) (OUMNH); OMUSATI, Narawandu road, Etosha National Park (18°51'4"S, 15°32'55"E), 24–25.xii.1999, Mann & Marais—1 ♀ (paratype) (OUMNH); OSHIKOTO, Mushara area, sandy road (18°36'24"S, 16°53'23"E), 21.xii.1999, Mann & Marais—1 ♂ (paratype) (OUMNH); Mushara Waterhole (18°35'19"S, 16°55'11"E), 23.xii.1999, Mann & Marais—1 ♂ (paratype) (OUMNH); OTJOZONDJUPA, Epupa Falls, 660 m (17°0'3"S, 13°14'36"E), 11–12.iv.2005, W. Schawaller—3 ♀♀, 4 ♂♂ (7 paratypes) (SMNS); **SOUTH AFRICA**: EASTERN CAPE, Willowmore (33°18'S, 23°29'E), ii.1916, Dr. Brauns—1 ♀, 1 ♂ (paratypes) (NMPC); NORTHERN CAPE, Farm Klipkoppies, 957 m (28°52'16.93"S, 21°18'33.98"E), 12–14.iii.2004, A.L.V. Davis & C. Deschodt—11 ♀♀, 12 ♂♂ (holotype, allotype, 21 paratypes) (BDGC, CMNC, FGIC, OUMNH, PMOC); Groblershoop, Farm Brulpan (28°53'56"S, 21°46'49"E), 23–26.iii.2001, A. Davis—2 ♂♂ (2 paratypes) (BMNH); Keograbie Farm (1), 1038 m (29°4'33.6"S, 21°46'5.63"E), 6–8.iii.2004, A.L.V. Davis & C. Deschodt—8 ♀♀, 7 ♂♂ (15 paratypes) (FGIC, PMOC); Rooiplato (31°26'S, 19°24'E), 14.i.1980, [anonymous]—1 ♂ (paratype) (BMNH); Upington (28°27'S, 21°15'E), 7.xii.1933, L. Ogilvie—1 ♀ (paratype) (BMNH).

Etymology. *Namaquensis* (from Namaqualand) a Latin adjective pertaining to the distribution of this species.

Natural history. Davis & Scholtz (2004), collected this species at the Brulpan Farm near Groblershoop, in Bushmanland Nama Karoo, in the south-west arid late summer rainfall region of Northern Cape. Specimens were collected in cow dung baited traps and the species is recorded in this work as a soil generalist. The current data indicates a Namibian savanna woodlands and a Nama karoo centered distribution. Some specimens collected in cow and elephant dung. A single specimen collected under old elephant dung. This species is attracted to mercury vapor and ultraviolet light traps.

Identification key to adult *Digitonthophagus* species

1. Vertex with an acute median conical process (Fig. 23–26) 2
1'. Vertex lacking median conical process (Figs. 27–54, 73–86) 3
2 (1). Anterior portion of pronotum with a distinct toothlike process in lateral view (Fig. 88); pronotal punctures restricted to anterior half (Fig. 87) . . . . . *D. bonasus* (Fabricius)
2'. Anterior portion of pronotum lacking distinct toothlike process, simply convex in lateral view (Fig. 90); pronotal punctures extending to posterior half (Fig. 89) . . . . . *D. uks* Génier
3 (1'). Cephalic horn of males strongly divergent (Figs. 27–28); clypeofrontal carina extending laterally to clypeal edge (Fig. 27); female with two cephalic horns (Fig. 73) . . . . . *D. sahelicus* Moretto
3'. Cephalic horns of males more-or-less curved but always upright (Figs. 29–54); clypeofrontal carina interrupted at gena (Figs. 29–54); female with a transverse carina on the vertex (Figs. 74–86) 4
4 (3'). Native species distribution from Pakistan eastward (Map. 5). . . . . *D. catta* (Fabricius)
4'. Native species distribution from Oman westward 5
5 (4'). Anterior hypomeral depression narrow and light colored (Fig. 187A); anterior hypomeral carina approximately straight on

most of distance anterior to coxal cavity (Fig. 187B); pronotum with smaller irregularly scattered, simple punctures on posterior half of disc; surface of anterior pronotal angles largely concave in male; distributed along a band south of the Sahara from Senegal to Oman (Map. 6) . . . . . *D. eucatta* Génier

5'. Anterior hypomeral depression wider and at least partly dark-colored (Fig. 188A); anterior hypomeral carina arcuate anteriorly (Fig. 188B); remaining combination of characters and distribution different 6

6 (5'). Overall body shape elongate and flat (Fig. 22); dorsum usually evenly light colored with slight green metallic sheen; pronotal posterolateral surface at most with weakly-defined, larger punctures (Fig. 70); male posterior surface of vertex higher than occipital surface, which is coarsely granulate (visible when head is slightly protruding) (Fig. 189); southwestern Angola, Namibia, and western South Africa (Map. 17) . . . . . *D. namaquensis* Génier

6' Overall body shape more robust and convex; dorsum variable in color but usually darker with some coppery to green metallic sheen; pronotal posterior surface usually with few coarse punctures; male posterior surface of the vertex in the same plane as occiput, which is coarsely granulate (visible when head is slightly protruding) (Fig. 190) 7

7 (6'). Pronotal surface with dense small punctures throughout (Fig. 20, 68); average size large, 9.0–15.0 mm; East Africa (Sudan, South Sudan, Somalia, Kenya, and Tanzania) (Map. 15) . . . . . *D. lusinganus* d'Orbigny

7'. Character combination and distribution different 8

8 (7'). Cephalic outline approximately triangular in dorsal view, lateral edge approximately straight at clypeogenal junction (Figs. 45, 51, 82, 85); male cephalic horns external edge set beyond genal edge, arcuate and with coarse granules internally at the apex (Figs. 46, 52); females can only be reliably identified by association with males and distribution 9

8'. Cephalic outline transverse in dorsal view, lateral edge usually distinctly angular at clypeogenal junction (*e.g.*, Figs. 33, 35, 37, 76, 77, 78); male cephalic horns external edge set inside genal edge, approximately straight and lacking coarse granules internally at apex (*e.g.*, Figs. 33–38); females can only be reliably identified by association with males and distribution 10

9 (8). Pronotal surface deeply concave behind anterior angles (Fig. 51); pronotal anteromedian tubercles well developed, produced into small acute denticles on each side of midline (Fig. 52); larger average size, 8.0–13.5 mm; Ethiopia, Somalia, Kenya, Tanzania (Map 16) . . . . . *D. ulcerosus* Génier

9'. Pronotal surface slightly concave and produced anteriorly at anterior angles (Fig. 45); pronotal anteromedian tubercle blunt (Fig. 46); smaller average size (7.5–12.0 mm); West Africa (Map. 13) . . . . . *D. dilatatus* Génier

10 (8'). Protibia elongate, with an apicointernal tooth (male) 11

10'. Protibia robust, lacking apicointernal tooth . . . . . females[1]

11 (10'). Pronotal surface with coarse granulate punctures usually extending on posterior half (Figs.19, 111); elytral intervals two and four usually with several granules (Fig. 19); FLP as in Figs. 171–173; West Africa and pastures in Central Africa, Ethiopian Plateau, and Uganda (Map 14) . . . . . *D. fimator* Génier

11'. Character combination and distribution different 12

12 (11'). West African species distributed from Cameroon westward (one doubtful record from Uganda) (Map 7); pronotal surface slightly convex or flat, never concave behind anterior angles; FLP with a distinctive falciform process on right preapical edge (Fig. 150). . . . . *D. falciger* Génier

12' Character combination and distribution different 13

13 (12'). Distribution centered on the southern portion of the Red Sea and northern portion of the Rift Valley (Map 12); clypeofrontal carina straight medially, set closer to anterior clypeal edge (Fig. 43); cephalic horns short, straight, and regularly tapering from base to apex (Fig. 44); FLP as in Figs. 165–167. . . . . *D. aksumensis* Génier

13'. Character combination and distribution different 14

14 (13'). Dorsum with coarse microsculpture, surface appearing dull between punctures (Fig. 63); anterior hypomeral depression light colored (similar to Fig. 1); FLP with subapicodorsal lobe large, extending beyond the apex of the apical lobe (Fig. 159–161); subaxial sclerite apical portion thin and long (Fig. 160); East Africa (Map 10). . . . . *D. petilus* Génier

14'. Character combination and distribution different 15

15 (14'). Pronotal punctation scattered and weakly impressed posteriorly (Fig. 61); FLP as in Figs. 153–155; the axial sclerite long, in line with or extending beyond SA (Fig. 153–154); East Africa (Map 8) . . . . . *D. biflagellatus* Génier

15'. Character combination and distribution different 16

16 (15'). Species distributed in Democratic Republic of the Congo (Bas-Congo), western Angola and west of Kavango region and north of Windhoek in Namibia (Map 11); cephalic lateral edge strongly angular at clypeogenal junction (Figs. 41); pronotal punctation scattered and weakly impressed posteriorly (Fig. 64); right lateral fold of FLP closed ventrally, lacking rows of large villi along external edge (Fig. 186). . . . . *D. viridicollis* Génier

16'. Species distributed southward of southern Angola in the west to southern Uganda in the east (Map 9), introduced worldwide in southern temperate zones and tropical pastures and savanna, including Comoros Islands, Mayotte, and Madagascar; cephalic lateral edge feebly angular at clypeogenal junction (Figs. 37); pronotal punctation rather dense and coarse posteriorly (Fig. 62); right lateral fold of FLP open ventrally, with a row of large villi along external edge (Fig. 185) . . . . . *D. gazella* (Fabricius)

Species checklist and distribution

1. Females belonging to species treated in couplet 11 to 16 can, in most instances, be identified by association with males from the same collecting event. In abraded individuals the protibia may appear less robust in dorsal view but the apicointernal tooth is always missing.

Digitonthophagus Balthasar, 1959

***Digitonthophagus bonasus* species group**

1. *Digitonthophagus bonasus* (Fabricius, 1775), **valid species**
   Distribution: Bangladesh, Cambodia, India, Laos, Malaysia, Myanmar, Nepal, Pakistan, Sri Lanka, Thailand, Vietnam
2. *Digitonthophagus uks* Génier, **new species**
   Distribution: Afghanistan, India, Iran, Pakistan
3. *Digitonthophagus sahelicus* Moretto, **new species**
   Distribution: Burkina Faso, Cameroon, Chad, Djibouti, Eritrea, Mali, Mauritania, Niger, Senegal, Sudan

***Digitonthophagus catta* species group**

4. *Digitonthophagus catta* (Fabricius, 1787), **valid species**
   Distribution: Afghanistan, Bangladesh, India, Nepal, Pakistan, Sri Lanka
5. *Digitonthophagus eucatta* Génier, **new species**
   Distribution: Benin, Burkina Faso, Cameroon, Chad, Eritrea, Ethiopia, Gambia, Mali, Mauritania, Niger, Nigeria, Oman, Senegal, Sudan

***Digitonthophagus falciger* species group**

6. *Digitonthophagus falciger* Génier, **new species**
   Distribution: Benin, Burkina Faso, Cameroon, Chad, Cote d'Ivoire, Gambia, Ghana, Guinea, Guinea-Bissau, Mauritania, Niger, Nigeria, Senegal, Sierra Leone, ?Uganda

***Digitonthophagus gazella* species group**

7. *Digitonthophagus biflagellatus* Génier, **new species**
   Distribution: Burundi, D.R. Congo, Kenya, Rwanda, Tanzania, Uganda, Zambia
8. *Digitonthophagus gazella* (Fabricius, 1787), **conservation of name in prevailing usage**
   Scarabaeus dorcas Olivier, 1789, **proposed new synonymy**
   Distribution: Angola, Botswana. Democratic Republic of the Congo, Kenya, Malawi, Mozambique, Namibia, South Africa, Swaziland, Tanzania, Uganda, Zambia, Zimbabwe; Introduced worldwide in tropical, subtropical, and southern temperate pastures (including the Comoros Islands, Mayotte, and Madagascar)
9. *Digitonthophagus petilus* Génier, **new species**
   Distribution: Ethiopia, Kenya, South Sudan, Sudan, Uganda
10. *Digitonthophagus viridicollis* Génier, **new species**
    Distribution: Angola, Congo, Democratic Republic of the Congo, Namibia

***Digitonthophagus lusinganus* species group**

11. *Digitonthophagus aksumensis* Génier, **new species**
    Distribution: Djibouti, Eritrea, Ethiopia, Saudi Arabia, Somalia, Sudan, Yemen
12. *Digitonthophagus dilatatus* Génier, **new species**
    Distribution: Burkina Faso, Cameroon, Chad, Côte d'Ivoire, Ghana, Nigeria
13. *Digitonthophagus fimator* Génier, **new species**
    Distribution: Benin, Burkina Faso, Cameroon, Central Africa republic, Chad, Côte d'Ivoire, Democratic Republic of the Congo, Ethiopia, Ghana, Guinea, Guinea-Bissau, Nigeria, Senegal, Sierra Leone, Togo, Uganda
14. *Digitonthophagus lusinganus* (d'Orbigny, 1905), **valid species**
    Distribution: Ethiopia, Kenya, Somalia, South Sudan, Sudan, Tanzania
15. *Digitonthophagus ulcerosus* Génier, **new species**
    Distribution: Ethiopia, Kenya, Somalia, Tanzania

***Digitonthophagus namaquensis* species group**

16. *Digitonthophagus namaquensis* Génier, **new species**
    Distribution: Angola, Namibia, South Africa

Phylogeny

Material and method

A morphology based phylogenetic analysis was performed on the 16 species of *Digitonthophagus* in order to organize the genus into species group. Four putative closely related species were included in the matrix as outgroups. These four species are currently known as *Caccobius castaneus* (Klug), *Onthophagus cameloides* d'Orbigny, *Onthophagus gonopygus* d'Orbigny, and *Phalops bubalus* (Harold). *Phalops bubalus* was selected to represent the genus *Phalops* as the species is hypothesized to be the most basal of the genus (Génier 2013). A total of 58 characters were scored as binaries:

1. clypeal edge of male overall shape ogival
    0 no, 1 yes
2. clypeofrontal carina of male set on anterior half of head
    0 yes, 1 no
3. anterior genal margin upturned
    0 no, 1 yes
4. posterolateral edge of gena emarginate
    0 no, 1 yes
5. vertex of male with fine, similarly-shaped, scattered punctures
    0 no, 1 yes
6. vertex of male with a central horn
    0 no, 1 yes
7. vertex of female granulate
    0 no, 1 yes
8. vertex of female with horns
    0 no, 1 yes
9. cephalic horns of male erect
    0 yes, 1 no
10. cephalic horns of male coarsely granulate internally
    0 no, 1 yes
11. cephalic horns of male external edge extending beyond gena
    0 no, 1 yes
12. cephalic horns of male posterointernal edge lacking tooth and straight in dorsal view
    0 no, 1 yes
13. median portion of posterior edge of male vertex in the same plane as the occiput
    0 no, 1 yes
14. pronotal posterolateral angles of male angular
    0 no, 1 yes
15. pronotal anterolateral surface of male sloping laterally
    0 no, 1 yes
16. pronotum of female with obliquely-oriented tubercles
    0 no, 1 yes
17. anterior pronotal angle of male concave
    0 no, 1 yes
18. anterior median sulcus of male wide and deep
    0 no, 1 yes

19. anterior pronotal angles with setae dorsally
    0 no, 1 yes
20. anterior pronotal tubercles of female atrophied
    0 no, 1 yes
21. anterior pronotal tubercles of female distinctly upturned anterolaterally
    0 no, 1 yes
22. ventrolateral portion of anterior pronotal tubercles of female largely concave
    0 no, 1 yes
23. elytra unicolor
    0 no, 1 yes
24. elytral juxtasutural interstria with metallic sheen
    0 no, 1 yes
25. elytral intervals 2 and 4 distinctly less granulate than interval 3
    0 no, 1 yes
26. mesosternum with a wide and smooth longitudinal carina medially
    0 no, 1 yes
27. metasternum anterior portion marginate
    0 yes, 1 no
28. metasternum anterior portion depressed
    0 no, 1 yes
29. metasternum with a short longitudinal carina anteriorly
    0 yes, 1 no
30. anterior tibia of male strongly arcuate on apical half
    0 no, 1 yes
31. protibia apicointernal tooth of male simply bent downward
    0 yes, 1 no
32. parameres basolateral lobe present
    0 yes, 1 no
33. parameres apicoventral portion with a transverse ridge
    0 no, 1 yes
34. axial and subaxial sclerites arrangement "*D. bonasus* type"
    0 no, 1 yes
35. axial and subaxial sclerites arrangement " *D.* catta type"
    0 no, 1 yes
36. axial and subaxial sclerites arrangement " *D. gazella* type"
    0 no, 1 yes
37. axial and subaxial sclerites arrangement " *D. falciger* type"
    0 no, 1 yes
38. subaxial sclerites with distinct villae apically
    0 no, 1 yes
39. FLP overall shape straight in lateral view
    0 no, 1 yes
40. ventral portion of FLP with medioventral carina(e)
    0 no, 1 yes
41. ventral portion of FLP with more than one medioventral carina
    0 no, 1 yes
42. ventral portion of FLP with single rectangular and slightly laterally angular carina
    0 no, 1 yes
43. left lateral apophysis of FLP present
    0 no, 1 yes
44. right lateral fold of FLP forming a concave structure apically
    0 no, 1 yes

45. right lateral fold of FLP sclerotized portion overall shape spoon-like apically
    0 no, 1 yes
46. right lateral fold of FLP with spoon-like process with a strongly sclerotized projection on opposite side
    0 no, 1 yes
47. subapicodorsal lobe of FLP present
    0 no, 1 yes
48. subapicodorsal lobe of FLP membranous
    0 yes, 1 no
49. subapicodorsal lobe of FLP narrow, detached, and set on left side apically
    0 no, 1 yes
50. subapicodorsal lobe of FLP sclerotized basolaterally
    0 no, 1 yes
51. subapicoventral lobe of FLP present
    0 no, 1 yes
52. subapicoventral lobe of FLP atrophied
    0 no, 1 yes
53. subapicoventral lobe of FLP pointing ventrally
    0 no, 1 yes
54. subapicoventral lobe of FLP approximately in line with left edge of apical lobe
    0 no, 1 yes
55. subapicoventral lobe of FLP apex semicircular in lateral view
    0 no, 1 yes
56. subapicoventral lobe of FLP appearing finely undulated with apex recurved dorsally
    0 no, 1 yes
57. apical lobe of FLP right portion with a well-sclerotized lateral concave projection
    0 no, 1 yes
58. apical lobe of FLP left edge emarginate as in *D. gazella*
    0 no, 1 yes

A total of 31 characters were coded from external morphology (Table 1). The head (13 characters) and thorax (nine characters) provided most of the external encodable characters. Due to extreme external morphological similarity, only nine additional characters presenting discretely encodable states could be found without disarticulating specimens. Mouthparts, especially epipharynx, were also investigated but were found to be rather homogenous within the genus and could only be used within a morphometric context. Male genitalia provided 27 characters and are hypothesized to be most informative as less subject to homoplasy. All characters are informative except for the autapomorphic character 37, which was included to code for the unique shape of the A + AS in *D. falciger*. The character matrix can be viewed online or downloaded from MorphoBank (http://www.morphobank.org; project 2504). The matrix was built using Mesquite version 3.10 (Maddison & Maddison 2009), the analysis was run through TNT version1.1 (Goloboff *et al*. 2003), and the resulting trees analyzed in Winclada (Nixon 2002).

The character set was run in TNT using traditional search options to find the most parsimonious trees under the following parameters: memory set to hold 10,000 trees, 1,000 TBR replicates, saving 1,000 trees per replicate, zero-length branches collapsed. A separate analysis was conducted with same setting options but using implied weights (Goloboff *et al*. 2003) with concavity factor 50. Cladogram branch support was calculated as Bremer support values (Bremer 1994) by searching for suboptimal trees using the trees obtained by the equal weights analyses. Bremer support was calculated from 4,709 trees up to 10 steps longer than the shortest one using TBR swapping on the most parsimonious trees (MPTs). Relative Bremer support was calculated from 1,323 trees.

TABLE 1. Character transformation matrix for the phylogenetic analysis of *Digitonthophagus*.

	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
C. castaneus	1	0	0	0	1	0	0	0	-	-	-	-	1	0	0	0	0	0	0	-	-	-	0	0	-	0	0	0	0
O. cameloides	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	1	0	0	1	1	1	1
O. gonopygus	0	-	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	1	0	0	0	1	1	1
P. bubalus	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	0	1	1	1	1	1	1
D. aksumensis	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	1	1	1	0	1	0
D. biflagellatus	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	1	1	1	0	1	0
D. bonasus	0	1	1	0	0	1	1	1	1	1	1	1	0	1	1	0	0	1	1	-	-	-	0	1	1	1	0	1	0
D. catta	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	1	0	1	1	1	0	1	0
D. dilatatus	1	0	1	0	1	0	0	0	0	1	1	1	1	0	0	1	1	0	1	0	0	0	0	1	1	1	0	1	0
D. eucatta	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	1	0	1	1	1	0	1	0
D. falciger	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	1	1	0	1	0
D. fimator	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	1	1	0	1	0
D. gazella	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	1	1	0	1	0
D. lusinganus	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	1	1	1	0	1	0
D. namaquensis	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	1	0	1	0
D. petilus	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	1	1	1	0	1	0
D. sahelicus	0	0	1	0	0	0	1	1	1	1	1	0	0	0	1	0	0	0	1	-	-	-	0	1	1	1	0	1	0
D. uks	0	1	1	0	0	1	1	1	1	1	1	1	0	1	1	0	0	1	1	-	-	-	0	1	1	1	0	1	0
D. ulcerosus	1	0	1	0	1	0	0	0	0	1	1	1	1	0	0	1	1	0	1	0	0	0	0	1	1	1	0	1	0
D. viridicollis	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	1	1	1	0	1	0

……continued on the next page

TABLE 1. (Continued)

	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58
C. castaneus	0	0	1	0	-	-	-	-	0	0	0	-	-	0	0	0	-	0	-	-	-	0	-	-	-	-	-	-	-
O. cameloides	0	0	1	0	-	-	-	-	0	0	0	-	-	0	0	0	-	0	-	-	-	0	-	-	-	-	-	-	-
O. gonopygus	0	0	0	0	-	-	-	-	0	0	0	-	-	0	0	0	-	0	-	-	-	0	-	-	-	-	-	-	-
P. bubalus	0	0	0	0	-	-	-	-	0	0	0	-	-	0	0	0	-	0	-	-	-	0	-	-	-	-	-	-	-
D. aksumensis	1	1	0	1	1	0	0	0	1	0	1	1	-	0	1	0	-	1	0	0	1	1	0	0	0	0	1	1	1
D. biflagellatus	1	1	0	1	0	0	1	0	1	0	0	-	-	0	1	1	1	1	0	0	0	1	0	0	0	1	0	0	1
D. bonasus	1	1	0	1	1	0	0	0	1	0	1	1	-	0	1	0	-	1	0	1	0	1	0	0	1	0	0	1	0
D. catta	1	1	0	1	0	1	0	0	1	1	1	0	0	1	0	0	-	1	1	0	0	1	1	1	0	1	0	0	0
D. dilatatus	1	1	0	1	1	0	0	0	1	0	1	0	1	0	1	0	-	1	0	0	1	1	0	0	0	0	1	0	0
D. eucatta	1	1	0	1	0	1	0	0	1	1	1	0	0	1	0	0	-	1	1	0	0	1	1	1	0	1	0	0	0
D. falciger	1	1	0	1	0	0	0	1	1	0	1	0	0	0	1	0	-	1	0	0	0	1	0	0	0	0	1	0	1
D. fimator	1	1	0	1	1	0	0	0	1	0	1	0	1	0	1	0	-	1	0	0	1	1	0	0	0	0	1	1	1
D. gazella	1	1	0	1	0	0	1	0	1	0	0	-	-	0	1	1	0	1	0	0	0	1	0	0	0	1	0	0	1
D. lusinganus	1	1	0	1	1	0	0	0	1	0	1	0	1	0	1	0	-	1	0	0	1	1	0	0	0	0	1	1	1
D. namaquensis	1	1	0	1	0	0	1	0	1	0	0	-	-	0	1	0	-	1	0	1	0	1	0	0	0	0	1	1	0
D. petilus	1	1	0	1	0	0	1	0	1	0	0	-	-	0	1	1	0	1	0	0	0	1	0	0	0	1	0	0	1
D. sahelicus	0	0	0	1	1	0	0	0	1	0	1	0	0	0	1	0	-	1	0	1	0	1	0	0	1	0	0	1	0
D. uks	1	1	0	1	1	0	0	0	1	0	1	1	-	0	1	0	-	1	0	1	0	1	0	0	1	0	0	1	0
D. ulcerosus	1	1	0	1	1	0	0	0	1	0	1	0	1	0	1	0	-	1	0	0	1	1	0	0	0	0	1	1	0
D. viridicollis	1	1	0	1	0	0	1	0	1	0	0	-	-	0	1	1	1	1	0	0	0	1	0	0	0	1	0	0	1

Results and discussion

The analyses under equal weights yielded four MPTs of length 84 with rather different topologies. The strict consensus tree (Fig. 191) consists of a polytomy for the genus with no support for *D. falciger* and *D. namaquensis*. Four other groups were retrieved with moderate to good Bremer support. The first group is the species pair *D. catta* and *D. eucatta* with the best Bremer and relative Bremer support. The second group is the triad consisting of *D. bonasus*, *D. sahelicus*, and *D. uks* with good Bremer support but lower relative Bremer support. The third group with moderate Bremer support includes four very closely related species, *D. biflagellatus*, *D. gazella*, *D. petilus*, and *D. viridicollis*. The fourth group comprises five species characterized by two synapomorphies and consists of *D. aksumensis*, *D. dilatatus*, *D. fimator*, *D. lusinganus*, and *D. ulcerosus*. The six species groups recognized here are based on these results.

When the analysis was performed with implied weight the resulting tree (Fig. 192) was completely resolved. This tree places *D. bonasus*, *D. sahelicus*, and *D. uks* basally as in two of the four most parsimonious trees. We favor this placement for two reasons, it is placing *D. sahelicus* basally, reflecting the putative primitive shorter configuration of the male protibia of this species and it also suggests a more distant relationship for this externally distinctive group of three species for which females possess horns on the vertex as opposed to a simple strong, transverse carina. It is not clear where *D. falciger* should be placed, the configuration of A + AS is similar to *D. biflagellatus* and might be a member of the *Digitonthophagus gazella* species group but the presence of a medioventral carina can also place it in the *Digitonthophagus lusinganus* species group. The relationship of *D. namaquensis* is perplexing with the truncate apex of the apical lobe of FLP similar to species of the *Digitonthophagus lusinganus* group. However, the much reduced right lateral fold of FLP, the overall shape of A + AS and the strongly developed basoventral apophysis suggest a rather distant relationship. These are preliminary results and a molecular phylogeny will certainly help in resolving the placement of *D. falciger* and *D. namaquensis*.

Concluding remarks

The recognition of more than a single species in Africa is opening up new possibilities for pasture improvement and biological control of pest flies. Distributional data of examined material suggest that a single *Digitonthophagus* species was introduced worldwide. Ecological studies for each of the currently recognized species should be performed to assess their suitability for possible introduction outside their native range. The current distributional analysis confirms that more than one species can coexist in a single locality. Investigating if a synergetic effect could be accomplished with the introduction of additional species would be interesting to test. We believe that species with preference for wetter (*D. fimator*) or dryer (*D. aksumensis*, *D. sahelicus*) habitats could be considered for introduction to complement the services already performed by *D. gazella* for pasture improvement. However, we caution that impact studies must be performed before the introduction of *D. fimator* as the species might be a possible competitor of local scarabaeine fauna in wetter open environment outside pastures. In addition, a molecular phylogeny testing the morphological phylogeny should be performed when DNA grade specimens are available. Morphologically, we could not differentiate the “even” or “cold strain” of *D. gazella* present on the south coast of Eastern Cape from individuals originating from the northern portion of the native distribution range. We believe that molecular data could be used to investigate if the population of the south coast of Eastern Cape is indeed the same taxon. With the exception of the pair *D. catta* and *D. eucatta*, all closely related species present parapatric distribution, which is incompatible with subspecies taxonomic level. Molecular data could be used to test the species level assigned to the pair *D. Catta* and *D. eucatta.* Finally, we suspect that the taxonomy of *D. bonasus* in continental Southeast Asia is not fully resolved. Sufficient material with precise distributional and especially ecological data was lacking to fully assess the observed morphological variation this problem should also be considered for further studies.

Author's contribution

FG: initiated the study, gathered material, studied and dissected specimens, acquired and analyzed data, recognized and described taxa, wrote the paper, and prepared the iconography. PM: gathered material, wrote a draft of the historical account, added to the natural history sections, and recognized *D. sahelicus* as a new species.

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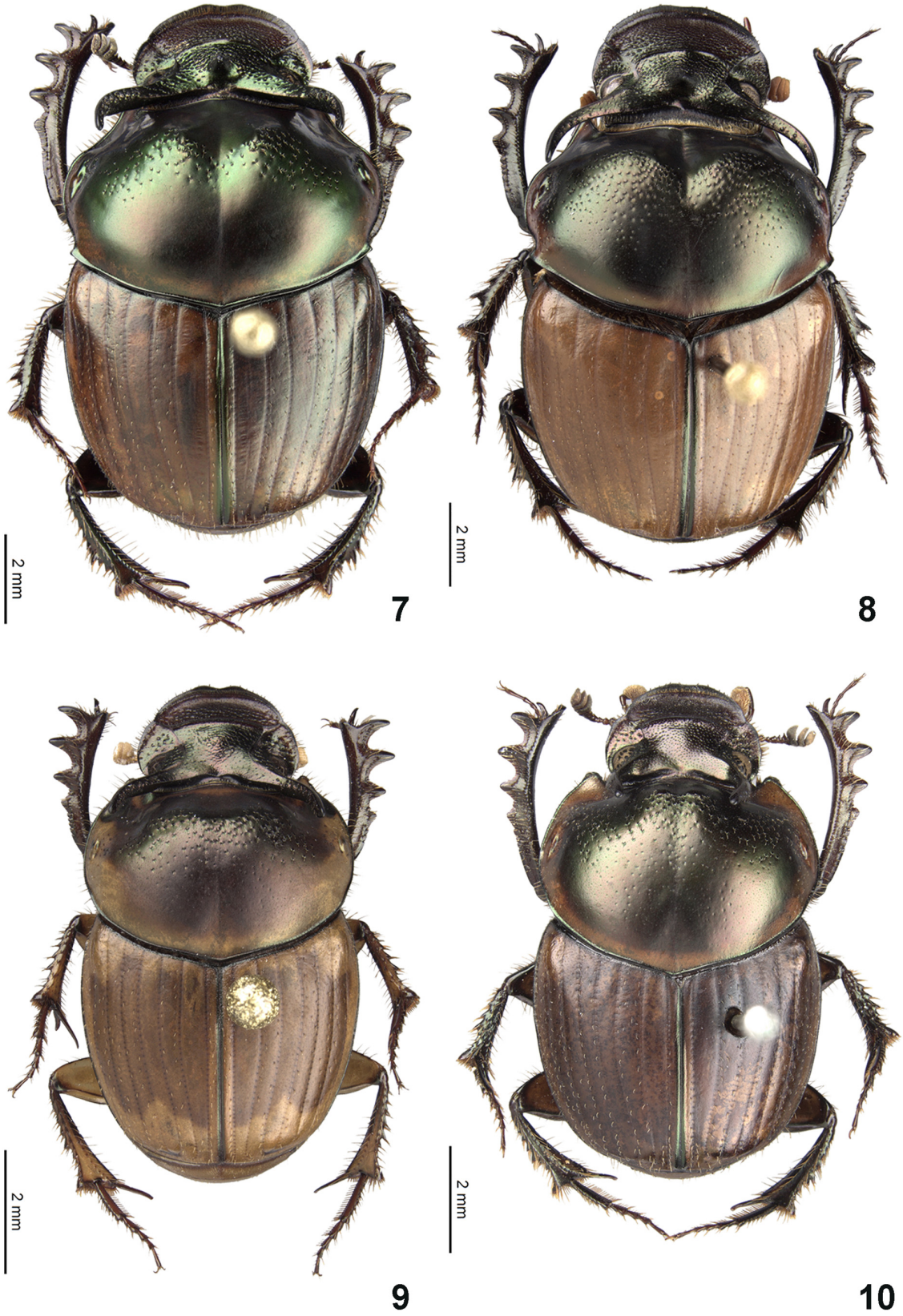
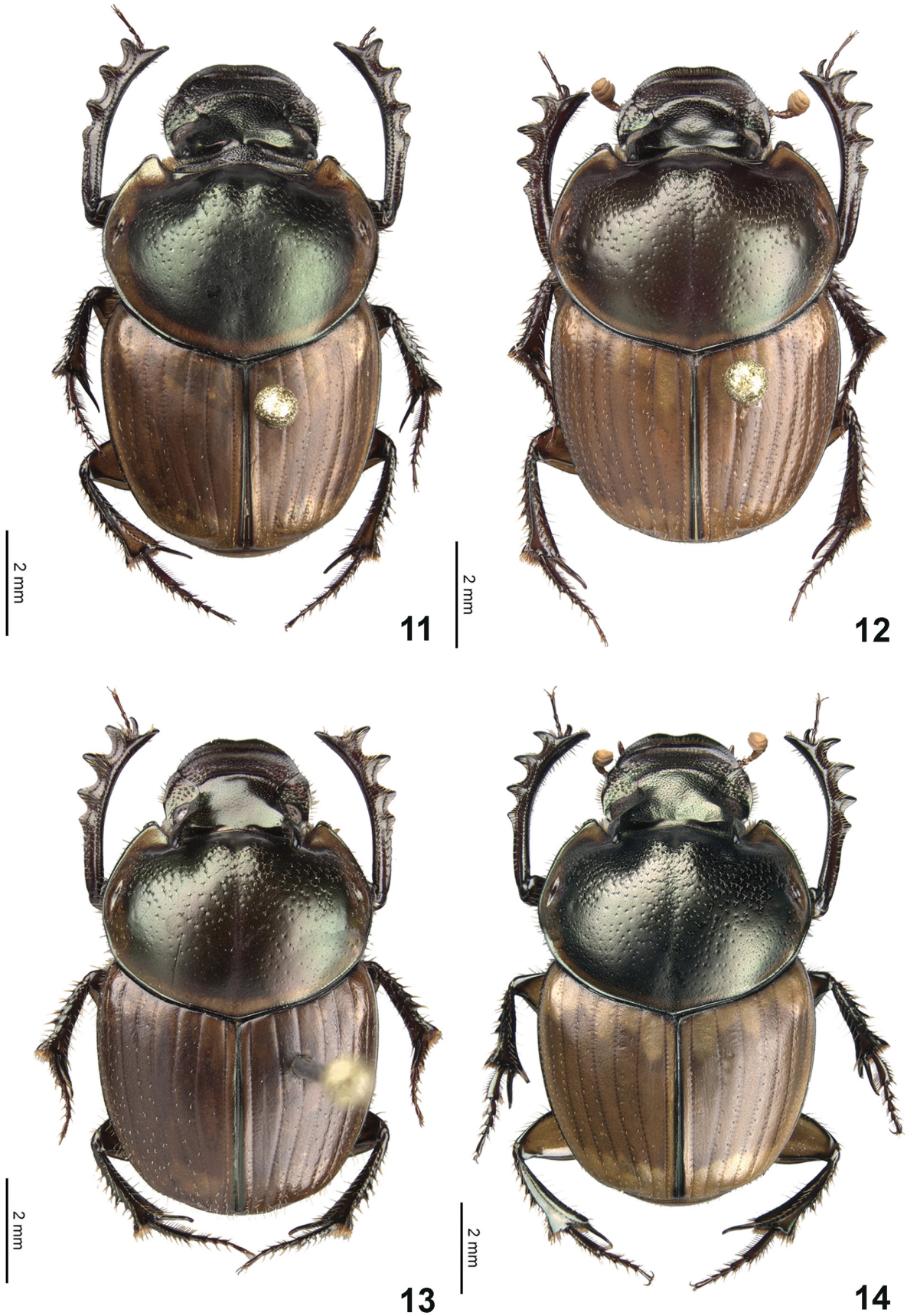
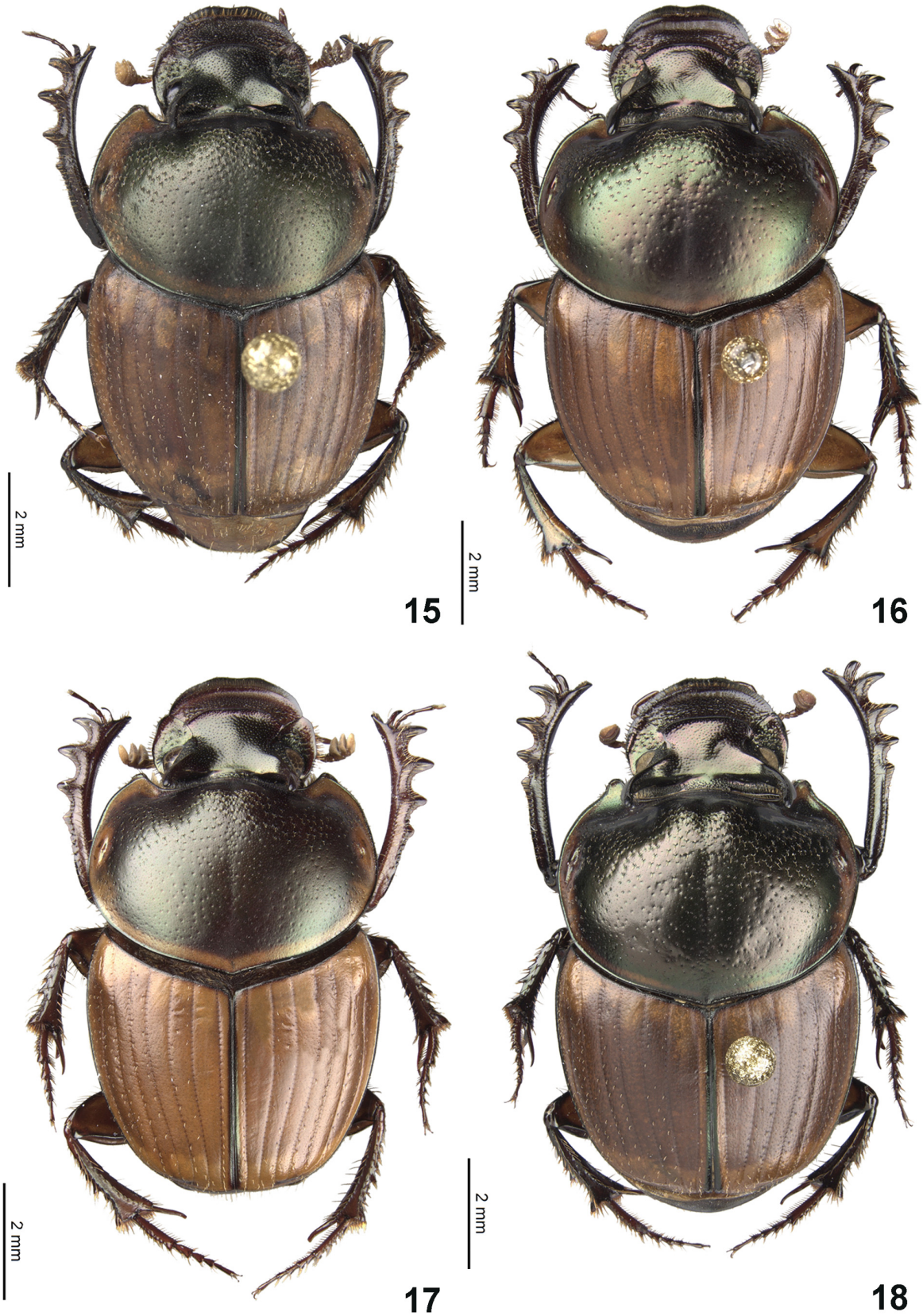


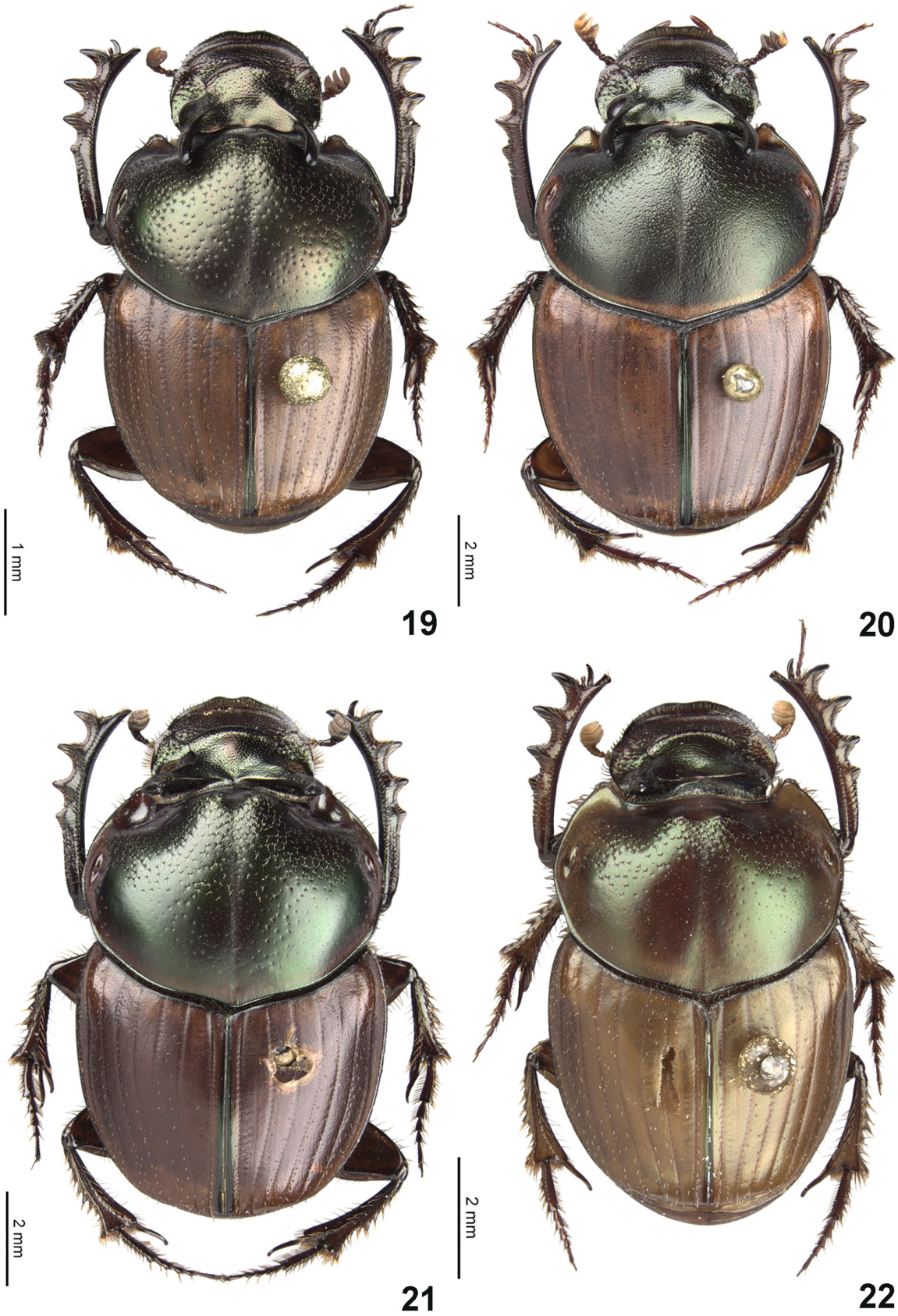
FIGURES 7–10. Male dorsal habitus. 7. *Digitonthophagus bonasus*, alloreferent (Tamil Nadu State, India); 8. *D. uks*, holotype; 9. *D. sahelicus*, holotype; 10. *D. catta*, alloreferent (Tamil Nadu State, India).



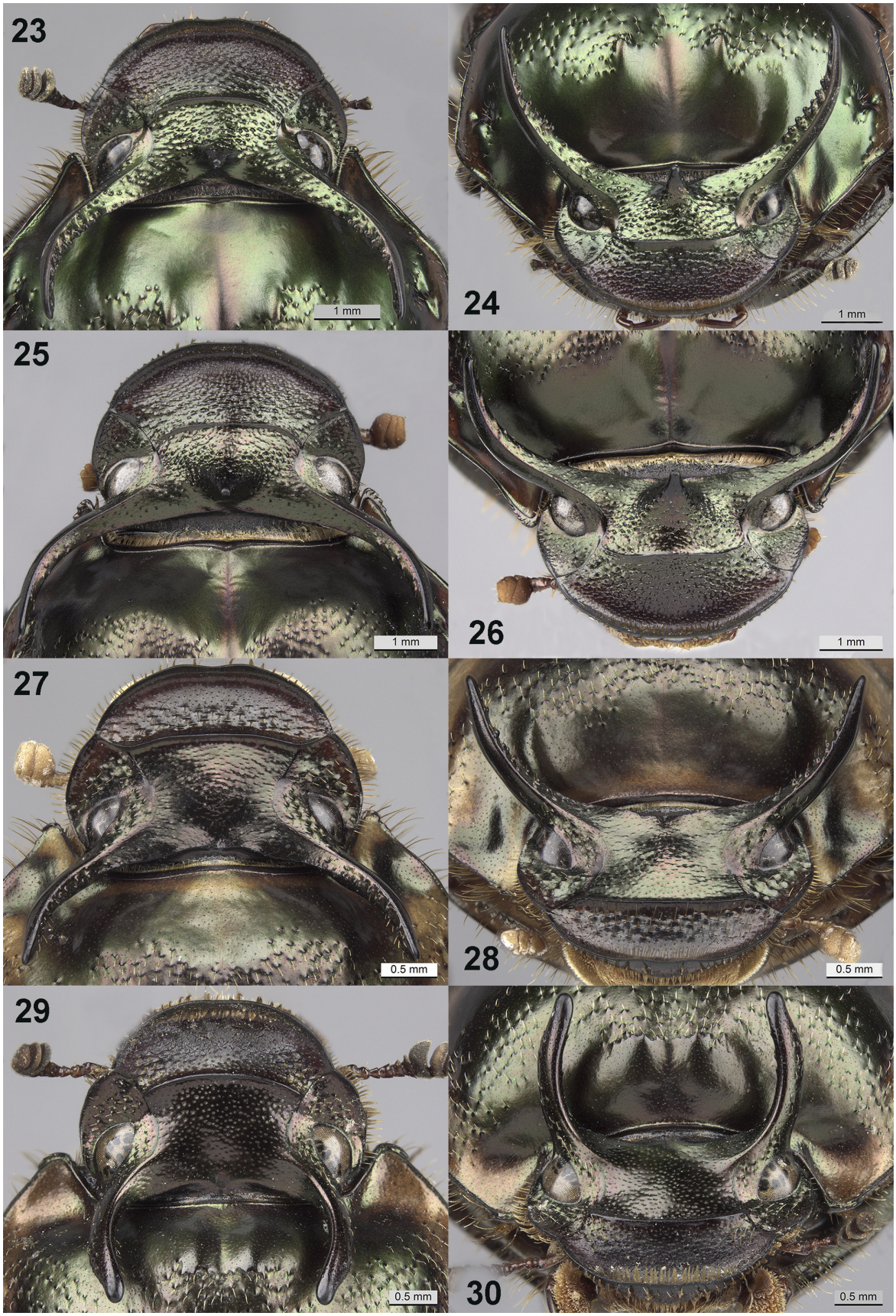
FIGURES 11–14. Male dorsal habitus.11. *D. eucatta*, holotype; 12. *D. falciger*, holotype; 13. *Digitonthophagus biflagellatus*, holotype; 14. *D. gazella*, non type (Central Province, Zambia).



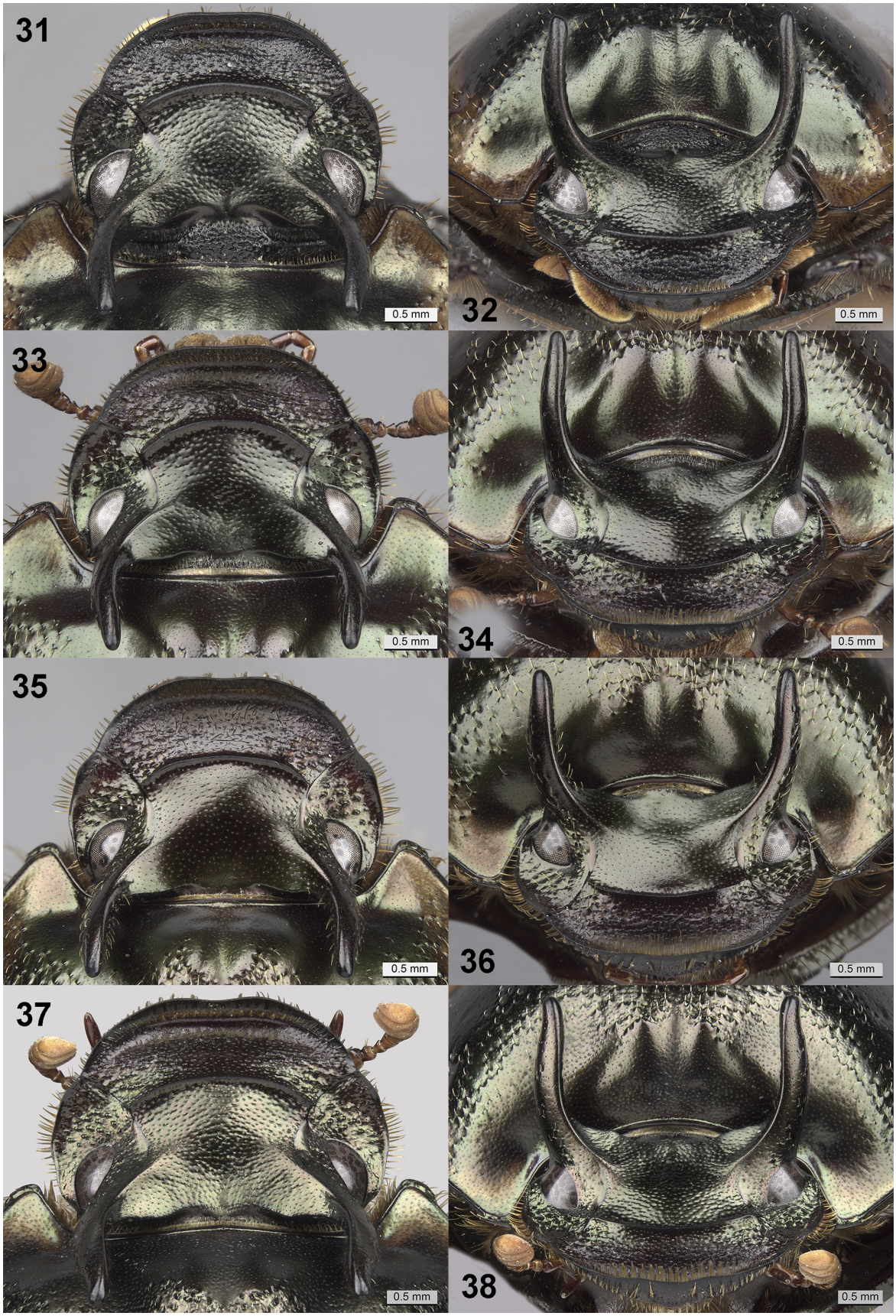
FIGURES 15–18. Male dorsal habitus. 15. *D. petilus*, holotype; 16. *D. viridicollis*, holotype; 17. *D. aksumensis*, holotype; 18. *D. dilatatus*, holotype.



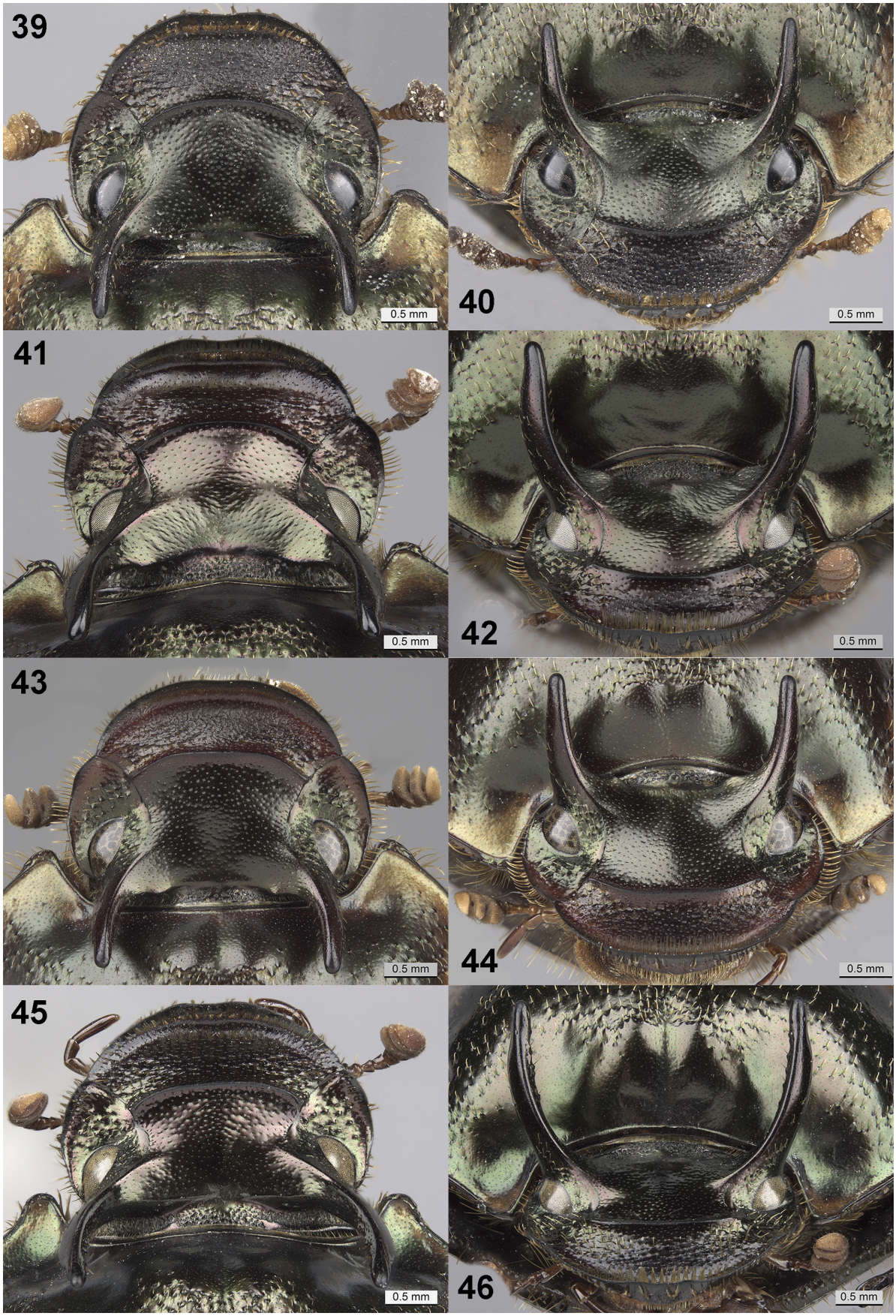
FIGURES 19–22. Male dorsal habitus. 19. *Digitonthophagus fimator*, holotype; 20. *D. lusinganus*, lectotype; 21. *D. ulcerosus*, holotype; 22. *D. namaquensis*, holotype.



FIGURES 23–30. 23, 25, 27, 29. Male head, dorsal view; 24, 26, 28, 30. Male head, frontal view. 23–24. *Digitonthophagus bonasus*, alloreferent (Tamil Nadu State, India); 25–26. *D. uks*, holotype; 27–28. *D. sahelicus*, holotype; 29–30. *D. catta*, alloreferent (Tamil Nadu State, India).

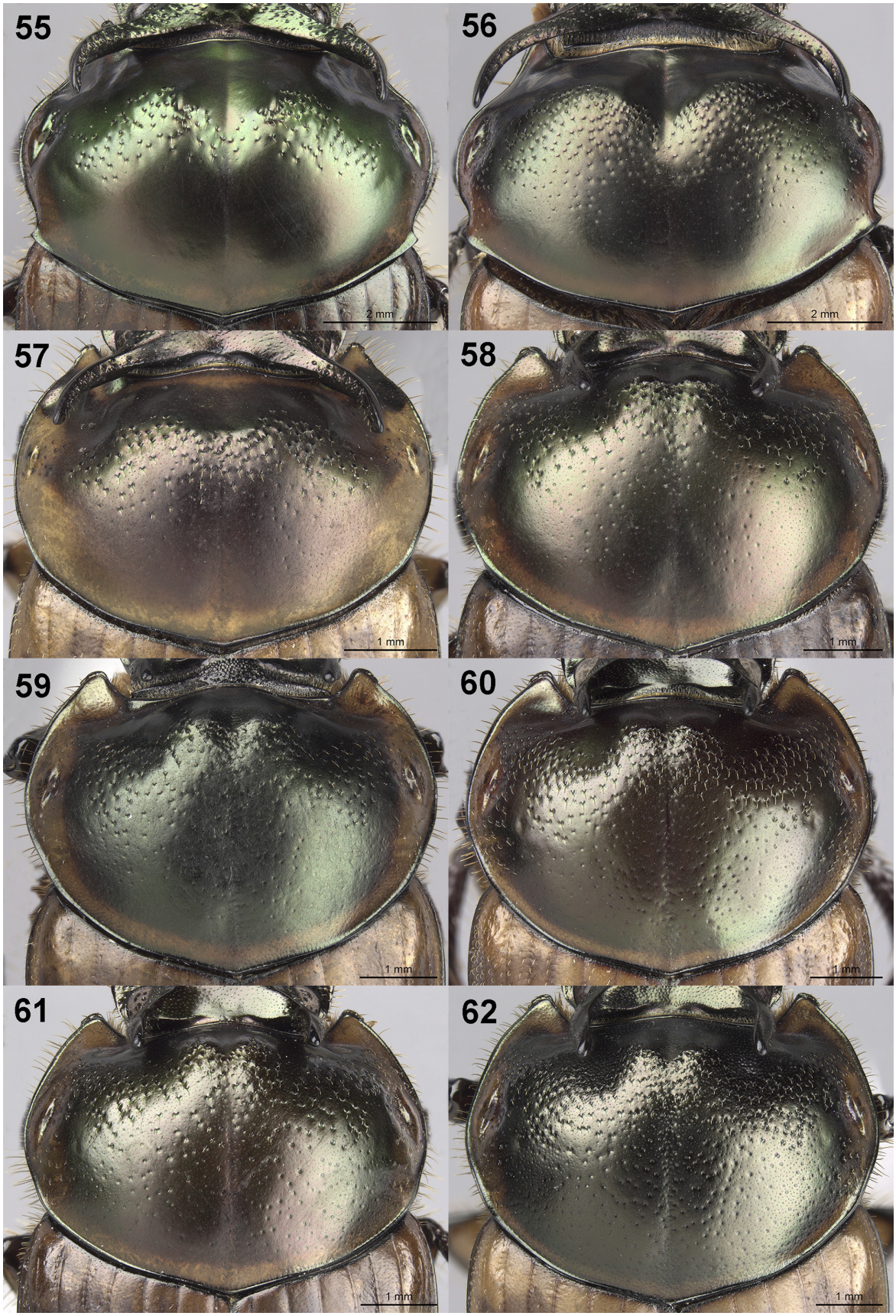


FIGURES 31–38. 31, 33, 35, 37. Male head, dorsal view; 32, 34, 36, 38. Male head, frontal view. 31–32. *Digitonthophagus eucatta*, alloreferent; 33–34. *D. falciger*, holotype; 35–36. *D. biflagellatus*, holotype; 37–38. *D. gazella*, non type (Central Province, Zambia).

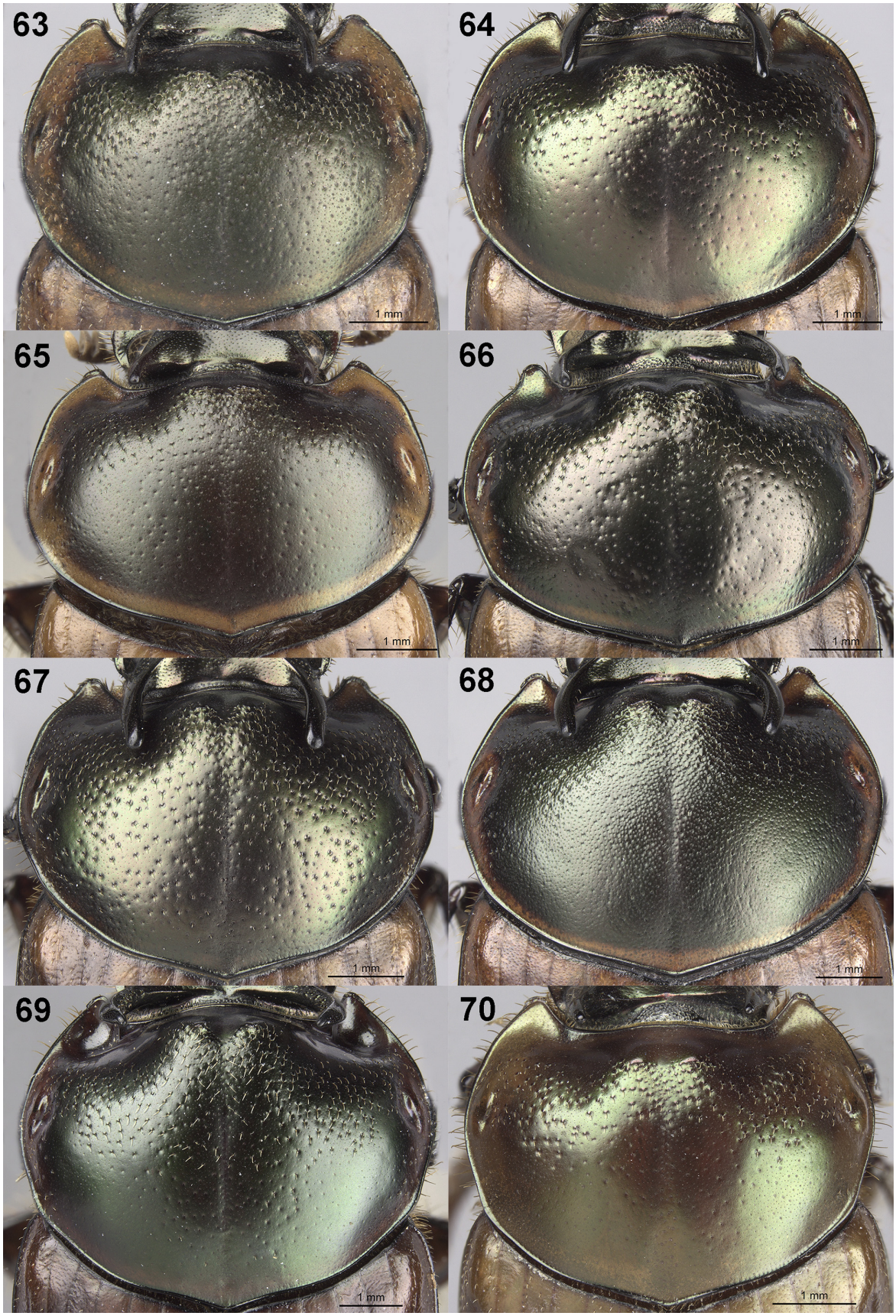


FIGURES 39–46. 39, 41, 43, 45. Male head, dorsal view; 40, 42, 44, 46. Male head, frontal view. 39–40. *Digitonthophagus petilus*, holotype; 41–42. *D. viridicollis*, holotype; 43–44. *D. aksumensis*, holotype; 45–46. *D. dilatatus*, holotype.

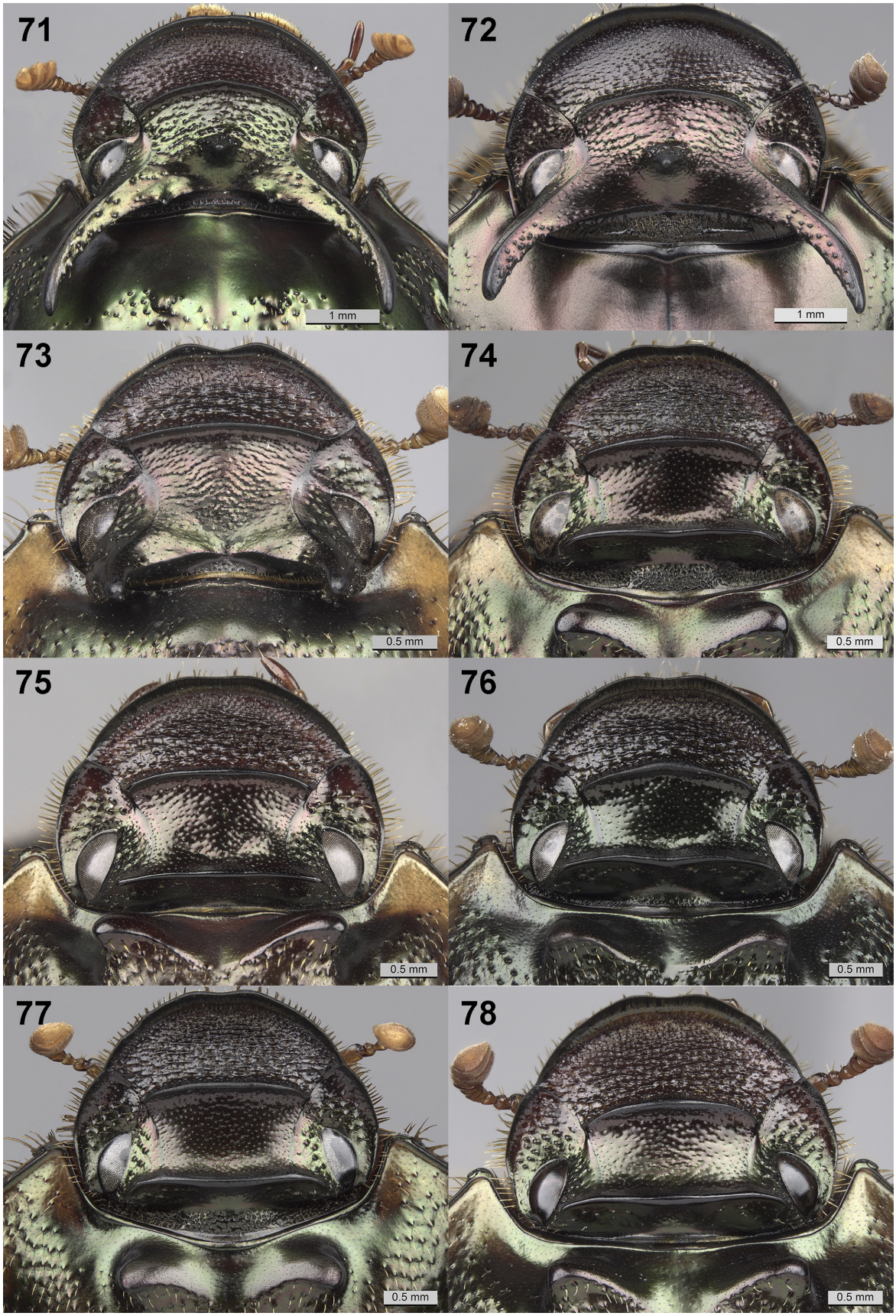
FIGURES 47–54. 47, 49, 51, 53. Male head, dorsal view; 48, 50, 52, 54. Male head, frontal view. 47–48. *Digitonthophagus fimator*, holotype; 49–50. *D. lusinganus*, lectotype; 51–52. *D. ulcerosus*, holotype; 53–54. *D. namaquensis*, holotype.



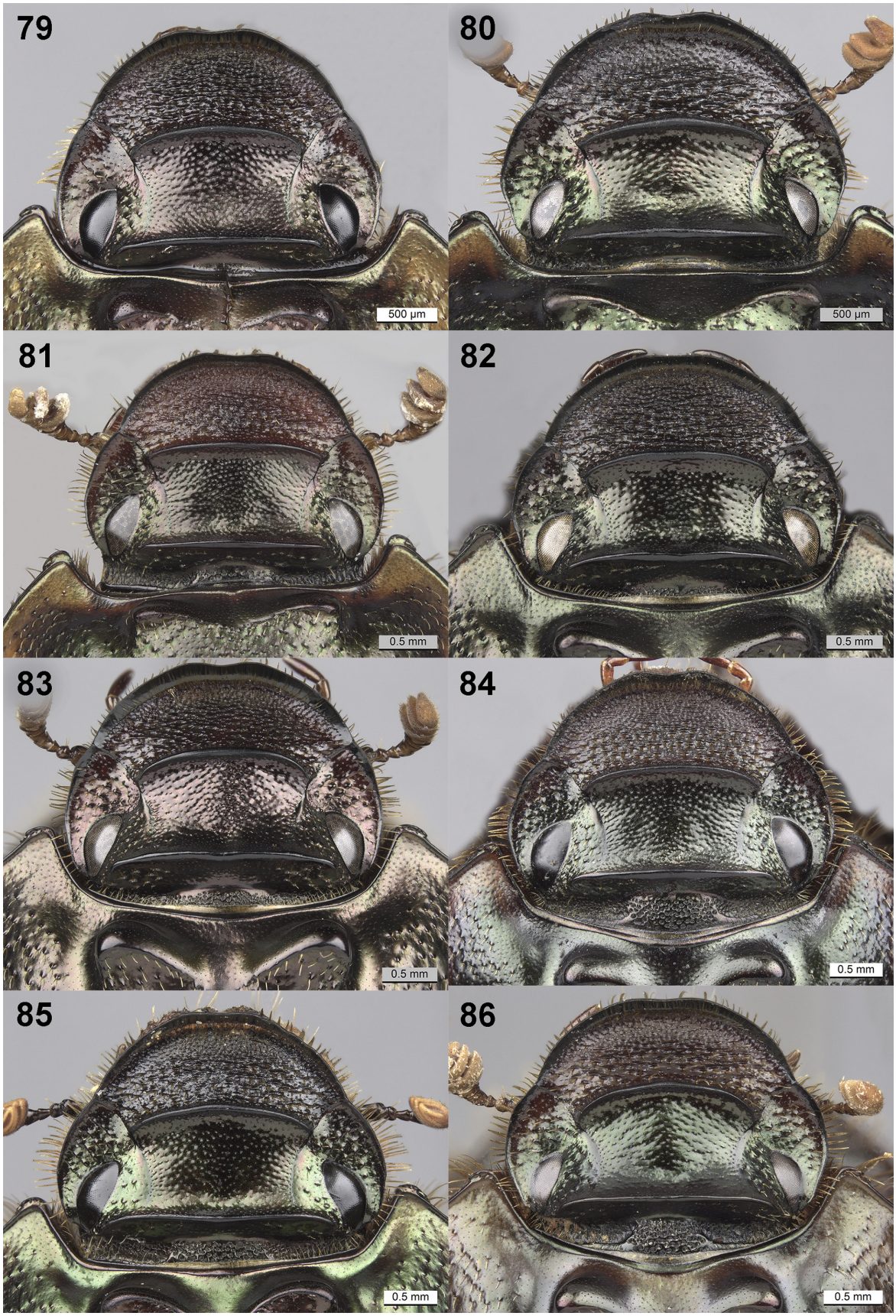
FIGURES 55–62. Male pronotum, dorsal view. 55. *Digitonthophagus bonasus*, alloreferent (Tamil Nadu State, India); 56. *D. uks*, holotype; 57. *D. sahelicus*, holotype; 58. *D. catta*, alloreferent (Tamil Nadu State, India); 59. *D. eucatta*, holotype; 60. *D. falciger*, holotype; 61. *D. biflagellatus*, holotype; 62. *D. gazella*, non type (Central Province, Zambia).



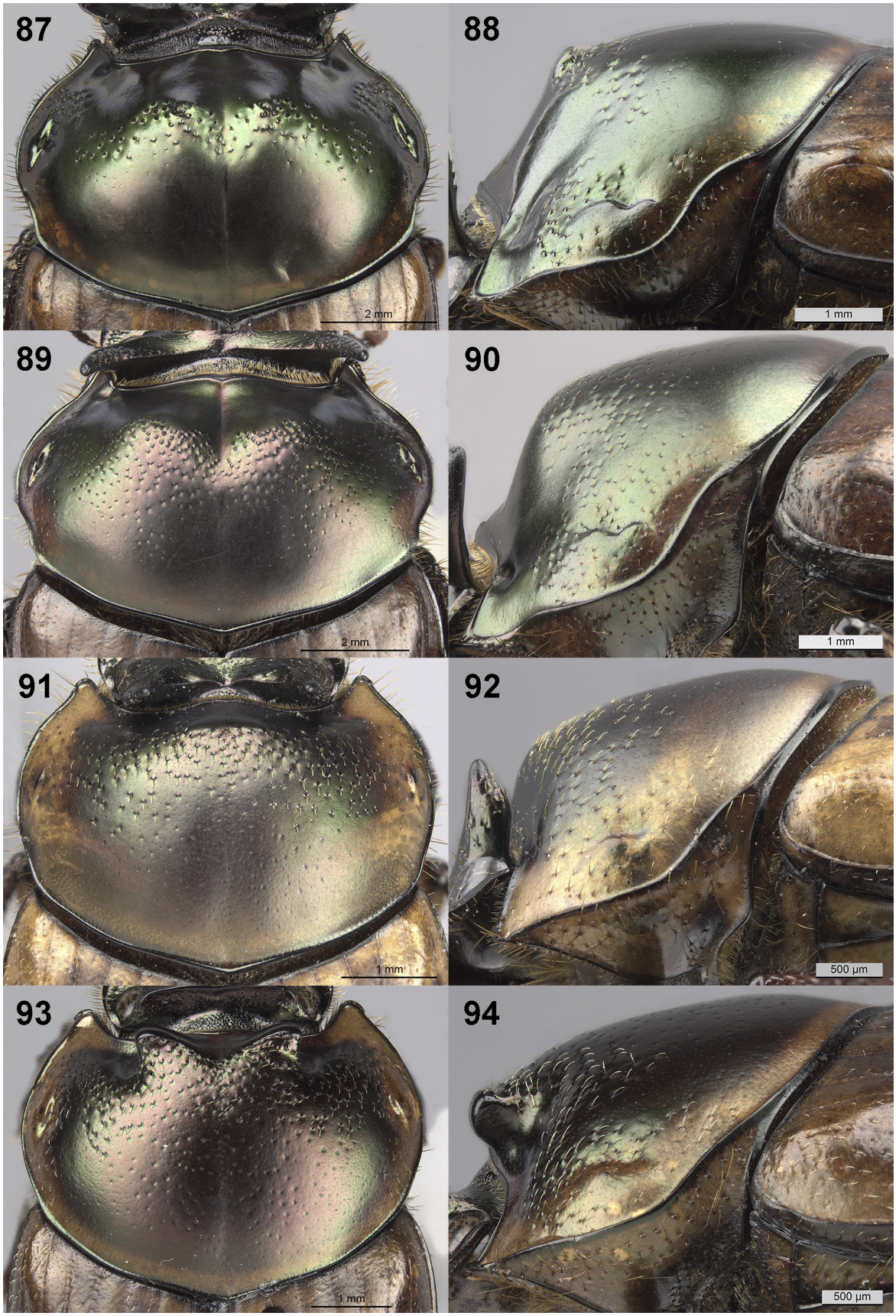
FIGURES 63–70. Male pronotum, dorsal view. 63. *D. petilus*, holotype; 64. *Digitonthophagus viridicollis*, holotype; 65. *D. aksumensis*, holotype; 66. *D. dilatatus*, holotype; 67. *D. fimator*, holotype; 68. *D. lusinganus*, lectotype; 69. *D. ulcerosus*, holotype 70. *D. namaquensis*, holotype.



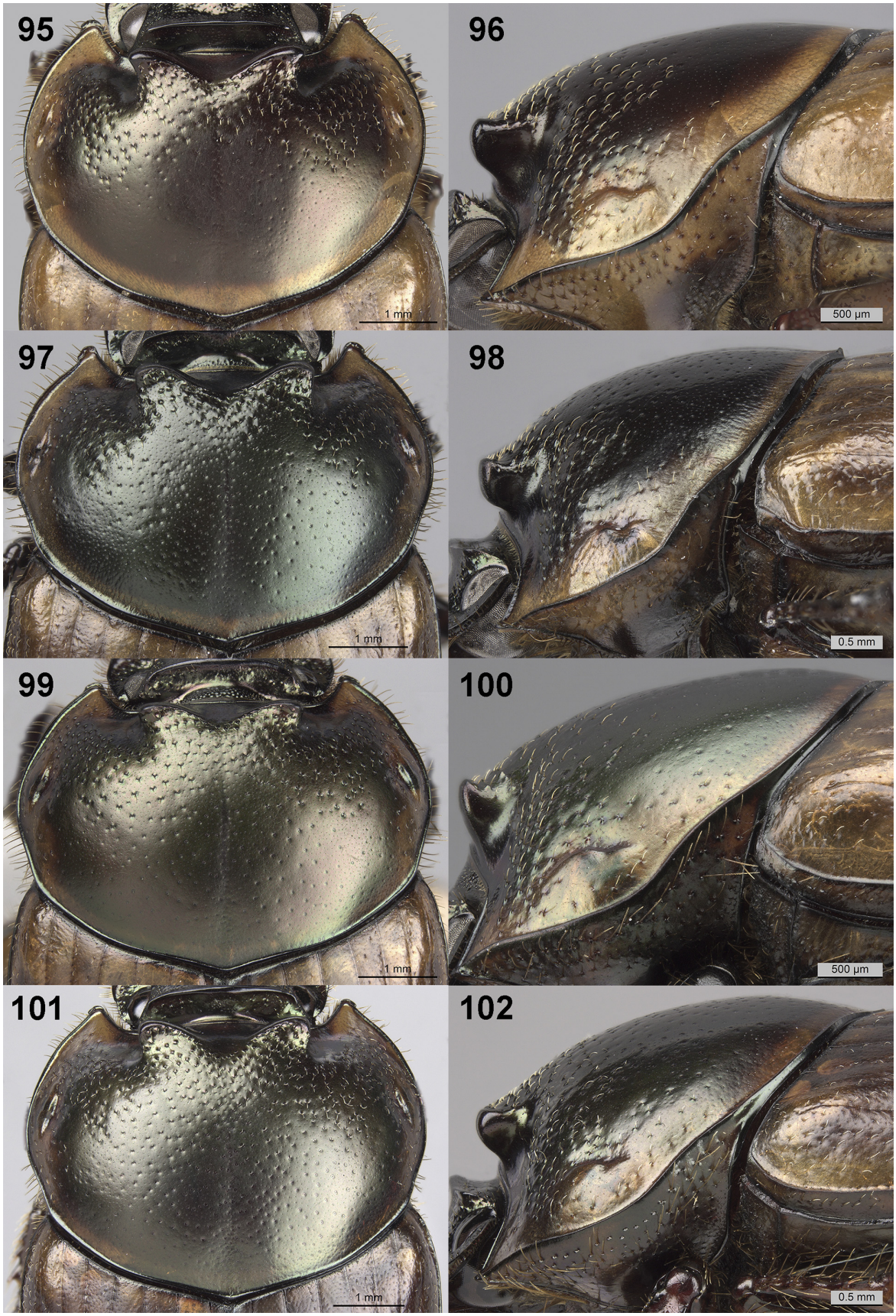
FIGURES 71–78. Female head, dorsal view. 71. *Digitonthophagus bonasus*, non type (Tamil Nadu State, India); 72. *D. uks*, allotype; 73. *D. sahelicus*, allotype; 74. *D. catta*, non type (India); 75. *D. eucatta*, allotype; 76. *D. falciger*, allotype; 77. *D. biflagellatus*, allotype; 78. *D. gazella*, non type (Antisiranana Province, Madagascar).



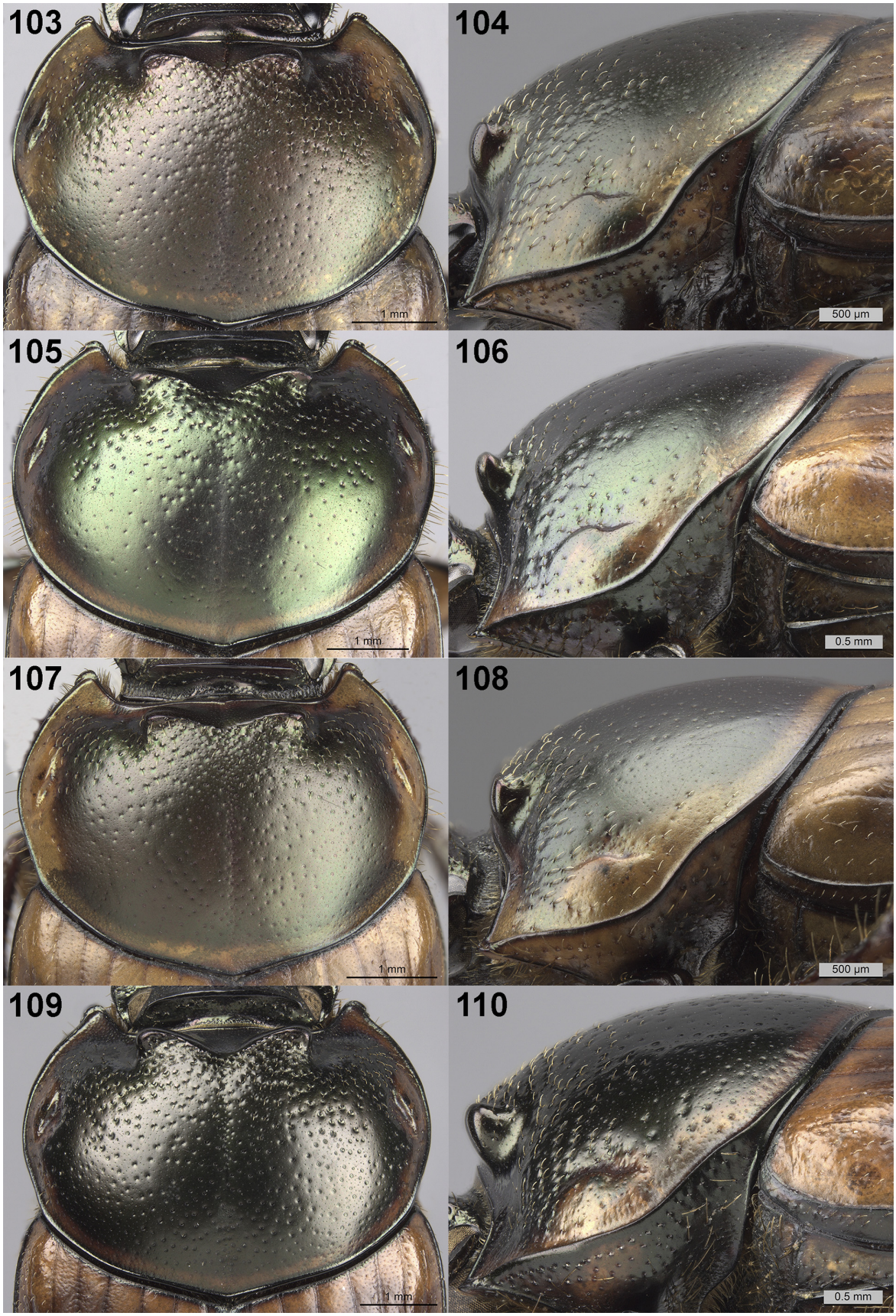
FIGURES 79–86. Female head, dorsal view. 79. *Digitonthophagus petilus*, allotype; 80. *D. viridicollis*, allotype; 81. *D. aksumensis*, allotype; 82. *D. dilatatus*, allotype; 83. *D. fimator*, allotype; 84. *D. lusinganus*, paralectotype; 85. *D. ulcerosus*, allotype 86. *D. namaquensis*, allotype.



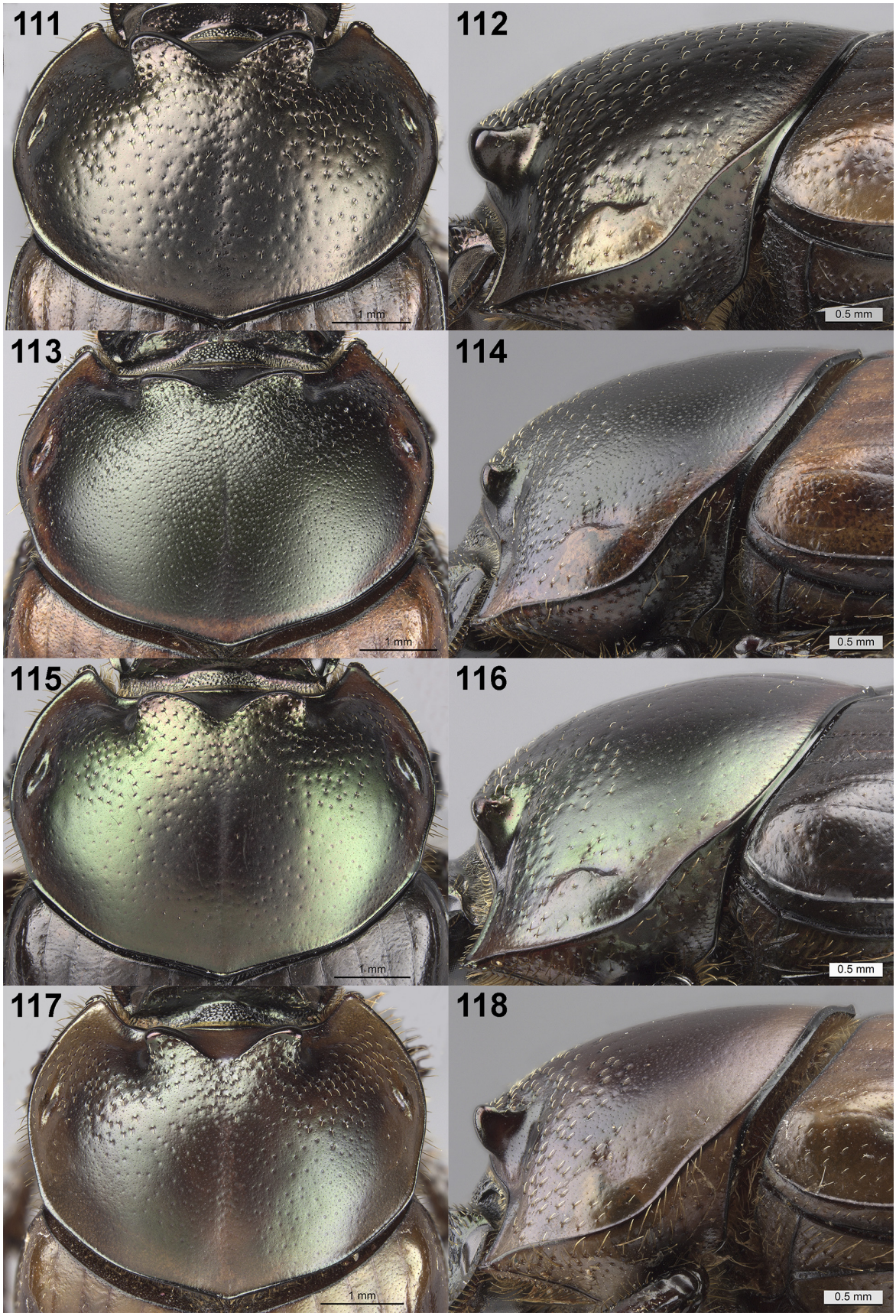
FIGURES 87–94. Female pronotum, 87, 89, 91, 93. Dorsal view; 88, 90, 92, 94. Lateral view. 87–88. *Digitonthophagus bonasus*, non type (Tamil Nadu State, India); 89–90. *D. uks*, allotype; 91–92. *D. sahelicus*, allotype; 93–94. *D. catta*, non type (India).



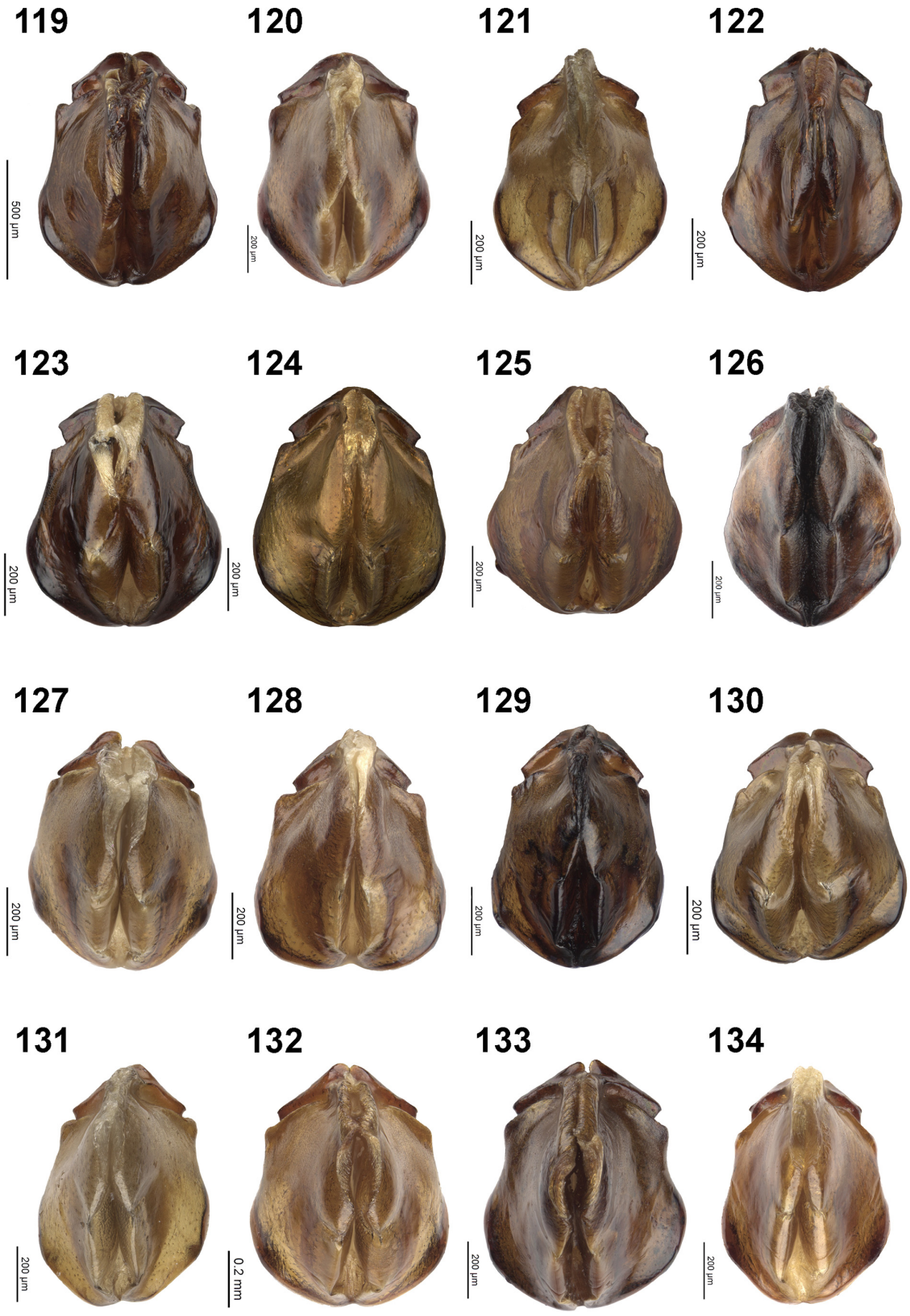
FIGURES 95–102. Female pronotum, 95, 97, 99, 101. Dorsal view; 96, 98, 100, 102. Lateral view. 95–96. *Digitonthophagus eucatta*, allotype; 97–98. *D. falciger*, allotype; 99–100. *D. biflagellatus*, allotype; 101–102. *D. gazella*, non type (Antisiranana Province, Madagascar).



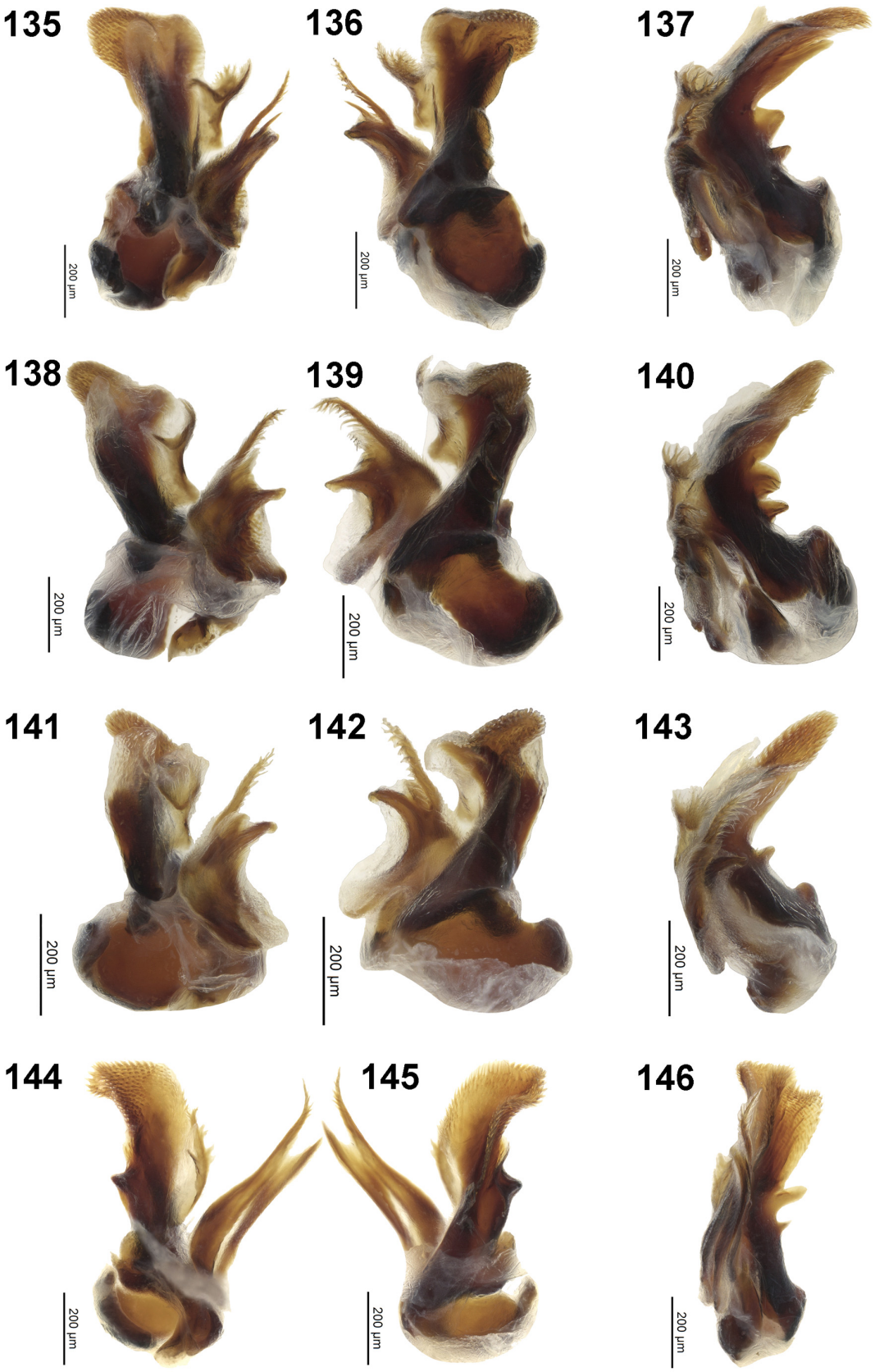
FIGURES 103–110. Female pronotum, 103, 105, 107, 109. Dorsal view; 104, 106, 108, 110. Lateral view. 103–104. *Digitonthophagus petillus*, allotype; 105–106. *D. viridicollis*, allotype; 107–108. *D. aksumensis*, allotype; 109–110. *D. dilatatus*, allotype.



FIGURES 111–118. Female pronotum, 111, 113, 115, 117. Dorsal view; 112, 114, 116, 118. Lateral view. 111–112. *Digitonthophagus fimator*, allotype; 113–114. *D. lusinganus*, paralectotype; 115–116. *D. ulcerosus*, allotype 117–118. *D. namaquensis*, allotype.

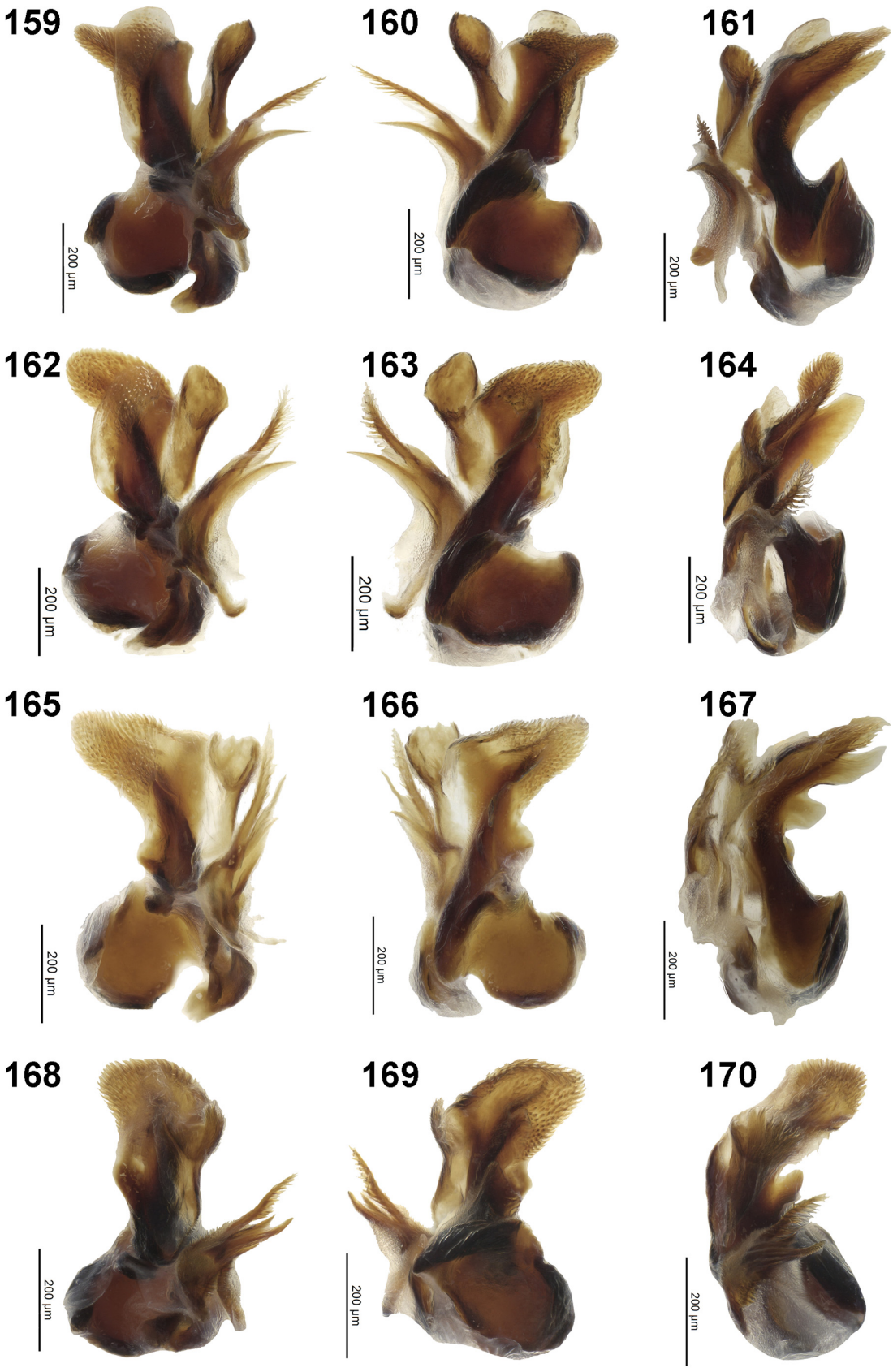


FIGURES 119–134. Parameres, dorsal view. 119. *D. bonasus*, alloreferent (Tamil Nadu State, India); 120. *Digitonthophagus uks*, holotype; 121. *D. sahelicus*, holotype; 122. *D. catta*, alloreferent (West Bengal, India); 123. *D. eucatta*, holotype; 124. *D. falciger*, holotype; 125. *D. biflagellatus*, holotype; 126. *D. gazella*, non type (Antisiranana Province, Madagascar); 127. *D. petillus*, holotype; 128. *D. viridicollis*, holotype; 129. *D. aksumensis*, holotype; 130. *D. dilatatus*, holotype; 131. *D. fimator*, holotype; 132. *D. lusinganus*, lectotype; 133. *D. ulcerosus*, holotype 134. *D. namaquensis*, holotype.

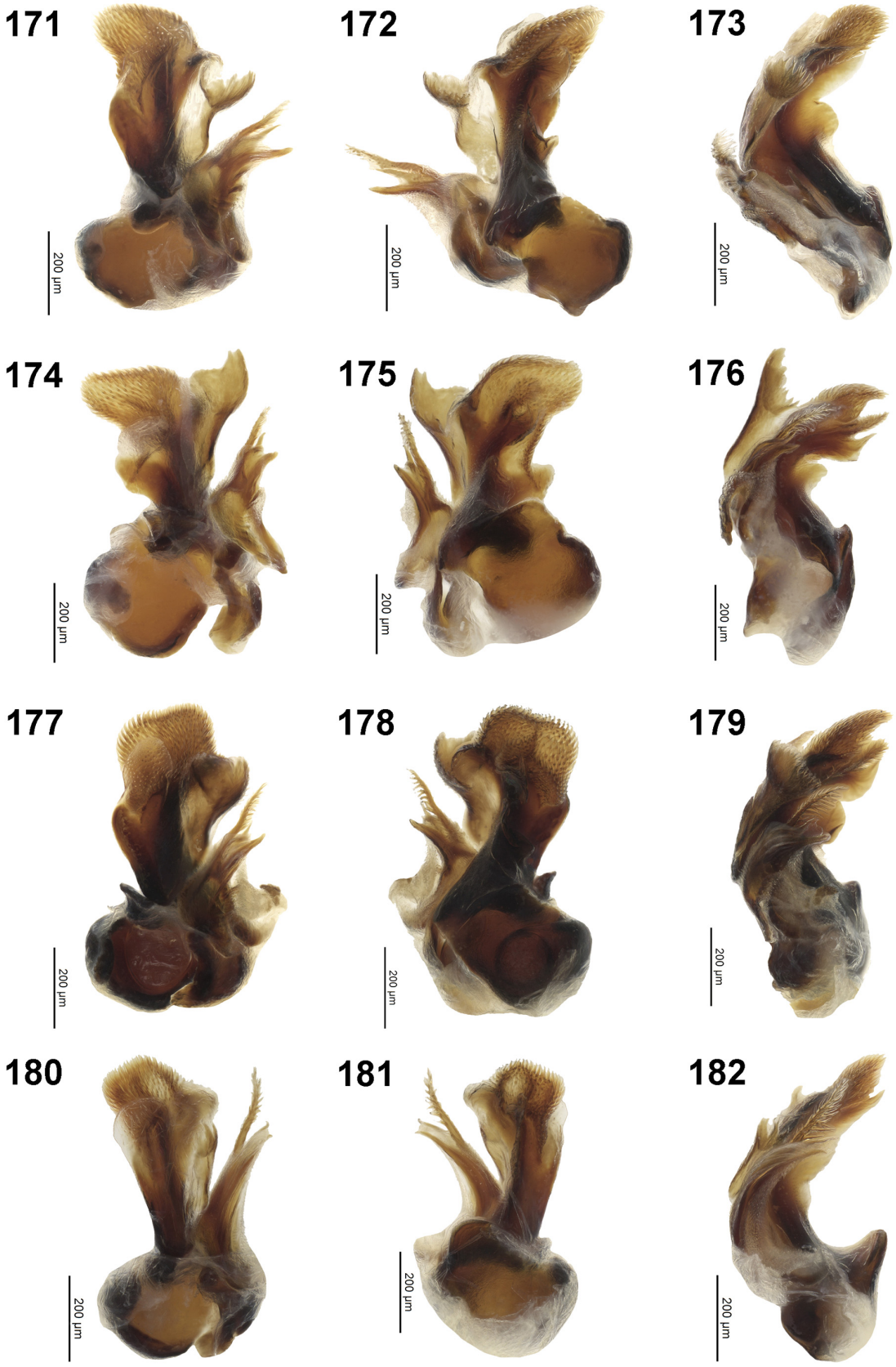


FIGURES 135–146. Internal sac sclerites (FLP, A + SA). 135, 138, 141, 144. Dorsal view; 136, 139, 142, 145. Ventral view. 137, 140, 143, 146. Right lateral view. 135–137. *Digitonthophagus bonasus*, alloreferent (Tamil Nadu State, India); 138–140. *D. uks*, holotype; 141–143. *D. sahelicus*, holotype; 144–146. *D. catta*, alloreferent.

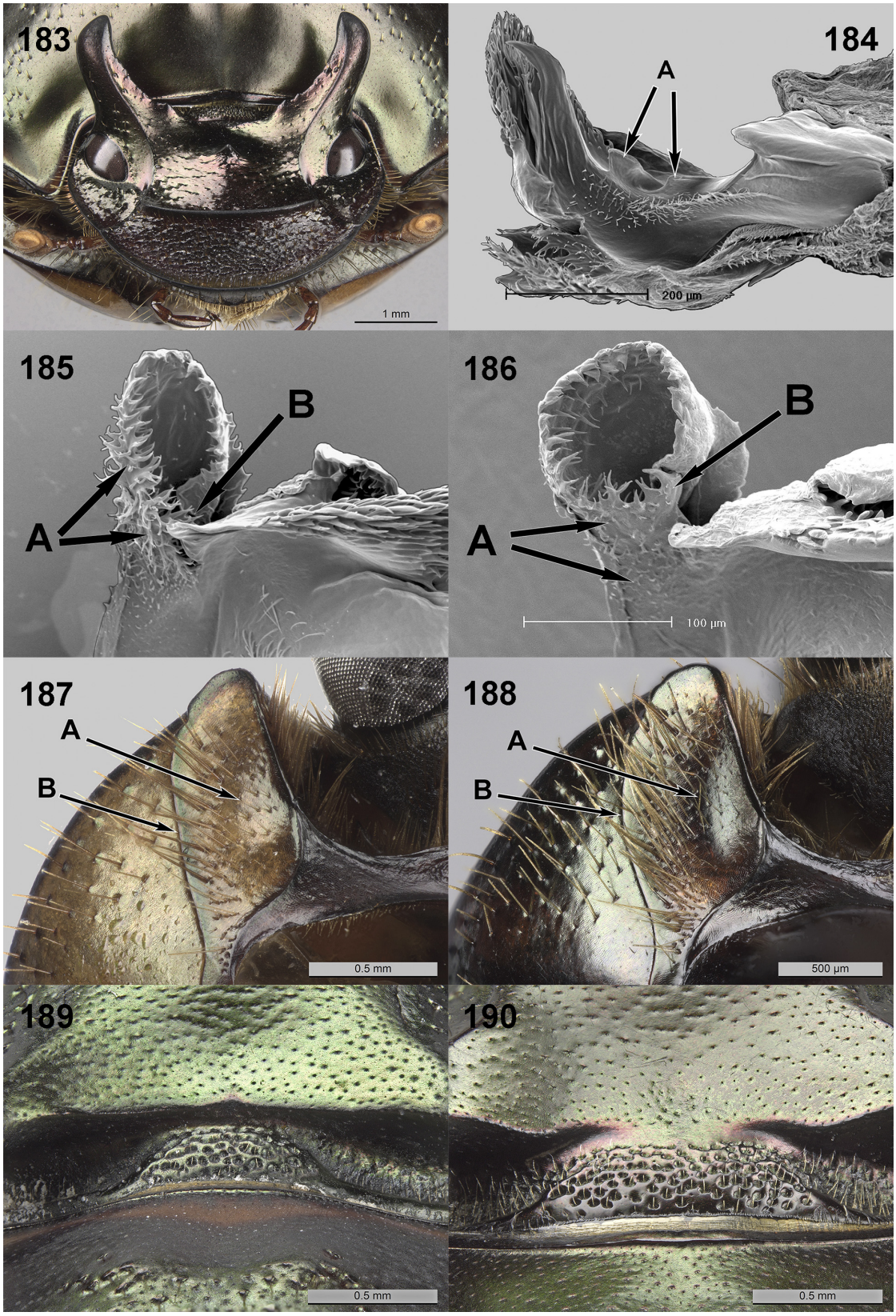
FIGURES 147–158. Internal sac sclerites (FLP, A + SA). 147, 150, 153, 156. Dorsal view; 148, 151, 154, 157. Ventral view. 149, 152, 155, 158. Right lateral view. 147–149. *Digitonthophagus eucatta*, alloreferent (Tamil Nadu State, India); 150–152. *D. falciger*, holotype; 153–155. *D. biflagellatus*, holotype; 156–158. *D. gazella*, non type (Antisiranana Province, Madagascar).



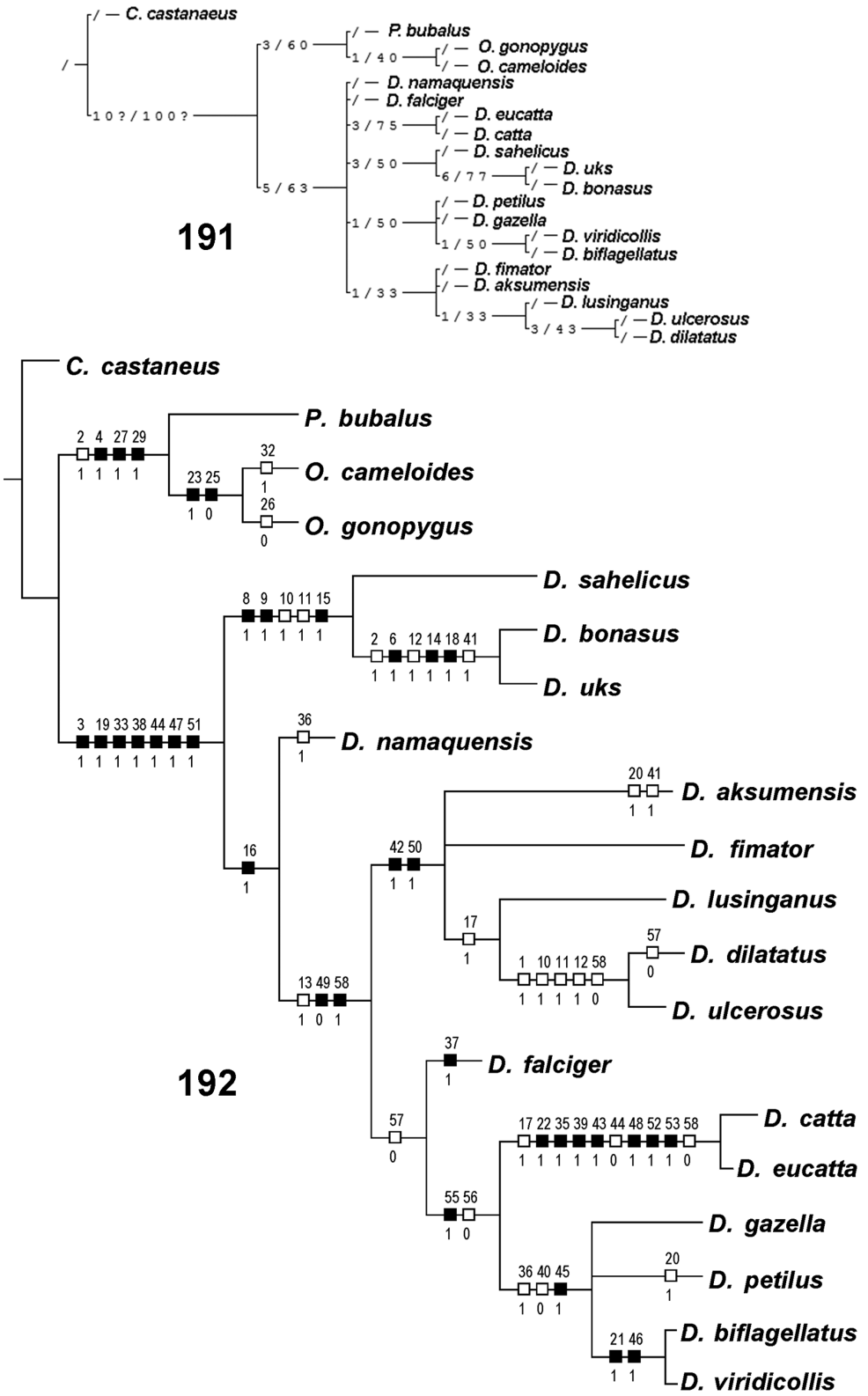
FIGURES 159–170. Internal sac sclerites (FLP, A + SA). 159, 162, 165, 168. Dorsal view; 160, 163, 166, 169. Ventral view. 161, 164, 167, 170. Right lateral view. 159–161. *Digitonthophagus petilus*, holotype; 162–164. *D. viridicollis*, holotype; 165–167. *D. aksumensis*, holotype; 168–170. *D. dilatatus*, holotype.



FIGURES 171–182. Internal sac sclerites (FLP, A + SA). 171, 174, 177, 180. Dorsal view; 172, 175, 178, 181. Ventral view. 173, 176, 179, 182. Right lateral view. 171–173. *Digitonthophagus fimator*, holotype; 174–176. *D. lusinganus*, lectotype; 177–179. *D. ulcerosus*, holotype; 180–182. *D. namaquensis*, holotype.



FIGURES 183–190. *Digitonthophagus bonasus*, female head, frontal view (Phongsaly Province, Laos); 184. *D. aksumensis*, FLP sclerite, right lateral view; 185. *D. gazella*, right lateral fold, ventral view; 186. *D. viridicollis*, right lateral fold, ventral view; 187. *D. eucatta*, hypomeron, ventral view, A. anterior hypomeral carina, B. anterior hypomeral depression; *D. gazella*, hypomeron, ventral view, A. anterior hypomeral carina, B. anterior hypomeral depression; 189. *D. namaquensis*, vertex dorsal view; 190. *D. gazella*, vertex dorsal view.



FIGURES 191–192. 191. Strict consensus phylogenetic tree of all known species of the genus *Digitonthophagus* based on morphology with Bremer support. The outgroup contains four putative closely related species. 192. Plotted implied weight trees showing character transformation for all known species of the genus *Digitonthophagus* and the four outgroup taxa. Above branch numbers indicate character and below branch numbers indicate state. Solid squares are showing non-homoplasious synapomorphies.