Annales de la Société entomologique de France (N.S.), 2020
Vol. 56, No. 5, 361–373, https://doi.org/10.1080/00379271.2020.1824589

Two new genera of Ochodaeinae for Africa (Coleoptera: Scarabaeoidea: Ochodaeidae)

Jean-Bernard Huchet *

Institut Systématique, Évolution, Biodiversité (ISYEB), CNRS, MNHN, SU, EPHE, UA, Muséum National d'Histoire Naturelle, CP 50, 45 Rue Buffon, F – 75005 Paris, France

(Accepté le 14 september 2020; publié en ligne le 21 octobre 2020)

Summary. This study conducted on African species of Ochodaeinae leads to the transfer of *Ochodaeus carinatus* Benderitter, 1913 to the genus *Parochodaeus*, Nikolajev, 1995, the first mention of this genus for the African continent. *Afrochodaeus* **n. gen.**, an endemic genus from South Africa, is described and illustrated. This new genus includes four species, namely: *Afrochodaeus corniger* (Scholtz & Evans, 1987) **n. comb.**, *A. quadridentatus* (Scholtz & Evans, 1987) **n. comb.**, *A. rectus* (Scholtz & Evans, 1987) **n. comb**. and *A. unicornis* (Scholtz & Evans, 1987) **n. comb**. An identification key to the genera as well as an updated catalogue of the Ochodaeinae species occurring on the African continent are provided.

Résumé. Deux nouveaux genres d'Ochodaeinae pour l'Afrique (Coleoptera : Scarabaeoidea : Ochodaeidae): L'étude des espèces africaines d'Ochodaeinae conduit à transférer *Ochodaeus carinatus* Benderitter, 1913 dans le genre *Parochodaeus* Nikolajev, 1995, première mention de ce genre pour le continent africain. *Afrochodaeus* **n. gen.**, genre endémique d'Afrique du Sud, est décrit et illustré. Ce nouveau genre comprend quatre espèces, à savoir : *Afrochodaeus corniger* (Scholtz & Evans, 1987) **n. comb.**, *A. quadridentatus* (Scholtz & Evans, 1987) **n. comb.**, *A. rectus* (Scholtz & Evans, 1987) **n. comb**. et *A. unicornis* (Scholtz & Evans, 1987) **n. comb**. Une clé d'identification des genres ainsi qu'un catalogue actualisé des Ochodaeinae d'Afrique sont proposés.

http://www.zoobank.org/urn:lsid:zoobank.org:pub:EF12ED28-4D20-426A-A167-0C116B22B98C

Keywords: Systematics; morphology; new genus; identification key

The Ochodaeidae is a relatively small family within the Scarabaeoidea, including 138 extant species arranged in 16 genera, six tribes and two subfamilies (Horn 1876; Fall 1909; Woodruff 1973; Carlson & Ritcher 1974; Paulian 1976; Scholtz & Evans 1987; Scholtz et al. 1988; Scholtz 1991; Nikolajev 1995; 2009; Carlson 2002; López-Colon et al. 2016; Paulsen 2007; Bouchard et al. 2011; Paulsen & Ocampo 2012; Huchet 2016 *inter alia*). Ochodaeidae representatives occur on all continents with the exception of Australia and Antarctica (Carlson 2002). All members of the family share the unique character of a pectinate/crenulate mesotibial spur as well as the virtual absence of a genal canthus intruding into the eye. These unusual characters provide strong arguments for the monophyly of the group (Scholtz 1990). According to Scholtz et al. (1988), the current status of the family suggests that it is fairly primitive, and closely related to Hybosoridae, Geotrupidae, Aclopidae, or Glaresidae. Recent molecular phylogenetic studies would support the Ochodaeidae to be the sister group to Glaphyridae (Smith et al. 2006; Ahrens et al. 2014; Bocak et al. 2014; Sabatinelli et al. 2020).

Until the second half of the twentieth century, species were grouped within a limited number of genera and the genus *Ochodaeus* Dejean, 1821 included the great majority of the species then described. On the basis of selected anatomical features, i.e. conformation of the mentum, elytral locking mechanism located on tergite VII ("propygidium"), stridulatory organ, and endophallic structures, the taxonomic works of Carlson and Ritcher (1974), Paulian (1976), Scholtz & Evans (1987), Nikolajev (1995, 2005), Paulsen (2007), Paulsen & Ocampo (2012), Huchet & Keith (2017), and Huchet (2017, 2019) greatly contributed to clarifying the systematics of the family. Consequently, 11 new genera were described to accommodate not only a significant number of new species but also many taxa previously misplaced within the genus *Ochodaeus*.

Within the family, one of the most relevant characters is related to the conformation of tergite VII which exhibits various structures ensuring elytral coaptation (e.g. furrows, pits and denticules). These formations, originally described and illustrated by Horn (1876), were reviewed and detailed by Arrow (1904). From the basis of these anatomical

*Corresponding author. Email: jean-bernard.huchet@mnhn.fr

structures, Nikolajev described the genera *Neochodaeus* and *Parochodaeus* (1995) to accommodate respectively two and six North American species, and *Nothochodaeus* (2005) for three Asian species. More recently, Paulsen (2007) established the genus *Xenochodaeus* based on the conformation of tergite VII. Another relevant character considered as phylogenetically significant is related to the conformation of the endophallus and its armature [i.e. sclerotized areas, series of spines, hooks, raspulae, and toothed sclerites, or "endophallites" according to the terminology recently proposed by Génier (2019)]. Carlson (1975) figures undoubtedly as a pioneer by having initiated the systematic study of the aedeagal sac, demonstrating the high taxonomic value of the inner structures. The study of the endophallus proved to be particularly useful since, unlike many other Scarabaeoidea, male external genitalia of Ochodaeidae, weakly sclerotized and indistinctive, proved to be most often unreliable for the delineation of species. From the study of seven genera and 17 species belonging to two subfamilies (Ochodaeinae and Chaetocanthinae), Hotman & Scholtz (1990) pointed out that the conformation of the endophallus can be an advantage in recognizing phylogenetic affinities between the various taxa of the family. These structures have since been represented and described for a relatively large number of taxa (Carlson & Ritcher 1974; Scholtz & Evans 1987; Ochi et al. 2006; Huchet 2014a, 2014b, 2016, 2017, 2018, 2019, 2020; Huchet & Li 2015; Huchet & Keith 2017; Paulsen 2019a).

Another relevant character widely used by the authors within the systematics of the Ochodaeidae is the shape of the stridulatory peg located on sternite VI. Horn (1876) was the first author to suggest stridulating power in *Ochodaeus* but was mistaken about the precise location of this organ. Arrow (1904), in a paper titled "Sound-production in the lamellicorn beetles", accurately described and illustrated these structures, and provided evidence that the shape of the stridulatory peg [sclerotized lobe that produces sound by acting as a plectrum rubbing against a striated thickening on the inner face of the elytra (Paulsen 2019a)] differs according to the species. Widely recognized as a taxonomically informative organ, many subsequent authors illustrated the stridulatory peg in their studies dealing with Ochodaeidae (Carlson 1975; Paulian 1976; Paulsen 2007; Paulsen & Ocampo 2012; Huchet 2014b; Paulsen 2019a, 2019b). The presence or absence of a stridulatory peg on the abdomen is often diagnostic and helps to establish taxonomic boundaries, especially in determining affinities at the generic and infrageneric levels.

Finally, another character of interest that seems, to our knowledge, undescribed and specific to the subfamily Ochodaeinae is the presence at the distal part of ventrites I–II of a cupuliform structure, the morphology and orientation of which differs according to the genera. It might be possible that this "cup-shaped" structure corresponds to a "resonance chamber" linked with the presence of a stridulatory apparatus. Anatomically, this structure appears as close to the mesotibial pectinate/crenulate spur and, internally, to the upper edge of the wing subcostal vein that presents a more or less distinct finely crenulate rim. Observations of living specimens with adapted acoustic material would be needed in order to identify the exact function of this anatomical structure.

Within the African continent, the revision proposed by Scholtz & Evans (1987) reports 20 species of Ochodaeidae belonging to four genera, namely: *Chaetocanthus* Péringuey, 1901, *Namibiotalpa* Scholtz & Evans, 1987, *Synochodaeus* Kolbe, 1907, and *Ochodaeus* Dejean, 1821. One year later, in a study dedicated to the phylogeny and systematics of the Ochodaeidae, Scholtz et al. (1988) proposed to split the African species into two subfamilies: Ochodaeinae Mulsant & Rey, 1871, and Chaetocanthinae Scholtz, 1988. From this date, while the Malagasy fauna has been the topic of recent studies (Paulsen 2019a, 2019b), no additional survey has been issued for continental Africa.

All African Ochodaeinae species are found in the sub-Saharan part, with the exception of *O. gigas* Marseul, 1878, which occurs in the northern part of Africa (Algeria, Egypt, Libya, Morocco, Tunisia) and, outside the continent, in Israel (López-Colon et al. 2016). The study of the African species originally placed within the genus *Ochodaeus* provided evidence that some species were not placed into the appropriate genus-level taxa and that nomenclatural rearrangement was necessary, resulting in the transfer of one species to the genus *Parochodaeus* Nikolajev, 1995, and the creation of a new genus warranted for four species exhibiting several distinctive characteristics detailed below.

Material and methods

Specimens and taxonomic material

The specimens studied in the frame of this study originated from the following institutions and collections:
CGML: Geoffrey Miessen collection, Liege, Belgium
CJBH: Jean-Bernard Huchet collection, Bordeaux, France
CMNO: Canadian Museum of Nature, Ottawa, Canada
CRAP: Richard Angus collection, Prague, Czech Republic
CSJP: Stanislav Jákl collection, Prague, Czech Republic
MNHN: Muséum national d'Histoire naturelle, Paris, France
NMNW: National Museum of Namibia, Windhoek, Namibia
SANC: South African National Collection, Queenswood, South Africa
NMPC: National Museum, Prague, Czech Republic
SMNS: Staatliches Museum für Naturkunde Stuttgart

Genitalia treatment

After removal of the entire abdomen to avoid any damage of the genital parts and other useful features, the genital apparatus was treated with 10% potassium hydroxide solution (KOH) to dissolve and remove the unneeded soft tissues, disassociate the aedeagus

from the genital segment (urite IX) and reveal the inner copulatory sclerites of the endophallus (male), or the sclerotized terminalia of the urite IX (female). The cleaned genital parts were then placed in 10% acetic acid to neutralize the effects of the KOH, rinsed with ethanol, and stored in a small glycerol vial pinned under the specimen. Finally, the abdomen was moved back to its original position and maintained in anatomical position using a small drop of hydrosoluble glue. Terminology of male genitalia follows Medina et al. (2013), Hotman & Scholtz (1990) and Génier (2019); female genitalia follow Dupuis (2005).

Illustrations

Digital images of the habitus were taken at the Entomology building (UGC Arthropodes terrestres, MNHN, Paris) with a Canon E0S 6D digital camera (zoom MP-E 65 mm) mounted on a Kaiser RTx column. The z-stepper was controlled through the focus stacking software Helicon Remote 3.8.6 w and images were processed using Helicon focus 7. The digital images were finally imported into Adobe Photoshop CS4 for post-processing, labeling and plate composition. Digital images of genitalia were done using an Olympus Tough TG-6 camera connected to a Leica MZ6 stereomicroscope. Drawings were made via a stereomicroscope Leica MZ6 using a *camera lucida* (drawing tube), scanned and then vectorized using Adobe Illustrator CS4.

Results

Systematics

Ochodaeidae Streubel, 1846
Ochodaeinae Streubel, 1846
Ochodaeini Streubel, 1846
***Parochodaeus* Nikolajev, 1995**

Parochodaeus Nikolajev 1995: 77.

Transfer of *Ochodaeus carinatus* Benderitter, 1913 to the genus *Parochodaeus* Nikolajev, 1995. The genus *Parochodaeus* was proposed by Nikolajev (1995) to accommodate a few Nearctic species originally placed within the genus *Ochodaeus*, namely: *O. pectoralis* LeConte, 1868, *O. biarmatus* LeConte, 1868, *O. inarmatus* Schaeffer, 1906, *O. kansanus* Fall, 1909 (subsequently synonymized with *O. duplex* LeConte, 1868 by Paulsen (2007)), *O. howdeni* Carlson, 1975, and *O. ritcheri* Carlson, 1975. The genus *Parochodaeus* includes the Ochodaeinae representatives bearing an elytral locking mechanism present on tergite VII, hooking with two corresponding structures located at the inner apical angle of each elytra. The genus *Parachodaeus* is undoubtedly the most important genus within the American continent, including 55% (25/45 sp.) of all the Nearctic and Neotropical Ochodaeidae. We recently demonstrated that this genus is also represented in the Old World (Huchet 2016).

Examination of the holotype of *Ochodaeus carinatus*, deposited at the MNHN, as well as a large series of specimens provide evidence that this taxon is very distinct from all the other species of the genus *Ochodaeus* and possesses the specific elytral locking mechanism of the genus *Parochodaeus* on tergite VII. This singular conformation was previously noticed by Scholtz & Evans (1987, p. 407) as specific to this species, without assigning it other taxonomic significance: "*Ochodaeus carinatus* is rather variable but is easy to distinguish from any other species by the very characteristic hooks on the elytral apices and corresponding hooks on the propygidium as well as by the absence of a stridulatory peg. It is the only African species with the above mentioned features". These morphological characters demonstrate, without ambiguity, that this species must be transferred to the genus *Parachodaeus* Nikolajev, 1995, resulting in the following new combination.

***Parachodaeus carinatus* (Benderitter, 1913) n. comb. (Figure 1–4)**

Ochodaeus carinatus Benderitter 1913: 359.
Syn. *Ochodaeus castaneus* Benderitter 1920: 116 (synonymized by Scholtz & Evans 1987).
Syn. *Ochodaeus ciliatus* Benderitter 1921: 113 (synonymized by Scholtz & Evans 1987).
Syn. *Ochodaeus minutus* Benderitter 1923: 5 (synonymized by Scholtz & Evans 1987).

Within the African continent, *Parochodaeus carinatus* occurs in Somalia (Carpaneto & Piattella 1990), Ethiopia, Kenya and Djibouti where it appears to be relatively common. Recent collections provided evidence that this species is also present outside the African continent and occurs in the Arabian Peninsula, more specifically in Yemen (Sommer et al. in press), and Oman.

Type material examined

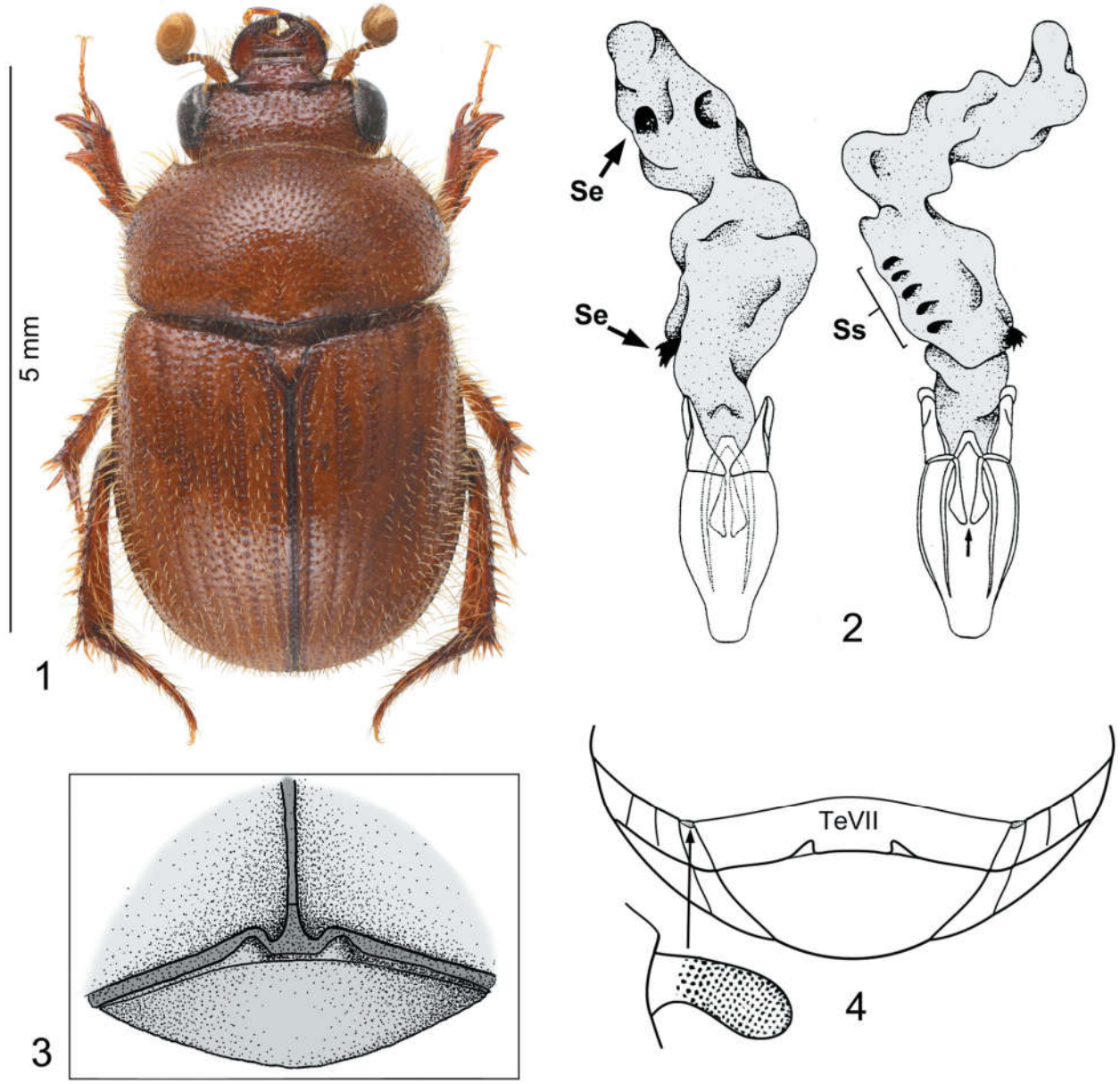
Ochodaeus carinatus Benderitter, 1913. Holotype (MNHN), labels: (a) rectangular, handwritten: Obock; (b) white label, rectangular, framed in black, handwritten and printed: Col. BENDERITTER, *Ochodaeus carinatus*, Type; (c) Muséum Paris, Coll. M. Pic; (d) red label, rectangular, printed: TYPE.

Ochodaeus castaneus Benderitter, 1920. Holotype (MNHN), labels: (a) printed: Musée du Congo, B.E.A.: Tsavo R., 4/21-V-1913, Dr Bayer; (b) printed: Muséum Paris; (c) handwritten and printed: *Ochodaeus castaneus* type, E. Benderitter, det.; (d) handwritten and printed: *Ochodaeus carinatus* Bend., det C. H. Scholtz 1986.

Ochodaeus ciliatus Benderitter, 1921. Paratype (MNHN): Muséum Paris, Coll. M. Pic/*Ochodaeus ciliatus* cotype, E. Benderitter, det./*Ochodaeus carinatus* Bend., det C. H. Scholtz 1986.

Other specimens examined (51)

Djibouti. *Ochodaeus rufus* Guér., Obock/Muséum Paris, 1906, coll. L. Fairmaire/*Ochodaeus carinatus* Bend., det C. H. Scholtz 1986 (1 ex./MNHN); Obock/Muséum Paris, Obok (ex coll. Dollé), M. Ley 1922/collection A. Lajoye/



Figures 1–4. *Parochodaeus carinatus* (Benderitter, 1913). **1**, Habitus, dorsal view. **2**, Male genitalia, the endophallus everted showing the well-developed endophallites (left, dorsal view; right, ventral view). Abbreviations: Se, serrated endophallites; Ss, sesamoïd sclerites. **3**, Dentate elytral apices and tergite VII interlocking mechanism, characteristic of the genus *Parochodaeus*. **4**, Location of the stridulatory peg on tergite VI. (Figure 1. Photo J.-B. Huchet; Figure 2, after Scholtz & Evans 1987, modified; Figure 3, drawing J.-B. Huchet; Figure 4, after Arrow 1911, modified).

Ochodaeus rufus Guér./Muséum Paris/*Ochodaeus carinatus* Bend., det C. H. Scholtz 1986 (1 ex./MNHN).

Ethiopia. Dire Dawa, 9°40.934′N, 41°57.930′E, 1055 m, 2.VI.2011, V. Hula & J. Niedobová leg. (1 ex./NMPC); Dire Dawa, 9°39.27′N, 41°55.813′E, 1133 m, 5.VI.2011, V. Hula & J. Niedobová leg. (5 ex./NMPC; 2 ex./CJBH); Dire Dawa, 9°41.842′N, 41°58.450′E, 1025 m, 6.VI.2011, V. Hula & J. Niedobová leg. (3 ex./NMPC); Abyssinie, Dire Daoua [sic] et environs, Dr J. Roger 1903 (4 ex./MNHN); 52/ Abyssinia Raffray/Muséum Paris, coll. M. Pic/*Ochodaeus carinatus* Bend., det C. H. Scholtz 1986 (1 ex./MNHN); Coll. Raffray, Abyssinia/Ex Musaeo N. Van de Poll/ Muséum Paris, 1936, coll. A. Boucomont/*Ochodaeus carinatus* Bend, E. Benderitter, det./*Ochodaeus carinatus* Bend., det C. H. Scholtz 1986 (1 ex./MNHN); Harrar (G. Kristensen)/ Muséum Paris, 1936, coll. A. Boucomont/*Ochodaeus ciliatus*

Bend., E. Benderitter, det./*Ochodaeus carinatus* Bend., det C. H. Scholtz 1986 (1 ex./MNHN). Ethiopia, 11 km SEE Goro, 1.V.2013, Martininů Ivo leg. (2 ex./CJBH); Sidamo, 60 km E. Negele, 8.V.2016, S. Prepsl leg. (4 ex./CJBH). Ethiopia South, GPS 110 km N Moyale, 04°33′N, 039°03′E, 21–24.V.2015, 1100 m, A. Kudrna JR lgt. (3 ex./CJBH); Ginir prov., forest in valley to Sof Omar cave, 16.VI.2011, 1249 m, J. Niedobová & M. Moradmand leg. (1 ex./CJBH).

Kenya. Kenya coast, Garissa, N. of Hola, 25.IV.2008, Snižek lgt (1 ex./CJBH); Eastern, 11 km NWN Dabel, 17. V.2017, S. Prepsl leg. (2 ex./CJBH). Rift Valley, 3 km W Oltepesi, 21.IV.2018, S. Prepsl leg. (1 ex./CJBH).

Somalia. Somalia, LasCanood; 47°22′E 8°28′N, Simonetta!, 8.XI.1980 (2 ex./MNHN).

Oman. Dhofar, Jabal al Qamar, 5 km NE Dhalqut, 16°43′22.48″N, 53°16′27.26″E, 22.IX.2011, R. Ambrus leg. (2 ex./CRAP; 2 ex./CJBH); Sultanate Oman, Dhofar prov., Jebel Samhan range, 900 m, VIII.1999, St. Jákl leg. (4 ex./CSJP; 1 ex./CJBH); Dhofar, 5 km E. Arift, 16. VIII.2018, S. Prepsl leg. (3 ex./CJBH; 3 ex. CGML).

Discussion

The endophallus of *P. carinatus* is very distinctive, including both a series of aligned sesamoïd sclerites (Figure 2: Ss), and serrated endophallites more or less related to those found in the genus *Ochodaeus* (Figure 2: Se). Interestingly, comparable aligned sesamoïd sclerites within the endophallus occur both in the Palaearctic species *Codocera ferruginea* (Eschscholtz, 1818), and the Nearctic species *C. gnatho* (Fall, 1909). Representatives of these two genera occurring both in the New World and the Old World raise interesting biogeographical issues.

Until very recently, *Parochodaeus* was considered as an endemic genus of the New World. Within the Americas, this genus includes 25 valid species (nine representatives in the Nearctic region, and 16 in the Neotropical region) (Nikolajev 1995; Paulsen 2007, 2011, 2012, 2014; Paulsen & Ocampo 2012) (Figure 5). Huchet (2016), on the basis of several morphological features, transferred the European species *Ochodaeus pocadioides* Motschulsky, 1859, to the genus *Parochodaeus*, resulting in the combination *Parochodaeus pocadioides* (Motschulsky 1859). After the recognition of a representative of this genus in the Palaearctic region, the presence of a second species of *Parochodaeus* within the Afrotropical region would suggest that the genus is very likely long established in the Old World (Figure 5). From a biogeographic point of view, this disjunct distribution model is certainly not unique. As an example, we can cite the Palaearctic genera *Codocera* Eschscholtz, 1821 (Ochodaeidae), or *Ceratophyus* Fischer, 1824 (Geotrupidae), which have a single representative in the south-western USA and northern Mexico (*Codocera gnatho* (Fall 1907)), and a species endemic to California (*Ceratophyus gopherinus* Cartwright, 1966). A thorough examination of Old World species might provide some insights by identifying possible affinities between these species and some representatives of the New World taxa. Interestingly, all the Nearctic species of *Parochodaeus* possess a stridulatory peg, which is not the case in Neotropical species where more than one-third of the representatives do not exhibit this organ. The lack of stridulatory apparatus in *P. pocadioides* and *P. carinatus* would suggest closer affinities between Old World taxa and Neotropical lineages rather than with the Nearctic representatives. A phylogenetic and/or molecular study based on Old World and New World *Parochodaeus* taxa may provide some relevant insight to address this biogeographic enigma.

Description of a new southern African genus

Afrochodaeus n. gen.
(Figures 6, 7, 8, 11, 13, 15–23)

Type species

Ochodaeus rectus Scholtz & Evans, 1987, here designated.

Diagnosis

This new genus includes species with quadridentate protibiae; horned clypeus (in both sexes); elytra long pubescent on the surface and lateral margins, the striae obsolete, except the juxta-sutural one (although superficially marked) (the striae always very distinct and well impressed within the genus *Ochodaeus*); abdominal sternites membranous, without distinct dorsolateral margin against which elytra close (abdominal sternites sclerotized, with distinct dorsolateral margin in *Ochodaeus*) (Figures 13 and 14); abdomen with five visible ventrites (IV–VIII), ventrite III invaginated into metacoxal cavity, only partly visible between the posterior coxae, in the form of a triangular apophysis (six visible ventrites in *Ochodaeus*) (Figures 13 and 14); tergite VII ("propygidium") membranous; stridulatory peg absent. Male genitalia: large parameres; endophallus membranous with folds, unarmed, without any endophallites, the surface locally covered with raspulae and fine spicules. Southern African species (Namibia and South Africa).

Etymology

Afrochodaeus (gender masculine; *Afro* from Latin "*Afer*", referring to Africa, + *Ochodaeus*), this new genus, close to *Ochodaeus*, being endemic to Africa.

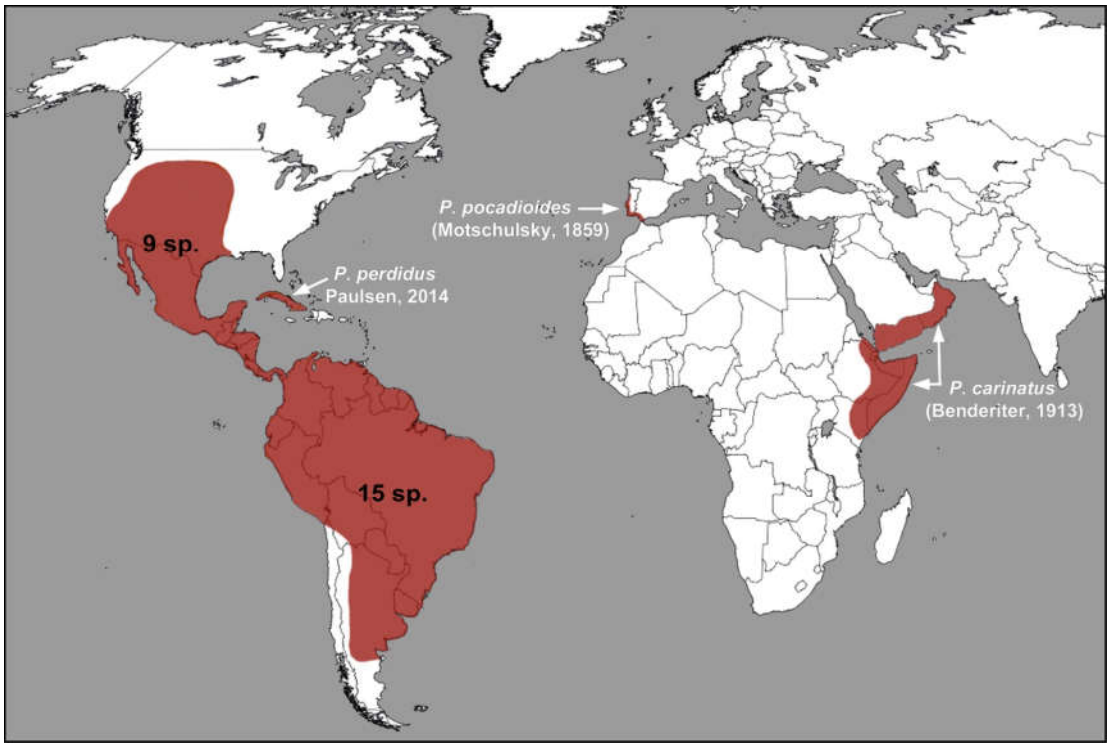


Figure 5. Worldwide distribution of the genus *Parochodaeus* Nikolajev, 1995.

Studied material

***Ochodaeus unicornis* Scholtz & Evans, 1987**

Holotype ♂ (NMNW), labels: (a) rectangular, handwritten: Okahandja, 6.IV.53; (b) rectangular, handwritten: Ochodaeinae, gen. ign. for *Synochodaeus*; (c) ♂; (d) white paper, rectangular, printed: GAERDES; (e) white label, rectangular, printed: H26278; (f) white label, rectangular, framed in red, handwritten and printed: *Ochodaeus unicornis* C.H.S. Scholtz + A.V. Evans 1986, HOLOTYPE; (g) blue label, rectangular, printed: Namibian National Insect Collection State Museum, P.O. Box 1203, Windhoek, Namibia.

Other specimens examined: Namibia, Karas prov., 11 km N Karasburg, 1000 m, 27°55′08″S 18°45′46″E, 3. IV.2017, J. Halada (1♂; 1♀/CJBH); N. Namibia, 45 km SE Okakarara, 1300 m 24–25.IV.2005, leg. W. Schawaller (2 ex./SMNS). Klein Nosib, SWA: Tsumeb District, 19° 28'S 17°50'E, 5–6.IV.1989, J. Irish, E. Marais (7 ex./ NMNW).

***Ochodaeus corniger* Scholtz & Evans, 1987**

Holotype (NMNW), labels: (a) white label, rectangular, printed: Kuruman N.W. Cape R.S.A., SE 2723 Ad, 21–22. II.1980, S. Louw M.-L. Penrith; (b) white label, rectangular, printed: H40751; (c) white label, rectangular, framed in red, handwritten and printed: *Ochodaeus corniger* C.H.S. Scholtz + A.V. Evans 1986, HOLOTYPE; (d) blue label, rectangular, printed: Namibian National Insect Collection State Museum, P.O. Box 1203, Windhoek, Namibia.

Paratype (NMNW) [head and pronotum missing]: Mukorob 14, Namaland, SE2518 Ac, 12–14.IV.1974/ H18405.

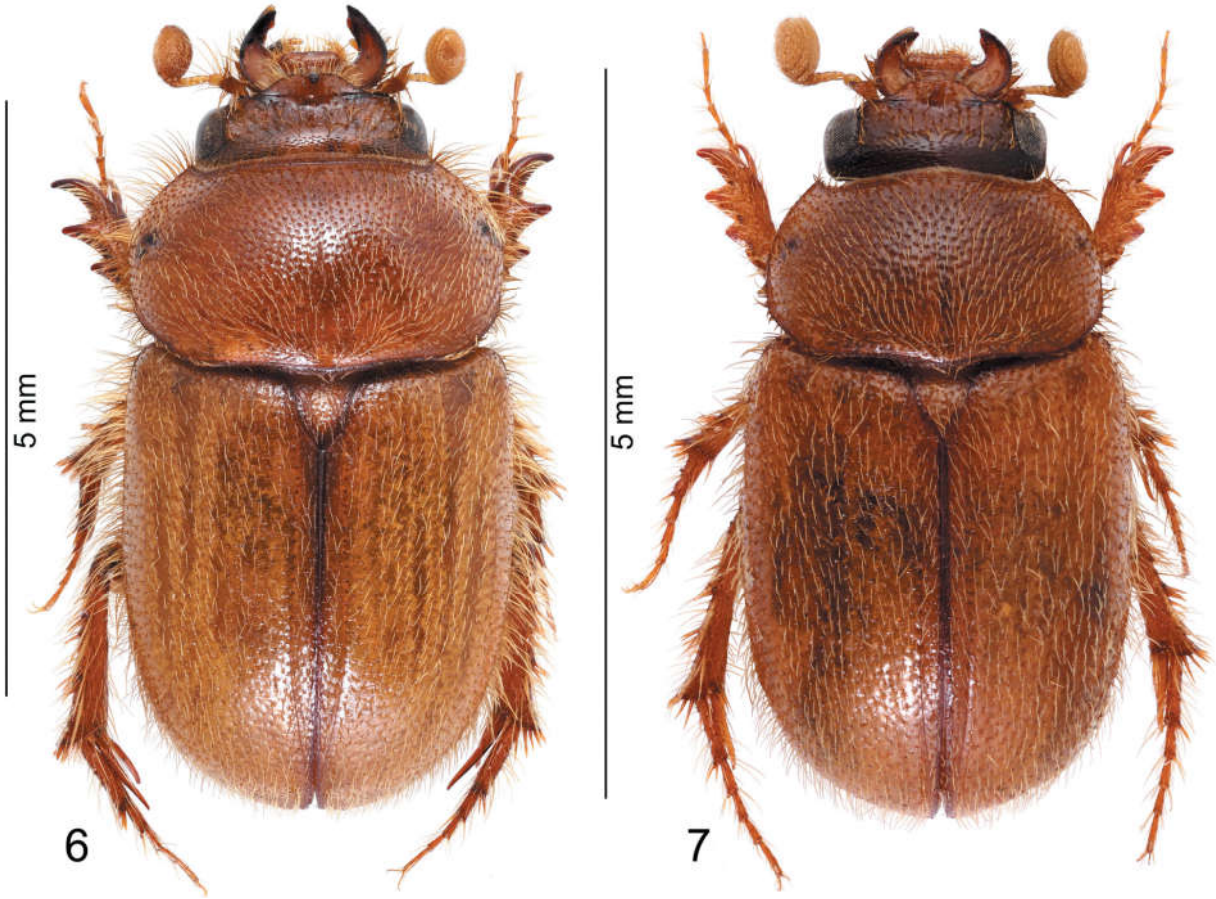
Other specimens examined: Namibia, Karas prov., 11 km N Karasburg, 1000 m, 27°55′08″S 18°45′46″E, 3. IV.2017, J. Halada (1♂; 2♀/CJBH).

***Ochodaeus rectus* Scholtz & Evans, 1987**

Namibia, Khomas prov., 60 km NW Dordabis, 150 m, 22°38′40″S 18°06′52″E, 7.IV.2017, J. Halada (1♂/CJBH).

***Ochodaeus quadridentatus* Scholtz & Evans, 1987**

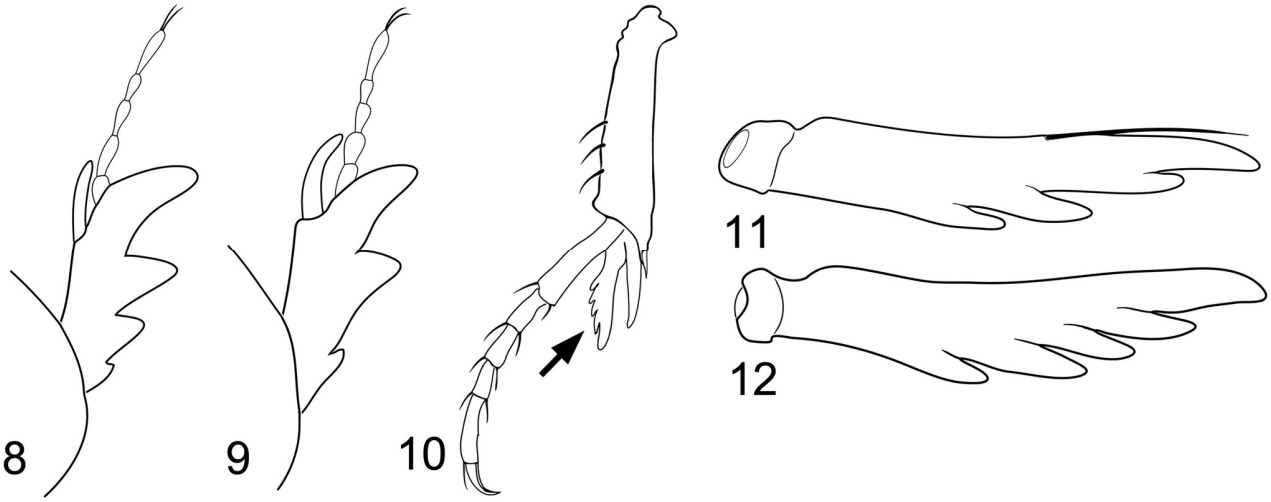
Holotype (SANC), labels: (a) rectangular, both printed and handwritten: 32 m SW Louis Trichardt, N. Tvl. S. Afr., 11.V.1967, II A, – 20. (b) white label, rectangular, printed, framed in black: National Coll. of Insects, Pretoria, S. Afr. (c) red label, rectangular, printed: 1298; (d) white label, rectangular, framed in red, handwritten and printed: *Ochodaeus quadridentatus* C.H.S. Scholtz + A.V. Evans 1986, HOLOTYPE.



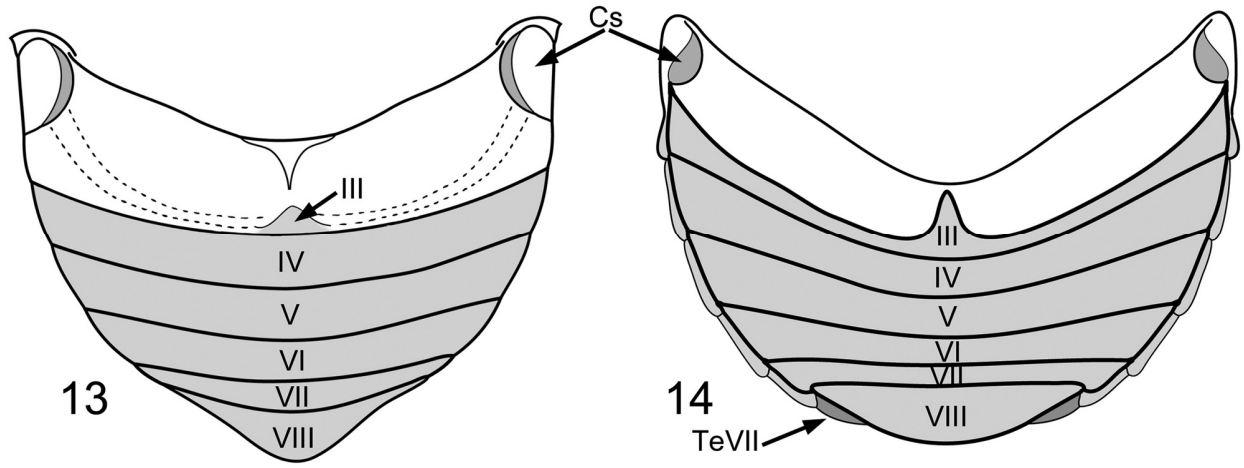
Figures 6, 7. *Afrochodaeus* species, habitus in dorsal view. **6**, *Afrochodaeus rectus* (Scholtz & Evans, 1987) **n. comb.** **7**, *Afrochodaeus corniger* (Scholtz & Evans, 1987) **n. comb.**

Description

Form convex, ovate, densely setose. Length 5–7 mm; width across humeri 2.5–3.5 mm. Color testaceous to pale orange-brown. Head: very transverse; clypeus with a distinct horn in both sexes; vertex separated to the frontal area by a transverse row of setose punctures, surface of the vertex with tight and confluent punctation. Labrum straight, or slightly emarginate according to the species. Eyes globose, prominent. Mentum subquadrangular; labial palps 3-jointed. Maxillae: lacinia and galea well sclerotized, distinctly separated, lacinia armed with a single acute tooth; maxillary palps 4-jointed. Mandibles moderately large, externally rounded, concave dorsally, visible beyond labrum in dorsal view. Antennae with 10 antennomeres, club with 3 antennomeres. Pronotum convex, entirely bordered on edges; surface densely punctate, punctures large, setigerous; setae moderately long, testaceous. Elytra strongly pubescent, surface punctate; humeral calli well-marked; elytral striae absent (except sutural), not impressed; surface punctate, punctures large, setigerous, and some scattered minute puncture; setae long and dense, testaceous. Legs: protibiae quadridentate (Figure 8), basal tooth reduced, apical spur long pubescent on edge; pollex absent. Mesotibial spur crenulate, with 4–5 teeth, and a long bristle on the upper edge (Figure 11). Meso- and metafemora without accessory teeth, their surface with two parallel rows of setose punctures. Upper spur of metatibiae slightly longer than the basitarsomere; tarsal formula 5-5-5, claws simple. Abdomen: abdominal ventrites membranous, without distinct dorsolateral margin against which elytra close (Figure 13); ventrites I–II cup-shaped chamber large, open-ended; stridulatory peg absent. Tergite VII ("propygidium") membranous. Male genitalia with well-developed membranous endophallus, unarmed, the membrane locally covered by patches of raspulae (Figures 15, 17–19); phallobase sub-translucent, strongly conxex dorsally, long tapered apically; parameres in wide plates, obtusely rounded apically, slightly divergent in dorsal view. Female terminalia (Figures 22 and 23): gonopods IX trimerous: subcoxites roughly triangular, concave, bearing a single elongated bristle at the end of the ventral edge; coxites elongated, roughly cylindrical in the middle and spatulated at the apex, bearing a wreath of six



Figures 8–12. *Afrochodaeus* and *Ochodaeus*, diagnostic characters. **8**, *Afrochodaeus unicornis* (Scholtz & Evans, 1987) **n. comb.**, quadridentate protibia. **9**, *Ochodaeus adsequa* Kolbe, 1907, tridentate protibia. **10**, *Ochodaeus* sp. mesotibia, the crenulate mesotibial spur indicated by an arrow. **11**, *A. unicornis*, mesotibial spur. **12**, *O. adsequa*, mesotibial spur (*auct. del.*).



Figures 13, 14. Abdomen, ventral view. **13**, *Afrochodaeus unicornis* (Scholtz & Evans, 1987) **n. comb. 14**, *Ochodaeus adsequa* Kolbe, 1907 (III–VIII: ventrites; TeVII: tergite VII); Cs: ventrites I–II cup-shaped chamber (*auct. del.*).

bristles elongated at the apex, and two bristles on outer edge; styli small, very short, digitiform, bearing two elongated bristles apically.

Composition

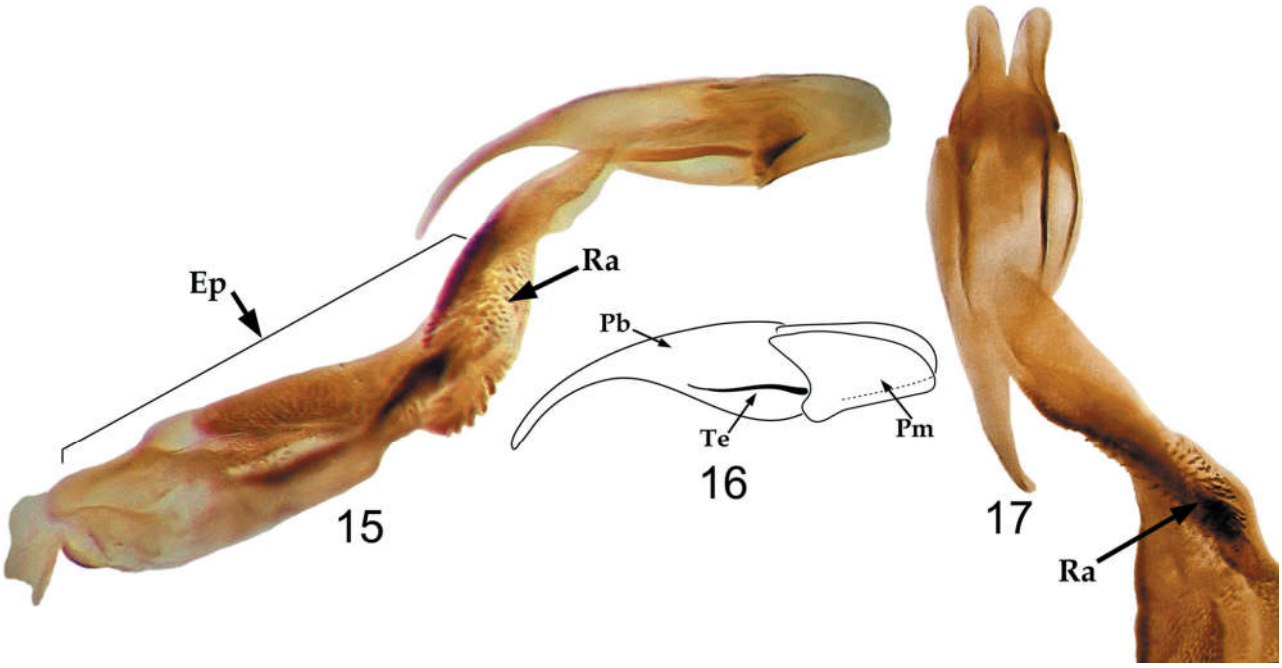
Four Afrotropical species transferred to *Afrochodaeus* include *A. corniger* (Scholtz & Evans, 1987) **n. comb.**, *A. quadridentatus* (Scholtz & Evans, 1987) **n. comb.**, *A. rectus* (Scholtz & Evans, 1987) **n. comb.**, and *A. unicornis* (Scholtz & Evans, 1987) **n. comb.**

Distribution

Restricted to the Southern part of Africa (Namibia and South Africa) (Figure 26).

Key to the genera of African Ochodaeinae

1. Protibiae tridentate (Figure 9). Elytra striae well marked; six visible sternites, all sclerotized, with distinct dorsolateral margin..... 2
– Protibiae quadridentate (Figure 8). Elytral striae obsolete, except the juxta-sutural one, although superficially marked; abdominal sternites membranous; five completely visible sternites (IV–VIII), sternite III only noticeable between the metacoxae, in the form of a triangular apophysis. Stridulatory peg absent. Clypeus always horned in both sexes. Male genitalia: large parameres, endophallus membranous, unarmed, without endophallites. Southern African species (Namibia and South Africa)..... ..... ***Afrochodaeus* n. gen.**



Figures 15–17. *Afrochodaeus unicornis* (Scholtz & Evans, 1987) **n. comb.**, male genitalia. **15**, aedeagus in lateral view, the endophallus not everted. **16**, ditto, schematic representation of the aedeagus. **17**, aedeagus, dorsal view. Abbreviations: Ep, endophallus; Pb, phallobase; Pm, parameres; Ra, raspulae; Te, temones.

2. Apex of elytra dentate, interlocking with two tubercles on tergite VII margin (Figure 3). Clypeus without horn. Stridulatory peg absent. Male genitalia: parameres pointed apically, endophallus armed*, with aligned sesamoïd sclerites, serrated endophallites and sclerotized areas. East African species (Somalia, Ethiopia, Kenya, Djibouti)..... ***Parochodaeus* Nikolajev, 1995**
– Elytral apex and tergite VII unarmed, without locking mechanism. Clypeus with a horn or not. Stridulatory peg present. Male genitalia: parameres pointed apically, endophallus armed, with serrated sclerites (North- and sub-Saharan Africa)..... ***Ochodaeus* Dejean, 1821**

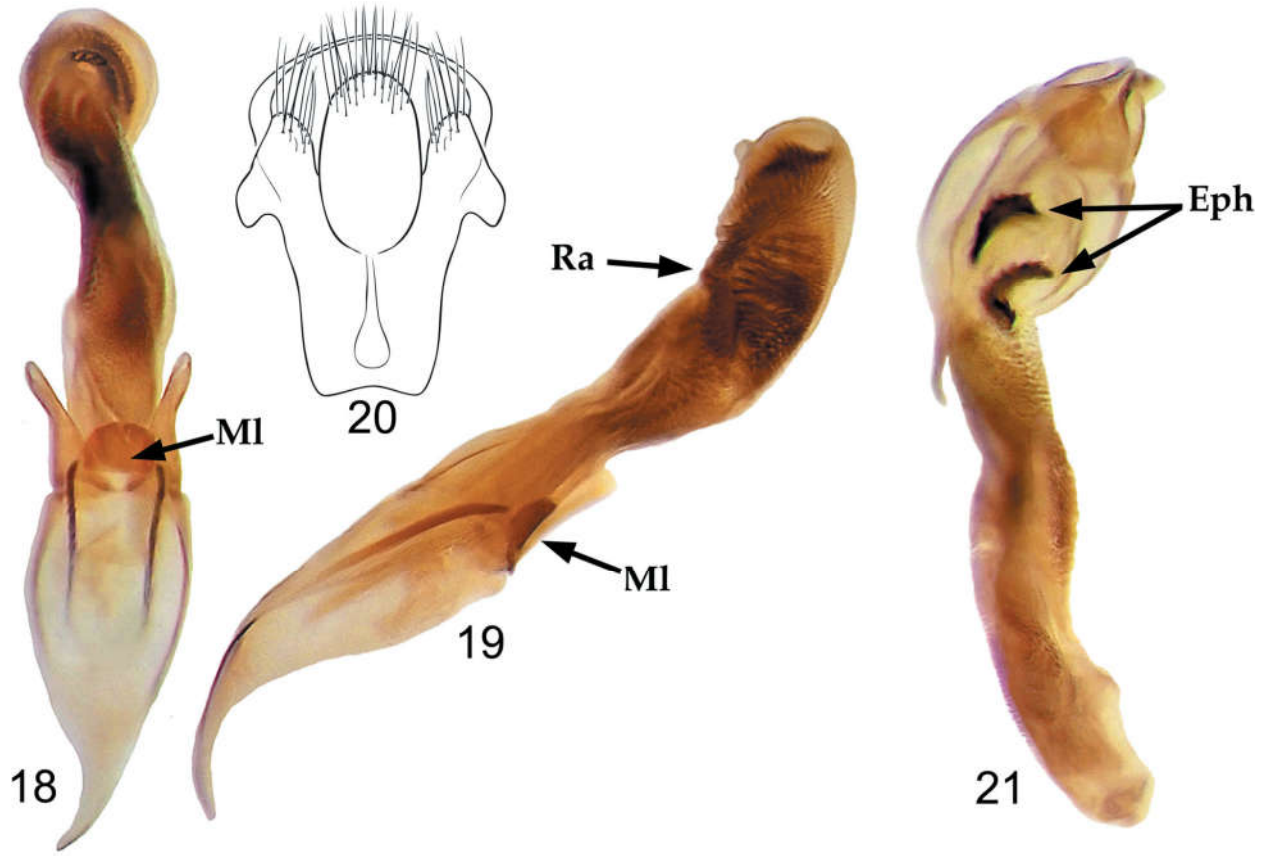
*NB: In the other Old World species, *P. pocadioides* (Spain and Portugal), the endophallus is unarmed.

Discussion

The discovery of a new genus of Ochodaeidae in Southern Africa is not surprising since this part of the continent figures among the regions of the world with the largest number of endemic taxa: 14 species distributed in two subfamilies (Ochodaeinae and Chaetocanthinae), three tribes (Ochodaeini, Chaetocanthini, and Synochodaeini), and five genera (including *Afrochodaeus* **n. gen.**): *Ochodaeus* Dejean, 1821, *Chaetocanthus* Péringuey, 1901, *Namibiotalpa* Scholtz & Evans, 1987, and *Synochodaeus* Kolbe, 1907). The only equivalent would be South America, but the area is much larger and the neotropical fauna only includes two subfamilies and three genera.

Compared to continental scale, at the specific level, 65% of African Ochodaeidae are endemic to the southern part of Africa (South Africa, Namibia and Botswana), and at the generic level four out of six genera (66%) are geographically restricted to the part of the continent south of the 20th parallel south.

With the exception of *A. quadridentatus* located in the far northeast of South Africa (Limpopo), the species belonging to *Afrochodaeus* **n. gen**. occur primarily in Namibia (Figure 26). This country, very biologically diverse, includes a high percentage of endemism (Simmons et al. 19981998). Ecologically, Namibia consists of four xeric or sub-xeric biomes, namely: the Namib desert, the Nama Karoo, the Succulent Karoo, and the Savanna, which extends into Botswana and South Africa (Pitzalis et al. 2014) (Figure 27). *Afrochodaeus* **n. gen**. mainly occupy the tree and shrub savanna biome and the Nama Karoo, a semi-arid inland biome dominated by dwarf shrubs with grasses while other genera such as *Synochodaeus* and *Namibiotalpa* (Chaetocanthinae), more adapted to survive in drier conditions, are located along the coast in sandy areas. *Namibiotalpa fossilis* Scholtz & Evans, 1987, a psammophilous species, only occurs in areas of deep sand in the Namib Desert.



Figures 18–21. *Afrochodaeus* and *Ochodaeus*, male genitalia comparison. **18–20**, *Afrochodaeus rectus* (Scholtz & Evans, 1987) **n. comb.**: **18, 19**, aedeagus, the unarmed endophallus everted (**18**, ventral view; **19**, lateral view); **20**, genital segment (urite IX). **21**, *Ochodaeus adsequa* Kolbe, 1907, aedeagus, the armed endophallus not everted, the serrated endophallites indicated by an arrow (Eph: endophallites; Ml: median lobe; Ra: raspulae).

Updated catalogue of the Ochodaeinae of Africa

Ochodaeini Mulsant & Rey, 1871

Afrochodaeus n. gen.

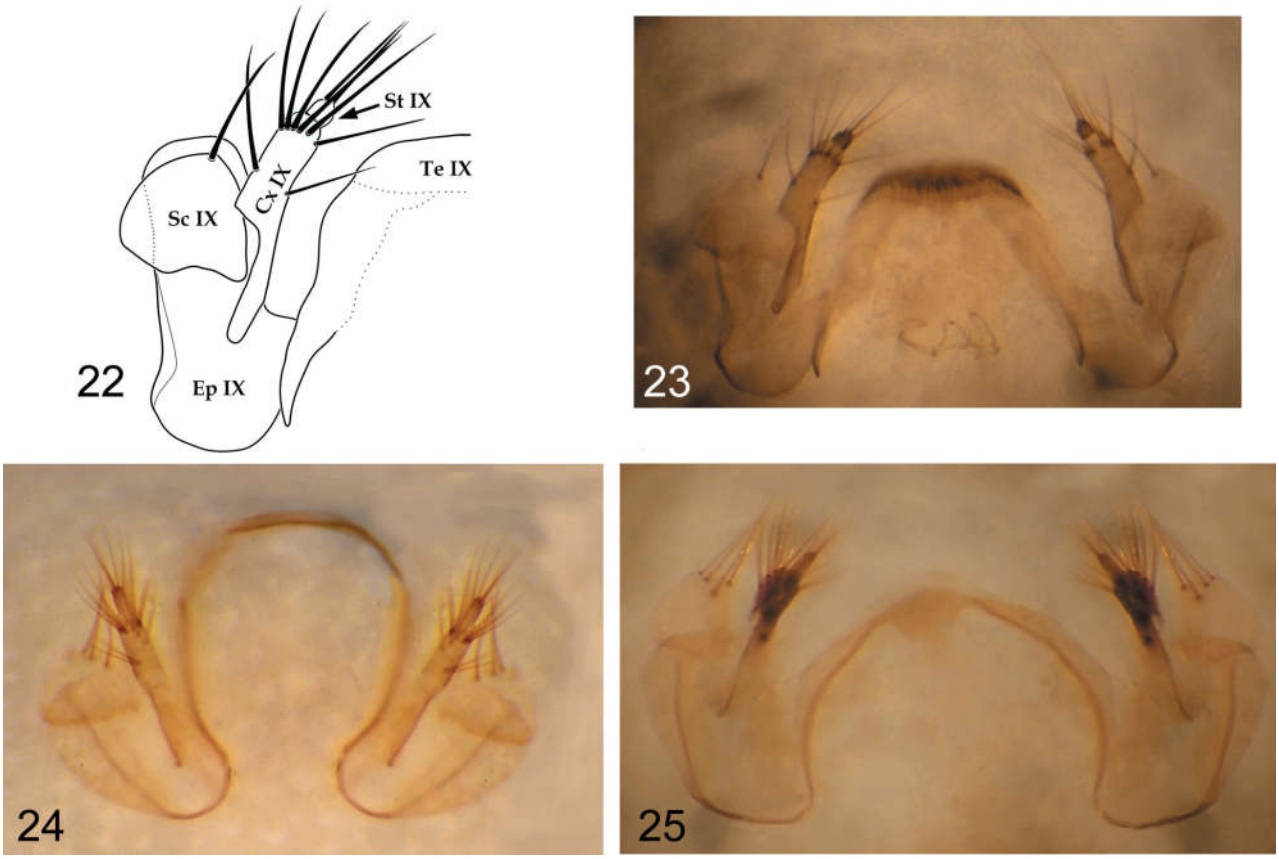
- *A. corniger* (1987) **n. comb**. (Cape Province, Namibia)
- *A. quadridentatus* (Scholtz & Evans, 1987) **n. comb**. (Transvaal)
- *A. rectus* (Scholtz & Evans, 1987) **n. comb**. (Cape Province, Namibia)
- *A. unicornis* (Scholtz & Evans, 1987) **n. comb**. (Namibia)

Ochodaeus Dejean, 1821

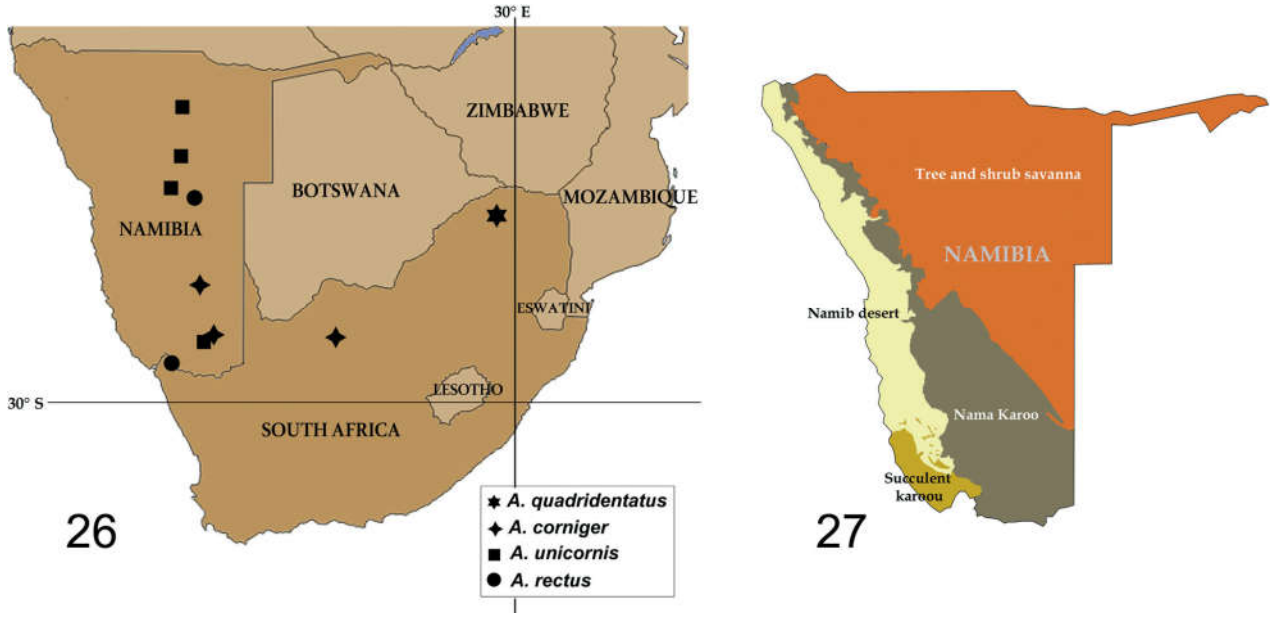
- *O. adsequa* Kolbe, 1907 (Namibia, Botswana)
- *O. alius* Scholtz & Evans, 1987 (Ivory Coast)
- *O. capicola* Péringuey, 1901 (South Africa)
- *O. congoensis* Benderitter, 1913 (Congo, Republic Central Africa, Burkina Faso, Ivory Coast, Mali, Tanzania, Zambia, and Angola (new country record))
- *O. femoratus* Scholtz & Evans, 1987 (Transvaal)
- *O. gigas* Marseul, 1878 (Algeria, Morocco, Tunisia, Egypt, Libya; Israel)
  - Syn. *Ochodaeus harterti* Reitter, 1913: 105 (syn. by Baraud 1985: 88)
- *O. singularis* Scholtz & Evans, 1987 (Kenya, Somalia)
- *O. stridulatus* Scholtz & Evans, 1987 (Central African Republic)

Parochodaeus Nikolajev, 1995

- *P. carinatus* (Benderitter, 1913) **n. comb**. (Somalia, Ethiopia, Kenya, Djibouti)
  - Syn. *Ochodaeus castaneus* Benderitter, 1920 (syn. by Scholtz & Evans 1987, p. 407)
  - Syn. *Ochodaeus ciliatus* Benderitter, 1921 (syn. by Scholtz & Evans 1987, p. 407)
  - Syn. *Ochodaeus minutus* Benderitter, 1923 (syn. by Scholtz & Evans 1987, p. 407)



Figures 22–25. Female terminalia. **22, 23**, *Afrochodaeus unicornis* (Scholtz & Evans, 1987): **22**, schematic representation (Cx: coxite; Ep: epipleurite; Sc: subcoxite; St: style; Te: tergite); **23**, photograph. **24**, *Ochodaeus congoensis* Benderitter, 1913. **25**, *O. adsequa* Kolbe, 1907.



Figures 26, 27. Geographic data. **26**, Geographic distribution of the species belonging to the genus *Afrochodaeus* **n. gen. 27**, The Namibian biomes (after Pitzalis et al. 2014, modified).

Acknowledgements

I would like to thank the following curators and colleagues for having allowed me to study the material mentioned in this paper: François S. Becker (National Museum of Namibia, Windhoek, Namibia) for having kindly allowed me to study the African Ochodaeidae specimens preserved within its institution, including the type material of *O. corniger*, and *O. unicornis*, François Génier (Canadian Museum for Nature, Ottawa, Canada) for providing me with the unique type specimen of *Ochodaeus alius*, Beth Grobbelaar (South African National Collection, Queenswood, South Africa), David Král (National Museum, Prague, Czech Republic), Arnaud Faille (Staatliches Museum für Naturkunde, Stuttgart, Germany), Olivier Montreuil and Antoine Mantilleri (Muséum national d'Histoire naturelle, Paris, France), Geoffrey Miessen (Liege, Belgium), Stanislav Jákl, David Sommer, and Richard Ambrus (Prague, Czech Republic). I am indebted to Amoret P. Whitaker (Natural History Museum, London, UK), for kindly improving the English version of the manuscript. Finally, I would like to address my sincere thanks to the two anonymous reviewers for their insightful comments that improved the paper.

ORCID

Jean-Bernard Huchet http://orcid.org/0000-0002-3906-6934

References

Ahrens D, Schwarzer J, Vogler AP. 2014. The evolution of scarab beetles tracks the sequential rise of angiosperms and mammals. Proceedings of the Royal Society B. 281 (1791):20141470. doi:10.1098/rspb.2014.1470.

Arrow GJ. 1904. XXVII. Sound-production in the Lamellicorn Beetles. Transactions of the Royal Entomological Society of London. 52(4):709–750. doi:10.1111/j.1365-2311.1904.tb02761.x.

Bocak L, Barton C, Crampton-Platt A, Chesters D, Ahrens D, Vogler AP. 2014. Building the Coleoptera tree-of-life for >8000 species: composition of public DNA data and fit with Linnaean classification. Systematic Entomology. 39 (1):97–110. doi:10.1111/syen.12037.

Bouchard P, Bousquet Y, Davies AE, Alonso-Zarazaga MA, Lawrence JF, Lyal CH, Newton AF, Reid CA, Schmitt M, Slipiński SA, et al. 2011. Family-group names in Coleoptera (Insecta). ZooKeys. 88:1–972. doi:10.3897/zookeys.88.807.

Carlson DC. 1975. Taxonomic characters of the genus Ochodaeus Serville with descriptions of two new species in the O. pectoralis LeConte species complex (Coleoptera: Scarabaeidae). Bulletin of the Southern California Academy of Sciences. 74: 49–65.

Carlson DC. 2002. Ochodaeidae Mulsant and Rey, 1870. In: Arnett R H, Thomas M C, Skelley P E and Frank J H, editors. American Beetles Vol. 2. Boca Raton: CRC Press; p. 861.

Carlson DC, Ritcher PO. 1974. A new genus of Ochodaeinae and a description of the larva of *Pseudochodaeus estriatus* (Schaeffer) (Coleoptera: Scarabaeidae). Pan Pacific Entomologist. 50:99–110.

Carpaneto GM, Piattella E. 1990. First records of Ochodaeidae from Somalia. Bollettino della Societa Entomologica Italiana. 122(2):115–118.

Dupuis F. 2005. L'abdomen et les genitalia des femelles de coléoptères Scarabaeoidea (Insecta, Coleoptera). Zoosystema. 27(4):733–823.

Fall HF. 1909. A short synopsis of the species of *Ochodaeus* inhabiting the United States. Journal of the New York Entomological Society. 17:30–38.

Génier F. 2019. Endophallites: a proposed neologism for naming the sclerotized elements of the insect endophallus (Arthropoda: Insecta). Annales de la Société entomologique de France. 55 (6):482–484. doi:10.1080/00379271.2019.1685907.

Horn GH. 1876. Revision of the United States species of *Ochodaeus* and other genera of Scarabaeidae. Transactions of the American Entomological Society. 5:177–198.

Hotman D (d'), Scholtz CH. 1990. Phylogenetic significance of the structure of the external male genitalia in the Scarabaeoidea (Coleoptera). Entomology Memoir. 77:iii+ 51.

Huchet J-B. 2014a. Un nouveau *Nothochodaeus* Nikolajev des Philippines (Coleoptera, Scarabaeoidea, Ochodaeidae). Coléoptères. 20(6):38–46.

Huchet J-B. 2014b. *Nothochodaeus mindanaoensis*, nouvelle espèce des Philippines (Coleoptera, Scarabaeoidea, Ochodaeidae). Coléoptères. 20(8):57–64.

Huchet J-B. 2016. Un nouveau genre et une nouvelle espèce d'Ochodaeidae pour la faune d'Europe (Coleoptera: Scarabaeoidea). Coléoptères. 22(5):38–53.

Huchet J-B. 2017. Un nouveau sous-genre et une nouvelle espèce d'Ochodaeidae des Philippines (Coleoptera, Scarabaeoidea). Coléoptères. 23(8):85–93.

Huchet J-B. 2018. Une nouvelle espèce du sous-genre *Ceratochodaeus* Huchet, 2017, de Luzon, Philippines (Coleoptera, Scarabaeoidea, Ochodaeidae). Coléoptères. 24 (7):63–70.

Huchet J-B. 2019. New data on the taxonomy and distribution of Philippine Ochodaeidae and description of a new species from Central Visayas (Coleoptera: Scarabaeoidea). Insecta Mundi. 0722:1–10.

Huchet J-B. 2020. Two new species of *Nothochodaeus* Nikolajev, 2005 from the Himalayan region (Coleoptera: Scarabaeoidea: Ochodaeidae). Insecta Mundi. 0778:1–11.

Huchet J-B, Keith D. 2017. Réhabilitation du genre *Mimochodaeus* Nikolajev, 2009 et description d'une nouvelle espèce du Sichuan, Chine (Coleoptera: Scarabaeoidea: Ochodaeidae). Coléoptères. 23(2):17–29.

Huchet J-B, Li CL. 2015. Une nouvelle espèce taïwanaise du genre *Nothochodaeus* Nikolajev (Coleoptera, Ochodaeidae). Coléoptères. 21(16):179–189.

López-Colon JI, Löbl I, Nikolajev GV. 2016. Ochodaeidae. In: Löbl I and Smetana A, editors. Catalogue of Palaearctic Coleoptera Vol. 3. Leiden (Boston): Brill; p. 983. Scarabaeoidea – Scirtoidea – Dascilloidea – Buprestoidea – Byrrhoidea. 2nd revised and updated edition.

Medina CA, Molano F, Scholtz CH. 2013. Morphology and terminology of dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) male genitalia. Zootaxa. 3626(4):455–476. doi:10.11646/zootaxa.3626.4.3.

Nikolajev GV. 1995. New data on the systematics of the subfamily Ochodaeinae (Coleoptera, Scarabaeidae). Zoologicheskiy Zhurnal. 74: 72–82. (in Russian).

Nikolajev GV. 2005. *Notochodaeus* [sic] gen. Nov, a new Ochodaeinae genus (Coleoptera, Scarabaeidae) from Asia. Euroasian Entomological Journal. 4:219–220.

Nikolajev GV. 2009. Ochodaeidae species of the Palaearctic's Asia. Euroasian Entomological Journal. 8: 205–211. in Russian with English abstract.

Ochi T, Kawahara M, Inagaki M. 2006. Taxonomic notes on some Japanese coprophagous lamellicorn beetles. VI.

Descriptions of three new taxa. Japanese Journal of Systematic Entomology. 12(1): 141–147.
Paulian R. 1976. Les Ochodaeidae (Coleoptera: Scarabaeoidea) de Madagascar. Nouvelle Revue d'Entomologie. 6:139–152.
Paulsen MJ. 2007. Nomenclatural changes in the Nearctic Ochodaeinae and description of two new genera (Coleoptera: Scarabaeoidea: Ochodaeidae). Insecta Mundi. 0021:1–13.
Paulsen MJ. 2011. A new species of *Parochodaeus* Nikolajev from the southwestern United States (Coleoptera: Scarabaeoidea: Ochodaeidae). Insecta Mundi. 0184:1–6.
Paulsen MJ. 2012. The Ochodaeidae (Coleoptera: Scarabaeoidea) of Guatemala. In: Cano E, editor. Biodiversidad de Guatemala. Vol. 2. Guatemala City: Universidad de Valle de Guatemala; 175–179.
Paulsen MJ. 2014. Correction of the misidentifications and confusion surrounding *Ochodaeus grandiceps* Fairmaire, 1897 (Coleoptera: Ochodaeidae), and the description of a new species of ochodaeid from Cuba. Insecta Mundi. 369:1–6.
Paulsen MJ. 2019a. Three new Madagascan species of *Ochodaeus* Dejean (Coleoptera: Scarabaeoidea: Ochodaeidae). Insecta Mundi. 0684:1–14. doi:10.5281/zenodo.2579565.
Paulsen MJ. 2019b. New species of *Ochodaeus* Dejean from Madagascar II (Coleoptera: Scarabaeoidea: Ochodaeidae). Insecta Mundi. 0706:1–10. doi:10.5281/zenodo.3673403.
Paulsen MJ, Ocampo FC. 2012. The Ochodaeidae of Argentina (Coleoptera, Scarabaeoidea). ZooKeys. 174:7–30. doi:10.3897/zookeys.174.2668.
Pitzalis M, Amore V, Montalto F, Luiselli L, Bologna MA. 2014. Rarity of blister beetles (Coleoptera: Meloidae) in Southern Africa correlates with their phylogeny and trophic habits, but not body size. European Journal of Entomology. 111(4):529–535. doi:10.14411/eje.2014.058.
Sabatinelli G, Eberle J, Fabrizi S, Ahrens D. 2020. A molecular phylogeny of Glaphyridae (Coleoptera: Scarabaeoidea): evolution of pollination and association with 'Poppy guild' flowers. Systematic Entomology. 45:838–848. doi:10.1111/syen.12429.
Scholtz CH. 1990. Phylogenetic trends in the Scarabaeoidea (Coleoptera). Journal of Natural History. 24: 1027–1066.
Scholtz CH. 1991. Nomenclatural changes in the Ochodaeidae (Coleoptera: Scarabaeoidea). The Coleopterists Bulletin. 45 (1):30.
Scholtz CH, d'Hotman D, Evans AV, Nel A. 1988. Phylogeny and systematics of the Ochodaeidae (Insecta: Coleoptera: Scarabaeoidea). Journal of the Entomological Society of Southern Africa. 51(2):207–240.
Scholtz CH, Evans AV. 1987. A revision of the African Ochodaeidae (Coleoptera: Scarabaeoidea). Journal of the Entomological Society of Southern Africa. 50:399–426.
Simmons RE, Griffin M, Griffin RE, Marais E, Kolberg H. 1998. Endemism in Namibia: patterns, processes and predictions. Biodiversity & Conservation. 7:513–530.
Smith ABT, Hawks DC, Heraty JM. 2006. An overview of the classification and evolution of the major scarab beetle clades (Coleoptera: Scarabaeoidea) based on preliminary molecular analyses. Coleopterists Society Monograph. 5:35–46.
Sommer D, Hrůzová L, Král D. in press. Occurrence of the family Ochodaeidae (Coleoptera: Scarabaeoidea) in the Arabian Peninsula. Acta Societatis Zoologicae Bohemicae. 84(1–2).
Woodruff RE. 1973. The scarab beetles of Florida (Coleoptera: Scarabaeidae). Part. I. The Laparosticti (subfamilies: Scarabaeinae, Aphodiinae, Hybosorinae, Ochodaeinae, Geotrupinae, Acanthocerinae). Arthropods of Florida and Neighboring Land Areas. 8:220.