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Historical and morphological review
of the subgenus *Indonthophagus* Kabakov, 2006
of *Onthophagus* Latreille, 1802 (Coleoptera: Scarabaeidae:
Scarabaeinae: Onthophagini)

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Historical and morphological review of the subgenus *Indonthophagus* Kabakov, 2006 of *Onthophagus* Latreille, 1802 (Coleoptera: Scarabaeidae: Scarabaeinae: Onthophagini)

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Abstract. The subgenus *Indonthophagus* Kabakov, 2006 of *Onthophagus* Latreille, 1802 (Coleoptera: Scarabaeidae: Scarabaeinae: Onthophagini) is reviewed. A morphological definition of it is provided. A diagnosis, based both on external and internal characters, of the seven species deemed to belong to the group according to literature, is supplied. As a result, *Onthophagus spinifex* (Fabricius, 1781), previously placed with some uncertainty in the subgenus, is definitively excluded. A key to *Indonthophagus* species is also provided, as well as images of male, aedeagus and endophallus for each species. New country records of *Onthophagus turbatus* Walker, 1858 for Pakistan, Nepal and Bhutan are given.

Key words. Taxonomy, faunistic, dung beetles, Palaearctic, new country records.

ZooBank registration. urn:lsid:zoobank.org:pub:9D0CE9F2-35CF-449D-8984-1B4C722762F7

Introduction

The subgenus *Indonthophagus* was described by Kabakov (2006), in a footnote, to accommodate *Onthophagus mopsus* (Fabricius, 1792) as type species, and *O. nitidulus* Klug, 1845, *O. turbatus* Walker, 1858, *O. hastifer* van Lansberge, 1885, *O. ensifer* Boucomont, 1914 and, “likely”, *O. spinifex* (Fabricius, 1781).

In this paper a review of *Indonthophagus* is provided. Specimens of all the species placed in the subgenus by Kabakov (2006) and subsequent literature (Ziani and Bezděk 2016; Král and Batelka 2017; Montreuil 2017; Gupta et al. 2018; Ziani et al. 2019; Ghosh et al. 2020; Kharel et al. 2020; Gupta et al. 2022; Schoolmeesters 2023; Ziani and Keith 2023) have been examined and studied. Furthermore, a historical review and images of male habitus, aedeagus and endophallus, are presented for each species, to provide the reader a better overview on the subject.

The main objective of the paper, other than to furnish a comprehensive historical and morphological review of the species involved, is to better define the subgenus *Indonthophagus*, maybe described a bit quickly by the author.

Materials and Methods

Terminology of external morphology is based on Génier and Moretto (2017), whereas terms and study criteria of male genitalia structures follow Tarasov and Solodovnikov (2011) and Génier (2019), except for the term “raspula” (*sensu* Binaghi et al. 1969), herein preferred to the term “bristle”. For the methodology see Ziani and Gudenzi (2006). Epipharynx terminology is according to Dellacasa et al. (2001). Habitus measurements are given in the corresponding diagnostic features.

Initialisms of the collections in which the quoted material is preserved are as following:

AIMB	ATREE Insect Museum, Bangalore, Karnataka state (India)
DKCC	Denis Keith private collection, Chartres (France)
EIHU	Hokkaido University Museum, Sapporo (Japan)
JSCS	Joachim Schönfeld private collection, Sinzig (Germany)

MCSN	Museo Civico di Storia Naturale “Giacomo Doria”, Genoa (Italy)
MHNG	Muséum d’Histoire Naturelle, Genève (Switzerland)
MNHN	Muséum National d’Histoire Naturelle, Paris (France)
MZH	Finnish Museum of Natural History - Zoological Museum, Helsinki (Finland)
NHMUK	Natural History Museum, London (United Kingdom)
NMPC	National Museum (Natural History), Prague (Czech Republic)
OUMNH	University Museum of Natural History, Oxford (United Kingdom)
STCH	Sergei Tarasov private collection, Helsinki (Finland)
SZCM	Stefano Ziani private collection, Meldola, Forlì (Italy)
ZMB	Museum für Naturkunde, Berlin (Germany)
ZMUK	Zoological Museum of Kiel University, Kiel (Germany)
ZSIK	National Zoological Collection at Western Ghats Regional Centre, Zoological Survey of India, Kozhikode (India)

Authors’ name spelling, titles and publication year of older books cited in the text are taken from Schmitt et al. (1998), Bousquet (2016) and Bouchard and Bousquet (2020). Particularly, following the latter paper, the authorship of the tribe Onthophagini, usually assigned to Burmeister (1846) by the literature, is here given to Streubel (1846).

Some bibliographic references particularly complicated to report, are cited according to Poggi (2010).

There is uncertainty around the publication year of the paper by Marcela Janíková regarding an Omani beetle checklist. No date is indicated on the cover or within the booklet. For this reason, it is usually referenced as undated by the literature (see, for example, Ambrus and Grosser (2012) or Král and Batelka (2017)). Requests to people that possibly could have provided information in this regard (such as author, reviser, supervisor of the paper) were left unanswered, and so I was not able to establish for certain the publication year of the book. Nevertheless, after consulting the final bibliography of the paper, it can be noticed that 45 out of 48 references belong to the important series “Fauna of Saudi Arabia”. The latest mentioned volume is the 16th, dated 1997. There are no references to the next volume, the 17th dated 1998, or to subsequent ones. It can then reasonably assume that the publication year can be later than 1997, most likely 1998, as already stated by Ziani et al. (2019).

In “Historical Remarks” of some taxa, I quoted also some *nomina nuda*, i.e. names published without a description, a definition or an indication of the taxon that they denote (Articles 12 and 13 of the Code; ICZN 1999). I know well that such names are unavailable for nomenclatorial purposes, but I believe that mentioning them is important to better understand the complexity of nomenclatorial history of some taxa, and also to make reading less monotonous.

Males belonging to *Indonthophagus*, as well as most of horned *Onthophagus* Latreille species, present different degrees of development of outgrowths on the head and pronotum. Specimens can range from hypotelic, called minor males, with gynecoid appearance, to hypertelic, major males, with maximum development of ornamentation. Of course, individuals with all sorts of intermediates ornamentations can be distinguished. In this paper I consider only the two extreme phenotypes for each species, with the exception of *O. turbatus*, described on an eutelic male, herein called for convenience but rather improperly “medium”.

Finally, the study of type material. I have endeavoured to study directly types, especially for the species involved in taxonomic and, or, nomenclatorial issues. But it was not always possible, since in recent times, managers of some European and Asian museums have decided not to send on loan type material for studying, to not-institutionalized entomologists at least. In some countries is even forbidden to send specimens abroad or sampling on the spot without a special permit. Therefore, in the impossibility to go personally to those museums for studying types or in those countries for collecting specimens, I was forced to examine some types or other critical specimens only by photos. To do so, I have taken advantage of the much-appreciated support of museums curators and their staff, and of some colleagues (all mentioned in “Acknowledgments”) who took the photos and made them available to me. For this very reason, I preferred to title this paper “review” rather than “revision”, well aware that the latter includes also the direct study of all types.

Systematic Account

Superfamily Scarabaeoidea Latreille, 1802

Family Scarabaeidae Latreille, 1802

Subfamily Scarabaeinae Latreille, 1802

Tribe Onthophagini Streubel, 1846

Genus *Onthophagus* Latreille, 1802

Subgenus *Indonthophagus* Kabakov, 2006

Indonthophagus Kabakov 2006: 154 (footnote); Krajcik 2012: 174; Krajcik 2013: 124; Ziani and Bezděk 2016: 188; Král and Batelka 2017: 131; Montreuil 2017: 269; Gupta et al. 2018: 483; Ziani et al. 2019: 18; Ghosh et al. 2020: 243; Kharel et al. 2020: 368/371; Gupta et al. 2022: 425; Schoolmeesters 2023; Ziani and Keith 2023: 1.

Type species. *Onthophagus mopsus* (Fabricius, 1792), by original designation.

Diagnosis. *Onthophagus* species of small or medium size (length 3.0 to 10.0 mm), colour blackish brown, sometimes with green or blue metallic lustre, elytra sometimes with dark red basal and apical spots, in one case elytra yellow ochre with symmetrical v-shaped black spots. Antennae yellow, more or less dark. Setation pale-yellow.

Head short, clypeus broadly round, barely or not at all emarginate anteriorly and not sinuate at sides; antenna with 9 antennomeres; clypeofrontal carina distinct, sometimes barely discernible, bent backward, in major males usually halfway between the base of the horn and the anterior clypeal margin, in one case nearly adjacent to the base of the horn; major males with the occipital carina extended in a long horn arising sometimes between eyes or slightly forward, sometimes in front of them, flat and more or less broad at base, directed backward, following the curvature of pronotum, often extending past the middle of the body; occipital carina reduced to a short tubercle in minor males or to a more or less straight carina, placed between eyes, or nearly so, in females (Fig. 1a); clypeal surface with transversely rugose, setigerous punctures, frontal surface sparsely punctate, punctures of two sizes.

Pronotum convex, declivous anteriorly, major males with a more or less appreciable anteromedian groove, with or without a tubercle on each side; minor males and females with an anteromedian transverse gibbosity, sometimes hardly appreciable, sometimes divided in two lobes; both sexes with a posterolateral area, more or less wide and depressed, dull with stronger microreticulation, on either side near pronotal posterior angles (Fig. 2), sometimes anteriorly with a tuft of few longer setae; anterior angles distinctly produced, sides not sinuate behind them; dorsal surface setigerously punctate, punctures more or less slightly impressed, usually subregular in distribution, bearing pale-yellow setae.

Elytral striae usually shiny, distinctly impressed, with punctures slightly larger than strial width and barely crenulating interstitial sides; interstriae flat to convex, all rather regularly densely granulate, granules with a more or less short thin setae.

Pygidium basally ridged, with rather regularly distributed, setigerous punctures; setae pale-yellow, thin, usually longer than those of elytra.

Apical margin of male protibiae either oblique or perpendicular to the inner protibial margin, in the latter case with a tuft of short pale-yellow bristles, always with a small denticle strongly curved downward at the inner angle of protibial apex; metatibiae distinctly widened apically.

Male genital armature. Parameres short, apices usually bent ventrally and diverging apically, without basolateral plate denticle, round at apex; endophallus with the presence of accessory endophallites, one (in *O. ensifer*), usually two evident raspulae and a U-shaped lamella copulatrix, with arms more or less slender, sometimes with spinelike processes or apically bifurcate.

Epipharynx (Fig. 1b). Rounded laterally, front edge not sinuate; acropariae long, rather densely arranged; epitorma very slender, almost indistinguishable, with some bristles along its length, the distal ones longer and stouter; corypha without spinules; chaetopariae stout; tomiae rounded at the end.

Distribution. East Palaearctic, east Afrotropical and west Oriental ecozone (Schoolmeesters 2023).

Historical review. The first author that somehow grouped most of the species treated in this paper was Boucomont (1914). He drawn up a key to some *Onthophagus* species with the following characteristics: “tête ♂ avec une

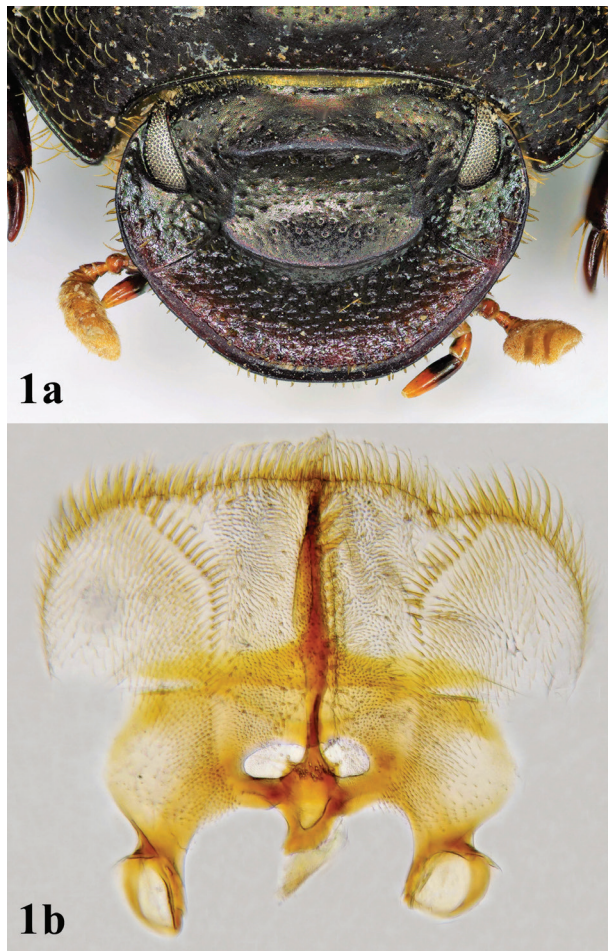


Figure 1. *Onthophagus (Indonthophagus) mopsus* (Fabricius, 1792) [Pakistan, Islamabad Capital Territory]. **1a** ♀ head, from above. **1b** Epipharynx. Photos by A. Degiovanni, edited by G. Fiumi.

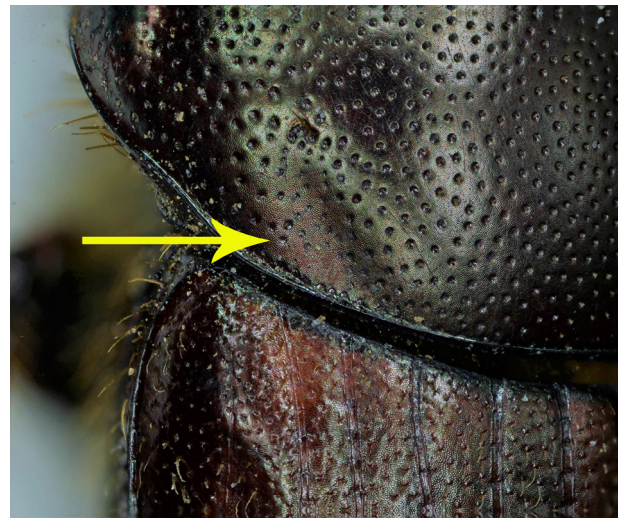


Figure 2. *Onthophagus (Indonthophagus) turbatus* Walker, 1858 [Sri Lanka, Uva prov.]. Detail of pronotal posterolateral area. Photos by A. Degiovanni, edited by G. Fiumi.

corne plus ou moins longue, non lamiforme, thorax ♂ sans saillies ni tubercules latéraux ou discaux, tout au plus avec deux petites dents au sommet; intervalles des élytres à ponctuation râpeuse; insectes concolores sans taches accusées” [head ♂ with a more or less long, not lamiform horn, pronotum without projections or lateral tubercles, at most with two small teeth anteriorly; interstriae with raspish punctation; insects unicoloured, without definite spots]. Five species were placed in this “group”: *Onthophagus spinifex* (Fabricius, 1781), *O. ensifer* Boucomont, 1914, *O. turbatus* Walker, 1858, *O. gracilicornis* (Germar, 1813) [now deemed as junior synonym of *O. mopsus*, see below] and *O. hastifer* van Lansberge, 1885.

Arrow (1931) proposed a “*mopsus* group” (Group 25) for *O. mopsus*, *O. turbatus*, *O. hastifer*, *O. ensifer* and for *O. nitidulus* Klug, 1845, together with other seventeen species. It’s worth noting that Arrow (1931) placed the male of *Onthophagus spinifex* in the Group 13 (*marginalis* group), whereas the female was placed in the Group 6 (*rudis* group).

Biswas and Chatterjee (1985), probably referring to Arrow (1931), mentioned a “*mopsus* group” without specifying any morphological characteristic.

Again, also Kabakov and Napolov (1999) placed *O. hastifer* in a vaguely defined “*mopsus* group”.

Later on, Kabakov (2006) described the subgenus *Indonthophagus* for all the species quoted by Boucomont (1914) and adding *Onthophagus nitidulus*.

The subgenus was then accepted and used by Ziani and Bezděk (2016), Král and Batelka (2017), Montreuil (2017), Gupta et al. (2018), Ziani et al. (2019), Ghosh et al. (2020), Kharel et al. (2020), Gupta et al. (2022) and Schoolmeesters (2023), even though none of them dealt with *Indonthophagus* more in depth.

Phonetic remarks. As explained some years ago (Ziani 2020a), *Indonthophagus*, having *Onthophagus* as suffix, is a proparoxytone word, that is, it has a heavy stress on the third-to-last syllable. It has to be pronounced Indontòfagus.

Biology. All the species cited in this paper should be strictly coprophagous. To confirm that, Mittal (1986) reported *O. mopsus* and *O. spinifex* attracted by human dung and Mittal (1999) by cattle and horse dung. Thomas et al. (2006) recorded *O. ensifer* in a trap baited with Indian elephant dung. Again, *O. ensifer* with *O. turbatus* have been recorded in gaur dung from Southern Western Ghats (India) by Thomas et al. (2007). According to Asha et al. (2022), this last two species (*O. ensifer* and *O. turbatus*) are specialists of non-ruminant dung, such as elephant and wild boar. And always regarding *O. ensifer* and *O. turbatus*, Sathiandran et al. (2021) specified that, in southern India, the two species attend dung of deer, elephant, gaur and especially boar, whereas only *O. turbatus* has been collected in macaque dung. For what I know, other eating preferences have never been reported. Taiwanese specimens of *O. hastifer* were collected in buffalo dung deposited in open pastures (D. Král, personal communication). In Western Ghats (India), *O. turbatus* seems to be abundant both in open and in shaded areas, with both day and night activity, whereas *O. spinifex* is a nocturnal species present in open areas (Asha et al. 2021). Three species at least (*O. turbatus*, *O. mopsus* and *O. spinifex*) present positive phototaxis, and were collected at light in Pakistan (unpublished data).

***Onthophagus (Indonthophagus) aeneopiceus* d'Orbigny, 1902**

(Fig. 3)

Onthophagus aeneopiceus d'Orbigny 1902: 156; d'Orbigny 1905: 488; d'Orbigny 1913: 376; d'Orbigny 1922: 609; Boucomont and Gillet 1927: 151; Balthasar 1963: 263; Balthasar 1969: 65; Ferreira 1972: 557; Balthasar 1972: 22; Zunino 1975: 153; Barbero et al. 1998: 243; Schoolmeesters 2023; Ziani and Keith 2023: 1.

Type locality. “Erythrée” [Eritrea].

Type material. Holotype, a minor ♂, fixed by monotypy, examined by photos, in d'Orbigny collection (MNHN).

Diagnostic features. Length 4.0 to 6.5 mm. Colour dark brown, moderately shiny, with distinct isodiametric microreticulation, elytra sometimes with dark red irregular humeral spots, clypeal sides dark red. Antennae yellow. Dorsal pubescence pale-yellow.

Head short, clearly wider than long, with clypeus broadly round, only very feebly sinuate anteriorly, sides not sinuate; clypeofrontal carina distinct and bent backward, slightly closer to the base of the horn than to the anterior margin of clypeus; occipital carina extended in a long horn arising between the eyes, where it is broad, broader than clypeofrontal carina, and flat, directed backward, tapering gradually to the extremity and following the curvature of pronotum, with moderately long yellow setae mainly at sides, in major males, reduced to a narrow straight lamina in minor males (holotype); clypeal surface with very transversely rugose, setigerous punctures, frontal surface doubly sparsely punctate.

Pronotum convex, declivous anteriorly, with a distinct anteromedian depressed area in major males (in minor male (holotype) without depression) and a small hardly distinguishable posterolateral dull area on either side near pronotal posterior angles; anterior angles distinctly produced, sides not sinuate behind them in dorsal view; dorsal surface setigerously punctate, punctures sub-regular in distribution, separated by 1-2 diameters on disc, smaller and more spaced on the anteromedian furrow; each puncture bears a small granule at its anterior margin, and a long pale-yellow seta, slightly longer than those on clypeus.

Elytral striae shiny, distinctly impressed, with punctures slightly larger than stria width and barely crenulating interstriae sides; interstriae flat to barely convex, all rather regularly granulate; granules slightly smaller than stria punctures; posterior margin of each granule with a small, indistinct, setigerous puncture; setae pale-yellow, thin, as long as pronotal ones.

Pygidium with rather regularly distributed, setigerous punctures; setae yellow, long, thin.

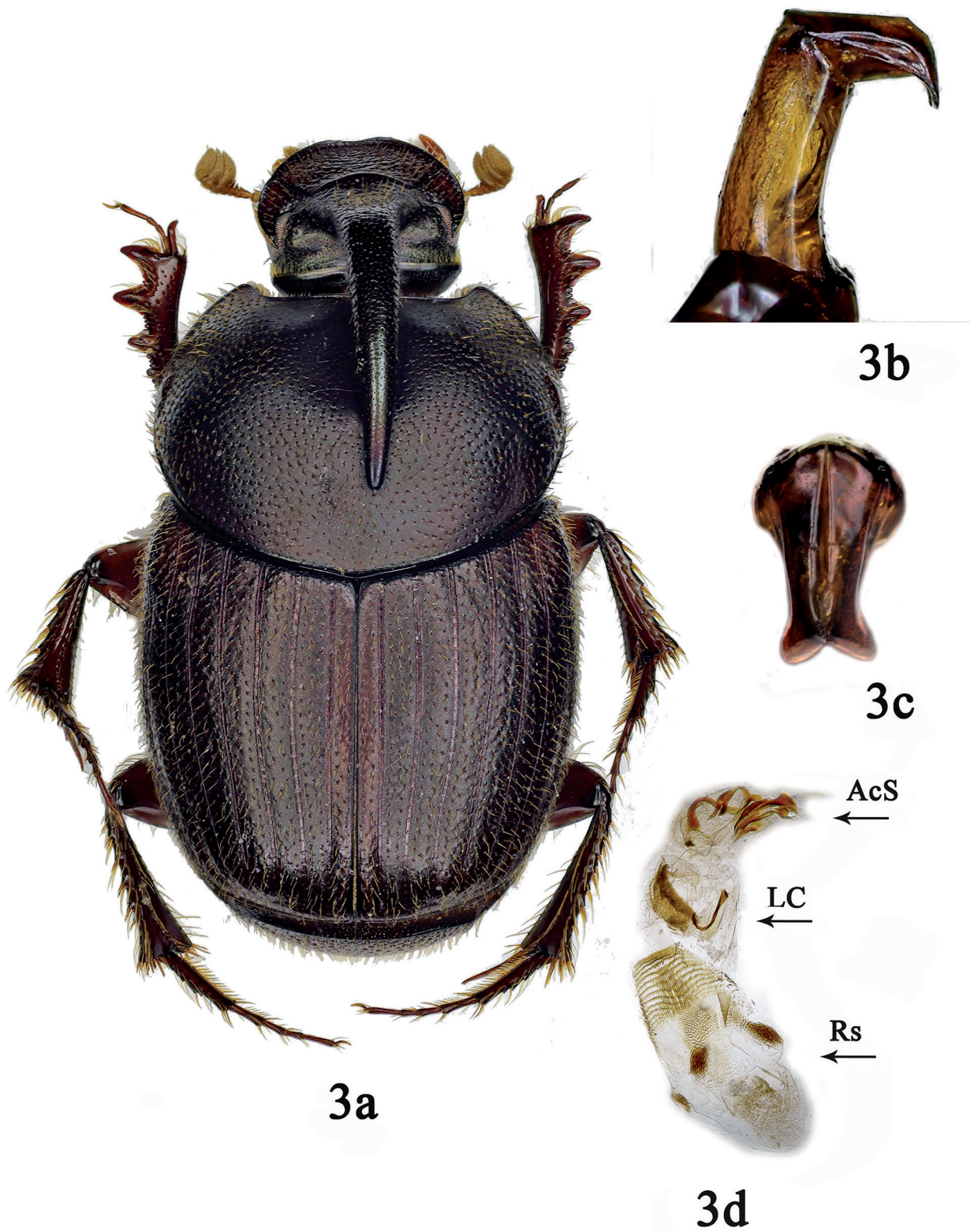


Figure 3. *Onthophagus (Indonthophagus) aeneopiceus* d'Orbigny, 1902 [major ♂: Yemen, Ibb gov.]. **3a)** Dorsal habitus. **3b)** Parameres, lateral view. **3c)** Parameres, dorsal view. **3d)** Endophallus. AcS: accessory endophallites. LC: lamella copulatrix. Rs: raspulae. Photos by A. Degiovanni, edited by G. Fiumi [from Ziani and Keith (2023)].

Males with protibial spur clearly bent downward apically, and with a small denticle strongly curved downward on the inner angle of protibial apex.

Female not examined. According to d'Orbigny (1913), females have the occipital carina extended in a backward bent lamina, placed between the eyes, in the middle of them, and a pronotal anteromedian transverse gibbosity, sometimes very slightly divided in two lobes.

Male genital armature. Parameres short, apices bent ventrally, obviously diverging apically, without basolateral plate denticle, round at apex (Fig. 3b–c); endophallus with the presence of accessory endophallites, two evident raspulae and a bracket-shaped lamella copulatrix, very thin (Fig. 3d).

Distribution. Eritrea (d'Orbigny 1902). Sudan, Ethiopia, Kenya (d'Orbigny 1913). Ivory Coast (Balthasar 1969, doubtful record). Yemen (Ziani and Keith 2023).

Material examined. Eritrea: “Erythrée” [Eritrea], examined by photos (holotype ♂ of *O. aeneopiceus*, MNHN). **Yemen:** Ibb gov., W of Jabal Hadish, 30.iii.1976, R. Naviaux leg. 1 ♂ (DKCC); Ibb gov., 5 km SW Najd al Jumai - Wadi Maytam 1600 m, 13°52'28"N 44°17'45" E, 26-27.x.2005, D. Král leg. 1 ♂ (NMPC).

Historical review. Despite *O. aeneopiceus* being described more than a century ago, its nomenclatorial and systematic history is relatively poor. According to d'Orbigny (1902), the holotype, a male, the sole available specimen for the description, was collected in Eritrea. Eleven years later, d'Orbigny (1913), evidently after examining further material, specified the presence of a long curved backward cephalic horn in major males, described the female and added other localities from three more countries. Balthasar (1963), whilst specifying that *O. aeneopiceus* was an Afrotropical species, hypothesized its presence also in the Palaearctic Africa. Balthasar (1969) reported the species for Ivory Coast, but this record, completely off the known distribution area of the species, was rightly regarded dubiously by Schoolmeesters (2023). Lastly, Ziani and Keith (2023) published the first record for the Palaearctic ecozone (*sensu* Löbl and Löbl 2016) after two males collected in Yemen.

Remarks. Ziani and Keith (2023), although preferring not to insert *O. aeneopiceus* in any known subgenus of *Onthophagus*, pointed out the similarity between the lamella copulatrix and the overall structures inside the endophallus of *O. aeneopiceus* with those of *O. mopsus*.

It is noteworthy that *O. aeneopiceus* is, so far, the sole species belonging to the group in which the male protibial spur is sinuate, clearly bent downward apically. This characteristic is common in those *Onthophagus* species somehow associated with burrows or nests of small mammals (Ziani and Gudenzi 2009). Only further investigation will be able to clarify whether the biology of this species is connected to pholeophily.

Onthophagus (Indonthophagus) ensifer Boucomont, 1914

(Fig. 4)

Onthophagus ensifer Boucomont 1914: 220; Boucomont and Gillet 1927: 136; Arrow 1931: 334; Petrovitz 1961: 102; Balthasar 1963: 342; Biswas and Chatterjee 1986a: 58; Biswas and Chatterjee 1986b: 88; Sewak 1986a: 138; Sewak 1986b: 14; Sewak and Yadva 1991: 26; Biswas and Mulay 2001: 140; Sewak 2003: 276; Sewak 2004: 118; Sewak 2005: 146; Shrestha 2005: 107; Krajcik 2006: 102; Rajan 2006: 124; Thomas et al. 2006: 5; Sewak 2006: 212; Vinod and Thomas 2006: 5; Thomas et al. 2007: 62; Sewak 2009a: 30; Sewak 2009b: 51; Sewak 2010: 108; Thomas et al. 2011: 33; Krajcik 2012: 178; Venugopal et al. 2012: 2687; Karimbunkara and Rajan 2013: 176; Krajcik 2013: 84; Rani and Sanjayan 2013: 242; Mittal and Jain 2015: 397; Sathiandran et al. 2015: 8254; Anu and Vinod 2017: 47; Latha and Thomas 2018a: 16123; Latha and Thomas 2018b: 1889; Latha 2019: 63; Sathiandran et al. 2021: 741; Asha et al. 2022: 7.

Onthophagus (incertae sedis) ensifer, Löbl et al. 2006: 174; Gupta et al. 2022: 426.

Onthophagus (Indonthophagus) ensifer, Kabakov 2006: 154 (footnote); Ziani and Bezděk 2016: 188; Gupta et al. 2018: 484; Kharel et al. 2020: 376; Schoolmeesters 2023.

Onthophagus (Onthophagus) ensifer, Sobhana et al. 2013: 95.

Type locality. “Nilghiris: Coonour”; “Madura distr.: Shembaganur”; “Madras” [South India, Tamil Nadu state].

Type material. Number of type specimens not specified in the original description, but more than one. One specimen, a major ♂, labelled as “type” and with a label handwritten by Boucomont himself, here considered a syntype, examined by photos (MNHN).

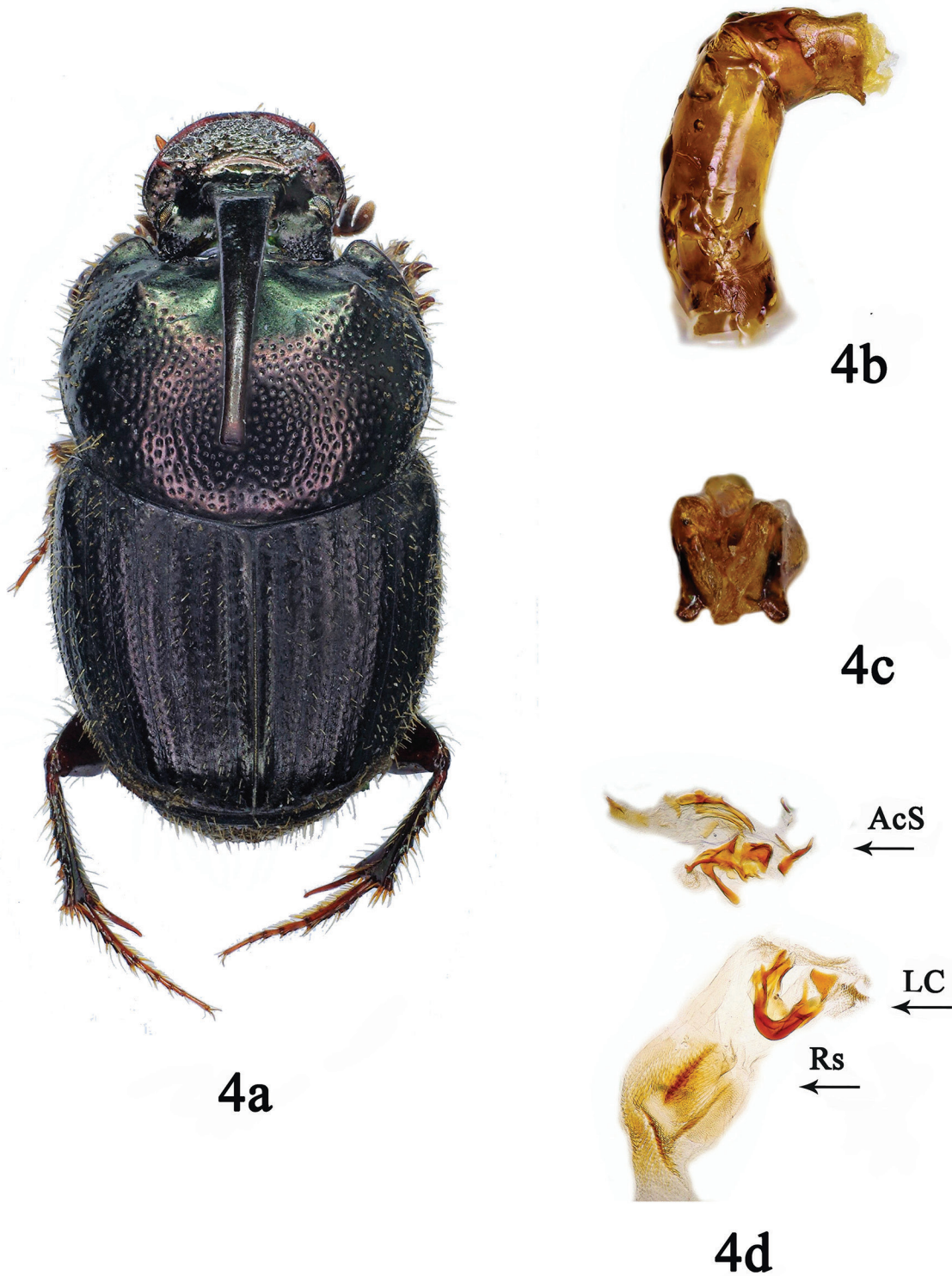


Figure 4. *Onthophagus (Indonthophagus) ensifer* Boucomont, 1914 [major ♂: India, Tamil Nadu st.]. **4a)** Dorsal habitus. **4b)** Parameres, lateral view. **4c)** Parameres, dorsal view. **4d)** Endophallus. AcS: accessory endophallites. LC: lamella copulatrix. Rs: *raspula*. Photos by A. Degiovanni, edited by G. Fiumi.

Diagnostic features. Length 5.0 to 7.5 mm. Colour brownish black, elytra moderately shiny, with distinct isodiametric microreticulation, head and pronotum shinier, with cupreous or greenish metallic lustre, almost lacquered, not microreticulate. Antennal scape, pedicel and funicle dark red, antennal club brown. Dorsal pubescence whitish yellow.

Head short, clearly wider than long, with clypeus broadly round, slightly or not at all sinuate anteriorly, sides not sinuate; clypeofrontal carina distinct, sometimes barely discernible, bent backward, clearly closer to the base of the horn than to clypeal anterior margin in major males, extended in a slightly sinuate lamina, placed between the eyes, in the middle of them, in females; occipital carina extended in a long horn arising in correspondence of the anterior margin of eyes, broad and flat at base, directed backward, tapering gradually to the extremity and following the curvature of pronotum, often extending past the middle of the body, sometimes bifurcate apically, in major males, reduced to a narrow straight lamina in minor males and females; clypeal surface with transversely rugose, setigerous punctures, frontal surface doubly sparsely punctate.

Pronotum convex, declivous anteriorly, with a distinct anteromedian depressed smooth and unpunctured area and an anterolateral small tubercle on either side, a little behind the front margin, in major males, without depression and with an anteromedian transverse row, usually bilobate, besides the anterolateral tubercle, sometimes hardly appreciable, on either side, in minor males and females; both sexes with a small, hardly distinguishable, in some specimens almost undiscernible, posterolateral groove on either side near pronotal posterior angles; anterior angles distinctly produced, sides not sinuate behind them in dorsal view; dorsal surface setigerously punctate, punctures broad, sub-regular in distribution, separated by 1/2 to 1 diameter on disc, absent in the median depression, bearing pale-yellow setae, shorter on disc, barely longer at sides.

Elytral striae barely shiny, distinctly impressed, with punctures slightly larger than strial width and barely crenulating interstrial sides; interstriae convex, particularly the external ones, all rather regularly granulate; granules smaller than strial punctures; posterior margin of each granule with a small, indistinct, setigerous puncture; setae short, pale-yellow, thin.

Pygidium with rather regularly distributed, setigerous punctures; setae pale-yellow, thin, clearly longer than those of elytra.

Males with protibial spur directed outward, and with a small denticle strongly curved downward at the inner angle of protibial apex.

Male genital armature. Parameres short, apices bent ventrally, slightly diverging apically, without basolateral plate denticle, round at apex (Fig. 4b–c); endophallus with the presence of accessory endophallites, a single *raspula* and a U-shaped lamella copulatrix, frayed at one end, enlarged and bifurcate at the other (Fig. 4d).

Distribution. South India (Boucomont 1914). Pakistan (Petrovitz 1961). North India (Sewak 1986). Nepal (Shrestha 2005).

Material examined. India: Tamil Nadu state, “Nilghiris / M. Maindron”, “Coonour / 15-30 Juill. 1901 / 1500-2000 m. alt.”, “Boucomont det. 1914 / *Onthophagus / ensifer* n. sp. ♂”, “*Typus*”, Muséum Paris / 1936 / Coll. A. Boucomont”, examined by photos (syntype ♂ of *O. ensifer*, MNHN); Tamil Nadu state, “Nilgiri Hills, 1922, H. L. Andrewes Bequest, compared with type. G. J. Arrow”, 2 ♂♂ and 1 ♀ (MCSN); Tamil Nadu state, “Shembaganur” [Senbahanoor], 3 ♂♂ and 4 ♀♀ (Balthasar collection, NMPC).

Historical review. Boucomont (1914) described *O. ensifer* on an unspecified number of specimens coming from three different localities, “Coonour”, “Shembaganur” and “Madras” whose present names are respectively Coonour, Senbahanoor and Chennai, all in the state of Tamil Nadu, South India. According the Article 73.2.3 of the Code (ICZN 1999), the type locality of the taxon encompasses all these places.

Boucomont (1914) also stated that the new species could be a junior synonym of *Onthophagus pardalis* (Fabricius, 1798), described, as *Copris*, from “India”. Unfortunately, always according to Boucomont (1914), Fabricius description was not sufficient for establishing the synonymy, and what’s more, the type of *O. pardalis* was lost.

Instead, Arrow (1931), citing Fabricius’ species, added an extensive description of both male and female and gave new records from central and southern India. He confirmed that *pardalis*’ type had disappeared, but its

original description appeared to him on the whole enough to apply to the concerned taxon. Therefore (Arrow 1931) considered it *bona species*, not conspecific with *O. ensifer*.

Balthasar (1963), placed *O. pardalis* in the subgenus *Colobonthophagus* despite expressing the same considerations exposed by Arrow (1931), concerning its relationship with *O. ensifer* and *O. mopsus*.

Shortly after, Zimsen (1964) added a little twist to the story, reporting the existence of a specimen of *O. pardalis* type series, preserved in Kiel Museum (Germany).

The existence of this specimen gave Scheuern (1996) the opportunity to provide another systematic interpretation of the issue. According to this author, the placement of *O. pardalis* by Balthasar (1963) was incorrect, as the species that Balthasar – and before him Arrow (1931) – called *O. pardalis* was not conspecific with Fabricius' species nor with *O. ensifer* or *O. mopsus*. Scheuern (1996), after having designated the lectotype of *O. pardalis*, claimed not to be able to insert the species in any known subgenera of *Onthophagus*.

Despite this, Thomas et al. (2011), Karimbunkara and Rayan (2013), Mittal and Jain (2015), Karel et al. (2020) and Gupta et al. (2022) considered *O. pardalis* a *Colobonthophagus*, probably referring to the *O. pardalis sensu* Arrow and *sensu* Balthasar, that Scheuern (1996) named *Onthophagus (Colobonthophagus) neocolobus* Scheuern, 1996. I could examine pictures of the lectotype of *Onthophagus pardalis* (Fabricius, 1798), and can confirm its exclusion to the group treated in this paper, as already stated by Scheuern (1996).

Remarks. I was able to study specimens coming from Tamil Nadu state (southern India) only. The records listed in literature from northern India, Pakistan and Nepal are reasonable but anyway should be confirmed.

The morphology of the aedeagus, particularly of paramera (Fig. 4b–c), short and not elongate as in the other species treated here, casts some doubts on the placement of *O. ensifer* in the subgenus *Indonthophagus*. Nevertheless, for now I prefer to keep the species in this group, based on the shape of the lamella copulatrix that follows the pattern of the other species assigned to the subgenus.

***Onthophagus (Indonthophagus) hastifer* van Lansberge, 1885**

(Fig. 5, 12a,c)

Onthophagus hastifer van Lansberge 1885: 380; Ritsema 1888: 214; Boucomont 1914: 221; Boucomont and Gillet 1921: 55; Boucomont and Gillet 1927: 138; Boucomont 1929: 773; Arrow 1931: 330; Balthasar 1935: 341; Balthasar 1942: 120; Paulian 1945: 118; Balthasar 1963: 378; Masumoto 1976b: 28; Kabakov and Napolov 1999: 84; Chen 2002: 223; Hua 2002: 154; Shrestha 2005: 108; Krajcik 2006: 108; Masumoto et al. 2006: 142; Aston and Vor 2008: 63; Krajcik 2012: 179; Krajcik 2013: 112; Mittal and Jain 2015: 398; Cheung et al. 2018: 236; Lau 2019: 95; ; Cheung et al. 2020: 27.

Onthophagus (incertae sedis) hastifer, Kabakov and Yanushev 1983: 162; Hanboonsong et al. 1999: 467.

Onthophagus (Onthophagus) hastifer, Löbl et al. 2006: 165.

Onthophagus (Indonthophagus) hastifer, Kabakov 2006: 154 (footnote); Ziani and Bezděk 2016: 188; Schoolmeesters 2023.

Onthophagus turmalis Gillet 1924: 66 [type locality: “Tainan, Formosa” (Taiwan)]; Boucomont and Gillet 1927: 149; Miwa 1930: 169 (as *O. turmaris*, misspelling); Arrow 1931: 330 (as junior synonym of *O. hastifer*); Matsumura 1938: 55 (as *O. turmaris*); Paulian 1945: 118 (as junior synonym of *O. hastifer*); Hwang 1952: 139; Balthasar 1963: 368 (as junior synonym of *O. hastifer*); Masumoto 1976b: 28 (as *O. turmaris*, junior synonym of *O. hastifer*); Chen 2002: 223 (as junior synonym of *O. hastifer*); Hua 2002: 156; Krajcik 2006: 108/138 (both as doubtful synonym of *O. hastifer* (p. 108) and valid species (p. 138), as *O. turmalis* Gillet, 1930); Löbl et al. 2006: 165 (as junior synonym of *O. hastifer*); Masumoto et al. 2006: 142 (as junior synonym of *O. hastifer*); Krajcik 2012: 187 (as *Onthophagus turmalis* Gillet, 1930, valid species); Krajcik 2013: 281 (as *Onthophagus turmalis* Gillet, 1930, valid species); Ziani and Bezděk 2016: 188 (as junior synonym of *O. hastifer*); Lau 2019: 95 (as junior synonym of *O. hastifer*); Schoolmeesters 2023 (as junior synonym of *O. hastifer*).

Onthophagus agilis Matsumura 1938: 56 [type locality: “Chokakurai, Formosa” (Taiwan)]; Hwang 1952: 138; Balthasar 1963: 266 (doubtful species); Masumoto 1976a: 2; Masumoto 1976b: 27; Chen 2002: 270; Hua 2002: 154; Krajcik 2006: 87 (doubtful as valid species); Löbl et al. 2006: 165 (as junior synonym of *O. hastifer*); Masumoto et al. 2006: 142 (as junior synonym of *O. hastifer*); Ziani and Bezděk 2016: 188 (as junior synonym of *O. hastifer*); Lau 2019: 95 (as junior synonym of *O. hastifer*).

Onthophagus putealis Matsumura 1938: 61 [type locality: “Chokakurai, Formosa” (Taiwan)]; Hwang 1952: 139; Balthasar 1963: 579 (as junior synonym of *O. viduus* von Harold, 1874); Nomura 1973: 48; Masumoto 1976a: 3 (as junior synonym of *O. hastifer*); Masumoto 1976b: 28 (as junior synonym of *O. hastifer*); Hua 2002: 155; Krajcik 2006: 141 (as junior synonym of *O. viduus*); Löbl et al. 2006: 164, 165 (both as junior synonym of *O. viduus* and, as *O. puetalis*, misspelling, junior synonym of *O. hastifer*); Masumoto et al. 2006: 142 (as junior synonym of *O. hastifer*); Ziani and Bezděk

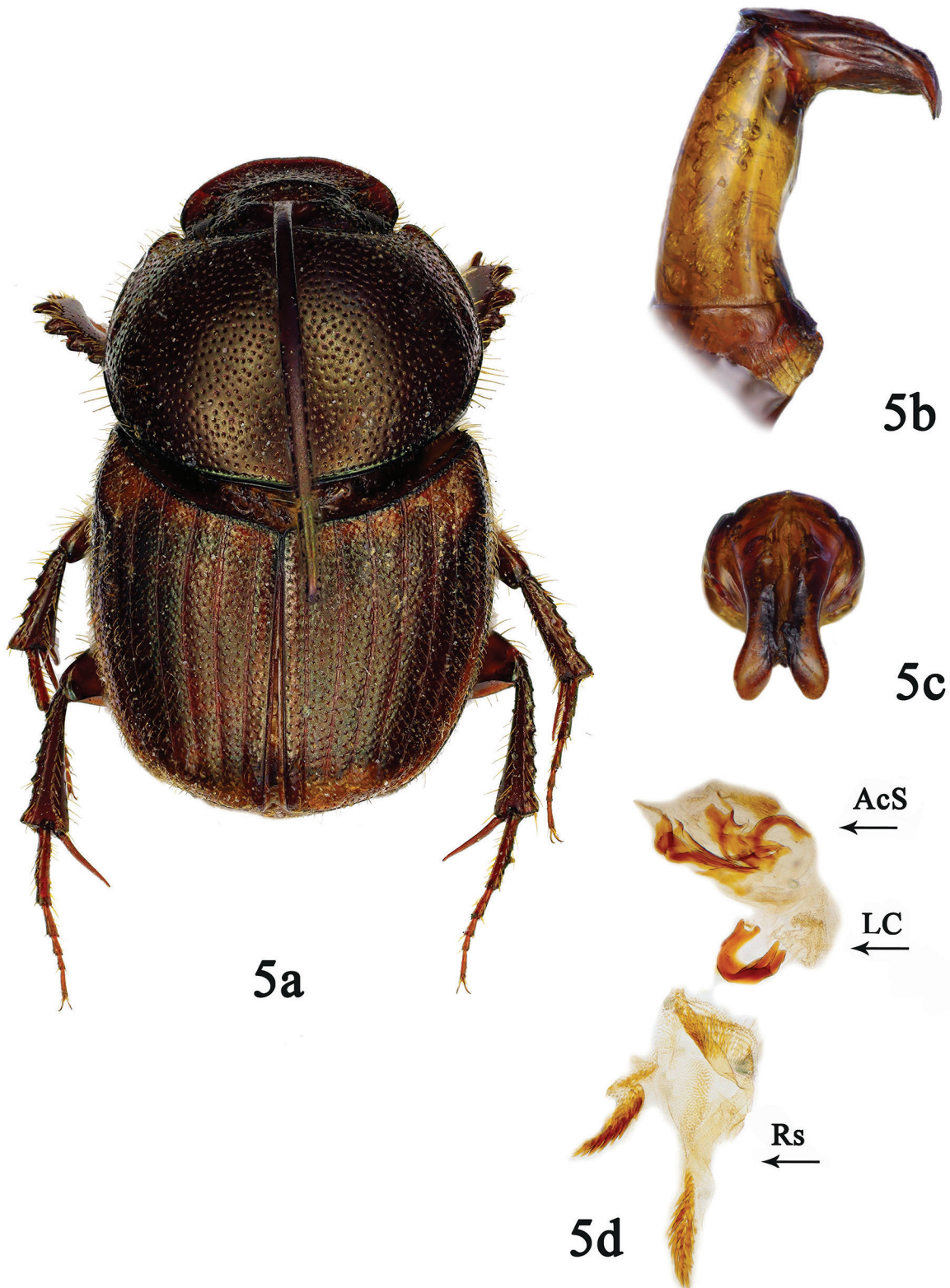


Figure 5. *Onthophagus (Indonthophagus) hastifer* von Lansberge, 1914 [holotype, major ♂: Myanmar, Minhla]. **5a**) Dorsal habitus. **5b**) Parameres, lateral view. **5c**) Parameres, dorsal view. **5d**) Endophallus. AcS: accessory endophallites. LC: lamella copulatrix. Rs: *raspulae*. Photos by A. Degiovanni, edited by G. Fiumi.

2016: 187, 188 (both as junior synonym of *O. viduus* and, as *O. puetalis*, misspelling, junior synonym of *O. hastifer*); Lau 2019: 95 (as *puetalis*, misspelling, junior synonym of *O. hastifer*).

Type locality. “Minhla, Birmania” [Minhla, Bago Region, Myanmar].

Type material.

Onthophagus hastifer van Lansberge, 1885: holotype, a major ♂, fixed by monotypy, studied (MCSN).

Onthophagus turmalis Gillet, 1924: 2 syntypes ♀♀, studied (NHMUK).

Onthophagus agilis Matsumura, 1938: holotype ♂, fixed by monotypy, examined by photos (EIHU).

Onthophagus putealis Matsumura, 1938: holotype ♀, fixed by monotypy, examined by photos (EIHU).

Diagnostic features. Length 6.0 to 8.0 mm. Colour reddish brown or bronzed, with slight metallic lustre, moderately shiny, with distinct isodiametric microreticulation. Elytra sometimes with dark red irregular basal and apical spots. Antennal scape, pedicel and funicle red, antennal club yellow. Dorsal pubescence whitish yellow.

Head short, slightly wider than long, with clypeus broadly round, slightly or not at all sinuate anteriorly, sides not sinuate; clypeofrontal carina distinct, bent backward, placed nearly halfway between base of the horn and anterior clypeal margin in major males; occipital carina with an extremely long and slender thread-like horn, slightly enlarged at base (Fig. 12a), arising between the eyes and curving backward, sometimes extending beyond the hind margin of pronotum, in major males, reduced to a short transverse tubercle between the eyes in minor males, and into a straight or slightly sinuate transverse carina (Fig. 12c), subequal in length to the clypeofrontal carina, in females; clypeal surface with transversely rugose, setigerous punctures, frontal surface doubly sparsely punctate.

Pronotum convex, declivous anteriorly, with a shallow anteromedian narrow groove in major males, with an anteromedian transverse gibbosity, sometimes hardly appreciable, in females; both sexes with a slightly depressed posterolateral area, duller than pronotal disc, on either side near pronotal posterior angles, anteriorly with a tuft of longer setae; anterior angles distinctly produced, sides not sinuate behind them in dorsal view; dorsal surface setigerously punctate, punctures slightly impressed, sub-regular in distribution, separated by 1 to 2 diameters on disc, subequal in size to the punctures of elytral striae, bearing pale-yellow setae, shorter on disc, barely longer at sides.

Elytral striae shiny, distinctly impressed, with punctures slightly larger than stria width and barely crenulating interstriae; interstriae flat to barely convex, all rather regularly densely granulate; granules smaller than stria punctures; posterior margin of each granule with a small, indistinct, setigerous puncture; setae pale-yellow, thin.

Pygidium with rather regularly distributed, setigerous punctures; setae hook-like at the extremity, pale-yellow, thin, clearly longer than those of elytra.

Males with protibial spurs directed outward. Distal margin of male protibiae at right angles to the inner margin, with a tuft of short pale-yellow bristles, and with a small denticle strongly curved downward at the inner angle of protibial apex.

Male genital armature. Parameres short, apices bent ventrally, diverging apically, without basolateral plate denticle, round at apex (Fig. 5b–c); endophallus with the presence of accessory endophallites, two evident raspulae of different sizes and a U-shaped lamella copulatrix, bifurcate at one end, clearly divided in two arms at the other (Fig. 5d).

Distribution. Myanmar (van Lansberge 1885). South-Eastern China, “Indochina” (Boucomont 1929). Taiwan (Arrow 1931). Central China (Balthasar 1963). Thailand (Hanboonsong et al. 1999; Kabakov and Napolov 1999). Vietnam (Kabakov and Napolov 1999). All the western records (Nepal (Shrestha 2005); India (Mittal and Jain 2015); Sri Lanka (Schoolmeesters 2023)) have to be considered incorrect until proven otherwise.

Material examined. Myanmar: “Minhla / Birmania / D[onavit]. Comotto 18__”, “Typus”, “hastifer / Lansb. / ♂”, “Onthophagus / Hastifer / Lansberge [Lansberge’s handwriting]”, “MUSEO CIVICO / GENOVA”, “HOLOTYPE / Onthophagus / hastifer / Lansberge”, (holotype ♂ of *O. hastifer*, MCSN); “Rangoon [Yangon]”, L. Fea leg., A. Boucomont det., 2 ♀♀, examined by photos (MCSN); “Bhamò [Bhamo], vi.1886, L. Fea leg., A. Boucomont det., 1 minor ♂ (MCSN); “Da Yonang-Young / a Mandalay, v.1886, L. Fea leg., A. Boucomont det.” 1 ♂ (MCSN).

Thailand: Pak Chong, i-iii 1989, S. Steinke leg. 1 ♂ and 1 ♀, J. Schönfeld det. (MCSN); Chonburi prov., Pattaya, 5 km E Elefantcamp, 30.i.1995, A. Weigel leg. 1 ♂ (JSCS). **Laos:** Champassak prov., 25 km SE Pakxe, 200 m, bank of Banglieng river, 14°58’N 105°55’E, 30.iii.1998, O. Merkl and G. Csorba leg. 2 ♂♂ (JSCS); Viang Chan prov.,

Ban Pa Kho resort, 50 km NE Vientiane, 90 m, 9-14.vi.2007, M. Štrba leg. 2 ♂♂ (JSCS). **Vietnam:** “Huế”, southern Vietnam, 2 ♂♂ (JSCS). **China:** Hong Kong, 2 ♂♂ (NHMUK); Fujian prov., Guangze, 24.ix.1937, J. Klapperich leg. 1 ♂ (JSCS). **Taiwan:** “Tainan / Formosa / H. Sauter, VII. 11 [date handwritten].” (2 syntypes ♀♀ of *O. turmalis*, NHMUK); “Chokakurai / Da Ibu, Formosa, 28-vi-1936, Coll. Y. Yano”, examined by photos (holotype ♂ of *O. agilis*, EIHU); “Chokakurai / Da Ibu, Formosa, 28-vi-1936, Coll. Y. Yano”, examined by photos (holotype ♀ of *O. putealis*, EIHU); Pingtung Co., Hengchun / Shuiwaku, 14.ix.2021, B.-H. Ho leg. 1 minor ♂ and 1 ♀ (SZCM); Pingtung, N of Shuiwaku, 80 m, 21°56'29"N 120°50'23"E, 20.vi.2023, D. Král and J. Růžička leg. 1 major ♂ and 4 ♀♀ (SZCM).

Historical review. *Onthophagus hastifer* was described by van Lansberge (1885) most probably on a major male only, from Minhla, Myanmar. According to R. Poggi (MCSN, personal communication), there is a sole specimen, a major male, in the collection of the Genoa Museum, with a label written by van Lansberge. This specimen is to be considered the holotype. The female was subsequently described by Boucomont (1914) on a specimen also from Myanmar and deposited in MCSN. Boucomont and Gillet (1921) ran into a misprint, and with a misplaced asterisk, excluded *O. hastifer* from the fauna of French Indochina, in favour of *O. turbatus*, described from Sri Lanka and most probably not distributed east of Bhutan (see below). Such mistake was later partially amended (Boucomont and Gillet 1927) with the citation of *O. turbatus* Boucomont, 1921, not Walker, junior synonym of *O. hastifer*.

Onthophagus turmalis Gillet, 1924 was described from Taiwan on at least a male and a female, and was synonymized with *O. hastifer* by Arrow (1931) after 7 years from its description. A misspelling involved this taxon, wrongly cited as “*O. turmaris*” by Miwa (1930), Matsumura (1938) and Masumoto (1976b). Krajcik (2006) listed twice *Onthophagus turmalis* both as valid species (as *Onthophagus turmalis* Gillet, 1930, wrong year) and, doubtfully, a junior synonym of *O. hastifer*. Later, the same author (Krajcik 2012, 2013) confirmed the validity of the species (always dated 1930).

Matsumura (1938) described 13 new species of Onthophagini from “Formosa” [Taiwan]. Of which only five are presently considered *bonae species*. Among those that were synonymized, there are two species treated in this paper: *Onthophagus agilis* and *Onthophagus putealis*, described from the same locality (Chokakurai), collected on the same day (28.vi.1936) and by the same entomologist (Y. Yano). *O. agilis*, described on a single male, was treated as a doubtful species by Balthasar (1963) and Masumoto (1976a; 1976b). This last author (Masumoto 1976b) affirmed “I still don’t know what it is” (verbatim, from the Japanese). But it was from Masumoto et al. (2006) that *O. agilis* was treated as a junior synonym of *O. hastifer*.

Onthophagus putealis, instead, has a little different nomenclatural history. Balthasar (1963), quoting Nakane (1956), considered *O. putealis* Matsumura, 1938, described on a sole female, as a junior synonym of *Onthophagus viduus* von Harold, 1874. Actually, Nakane (1956) excluded *O. putealis* from the twenty species consider as junior synonym of *O. viduus*. The synonymy by Balthasar (1963) is to be considered incorrect. So, as stated for the first time by Masumoto (1976a), the correct synonymy is *Onthophagus putealis* Matsumura, 1938 = *Onthophagus hastifer* van Lansberge, 1885. It should be noted that *O. putealis* has been listed twice in Löbl et al. (2006) and in Ziani and Bezděk (2016), both as a junior synonym of *O. viduus* and, as *O. puetalis*, misprint, as junior synonym of *O. hastifer*. As mentioned above, the first reference is wrong and should be deleted.

There is another species described by Matsumura (1938), *Onthophagus komabellus*, supposed to be a junior synonym of *O. hastifer* by Balthasar (1942). Later though, Nakane (1956) proposed *O. komabellus* as junior synonym of *O. viduus*, and all the subsequent authors, from Balthasar (1963), followed this synonymy.

Remarks. Present literature (Ziani and Bezděk 2016 and Schoolmeesters 2023) considers *O. turmalis*, *O. agilis* and *O. putealis* as junior synonyms of *O. hastifer*. After studying directly two syntypes of the first species and examining high resolution images of holotypes of the other two species, I can confirm such synonymies.

Onthophagus (Indonthophagus) mopsus (Fabricius, 1792)

(Fig. 1, 6–7)

Scarabaeus mopsus Fabricius 1792: 58.

Copris mopsus, Fabricius 1801: 49; Schönherr 1806: 50.

Onthophagus mopsus, Dejean 1833: 142 (with a question mark); von Harold 1869: 1033; von Harold 1872: 206; Boucomont and Gillet 1927: 141; Arrow 1931: 328; Balthasar 1956: 435; Petrovitz 1961: 102; Balthasar 1963: 441; Petrovitz

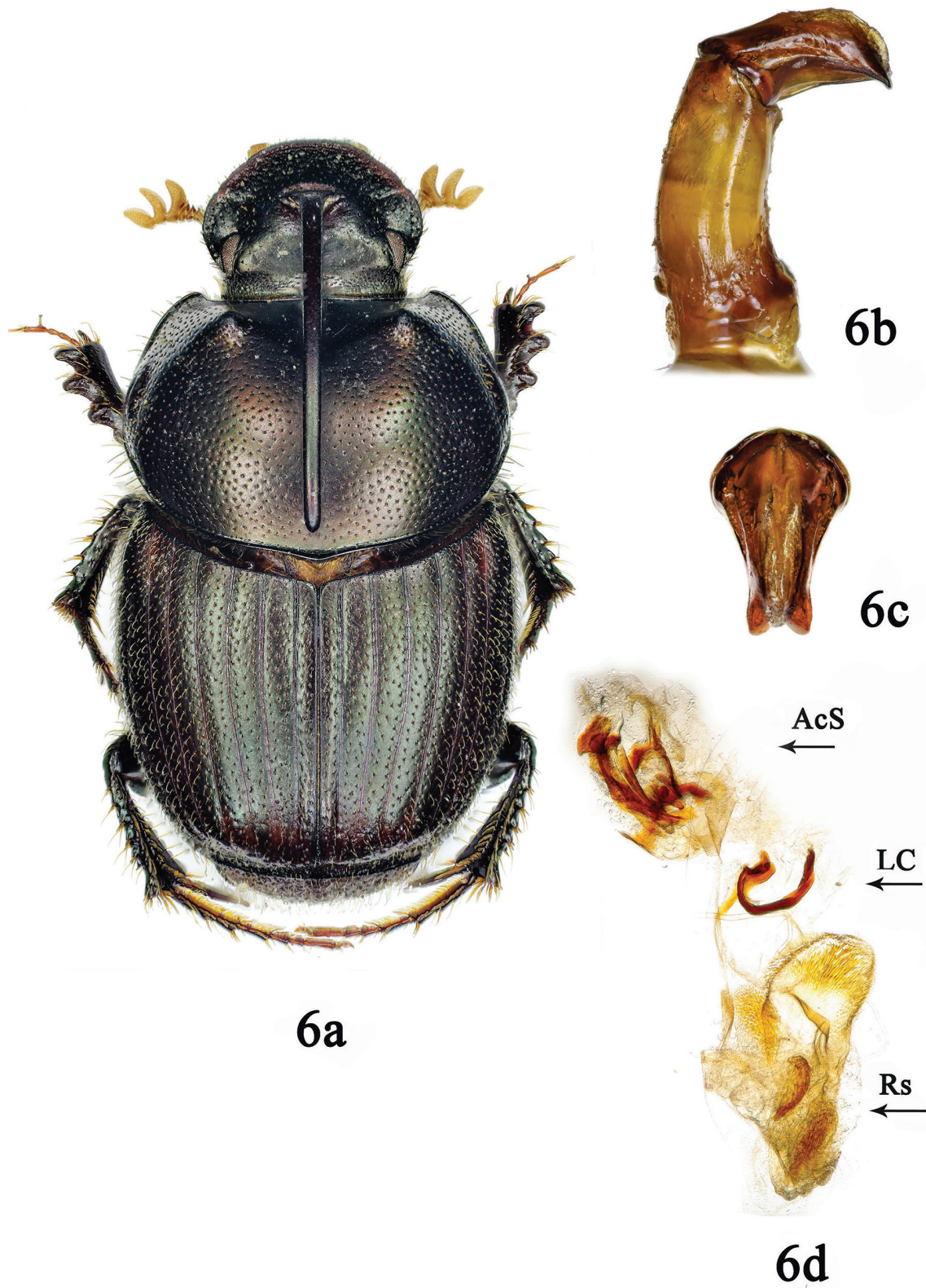


Figure 6. *Onthophagus (Indonthophagus) mopsus* (Fabricius, 1792) [major ♂: Pakistan, Islamabad Capital Territory]. **6a)** Dorsal habitus; **6b)** Parameres, lateral view. **6c)** Parameres, dorsal view. **6d)** Endophallus. AcS: accessory endophallites. LC: lamella copulatrix. Rs: *raspulae*. Photos by A. Degiovanni, edited by G. Fiumi.

1967: 479; Balthasar 1968: 153; Endrödi 1974: 3; Mittal 1981: 80; Gupta and Mittal 1987: 52; Gupta 1989: 25; Hashmi and Tashfeen 1992: 148; Mittal 1999: 34; Biswas and Ghosh 2000: 590; Mittal 2000: 264; Chandra 2005: 149; Mittal 2005: 46; Krajcik 2006: 119; Rajan 2006: 128; Chandra and Gupta 2012: 100; Krajcik 2012: 182; Karimbumkara and Rajan 2013: 176; Krajcik 2013: 174; Kaur and Yadav 2014: 4; Mittal and Jain 2015: 399; Singh et al. 2017: 18; Kaur and Yadav 2018: 405; Singh 2020: 522.

Onthophagus (incertae sedis) mopsus, Löbl et al. 2006: 175; Siddiqui and Kamaluddin 2011: 349.

Onthophagus (Furconthophagus) mopsus, Siddiqui et al. 2014: 304.

Onthophagus (Indonthophagus) mopsus, Kabakov 2006: 154 (footnote); Ziani and Bezděk 2016: 188; Gupta et al. 2018: 484; Ghosh et al. 2020: 243; Kharel et al. 2020: 368; Ghosh et al. 2022a: 11; Ghosh et al. 2022b: 42; Gupta et al. 2022: 425; Schoolmeesters 2023.

Copris gracilicornis Germar 1813: 114 [type locality: "America", *patria errata*]; Arrow 1931: 328 (as junior synonym of *O. mopsus*).

Onthophagus gracilicornis, Dejean 1821: 53 (as "*gracilicornis* Meg."); Sturm 1826: 178 (as "*gracilicornis* Meg."); Dejean 1833: 141 (as "*O. gracilicornis* Dej."); Dejean 1836: 157 (as "*O. gracilicornis* Dej."); Sturm 1843: 107 (as "*gracilicornis* Megerl."); von Harold 1869: 1030; van Lansberge 1885: 381; Boucomont 1914: 220; Boucomont and Gillet 1927: 138; Arrow 1931: 328 (as *O. gracilicornis* Boucomont, 1914, junior synonym of *O. mopsus*); Balthasar 1963: 441 (as junior synonym of *O. mopsus*); Krajcik 2006: 119 (as junior synonym of *O. mopsus*); Löbl et al. 2006: 175 (as junior synonym of *O. mopsus*); Rajan 2006: 128 (as *O. gracilicornis* Boucomont, 1914, junior synonym of *O. mopsus*); Ziani and Bezděk 2016: 188 (as junior synonym of *O. mopsus*).

Onthophagus mopsus ssp. *gracilicornis*, Kaur and Yadav 2014: 4; Kaur and Yadav 2018: 405.

Type locality. "...in India orientali" [East Indies].

Type material.

Scarabaeus mopsus Fabricius, 1792: lectotype, a minor ♂, designated by Arrow (1931), examined by photos (OUMNH); 4 paralectotypes, 2 ♂♂ and 2 ♀♀, all examined by photos (ZMUK).

Copris gracilicornis Germar, 1813: a syntype ♂, examined by photos (ZMB).

Diagnostic features. Length 6.0 to 8.0 mm. Colour blackish brown or bronzed, sometimes with slight metallic lustre, moderately shiny, with distinct isodiametric microreticulation. Elytra sometimes with dark red irregular humeral and apical spots. Antennae reddish yellow more or less pale. Dorsal pubescence whitish yellow.

Head short, slightly wider than long, with clypeus broadly round, slightly or not at all sinuate anteriorly, sides not sinuate; clypeofrontal carina distinct, bent backward; occipital carina of major males extended in an extremely long and slender thread-like horn, its base a little enlarged and very close, nearly adjacent to the clypeofrontal carina, horn arising in front of the eyes and curving backward, sometimes extending beyond the hind margin of pronotum, reduced to a very short, erected conical tubercle, placed between the eyes, in minor males, to a straight carina between the eyes, sometimes slightly downwards at the ends, shorter than or subequal to clypeofrontal carina, in females (Fig. 1a); clypeal surface transversely rugose, setigerous punctate, frontal surface doubly sparsely punctate.

Pronotum convex, declivous anteriorly, with a distinct anteromedian smooth and unpunctured area delimited by a strong tubercle on either side, a little behind the front margin in major males, with a smooth vertical anterior margin, delimited by a short straight carina in the middle of its upper edge, sometimes divided in two, in minor males and females; both sexes with a small – in some specimens, particularly females, almost undiscernible – posterolateral depressed area on either side near pronotal posterior angles, sometimes distinguishable only because it is slightly duller than the surrounding surface; anterior angles distinctly produced, sides not sinuate behind them in dorsal view; dorsal surface setigerously punctate, punctures sub-regular in distribution, separated by 2 to 3 diameter on disc, bearing pale-yellow setae.

Elytral striae moderately shiny, distinctly impressed, with punctures slightly larger than strial width and barely crenulating interstrial sides; interstriae flat to barely convex, all rather regularly granulate; granules smaller than strial punctures; posterior margin of each granule with a small, indistinct, setigerous puncture; setae short, pale-yellow, thin.

Pygidium with rather regularly distributed, setigerous punctures; setae pale-yellow, thin, a little longer than those of elytra.

Males with protibial spur outward, and with a small denticle strongly curved downward at the inner angle of protibial apex.

Male genital armature. Parameres short, apices bent ventrally, little diverging apically, without basolateral plate denticle, latero-apical angle round or almost so (Fig. 6b–c); endophallus with the presence of accessory endophallites, two evident raspulae and a U-shaped very thin lamella copulatrix, sharp at one end, broad and slightly fringed or bifurcate at the other (Fig. 6d).

Distribution. West Bengal [India] (von Harold 1869). Nepal (Boucomont 1914, as *O. gracilicornis*). Pakistan, North India, Kashmir (Arrow 1931). Afghanistan (Balthasar 1956). South India (Rajan 2006).

Material examined. Pakistan. Islamabad Capital Territory, Islamabad, 6.vi.1991, S. Prepsl leg. 1 ex. (SZCM); Islamabad Capital Territory, Marghalla hills, 1000 m, 15.vii.2010, G. Sabatinelli leg. 3 exx. (SZCM); Islamabad Capital Territory, Islamabad, 15.ix.2010, G. Sabatinelli leg. 5 exx. (SZCM); Islamabad Capital Territory, Marghalla hills, 23.iv.2011, S. Ziani leg. 10 exx. (SZCM); Islamabad Capital Territory, Islamabad, sect. E7, 600 m, 20.vi.2011, G. Sabatinelli leg. 1 ex. (SZCM); Islamabad Capital Territory, Marghalla hills, 1060 m, 22.vi.2011, G. Sabatinelli leg. 1 ex. (SZCM); Islamabad Capital Territory, Marghalla hills, 1060 m, 16.vii.2012, G. Sabatinelli leg. 3 exx. (SZCM); Balochistan, Avaran (Khuzdar), 4.iv.1993, Bečvář leg. 3 exx. (SZCM); Balochistan, Bela, 21.iv.1993, Bečvář leg. 1 ex. (SZCM); Punjab, Kallar Kahar, 14.iii.2007, Z. Ahmed leg. 1 ex. (SZCM); Punjab, Bhan Kotly Sathia, 25.iv.2011, S. Ziani leg. 6 exx. (SZCM); Punjab, Melod, 27.iv.2011, S. Ziani leg. 5 exx. (SZCM); Punjab, Chakri, 26.vi.2011, Z. Ahmed leg. 2 exx. (SZCM); Punjab, Ransial (Kallar Kahar), 800 m, 11.iv.2012, S. Ziani leg. 2 exx. (SZCM); Gilgit - Baltistan, Goner Farm/25 km E Chilas, 1100 m, 2.vi.2007, G. Carpaneto leg. 2 exx. (SZCM); Khyber Pakhtunkhwa, Mansehra, vi.2009, G. Sabatinelli leg. 3 exx. (SZCM); Khyber Pakhtunkhwa, Mansehra – Jaba Dara, 28.iv.2011, S. Ziani leg. 5 exx. (SZCM); Khyber Pakhtunkhwa, Mansehra, 10.vii.2011, G. Sabatinelli leg. 1 ex. (SZCM); Khyber Pakhtunkhwa, Mansehra, viii.2011, G. Sabatinelli leg. 3 exx. (SZCM); Khyber Pakhtunkhwa, 21 km N Mingora, 1024 m, 7.iv.2012, S. Ziani leg. 3 exx. (SZCM); Azad Kashmir, Sawa Hill, 3566 m, 26.iv.2011, G. Sabatinelli leg. 1 ex. (SZCM); Azad Kashmir, Rawala Kot – Banjosa lake 1980 m, 26.iv.2011, G. Sabatinelli leg. 2 exx. (SZCM). **India:** “*Mopsus* / [illegible]”, “in India or. / Monson *mopsus* Fabr.”, “*Onthophagus / mopsus* / type”, “Type / *Onthophagus / mopsus*, F. / G. J. Arrow det. / Faun. Brit. Ind. / Lamellicornia. / iii, Coprinae. / Dec. 1931”, “Type Col: 458 / *Onthophagus / mopsus* Fabr. / Hope Dept. Oxford”, examined by photos (lectotype of *O. mopsus*, OUMNH); “*Mopsus*”, “Type i Oxford”, examined by photos (4 paralectotypes, 2 ♂♂ and 2 ♀♀, of *O. mopsus*, ZMUC); Himachal Pradesh state, W Himalaya - Pirpandzhal range near Kullu, 1500 m, 21.vii.2003, A. Gorodinski leg. 3 exx. (SZCM). **Nepal:** Bagmati Prov., Chitwan National Park – Sauraha 213 m, 4.vi.1983, M.J.D. Brendell leg. 19 exx. (NHMUK); Bagmati Prov., Chitwan National Park – Sauraha, 11.iv.2009, L. Nádai leg. 1 ex. (SZCM); Karnali prov., Humla distr., between Simikot – 29°56'33"N 81°51'27"E – and 29°54'23"N 81°55'7"E, 2975 m–2990 m, 16.vi.2022, D. Telnov leg. 4 exx. (NHMUK). **Without locality:** “*Germari* / typ.”, “*gracilicornis* / Gr.”, “Holotype ♂”, “Ex-Musaeo / E. Harold”, examined by photos (syntype ♂ of *O. gracilicornis*, ZMB).

Historical review. Fabricius (1792) described *Onthophagus mopsus*, as *Scarabaeus mopsus*, from “East Indies”, that presently encompasses, in its broadest context, India, the mainland Southeast Asia, the Malay Archipelago including the Philippines, and the Republic of Indonesia (Encyclopaedia Britannica 2018). It is not possible to know exactly where the specimen or the specimens described by Fabricius came from, but according to the present distribution of the species, it is reasonable to think that the type locality was in the Western portion of this area.

“*Onthophagus brunneus* Meg[erle]” was given as a possible synonym of *O. mopsus* by Dejean (1821, 1833, 1836). Later von Harold (1869) pointed out that *Onthophagus brunneus* Megerle von Mühlfeld was a “*nomen nudum*” and, as such, not available in the light of the current nomenclatural rules (Article 12 of the Code, ICZN 1999).

In the taxonomic history of taxa involved with *O. mopsus*, there are another two possible cases of “*nomina nuda*”. The first one concerns *Onthophagus rupicapra* Illiger, cited by Dejean (1833, 1836) as “var.” of *O. mopsus*. As far as I know, Illiger never described a taxon named as such. Therefore, the same nomenclatural rule applies for *Onthophagus rupicapra* Illiger and consequently the name is not available. Beware, though, because the epithet *rupicapra* is currently in use for a valid Australian species, *Onthophagus rupicapra* Waterhouse, 1894 (Schoolmeesters 2023).

A second case is represented by “*Onthophagus longicornis* Westermann”, deemed as a synonym of *O. mopsus* by Dejean (1833, 1836). Bernt Wilhelm Westermann (1781–1868) was a Danish merchant, amateur entomologist and tropical insect collector (Dohrn 1868). He published only one paper on entomology (Westermann 1821),

where *Onthophagus* is not cited. Therefore, in agreement with von Harold (1869), it can be concluded that *O. longicornis* Westermann is a “*nomen nudum*”, never published. The name was probably assigned by Westermann himself to one or more specimens present in his collection.

Germar (1813) mentioned *Copris gracilicornis*, attributing its authorship to Megerle von Mühlfeld, who, indeed, described the species and made the name available in his paper dated 1803 (Megerle von Mühlfeld 1803). Nevertheless, this last work, together with ten more authored by Megerle von Mühlfeld between 1801 and 1805, the so-called “J.C. Megerle’s (1801–1805) auction catalogues of insects” (ICZN 1993), have been suppressed for nomenclatural purposes by the International Commission on Zoological Nomenclature (ICZN 1993). Almost all the names featured in those publications were ruled not to be available, including *Copris gracilicornis*. Because of it, the name *Copris gracilicornis* became available from Germar (1813), who redescribed it on one male and one female at least. Furthermore, it must also be said that “America”, the specimen(s) locality indicated by Germar (1813), is clearly incorrect, as evidenced by the collecting place (“Beng.” [Bengal]) presented in Megerle von Mühlfeld (1803) paper.

Arrow (1931) distinguished two “*gracilicornis*”: the first, as *Copris gracilicornis*, attributed to Germar (1813), the second, as *Onthophagus gracilicornis*, attributed to Boucomont (1914). Both taxa are deemed junior synonyms of *O. mopsus*. Why this distinction, since Boucomont never described an *Onthophagus gracilicornis*? Was it a simple mistake? It would be unusual for Arrow. Maybe he referred to the claim of Boucomont (1914) that *Onthophagus ensifer*, just described in that paper, was present as *O. gracilicornis* in most entomological collections at that time. But this explanation is not convincing since Arrow (1931) did list also *O. ensifer* Boucomont, 1914 as valid species. I was unable to find a nomenclatorial or systematic meaning for this distinction and for the citation of *Onthophagus gracilicornis* Boucomont, 1914, done by Arrow (1931). Unfortunately, the same distinction, maybe a copy and paste operation, is present also in Rajan (2006). Therefore, I am forced to leave the problem unsolved.

The name *gracilicornis* has a nomenclatorial convoluted history. Howden and Cartwright (1963) mentioned *O. gracilicornis* Sturm, 1843 as junior homonym of *O. gracilicornis* Germar. But in this case such authorship is clearly a mistake: Howden and Cartwright (1963) missed the fact that Sturm (1843) never described the species and indeed, he correctly attributed the name to Megerle von Mühlfeld.

Kaur and Yadav (2014, 2018) considered *gracilicornis* Germar as a subspecies of *O. mopsus*. No other authors have subsequently shared this taxonomic concept.

The name *Onthophagus gracilicornis* Germar, 1813 gave rise to two homonyms, at least: *Onthophagus gracilicornis* Fåhraeus, 1857 and *Onthophagus gracilicornis* Raffray, 1877, both Afrotropical. However, the nomenclatorial problems connected to these taxa are beyond the scopes of this paper.

Remarks. It is not known how many specimens Fabricius (1792) examined for describing *Scarabaeus mopsus*. According to Zimsen (1964), the type series currently available is composed by six specimens, one housed in OUMNH, five in ZMUK. Among these six specimens, Arrow (1931) selected the specimen in OUMNH, naming it “Type” both in the book “The Fauna of the British India...” (Arrow 1931) and in the label that he added to the specimen in OUMNH (Fig. 7). According to the Article 74.5 of the Code (ICZN 1999), this has to be considered a valid designation of a lectotype. This designation, not taken into account in subsequent literature, turned out to be very important to stabilise the nomenclature, especially because the five specimens in ZMUK are not conspecific. After Arrow’s nomenclatorial act, such specimens became automatically paralectotypes, all but one, to which I added the label “not conspecific with the lectotype and the paralectotypes of *Scarabaeus mopsus* Fabricius, 1792”.

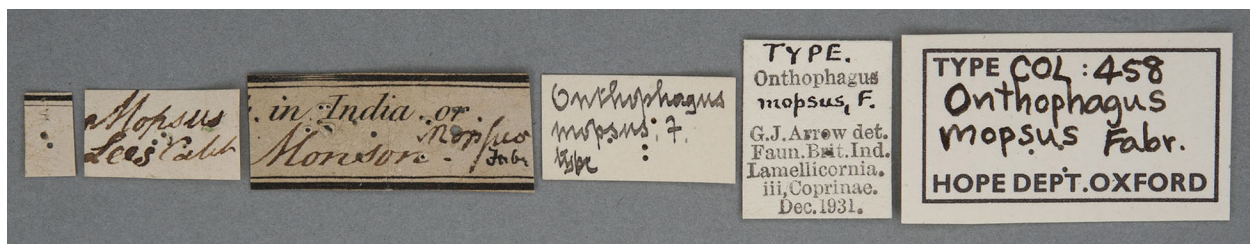


Figure 7. *Onthophagus (Indonthophagus) mopsus* (Fabricius, 1792), lectotype labels. Photo by Katerine Child (OUMNH).

***Onthophagus (Indonthophagus) nitidulus* Klug, 1845**

(Fig. 8)

Onthophagus nitidulus Klug 1845: [4], pl. xli; Marseul 1866: 52; von Harold 1869: 1033; Gestro 1889: 16; Reitter 1892: 184; d'Orbigny 1898: 203; d'Orbigny 1900: 297; d'Orbigny 1904: 303; d'Orbigny 1913: 381; Boucomont 1927: 188; Boucomont and Gillet 1927: 184; Winkler 1929: 1034; Arrow 1931: 348; Schatzmayr 1946: 47; Scott in Paulian 1948: 151; El-Zoheiry and Mohamed 1949: 58; Balthasar 1956: 435; Frey 1956: 654; Balthasar 1963: 452; Baraud 1968: 920; Ferreira 1972: 697; Alfieri 1976: 205; Paulian 1980: 153; Zunino 1981: 412; Baraud 1985: 287; Carpaneto and Piattella 1990: 271; Gillett 1995: 20; Gillett and Gillett 2005: 355; Van Harten 2005: 21; Krajcik 2006: 120; Krajcik 2012: 183; Krajcik 2013: 185.

Onthophagus (Palaeonthophagus) nitidulus, Janíková 1998: 30; Bunalski et al. 2014: 158.

Onthophagus (incertae sedis) nitidulus, Löbl et al. 2006: 175.

Onthophagus (Indonthophagus) nitidulus, Kabakov 2006: 154 (footnote); Král and Batelka 2017: 131; Ziani and Bezděk 2016: 188; Montreuil 2017: 269; Ziani et al. 2019: 18; Schoolmeesters 2023.

Onthophagus nitidulus var. *mediofasciatus* d'Orbigny 1898: 203 [type locality: "Egypte: Le Caire" (Cairo, Egypt); "Sind : Kurrachee (Karachi, Pakistan)"]; d'Orbigny 1913: 380; Boucomont and Gillet 1927: 184; Winkler 1929: 1034 (as aberration of *O. nitidulus*); Balthasar 1963: 452 (as aberration of *O. nitidulus*); Ferreira 1972: 697; Alfieri 1976: 205; Balthasar 1963: 452 (as aberration of *O. nitidulus*); Baraud 1985: 287 (as aberration of *O. nitidulus*); Krajcik 2006: 121 (as junior synonym of *O. nitidulus*); Löbl et al. 2006: 175 (as junior synonym of *O. nitidulus*); Ziani and Bezděk 2016: 188 (as junior synonym of *O. nitidulus*); Schoolmeesters 2023 (as junior synonym of *O. nitidulus*).

Onthophagus tetraspilus Fairmaire 1887: 114 [type locality: "Somâlis" [Côte française des Somalis, presently Djibouti]]; d'Orbigny 1898: 202 (as junior synonym (= chromatic variety) of *O. nitidulus*); d'Orbigny 1900: 297 (as *O. nitidulus* var. *tetraspilus*); d'Orbigny 1904: 303 (as *O. nitidulus* var. *tetraspilus*); d'Orbigny, 1913: 380 (as junior synonym (= chromatic variety) of *O. nitidulus*); Boucomont and Gillet 1927: 184 (as junior synonym of *O. nitidulus*); Winkler 1929: 1034 (as aberration of *O. nitidulus*); Balthasar 1963: 452 (as aberration of *O. nitidulus*); Ferreira 1972: 697 (as *O. nitidulus* var. *tetraspilus*); Alfieri 1976: 205 (as *O. nitidulus* var. *tetraspilus*); Baraud 1985: 287 (as aberration of *O. nitidulus*); Krajcik 2006: 121 (as junior synonym of *O. nitidulus*); Löbl et al. 2006: 175 (as junior synonym of *O. nitidulus*); Ziani and Bezděk 2016: 188 (as junior synonym of *O. nitidulus*); Schoolmeesters 2023 (as junior synonym of *O. nitidulus*).

Type locality. "Benisuef" [Beni Suef, Egypt]; "Syenam" [Aswan, Egypt]; "Ambukohl" [Ambigol, Sudan].

Type material.

Onthophagus nitidulus Klug, 1845: 4 syntypes (1 ♂ and 3 ♀), examined by photos (ZMB).

Onthophagus tetraspilus Fairmaire, 1887: presumably, holotype ♀, fixed by monotypy, not traced.

Onthophagus nitidulus var. *mediofasciatus* d'Orbigny, 1898: number of type specimens not specified in the original description, but at last two. A syntype, a minor ♂, examined by photos (MNHN).

Diagnostic features. Length 3.0 to 6.0 mm. Colour black, with distinct isodiametric microreticulation and slight metallic lustre, elytra yellow ochre, usually with dark brown symmetrical spots arranged in a V-shaped pattern, at third, fifth and seventh interstria, and the first interstria brown along entire length; sometimes spots are joined to each other, sometimes lacking in some interstriae. Antennae and dorsal pubescence yellow.

Head short, slightly wider than long, with clypeus broadly round, slightly sinuate anteriorly, sides not sinuate; clypeofrontal carina distinct, bent backward, placed slightly closer to the base of the horn than to the anterior margin of clypeus in major males; occipital carina with a long slender thread-like horn, thickened and flat at base, arising in correspondence of the anterior margin of eyes, directed backward and tapering gradually to the extremity, in major males, reduced to a short, erected conical tubercle, in minor males, to a sinuate carina, longer than the clypeofrontal one, placed between the eyes or little further back in females; clypeal surface with transversely rugose, setigerous punctures, frontal surface double sparsely punctate.

Pronotum convex, declivous anteriorly, with an almost undistinguishable anteromedian smooth and unpunctured area, in major males, with an anteromedian slightly bilobate prominence, in minor males and females; both sexes with a small unpunctured area, duller than the surrounding surface, on either side near pronotal posterior angles; anterior angles distinctly produced, sides not sinuate behind them in dorsal view; dorsal surface setigerously punctate, punctures broad, sub-regular in distribution, separated by 2 to 3 diameter on disc, bearing pale-yellow setae.

Elytral striae little or not at all shiny, barely impressed, with punctures slightly larger than stria width and crenulating interstitial sides; interstriae barely convex, all rather regularly granulate; granules spread, smaller than

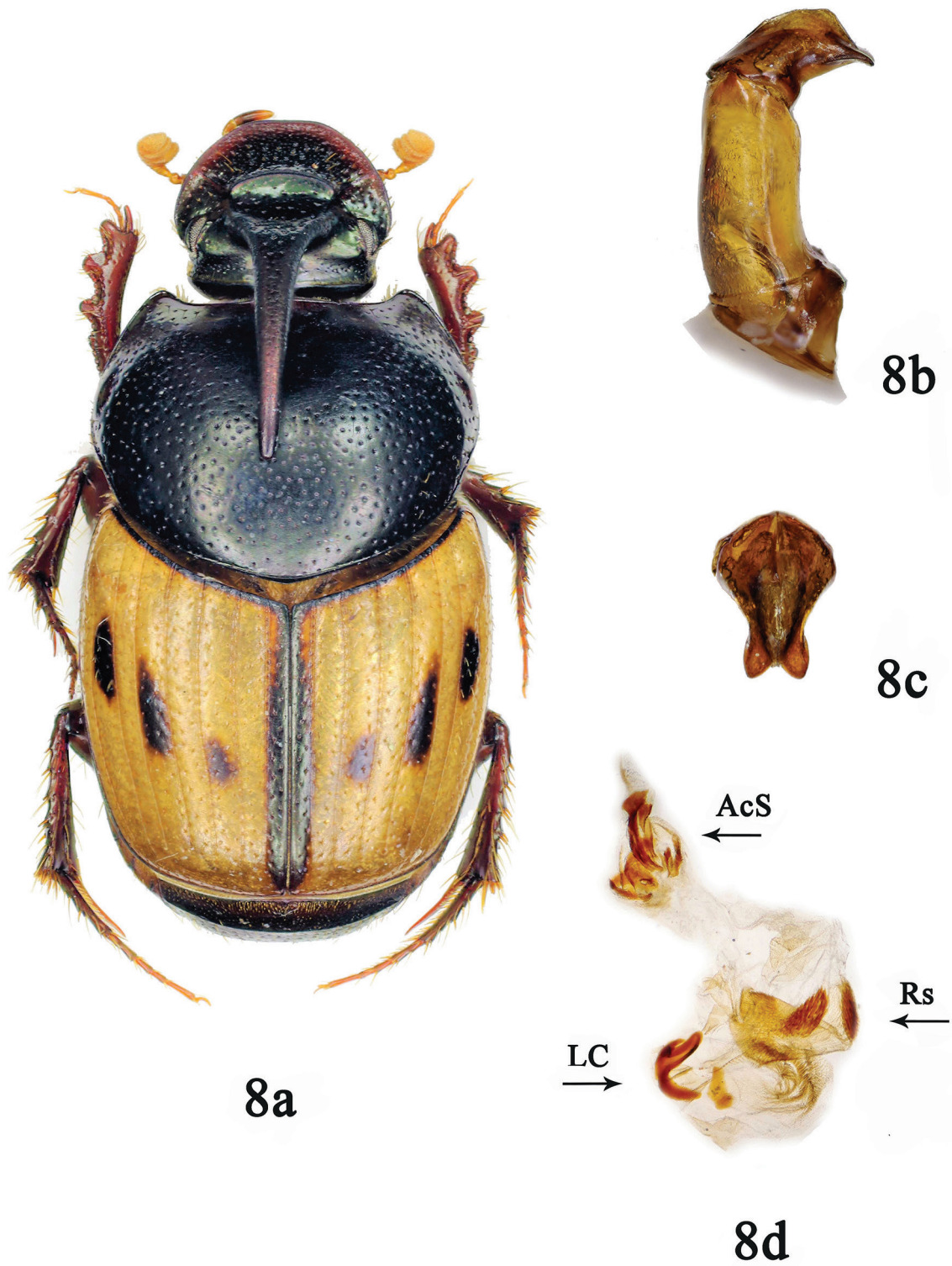


Figure 8. *Onthophagus (Indonthophagus) nitidulus* Klug, 1845 [major ♂: Yemen, Abyan gov.]. **8a)** Dorsal habitus. **8b)** Parameres, lateral view. **8c)** Parameres, dorsal view. **8d)** Endophallus. AcS: accessory endophallites. LC: lamella copulatrix. Rs: raspulae. Photos by A. Degiovanni, edited by G. Fiumi.

strial punctures, each granule with a small, indistinct, setigerous puncture; setae short, pale-yellow, thin.

Pygidium with rather regularly distributed, setigerous punctures; setae pale-yellow, thin, longer than those of elytra.

Males with protibial spur outward and with a strongly curved downward denticle on the inner angle of protibial apex.

Male genital armature. Parameres short, apices slightly bent ventrally, slightly diverging apically, without latero-proximal denticle, round at apex (Fig. 8b–c); endophallus with the presence of accessory endophallites, two evident raspulae and a U-shaped lamella copulatrix, with an arm straight, the other broad and clearly divided in two unequal branches (Fig. 8d).

Distribution. Egypt, Sudan (Klug 1845). Eritrea, “Arabia” (Gestro 1889). Iraq, Djibouti, Somalia, Saudi Arabia, Yemen, Pakistan (d’Orbigny 1898). Afghanistan (Balthasar 1956). Rajasthan, India (Frey 1956). Ethiopia (Balthasar 1963). Iran (Baraud 1968). United Arab Emirates, Oman (Gillett 1995).

Material examined. **Egypt:** “Aegypt Ehrenb./ [...], “*nitidulus* / Klug”, examined by photos (4 syntypes of *O. nitidulus*, 1 ♂ and 3 ♀♀, ZMB). **Saudi Arabia:** Madinah prov., 10 km N Wadi Reem, 200 m, 17°55’28”N; 42°15’20”E, 30.iii.2017, G. Magnani leg. 1 ex. (SZCM). **Yemen:** Abyan gov., W Lawdar, env. 1150 m, 13°52’36”N 45°48’01”E, 22.x.2005, D. Král leg. 1 ex. (SZCM); Al Hudaydah gov., Al Munirah, 21 m, 15°20’10”N 42°50’12”E, 31.x.2005, D. Král leg. 1 ex. (SZCM). **Oman:** Dhofar gov., Road 47 before Al Mughssyl, 61 m, 16°54’11”N 53°49’20”E, 11.ix.2000, M. Dellacasa leg. 3 exx. (SZCM); Dhofar gov., Khor Rori, 37 m, 17°02’27”N 54°26’16”E, 12.ix.2000, M. Dellacasa leg. 3 exx. (SZCM); Dhofar gov., Salalah - Wadi Darbat, 41 m, 17°04’23”N 54°25’56”E, 10.vii.2018, I. Zappi leg. 1 ex. (SZCM); Dhofar gov., Rakhyut, 27.x.2022, L. Melloni leg. 4 exx. (SZCM); Dhofar gov., 15 km W Salalah, 20 m, 16°56’52”N 53°57’37”E, 4.iv.2023, S. Ziani leg. 8 exx. (SZCM); Dhofar gov., Wadi Ayun 840 m, 17°15’14”N 53°53’33”E, 5.iv.2023, S. Ziani leg. 4 exx. (SZCM). **Iran:** Lorestan prov., Kumas, 2.iv.2015 (SZCM); Hormozgan prov., Ahmadi, 10.iii.2017, 2 exx. (SZCM); Hormozgan prov., Chah Faleh, 19 m, 30.iii.2018, G. Saba-tinelli leg. 2 exx. (SZCM). **Pakistan:** “Kurrachee” [Karachi], viii-ix, Maindron leg. 1 ♂, examined by photos (syntype ♂ of *O. nitidulus* var. *mediofasciatus*, d’Orbigny collection, MNHN); Punjab prov., Chakri, motorway for Islamabad, 26.vi.2011 (SZCM).

Historical review. The specimens (syntypes) examined and used by Klug (1845) for describing *Onthophagus nitidulus* came from three localities, “Benisuef” [Beni Suef], “Syenam” [Aswan] and “Ambukohl” [Ambigol], respectively in northern Egypt, in southern Egypt, and in northern Sudan. The type locality of the taxon encompasses all these three localities (Article 73.2.3 of the Code, ICZN 1999).

Kolenati (1846) and von Harold (1867, 1869) mentioned *Onthophagus sexstriatus* Waltl [“6-striatus Waltl.”] and *Onthophagus niloticus* Reiche, presumably as junior synonyms of *O. nitidulus*. As specified by von Harold (1867), in the first half of the nineteenth century, specimens of this last species were often found in entomological collections under the names “*niloticus*” and “6-striatus”. It does not appear that Joseph Waltl and Louis Jérôme Reiche published papers where, respectively, *Onthophagus sexstriatus* and *Onthophagus niloticus* have been described. Therefore, as specified by von Harold (1869), it can be reasonably presumed that these names are “*nomina nuda*”, hence not available. It should be noted that, later on, Montrouzier (1855) and von Harold (1879) described, respectively, *Onthophagus sexstriatus* from “Woodlark” [Papua New Guinea] and *Onthophagus niloticus* from “Kordofan, Nilus coeruleus” [Sudan], valid names of taxa that, obviously, have nothing to do with *Onthophagus sexstriatus* Waltl, *nomen nudum*, with *Onthophagus niloticus* Reiche, *nomen nudum*, and with *Onthophagus nitidulus* Klug.

Ten years after having described *Onthophagus nitidulus*, Klug (1855) described “another” *Onthophagus nitidulus* – clearly different from *Onthophagus nitidulus* Klug, 1845 – from Sena, Mozambique, description confirmed a few years later (Klug 1862) with, in addition, the statement “*nova spec.*” after the name of the species, as if the 1855 paper had never been published. Whatever happened, Klug most likely forgot his 1845 paper and his “first” *Onthophagus nitidulus*. Aware of this clear primary homonymy (*Onthophagus nitidulus* Klug, 1845 and *Onthophagus nitidulus* Klug, 1855), von Harold (1867) replaced the junior homonym with the new name *virescens*.

Onthophagus tetraspilus Fairmaire, 1887 was described from the then “Côte française des Somalis”, presently Djibouti, and considered close to the female of *O. nitidulus*. Later d’Orbigny (1898) deemed *O. tetraspilus* as a simple chromatic variation of *O. nitidulus*, with elytral spot only on the 3rd and 7th interstriae or even just on 7th.

In 1898 d’Orbigny described the variety *mediofasciatus* of *O. nitidulus*, from Cairo, Egypt, and from Karachi, Pakistan, with elytral spots joint to form a transversal V-shaped band, sometimes interrupted on the 6th interstria. Since d’Orbigny’s taxon was published before 1961, it must be considered of subspecific rank according the Article 45.6.4 of the Code (ICZN 1999). From Winkler (1929), *mediofasciatus* was deemed to be an aberration of *O. nitidulus*, hence its junior synonym.

Janíková (1998) and Bunalski (2014) inserted *O. nitidulus* in the subgenus *Palaeonthophagus* Zunino, 1979 without any explanation. No subsequent authors followed this systematic concept.

Remarks. The current systematic literature (Balthasar 1963; Krajcik 2006; Löbl et al. 2006; Ziani and Bezděk 2016; Schoolmeesters 2023) considers *O. tetraspilus* and *O. nitidulus* ssp. *mediofasciatus* junior synonyms of *O. nitidulus*. This paper follows such direction.

According to Zunino (1981), *O. nitidulus* has phylogenetic affinities with *Onthophagus sellatus* Klug, 1845 (tentatively inserted in the subgenus *Furconthophagus* Zunino, 1979 by Ziani 2020b), and *Onthophagus margaritifera* d’Orbigny, 1898 (inserted in *Onthophagus sensu lato*, without a subgeneric placement, by Ziani and Bezděk 2016). After studying the external morphology and the structures of the endophallus of the last two species, I prefer not to insert them in *Indonthophagus*.

***Onthophagus (Indonthophagus) turbatus* Walker, 1858**

(Fig. 2, 9–10, 12b,d)

Onthophagus turbatus Walker 1858: 209; von Harold 1862: 402 (as junior synonym of *O. spinifex*); von Harold 1869: 1036 (as junior synonym of *O. spinifex*); Arrow 1907: 429; Boucomont 1914: 222 (as possible junior synonym of *O. mopsus*); Boucomont and Gillet 1921: 38; Boucomont and Gillet 1927: 149; Arrow 1931: 329; Paulian 1945: 118 (as “*Onthophagus turbatus* Boucomont (*nec* Walker)”, junior synonym of *O. hastifer*); Balthasar 1963: 569; Endrödi 1974: 2; Krajcik 2006: 138; Biswas and Mulay 2001: 140; Rajan 2006: 133; Vinod and Thomas 2006: 5; Jadhav and Sharma 2012: 491; Krajcik 2012: 187; Thakare et al. 2012: 78; Karimumkara and Rajan 2013: 177; Krajcik 2013: 281; Rani and Sanjayan 2013: 242; Mittal and Jain 2015: 402; Sathiantran et al. 2015: 8256; Latha and Thomas 2018a: 16123; Lau 2019: 95 (as “*Onthophagus turbatus* Boucomont & Gillet (*nec* Walker 1858)”; Latha 2019: 59; Kalawate et al. 2021: 17583; Sathiantran et al. 2021: 741; Asha et al. 2022: 7; Rajagopal et al. 2023: 329.

Onthophagus (Indonthophagus) turbatus, Kabakov 2006: 154 (footnote); Kharel et al. 2020: 371; Schoolmeesters 2023.

Onthophagus (Colobonthophagus) turbatus, Gupta et al. 2022: 425.

Onthophagus (Onthophagus) turbatus, Sobhana et al. 2013: 95; Kalawate et al. 2021: 17583.

Type localities. “Ceylon” [Sri Lanka].

Type material. 2 syntypes, a medium ♂ and a ♀, studied (NHMUK).

Diagnostic features. Length 7.0 to 8.0 mm. Colour reddish brown or bronzed, with slight metallic lustre, moderately shiny, with distinct isodiametric microreticulation. Elytra dark red, sometimes with lighter red irregular basal and apical spots. Antennal scape, pedicel and funicle reddish yellow, antennal club yellow. Dorsal pubescence whitish yellow.

Head short, distinctly wider than long, with clypeus broadly round, slightly or not at all sinuate anteriorly, sides not sinuate; clypeofrontal carina distinct, bent backward, placed nearly halfway between base of the horn and anterior clypeal margin; occipital carina with a long and slender thread-like horn, flat and clearly moderately enlarged at base (Fig. 12b), curving backward, sometimes reaching and also exceeding the pronotal hind margin, in major males, reduced to a short transverse tubercle between the eyes in minor males, and into a straight, sometimes sinuate transverse carina in females (Fig. 12d), clearly broader than clypeofrontal one, almost reaching inner margin of eyes; clypeal surface with transversely rugose, setigerous punctures, frontal surface doubly sparsely punctate.

Pronotum convex, declivous anteriorly, with a slight anteromedian depression in major males, front pronotal margin vertical in the middle, the upper edge of the declivity forming a more or less evident anteromedian prominence in minor males and in females, in the latter the prominence being slightly bilobate; medium males,

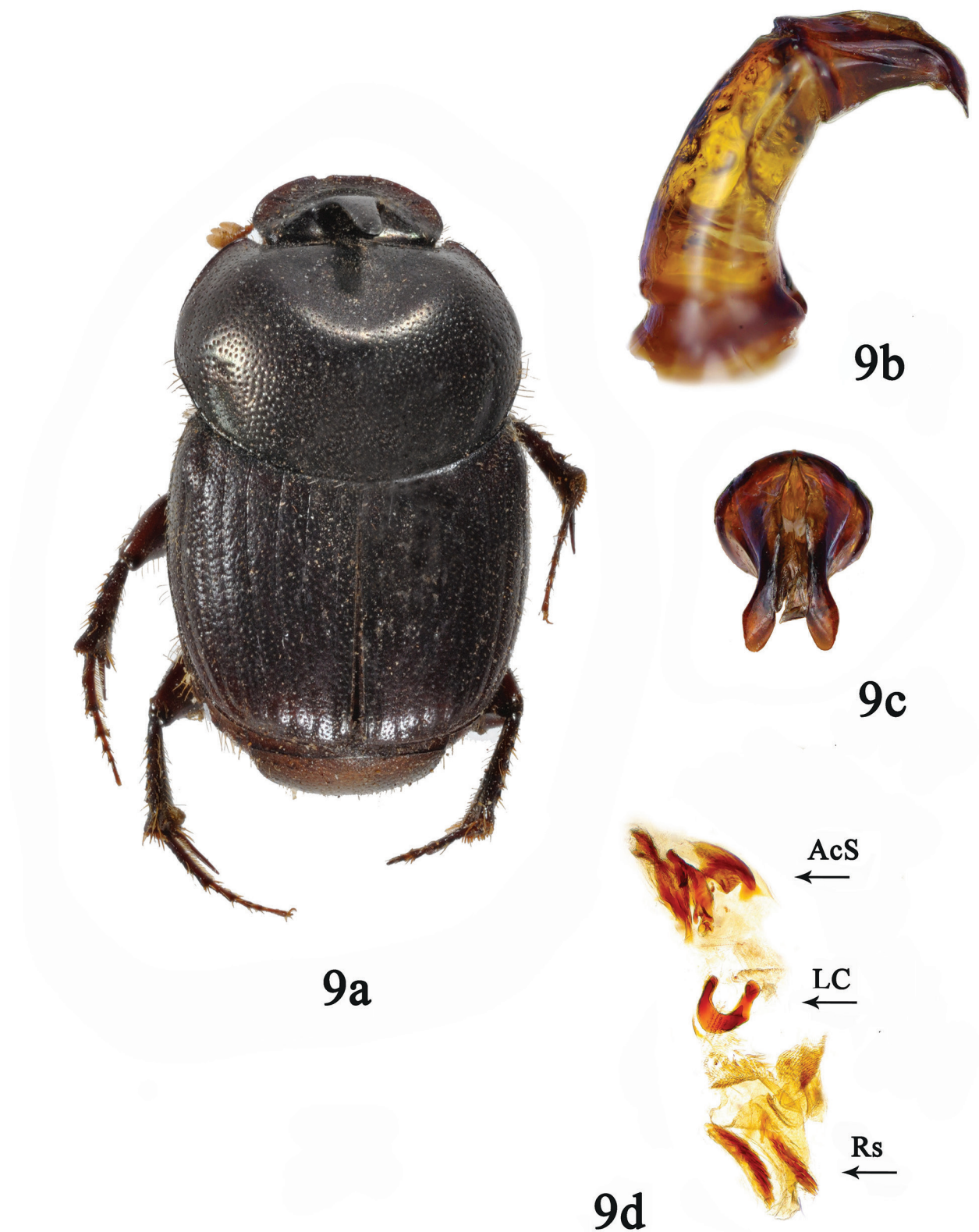


Figure 9. *Onthophagus (Indonthophagus) turbatus* Walker, 1858 [syntype, medium ♂: Sri Lanka]. **9a)** Male dorsal habitus [photo and editing by G. Fiumi]. **9b)** Parameres, lateral view. **9c)** Parameres, dorsal view. **9d)** Endophallus. AcS: accessory endophallites. LC: lamella copulatrix. Rs: *raspulae*. Photos by A. Degiovanni, edited by G. Fiumi.



Figure 10. *Onthophagus (Indonthophagus) turbatus* Walker, 1858 [major ♂: Pakistan, Mansehra prov.]. Dorsal habitus. Photos by A. Degiovanni, edited by G. Fiumi.

including the syntype, with horn shortened sometime by half, and a deep wide pronotal anteromedian hollow, its surface smooth and scarcely simply punctate; both sexes with a slightly depressed posterolateral area (Fig. 2), duller than pronotal disc, on either side near pronotal posterior angles, anteriorly with a tuft of longer setae; anterior angles distinctly produced, sides not sinuate behind them in dorsal view; dorsal surface setigerously punctate, punctures slightly impressed, sub-regular in distribution, separated by 1 to 3 diameters on disc, smaller than the punctures of elytral striae, bearing pale-yellow setae, shorter on disc, barely longer at sides.

Elytral striae shiny, distinctly impressed, with punctures slightly larger than stria width and barely crenulating interstitial sides; interstriae flat to barely convex, all rather regularly granulate; granules smaller than stria punctures, each granule with a short, pale-yellow, thin seta.

Pygidium with regularly or sub-regularly distributed, setigerous punctures; setae pale-yellow, thin, clearly longer than those of elytra.

Males with protibial spur outward. Terminal margin of male protibiae at right angle to the inner margin, with a tuft of short pale-yellow bristles, and with a small denticle curved downward on the inner angle of protibial apex.

Male genital armature. Parameres short, apices bent ventrally and rhombus-shape, diverging apically, without basolateral plate denticle (Fig. 10b–c); endophallus with the presence of accessory endophallites, two evident and large raspulae of different sizes and a U-shaped lamella copulatrix, with one arm bifurcate apically, the other with a spinelike process, more or less long but never reaching the apex that appears clearly lobate (Fig. 10d).

Distribution. Sri Lanka (Walker 1858). India (Boucomont 1914). First records for Pakistan, Nepal and Bhutan.

Material examined. Pakistan: Islamabad Capital Territory, Marghalla hills, 1000 m, 15.viii.2010, G. Sabatinelli leg. 3 ♂♂ and 2 ♀♀ (SZCM); Islamabad Capital Territory, Islamabad, sect. E7, 600 m, 1.ix.2012, G. Sabatinelli leg. 2 ♂♂ at light (SZCM); Khyber Pakhtunkhwa, Jaba Dara (Manshera), 28.iv.2011, S. Ziani leg. 3 ♂♂ and 1 ♀ (SZCM). **India:** Kerala state, Cardamon H., Periyar, env. Aranya Nivas, 950 m, 4.xi.1972, C. Besuchet, I. Löbl, R. Mussard leg. 1 ♀ (MHNG); Karnataka state, Bangalore University Campus, Bangalore, 6.vii.2004, R. Ramalingam leg. 3 major ♂♂ and 1 medium ♂, examined by photos (AIMB); West Bengal state, Siliguri distr., Sevoke, 200 m, 7.vi.2008, V. Patrikeev leg. 1 minor ♂ (STCH); Arunachal Pradesh state, West Kameng, Bhalukpong, 150 m, 27°00'48"N 92°39'08"E, 1/8.v.2012. L. Dembický leg. 1 major ♂ (SZCM); Kerala state, Nelliampathy/Palakkad, 97 m, 23.iii.2022, K. A. Sobhana leg. 1 medium ♂, examined by photos (ZSIK); Kerala state, Meppadi/Wayanad, 987 m, 29.xi.2022, J. Subha Babu leg. 2 medium ♂♂, examined by photos (ZSIK). **Sri Lanka:** “Typus”, “Ceylon”, “*Onth. turbatus* / Walker / (type)”, “*turbatus*” (syntype ♂ of *O. turbatus*, NHMUK); “Ceylon”, “*Onth. turbatus* / Walker / (type)” (syntype ♀ of *O. turbatus*, NHMUK); Central Province, Kandy, 1892, E. Simon leg. 1 ♂ and 1 ♀ (Balthasar collection, NMPC); Uva prov., Inginiyagala, 12.ii.1970, Mussard, Besuchet, Löbl leg. 1 ♂ (NMPC); Sabaragamuwa prov., Pinnawala – Rambukkana, 2.ii.2024, M. Rivalta and P. Subini leg. 1 ♀ (SZCM). **Nepal:** Central region, Annapurna - Himalaya / near Tatopani, 1300 m, 3.vi.1996, L. Nádai leg. 1 ♂ (SZCM). **Bhutan:** Punakha, Sobsokha, 1200 m, 13.vii.2016, S. Ziani leg. 2 ♀♀ (SZCM).

Historical review. *Onthophagus turbatus* was described on one male and one female at least, since Walker (1858) has featured both sexes. The “types” present in NHMUK, with Walker’s handwritten labels, are therefore to be considered syntypes.

The taxon did not appear to be born under a lucky star: only four years after its description, *O. turbatus* was synonymized by von Harold (1862). He affirmed that Walker described the species on a female of *O. spinifex* (Fabricius, 1781), and later confirmed such synonymy (von Harold 1869).

On the contrary, Arrow (1907), claiming to have examined the type material of both species, stated that *O. turbatus* and *O. spinifex* were absolutely not conspecific.

Boucomont (1914), in a footnote at p. 222, asserted that “Ce nom [*O. turbatus*] est probablement synonyme de *mopsus* F., (...), malheureusement le type de Fabricius est perdu et la description est insuffisante” [This name [*O. turbatus*] is probably a synonym of *mopsus* F., (...), unfortunately Fabricius’ type has been lost and the description is insufficient]. Later, Boucomont, with Gillet, accepted the validity of the species, first in “Faune entomologique de l’Indochine française” (Boucomont and Gillet 1921), then in “Coleopterorum Catalogus” (Boucomont and

Gillet 1927). It is worth noting that Boucomont and Gillet (1921) recorded this species from Vietnam (“Tonkin: Quang Yen; Annam: Quang-tri), whereas Arrow (1931) specified that these records were wrong.

Paulian (1945) hypothesized that *O. turbatus sensu* Boucomont [and Gillet] (1921), which is the species recorded from Vietnam by Boucomont and Gillet (1921) – and from Myanmar, China and Taiwan by himself – was not conspecific with *O. turbatus* Walker. This last taxon, always according to Paulian (1945), is distributed in Sri Lanka and south India, whereas in north-western India “l’espèce est représentée par le vicariant *O. mopsus* Fabricius” [the species is represented by the vicariant *O. mopsus* Fabricius]. *O. turbatus sensu* Boucomont [and Gillet] 1921, always according to Paulian (1945), is a junior synonym of *O. hastifer*.

Lau (2019) quoted, in the “Checklist of Insects of Hong Kong”, “*Onthophagus turbatus* Boucomont and Gillet (*nec* Walker, 1858)”, but as *bona species*.

Kharel et al. (2020) recorded the species, cited as *O. turbatus* Walker, also from Thailand. Regarding its subgeneric placement, the taxon was mentioned twice by Kalawate et al. (2021), either belonging to the subgenus *Onthophagus* and as “*species incertae sedis*”.

Remarks. After the study of type material of *O. turbatus* and *O. hastifer*, as well as other specimens belonging to both taxa, I fully agree with Paulian (1945) in considering *O. turbatus sensu* Boucomont [and Gillet] 1921 not conspecific with *O. turbatus* Walker, and a junior synonym of *O. hastifer*. Consequently, the distribution of *O. turbatus* Walker does not include localities eastward of Bhutan. Most probably *O. turbatus* and *O. hastifer* are sister species and, for what I know, their distributional areas are not overlapping.

All the morphological descriptions of *O. turbatus* published in the literature (Boucomont 1914; Boucomont and Gillet 1921; Arrow 1931; Balthasar 1963), including the original description (Walker 1858), report as the main distinctive characters of males, the cephalic horn, short and far from reaching the pronotal hind margin, and the pronotal deep and wide antero-median depression. The authors who pointed out such features had clearly described the syntype male or had reported a previous description of the syntype male, without noticing, or stressing at least, that the specimen was not a major male, but a so-called “medium” male, with all the characteristics of moderately developed males, such as shorter cephalic horn and evident pronotal antero-median depression (Fig. 10a). Actually, major males of *O. turbatus* have the cephalic horn reaching and sometimes exceeding the pronotal hind margin, and a very shallow anteromedian hollow, if any (Fig. 11). The morphology of lamella copulatrix leaves no doubts about the conspecificity of major and medium specimens. For these reasons, in the dichotomous key to the *Indonthophagus* species provided below, also other characters for discriminating *O. turbatus* from other species, particularly *O. hastifer*, the taxon in the same couplet, are used.

[*Onthophagus (sensu lato) spinifex* (Fabricius, 1781)]

(Fig. 11)

Scarabaeus spinifex Fabricius, 1781: 29; Fabricius 1787: 15; Jablonsky and Herbst 1789: 240; Olivier 1789: 148 (as *S. spinifer*, misprint); Gmelin 1790: 1543; Fabricius 1792: 58; Illiger 1800: 263 (as *S. spinifer*, misprint); Sturm 1802: 92 (as *S. spinifer*, misprint); Zimsen 1964: 28.

Copris spinifex, Olivier 1790: 170; Fabricius 1801: 49; Illiger 1802: 316; Schönherr 1806: 50.

Onthophagus spinifex, Hope 1837: 33; Hope 1838: 315 (as *spinifer*, misprinting); Westwood 1842: 2; Motschulsky 1859: 154; von Harold 1869: 1036; Arrow 1907: 430 (as *spinifer*, misprint); Boucomont 1914: 222; Boucomont and Gillet 1927: 147; Arrow 1931: 200; Balthasar 1963: 535; Gupta and Mittal 1987: 50; Gupta 1989: 24; Mittal 1999: 35; Biswas and Mulay 2001: 137; Krajcik 2006: 133; Chandra and Gupta 2011: 254; Chandra and Gupta 2012: 105; Chandra et al. 2012: 53; Jadhav and Sharma 2012: 491; Krajcik 2012: 186; Chandra and Gupta 2013a: 4665; Chandra and Gupta 2013b: 345; Karimbumkara and Rajan 2013: 176; Krajcik 2013: 257; Gupta et al. 2014: 233; Mittal and Jain 2015: 401; Ziani 2015: 19; Gajendra and Prasad 2016: 711; Kharel et al. 2020: 380; Ghosh et al. 2021: 387; Ghosh et al. 2022a: 11.

Onthophagus (Indonthophagus?) spinifex, Kabakov 2006: 154 (footnote).

Onthophagus (Onthophagus) spinifex, Sobhana et al. 2013: 95; Kalawate et al. 2021: 17583.

Onthophagus (incertae sedis) spinifex, Löbl et al. 2006: 176; Ziani and Bezděk 2016: 203; Gupta et al. 2018: 484; Ghosh et al. 2020: 246; Ghosh et al. 2022b: 120; Gupta et al. 2022: 426.

Scarabaeus aeneus Fabricius 1781: 34 [type locality: “Coromandel” (south-eastern India)]; Fabricius 1787: 18; Jablonsky and Herbst 1789: 328; Olivier 1789: 131; Gmelin 1790: 1557; Fabricius 1792: 59; Illiger 1800: 238; Sturm 1802: 80.

Copris aeneus, Olivier 1790: 163.

Copris aenea, Fabricius 1801: 51; Schönherr 1806: 53.

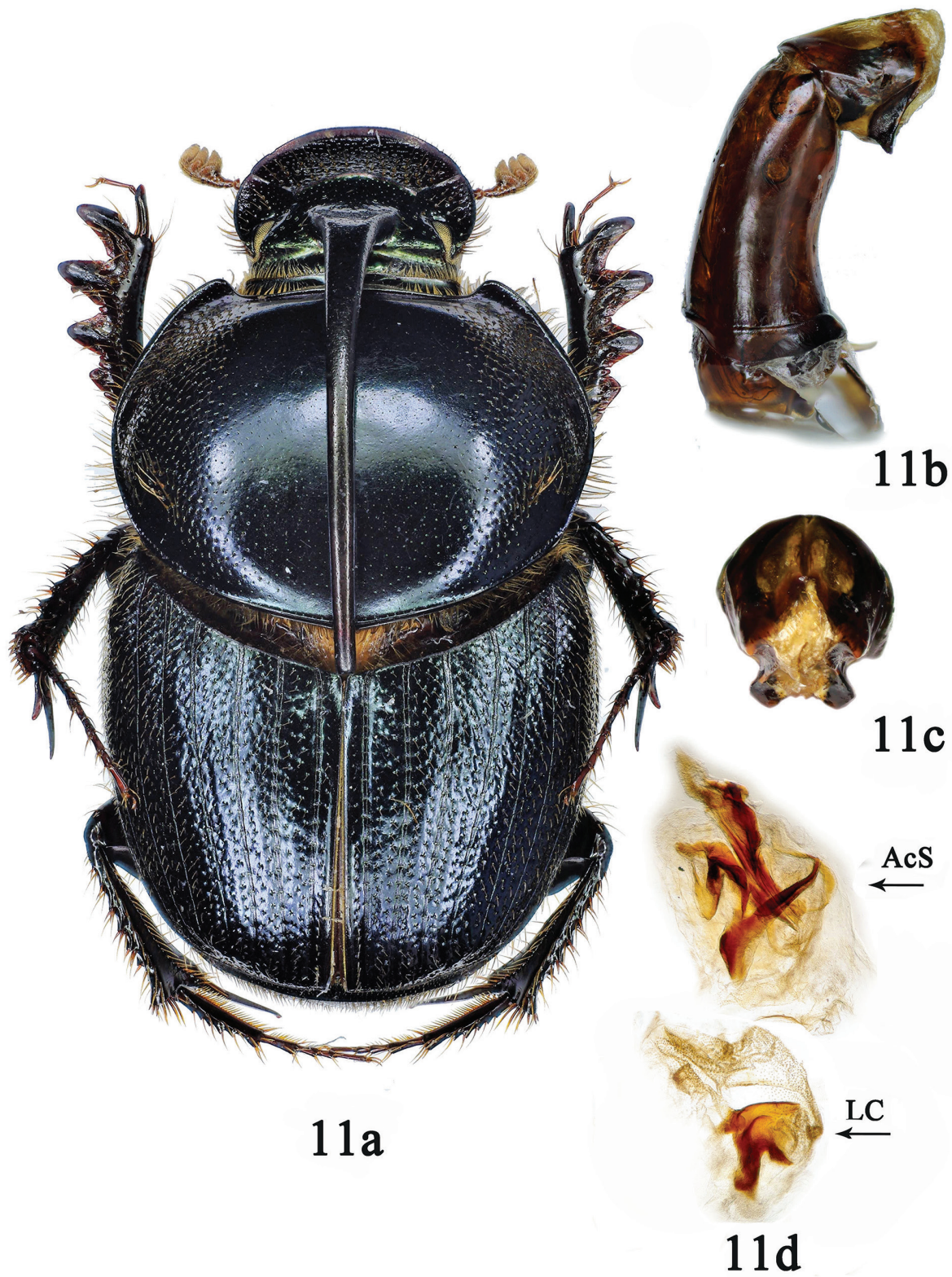


Figure 11. *Onthophagus (incertae sedis) spinifex* (Fabricius, 1781) [major ♂: Pakistan, Capital Territory]. **11a**) Dorsal habitus. **11b**) Parameres, lateral view. **11c**) Parameres, dorsal view. **11d**) Endophallus. AcS: accessory endophallites. LC: lamella copulatrix. Photos by A. Degiovanni, edited by G. Fiumi.

- Onthophagus aeneus*, von Harold 1869: 1024; von Harold 1880: 154 (as junior synonym of *O. spinifex*); Shipp 1895: 179 (as junior synonym of *O. spinifex*); Boucomont and Gillet 1927: 147 (as junior synonym of *O. spinifex*); Arrow 1931: 200 (as junior synonym of *O. spinifex*); Balthasar 1963: 535 (as junior synonym of *O. spinifex*); Krajcik 2006: 133 (as junior synonym of *O. spinifex*); Löbl et al. 2006: 176 (as junior synonym of *O. spinifex*); Ziani and Bezděk 2016: 203 (as junior synonym of *O. spinifex*).
- Scarabaeus truncaticornis* Herbst 1786: 154; [type locality: "Ostindien" (East India)]; Jablonsky and Herbst 1789: 209 (as junior synonym of *S. truncaticornis* Schaller, 1783); Fabricius 1792: 59 (as junior synonym of *S. aeneus* Fabricius, 1781); Illiger 1800: 239 (as junior synonym of *S. aeneus*); Schönherr 1806: 53 (as junior synonym of *Copris aenea*).
- Onthophagus truncaticornis*, von Harold 1869: 1024 (as junior synonym of *O. aeneus*); von Harold 1880: 154 (as junior synonym of *O. aeneus*); Shipp 1895: 179 (as junior synonym of *O. aeneus* and junior synonym of *O. spinifex*); Boucomont and Gillet 1927: 147 (as junior synonym of *O. spinifex*); Balthasar 1963: 535 (as junior synonym of *O. spinifex*); Krajcik 2006: 133 (as *O. truncaticornis* Herbst in Jablonsky 1789, junior synonym of *O. spinifex*); Löbl et al. 2006: 176 (as junior synonym of *O. spinifex*); Ziani and Bezděk 2016: 203 (as junior synonym of *O. spinifex*).
- Onthophagus reflexicornis* Redtenbacher 1868: 57 [type locality: "Ceylon" (Sri Lanka)]; von Harold 1872: 206 (as junior synonym of *O. spinifex*); Boucomont and Gillet 1927: 147 (as junior synonym of *O. spinifex*); Arrow 1931: 200 (as junior synonym of *O. spinifex*); Balthasar 1963: 535 (as junior synonym of *O. spinifex*); Krajcik 2006: 133 (as junior synonym of *O. spinifex*); Löbl et al. 2006: 176 (as "*O. reflexicornis* L. Redtenbacher 1867", junior synonym of *O. spinifex*); Ziani and Bezděk 2016: 203 (as junior synonym of *O. spinifex*); Schoolmeesters 2023 (as junior synonym of *O. spinifex*).
- Onthophagus bifossus* d'Orbigny 1902: 145 [type locality: "Sénégal" (Senegal)]; d'Orbigny 1908: 155 (as junior synonym of *O. spinifex*); d'Orbigny 1913: 726 (as junior synonym of *O. spinifex*); Boucomont and Gillet 1927: 144 (as junior synonym of *O. spinifex*); Balthasar 1963: 535 (as junior synonym of *O. spinifex*); Krajcik 2006: 133 (as junior synonym of *O. spinifex*); Löbl et al. 2006: 176 (as junior synonym of *O. spinifex*); Ziani and Bezděk 2016: 203 (as junior synonym of *O. spinifex*); Schoolmeesters 2023 (as junior synonym of *O. spinifex*).

Type localities. "Coromandel" [south-eastern India].

Type material.

Scarabaeus spinifex Fabricius, 1781: a syntype (holotype?), a major male, examined by photos (NHMUK).

Scarabaeus aeneus Fabricius, 1781: a syntype (holotype?) female, examined by photos (NHMUK).

Scarabaeus truncaticornis Herbst, 1786: holotype (?) not traced.

Scarabaeus truncaticornis Schaller, 1783: type lost/destroyed (Hendrick Müller, Martin-Luther-Universität, Halle-Wittenberg, personal communication).

Onthophagus reflexicornis Redtenbacher, 1868: holotype male, fixed by monotypy, not traced.

Onthophagus bifossus d'Orbigny, 1902: holotype female, fixed by monotypy, examined by photos (MNHN).

Diagnostic features. Length 7.5 to 10.0 mm. Colour dark metallic blue or dark metallic green, glossy, without distinct isodiametric microreticulation. Antennal scape, pedicel and funicle brownish reddish yellow, antennal club yellow. Dorsal pubescence yellow.

Head very slightly wider than long, with clypeus broadly rounded, not sinuate anteriorly, sides not sinuate; clypeofrontal carina distinct, bent backward, very slightly closer to the occipital carina than to clypeal anterior margin in major males; occipital carina bearing a long slender horn, flattened and broad in its basal part, curving and tapering backward, sometimes extending beyond the middle of the body in major males, reduced to a short, erected conical tubercle, placed between the eyes, or to a transverse carina, in minor males, to a strongly elevated carina, curved backward, clearly longer than clypeofrontal carina and extended from eye to eye, in females; clypeal surface with transversely rugose, setigerous punctures, frontal surface sparsely punctate.

Pronotum convex, declivous anteriorly, with a longitudinal smooth and almost unpunctured very slight median groove, in major males, with a short anteromedian steep declivity bearing a pair of small tubercles rather close to each other, in minor males, and with an anteromedian curved prominence, slightly elevated, a little depressed in the middle, with a smooth hollow on either side, in females; both sexes with a small posterolateral area on either side near pronotal posterior angles, slightly duller than the surrounding surface and simply sparsely punctate, anteriorly with a line of longer setae; anterior angles produced, sides not sinuate behind them in dorsal view; dorsal surface setigerously punctate, punctures small on disc, very sparse, simple, in major males, a slightly rough in minor males, clearly rough and closer in females, each puncture bearing a short pale-yellow seta, longer at sides.

Elytral striae distinctly impressed, with punctures slightly larger than stria width and crenulating interstitial sides; interstriae barely convex, wrinkling granulate; granules spread, equal in size to stria punctures, each granule with a short, pale-yellow, thin seta.

Pygidium with rather regularly distributed, setigerous punctures; setae pale-yellow, thin, a clearly longer than those of elytra.

Males with protibial spur very slightly bent downward, and with a small denticle curved downward on the inner angle of protibial apex.

Male genital armature. Parameres very short, with two symmetrical denticles apically, and two spatulae, slightly diverging, ventrally (Fig. 9b–c); endophallus with the presence of accessory endophallites and a sub-quadrangular lamella copulatrix, with three arms at least, one arms longer than the others, and a sinuate side (Fig. 9d).

Distribution. India (Fabricius 1781). Sri Lanka (Boucomont 1914). Nepal (Löbl et al. 2006). Pakistan (Ziani 2015). Bangladesh (Kharel et al. 2020).

Material examined. Pakistan: Azad Kashmir, Muzaffarabad, 800 m, 15.v.2012, G. Sabatinelli leg. 17 exx. (SZCM); Azad Kashmir, Rawalakot – Tatapani, 7.vi.2012, G. Sabatinelli leg. 1 ex. (SZCM); Khyber Pakhtunkhwa prov., Kalam, 1900 m, 28.ix.2012, G. Sabatinelli leg. 1 ex. (SZCM); Islamabad Capital Territory, Islamabad, sect. E7, 600 m, 15.vii.2012, G. Sabatinelli leg. 1 ex. (SZCM); *ibidem*, 1.ix.2012, G. Sabatinelli leg. 4 exx. (SZCM); *ibidem*, 15.ix.2012, G. Sabatinelli leg. 1 ex. (SZCM); Islamabad Capital Territory, Marghalla hills, 1056 m, 16.vii.2012, G. Sabatinelli leg. 2 exx. (SZCM). **India:** [Coromandel], “*Scarab. spinifex* / Fabr. [...]”, “*Syntypus*”, examined by photos (syntype [holotype?] major ♂ of *O. spinifex*, NHMUK); [Coromandel], “*Scarab. aeneus*. / Fabr. [...]”, examined by photos (syntype [holotype?] ♀ of *O. aeneus*, NHMUK). **Sri Lanka:** Western prov., Negombo, 1.ii.1971, L. Lindgren leg. 1 ♂ (MZH). Northern Prov., Madhu, 8.ii.1971, L. Lindgren leg. 1 ♀. (MZH); Uva prov., Kataragama env., 1-3.vii.2003, O. Mehl leg. 1 ♀ (SZCM). **Without locality:** “Senegal” [*patria errata*] / *Ex-Musaeo* / Van Lansberge”, “H. d’Orbigny / Onth. Afr. 1902”, “*bifossus* / n. sp. d’Orb.”, “Holotype”, examined by photos ((syntype [holotype?] ♀ of *O. bifossus*, MNHN).

Historical review. Fabricius (1781) described *Onthophagus spinifex*, as *Scarabaeus spinifex*, from “Coromandel”. Presently Coromandel is the name of a southeastern coastal region of the Indian subcontinent, comprising the states of Tamil Nadu and Andhra Pradesh, but historically Coromandel stretch of coast was shorter, from the mouth of the river Krishna to, southward, the Cape of Calimere (“Kodiakarai”).

Olivier (1789) wrongly reported the specific name “*spinifer*” for *Scarabaeus spinifex*. This misprint is to be considered an incorrect subsequent spelling, also because the same author, one year later (Olivier 1790), returned to use the original spelling *spinifex*, a clear evidence that his 1789 change was not an emendation – i.e. an intentional change – but simply a misprint. As such, the name “*spinifer*”, as incorrect subsequent spelling, is not available and does not enter in homonymy (Article 33.3 of the Code, ICZN 1999). Unfortunately the “copy and paste” operations were very fashionable also more than two centuries ago. And so, Illiger (1800) [who two year later (Illiger 1802) realized the mistake and remedied], Sturm (1802), Hope (1838) and even Arrow (1907) fell into Olivier’s misprint and wrongly used “*spinifer*”.

Fabricius (1781) described also *Scarabaeus aeneus* from “Coromandel”, just in the same volume in which he described *Scarabaeus spinifex*. Almost a century later, von Harold (1880), claiming that Fabricius’s *aeneus* was nothing but the female of *spinifex*, acted as First Reviser (Article 24.2.1 of the Code, ICZN 1999) and gave the precedence to the name *Onthophagus spinifex*. The synonymy was followed by all the subsequent authors.

According to some recent literature, *Onthophagus aeneus*, as *Scarabaeus*, was described twice, by two different authors. Let’s see how. At page 131 of “Entomologie, ou Histoire Naturelle des Insectes...” Olivier (1789) quoted *Scarabaeus aeneus* Fabricius, 1781. It was simply a citation, not a description of a new species. Also, in “Dictionnaire encyclopédique de l’histoire naturelle”, the same author (Olivier 1790), even referring to the image of the beetle in Olivier (1789), clearly gave the authorship of *Scarabaeus aeneus* to Fabricius (1781). But despite this, some authors (among them Balthasar 1963, Löbl et al. 2006, Rossini et al. 2014, Ziani and Bezděk 2016) considered *Scarabaeus aeneus* as described twice, the first time in 1781 by Fabricius, then in 1789 by Olivier. In particular, according to Balthasar 1963, Löbl et al. 2006 and Ziani and Bezděk 2016, *Scarabaeus aeneus* Fabricius, 1781 is a junior synonym of *Onthophagus spinifex*, whereas *Scarabaeus aeneus* Olivier 1789 is a junior synonym of *Onthophagus dama* (Fabricius, 1789). Actually, as stated above, Olivier (1789) cited the *Scarabaeus aeneus* described by Fabricius (1781), with indications and bibliographical references, even with the same type locality

(“Coromandel”, south-eastern India), of Fabricius’s species. Therefore, *Scarabaeus aeneus* Olivier, 1789 was never described and doesn’t enter in any kind of synonymy or homonymy.

Blanchard (1847) described *Onthophagus aeneus* from Argentina. Since this name was a secondary homonym of *Onthophagus aeneus* (Fabricius, 1781), it was replaced by von Harold (1859) with *Onthophagus brasiliensis nomen novum*. This taxon is currently considered a junior synonym of *Onthophagus hircus* Billberg, 1815 (Schoolmeesters 2023).

There is also a *Scarabaeus aeneus* described by Linnaeus (1764) from South Africa but, as already noticed by Jablonsky and Herbst (1789), it is a Cetoniinae (Scarabaeidae) and all the issues related to its homonymies or synonymies are not discussed here.

Since it also concerns *O. aeneus*, it is now necessary to mention the very complicated and tangled story, under a systematic/nomenclatorial point of view, of *Onthophagus truncaticornis*. It was described for the first time, as *Scarabaeus truncaticornis*, by Schaller (1783), on an unknown number of specimens from Malabar (southwestern India). Three years later Herbst (1786) claimed the authorship of the name, based on reasons irrelevant under nomenclatorial conventions. He asserted that “his” *S. truncaticornis* differed from Schaller *S. truncaticornis* only by the presence of head carinae. Strangely enough, Jablonsky and Herbst (1789) gave the precedence to Schaller as author of *Scarabaeus truncaticornis*. Are the two *Scarabaeus truncaticornis* really different species? We cannot say it with certainty. According to von Harold (1880) and the current literature, they are so.

Anyway, despite the confusion about the authorship, the systematic fate of *Scarabaeus truncaticornis* intertwined that of *Scarabaeus aeneus* Fabricius, 1781 – as stated before, junior synonym of *O. spinifex* – after Fabricius (1792), who affirmed that Herbst’s *Scarabaeus truncaticornis* was nothing but the female of *Scarabaeus aeneus*. Later, Sturm (1800) followed Fabricius (1792) synonymy, namely *S. truncaticornis* Herbst, 1786 = *S. aeneus* Fabricius, 1781 but added to the synonymy “the other” *Scarabaeus truncaticornis* by Schaller (1783). Gmelin (1790) gave the authorship of *S. truncaticornis* to Schaller (1781) only. Fabricius (1792) resumed the synonymy *Scarabaeus aeneus* versus *Scarabaeus truncaticornis* Schaller, confirming that *S. truncaticornis* Herbst was the female of *S. aeneus*. According to Illiger (1800), *S. truncaticornis* Schaller was a junior synonym of *S. aeneus*, whereas according to Schönherr (1802), was instead *S. truncaticornis* Herbst a junior synonym of *S. aeneus* (as *Copris aenea*). As it can be seen, nomenclatorial and taxonomic chaos were dominant. Only after Latreille (1802), when all these taxa had been moved into the genus *Onthophagus* by subsequent authors, it became less mystifying mainly thanks to von Harold (1869) and especially to von Harold (1880). In this last paper von Harold clearly suggested, after seeing the type of *Onthophagus truncaticornis* (Herbst) preserved in Berlin Museum, that the latter was absolutely conspecific with *O. aeneus* (Fabricius) – in turn conspecific with *O. spinifex* – but different from *O. truncaticornis* (Schaller). All the subsequent authors followed von Harold’s systematic statement, so the nomenclatorial chaos problem is seemingly solved.

The choice by Krajcik (2006) to reference “Herbst in Jablonsky, 1789” as the authorship and year of description of *O. truncaticornis* is not clear to me and even, also in view of Bousquet (2016), seems to be incorrect.

And Schaller’s *Onthophagus truncaticornis*? It is presently accepted as a species recorded from India (Schoolmeesters 2023) and belonging to the *O. pusillus* group (Palestrini 1983). The treatment of this taxon is, however, out of the topic of this paper.

Finally, to make nomenclatorial matter worse, Boheman (1860) described “another” *Onthophagus truncaticornis* from Botswana (Africa), a secondary homonym replaced by von Harold (1870) with the new name *Onthophagus trucidatus*. *O. trucidatus* is presently considered a junior synonym of *O. quadrinodosus* Fåhraeus, 1857 (Schoolmeesters 2023).

Onthophagus reflexicornis, described by Redtenbacher (1868) on a single male from Ceylon, was soon synonymized with *O. spinifex* by von Harold (1872), after examining the type. This synonymy was followed by all subsequent authors.

Onthophagus bifossus, described by d’Orbigny (1902) on a single female from Senegal, was synonymized with *O. spinifex* by d’Orbigny himself (d’Orbigny 1908), on the ground of a possible mislabelled specimen.

Remarks. Some characteristics of *O. spinifex* external morphology, such as the depressed and dull area on either side near pronotal posterior angles and the major males’ long thin horn, curved backward, suggest the species could belong to *Indonthophagus*. And in that subgenus the species was inserted by Kabakov (2006) based on these

characters. Actually, females of *O. spinifex* have a strongly elevated occipital carina, curved backward, clearly longer than the clypeofrontal carina and extended from eye to eye, whereas female members of *Indonthophagus* have a simple occipital carina, nearly straight, placed between the eyes and more or less extended but never from eye to eye. As to male genitalia, *O. spinifex* parameres and structures of the endophallus are definitively far from the ones of the other species here included in the subgenus *Indonthophagus*. Particularly, the lamella copulatrix is not U-shaped but sub-quadrangular. Additionally, the endophallus is lacking raspulae. For the abovementioned reasons, I decided to exclude definitively *O. spinifex* from the subgenus *Indonthophagus*, and to insert it in *mare magnum* of the *Onthophagus* species needing a subgeneric placement.

There is a little mystery in Ghosh et al. (2021): in the geographical distribution of *O. spinifex*, the code “CH” is cited. Nevertheless, such code is not present in the section of that paper called “abbreviations” which specifies countries matching the initialisms. What does “CH” mean? From a geographical point of view, CH can mean “China”, as in Löbl and Smetana (2006) and Löbl and Löbl (2016), but this Country, although not in *O. spinifex* distribution, is already present in Ghosh et al. (2021) under the code “CN”. Switzerland, the other Country that is often abridged as “CH”, can be definitely ruled out. So, is CH a misprint for CN, which would be China? If this is the case, should China be added to the distribution of the species? For the moment and until verified records are available, I prudently exclude *O. spinifex* from the Chinese fauna.

Discussion

The subgenus *Indonthophagus* was established by Kabakov (2006) to accommodate the *Onthophagus* species whose major males share a long thin horn, curved backward, sometimes exceeding the pronotal base. According to the author (Kabakov 2006), the subgenus is characterized by two taxonomic features, deemed not to be present in any other *Onthophagus* subgenus, namely:

- base of the horn very close to the clypeofrontal carina, in males;
- hind pronotal angles, with a little concave area.

Moreover, in the key to the *Onthophagus* subgenera, Kabakov (2006) added other characters that presumably should better define *Indonthophagus*, which are:

- large roundish and convex eyes, their “lower lobes” much larger than antennal club;
- antennal club usually yellowish;
- male occipital carina often extended in a long horn, the base of which is rather close to the clypeofrontal carina;
- anterior margin of male protibiae more or less perpendicularly truncate;
- parameres weakly flattened dorsally, with apex simple and turned downward;
- various colour, often dark with metallic shines.

Actually, none of these characters is exclusive of the species placed in the subgenus, as well as not all those species share these characters.

Regarding the two features that according to Kabakov (2006) denote the subgenus, the first, that is, the base of the male horn very close to the clypeofrontal carina, can be observed only in *O. mopsus*. In the other species, the base of the horn is sometimes slightly closer to the clypeofrontal carina than to the anterior clypeal margin, but usually the clypeofrontal carina is at the same distance from the base of the horn and the clypeal anterior margin. It is interesting to note that also in other Palaearctic *Onthophagini*, apparently phylogenetically far from the species of the subgenus *Indonthophagus*, the base of the occipital carina, from where horns or erected laminae arise, is adjacent to the clypeofrontal carina, when it is present, or almost in contact with it. That is the case, for example, with *Onthophagus (Palaeonthophagus) koryoensis* Kim, 1985, and *Onthophagus (Eremonthophagus) heydeni* von Harold, 1875.

The second character highlighted by Kabakov (2006) is the pronotal posterolateral small area, sometimes depressed and/or strongly microreticulate, hence dull. This spot, more or less distinguishable in both sexes, is present in all the *Indonthophagus* species, but is a feature shared with many other *Palaeonthophagus* and

Furconthophagus species, and even with some Afrotropical taxa, particularly the species belonging to the genus *Tiaronthophagus* Roggero, Moretto, Barbero and Palestirini, 2019.

Regarding the characteristics given by Kabakov (2006) in the key, it can be said that anterior margin of male protibiae is clearly perpendicularly truncate, somehow like that of the species belonging to the genus *Caccobius* Thomson, 1859, only in *O. hastifer* and *O. turbatus*, normally shaped in the other species. As for parameres, they are weakly flattened dorsally with apex simple and turned downward, but this is a characteristic present in several Onthophagini species, belonging to different groups, subgenera up to genera. Some other features cited by Kabakov (2006) seem, in this case at least, to be lacking of taxonomic meaning.

As often happens in the tribe Onthophagini, it is the structures inside the endophallus that can help to better understand and define the group. All the species placed in the subgenus have a U-shaped lamella copulatrix, with the two parallel branches more or less slender, sometimes enlarged, fringed or bifurcate apically. In addition, in their endophalli there are usually two large raspulae, in *O. ensifer* only one.

Therefore, in light of above, the group can be recognized by the combination of the following characters:

- pronotal hind angles with a small sometimes depressed area, always dull and more strongly micro-reticulated;
- distal inner edge of male protibia with a small denticle strongly curved downward;
- antennae yellow;
- major males with a long or very long thin horn, curved backward;
- females with a more or less straight occipital carina placed between the eyes, or nearly so;
- endophallus with a U-shaped lamella copulatrix;
- endophallus with at least one, usually two large raspulae.

Under these conditions, it can be assumed that *Indonthophagus* is a homogeneous group, within the genus *Onthophagus*. This is a cautious approach, however. Right now, such grouping can be considered “useful”, in operational term, for species identification. We can of course discuss on the opportunity to deem it as subgenus, or rather as a simple group of species, without nomenclatorial value. This choice being subjective, hence not definitive, I prefer for now not to make nomenclatural changes and to maintain the subgeneric rank given by Kabakov (2006).

As seen before, the subgenus *Indonthophagus* has been sometimes related, in the literature (Thomas et al. 2011, Karimbunkara and Rayan 2013, Mittal and Jain 2015, Karel et al. 2020, Gupta et al. 2022 and, indirectly, Balthasar 1963), to the subgenus *Colobonthophagus* Balthasar, 1963. The two taxa are however easily distinguishable at least for the feature that mainly characterizes *Colobonthophagus*, according to the original description (Balthasar 1963) and its latest and reliable taxonomic interpretation (Scheuern 1995), which is the presence of a bulbous elevation at base of the elytral sutural interstria, whereas the sutural interstria is levelled in the species belonging to *Indonthophagus*.

Some Afrotropical *Onthophagus* species are waiting to be deeper studied and, most probably, inserted in *Indonthophagus*. For example, *Onthophagus mixticeps* d’Orbigny, 1905, who according to the original description, is close to *O. aeneopiceus* d’Orbigny 1902, and many more. The subgenus *Indonthophagus* is therefore expected to numerically increase when the Afrotropical fauna will be thoroughly studied.

Key to Palaearctic *Indonthophagus*

1. Species relatively large (from 7.5 to 10.0 mm). Dorsal surface completely dark metallic blue or dark metallic green, glossy, without distinct isodiametric microreticulation (Fig. 11a). Females with clypeofrontal carina extended from eye to eye. Pakistan, India, Nepal, Sri Lanka, Bangladesh [*O. spinifex* (Fabricius, 1781)]
- Species relatively small (from 3.0 to 8.0 mm). Dorsal surface usually without strong metallic lustre, at most present only on head and pronotum. At least elytra always with distinct isodiametric microreticulation. Females with clypeofrontal carina more or less wide, but never extended from eye to eye 2
2. Elytra yellow ochre, usually with dark brown symmetrical V-shaped spots (Fig. 8a); first interstria brown along entire length. Length 3.0 to 6.0 mm. Egypt, Eastern Africa; Arabian Peninsula, Iraq, Iran, Afghanistan, Pakistan, India *O. nitidulus* Klug, 1845

- Elytra monochromatic dark brown, dark red or bronzed, at most with basal or apical red spots 3
3. Head and pronotum with strong cupreous or greenish metallic lustre (Fig. 4a). Pronotal punctuation strongly impressed and large, larger than elytral striae punctures. Females: pronotum with an anterolateral tubercle, sometime hardly distinguishable, on either side, a little behind frontal margin, anteromedian gibbosity usually bilobate or divided in two. Length 5.0 to 7.5 mm. Pakistan, India, Nepal ***O. ensifer* Boucomont, 1914**
- Head and pronotum without strong metallic lustre. Pronotal punctuation as large as elytral stria punctures or a slightly smaller. Females: pronotum with a single anteromedian gibbosity, sometimes very slightly developed 4
4. Major males: pronotum with an anterolateral tubercle, on each side (Fig. 6a); horn arising clearly in front of eyes, adjacent to clypeofrontal carina. Length 6.0 to 8.0 mm. Afghanistan, Pakistan, India, Nepal ***O. mopsus* (Fabricius, 1792)**
- Major males: pronotum without anterolateral tubercles; horn arising between eyes, or at most in line with eyes anterior edge, not adjacent to clypeofrontal carina 5
5. Major males: base of cephalic horn broader than or as broad as clypeofrontal carina (Fig. 3a); dorsal surface of horn rugose-punctate on basal half, with some setae laterally. Length 4.0 to 6.5 mm. Sudan, Ethiopia, Kenya; Yemen ***O. aeneopiceus* d'Orbigny, 1902**
- Major males: base of cephalic horn more or less shorter than clypeofrontal carina; dorsal surface of horn simply punctate, completely hairless 6
6. Major males: base of cephalic horn clearly shorter than clypeofrontal carina (Fig. 12a). Medium males, with horn not reaching pronotal hind margin: pronotum with a barely appreciable antero-median narrow groove. Females: occipital carina as long as or shorter than clypeofrontal carina (Fig. 12c). Pronotal punctures more deeply impressed, subequal in size to punctures of elytral striae. Length 6.0 to 8.0 mm. Myanmar, China, Thailand, Vietnam, Taiwan ***O. hastifer* van Lansberge, 1885**
- Major males: base of cephalic horn slightly shorter than clypeofrontal carina (Fig. 12b). Medium males, with horn not reaching pronotal hind margin: pronotum with a deep wide antero-median hollow. Females: occipital carina clearly broader than clypeofrontal one, almost reaching inner margin of eyes (Fig. 12d). Pronotal punctures slightly impressed, smaller than punctures of elytral striae. Length 7.0 to 8.0 mm. Pakistan, India, Sri Lanka, Nepal, Bhutan ***O. turbatus* Walker, 1858**

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12a



12b



12c



12d

Figure 12. Head from above: **12a** *Onthophagus (Indonthophagus) hastifer* von Lansberge, 1914 [major ♂: Taiwan, Pingtung]. **12b** *Onthophagus (Indonthophagus) turbatus* Walker, 1858 [major ♂: India, Arunachal Pradesh st.]. **12c** *Onthophagus (Indonthophagus) hastifer* von Lansberge, 1914 [♀: Taiwan, Pingtung]. **12d** *Onthophagus (Indonthophagus) turbatus* Walker, 1858 [♀: Pakistan, Islamabad Capital Territory]. Photos by A. Degiovanni, edited by G. Fiumi.

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