Preliminary considerations on the genus-group Furconthophagus and the Palaearctic species assigned to it in the literature (Coleoptera: Scarabaeidae: Onthophagini)

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Abstract. The Palaearctic species, which according to the literature belong to the subgenus *Furconthophagus* Zunino, 1979 of *Onthophagus* Latreille, 1802, were considered and examined. This revealed considerable morphological heterogeneity in this group, for which it was not possible to provide a complete and satisfactory phylogenetic hypothesis. Nevertheless, a diagnosis based both on external and internal characters is provided, as a result of which, *Onthophagus centricornis* (Fabricius, 1798), placed in the group by Kabakov (2006), is moved from *Furconthophagus* to "*Onthophagus*, species incertae sedis". In addition, images of the aedeagus and endophallus of some relevant species are provided and a new country record (*Onthophagus variegatus* (Fabricius, 1789) from Morocco) is given.

Key words. Taxonomy, dung beetles, scarabs, species-group, Scarabaeoidea, Onthophagus, new country record.

INTRODUCTION

Furconthophagus Zunino, 1979, described as a subgenus of Onthophagus Latreille, 1802, is a seemingly monophyletic group spread in the Palaearctic, Afrotropical and Oriental realms. It was erected by Zunino (1979) on the basis of male and female genital armatures. Its type species is Scarabaeus furcatus Fabricius, 1781, presently Onthophagus furcatus, distributed in central and southern Europe, Morocco, Middle East, and Central Asia. According to Ziani & Bezděk (2016) and Ziani et al. (2019) there are twelve species in this subgenus recorded in the Palaearctic region. Nevertheless, a completely satisfying morphological and aedeagal definition of the group is lacking.

This paper considers the species that in the literature are assigned to the subgenus *Furcontho-phagus*, and verifies the external and aedeagal characters that such species share with each other and the type species. Given the great morphological heterogeneity of the involved taxa, no attempt is made to present a phylogenetic hypothesis for this group, but only a preliminary morphological diagnosis, with emphasis on characters of the endophallus sclerites.

MATERIAL AND METHODS

Terminology of external morphology is based on Génier & Moretto (2017), whereas terms and study criteria of male genitalia structures follow Tarasov & Solodovnikov (2011), except for the term "raspula" (sensu Binaghi et al. 1969), herein preferred to the term "bristle". Initialisms of collections cited in the paper are as follows:

HNHM - Hungarian Natural History Museum, Budapest, Hungary;

MHNG – Muséum d'histoire naturelle, Genève, Switzerland;

NMEG - Naturkundemuseum Erfurt, Germany;

NMPC - National Museum, Prague, Czech Republic;

PMCT – Philippe Moretto personal collection, Toulon, France;

SZCM - Stefano Ziani personal collection, Meldola FC, Italy.

MATERIAL EXAMINED. *Onthophagus aethiopicus* d'Orbigny, 1902: specimens from Saudi Arabia and Yemen (SZCM); *O. amicus* (Gillet, 1925): specimens from Pakistan (SZCM); *O. centricornis* (Fabricius, 1798): specimens from Afghanistan (SZCM), southern India, Sri Lanka, Nepal (HNHM, MHNG, NMPC); *O. dapcauensis* Boucomont, 1921: 1 specimen from Vietnam (HNHM), 4 specimens from Taiwan (SZCM); *O. frontalis* Raffray, 1877: 2 specimens from Yemen (MHNG, NMPC); *O. furcatus* (Fabricius, 1781): specimens from central-southern Europe, Middle East, Caucasus (SZCM); *O. furcillifer* Bates, 1891: specimens from Pakistan, India, Nepal and Bhutan (SZCM); *O. furcicollis* Arrow, 1931: 1 specimen from Nepal (SZCM); *O. kchatriya* Boucomont, 1914: 2 specimens from Nepal (SZCM); *O. parvulus* (Fabricius, 1798): specimens from Pakistan (SZCM), India (HNHM), Sri Lanka (MHNG); *O. rugulipennis* Fairmaire, 1887: specimens from Saudi Arabia and Yemen (SZCM); *O. schawalleri* Scheuern, 1996: 2 paratypes from Nepal (MHNG); *O. sellatus* Klug, 1845: specimens from Egypt, Israel, Saudi Arabia (SZCM); *O. stellio* Erichson, 1843: 1 specimen from Namibia (NMPC), 4 specimens from southern Africa (NMEG); *O. troglodyta* Wiedemann, 1823: specimens from Nepal (MHNG, SZCM), Afghanistan and Pakistan (NMPC); *O. variegatus* (Fabricius, 1798): specimens from Iran, Saudi Arabia, Yemen, Oman, United Arab Emirates, Pakistan (SZCM), 4 specimens from Morocco, Volubilis (Moulay Idriss), 14 May 1989, H. Tussac leg. (PMCT) (new country record for Morocco).

Unfortunately, it was not possible to examine specimens of *Onthophagus (Furconthophagus) schoolmeestersi* Ochi et Kon, 2007, and therefore any observations on it are based on the original description. Finally, and once more, for the species concerned, the morphology of female genitalia turned out to be scarcely evaluable and its study, albeit attempted, was deemed not essential for any systematic consideration.

HISTORICAL OVERVIEW AND SYSTEMATIC REMARKS

In describing the subgenus Furconthophagus, Zunino (1979) did not specify any external morphological features characterizing the species included in this group. He only pointed out the characteristics of male and female genital armature, namely, for male genitalia, parameres very elongate with apex clearly bent ventrally, and endophallus with the lamina copulatrix large, composed of three branches joined at vertex of an irregular pyramid, usually with small but distinct raspulae. In this subgenus, in addition to the type species, Onthophagus furcatus, Zunino (1979) included O. dapcauensis, O. variegatus and other unspecified taxa from the "Vecchio Continente", that is, Afro-Eurasia.

Before Zunino (1979) described *Furconthophagus*, other authors established some groups in which species later assigned to the subgenus were inserted.

The first was d'Orbigny (1913), who for the African fauna of the Onthophagini, instituted and diagnosed (see below) a group within the genus *Onthophagus*, called "31st group", consisting of 35 species. Some of them are now included in the subgenus. In all respects, this was the first attempt to outline the external morphological characteristics of the group or of part of the group that later on Zunino (1979) would called *Furconthophagus*. Among other characters, d'Orbigny (1913) pointed out the importance of the anterior hypomeral carina reaching directly the pronotal anterior angle.

Arrow (1931) in a key to the groups of *Onthophagus* of British India, selected a group called "Group 8 (*variegatus* group)" in which five species were included, three of them (*O. parvulus*, *O. troglodyta* and *O. variegatus*), occurred also in the east Palaearctic realm. Yet, no definition of the group was provided by the author.

After Furconthophagus was described, some authors tried to define external morphological features for distinguishing the subgenus. Keys to the subgenera of Onthophagus based on the external morphology were tentatively attempted by Martín-Piera (1983, 2000) for the Spanish fauna and by Baraud (1992) for Europe, but the results were not very satisfactory, because only one species, O. furcatus, the sole European species, was included in these keys.

Kabakov (2006) gave a definition of the subgenus *Furconthophagus* based mainly on characters already furnished by d'Orbigny (1913), among them the anterior hypomeral carina reaching the pronotal anterior angle both in a straight and curvilinear way, to form a small hollow (anterior

hypomeral depression sensu Génier & Moretto 2017). Within the tribe Onthophagini, this last character is shared, according to Kabakov (2006), by the subgenera *Indachorius* Balthasar, 1941 and *Micronthophagus* Balthasar, 1963, and to some extent by the genera *Caccobius* Thomson, 1859 and *Milichus* Péringuey, 1901. Kabakov (2006) tried to consider aedeagal characteristics for defining the subgenus *Furconthophagus*, but only said that the parameres of the species belonging to this subgenus are differently shaped and, generally, beak-like. He included in *Furconthophagus* 13 species, eight of which (*O. aethiopicus*, *O. centricornis*, *O. dapcauensis*, *O. furcatus*, *O. parvulus*, *O. sellatus*, *O. troglodyta* and *O. variegatus*) with a distribution comprising also some central-east Palaearctic regions.

Ochi & Kon (2007), in trying to define this group, also referred to the anterior hypomeral carina and specified that the subgenus *Furconthophagus* is characterized by "prothorax with anterior angle shallowly but clearly hollowed on the ventral side, each hollow clearly defined by a strong carina on the external upper edge, the carina extended to tip of anterior angle".

In the Catalogue of Palaearctic Scarabaeoidea, Ziani & Bezděk (2016) listed 9 species included in the subgenus, namely *Onthophagus amicus*, *O. centricornis*, *O. dapcauensis*, *O. furcatus*, *O. parvulus*, *O. schoolmeestersi*, *O. sellatus*, *O. troglodyta* and *O. variegatus*. To these, Ziani et al. (2019) have added some Afrotropical species recently recorded from the Arabian Peninsula, namely *Onthophagus aethiopicus*, *O. frontalis* and *O. rugulipennis*.

Considering only the external morphology, it is reasonable to say that the definition of the 31st group given by d'Orbigny (1913), if applied to the subgenus *Furconthophagus*, is still the most acceptable, even with the very fitting distinctions. Moreover, as already mentioned, it is noteworthy that d'Orbigny did not miss the main character, or one of the main characters, that can help in characterizing the group, namely the direction of the carina in the anterior hypomeral region.

The definition provided by d'Orbigny (1913) is as follows:

"31e GROUPE. Tête de grandeur normale, ayant sa plus grande largeur en ayant du milieu des yeux, garnie de granules, ou de gros points, ou de rugosités; épistome nettement échancré, sauf parfois chez le suffusus et l'immundus qui ont l'armature du vertex située en arrière des yeux; front avec une carène, ou parfois d'sans carène; vertex très rarement muni d'un seul tubercule, ordinairement ayant soit deux cornes ou tubercules souvent reliés par une lame ou par une carène, et souvent, en outre, un tubercule médian situé plus en avant, soit seulement une lame échancrée à son sommet, ou une carène dentée à ses extrémités, ou une forte carène simple, ou une assez fine carène fortement arquée. Prothorax entièrement garni de granules ou d'une ponctuation au moins en partie râpeuse; les côtés non ou à peine sinués près des angles postérieurs, sauf chez des insectes avant les angles antérieurs à sommet vif ou presque vif et faisant ordinairement un peu saillie en dehors; la base entièrement mais parfois très finement rebordée. Élytres sans taches, ou avec des taches situées symétriquement sur les deux élytres; interstries entièrement et très distinctement garnis de granules; la 7^e strie nettement arquée ou sinueuse. Base du pygidium avec une carène transverse. Ligne cariniforme des flancs du prosternum se prolongeant très distinctement et à peine sinueusement jusqu'au sommet des angles antérieurs. Dessus du corps entièrement à courte pubescence jaune, sauf souvent *la tête* et le devant du prothorax à pubescence un peu plus longue. Taille petite ou assez petite (3–6 mill.)".

["31st GROUP. Head normal size, with the largest width in front of the middle of the eyes, with granules or large punctures, or broadly wrinkled; epistome clearly dentate, except sometimes in *suffusus* [Onthophagus suffusus Klug, 1855] and *immundus* [Onthophagus immundus Boheman, 1858] in which the vertex armature is behind the eyes; clypeofrontal carina present, or sometimes males without carina; vertex very rarely with a single tubercle, usually either with two horns or tubercles often connected by a ridge or a keel, or also, moreover, with a median tubercle situated

forward, or only a carina notched at the top, or a keel dentate at sides, or a strong simple carina, or a strongly curved very fine ridge. Pronotum with granules or with punctuation at least partially rasp-like; pronotal sides not or barely sinuate near the posterior angles, except in insects with anterior angles with sharp or almost sharp edges and usually projected outward; base completely, sometimes finely emarginate. Elytra without spots or with symmetrical spots; interstriae totally and distinctly granulate; 7th stria clearly curved or sinuous. Base of pygidium with a transverse carina. Cariniform line on prosternal sides extending very distinctly and barely sinuously to the apex of the anterior angles. Upper side with short yellow pubescence, except on the head and the anterior area of pronotum, with slightly longer setae. Small or fairly small (3–6 mm)"].

Difficulties in providing a comprehensive definition of *Furconthophagus* as meant by Ziani & Bezděk (2016) and Ziani et al. (2019), namely in finding distinctive features that all the members of the subgenus share with the type species, *O. furcatus*, also affected this study. This group turned out to be morphologically very heterogeneous. However, a diagnosis is attempted below.

RESULTS AND DISCUSSION

Onthophagus (Furconthophagus) Zunino, 1979

Type species. Scarabaeus furcatus Fabricius, 1781, by original designation.

DIAGNOSIS. Onthophagini species of small size (length 2.5–5.5 mm), black, with or without apical and basal symmetrically red spots, some species with yellow pronotum and elytra, or only yellow elytra, symmetrically black spotted. Upper side with rather long yellow setae.

Head with clypeal margin medially strongly emarginate, often v-shaped; clypeofrontal carina distinct, sometimes faint or absent in males; occipital carina in males with two lateral horns, or a lamina bifurcate at apex, or simply a strong carina, rarely a single tubercle or horn; female occipital carina simple, more or less elevated, bent backwards at sides.

Pronotal dorsal surface granulate, punctate-granulate or with broad rasp-like punctures; pronotum usually unarmed, without outgrowths or distinct gibbosities, sometimes strongly declivous towards anterior edge, rarely with a faint anteromedian bump but always without anterolateral tubercles; pronotal anterior angles distinct, sides more or less obviously sinuate just behind them. Hypomeral carina directly connected, slightly curved outward, to the anterior angle, and clearly visible from above. Mesometasternal suture faintly impressed, sometimes indistinct.

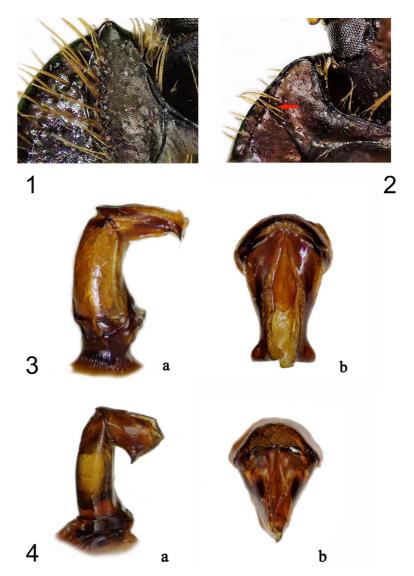
Aedeagus with parameres that can be straight and beak-shaped or short and truncate apically, apical *spatulae* ("distal-inferior paramerites" *sensu* Krikken & Huijbregts 2009) always clearly bent ventrally, more or less diverging, rarely parallel; in one case parameres with a lateral tooth before the apex. Lamina copulatrix variously shaped, strongly emarginate, to form a sort of horseshoe with three usually very slender branches, sometimes two of them overlap and hardly discernible one from another; accessory sclerites usually large, sclerotized, combined with one or more *spiculae*.

Secondary sexual characters usually well marked in males, with outgrowths on head, and with protibial spur short, clearly bent outwards, whereas it is long, longer than the first three tarsal segments combined, in female.

DISTRIBUTION. Palaearctic, Oriental and Afrotropical realms (Schoolmeesters 2020).

PHONETIC REMARKS. As explained by Ziani (in press), *Furconthophagus*, having *Onthophagus* as a suffix, is a proparoxytone word, that is, it has a heavy stress on the third-to-last syllable. It has to be pronounced Furcontòfagus.

The anterior hypomeral carina reaching directly, slightly curving outwards, the anterior angle (Fig. 1) is a character always used in past attempts to define this subgenus. As a matter of fact, this feature characterizes all the species of *Furconthophagus* but is also present in other

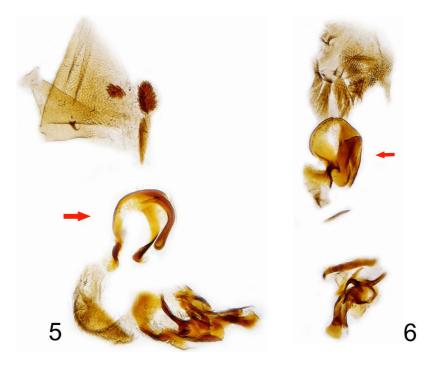


Figs. 1–4. Morphology of *Onthophagus*. 1 – *O.* (*Furconthophagus*) *furcatus* (Fabricius, 1781), Italy: Tirrenia (Tuscany). Anterior hypomeral carina. 2 – *O.* (s. l.) *centricornis* (Fabricius, 1798), India: Palakkad (Kerala). Anterior hypomeral carina. The carina extending to the side of the pronotum is indicated by an arrow. 3 – *O.* (*Furconthophagus*) *furcatus* (Fabricius, 1781), Italy: Tirrenia (Tuscany). Aedeagus. A: lateral view; B: dorsal view. 4 – *O.* (*Furconthophagus*) *variegatus* (Fabricius, 1798), Saudi Arabia: Al Makhwah (Baha). Aedeagus. A: lateral view; B: dorsal view.

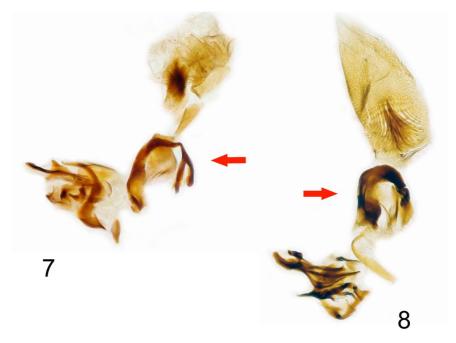
Onthophagini genus-group taxa, such as *Indachorius* and *Micronthophagus* (Kabakov 2006) and *Digitonthophagus* Balthasar, 1959 and on its own, is not meaningful either as a taxonomic instrument of identification or as phylogenetic support for understanding the relationship between *Furconthophagus* and other generic and subgeneric taxa within the tribe. Also the pronotal side, more or less clearly sinuate behind the anterior angle, is another character common to all species in this group. But also in this case the same pronotal feature is present in species placed in other *Onthophagus* lineages. These external morphological features are what Martín-Piera & Zunino (1983) call "caratteri neutri", neutral characters, that can hardly be interpreted phylogenetically, if they are not connected with a study of the characters of the male genital armature.

Parameres in Furconthophagus can be straight, beak-shaped (O. furcatus (Figs. 3A, B), O. aethiopicus, O. dapcauensis, O. parvulus, O. sellatus) or short, almost truncate apically (O. amicus, O. rugulipennis, O. schoolmeestersi, O. troglodyta, O. variegatus; Figs. 4A, B). Also within these divisions, their morphology is very heterogeneous, mainly in shape and in degree of divergence of the apical spatulae.

Other than the parameres and their apex, the most important taxonomic information is given by the shape of the lamina copulatrix. Zunino (1979), in defining the subgenus, pointed out the pattern of the lamina copulatrix, i.e. a large sclerite with three branches forming a pyramid. Species placed in *Furconthophagus* match more or less consistently this definition. Some of them have a lamina copulatrix with three branches more or less slender, of the same length and connected



Figs. 5, 6. Endophallus of *Onthophagus* (*Furconthophagus*); the lamina copulatrix is indicated by an arrow. 5 – *O.* (*F.*) *furcatus* (Fabricius, 1781), Italy: Tirrenia (Tuscany). 6 – *O.* (*F.*) *variegatus* (Fabricius, 1798), Saudi Arabia: Al Makhwah (Baha).



Figs. 7, 8. Endophallus of *Onthophagus* (*Furconthophagus*); the lamina copulatrix is indicated by an arrow. 7 – 0. (F.) *rugulipennis* Fairmaire, 1887, Yemen: Haddah (Sana'a). 8 – 0. (F.) *sellatus* Klug, 1845, Egypt: Aswan (Aswan).

at apex (*O. aethiopicus*, *O. amicus*, *O. furcatus* (Fig. 5), *O. troglodyta*), or with the left branch simple and the right one divided into two short arms (*O. dapcauensis*, *O. parvulus*, *O. variegatus*; Fig. 6). However, a similar shaped lamina, with three arms, even if sharp and not round apically, is present also in another subgenus of *Onthophagus*, *Amphionthophagus* Martín Piera et Zunino, 1983, which is considered to be phylogenetically not strictly related to *Furconthophagus*.

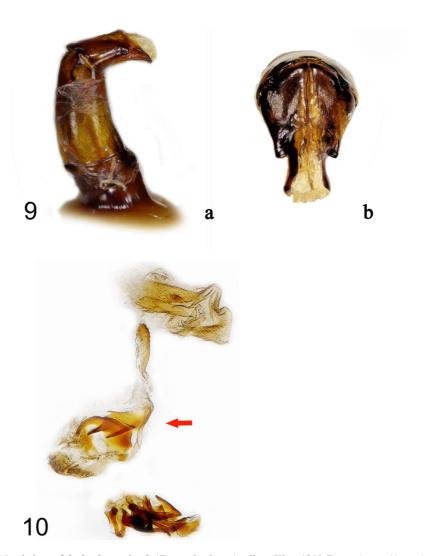
In this perspective, *Onthophagus rugulipennis* and *O. sellatus* are tentatively placed in *Furconthophagus*. Doubts have arisen for the shape of the lamina copulatrix (Fig. 7), with very slender branches, the left one simple and right one clearly bifurcate, in *O. rugulipennis*, and for the shape of the lamina copulatrix (Fig. 8), of which the third branch is only outlined and hardly discernable, and mainly for the lateral tooth below the apex of the parameres in *O. sellatus*, a feature that is not present in any other species of *Furconthophagus*.

As stated above, I was not able to examine *Onthophagus schoolmeestersi*, described as *Furconthophagus* by Ochi & Kon (2007). After studying the original description and the drawing of the endophallus, I also tentatively include this species in this subgenus.

In the light of this study, however, it is not possible to confirm the placement of *Onthophagus centricornis* in the subgenus *Furconthophagus*, as proposed by Kabakov (2006). The lamina copulatrix of this species (Fig. 10), with two horizontally overlapping branches, one of which is bifurcate, is clearly different from that of *Furconthophagus* cited by Zunino (1979) and confirmed by this study. Furthermore, the hypomeral carina of *O. centricornis* does not directly reach the anterior angle but extends to the pronotal side and then bends at a right angle to reach the anterior angle and so forms a deep anterior hypomeral depression (Fig. 2). As a consequence the

anterior angle of this species is more rounded, whereas it is sharper in the other taxa, and the pronotal sides are only very slightly sinuate anteriorly. For all these reasons, it is very likely that *O. centricornis* does not belong to this subgenus and has to be moved to "*Onthophagus*, *species incertae sedis*".

Thus, an updated checklist for Palaearctic *Furconthophagus* is presented below. There are eleven species in this group. Within square brackets are their geographical distributions (according to Ziani & Bezděk 2016 and Ziani et al. 2019).



Figs. 9, 10. Morphology of *Onthophagus*. 9 – *O.* (*Furconthophagus*) sellatus Klug, 1845, Egypt: Aswan (Aswan). Aedeagus. A: lateral view; B: dorsal view. 10 – *Onthophagus* (s. l.) *centricornis* (Fabricius, 1798), Nepal: Bahrabise (Bagmati). Endophallus. The lamina copulatrix is indicated by an arrow.

CHECKLIST OF THE PALAEARCTIC SPECIES

Onthophagus (Furconthophagus) aethiopicus d'Orbigny, 1902: Saudi Arabia, Yemen; Afrotropical realm;

Onthophagus (Furconthophagus) amicus (Gillet, 1925): Nepal, north India; Oriental realm;

Onthophagus (Furconthophagus) dapcauensis Boucomont, 1921: south-eastern China, Taiwan; Oriental realm;

Onthophagus (Furconthophagus) frontalis Raffray, 1877: Yemen; Afrotropical realm;

Onthophagus (Furconthophagus) furcatus (Fabricius, 1781): central and southern Europe, Middle East, Central Asia, Morocco;

Onthophagus (Furconthophagus) parvulus (Fabricius, 1798): Pakistan; Oriental realm;

Onthophagus (Furconthophagus) rugulipennis Fairmaire, 1887: Saudi Arabia, Yemen; Afrotropical realm;

Onthophagus (Furconthophagus) schoolmeestersi Ochi & Kon, 2007: Nepal;

Onthophagus (Furconthophagus) sellatus Klug, 1845: Cyprus, Levant, Oman, Yemen, Lybia, Egypt; Afrotropical realm;

Onthophagus (Furconthophagus) troglodyta Wiedemann, 1823: Afghanistan, Pakistan, north India; Oriental realm;

Onthophagus (Furconthophagus) variegatus (Fabricius, 1798): Cyprus, Arabian Peninsula, Iraq, Iran, Afghanistan, Pakistan, Morocco (new country record), Egypt; Afrotropical and Oriental realms;

Kabakov (1988) placed in the subgenus *Furconthophagus* another species recorded also from Palaeartic. It is *Onthophagus lilliputanus* van Lansberge, 1883, widespread in the Oriental realm, but also in Himachal Pradesh, Kashmir and Uttarakhand (Ziani & Bezděk 2016), Palaearctic Indian states and territories according to Löbl & Löbl (2016). This placement was adopted by other authors, such as Mittal & Jain (2015), Ueda et al. (2017), Kharel et al. (2020) and Schoolmeesters (2020). Kabakov himself (Kabakov & Napolov 1999), however, subsequently moved this species to *Relictonthophagus* Kabakov, 1979 (presently *Parentius* Zunino, 1979). *Onthophagus lilliputanus*, therefore, does not belong to the subgenus *Furconthophagus*, as already stated by Ziani & Bezděk (2016).

As mentioned above, the subgenus *Furconthophagus* does not only occur in the Palaearctic realm. According to Schoolmeesters (2020), another 6 species that occur only in the Oriental and 11 only in the Afrotropical realms are currently in this group, but most probably many others could also be assigned to it, especially species from Sub-Saharan Africa. Covering only the Palaearctic area, the present paper is necessarily a partial and hence preliminary study. It could be, however, the starting point for a comprehensive worldwide review that could provide a more satisfying morphological definition of *Furconthophagus* by adding some species and eliminating others, and a more thorough overall view of the phylogenetic relationships of this subgenus with other Onthophagini genus-group taxa. Such an analysis may also help in establishing whether *Furconthophagus*, from a systematic point of view, can be considered a subgenus of *Onthophagus* or a distinct genus, as proposed by some authors (Josso & Prévost 2006, Moretto 2007, Negrobov 2009, Negrobov & Batischcheva 2013, Moretto et al. 2019).

$A\,c\,k\,n\,o\,w\,l\,e\,d\,g\,e\,m\,e\,n\,t\,s$

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REFERENCES

- Arrow G. J. 1931: The Fauna of British India, including Ceylon and Burma. Coleoptera Lamellicornia. Part III (Coprinae). London: Taylor & Francis, 428 pp.
- BARAUD J. 1992: Coléoptères Scarabaeoidea d'Europe. Faune de France et régions limitrophes. 78. Paris-Lyon: Fédération française des Sociétés de Sciences naturelles and Société linnéenne de Lyon, ix+856 pp.
- BINAGHI G., DELLACASA G. & POGGI R. 1969: Nuovi caratteri diagnostici per la determinazione degli Onthophagus del gruppo ovatus (L.) e geonemia controllata delle specie italiane del gruppo. Memorie della Società Entomologica Italiana 48: 29–46.
- GÉNIER F. & MORETTO P. 2017: Digitonthophagus Balthasar, 1959: taxonomy, systematics, and morphological phylogeny of the genus revealing an African species complex (Coleoptera: Scarabaeidae: Scarabaeinae). Zootaxa 4248: 1–110.
- Josso J.-F. & Prevost P. 2006: Description de cinq Onthophagini nouveaux pour l'Afrique de l'Ouest (Parc du W) (Coleoptera, Scarabaeidae, Coprinae). Les Cahiers Magellanes, Hors Série 21: 1–10.
- KABAKOV O. N. 2006: Plastinčatousye žuki podsemejstva Scarabaeinae (Insecta: Coleoptera: Scarabaeidae) fauny Rossii i sopredelenyh stran [The Lamellicorn Beetle of the Subfamily Scarabaeinae (Insecta: Coleoptera: Scarabaeidae) in the Fauna of Russia and Adjacent Countries]. Moskva: Tovariŝestvo naučnyh izdanij KMK, 374 pp (in Russian).
- KABAKOV O. N & NAPOLOV A. 1999: Fauna and ecology of Lamellicornia of subfamily Scarabaeinae (Coleoptera, Scarabaeidae) of Vietnam and some parts of adjacent countries: South China, Laos and Thailand. *Latvijas Entomologs* 37: 58–96
- KHAREL B. P., SCHOOLMEESTERS P. & SARKAR S. K. 2020: A first faunistic account on the *Onthophagus* Latreille, 1802 (Coleoptera, Scarabaeidae, Scarabaeinae) of the Nadia district, West Bengal, with a preliminary checklist from India. *Check List* 16: 361–381.
- Krikken J. & Hulibregts J. 2009: Onthophagus pilularius and its close relatives in Sundaland: a taxonomic reappraisal (Coleoptera, Scarabaeidae, Scarabaeinae). *Deutsche Entomologische Zeitschrift* 56: 41–55.
- LÖBL I. & LÖBL D. 2016 (eds): Catalogue of Palaearctic Coleoptera. Volume 3. Scarabaeoidea Scirtoidea Dascilloidea Buprestoidea Byrrhoidea. Revised and Updated Edition. Leiden-Boston: Brill, 983 pp.
- MARTÍN-PIERA F. 1983: Los Onthophagini Ibero-Baleares (Col. Scarabaeoidea). I. Claves de identificación. Eos 59: 109–125.
- Martín-Piera F. 2000: Familia Scarabaeidae. Pp.: 207–432. In: Martín-Piera F. & J. I. Lòpez-Colòn J. I. (eds): Coleoptera Scarabaeoidea I. Fauna Ibérica, Volume 14. Madrid: Museo Nacional de Ciencias Naturales, CSIC, 526 pp.
- MARTÍN-PIERA F. & ZUNINO M. 1983: Amphionthophagus, nuovo sottogenere di Onthophagus Latr. (Coleoptera, Scarabaeidae). Bollettino del Museo Regionale di Scienze Naturali di Torino 1: 59–76.
- MITTAL I. C. & JAIN R. 2015: A checklist of Indian dung beetles (Coleoptera: Scarabaeidae). Indian Journal of Entomology 77: 383–404.
- MORETTO P. 2007: Partie 1. Scarabaeidae. Pp.: 115–134. In: MORETTO P. & BORDAT P. (eds): Les scarabéides coprophages du Parc National du Niokolo-Kobo au Sénégal (Coleoptera, Scarabaeoidea). Nouvelle Revue d'Entomologie (Novelle Série) 23 (2006): 115–145.
- MORETTO P., COSSON B., KRELL F.-T. & ARISTOPHANOUS M. 2019: Pollination of Amorphophallus barthlottii and A. abyssinicus subsp. akeassii (Araceae) by dung beetles (Insecta: Coleoptera: Scarabaeoidea). *Catharsius La Revue* 18: 19–36.
- Negrobov S. O. 2009: Seasonal dynamics of Scarab Beetles (Coleoptera, Lamellicornia) in Voronezh Province. Entomological Review 89: 113-115.
- Negrobov S. O. & Batischcheva E. N. 2013: Scarabaeidae family observation of Voronezh region. *Ekologiâ Centralno-Černozemnoj Oblasti Russkoj Federacii* 1–2: 140–143.
- OCHI T. & Kon M. 2007: A new species of Onthophagus (Furconthophagus) (Coleoptera, Scarabaeidae) from Nepal. *Kogane* 8: 81–84.
- D'Orbigny H. 1913: Synopsis des Onthophagides d'Afrique. Annales de la Société Entomologique de France 82: 1–742.
- Schoolmeesters P. 2020: Scarabs, World Scarabaeidae Database (version 2020-05-31). In: Roskov Y., Ower G., Orrell T., Nicolson D., Bailly N., Kirk P. M., Bourgoin T., DeWalt R. E., Decock W., van Neukerken E. & Penev L. (eds): Species 2000 & ITIS Catalogue of Life, 2020-06-04 Beta. Species 2000. Leiden: Naturalis. URL: www.catalogueoflife. org/col.

- TARASOV S. I. & SOLODOVNIKOV A. Y. 2011: Phylogenetic analyses reveal reliable morphological markers to classify megadiversity in Onthophagini dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). Cladistics 27: 1–39.
- UEDA A., DWIBADRA D., NOERDJITO W. A., SUGIARTO, KON M., OCHI T., TAKAHASHI M. & FUKUYAMA K. 2017: List of dung beetles (Coleoptera: Coprophagous group of Scarabaeoidea) collected in lowland near Balikpapan, East Kalimantan, Indonesia. *Bulletin of FFPRI* 16(2): 109–119.
- ZIANI S. (in press): Some phonetic remarks on the pronunciation of the name Onthophagus (Insecta: Coleoptera: Scarabaeidae: Onthophagini). Quaderno di Studi e Notizie di Storia Naturale della Romagna 52.
- ZIANI S. & BEZDĚK A. 2016: Scarabaeidae, subfamily Scarabaeinae, tribe Onthophagini. Pp.: 180–204. In: LÖBL I. & LÖBL D. (eds): Catalogue of Palaearctic Coleoptera. Volume 3. Scarabaeoidea Scirtoidea Dascilloidea Buprestoidea Byrrhoidea. Revised and Updated Edition. Leiden-Boston: Brill, 983 pp.
- ZIANI Ś., ABDEL-DAYEM M. S., ALDHAFER H. M. & BARBERO E. 2019: An overview of the Onthophagini from the Arabian Peninsula (Coleoptera: Scarabaeoidea: Scarabaeoidea). *Zootaxa* 4658: 1–36.
- ZUNINO M. 1979: Gruppi artificiali e gruppi naturali negli Onthophagus (Coleoptera, Scarabaeoidea). *Bollettino del Museo di Zoologia dell' Università di Torino* 1: 1–18.