

SYSTEMATICS, PHYLOGENY AND BIOGEOGRAPHY OF THE SUBGENUS *HYALONTHOPHAGUS* PALESTRINI AND GIACONE, 1988 (COLEOPTERA, SCARABAEIDAE: GEN. *ONTHOPHAGUS* LATREILLE)

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SUMMARY

Systematic, Phylogeny and Biogeography of the subgenus *Hyalonthophagus* PALESTRINI & GIACONE 1988. (Coleoptera, Scarabaeidae: gen. *Onthophagus* LATREILLE).

This paper is the fourth contribution to the study of the subgenus *Proagoderus* (genus *Onthophagus*). We reviewed the 6th group *sensu* D'ORBIGNY of *Proagoderus* as part of the overall project. Our results indicate that the nine species ascribed to the 6th group, according to literature, do not belong to *Proagoderus*, but represent a distinct subgenus, preliminary described as *Hyalonthophagus* at the XVth National Italian Congress of Entomology (L'Aquila, June 12-17, 1988).

The degree of homogeneity within the group is stressed, and a new species, *O. (H.) hyalcyon*, is also described. Furthermore, some biogeographical accounts are provided, on the basis of the close relationships between the subgenera *Hyalonthophagus* and *Trichonthophagus* and the respective phylogeny and distribution.

RIASSUNTO

La presente ricerca costituisce il quarto contributo allo studio del sottogenere *Proagoderus* (genere *Onthophagus*, *sensu* Auctorum). In tale ambito è stata effettuata la revisione del sesto gruppo *sensu* D'ORBIGNY di tale sottogenere. Le nove specie del gruppo costituiscono in realtà un sottogenere a parte, descritto (PALESTRINI & GIACONE, 1988) come *Hyalonthophagus*. Si sottolinea la notevole omogeneità del gruppo, una nuova specie, *O. (H.) hyalcyon*, viene descritta. Si intraprende inoltre un'analisi biogeografica sulla base delle strette relazioni emerse fra i sottogeneri *Hyalonthophagus* e *Trichonthophagus*.

Key words: Coleoptera, Scarabaeidae, genus *Onthophagus*, subgenus *Hyalonthophagus*, Africa.

INTRODUCTION

In previous papers (see PALESTRINI, 1982b, 1983, 1984, 1985 and 1988) systematical, phylogenetical and biogeographical aspects of some Indoafriean groups of *Onthophagini* have been discussed. The present paper is the fourth study on the Indoafriean subgenus *Proagoderus* (genus *Onthophagus*). The subgenus *Pro-*

*agoderus** was described in 1883 by LANSBERGE; currently over one hundred species are known. In 1913 D'ORBIGNY classed them in 9 groups mainly for practical purposes. In 1917 MARCUS had suggested that D'ORBIGNY's classification was incomplete. He also questioned D'ORBIGNY's specific diagnoses because not only was it inadequate, but it did not make use of the evolutionary approach which in turn has to be integrated by eco-geographical data. Recent advances in the systematics of Scarabaeidae confirm that the classification of D'ORBIGNY requires a deep revision.

In this paper we only consider D'ORBIGNY's sixth group, also known as the *O. alcyon* group which is very homogeneous, as our research confirms. This is consistent with MARCUS.

However, our results also show that the nine species ascribed in literature (D'ORBIGNY, 1913; FERREIRA 1967, 1972) to the 6th group of the subgenus *Proagoderus* must be separated from this subgenus. A comparative analysis of their anatomy and physiology stresses the very high degree of homogeneity as a group and does not confirm their belonging to the subgenus *Proagoderus*.

Considering the above mentioned and the degree of differences occurring amongst the recently revised subgenera of *Onthophagus* (KABAKOV, 1979; MARTÍN PIERA & ZUNINO, 1983; PALESTRINI, 1980, 1982 a; VAROLA & ZUNINO, 1981; ZUNINO, 1979), the group represents a subgenus, which we named *Hyalonthophagus*.

SUBGEN. HYALONTHOPHAGUS PALESTRINI & GIACONE, 1988

The subgenus *Hyalonthophagus* is defined by the following combinations of characters.

Head: smooth or non granulated surface which (Fig. 1) may be slightly punctate with some large punctures; vertex with horn, or tubercle or a flattened carina, sometimes with a central tooth; pronotum smooth or with a few large punctures (simple or raspous) or entirely with simple punctures (sometimes anteriorly and laterally raspous). Cephalic portion of the pronotum simple or with a small median groove. Caudal margin prolonged into a strong angle, often blunt; elytra: very tapered caudally, laterally straight or slightly concave, with a depression next to the humeral callus; interstriae prevalently smooth or granulated; length: 5,5 - 10,5 mm.

Male. Primitive phallosome with slightly elongated and rounded parameres apices. Plain copulating lamella (Fig. 2) developing mainly lengthwise with a complex transverse ridge dividing it asymmetrically. The apex of the larger side of the principal lamella articulates with a secondary lamella, more or less complex depending on the species. Three orders of raspulae, one of which may connect with the lamellar spinous belt, though it is separate. This raspula appears to be exclusive to the subgenus.

Female. Vagina: the ventral wall shows a sideways E-shaped sclerotization (Fig. 2), the middle branch of which joins the groove of the insertion of the infundibulum (Fig. 2).

The apical portion of the vagina expands in varying degrees and has small cerebroid folds. Infundibulum: little or no sclerotization (Fig. 2) in the basal portion of the tubular tract.

*PAULIAN (1986), from a strictly nomenclatorial point of view, refers to the 2nd edition of the International Code of Zoological Nomenclature (I.C.Z.N.) (that does not mention the "nomen oblitum" rule considered by the 1st edition) and considers *Proagoderus* LANSBERGE, 1883, to be synonym of *Onthotrogus* MOTSCHULSKY, 1859. At any rate, this latter name became immediately out of use, whereas the LANSBERGE's continued to be used.

We feel that PAULIAN's approach, formally quite correct, is not completely in accordance with the main aim of the I.C.Z.N., which is to provide the maximum stability of nomenclature.

Therefore we decided, waiting for any further development of the above, to use the LANSBERGE's name, *Proagoderus*.

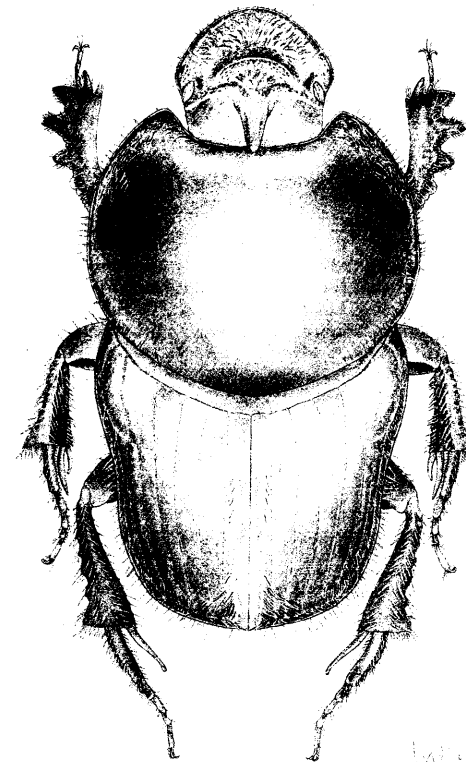


Fig. 1: *Onthophagus (Hyalonthophagus) alcyon* KLUG, male habitus.

Typus subgeneris: *Onthophagus viridiceps* D'ORBIGNY, 1911, *Bull. Mus. Hist. nat.*, 1910, 6: 308-309. Holotype described from Uganda and former British East Africa.

The subgenus *Hyalonthophagus* includes ten species: *O. alcyon* KLUG, *O. alcedo* D'ORBIGNY, *O. alcyonides* D'ORBIGNY, *O. hyalcyon* n. sp., *O. mixtifrons* D'ORBIGNY, *O. nigroviolaceus* D'ORBIGNY, *O. pseudoalcyon* D'ORBIGNY, *O. pseudovirens* D'ORBIGNY, *O. virens* D'ORBIGNY and *O. viridiceps* D'ORBIGNY.

Key to species of the subgenus *Hyalonthophagus*

The following keys are more informative than usual. We included all the morphological characters of a certain significance, mainly in order to avoid repetitive description of every species.

As a rule, such descriptions do not give any useful information for the identification of species that can be correctly reached only by means of an accurate dissection of the specimen.

- 1(18) Pronotum slightly punctured except for the antero-lateral portion, where the sculpture is more marked. Elytral striae narrow, except for the first one or the first two. Interstriae on the elytral disk with light punctures. Pygidium with distinct simple punctures. In general head with light punctures.

- 2(17) Elytral interstriae with fine but distinct punctures on the disk.
- 3(8) Pygidium with very marked, spaced punctures with finer punctation in-between.
- 4(5) Females with frontal carina gently arched, vertex carina long and straight. Males with front carina short, straight and not very evident. Vertex carina positioned forward, evident in the middle forming a triangular based horn with two lateral effaced teeth. Anterior portion of the head densely punctured with a small number of larger punctures; remaining surface finely punctured. Length 9 mm. Max. width 5 mm posteriorly to the humeral callus *alcyon* KLUG
- 5(4) Females with a long straight, or nearly straight distinct vertex carina which may be more elevated in the middle.
- 6(7) Base of pygidium intensely punctured; remaining surface sparsely punctate with some large and very few fine punctures. Lateral declivity of the pronotal base above the posterior angles and sides of the pronotal shield often with large, marked punctures. Elytral sides mostly distinctly punctate; some punctures, mainly near the apex, even more marked. Head surface feebly punctulate, with more consistent punctures anteriorly. Length 9 mm. Max. width 3.8 mm post. to the humeral callus *hyalcyon* n. sp.
- 7(6) All the pygidial surface with scattered punctures of different size. Pronotum devoid of basal declivities; no marked punctures. Elytral sides barely punctulate, occasionally with a few marked punctures. Head surface with fine, but distinct punctures. Length 11 mm. Max. width 5.5 mm post. to humeral callus *alcyonides* D'ORBIGNY
- 8(3) Pygidium with weak or moderately marked punctures, more or less dense.
- 9(10) Head surface densely punctulated, with some sizeable rasposus punctures. Elytral surface devoid of anterior depression, or with a small depression on the bases of the 4th interstriae, even extending to the 5th. Elytral sides and apices punctate.

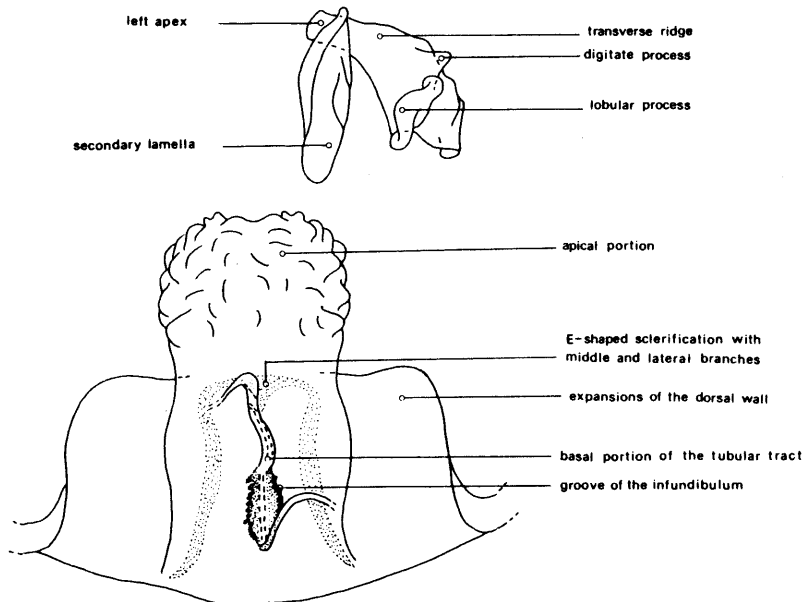


Fig. 2: General scheme illustrating the several parts of vagina and copulating lamella.

- Basal declivities of the pronotum very gentle, their surfaces with some large punctures extending just above. Pygidium punctures relatively strong, very dense or sparse. Length 9.5 mm. Max. width 5 mm. post. to the humeral callus *mixtifrons* D'ORBIGNY
- 10(9) Head surface very thickly punctate forward. Pygidium quite densely punctate.
- 11(16) Elytral surface devoid of anterior depression, or merely with a very slight one on the 2nd interstria.
- 12(13) Second elytral interstria markedly convex at the base, only slightly depressed at the anterior third, flat or barely convex on the back. Elytral sides finely punctate, with at least a few larger punctures towards the apex and on the outer edge. Basal sides of the pronotal shield gently curved near the posterior angles, with a single line of punctures along the edge. Punctures tend to be finer on the declivity and just above it. Head surface densely or anteriorly more sparsely punctulated with few irregular larger punctures. Male head armed with a horn situated in correspondence to the anterior rim of the eyes or more forward. The horn base extends laterally on either side into a fine carina which slants backwards to the posterior eye rim. Female: vertex carina short, straight or just slightly curved, with a marked median tooth and blunt apices. Such a carina situated a little posteriorly to the middle of the interocular space occupies about half the distance between eyes. Length 9.5 mm. Max. width 5 mm post. to the humeral callus *alcedo* D'ORBIGNY
- 13(12) Second elytral interstria flat or slightly convex lacking the depression towards the anterior third. Head finely and rather densely punctate. Female with vertex carina simple, straight or nearly straight, situated just behind the posterior rim of the eyes.
- 14(15) Basal sides of the pronotal shield slightly curved, with nearly imperceptible punctures up to the posterior angle, with the exception of a row of medium sized punctures along the margin. At times one or two isolated, fine, distinct punctures. Elytral surface with punctures of irregular size, occasionally some larger punctures. Male head armed with a vertex horn situated in correspondence to the anterior rim of the eyes. On either side its base forms a laminar, triangular, evenly thin arched carina, extending backward up to the posterior rim of the eye. Female: vertex carina long but extending through all the interocular space. Length 10 mm. Max. width 5 mm post. to the humeral callus *virens* D'ORBIGNY
- 15(14) Basal sides of the pronotal shield with very narrowly but strongly curved angles. Some large punctures near the edge and some others on the declivity beyond. Some rather fine punctures on the posterior angles and next to the declivity. Elytral disk with punctures of irregular size; larger punctures along the outer margin and apices. Female: vertex carina straight extending through more than half of the interocular space. Length 9.5 mm. Max. width 4.5 mm post. to the humeral callus *pseudovirens* D'ORBIGNY
- 16(11) Elytral surface with a marked transverse depression on the whole front third. Second interstria convex backward. Elytral sides (punctate in varying degrees). First interval with more marked punctures. Basal declivities of the pronotum very narrow with a transversal row of large punctures along the edge. A few larger punctures scattered just above. Pygidium with very dense and irregular punctures, normally veiled by setae. Head very strongly and intensely punctate. Male vertex with a horn in the center, just in front of the anterior rim of the eye. Its base extends on both sides with a short and nearly straight carina. Female vertex carina rather short, slightly arched or nearly straight, distinct and located between the anterior eyerims, taking up roughly half of the interocular space. Length 10 mm. Max. width 5 mm post. to the humeral callus *viridiceps* D'ORBIGNY
- 17(2) Elytral interstriae with very fine punctures on the disk, and with a few large punctures at the apex of the 1st, 3rd, 5th and 6th; the 7th and 8th with numerous well marked, punctures along its length except on the humeral callus. Pygidium with marked, moderately close punctures mixed with smaller ones. Length 9-10 mm. Max. width 5.5 mm post. to the humeral callus *pseudoalcyon* D'ORBIGNY

- 18(1) Pronotal punctures of irregular size, dense and raspy forward in the anterior portion. Elytral striae wide, double, strongly punctate. Interstriae with dense, granulate or raspy punctures. Pygidium with irregular, coarse raspy punctures. Head margin rounded, surface with scarce, irregular, but very conspicuous punctures mixed with fine scattered ones. Length 7 mm. Max. width 4 mm post. to the humeral callus *nigroviolaceus* D'ORBIGNY

O. (*Hyalonthophagus*) *alcyon* KLUG

KLUG, 1855. *Monatsber. Akad. Berlin*, 1855, 20: 653.

Described from Mozambique: Tete and Sena. Known from Tanzania, Kenya, Zimbabwe (formerly: Rhodesia), Mozambique, Botswana, Natal and Transvaal.

The following typical material was examined: Lectotype (herein designated): a male from Mozambique: Tete and Sena (M. Nat. H. Univ. Collection, Berlin). Paralectotype: a female from Mozambique: Tete and Sena. (M. Nat. H. Univ. Collection, Berlin).

Specimens from all the above mentioned countries were examined.

Male genitalia (Figs. 3 a, b, c, d, e, f, and g).

Parameres moderately elongated with slightly divergent, rounded apices and a finely dentate or serrate appearance. Copulating lamella complex with a transverse ridge extending to the left of the lamella. Secondary lamella developing from its diversified apex, lengthwise and wider in the middle portion with a reflected lobe rich in squamous elements.

Raspulae (Figs. 3 e, f and g):

—(Fig. e) formed by sparse, minute spines with a single complex of elongated sclerotized processes.

—(Fig. f) formed by reduced squamoid elements.

—(Fig. g) formed by extremely elongated, large squamae parallel oriented. This kind of raspula appears related to the lamellar belt, without belonging to it.

Female genitalia (Figs. 3 h and i). The vagina quite large on the whole. Apical portion relatively small and more or less sclerotized, small cerebriform folds are present throughout. Dorsal wall: lateral growths with a relatively low degree of sclerotization; folds develop lengthwise. Ventral wall with support sclerotization forming a sideways E-shape; its scarcely developed middle branch joins the excavation of the infundibulum insertion whilst lateral branches have a bottle-neck in the subapical tract. Infundibulum long and highly sclerotized in the groove; margins not linear. Basal portion clearly not continuous in the tubular tract, which is quite well developed.

O. (*Hyalonthophagus*) *alcedo* D'ORBIGNY

D'ORBIGNY, 1913. *Syn Onth. Afr.*, 82: 553.

Described from Zimbabwe (formerly Rhodesia): Zambesi, Sebakwe; Botswana; Transvaal: Shilouvane. Known from Zimbabwe, Botswana, Transvaal, Zambia and Tanzania.

Lectotype (herein designated): a male from Botswana (M.N.H.N. Collection, Paris). Paralectotypes: a male from Zimbabwe: Sebakwe (M.N.H.N. Collection, Paris); a female from Zimbabwe: Sebakwe (M.N.H.N. Collection, Paris).

Moreover, material from all above mentioned countries was examined.

Male genitalia (Figs. 4 a, b, c, d, e, f, and g).

Parameres elongated with slightly divergent rounded apices ending with a minute tooth. Copulating lamella with a highly developed transverse ridge with a subquadratic shape showing a subtriangular digitate prominence. Secondary lamella elongated and spatula shaped. Three orders of regular raspulae.

Female genitalia (Figs. 4 h and i). Apical vaginal tract with marked cerebriform

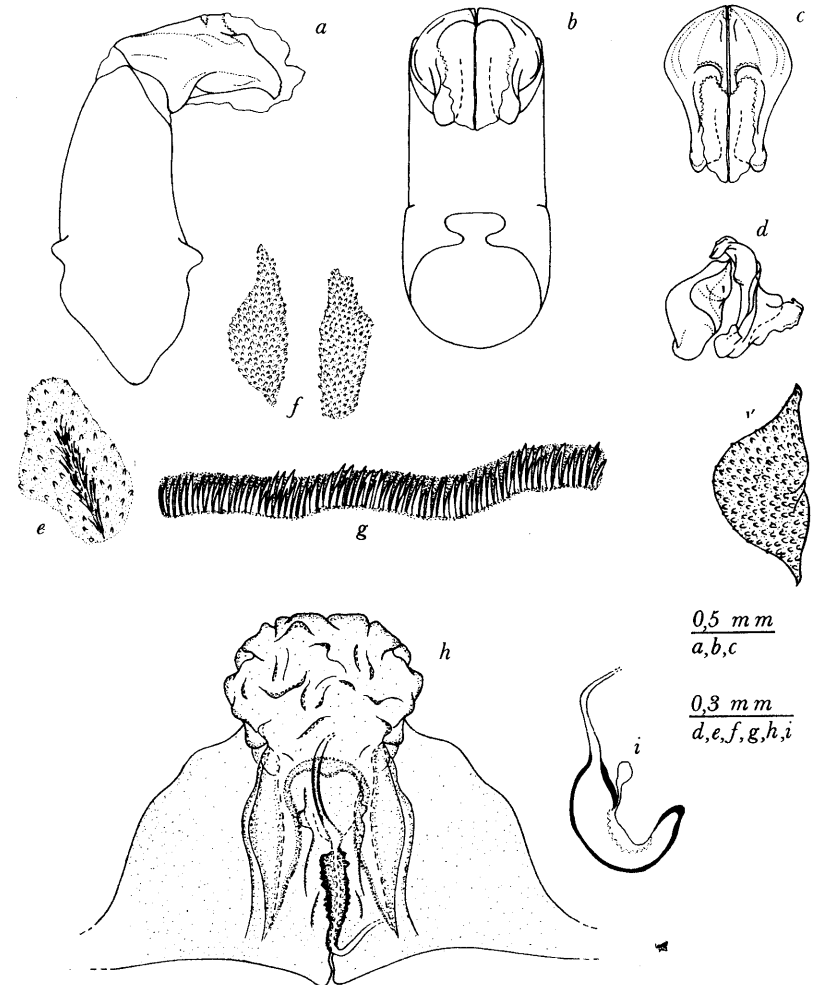


Fig. 3: *Onthophagus (Hyalonthophagus) alcyon* KLUG. Male genitalia: phallosome (a, b); parameres, dorsal view (c); copulating lamella (d); secondary lamella (1), secondary lamella at a higher magnification (1'); raspulae (e, f, g). Female genitalia: vagina, ventral view (h); receptaculum seminis (i).

folds and a medium degree of sclerotization. Ventral wall with mainly transverse development and a sideways E-shaped sclerotization. Infundibulum highly sclerotized in the groove, which expands irregularly towards the apex. Basal portion visibly discontinuous.

O. (*Hyalonthophagus*) *alcyonides* D'ORBIGNY

D'ORBIGNY, 1913. *Syn. Onth. Afr.*, 82: 551-552.

Described from Botswana: Lake Ngami; Transvaal: Shilouvane near Leydsdorp;

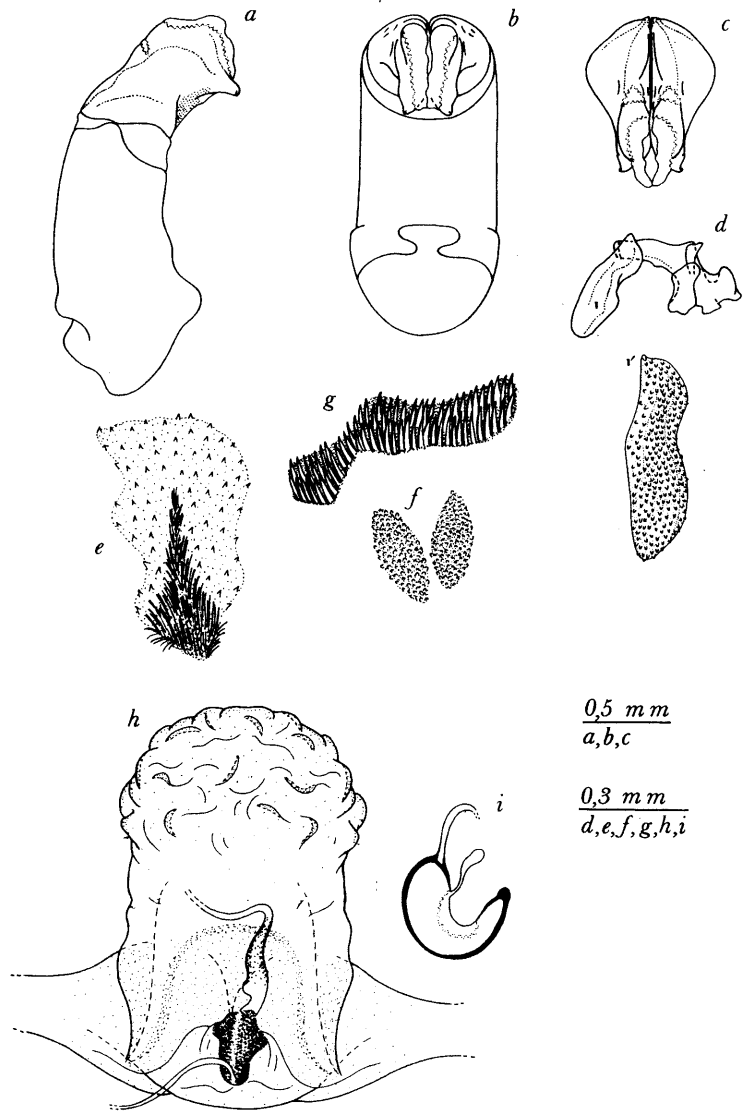


Fig. 4: *Onthophagus (Hyalonthophagus) alcedo* D'ORBIGNY. Male genitalia: phallosome (a, b); parameres, dorsal view (c); copulating lamella (d): secondary lamella (1), secondary lamella at a higher magnification (1'); raspulae (e, f, g). Female genitalia: vagina, ventral view (h); receptaculum seminis (i).

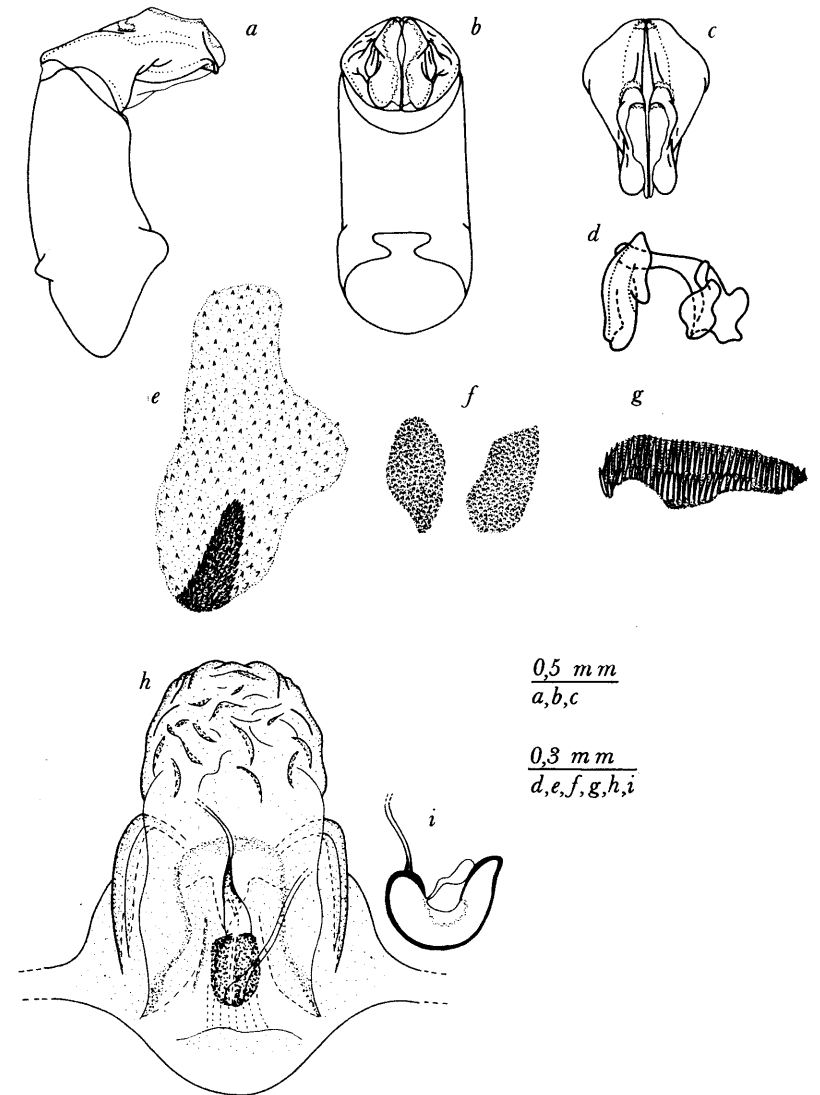


Fig. 5: *Onthophagus (Hyalonthophagus) alcyonides* D'ORBIGNY. Male genitalia: phallosome (a, b); parameres, dorsal view (c); copulating lamella (d); raspulae (e, f, g). Female genitalia: vagina, ventral view (h); receptaculum seminis (i).

Natal: Ladysmith; Cape Town Province: Port Elisabeth. Known from Transvaal, Southern Africa, Natal, Mozambique and Botswana.

The following typical material was examined: Lectotype (herein designated): a male from Transvaal: Shilouvane (M.N.H.N. Collection, Paris), Paralectotypes: 2 males from Transvaal: Shilouvane (M.N.H.N. Collection, Paris); 3 females from Transvaal: Shilouvane (M.N.H.N. Collection, Paris); 1 female from Botswana: Lake Ngami (M.N.H.N. Collection, Paris); 1 female from Natal: Ladysmith (M.N.H.N. Collection, Paris). Specimens of other findings from all the above mentioned countries were examined.

Male genitalia (Figs. 5 a, b, c, d, e, f, and g). Parameres slightly elongated with markedly rounded apices. Copulating lamella with a discontinuous development of the transverse ridge with a digitate prominence at the apex. Secondary lamella spatula-shaped, complicated by secondary reflective plicae folded back. Three orders of regular raspulae.

Female genitalia (Figs. 5 h and i). Vagina, generally with a mainly longitudinal development. A number of cerebroid folds in the expanded apical tract. Dorsal wall with lateral growths tending to be complex, scarcely expanded and sclerotized. Ventral wall: sideways E-shaped sclerotization, the middle branch of which is not especially developed, joins the excavation of the infundibulum insertion. Lateral branches, elongated with a bottle-neck in the middle portion. The groove of the infundibulum highly sclerotized and with very definite edges. Basal portion clearly discontinuous.

O. (*Hyalonthophagus*) *hyalcyon* n. sp.

Type material. Holotype: a male from Tanzania: Dodoma District (3000 ft) (British Museum N.H. Collection, London). Paratypes: a female from Tanzania: Dodoma District (3000 ft) (British Museum N.H. Collection, London); a male from Mozambique: Delagoa (M. Zunino Collection, Turin).

Description. Length 9 mm. Max. width 5 mm post. to the humeral callus.

Head and pronotum shiny black with metal green highlights. Elytra and pygidium chestnut brown with weak green highlights. Leg surface and antennae brown. Head with light, sparse, minute and straight setae. Pronotum setae light, thin, minute and flattened, mainly located along the sides. Elytra setae light and mainly grown at the apex and along outer margins. Setae on the pygidium light, erect. Clypeus margin rounded, folded inwards. Genae flattened and suturae genales marked.

Male front carina short, arched and not especially raised. The vertex carina is rather forward, raised in the middle with a triangular based horn. Female front carina arched; the vertex one straight and long. Head surface slightly punctulate, with more consistent punctures anteriorly. Lateral declivity of the pronotal base above the posterior angles and sides of the pronotal shield often with large, marked punctures. Micro-sculpture reticulate; pronotum with a small border, apparently uninterrupted; the medial line not visible. Elytral striae narrow except for the first or the first two; punctures marked. Interstriae finely punctate and mixed in with even smaller punctures. A few large and irregular punctures on the apex. Juxta-sutural interstriae convex posteriorly.

Microsculpture shining reticular. Both basal and free margin of pygidium with continuous border. Base of pygidium intensely punctate; remaining surface sparsely punctate with some large and very few fine punctures.

Male genitalia (Figs. 6 a, b, c, d, e, f and g). Parameres elongated, laterally curved, apices smallish, divergent and slightly blunt. Transverse ridge of the copulative lamella evident, strong but not continuous, the apex produced in a digitate process followed by a second, lobular one, directed longitudinally. Secondary lamella elongated, spatula shaped, folding back over the left lateral edge. Three orders of regular raspulae.

Female genitalia (Figs. 6 h and i). Apical portion of the vagina scarcely expanded, more or less sclerotized, with many small cerebroid folds. Expansions of the dorsal wall wide, scarcely sclerotized. Ventral wall longitudinal, strengthened by a sideways E-shaped sclerotization. Middle branch of such sclerotization hardly developed, joining the excavation of the infundibulum insertion. Lateral branches elongated, not regularly straight, but sinuous. Infundibulum highly sclerotized, mainly in the groove portion; this one elongated, with several lateral expansions, more strongly sclerotized. Basal portion of the tubular tract devoid of sclerotization.

O. (*Hyalonthophagus*) *mixtifrons* D'ORBIGNY

D'ORBIGNY, 1911. *Bull. Mus. Hist. nat.*, 1910, 6: 308.

Described from Southern Ethiopia: Endessa, High Awash (between Yaba and Endessa). Also mentioned in the 'Afrique Orientale Anglaise'.

Known from Southern Ethiopia, Kenya and Tanzania.

We examined the following typical material: Lectotype (herein designated): a male from Southern Ethiopia: High Awash (M.N.H.N. Collection, Paris). Paralectotype: a male from Southern Ethiopia- High Awash (M.N.H.N. Collection, Paris).

Moreover, material from all the above mentioned countries was examined.

Male genitalia (Figs. 7 a, b, c, d, e, and f). Parameres moderately elongated with rounded divergent apices ending with a small tooth. Copulating lamella with complex transverse ridge; secondary lamella elongated.

Due to the limited amount of available material we were unable to examine raspulae in detail: those observed are regular (Figs. e and f).

Female genitalia (Figs. 7 g and h). Cephalic portion of vagina more or less sclerotized, scarcely expanded, having thin cerebroid folds which are replaced in the caudal portion with folds longitudinally oriented. Dorsal wall: lateral growths relatively developed, low degree of sclerotization. Ventral wall with longitudinal development generally not too elongated. Support sclerotization is of a sideways E-shape, though rather short and thick; the middle branch is well developed and highly sclerotized. Lateral branches markedly arched at the base. Infundibulum groove markedly sclerotized, elongated and with linear margins. Basal portion markedly discontinuous.

O. (*Hyalonthophagus*) *nigroviolaceus* D'ORBIGNY

D'ORBIGNY, 1902. *Ann. Soc. ent. Fr.*, 1902, 71: 291-292.

Described from Senegal and Gambia: Sédhiou. Known from Senegal, Gambia, Ivory Coast and Guinea.

We examined the following typical material: Lectotype (herein designated): a male from Gambia: Sédhiou (M.N.H.N. Collection, Paris). Paralectotype: a male from Gambia: Sédhiou (M.N.H.N. Collection, Paris).

Moreover, material from Senegal, Guinea Bissau (former Portuguese Guinea) and Gambia was examined.

Male genitalia (Figs. 8 a, b, c, d, e, f, and g). Phalloteca small. Parameres slightly elongated with rounded and barely divergent apices.

Copulating lamella with a highly complex transverse ridge, secondary lamella elongated with a clear reflective fold.

Raspulae, on the whole, regular except for the one presumed to be in contact with the lamellar spinous fascia where scales are concentrated and slightly elongated.

Female genitalia (Figs. 8 h and i). Vagina minute with no great development of the apical portion; cerebroid folds small. Dorsal wall with reduced and relatively sclerotized growths.

The sideways E-shaped sclerotization is quite complex, the middle branch joining the infundibulum excavation. Lateral branches show a limited lateral secondary cephalic expansion.

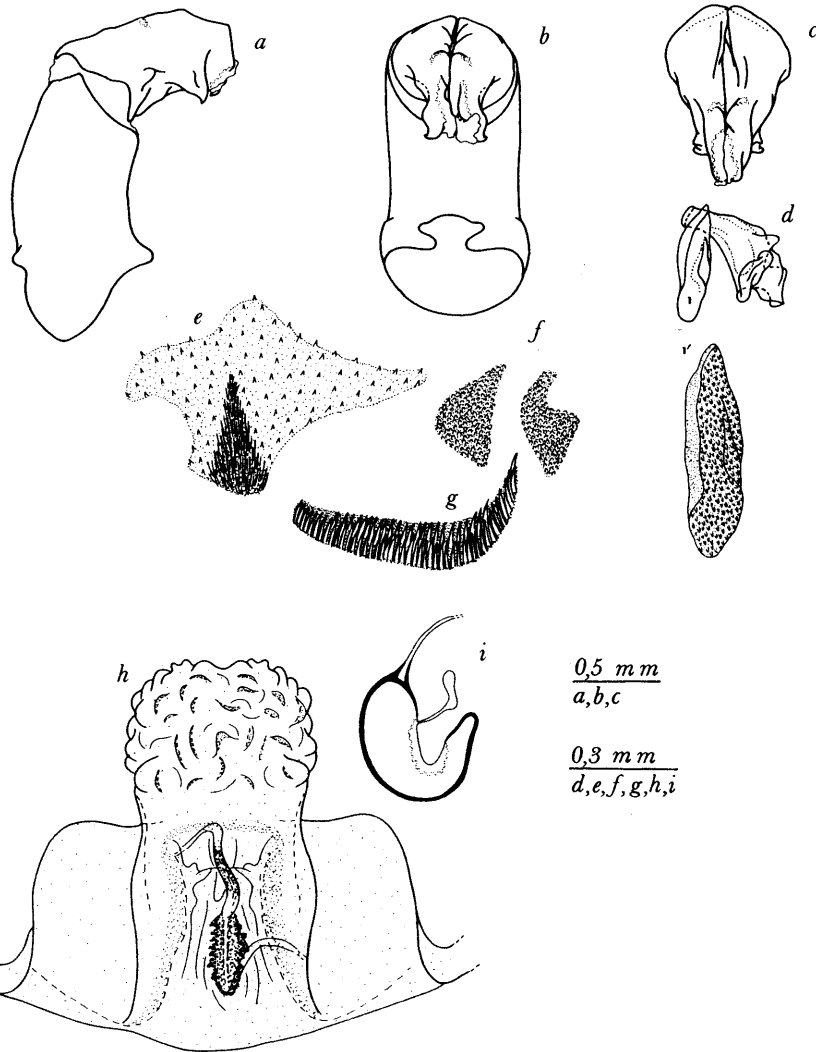
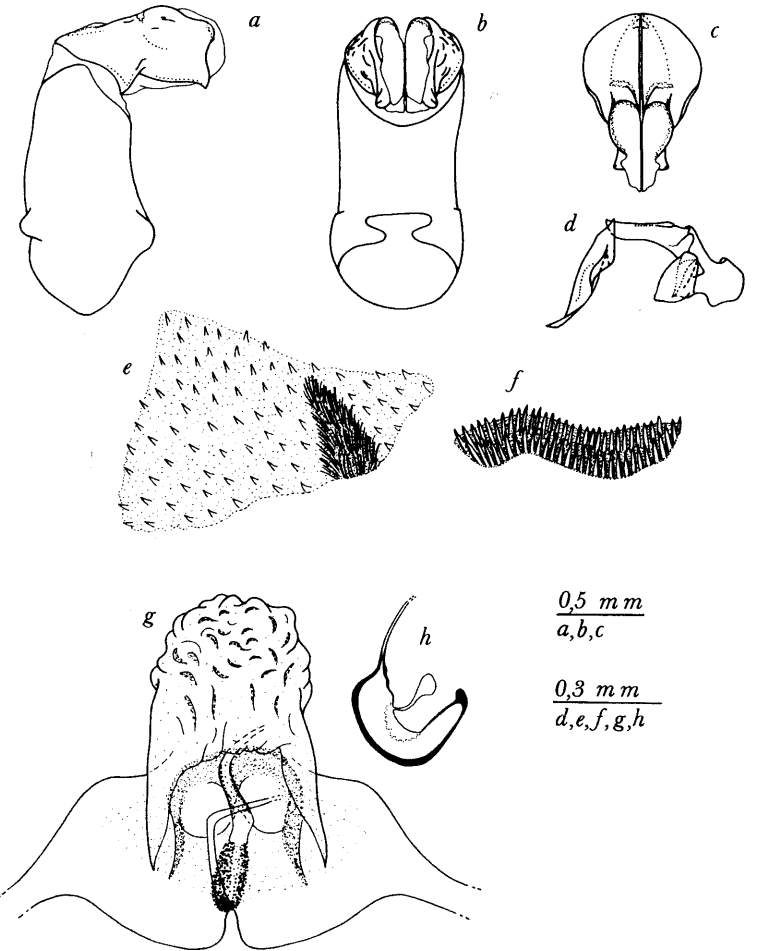


Fig. 6: *Onthophagus (Hyalonthophagus) hyalcyon* n. sp. Male genitalia: phallosome (a, b); parameres, dorsal view (c); copulating lamella (d); secondary lamella (1), secondary lamella at a higher magnification (1'); raspulae (e, f, g). Female genitalia: vagina, ventral view (h); receptaculum seminis (i).

$\frac{0,5 \text{ mm}}{a, b, c}$

$\frac{0,3 \text{ mm}}{d, e, f, g, h, i}$



$\frac{0,5 \text{ mm}}{a, b, c}$

$\frac{0,3 \text{ mm}}{d, e, f, g, h}$

Fig. 7: *Onthophagus (Hyalonthophagus) mixtifrons* D'ORBIGNY. Male genitalia: phallosome (a, b); parameres, dorsal view (c); copulating lamella (d); raspulae (e, f). Female genitalia: vagina, ventral view (g); receptaculum seminis (h).

The groove portion of the infundibulum relatively sclerotized, expanded, with well defined non-linear margins. Basal portion of the tubular tract discontinuous.

O. (Hyalonthophagus) pseudoalcyon D'ORBIGNY

D'ORBIGNY, 1913. *Syn. Onth. Afr.*, 82: 555.

Described from Senegal, Guinea, Central African Republic: Fort Crampel. Known from Senegal, Guinea, Ivory Coast, Central African Republic, Zaire.

We examined the following typical material: Lectotype (herein designated): a male from the Central African Republic: Fort Crampel (M.N.H.N. Collection,

Paris). Paralectotype: a male from the Central Africa Republic: Fort Crampel (M.N.H.N. Collection, Paris).

Moreover, material from all the above mentioned countries was examined.

Male genitalia (Figs. 9 a, b, c, d, e, f, and g). Parameres not particularly elongated, with rounded, slightly divergent apices. Copulating lamella highly complex with transverse ridge developing into minute rounded processes. Secondary lamella spatula-like with a markedly subtriangular shape. The left lateral margin with a large reflective fold.

Three orders of regular raspulae.

Female genitalia (Figs. 9 h and i). Vagina with the apical portion not particularly developed, varying degrees of sclerotization, small cerebroid folds. Dorsal wall with comparatively small lateral expansions with a high degree of sclerotization, especially in the folds. Ventral wall developing longitudinally with

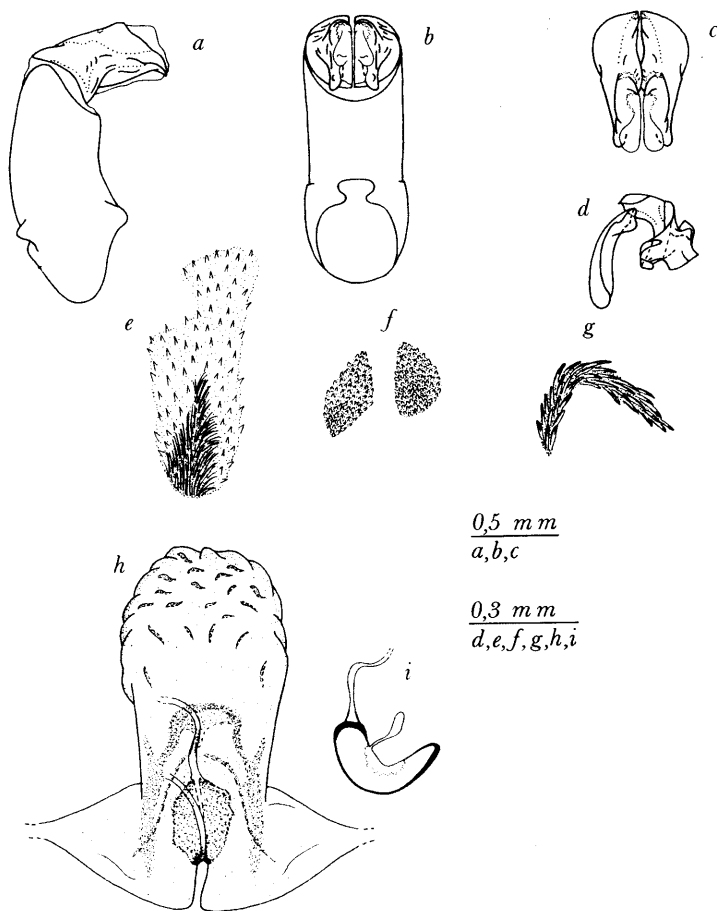


Fig. 8: *Onthophagus (Hyalonthophagus) nigroviolaceus* D'ORBIGNY. Male genitalia: phallosome (a, b); parameres, dorsal view (c); copulating lamella (d); raspulae (e, f, g). Female genitalia: vagina, ventral view (h); receptaculum seminis (i).

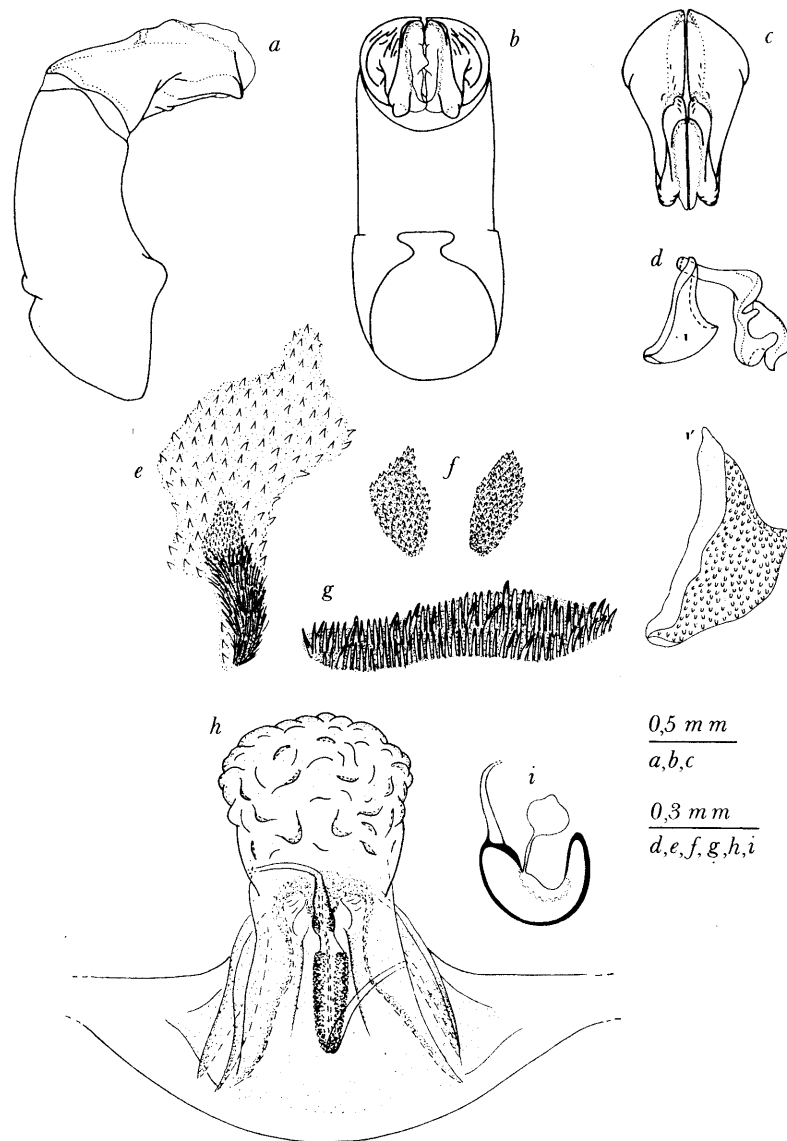


Fig. 9: *Onthophagus (Hyalonthophagus) pseudoalcyon* D'ORBIGNY. Male genitalia: phallosome (a, b); parameres, dorsal view (c); copulating lamella (d); secondary lamella (1), secondary lamella at a higher magnification (1'); raspulae (e, f, g). Female genitalia: vagina, ventral view (h); receptaculum seminis (i).

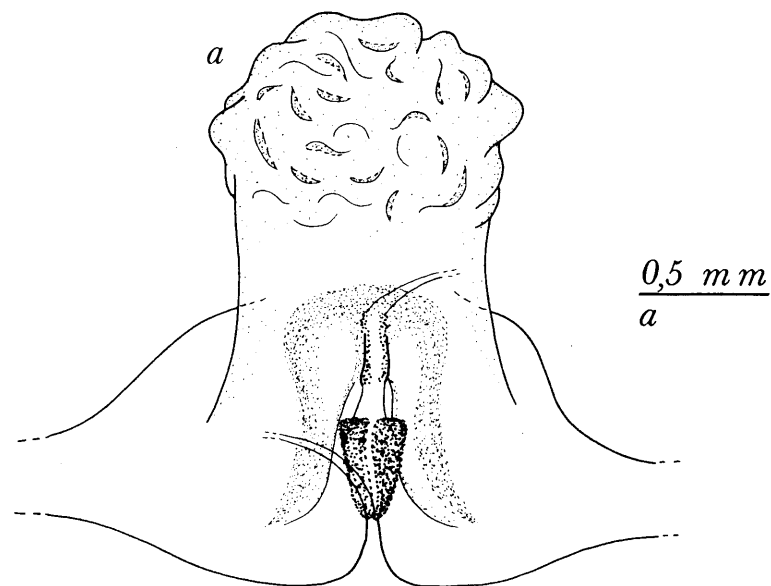


Fig. 10: *Onthophagus (Hyalonthophagus) pseudovirens* D'ORBIGNY. Male genitalia: vagina, ventral view (a).

sideways E-shaped sclerotization, the middle branch of which joins the excavation of the infundibulum insertion, lateral branches well developed with a marked sub-apical narrowing.

Infundibulum highly sclerotized, especially in the groove which is elongated and has well defined margins. Basal portion of the tubular tract clearly discontinuous.

O. (Hyalonthophagus) pseudovirens D'ORBIGNY

D'ORBIGNY, 1913. *Syn. Onth. Afr.*, 82: 554.

Described from Mozambique: Lugenda. Known from: Mozambique. We only examined the type. Holotype by monotypy, a female (M.N.H.N. Collection, Paris).

Female genitalia (Fig. 10a). Vaginal apical portion: no marked expansion with a varying degree of sclerotization. Cerebroid folds small.

Dorsal wall comparatively large and scarcely sclerotized lateral expansions; ventral wall developed lengthwise and scarcely sclerotized—except for the rather limited sideways E-shaped sclerotization. Infundibulum with a high degree of sclerotization, especially in the groove which is elongated and has linear rims. Basal portion of the tubular tract of the infundibulum markedly discontinuous.

O. (Hyalonthophagus) virens D'ORBIGNY

D'ORBIGNY, 1913. *Syn. Onth. Afr.*, 82: 553-554.

Described from: Tanzania: Mpwapwa. Known from: Tanzania.

We examined the following typical material: Lectotype (herein designated): a

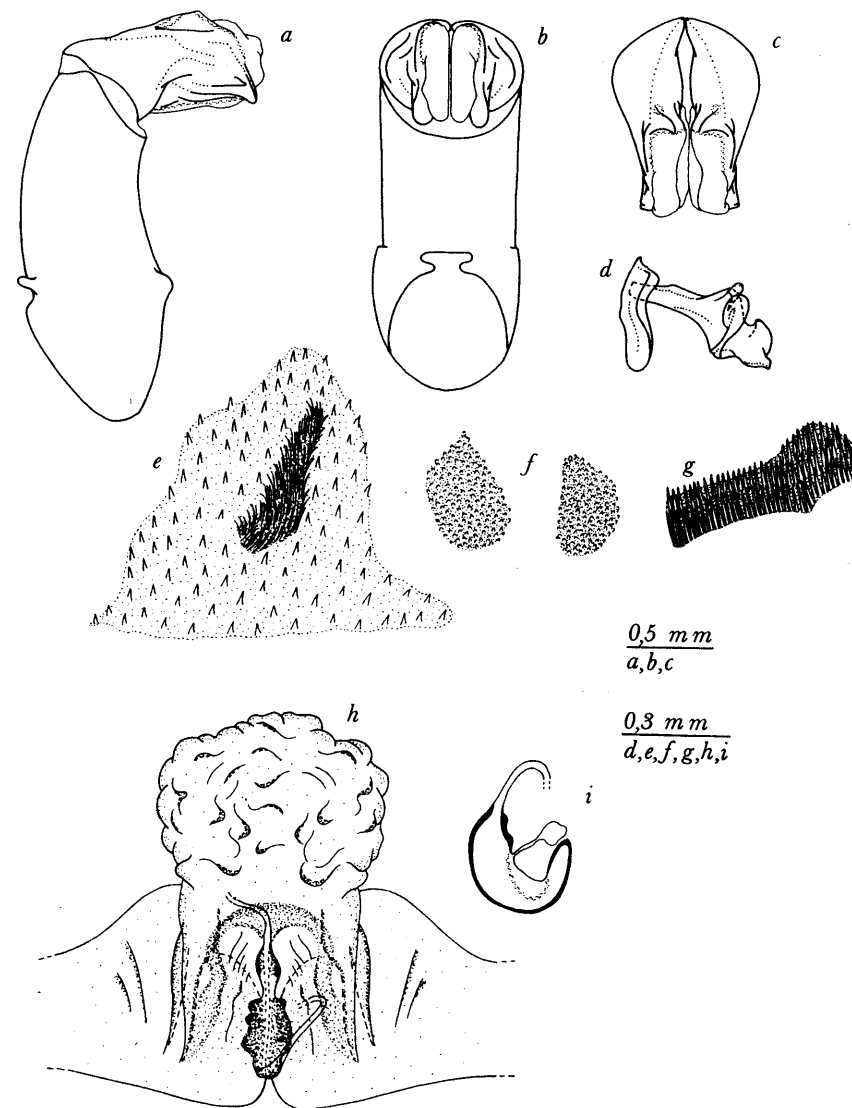


Fig. 11: *Onthophagus (Hyalonthophagus) virens* D'ORBIGNY. Male genitalia: phallosome (a, b); parameres, dorsal view (c); copulating lamella (d); raspulae (e, f, g). Female genitalia: vagina, ventral view (h); receptaculum seminis (i).

male from Tanzania: Mpwapwa (M.N.H.N. Collection, Paris). Paralectotypes: 2 males from Tanzania: Mpwapwa (M.N.H.N. Collection, Paris); a female from Tanzania: Mpwapwa (M.N.H.N. Collection, Paris).

Moreover non typical material also from Tanzania was examined.

Male genitalia (Figs. 11 a, b, c, d, e, f, and g). Parameres not especially elongated, with rounded apices and a smallish, barely rounded lateral ridge. Copulating lamella with a discontinuous transverse ridge and a digitate apical expansion. Secondary lamella elongated with a marked carina on the right lateral margin. Three orders of regular raspulae.

Female genitalia (Figs. 11 h and i). Vagina: apical portion relatively expanded with longitudinal cerebroid folds. Dorsal wall with large lateral growths slightly sclerotized and longitudinal plicae. Ventral wall with sideways E-shaped sclerotization, the middle branch of which joins the excavation of the infundibulum insertion. Lateral branches narrow in the middle portion. Infundibulum groove highly sclerotized with a marked, wavy and more intensely sclerotized margin. Basal portion discontinuous.

O. (*Hyalonthophagus*) *viridiceps* D'ORBIGNY

D'ORBIGNY, 1911. *Bull. Mus. nat.*, 1910, 6: 308-309.

This taxon reported as "*O. alcyon* var. *viridiceps* nov." on the basis of material from Kenya: Oukamba, Teita (D'ORBIGNY, *Ann. Soc. ent. Fr.*, 1902: 291) and then subsequently upgraded to a species (D'ORBIGNY 1911: 308-309). Known from Uganda, Kenya, Tanzania and Somalia.

We examined the following typical material: Lectotype (herein designated): a male from Kenya: Teita (M.N.H.N. Collection, Paris). Paralectotype: a female from Kenya, Teita (M.N.H.N. Collection, Paris).

Moreover, material from all the above mentioned countries was examined.

Male genitalia (Figs. 12 a, b, c, d, e, f, and g). Parameres moderately elongated with barely divergent and definitely rounded apices. Copulating lamella relatively developed on the whole, transverse ridge distinct and markedly discontinuous. Left portion of the lamella squat and scarcely developed. Secondary lamella elongated, spatula-like with plicae folding back on the left lateral margin and roughly as long as the branch itself. Three orders of regular raspulae.

Female genitalia (Figs. 12 h and i). Vagina small and prevalently longitudinal; its cephalic portion scarcely expanded and sclerotized, with small cerebroid folds. Dorsal wall: lateral expansions limited with folds scarcely sclerotized.

Sideways E-shaped support sclerotization with a well developed middle branch joining the excavation of the infundibulum insertion. Infundibulum highly sclerotized, especially in the diamond-shaped groove, the margins of which are not very well defined.

DISCUSSION

We examined sample specimens of nearly all the *Onthophagus* species, which literature ascribes to the subgenus *Proagoderus*. No character which can be interpreted as a synapomorphy was shared by subgenera *Proagoderus* and *Hyalonthophagus*. Conversely, a series of characters such as the support sclerotization of the vaginal ventral wall and of the copulating lamella show a strong degree of affinity with the subgenus *Trichonthophagus* (as defined by ZUNINO, 1979 and PALESTRINI 1985). Recent results on the systematics of the genus *Onthophagus* —at subgenus level (see Introduction) —confirm these findings. Consequently, we analyzed the relationships among species belonging to the subgenus *Hyalonthophagus* utilizing *Trichonthophagus* as out-group.

From such an analysis it resulted that the subgenus *Hyalonthophagus* consists of three species-complexes (sensu ZUNINO & HALFFTER, 1981): *nigroviolaceus*,



0,5 mm
a,b,c

0,3 mm
d,e,f,g,h,i

Fig. 12: *Onthophagus* (*Hyalonthophagus*) *viridiceps* D'ORBIGNY. Male genitalia: phallosome (a, b); parameres, dorsal view (c); copulating lamella (d): secondary lamella (1), secondary lamella at a higher magnification (1'); raspulae (e, f, g). Female genitalia: vagina, ventral view (h); receptaculum seminis (i).

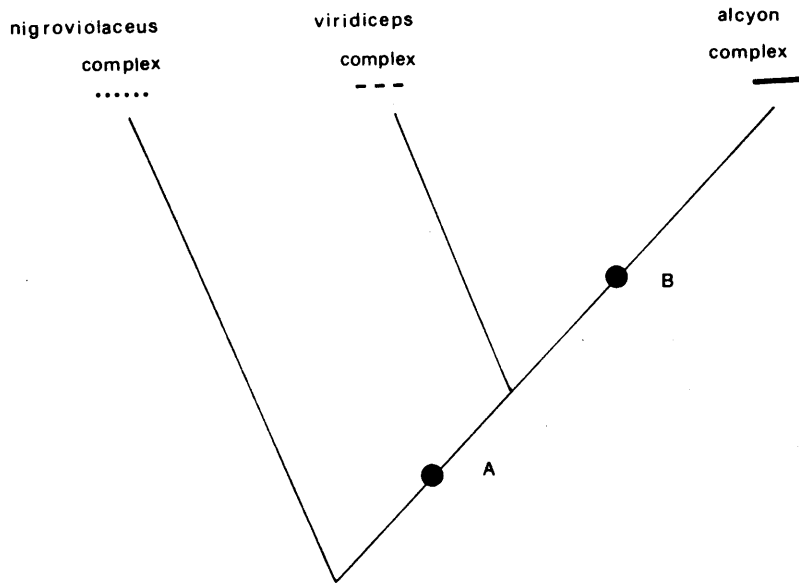


Fig. 13: Outline of the supposed phyletic relations among the three species-complexes of subgenus *Hyalonthophagus*. Main synapomorphies considered: (A) Infundibulum: groove portion transversally reduced. Vaginal ventral wall: the support sclerotization transversally reduced, with no later-cephalic outgrowths. Lateral vaginal outgrowths relatively large. Copulating lamella: left branch transversal. (B) Infundibulum: groove portion markedly longitudinal. Vaginal ventral wall: sideways E-shaped support sclerotization developing lengthwise and with a reduced middle branch. Lateral expansions large or complicated by longitudinal folds. Copulating lamella: increasingly complex, as well as the secondary lamella.

viridiceps and *alcyon*. The *nigroviolaceus* complex consists of only *O. (H.) nigroviolaceus* D'ORBIGNY. It is defined by the set of genital characters below: (see Fig. 8).

Male: left branch of copulating lamella roughly isodiametrical. Female: infundibulum groove with a extremely marked expansion; support sclerotization of vaginal ventral wall of a sideways E-shape, regular, with moderate latero-cephalic expansions. Vaginal lateral outgrowths moderately developed.

Distribution: (Fig. 14).

The *viridiceps* complex comprises the following species: *O. (H.) viridiceps* D'ORBIGNY, *O. (H.) alcedo* D'ORBIGNY, *O. mixtifrons* D'ORBIGNY, *O. (H.) virens* D'ORBIGNY, *O. (H.) alcyonides* D'ORBIGNY. It is characterized by the genital characters below (Figs. 12, 4, 7, 11 and 5).

Male: left branch of the copulating lamella transversal.

Female: groove portion of the infundibulum transversally reduced; support sclerotization of vaginal ventral wall transversally reduced with no latero-cephalic outgrowths. Vaginal lateral outgrowth relatively large.

Distribution: (Fig. 14).

The *alcyon* complex comprises the following species: *O. (H.) alcyon* KLUG, *O. (H.) pseudoalcyon* D'ORBIGNY, *O. (H.) hyalcyon* n. sp. It is identified by the genital characters below: (Figs. 3, 9 and 6).

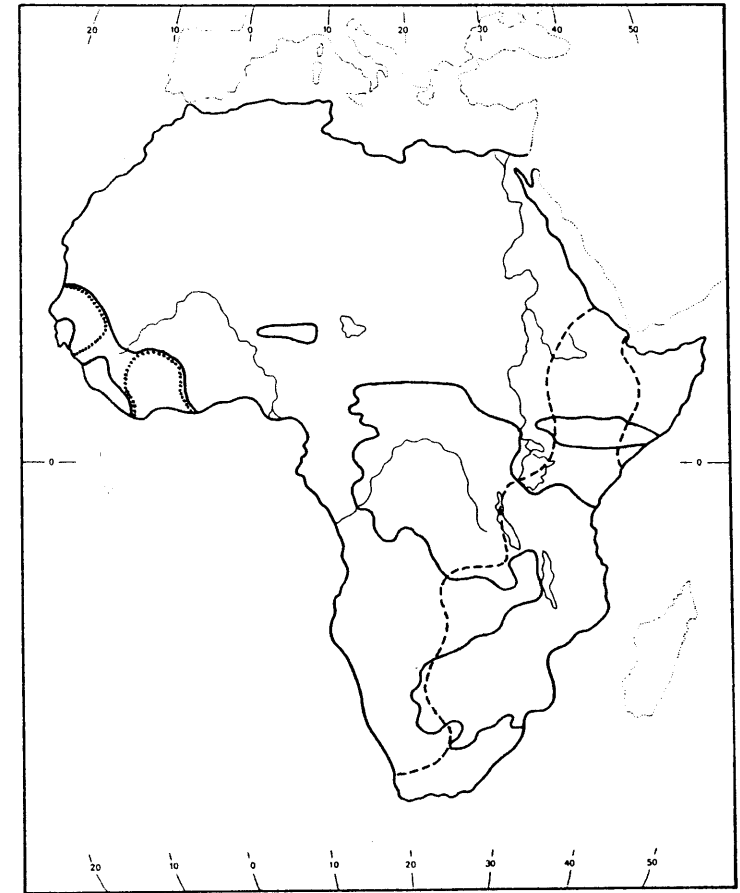


Fig. 14: Geographical Distribution of the *nigroviolaceus* (.....), *viridiceps* (-----) and *alcyon* (—) species-complexes.

Male: a higher degree of complexity involving both copulating lamella and secondary lamella.

Female: infundibulum groove markedly longitudinal; sideways E-shaped support sclerotization of ventral wall of the vagina developing lengthwise and with short middle branch. Lateral expansions very large or complicated by longitudinal folds.

Such phylogenetic hypotheses are summarized in Figure 13.

General distribution (Fig. 14).

The subgenus *Hyalonthophagus* appears to be limited to tropical Africa. Biometric information is scanty and mostly derived from the place of capture (MARCUS, 1917). On the whole, the scarce amount of available material of each species may account for their absence in some geographical areas. According to BERNON's

(1981) and CAMBEFORT's (1984) data at least some species have a tendency to cleptoparasitism.

A zoogeographical interpretation of the distribution we have just outlined may be attempted by considering jointly both subgenera *Hyalonthophagus* and *Trichonthophagus*. Eleven species have been attributed so far (PALESTRINI, 1985) to the subgenus *Trichonthophagus*, forming two groups, i.e.:

- i) *tarandus* group, with *-quadricuspis*, *-juvencus* and *tarandus* species-complexes.
- ii) *hirtus* group, with *-hirtus* and *-maki* species-complexes.

From a zoogeographical standpoint, present distribution of the subgenus corresponds to the defined Indoafrican Distribution Pattern (PALESTRINI, SIMONIS & ZUNINO, 1984, 1987).

The *Trichonthophagus* ancestral line supposedly originated in an area including what is the present day Ibero-Maghrebian district. Analyses of the phyletic relationships within the subgenus are still incomplete; however, we consider the palaearctic distribution of the *hirtus* group —the most primitive one with the subgenus as a relic of an ancient tropical Euromediterranean fauna.

Within the *Hyalonthophagus* groups of species, there is little doubt that the *nigroviolaceus* complex (with more north-western distribution) represents the primitive phyletic line.

According to the main tenets of the phylogenetic biogeography (HENNIG, 1966; BRUNDIN, 1966, 1972, 1981), and especially to the deviation/progression rule, the north-western distribution of the primitive elements in both subgenera, suggests that the present situation should be considered as the outcome of a prevalently eastward-oriented distribution.

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LITERATURE

- BERNON, G.— 1981. *Species abundance and diversity of the Coleoptera component of a South African cow dung community, and associated insect predators*. Ph. D. Thesis, Bowling Green Univ. (U.S.A.), 173 pp.
- BRUNDIN, L.— 1966. *Transantarctic relationship and their significance, as evidenced by Chironomid midges*. Kungl. Svenska Vetensk. Akad. Handl., 4 (11), 472 pp.
- BRUNDIN, L.— 1972. *Phylogenetics and Biogeography*. *Syst. Zool.*, 21: 69-79.
- BRUNDIN, L.— 1981. *Croizat's Panbiogeography versus Phylogenetic Biogeography*. In: *Nelson G. & D. Rosen, Eds., Vicariance Biogeography: a critique*, pp. 94-158. Columbia Univ. Press, New York.
- CAMBEFORT, V.— 1984. *Etude écologique des Coléoptères Scarabaeidae de Côte d'Ivoire. Travaux des chercheurs de la station de Lamto, Univ. Abidjan*, 3, VIII + 294 pp.
- FERREIRA, M.C.— 1967. Os Escarabádeos de Moçambique. I. *Revta Ent. Moçamb.*, 10 (1, 2): 5-778.
- FERREIRA, M.C.— 1972. Os Escarabádeos de Africa (Sul do Sáara). I. *Revta Ent. Moçamb.*, 11: 1-1088.
- HENNIG, W.— 1966. *Phylogenetic systematics*. Univ. Illinois Press, Urbana, 263 pp.
- KABAKOV, O.N.— 1979. Obzor platinčatousykh zhukov podsemejstva *Coprinae* (Scarabaeidae, Coleoptera) dal' nego vostočka SSSR i sopro del'nykh territorij. *Zhuki dal' nego vostočka i vostočnoj Sibiri*: 58-98. Vladivostok.

- KLUG, J.— 1855. Diagnosen neuer Coleopteren aus Mossambique. *Monatsber. Akad. Wiss. Berlin*, 20: 643-660.
- LANSBERGE, G. VAN.— 1833. Révision des *Onthophagus* de l'Archipel Indo-Néerlandais, avec description d'espèces nouvelles. *Notes Leyden Museum*, 5: 41-82.
- MARCUS, E.— 1917. Studien zur Kenntnis der coprophagen *Lamellicornia*. Untersuchungen über System, Morphologie, Phylogenese und Verbreith der *Proagoderus* auf Grund des Materials des Zoologischen Museum zu Berlin. *Arch. Naturgesch.*, 83, A, (10): 1-122.
- MARTIN PIERA, F.— 1986. The palaearctic species of the subgenus *Parentius* Zunino, 1979 (Coleoptera, Scarabaeoidea, Onthophagini). *Boll. Mus. Reg. Sci. Nat. Torino*, 4 (19): 77-122.
- MARTIN PIERA, F. & ZUNINO, M.— 1983. *Amphionthophagus*, nuovo sottogenere di *Onthophagus* Latr., (Coleoptera, Scarabaeidae). *Boll. Mus. Reg. Sci. Nat. Torino*, 1 (1): 59-76.
- MOTSCHULSKY, V. DE.— 1859. Sur les Collections Coléoptérologiques de Linné et de Fabricius. (Cont.) XXII, *Lamellicornes. Etud. Entom. Helsingfors*, 8: 147-162.
- ORBIGNY, H.D'.— 1902. Mémoire sur les Onthophagides d'Afrique. *Ann. Soc. ent. Fr.*, 71: 1-324.
- ORBIGNY, H.D'.— 1911. Collections Recueillies par M. Maurice de Rothschild en Abyssinie et dans l'Afrique Orientale Anglaise. Coléoptères: *Onthophagus* (2 partie). *Bull. Mus. Hist. nat.* 1910, 6: 308-309.
- ORBIGNY, H.D'.— 1913. Synopsis des Onthophagides d'Afrique. *Ann. Soc. ent. Fr.*, 82: 1-742.
- PALESTRINI, C.— 1980. Il "sottogenere" *Serrophorus* Balth. (Coleoptera Scarabaeoidea, Onthophagini). *Boll. Mus. Zool. Univ., Torino*, 1980, (3): 13-20.
- PALESTRINI, C.— 1982a. Il "sottogenere" *Pseudonthophagus* Balth. (Coleoptera, Scarabaeoidea, Onthophagini). *Boll. Soc. ent. ital., Genova*, 114 (4-7): 97-102.
- PALESTRINI, C.— 1982b. Le specie orientali del sottogenere *Proagoderus* Lansb. (Coleoptera, Scarabaeoidea, Onthophagini: genere *Onthophagus*). *Boll. Mus. Zool. Univ. Torino*, 1982, (3): 29-46.
- PALESTRINI, C.— 1983. Note preliminari su un gruppo indo-africano di *Onthophagus* (Coleoptera, Scarabaeidae). *Atti XIII Congr. Naz. It. Ent. Sestriere-Torino*, 1983: 71-74.
- PALESTRINI, C.— 1984. Revisione del sottogenere *Proagoderus* Lansb. (Coleoptera, Scarabaeoidea, Onthophagini: genere *Onthophagus*). II. I tipi di R. Gestro e H. d'Orbigny nel Museo Civico di Storia Naturale di Genova. *Boll. Mus. Reg. Sci. Nat. Torino*, 2 (2): 483-494.
- PALESTRINI, C.— 1985. Note sistematiche e zoogeografiche su un sottogenere indoafricano di *Onthophagus* (Coleoptera, Scarabaeoidea: Onthophagini). *Boll. Mus. Reg. Sci. Nat. Torino*, 3 (1): 29-52.
- PALESTRINI, C. & GIACONE, P.— 1988. Filogenesi e zoogeografia del sottogenere *Hyalonthophagus* nov. (Coleoptera, Scarabaeoidea, gen. Onthophagini). *Atti XV Congr. Naz. It. Ent. L'Aquila*, 1988: 319-327.
- PALESTRINI, C., SIMONIS, A. & ZUNINO, M.— 1984. Modelli di distribuzione dell'entomofauna della Zona di Transizione Cinese, analisi di esempi ed ipotesi sulle sue origini. *RIASS. Com. XXV Congr. Soc. It. Biogeografia, Rifreddo (Potenza)*, 21-24 maggio: 27.
- PALESTRINI, C., SIMONIS, A. & ZUNINO, M.— 1987. Modelli di distribuzione dell'entomofauna della Zona di Transizione Cinese, analisi di esempi ed ipotesi sulle sue origini. *Bio-geografia, N.S., X. Suppl.*: 193-207.
- PAULIAN, R.— 1986. Quelques modifications dans la nomenclature des coléoptères Scarabaeides. *Nouv. Revue Ent. (N.S.)*, 1986, 3 (2): 214.
- VAROLA, P. & ZUNINO, M.— 1981. Il "sottogenere" *Endroedius* Balth. (Coleoptera, Scarabaeoidea, Onthophagini). *Boll. Mus. Zool. Univ. Torino*, 1981, 5: 65-74.
- ZUNINO, M.— 1979. Gruppi artificiali e gruppi naturali negli *Onthophagus* (Coleoptera, Scarabaeoidea). *Boll. Mus. Zool. Univ. Torino*, 1979, (1): 1-18.
- ZUNINO, M. & HALFFTER, G.— 1981. Descrizione di *Onthophagus micropterus* n. sp. (Coleoptera, Scarabaeidae), note sulla sua distribuzione geografica e sulla riduzione alare nel genere. *Boll. Mus. Zool. Univ. Torino*, 1981 (8): 95-110.

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