

**A taxonomic review of the genus *Clitobius*
with description of a new species from Oman
(Coleoptera: Tenebrionidae)**

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Abstract. Based on external and internal morphological characters, *Apithesis obesa* Waterhouse, 1881 (of the monotypical genus *Apithesis* Waterhouse, 1881) is redescribed and transferred from the tribe Ulomini to the tribe Opatrini where it is incorporated in *Clitobius* Mulsant & Rey, 1859. Preliminary review of the taxonomy and distribution of *Clitobius* is performed. The following names are placed in synonymy: *Clitobius* Mulsant & Rey, 1859 = *Apithesis* Waterhouse, 1881, syn. nov. = *Apteroclitobius* Koch, 1960, syn. nov.; *Clitobius ovatus* (Erichson, 1843) = *Halonomus salinicola* Wollaston, 1861, syn. nov.; *Clitobius oblongiusculus* (Fairmaire, 1875) = *Clitobius ovatus borkouensis* Pierre, 1961, syn. nov.; *Clitobius obesus* (Waterhouse, 1881), comb. nov. = *Clitobius pseudalatus* Koch, 1960, syn. nov. *Clitobius omanicus* sp. nov. is described from Oman. A key to the species of *Clitobius* is presented. Distributional patterns within the genus are analysed and discussed.

Key words. Coleoptera, Tenebrionidae, Ulomini, Opatrini, Ammobiina, *Apithesis*, *Apteroclitobius*, *Clitobius*, taxonomy, new species, new synonymy, Oman, Socotra, Yemen

Introduction

The insect fauna of Socotra Archipelago (Yemen) has been subject to intensive study by Czech entomologists for the last several years that led to discoveries of many species new to science. A part of these results has already been published (HÁJEK & BEZDĚK 2012, 2014).

The research was focused also on the family Tenebrionidae, one of the most diverse beetle families that occur on the island. Based on the material mentioned above, the following genera have been treated so far: *Deretus* Gahan, 1900 (PURCHART 2012, 2013; PURCHART & NABOZHENKO 2012), *Corticeus* Piller & Mitterpacher, 1783 (PURCHART & SCHAWALLER 2012), *Socotralia* Novák, 2004 (NOVÁK & PURCHART 2012), *Nanocaecus* Schawaller & Purchart, 2012 (SCHAWALLER & PURCHART 2012), *Histeromorphus* Kraatz, 1865 (PURCHART 2014a), *Zophosis* Latreille, 1802, *Oxycara* Solier, 1835, *Freyula* Koch, 1959 (PURCHART 2014b) and *Trachyscelis* Latreille, 1809 (NABOZHENKO & PURCHART 2017). This paper presents a further part of these results and deals with the genus *Apithesis* Waterhouse, 1881.

A large series of *Apithesis obesa* Waterhouse, 1881 collected in Socotra Island was studied in order to verify its taxonomic position. Moreover, a similar new species was discovered within the material collected in Oman. Close examination of morphology of both taxa revealed that they should be treated as representatives of the tribe Opatrini, where they belong to the genus *Clitobius* Mulsant & Rey, 1859 (for details see below).

The aim of this study was to incorporate the above-mentioned species within *Clitobius*. Moreover, based on available type material, a preliminary revision of this genus was performed.

Material and methods

Material of *Apithesis obesa* was obtained under the research project implemented by a research team of the Mendel University in Brno (Czech Republic) (for details see PURCHART 2012). Dissection and preparation of female internal structures followed IWAN & KAMIŃSKI (2016). Photographs were taken using a KEYENCE microscope with VH-Z20R and VH-Z100R lenses at the Faculty of Forestry and Wood Technology (Mendel University in Brno). SEM images were acquired using a Hitachi S-3400N microscope at the Museum and Institute of Zoology (Polish Academy of Sciences, Warsaw). Terminology of female internal structures follows TSCHINKEL & DOYEN (1980) and MATTHEWS & BOUCHARD (2008).

Stated lengths and widths represent the maximum values of the measured parts. Body length is the distance from the clypeus to the elytral apex with head in its natural position. Width of elytra is the combined maximum width of both elytra.

Exact label data are cited for the type specimens; a double slash (//) divides the data on different labels. All specimens of the newly described species bear one printed red label: 'HOLOTYPE [PARATYPE], *Clitobius omanicus* sp. nov., det. Purchart & Kamiński 2017'.

Socotran local names stated in the text below may represent one of many alternative transcriptions of the same place. For more information see BEZDĚK et al. (2012).

The material studied is deposited in the following collections:

BMNH	The Natural History Museum, London, United Kingdom (Maxwell V. L. Barclay);
CULS	Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Prague, Czech Republic (Jan Farkač);
LPCB	Luboš Purchart collection, Brno, Czech Republic;
MIIZ	Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw, Poland (Marcin Jan Kamiński);
MZSF	Museo Zoologico 'La Specola', Florence (Luca Bartolozzi);
NMPC	Národní muzeum, Prague, Czech Republic (Jiří Hájek);
ZSMG	Zoologische Staatssammlung München, Munich, Germany (Ditta Amran Balke).

The distribution of species was illustrated using Quantum GIS (QGIS) v. 2.4. The raster layer used for creating the digital elevation model was downloaded from the WorldClim website (<http://www.worldclim.org/>). The list of localities was built by consulting available literature and including label data of the investigated specimens (Appendix 1). Geographic data with low degree of accuracy (countries or states) was not georeferenced, and therefore is absent on the maps and distributional sections of particular taxa.

Potential distributions of chosen *Clitobius* species were modelled with a presence-only method due to the lack of reliable absence data. MaxEnt approach (Maximum Entropy Modelling) was employed (HERNANDEZ et al. 2006, ELITH et al. 2006). *Clitobius ovatus* and *C. oblongiusculus* were the only species included in the analysis, due to the scarcity of distributional data reported for other taxa (Appendix 1). Clustered localities were excluded prior to the modelling process to reduce spatial autocorrelation (for details see Appendix 1). A set of WorldClim (HIJMAN et al. 2005) environmental layers (continuous variables, resolution of 2.5 minutes) was used in the calculations. The area of the analysis was not restricted to any particular parts of the globe. Models were run 25 times, with random test percentage set to 25 and ‘Subsample’ as the sampling technique. The model evaluation was assessed by estimating the Area Under Curve value (AUC) (FIELDING & BELL 1997). After mapping the ecological niche of the studied species, the obtained prediction values (ranging from 0 to 1) were converted into binary (presence/absence) using the threshold rule of equal training sensitivity and specificity. This approach refers to the choice of a model that has an equal probability of being sensitive (predicting true presences) and being specific (predicting true absences) (CANRAN et al. 2005, FREEMAN & MOISEN 2008, FIKÁČEK & VONDRÁČEK 2014). The primary goal of the performed analysis was to verify the credibility of the disjunct localities provided by MULSANT & REY (1859) and ALLARD (1891) respectively for *C. ovatus* and *C. oblongiusculus* (Fig. 4). Moreover, the conducted analysis enabled verification of the abiotic factors strongly influencing distribution of the studied species.

History of classification

The monotypic genus *Apithesis*, with *Apithesis obesa* Waterhouse, 1881 as type species of the genus, was described by WATERHOUSE (1881) from Socotra Island and it was considered endemic for the Socotra Archipelago (KOCH 1970, SCHAWALLER 2004, BATELKA 2012). It was provisionally placed by WATERHOUSE (1881) in the tribe Ulomini as closely related to the genus *Alphitobius* Stephens, 1829, but its systematic position remained unclear (KOCH 1970).

The genus *Clitobius* was established by MULSANT & REY (1859) for *Clitobius sabulicola* Mulsant & Rey, 1859 (by monotypy) from Bengal (‘Le Bengale’), which was later synonymised by FAIRMAIRE (1885) with *Opatrum ovatum* Erichson, 1843. FAIRMAIRE (1856, 1888) described *Platydemia subplumbea* Fairmaire, 1856 and *Clitobius immarginatus* Fairmaire, 1888. Both names are presently considered synonyms of *C. ovatus*. Later FAIRMAIRE (1892, 1896) described *Clitobius laevipennis* Fairmaire, 1892, *C. strongyloides* Fairmaire, 1892, *C. grandis* Fairmaire, 1896, and *C. rugulipennis* Fairmaire, 1896. *Clitobius laevipennis* and *C. rugulipennis* were later transferred to the genus *Falsammidium* Koch, 1960. Just as an interesting fact, BEDEL (1896) had serious doubts about the origin of *C. rugulipennis* that was

described as coming from Djibouti. BEDEL (1896) believed that types of this species in fact come from Sheikh Othman or Perim Island, both in Yemen.

REITTER (1904) established the subgenus *Pentholasius* Reitter, 1904 for *Halonomus vario-latus* Allard, 1884. *Pentholasius* was later synonymised by FERRER (2001) with *Mesomorphus* Miedel, 1880.

ESCALERA (1914) described *Clitobius fossulatus* Escalera, 1914 for which ESPAÑOL (1943) established a separate subgenus *Falsocaedius* Español, 1943. KOCH (1959b) transferred *C. fossulatus* to the genus *Ammidium* Erichson, 1843 as *A. (Falsocaedius) fossulatum*. The same author (KOCH 1960) promoted the subgenus *Falsocaedius* to generic level. In the same paper Koch divided *Clitobius* into two subgenera – a newly described *Apteroclitobius* (type species: *C. grandis*) and the nominal one. Besides, he also described *Clitobius pseudalatus* Koch, 1960, which is treated as a new synonym for *Apithesis obesa* in this paper. PIERRE (1961) described *Clitobius ovatus borkouensis* from Chad. The last two species, *C. kochi* Ferrer 1995 and *C. endroediorum* Ferrer, 2001, were incorporated by FERRER (1995, 2001).

Meanwhile, WOLLASTON (1861) established the genus *Halonomus* Wollaston, 1861 for two species, *H. grayii* Wollaston, 1861 and *H. salinicola* Wollaston, 1861 (the latter treated as a new synonym of *C. ovatus* in this paper), from Canary Islands without designating the type species of the genus. Thus, type species designation has formally been performed for *H. grayii* by IWAN & LÖBL (2007). WOLLASTON (1867) himself synonymised *H. grayii* with *Clitobius ovatus*. FAIRMAIRE (1875, 1879b) added *Halonomus oblongiusculus* Fairmaire, 1875 from Algeria and *H. lineicollis* Fairmaire, 1879 from the Sinai Peninsula. The latter species, however, is a synonym of the previous one (GEBIEN 1910). ALLARD (1882) described *H. cribricollis* Allard, 1882 from Abyssinia (= Ethiopia) and *H. schneideri* Allard, 1882 from Cairo (Egypt). ALLARD (1884) described *H. variolatus* Allard, 1884 (= *Penthicus subpubescens* Reitter, 1896) from Syria which has later been transferred by FERRER (2001) to the genus *Mesomorphus* (see also *Pentholasius* above). The genus *Halonomus*, however, was later synonymised by FAIRMAIRE (1885) with the genus *Clitobius*.

Prior to this publication, *Clitobius* contained two subgenera and nine species and subspecies (KOCH 1960, FERRER 2001, LÖBL et al. 2008).

Taxonomy

Genus *Clitobius* Mulsant & Rey, 1859

(Figs 1, 2, 3C–I, 4)

Clitobius Mulsant & Rey, 1859: 141 (original description). Type species: *Clitobius sabulicola* Mulsant & Rey, 1859 (= *Opatrum ovatum* Erichson, 1843). MULSANT & REY (1860): 49 (repeated description); FAIRMAIRE (1885): ccvi (catalogue); SEIDLITZ (1891): 130 (key to Tenebrionidae of Transylvania); SEIDLITZ (1898): 410 (key to Opatrini), 452 (key to Melanimonina); CHAMPION (1895): 111 (catalogue); REITTER (1904): 136 (key to Opatrini), 178 (new subgenus); GEBIEN (1910): 340 (catalogue); REICHARDT (1936): 81 (key to Palaearctic Opatrini), 200 (key to subgenera), 201 (key to species); ESPAÑOL (1943): 142 (key to *Clitobius* subgenera); ESPAÑOL (1944): 30 (key to palaearctic Opatrina); ESPAÑOL (1962a): 219 (key to Opatrinae of Canary Islands); HAR. LINDBERG (1950): 12 (new species); KOCH (1959a): 11 (definition and key of *Clitobius* group of genera); KOCH (1959b): 592 (key to *Clitobius* group of genera); KOCH (1960): 391 (key to *Apteroclitobius* species), 403 (key to *Clitobius* generic group); ABDURAKHMANOV & NABOZHENKO (2011): 103 (key to Opatrina).

Apithesis Waterhouse, 1881: 476 (**syn. nov.**). Type species: *Apithesis obesa* Waterhouse, 1881. GAHAN (1903): 280 (repeated description; with figure of habitus); GEBIEN (1940): 781 [588] (catalogue); KOCH (1970): 115; SCHAWALLER (2004): 455 (new records); LÖBL et al. (2008): 302 (catalogue).

Apteroclitobius Koch, 1960: 391 (**syn. nov.**). Type species: *Clitobius grandis* Fairmaire, 1896.

Halonomus Wollaston, 1861: 201 (syn. by FAIRMAIRE 1885: ccv). Type species: *Halonomus grayii* Wollaston, 1861. WOLLASTON (1864): 490; WOLLASTON (1865): 415 (discussion); WOLLASTON (1867): 191 (redescription); ALLARD (1883): 30 (key to species); IWAN & LÖBL (2007): 733 (type species designation).

Halanomus [sic!]: ESCALERA (1914): 339.

Note. The above-listed publications concern only the most important nomenclatural acts and taxonomic works. For justification of the newly proposed synonymies see the discussion.

Diagnostic characters. According to KOCH (1960) and subsequent authors (e.g. SCHAWALLER 2009) *Clitobius* together with *Ammidium* Erichson, 1843, *Diaderma* Koch, 1960, *Falsammidium* Koch, 1960, *Falsocaedius* Español, 1943, and *Freyula* Koch, 1959 form a separate generic complex. All these taxa, together with some other genera representing Opatrini, were recently classified within the restituted subtribe *Ammobiina* (see IWAN & KAMIŃSKI 2016). Taxonomic distinctiveness of *Clitobius* within the above-mentioned generic complex is grounded in the following characters: base of pronotal disc bisinuate, with complete margination (Figs 2B vs 3A); prosternal apophysis, in lateral view, horizontal, not gradually depressed or saddle-like (Figs 3B vs 3C); sides of pronotum and elytra glabrous or covered with fine and short setae; primary rows coarse (Figs 2F vs 3A); protibia with relatively small apical tooth and without median tooth (Fig. 1).

Checklist of the genus *Clitobius*

<i>C. cribricollis</i> (Allard, 1882)	Ethiopia, Yemen
<i>C. endroediorum</i> Ferrer, 2001	Namibia, RSA
<i>C. grandis</i> Fairmaire, 1896	Djibouti
<i>C. kochi</i> Ferrer, 1995	Somalia
<i>C. obesus</i> (Waterhouse, 1881), comb. nov. = <i>Clitobius pseudalatus</i> Koch 1960, syn. nov.	Somalia, Yemen (Socotra Archipelago)
<i>C. oblongiusculus</i> (Fairmaire, 1875) = <i>Halonomus lineicollis</i> Fairmaire, 1879 = <i>Halonomus schneideri</i> Allard, 1882	north Africa, Arabian Peninsula, Cyprus, Azerbaijan, Iran, Tajikistan
<i>C. omanicus</i> sp. nov.	Oman
<i>C. ovatus</i> (Erichson, 1843) = <i>Halonomus grayii</i> Wollaston, 1861 = <i>Clitobius immarginatus</i> Fairmaire, 1888 = <i>Clitobius opacus</i> Har. Lindberg, 1950 = <i>Clitobius ovatus borkouensis</i> Pierre, 1961, syn. nov. = <i>Clitobius sabulicola</i> Mulsant & Rey, 1859 = <i>Halonomus salinicola</i> Wollaston, 1861, syn. nov. = <i>Platydemus subplumbea</i> Fairmaire, 1856	widely distributed in Africa, Malta Island
<i>C. strongyloides</i> Fairmaire, 1892	Namibia

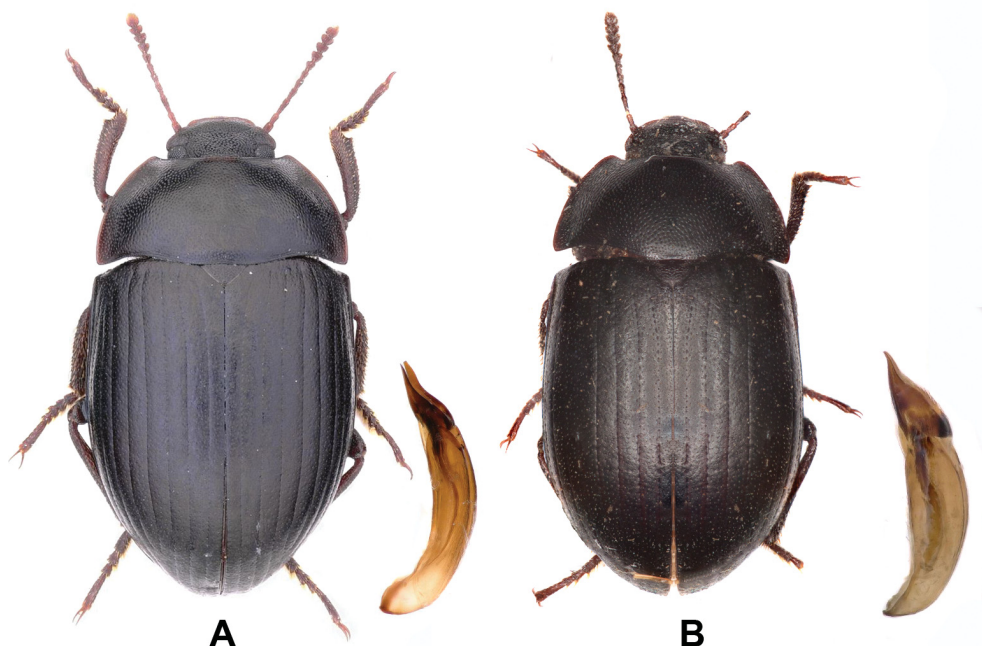


Fig. 1. *Clitobius obesus* (Waterhouse, 1881) (A) and *C. omanicus* sp. nov. (B). Habitus (dorsal view) and aedeagal tegmen (lateral view).

***Clitobius obesus* (Waterhouse, 1881) comb. nov.**

(Figs 1A, 2A–C, 3C–D, 4)

Apithesis obesa Waterhouse, 1881: 477 (original description; with figure of habitus). GAHAN (1903): 280 (redescription; with figure of habitus); GEBIEN (1940): 781 [588] (catalogue); KOCH (1970): 115 (discussion); SCHAWALLER (2004): 455 (new records); LÖBL et al. 2008: 302 (catalogue).

Clitobius pseudalatus Koch 1960: 391 (original description), **syn. nov.**

Type material. *Apithesis obesa* Waterhouse, 1881. SYNTYPES: 1 unsexed spec. (BMNH): Type // Socotra / 81.51 // *Apithesis / obesus* / (Type) Waterh.; 1 unsexed spec. (BMNH): Socotra / 81.51.

Clitobius pseudalatus Koch 1960. PARATYPE, sex undetermined (ZSMG), labelled: CARIN / IX.1959 / C. KOCH // Paratypus / *Clitobius / pseudalatus* / C. Koch sp. n.

Additional material examined. (45 spec.), labelled: YEMEN, Socotra Island / Halla area, Arher / freshwater spring in sand dune / 9-10. + 15.vi.2012 / 12°33.0'N, 54°27.6', 5m // SOCOTRA expedition 2012 / J. Bezděk, J. Hájek, V. Hula, / P. Kment, I. Malenovský, / J. Niedobová & L. Purchart leg. (35 spec.; LPCB, MIIZ, NMPC); YEMEN, SOCOTRA Island / Deiqub cave env. / 10.vi.2010 / V. Hula & J. Niedobová leg. (1 spec.; LPCB); YEMEN, SOCOTRA Island / DEIQUB cave, 12.vi.2012 / cave & *Croton socotranus* + *Jatropha unicosata* shrubland / 12°23.1'N, 54°00.9'E, 115 m // SOCOTRA expedition 2012 / J. Bezděk, J. Hájek, V. Hula, / P. Kment, I. Malenovský, / J. Niedobová & L. Purchart leg. (6 spec.; LPCB, NMPC); Yemen, Soqotra Is. / GUBBAH vill. env. / 23.xi.2003, 7 m / N12°36'35" E53°46'56" // [GPS], David Král lgt. // YEMEN - SOQOTRA 2003 / Expedition; Jan Farkač, Petr Kabátek & David Král (1 spec.; NMPC); same as previous but Jan Farkač lgt. (1 spec.; CULS); Zoologische Excursion / Hadibo / März 1999 / leg. Wranik (1 spec.; NMPC); Yemen: Soqotra Archipelago / Samha I., under stones along wadi / near village / 12°10.392'N 53°00.919'E / 9.II.2000, leg. S Taiti & R. Argano (1 ♀; MZSF).

Redescription. Body length = 5.6–7.4 mm ($n = 25$). Habitus as in Fig. 1A.

Dorsal side of head dull, with fine, but often merging punctures. Frontoclypeal suture extremely fine. Canthus rounded in basal part. Clypeal emargination relatively shallow (clypeal emargination width / depth ratio ca. 9.0). Labrum wide (width / length ratio ca. 1.9); delicately emarginated in middle. Sides of mentum subparallel. Mentum with median keel; lateral wings directed towards body front; not covering cardines or basistipites. Submentum pentagonal. Apical maxillary palpomere trapezoidal; with relatively large sensory field (occupying whole proximal edge). Maxillary palpomere II elongated (length to width ratio ca. 3.0). Palpifer with bunch of setae located near base. Anterior tentorial pits circular. Dorsally eye not shielded by longitudinal keel. Eye partly divided by canthus (three rows of ocelli visible between canthus and gena); ventral portion contains slightly more ocelli than dorsal one. Antenna relatively long (length of antenna / maximal length of pronotum ca. 1.3); antennomere III slender (ratio of its length to length of antennomere II ca. 1.4); antennomeres VIII–XI forming a loosely joined club.

Pronotum narrower than elytra (width ratio elytra / pronotum ca. 1.1). Length to width ratio of pronotal disc ca. 0.6. Pronotal disc dull; with conspicuous microsculpture (magnification 40 \times); covered with fine and shallow punctures (1–2 diameters apart); covered with short and extremely fine setae. Lateral sides of pronotal disc rounded; widest in basal third; without apophyseal depressions. Lateral emargination of pronotum narrow and complete; basal emargination complete (clearly visible, relatively broad); anterior emargination slightly interrupted in middle. Middle of prosternum and basal part of hypomerone covered with coarse setae. The latter structure flattened near lateral edges. Intercostal process of prosternum slightly depressed apically (lateral view). Procoxae situated closely (width ratio of procoxa and intercostal process ca. 1.4).

Elytra dull; glabrous. Elytral striae impressed on their whole length, visible as nine rows of conspicuous punctures on each elytron (1–2 diameters apart). Intervals convex, with fine punctures (2–3 diameters apart). Elytral base sinusoidal; not emarginate. Epipleuron straight in most of its length, terminating at level of abdominal ventrite V; situated ventrally, only basal part visible in dorsal aspect near elytral slope. Elytral humerus obtuse. Scutellum relatively large; triangular. Metathoracic wings reduced (Fig. 3D).

Mesoventrite without processes. Metaventrite relatively elongated (length ratio cavity of metacoxa / metaventrite between insertions of meso- and metacoxae ca. 0.9); without processes, however in apical part slightly elevated; with median carina reaching base of elevated part. Process of abdominal ventrite I narrow and sharp (ratio of distances between meso- and metacoxae ca. 0.5). Abdominal ventrite V not bordered.

Protochanters of opatrinoid type (with elongated base). Meso- and metatrochanters only slightly covered by respective femora. Metacoxa elongated. Male and female tarsi, tibiae and femora simple.

Aedeagal tegmen as in Fig. 1A. Parameres evenly narrowing towards apex. Clavae absent. Penis basally covered by fused parameres. Ovipositor with paraprocts equal in length to coxites. Paraproct does not shield valvifer and other lobes (directed basally). Valvifer wide and short; third and fourth lobes of coxities elongated. Gonostylus situated laterally. Vagina and bursa copulatrix without sclerites. Spiculum ventrale short.

Distribution. Somalia, Yemen (Samha Island, Socotra) (Fig. 4).

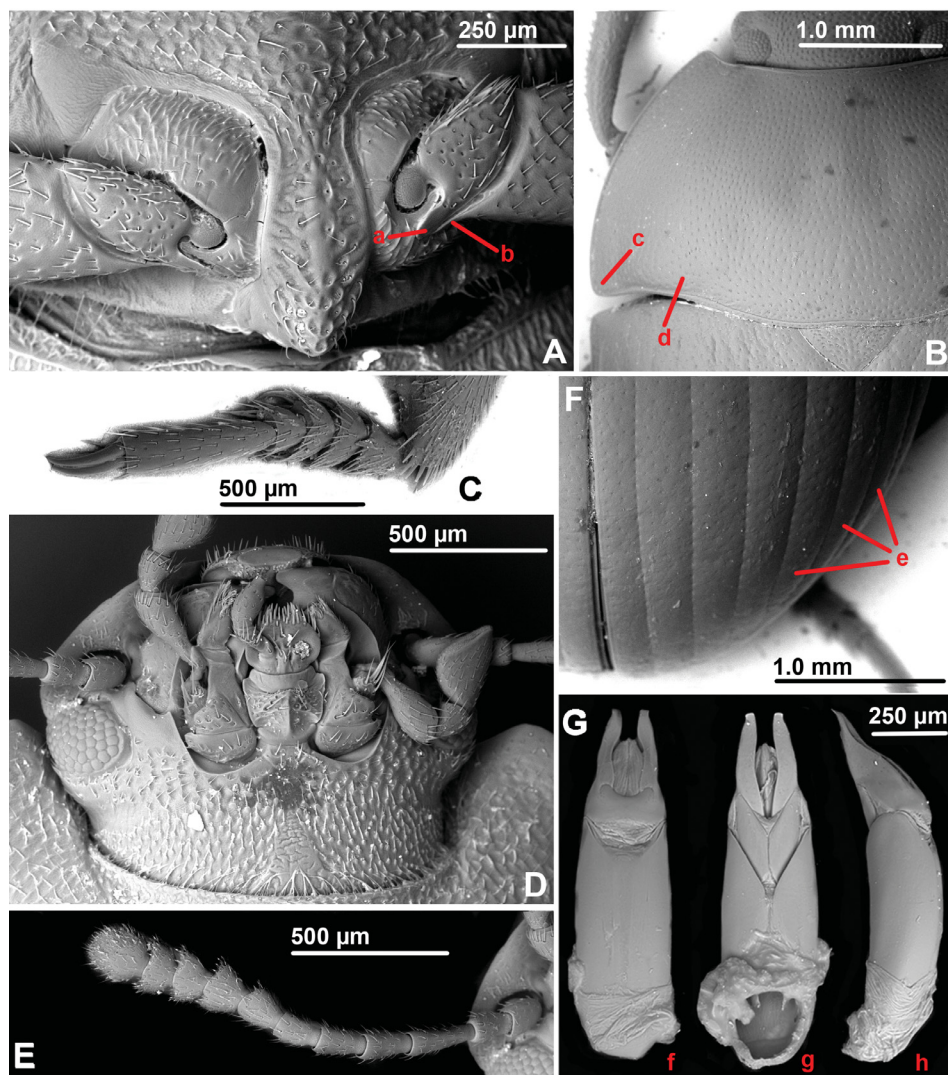
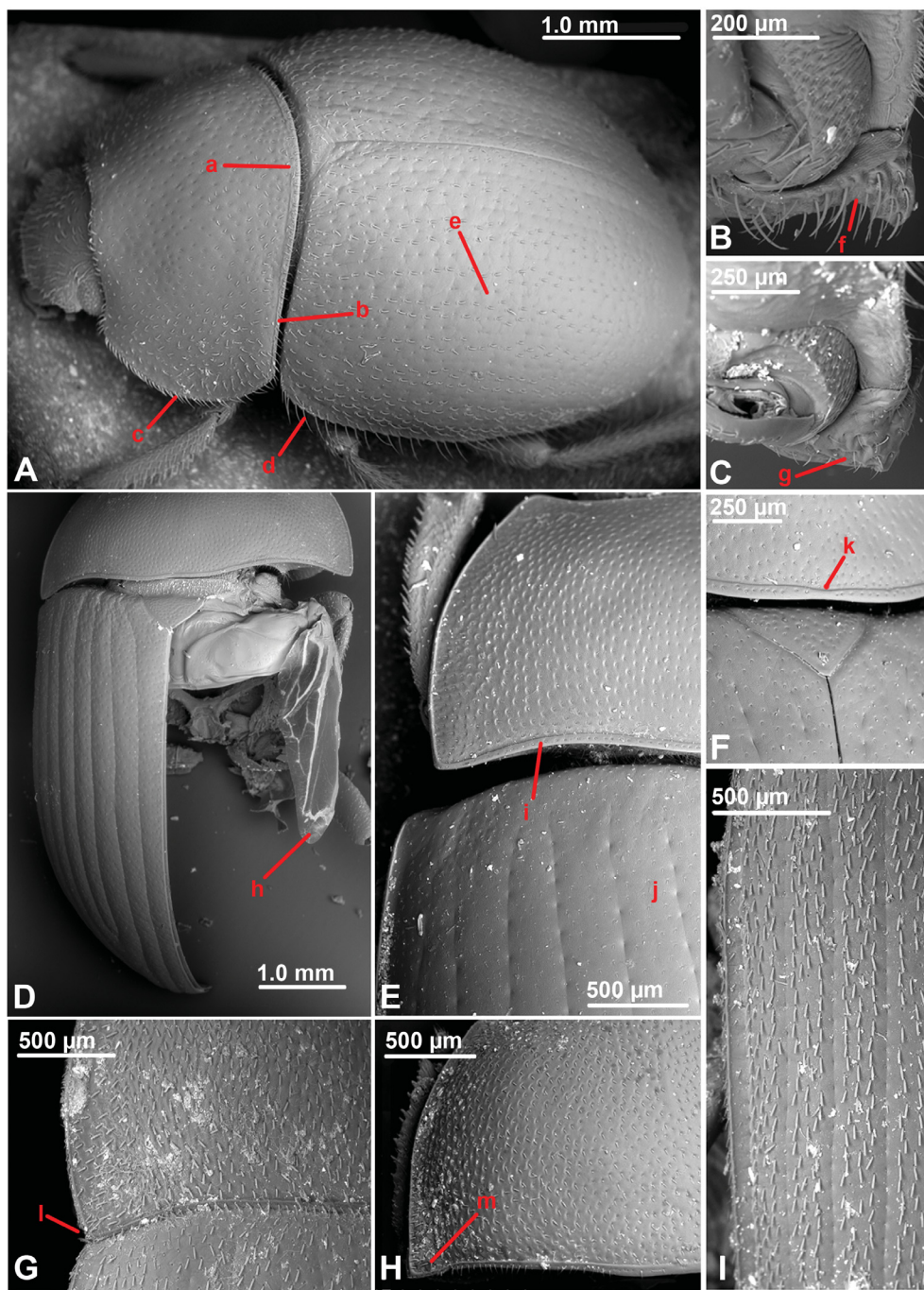


Fig. 2. Detailed morphology of *Clitobius obesus* (Waterhouse, 1881) (A–C, F) and *C. omanicus* sp. nov. (D, E, G). Abbreviations: a – trochanter base; b – femur base; c – rounded posterior angle of pronotal disc; d – not depressed sides of pronotal disc; e – convex intervals; f – ventral; g – dorsal; h – lateral view.

Fig. 3. Diagnostic characters of *Falsocaedius* and *Clitobius*. A–B – *Falsocaedius fossulatus* (Escalera, 1914); C–D – *Clitobius obesus* (Waterhouse, 1881); E–F – *C. grandis* Fairmaire, 1896; G–I – *C. ovatus* (Erichson, 1843); H – *C. oblongiusculus* (Fairmaire, 1875). Abbreviations: a – interrupted basal margination of pronotum; b – straight pronotal base; c–d – long setae on body sides; e – finely marked elytral rows; f – saddle-like tip of prosternal process (lateral view); g – angular tip of prosternal process (lateral view); h – reduced metathoracic wing; i – bi-sinuate base of pronotum; j – sulcate-punctate elytral rows; k – complete margination of pronotal base; l – rounded posterior angle of pronotal disc; m – sharp posterior angle of pronotal disc.



***Clitobius oblongiusculus* (Fairmaire, 1875)**

(Figs 3H, 4)

Halonomus oblongiusculus Fairmaire, 1875: 495 (original description). FAIRMAIRE (1879a): 196 (redescription).*Clitobius oblongiusculus oblongiusculus*: FAIRMAIRE (1885): ccvi (checklist); CHAMPION (1895): 111 (catalogue); REITTER (1904): 179 (key to species); GEBIEN (1910): 340 (catalogue); SAHLBERG (1913): 177 (new record); HOLDHAUS (1919): 44 (new record); BLAIR (1925): 434 (new record); GRIDELLI (1930): 303 (new record), GRIDELLI (1933): 247 (new record); GRIDELLI (1953): 64 (catalogue); REICHARDT (1936): 202 (redescription, distribution, ecology); ESPAÑOL (1943): 143 (new record); ESPAÑOL (1967): 43 (new record); ALFIERI (1976): 197 (new record); KASZAB (1982): 172 (new record, with picture of habitus); JOHNSON (1989): 131 (new record); GRIMM (1991): 30 (new record); CARL (1991): 278 (new record); LILLIG & PAVLIČEK (2003): 48 (new records); SOLDATI (2009): 61 (new record, with photo of habitus); ABDURAKHMANOV & NABOZHENKO (2011): 106 (with drawing of habitus); GRIMM (2015): 312 (new record).*Clitobius oblongiusculus* [sic!]: ANDRES (1913): 121 (new record).*Halonomus lineicollis* Fairmaire, 1879b: 4 (original description). FAIRMAIRE (1879a): 197 (redescription); GEBIEN (1910): 340 (synonymy with *C. oblongiusculus*).*Clitobius lineicollis*: FAIRMAIRE (1885): ccvi (checklist); CHAMPION (1895): 111 (catalogue).*Clitobius oblongiusculus lineicollis*: REITTER (1904): 179 (key to species); ALFIERI (1976): 197 (new record).*Halonomus schneideri* Allard, 1882: lxxxvi (original description). ALLARD (1883): 31 (key to species); ALLARD (1891): 235 (new record); FAIRMAIRE (1885): ccvi (synonymy with *C. lineicollis*).*Clitobius schneideri*: CHAMPION (1895): 111 (catalogue).*Clitobius oblongiusculus schneideri*: ARDOIN 1972: 11 (new record); ALFIERI (1976): 197 (new record).*Clitobius ovatus borkouensis* Pierre, 1961: 1043 (original description). ESPAÑOL 1967: 43 (new record); **syn. nov.****Material examined.** (3 spec.; MIIZ), labelled: Sahara algérien // crue / 26-3-48 / P. Pierre; (1 spec.; ZSMG), labelled: Cairo / [unreadable, handwritten], Sammlung / Haag- / Rutenberg.**Taxonomic remark.** Investigation of a topotype (Cairo, Egypt) of *C. oblongiusculus schneideri* did not reveal any characters to support taxonomic distinctiveness of this entity in relation to the typical form. Furthermore, the hitherto accepted subspecific division of *Clitobius oblongiusculus* is not supported by available distributional records. Therefore, the synonymy between *Halonomus schneideri* and *H. oblongiusculus* is confirmed.According to the description provided by PIERRE (1961), *Clitobius ovatus borkouensis* differs from the nominotypical form only in having sharp anterior pronotal angles. Since the taxonomic concept of *Clitobius ovatus* presented here is, inter alia, based on rounded pronotal angles, *Clitobius ovatus borkouensis* seems to fall out. Taking into consideration the other information provided by PIERRE (1961), the concept of this subspecies is consistent with the one presented here for *C. oblongiusculus*. In conclusion, the following synonymy is proposed: *C. oblongiusculus* = *Clitobius ovatus borkouensis*, **syn. nov.****Distribution.** Algeria, Azerbaijan, Chad, Cyprus, Egypt, Israel, Iran, Iraq, Jordan, Libya, Morocco, Qatar, Saudi Arabia, Sudan, Syria, Tajikistan, and Western Sahara (Fig. 4).ALLARD (1891) described *C. oblongiusculus* from Cambodia, an area that is extremely isolated from the known distributional area of the genus *Clitobius*, and thus we consider this record highly improbable and believe that the type material was mislabelled. This assumption has also been supported by the conducted ecological niche modelling (Fig. 4B).

Clitobius omanicus sp. nov.

(Figs 1B, 2D, E, G, 4)

Type locality. Oman, Dhofar Province, Wadi Ain.

Type material. HOLOTYPE, ♂ (NMPC), labelled: OMAN, Dhofar Prov. / WADI AIN, 59 m a.s.l. / 13 km E of Mirbat / 17°01'N; 54°47'E [GPS] / 29. iii. 2012, A. REITER lgt. PARATYPES (1 ♂ 2 ♀♀ NMPC, 1 ♂ LPCB, 1 ♂ MIIZ): same data as holotype.

Description. Body length = 5.8–6.5 mm (n = 6). Habitus as in Fig. 1B.

Dorsal side of head dull, with fine, but often merging punctures. Frontoclypeal suture extremely fine. Canthus rounded in basal part. Clypeal emargination relatively shallow (clypeal emargination width / depth ratio ca. 10.0). Labrum wide (width / length ratio ca. 1.8); delicately emarginated in middle. Sides of mentum subparallel. Mentum with median keel; lateral wings directed towards body front; not covering cardines or basistipites. Submentum pentagonal. Apical maxillary palpomere trapezoidal; with relatively large sensory field (occupying the whole proximal edge). Maxillary palpomere II elongated (length to width ratio ca. 3.0). Palpifer with bunch of setae located near base. Anterior tentorial pits circular. Dorsally eye not shielded by longitudinal keel. Eye partly divided by canthus (three rows of ocelli visible between canthus and gena); ventral portion contains slightly more ocelli than dorsal one. Antenna relatively long (length of antenna / maximal length of pronotum ca. 1.3); antennomere III slender (ratio of its length to length of antennomere II ca. 1.5); antennomeres VII–XI forming a loosely joined club.

Pronotum narrower than elytra (width ratio elytra / pronotum ca. 1.2). Length to width ratio of pronotal disc ca. 0.6. Pronotal disc dull; with conspicuous microsculpture (magnification 40×); covered with fine and shallow punctures (1–2 diameters apart); covered with short and extremely fine setae. Lateral sides of pronotal disc rounded; widest in basal third; without apophyseal depressions. Lateral emargination of pronotum narrow and complete; basal emargination complete (clearly visible, relatively broad); anterior slightly interrupted in middle. Middle of prosternum and basal part of hypomeron covered with coarse setae. The latter structure flattened near lateral edges. Intercoxal process of prosternum not depressed apically, with sharp tip slightly projecting outwards (lateral view). Procoxae situated closely (width ratio of procoxa and intercoxal process ca. 1.3).

Elytra dull; glabrous. Elytral striae impressed on whole length, visible as nine rows of conspicuous punctures on each elytron (2 diameters apart). Intervals flat, with fine punctures (3–4 diameters apart). Elytral base sinusoidal; not emarginate. Epipleuron straight in most of its length, terminating at level of abdominal ventrite V; situated ventrally, only basal part visible in dorsal aspect near elytral slope. Elytral humerus obtuse. Scutellum relatively large; triangular. Metathoracic wings fully developed.

Mesoventrite without processes. Metaventrite relatively elongated (length ratio cavity of metacoxa / metaventrite between insertions of meso- and metacoxae ca. 0.9); without processes, however in apical part slightly elevated; with median carina reaching base of elevated part. Process of abdominal ventrite I narrow and sharp (ratio of distances between meso- and metacoxae ca. 0.5). Abdominal ventrite V not bordered.

Protrochanters of opatrinoid type (with elongated base). Meso- and metatrochanters only slightly covered by respective femora. Metacoxa elongated. Male and female tarsi, tibiae and femora simple.

Aedeagal tegmen as in Figs 1B, 2G. Parameres evenly narrowing towards apex; tip sinu-soidal (lateral view). Clavae absent. Penis basally covered by fused parameres. Ovipositor with paraprocts equal in length to coxites. Paraproct does not shield valvifer and other lobes (directed basally). Valvifer wide and short; third and fourth lobes of coxities elongated. Gonostylus situated laterally. Vagina and bursa copulatrix without sclerites. Spiculum ventrale short. **Differential diagnosis.** This species is similar to *Clitobius oblongiusculus* in sharing the following features: dorsal side of the body glabrous or covered with fine setae (Fig. 1B), metathoracic wings fully developed, pronotum widest in the middle or near the base (Fig. 1B), elytral humeri not protruding outwards (Fig. 1B), protibiae slender, without a prominent apical tooth (Fig. 1B), and male protarsi not widened. Both species can be distinguished by different body shape (*C. oblongiusculus* – elongate; *C. omanicus* sp. nov. – oval), shape of antennomere III (*C. oblongiusculus* – short; *C. omanicus* sp. nov. – elongate), and shape of the posterior pronotal angles (*C. oblongiusculus* – sharp; *C. omanicus* sp. nov. – rounded). For details and additional characters, see the identification key attached below.

Etymology. The name refers to country name Oman, where the new species was collected.

Distribution. Oman – so far known from the type locality only (Fig. 5).

Clitobius ovatus (Erichson, 1843)

(Figs 3G, I, 4)

Opatrum ovatum Erichson, 1843: 249 (original description).

Clitobius ovatus ovatus: FAIRMAIRE (1885): ccvi (checklist); SEIDLITZ (1891): 130 (key to Opatrini); SEIDLITZ (1898): 452 (key to Melanimonina); RAGUSA (1898): 126 (catalogue); REITTER (1904): 179 (key to species); ESCALERA (1914): 339 (new record); GEBIEN (1910): 340 (catalogue); GEBIEN (1920a): 133 (new record); GEBIEN (1920b): 234 (catalogue); KNEUCKER & ANDRES (1920): 73 (new record); EBNER (1923): 190 (new record); GRIDELLI (1930): 303 (new record); GRIDELLI (1933): 247 (new record); GRIDELLI (1954): 79 (new record); REICHARDT (1936): 201 (distribution); ESPAÑOL (1943): 141 (new record, with drawing of habitus); KASZAB (1963): 345 (new record); ARDOIN (1963): 385 (new record); ARDOIN (1971): 115 (new record); ALFIERI (1976): 197 (new record); GRIMM (1995): 44 (distribution); GRIMM (1986): 11 (new record); ALIQUÒ & LEO (1999): 11 (new record); FERRER (2004): 205 (new record); ALIQUÒ & SOLDATI (2010): 88 (new record); LILLIG et al. (2012): 130, 139 (key to Tenebrionidae of Malta, biology).

Halonomus ovatus: WOLLASTON (1867): 192 (redescription); FAIRMAIRE (1879c): 389 (discussion); ALLARD (1883): 30 (key to species); DESBROCHERS DES LOGES (1898): 2 (new record).

Halonomus grayii Wollaston, 1861: 203 (original description). WOLLASTON (1867): 193 (synonymy with *Clitobius ovatus*).

Clitobius grayi: FAIRMAIRE (1885): ccvi (checklist).

Clitobius immarginatus Fairmaire, 1888: 195 (original description). CHAMPION (1895): 111 (catalogue); GEBIEN (1910): 340 (catalogue); GEBIEN (1920a): 133 (synonymy with *C. ovatus*).

Clitobius sabulicola Mulsant & Rey, 1859: 141 (original description). MULSANT & REY (1860): 49 (redescription); GEMMINGER (1870): 1927 (catalogue); FAIRMAIRE (1885): ccvi (synonymy with *C. ovatus*); SEIDLITZ (1891): 130 (key to Opatrini); SEIDLITZ (1898): 452 (key to Melanimonina).

Halonomus salinicola Wollaston, 1861: 203 (original description). WOLLASTON (1864): 490 (redescription); WOLLASTON (1865): 415 (catalogue); FAIRMAIRE (1879a): 196 (redescription); FAIRMAIRE (1879c): 389 (discussion); ALLARD (1883): 31 (key to species); **syn. nov.**

Clitobius salinicola: FAIRMAIRE (1885): ccvi (checklist); GEBIEN (1910): 340 (catalogue); REICHARDT (1936): 202 (distribution).

Clitobius ovatus salinicola: ESPAÑOL (1962a): 212, 219 (drawing of aedeagus, key to subspecies); ESPAÑOL (1962b): 233 (new record); ESPAÑOL (1963): 208 (new record); ESPAÑOL (1967): 43 (new record); HÅK. LINDBERG (1962): 49 (habitus figure); OROMÍ (1982): 272 (checklist); FAUCHEUX (2011): 55 (new record).

Platyedema subplumbea Fairmaire, 1856: 533 (original description). FAIRMAIRE (1879c): 389 (discussion); FAIRMAIRE (1885): ccvi (synonymy with *C. ovatus*).

Halonomus subplumbeus: ROTTENBERG (1870): 252 (redescription, with drawing of habitus); SEIDLITZ (1891): 130 (key to Opatrini); SEIDLITZ (1898): 452 (key to Melanimonina).

Clitobius subplumbeus: CHAMPION (1895): 111 (catalogue).

Clitobius opacus Har. Lindberg, 1950: 12 (original description). GRIMM (1995): 44 (synonymy with *C. ovatus*).

Clitobius ovatus opacus: ESPAÑOL (1962a): 212, 219 (with drawing of aedeagus, key to subspecies); ESPAÑOL (1962b): 233 (new record); ESPAÑOL (1967): 43 (distribution); HÅK. LINDBERG (1962): 50 (habitus figure); OROMÍ (1982): 272 (checklist).

Type material. *Halonomus salinicola* Wollaston, 1861. HOLOTYPE, sex undetermined (ZSMG), labelled: Type Clitobius / salinicola / Woll // salinicola / typ Woll // Sammlung / Haag- / Rutenberg.

Additional material examined. 5 spec. (MIIZ), labelled: Tunis // Clitobius / ovatus Er. / H. Gebien det. 1938.

Taxonomic remarks. During the present investigation of morphology and available literature concerning *C. ovatus salinicola* it was noted that there are no unambiguous characters to separate it from the nominotypical subspecies. This problem was also highlighted by some previous authors (see GRIMM 1995). Moreover, the analyzed distributional data suggest that both alleged subspecies occur sympatrically. Taking into account the above-mentioned facts it is clear that *C. ovatus salinicola* does not satisfy any criteria commonly used to designate subspecies, i.e. it is not allopatric and phenotypically distinct (e.g. BRABY et al. 2012, LAMB et al. 2013). Therefore, *Halonomus salinicola* is considered here a junior synonym of *Clitobius ovatus*.

Bionomy. According to WOLLASTON (1867) it is a strictly halophilous species. OROMÍ (1982) noted that in the Canary Islands *C. ovatus* inhabits beaches and white sand dunes (of mineral or organic origin). In the Maltese Islands it is generally found under stones close to salt marshes and coastal habitats having fine dust alluvial deposits (LILLIG et al. 2012).

Distribution. Angola, Botswana, Canary Islands (Tenerife, Gran Canaria, Fuerteventura, Lobos, Lanzarote), Cape Verde Islands, Egypt, Islands of the lake Chad, Italy (Sicily, Lampedusa), Libya, Maltese Islands, Morocco, Namibia, Senegal, South Africa, Sudan, Tunisia, Western Sahara (Fig. 4).

MULSANT & REY (1859) described *C. sabulicola* from Bengal ('Le Bengale') an area that is extremely isolated from the known distributional area of the genus *Clitobius* and thus we consider this record highly improbable and believe that the type material was mislabelled. This assumption has also been supported by the conducted ecological niche modelling (Fig. 4A).

Key to the species of *Clitobius*

1. Metathoracic wings absent or reduced (e.g., Fig. 3D). 2
 - Metathoracic wings fully developed. 5
2. Elytral intervals flat (Fig. 3E). 3
 - Elytral intervals convex (Fig. 2F). 4
3. Body size: 6.2–7.0 mm. Sides of pronotal disc with sparsely punctured distinct submarginal groove or depression along the lateral edge. ... *Clitobius grandis* Fairmaire, 1896

- Body size ca. 5.0 mm. Sides of pronotal disc without submarginal groove or depression; surface with coarse punctuation; in some cases lateral margination slightly widened near the posterior ends. *Clitobius strongyloides* Fairmaire, 1892
- 4. Body size: 5.0–5.5 mm. Metathoracic wings absent. Hypomera covered with extremely fine punctures. Elytra black and shiny. Elytral rows with coarse punctures (distributed densely than those on pronotal disc). *Clitobius cribricollis* (Allard, 1882)
- Body size: 6.6–7.0 mm. Metathoracic wings reduced but present (Fig. 3D). Hypomera covered with dense and coarse punctures. Elytra dull with greenish metallic shimmer. Elytral rows with fine and elongated punctures (distributed similarly to those on pronotal disc). *Clitobius obesus* (Waterhouse, 1881)
- 5. Pronotum widest directly at base. Elytral humeri strongly protruding outwards.
..... *Clitobius kochi* Ferrer, 1995
- Pronotum widest in the middle or near base (Fig. 3G). Elytral humeri not protruding outwards (Fig. 3G). 6
- 6. Protibiae equipped with a prominent apical tooth. Male protarsi widened (see FERRER 2001). *Clitobius endroediorum* Ferrer, 2001
- Protibiae slender, without a prominent apical tooth. Male protarsi not widened. 7
- 7. Dorsal side of the body covered with coarse and noticeable setae, arranged on each elytral interval in three parallel rows (Fig. 3I). Posterior pronotal angles rounded (Fig. 3G). *Clitobius ovatus* (Erichson, 1843)
- Dorsal side of the body glabrous or covered with fine setae (Fig. 3H). Posterior pronotal angles rounded or sharp (e.g., Fig. 3H). 8
- 8. Body elongated (body length to maximum width ratio = 2.0–2.3). Antennomere III relatively short (length ratio antennomeres II / III ca. 1.4). Antennomeres evenly widened, not forming well designated club. Posterior pronotal angles sharp (Fig. 3H). In some cases, pronotal disc with a longitudinal midline without punctures.
..... *Clitobius oblongiusculus* (Fairmaire, 1875)
- Body oval (body length to maximum width ratio = 1.6–1.9). Antennomere III relatively elongated (length ratio antennomeres II / III ca. 2.1). Five terminal antennomeres forming a club (Fig. 2E). Posterior pronotal angles rounded (Fig. 1B). Centre of pronotal disc evenly covered with punctures. *Clitobius omanicus* sp. nov.

Discussion

WATERHOUSE (1881) had great difficulty in placing the genus *Apithesis* in the family Tenebrionidae but, based exclusively on the similar appearance, he finally placed it close to the genus *Alphitobius* in the tribe Ulomini. He also stated that: ‘it is apterous, a character which is hitherto foreign to the Ulominae, but which I do not consider a fatal bar to its being placed in this subfamily’. The authors of this paper examined a series of specimens from the Socotri population (including the syntypes of *Apithesis obesa*) and surprisingly, found out that they possess reduced wings (but they are not completely apterous) and thus can only partly confirm Waterhouse’s observation.

The tribe Ulomini is recognisable by the presence of placoid sensoria on the antennae,

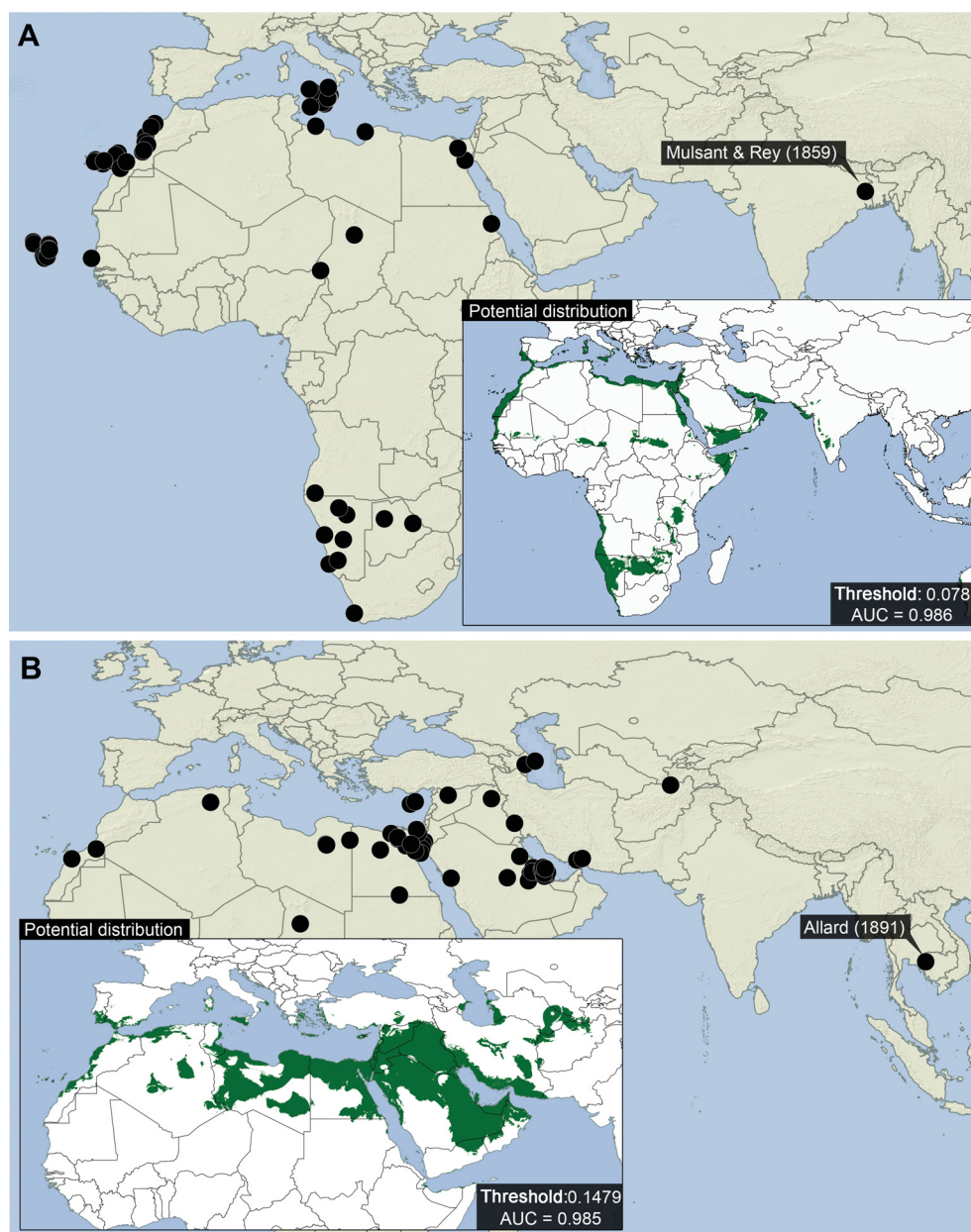


Fig. 4. Analysed localities and potential distribution of *Clitobius ovatus* (Erichson, 1843) (A) and *C. oblongiusculus* (Fairmaire, 1875) (B). Average AUC and habitat suitability threshold values for each analysis are presented.

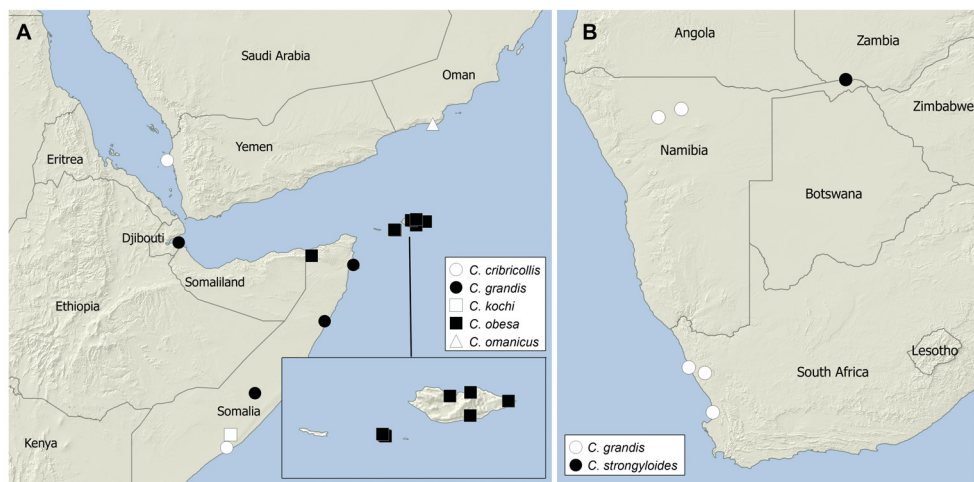


Fig. 5. Distribution of chosen species representing *Clitobius*: taxa restricted to the Horn of Africa and its surroundings (A), and Southern Africa (B).

and a partially exposed last abdominal tergite (AALBU et al. 2002, MATHEWS & BOUCHARD 2008). Those characters, however, are not present in the examined *Apithesis* specimens from the Socotra Archipelago (including two syntypes). On the other hand, having aedeagus with ventral apophyses and well developed inflexed alae on basal part, diagonally oriented baculi of paraproct and coxites, and mainly protrochanter with elongated base ('opatrinoïd type of protrochanter'; Fig. 2A) a character unique within the whole subfamily Tenebrioninae (TSCHINKEL & DOYEN 1980; IWAN 2001, 2004; IWAN & KAMIŃSKI 2016), *A. obesa* must be without any doubts placed in the tribe Opatrini. Last but not least, Ulomini are forest dwellers feeding on well-rotted wood while Opatrini are xerophilic and soil inhabiting animals (MATHEWS & BOUCHARD 2008) similarly to all newly collected *A. obesa* specimens from the Socotra Island that were exclusively found on sandy dunes showing crepuscular and nocturnal activity (L. Purchart, pers. observ.).

Using the key proposed by IWAN & KAMIŃSKI (2016), due to the eyes partly divided by extending genae, pronotum without basal depressions, flat apical portion of the prosternal process, evenly narrowing elytral epipleuron, protibiae slightly expanded towards the apex, relatively narrow protarsi, with preapical tarsomere not reduced, paraprocts not rotated laterodorsally and with simple proximal tips, middle coxites not elongate, vagina simple without sclerites, spiculum ventrale relatively short, *A. obesa* belongs to Ammobiina which presently contains 40 genera. Close morphological examination of the representatives of this subtribe revealed that *A. obesa* fits the concept of the genus *Clitobius* (KOCH 1960), where it is conspecific with *C. pseudalatus* Koch, 1960.

Taxonomy of most genera representing Ammobiina is poorly investigated. Majority of the available papers concern only single species descriptions (e.g. FERRER 1995, 2001; SCHAWALLER 2009) or faunistic records (e.g. KASZAB 1982, JOHNSON 1989, GRIMM 1995, FERRER 2004, SOLDATI

2009). The present investigation of the newly available material and its comparison with the type specimens of previously described species revealed a need for crucial taxonomic changes within *Clitobius* (see the taxonomy section). The major one concerned the subdivision of this genus into two separate subgenera, which exclusively relied on the wing structure (KOCH 1960, FERRER 1995). According to the commonly accepted concept, *Apteroclitobius* differed from *Clitobius* only in having reduced or absent metathoracic wings, which are fully developed in the case of the nominotypical subgenus (Fig. 3D). Because the present investigation did not reveal any autapomorphic characters for the subgenus *Clitobius* and due to the fact that designation of a taxonomic entity based only on the lack of an apomorphic feature reported for a closely related taxon might easily lead to introduction of a paraphyletic taxon, the authors of this paper decided to propose a synonymy between *Apteroclitobius* and *Clitobius*.

The biogeographic dataset constructed here suggests that *Clitobius* is widely distributed through the south-western Palaearctic Region (Figs 4, 5). However, the most species-rich regions were identified in the surrounding area of the Horn of Africa (5 species) and southern part of the African continent (3 species). Majority of taxa inhabiting particular hotspots were reported exclusively from a few clustered localities (Figs 4, 5), with the only exception of *C. ovatus* which has a wide distribution and is also present in southern Africa. Taking into account the potential dispersal abilities (Fig. 4), it is surprising that the presence of either *C. ovatus* or *C. oblongiusculus* was not noticed in the Horn of Africa and its closest surroundings (Figs 5A). According to the ecological niche modelling results, the distribution of both species is strongly influenced by the mean levels of precipitation — namely the precipitation of the driest month for *C. ovatus* (41.1% contribution) and the precipitation of warmest quarter for *C. oblongiusculus* (79.7% contribution). Since both species seem to prefer low levels of this factor, it is possible to conclude that their absence in the area of the Horn of Africa is caused by this climatic variable. A trend for the widespread species to occur in distinct ecological conditions compared to their endemic congeners is common and has been reported for many groups of organisms (e.g. LAVERGNE et al. 2004; KAMIŃSKI 2011, 2015).

On the other hand, the revealed distributional pattern within *Clitobius* might also be the result of collecting bias. However, this is highly improbable since the dataset analysed here contains over 150 records gathered for more than 150 years by different collectors (Appendix 1).

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References

- ABDURAKHMANOV G. M. & NABOZHENKO M. V. 2011: *Keys and catalogue to Darkling beetles (Coleoptera: Tenebrionidae s. str.) of the Caucasus and South of European part of Russia*. KMK Scientific Press Ltd., Moscow, 361 pp.
- ALFIERI A. 1976: The Coleoptera of Egypt. *Mémoires de la Société Entomologique d'Égypte* **5**: i–xvi + 1–361.
- ALLARD E. 1882: [new taxa]. *Bulletin de la Société Entomologique de France* **1882**: lxxxvi–lxxxvii.
- ALLARD E. 1883: Mélanges entomologiques. *Annales de la Société Entomologique de Belgique* **27**: 5–49.
- ALLARD E. 1884: Diagnoses de quatre nouveaux coléoptères. *Wiener Entomologische Zeitung* **3**: 248.
- ALLARD E. 1891: Coléoptères, Hétéromères. *Nouvelles Archives du Muséum d'Histoire Naturelle* **3**: 235–236.
- ALIQUÒ V. & LEO P. 1999: I coleotteri Tenebrionidi della regione Iblea (Sicilia sudorientale). *Ente Fauna Siciliana* **5**: 1–21.
- ALIQUÒ V. & SOLDATI F. 2010: *Coleotteri Tenebrionidi di Sicilia (Insecta: Coleoptera Tenebrionidae)*. Monografie Naturalistiche, 1, Edizioni Danaus, Palermo, 176 pp.
- ANDRES A. 1913: Note Bibliographique. *Bulletin de la Société Entomologique de d'Égypte* **3**: 51–132.
- ARDOIN P. 1963: Récoltes de M. A. Villiers dans les dunes côtières du Sénégal (1961). Coléoptères, Tenebrionidae. *Bulletin de l'Institut Français d'Afrique Noire, Série A* **25**: 372–388.
- ARDOIN P. 1971: Contribution à l'étude biologique du Sénégal septentrional. VIII. Coléoptères Tenebrionidae. *Bulletin de l'Institut Français d'Afrique Noire, Série A* **33**: 103–124.
- ARDOIN P. 1972: Liste de espèces de Tenebrionidae (Coleoptera) récoltées au Sudan par les expéditions finlandaises (1962–1964). *Commentationes Biologicae* **49**: 3–20.
- ARDOIN P. 1979: Mission Balachowsky-Menier dans l'ancien Territoire français des Afars et Issas. Coleoptera Tenebrionidae. *Bulletin de la Société Entomologique de France* **84**: 58–61.
- BATELKA J. 2012: Socotra Archipelago – a lifeboat in the sea of changes: advancement in Socotran insect biodiversity survey. Pp. 1–26. In: HÁJEK J. & BEZDĚK J. (eds.): Insect biodiversity of the Socotra Archipelago. *Acta Entomologica Musei Nationalis Pragae* **52 (supplementum 2)**: i–vi + 1–557.
- BEDEL L. 1896: Provenance du *Clitobius rugulipennis* Fairm. (Col.). *Bulletin de la Société Entomologique de France* **1896**: 346.
- BEZDĚK J., PURCHART L., KRÁL K. & HULA V. 2012: List of local Socotran geographical names used in entomological literature. Pp. 27–67. In: HÁJEK J. & BEZDĚK J. (eds): Insect biodiversity of the Socotra Archipelago. *Acta Entomologica Musei Nationalis Pragae* **52 (supplementum 2)**: i–vi + 1–557.
- BLAIR K. G. 1925: A list of heteromorous coleoptera collected mainly during the war by various members of H. M. Forces in Mesopotamia. *Journal of the Bombay Natural History Society* **30**: 428–440.
- BRABY M. F., EASTWOOD R. & MURRAY N. 2012: The subspecies concept in butterflies: has its application in taxonomy and conservation biology outlived its usefulness? *Biological Journal of the Linnean Society* **106**: 699–716.
- CANRAN L., BERRY P., DAWSON T. P. & PEARSON R. G. 2005: Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* **28**: 385–393.
- CARL M. 1991: Beitrag zur Schwarzkäferfauna Tadschikistans (UdSSR) (Coleoptera, Tenebrionidae). *Spixiana* **14**: 275–279.
- CHAMPION G. C. 1895: A list of Tenebrionidae supplementary to the “Munich” Catalogue. *Mémoires de la Société Entomologique de Belgique* **1(3)**: 1–264.
- DESBROCHERS DES LOGES J. 1898: Quelques matériaux pour la faune des coléoptères de Barbarie. *Le Frelon* **7**: 1–16.
- EBNER R. 1923: Wissenschaftliche Ergebnisse der mit Unterstützung der Akademie der Wissenschaften in Wien aus der Erbschaft Treitl von F. Werner unternommenen zoologischen Expedition nach dem Anglo-ägyptischen Sudan (Kordofan) 1914. XI. Coleoptera A. *Denkschriften der Kaiserlichen Akademie der Wissenschaften* **98**: 167–199.
- ELITH J., GRAHAM C. H., ANDERSON R. P., DUDÍK M., FERRIER S., GUIAN A., HIJMANS R. J., HUETT-MANN F., LEATHWICK J. R., LEHMANN A., LI J., LOHMANN L. G., LOISELLE B. A., MANION G., MORITZ C., NAKAMURA M., NAKAZAWA Y., MCC J., OVERTON M., PETERSON A. T., PHILLIPS S. J., RICHARDSON K., SCACHETTI-PEREIRA R., SCHAPIRE R. E., SOBERÓN J., WILLIAMS S., WISZ S. M. & ZIMMERMANN N. E. 2006: Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**: 129–151.

- ERICHSON W. F. 1843: Beitrag zur Insecten-Fauna von Angola in besonderer Beziehung zur geographischen Verbreitung der Insecten in Afrika. *Archiv für Naturgeschichte* **9**: 199–267.
- ESCALERA M. M. DE LA 1914: Los coleópteros de Marruecos. *Trabajos del Museo Nacional de Ciencias Naturales, Serie Zoológica* **11**: 4–553.
- ESPAÑOL F. 1943: Misión Científica E. Morales Agacino, Ch. Rungs y B. Zolotarevsky a Ifni y Sáhara Español. Tenebrionidae (Col.). I.ª Parte. *Eos, Revista Española de Entomología* **19**: 119–148.
- ESPAÑOL F. 1944: Nuevos datos para el conocimiento de los Tenebriónidos (Col.) del Sáhara español. *Eos, Revista Española de Entomología* **20**: 7–30.
- ESPAÑOL F. 1946: Tenebriónidos (Col.) nuevos o interesantes recogidos por D. Eugenio Morales y D. Joaquín Matéu en el Sáhara español. *Eos, Revista Española de Entomología* **22**: 107–122.
- ESPAÑOL F. 1962a: Los Opatrinæ de las islas Canarias (Col. Tenebrionidae). *Eos, Revista Española de Entomología* **38**: 203–211.
- ESPAÑOL F. 1962b: Tenebrionidos del Medano (Tenerife) (Coleoptera). *Graellsia* **19**: 229–235.
- ESPAÑOL F. 1963: Datos para el conocimiento de los Tenebrionidos del Mediterraneo occidental (Coleoptera). XXV. Sobre algunos Tenebrionidos recogidos por el Dr. C. Gonzalez en las pequeñas islas de las Canarias orientales. *Eos, Revista Española de Entomología* **39**: 203–209.
- ESPAÑOL F. 1967: Misión entomológica Hakan Lindberg y M. Meinander a Marruecos. Col. tenebriónidos. *Publicaciones del Instituto de Biología Aplicada* (Barcelona) **42**: 17–47.
- ESPAÑOL F. & LINDBERG H. 1963: Coleópteros tenebriónidos de las Islas de Cabo Verde. *Commentationes Biologicae* **25**: 1–51.
- FAIRMAIRE L. 1856: Miscellanea entomologica. *Annales de la Société Entomologique de France, Série 3* **4**: 517–548, pl. 16.
- FAIRMAIRE L. 1875: Diagnose de quelques coléoptères nouveaux d'Algérie. *Petites Nouvelles Entomologiques* **1** [1869–1875]: 495–496.
- FAIRMAIRE L. 1879a: Coléoptères du nord de l'Afrique. *Revue et Magasin de Zoologie Pure et Appliquée, Série 3* **7**: 178–218.
- FAIRMAIRE L. 1879b: Diagnoses de coléoptères du nord de l'Afrique. *Le Naturaliste* **1**(2): 3–4.
- FAIRMAIRE L. 1879c: Note sur une espèce européenne du genre Halonomus Woll. *Petites Nouvelles Entomologiques* **6**: 389.
- FAIRMAIRE L. 1885: [Note]. *Bulletin des Séances et Bulletin Bibliographique de la Société Entomologique de France* **4**: ccv–ccvi.
- FAIRMAIRE L. 1888: Enumeration des coléoptères recueillis par M. le Dr Hans Schinz dans le sud de l'Afrique. *Annales de la Société Entomologique de France, Série 6* **8**: 173–202.
- FAIRMAIRE L. 1892: Coléoptères d'Obock. Troisième partie. *Revue d'Entomologie* **11**: 77–127.
- FAIRMAIRE L. 1894: Coléoptères de l'Afrique intertropicale et australe. Deuxième note. *Annales de la Société Entomologique de Belgique* **38**: 314–335.
- FAIRMAIRE L. 1896: Description de coléoptères recueillis par le Dr. Ch. Marin à Obock, Djibouti et Aden. *Bulletin de la Société Entomologique de France* **1896**: 223–225.
- FAUCHEUX M. J. 2011: Coléoptères Ténébrionidés de Larache et Oualidia (Maroc atlantique): prospections de 2006 a 2009. *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France, Nouvelle Série* **33**: 54–56.
- FERRER J. 1995: Contribution to the knowledge of the Tenebrionidae of Somalia. Coleoptera. *Frustula Entomologica, Nuova Serie* **18**(21): 1–76.
- FERRER J. 2001: Contribution à l'étude des Opatrini africains: description d'une nouvelle espèce du genre Clitobius Mulsant & Ray 1859 d'Afrique du Sud (Coleoptera, Tenebrionidae, Opatrini). *Nouvelle Revue d'Entomologie (Nouvelle Série)* **18**: 375–380.
- FERRER J. 2004: Tenebrionidae (Coleoptera) de Namibia, avec descriptions de 12 espèces nouvelles. *Mitteilungen aus dem Museum für Naturkunde in Berlin. Zoologische Reihe* **80**: 181–250.
- FIELDING A. H. & BELL J. F. 1997: A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* **24**: 38–49.
- FIKÁČEK M. & VONDRÁČEK D. 2014: A review of Pseudorygmodus (Coleoptera: Hydrophilidae), with notes on the classification of the Anacaenini and on distribution of genera endemic to southern South America. *Acta Entomologica Musei Nationalis Pragae* **54**: 479–514.

- FOCARILE A. 1969: Sintesi preliminare sulle attuali conoscenze sui Coleotteri Tenebrionidi delle piccole isole circum-siciliane (Col. Tenebrionidae). *Memorie della Società Entomologica Italiana* **48**: 402–416.
- FREEMAN E. A. & MOISEN G. G. 2008: A comparison of the performance of threshold criteria for binary classification in terms of predicted prevalence and kappa. *Ecological Modelling* **217**: 48–58.
- GAHAN C. J. 1903: Insecta: Coleoptera. Pp. 261–292. In: FORBES H. O. (ed.): The natural history of Sokotra and Abd-el-Kuri: Being the report upon the results of the conjoint expedition to these islands in 1898–9. *Special Bulletin of the Liverpool Museums*, xlvii + 598 pp.
- GEBIEN H. 1910: Tenebrionidae I, II. Pars 15, 22. In: SCHENKLING S. (ed.): *Coleopterorum Catalogus. Volumen 18*. W. Junk, Berlin, 354 pp.
- GEBIEN H. 1920a: Käfer aus der Familie Tenebrionidae gesammelt auf der “Hamburger deutsch-südwestafrikanischen Studienreise 1911”. *Hamburgische Universität Abhandlungen aus dem Gebiet der Auslandskunde* **5**: 1–168.
- GEBIEN H. 1920b: Die Tenebrioniden Westafrikas. *Archiv für Naturgeschichte* **86**(6): 1–256.
- GEBIEN H. 1940: Katalog der Tenebrioniden. Teil II. *Mitteilungen der Münchener Entomologischen Gesellschaft* **30**: 405–625 [530–1092].
- GEMMINGER M. 1870: [new names]. In: GEMMINGER M. & HAROLD E. von: *Catalogus coleopterorum hucusque descriptorum synonymicus et systematicus. Tom. VII. Tenebrionidae, Nilionidae, Pythidae, Melandryidae, Lagriidae, Pedilidae, Anthicidae, Pyrochroidae, Mordellidae, Rhipidophoridae, Cantharidae, Oedemeridae*. E. H. Gummi, Monachii, pp. 1801–2180 + [9].
- GRIDELLI E. 1930: Risultati zoologici della Missione inviata dalla R. Società Geografica Italiana per l'esplorazione dell' oasi di Giarabub (1926–1927). Coleotteri. *Annali del Museo Civico di Storia Naturale di Genova* **54**: 1–485 + [1], 1 map.
- GRIDELLI E. 1933: Spedizione scientifica all'Oasi di Cufra (Marzo–Guglio 1931). Coleotteri. *Annali del Museo Civico di Storia Naturale di Genova* **56**: 155–258 + pl. V.
- GRIDELLI E. 1953: Catalogo ragionato delle specie di coleotteri Tenebrionidi dell'Arabia. *Atti del Museo Civico di Storia naturale di Trieste* **19**: 1–70.
- GRIDELLI E. 1954: Fauna coleopterologica delle isole del Capo Verde. *Annali del Museo Civico di Storia Naturale Giacomo Doria* **68**: 45–84.
- GRIMM R. 1986: Tenebrionidae vom Maltesischen Archipel (Insecta: Coleoptera). *Stuttgarter Beiträge zur Naturkunde, Serie A (Biologie)* **392**: 1–17.
- GRIMM R. 1991: Tenebrioniden (Coleoptera) von der Insel Zypern. *Biocosme Méditerranéenne* **8**: 15–49.
- GRIMM R. 1995: Beitrag zur Kenntnis der Schwarzkäferfauna der Kanarischen Inseln (Coleoptera, Tenebrionidae). *Mitteilungen der Münchner Entomologischen Gesellschaft* **85**: 33–50.
- GRIMM R. 2015: Tenebrionidae (Insecta: Coleoptera) from Iran. *Vernate* **34**: 299–318.
- HERNANDEZ P. A., GRAHAM C. H., MASTER L. L. & ALBERT D. L. 2006: The effect of sample size and species characteristics on performance of different species distribution modelling methods. *Ecography* **2**: 773–785.
- HIJMANS R. J., CAMERON S. E., PARRA J. L., JONES P. G. & JARVIS A. 2005: Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**: 1965–1978.
- HÁJEK J. & BEZDĚK J. (eds) 2012: Insect biodiversity of the Socotra Archipelago. *Acta Entomologica Musei Nationalis Pragae* **52** (Supplementum 2): i–vi + 1–557.
- HÁJEK J. & BEZDĚK J. (eds) 2014: Insect biodiversity of the Socotra Archipelago. *Acta Entomologica Musei Nationalis Pragae* **54** (Supplementum): i–vi + 1–440.
- HOLDHAUS K. 1919: Ergebnisse der wissenschaftlichen Expedition nach Mesopotamien, 1910. Koleopteren aus Mesopotamien. *Annalen des Naturhistorischen Museums in Wien* **33**: 39–58.
- IWAN D. 2001: Comparative study of male genitalia in Opatrinae sensu Medvedev (1968) (Coleoptera: Tenebrionidae), with notes on the tribal classification. Part I. *Annales Zoologici* **51**: 351–390.
- IWAN D. 2004: A comparative study of male genitalia in Opatrinae sensu Medvedev (1968) (Coleoptera: Tenebrionidae), with notes on the reinterpreted tribal classification. Part II. *Annales Zoologici* **54**: 735–765.
- IWAN D. & LÖBL I. 2007: Nomenclatural notes on tenebrionid beetles of the palaearctic region (Insecta: Coleoptera). *Annales Zoologici* **57**: 733–739.
- IWAN D. & KAMIŃSKI M. J. 2016: Toward a natural classification of opatrine darkling beetles: comparative study of female terminalia. *Zoomorphology* **135**: 453–485.

- JOHNSON C. 1989: Tenebrionidae (Coleoptera) collected in the eastern province of Saudi Arabia. *Fauna of Saudi Arabia* **10**: 123–133.
- KAMIŃSKI M. J. 2011: Catalogue of the World Melambiina Mulsant et Rey, 1854 (Coleoptera, Tenebrionidae, Pedinini). *Annales Zoologici* **61**: 281–333.
- KAMIŃSKI M. J. 2015: Phylogenetic reassessment and biogeography of the Ectateus generic group (Coleoptera: Tenebrionidae: Platynotina). *Zoological Journal of the Linnean Society* **175**: 73–106.
- KASZAB Z. 1963: Angaben zur Kenntnis der Tenebrioniden des Tschadsee-Gebietes, nebst einer Revision der afrikanischen Mesomorphus-Arten (Coleoptera). *Revue de Zoologie et de Botanique Africaines* **67**: 341–387.
- KASZAB Z. 1982: Insects of Saudi Arabia, Coleoptera: Fam. Tenebrionidae (Part 2). *Fauna of Saudi Arabia* **4**: 124–243.
- KNEUCKER A. & ANDRES A. 1920: Zoologische Ergebnisse zweier in den Jahren 1902 und 1904 durch die Sinaihalbinsel unternommener botanischer Studienreisen. II. Teil. *Entomologische Blätter* **16**: 59–82.
- KOCH C. 1935: Wissenschaftliche Ergebnisse der entomologischen Expedition seiner Durchlaucht des Fürsten A. della Torre e Tasso nach Ägypten und auf der Halbinsel Sinai. VII. Tenebrionidae (Coleoptera). *Bulletin de la Société Royale Entomologique d'Égypte* **19**: 2–111.
- KOCH C. 1959a: The Tenebrionidae of Southern Africa XXVIII. On a new faunistic link between the African Continent and Cape Verde Islands (Ammidium Erichson). *Novos Taxa Entomologicos* **19**: 1–15.
- KOCH C. 1959b: Erster taxonomischer Beitrag zur Kenntnis der Tenebrioniden Somalias. *Entomologische Arbeiten aus dem Museum G. Frey* **10**: 568–596.
- KOCH C. 1960: Zweiter taxonomischer Beitrag zur Kenntnis der Tenebrioniden Somalias. *Entomologische Arbeiten aus dem Museum G. Frey* **11**: 325–411.
- KOCH C. 1970: Die Tenebrioniden (Coleoptera) des Archipels von Socotra. *Italian Journal of Zoology* **4**: 69–132.
- KOCHER L. 1958: Catalogue commenté des Coléoptères du Maroc. *Travaux de l'Institut Scientifique Chérifien, Série Zoologie* **12(6)**: 7–185.
- LAMB T., POLLARD R. & BOND J. E. 2013: Genetic variation corroborates subspecific delimitation in the Namib fog-basking beetle, *Onymacris unguicularis* (Haag) (Tenebrionidae, Coleoptera). *ZooKeys* **353**: 47–60.
- LAVERGNE S., THOMPSON J. D., GARNIER E. & DEBUSSCHE M. 2004: The biology and ecology of narrow endemic and widespread plants: a comparative study of trait variation in 20 congeneric pairs. *Oikos* **107**: 505–518.
- LILLIG M., BARTHET H. B. & MIFSUD D. 2012: An identification and informative guide to the Tenebrionidae of Malta (Coleoptera). *Bulletin of the Entomological Society of Malta* **5**: 121–160.
- LILLIG M. & PAVLÍČEK T. 2003: The darkling beetles of the Sinai Peninsula. Coleoptera: Tenebrionidae (excl. Lagriinae et Alleculinae). *Zoology in the Middle East, Supplementum* **1**: 3–87.
- LINDBERG HAR. 1950: Beitrag zur Kenntnis der Käferfauna der Kanarischen Inseln. *Societas Scientiarum Fennica Commentationes Biologicae* **10(18)**: 1–20.
- LINDBERG HÅK. 1962: Coleoptera Insularum Canariensium. III. Tenebrionidae. *Societas Scientiarum Fennica Commentationes Biologicae* **25**: 1–85 + 11 pls.
- LÖBL I., MERKL O., ANDO K., BOUCHARD P., EGOROV L. V., IWAN D., LILLIG M., MASUMOTO K., NABOZHENKO M., NOVÁK V., PETTERSON R., SCHAWALLER W. & SOLDATI F. 2008: Family Tenebrionidae Latreille, 1802. Pp. 105–352. In: LÖBL I. & SMETANAA. (eds): *Catalogue of Palaearctic Coleoptera. Volume 5. Tenebrionoidea*. Apollo Books, Stenstrup, 670 pp.
- MARCUZZI M. 1970: I tenebrionidi delle isole Eolie e di Ustica. *Atti dell'Accademia Gioenia di Scienze Naturali in Catania* **2**: 1–26.
- MATTHEWS E. G. & BOUCHARD P. 2008: *Tenebrionid beetles of Australia: descriptions of tribes, keys to genera, catalogue of species*. Australian Biological Resources Study, Canberra, viii + 398 pp.
- MIFSUD D. & SCUPOLAA. 1998: The Tenebrionidae (Coleoptera) of the Maltese Islands (Central Mediterranean). *Annali del Museo Civico di Storia Naturale "G. Doria" Genova* **92**: 191–229.
- MULSANT É. & REY C. 1859: Essai d'une division des derniers mélasomes, famille des parvilabres, quatrième tribu opatrites. *Opusculs Entomologiques* **10**: 1–160.
- MULSANT É. & REY C. 1860: Essai d'une division des derniers mélasomes. Famille des parvilabres quatrième tribu opatrites. *Mémoires de l'Académie des Sciences, Belles-Lettres et Arts de Lyon, Classe des Sciences, Nouvelle Série* **10**: 1–68.

- NABOZHENKO M. V. & PURCHART L. 2017: Western Palaearctic *Trachyscelis* Latreille, 1809 (Coleoptera: Tenebrionidae: Trachyscelini). *Annales Zoologici* **67**: 561–575.
- NOVÁK V. & PURCHART L. 2012: Review of the genus *Socotralia* Novák, 2007 from Socotra Island, with description of new species. Pp. 323–336. In: HÁJEK J. & BEZDĚK J. (eds): Insect biodiversity of the Socotra Archipelago. *Acta Entomologica Musei Nationalis Pragae* **52 (Supplementum 2)**: i–vi + 1–557.
- OROMÍ P. 1982: Los Tenebriónidos de las Islas Canarias. Pp. 267–292. In: *Instituto de Estudios Canarios, 50 Aniversario (1932–1982). I. Ciencias*. Instituto de Estudios Canarios, Santa Cruz de Tenerife, xl + 352 pp.
- PEYERIMHOFF P. DE 1907: Liste de coléoptères du Sinai. *L Abeille, Journal d'Entomologie* **31**: 1–48.
- PIERRE F. 1961: Les Ténébrionides du Tibesti et du Borkou (Missions P. de Miré et P. Quézel). *Bulletin de l'Institut Français d'Afrique Noire, Série A* **23**: 1030–1053.
- PURCHART L. 2012: Biodiversity research of darkling beetles on Socotra Island. Part I. – The genus *Deretus* Gahan, 1900 (Coleoptera: Tenebrionidae). *Zootaxa* **3153**: 57–68.
- PURCHART L. 2013: A new species of the genus *Deretus* Gahan, 1900 (Coleoptera: Tenebrionidae) from the island of Socotra. *Annales Zoologici* **63**: 79–83.
- PURCHART L. 2014a: Revision of the genus *Histeromorpha* (Coleoptera: Tenebrionidae) from the Socotra Archipelago with descriptions of three new species. Pp. 211–230. In: HÁJEK J. & BEZDĚK J. (eds): Insect biodiversity of the Socotra Archipelago. *Acta Entomologica Musei Nationalis Pragae* **54 (Supplementum)**: i–vi + 1–440.
- PURCHART L. 2014b: Two new species of the genera *Zophosis* and *Oxyacara*, and a new record of the genus *Freyula* from the Island of Socotra (Coleoptera: Tenebrionidae). Pp. 231–240. In: HÁJEK J. & BEZDĚK J. (eds): Insect biodiversity of the Socotra Archipelago. *Acta Entomologica Musei Nationalis Pragae* **54 (Supplementum)**: i–vi + 1–440.
- PURCHART L. & NABOZHENKO M. V. 2012: First description of larva and pupa of the genus *Deretus* (Coleoptera: Tenebrionidae) with key to the larvae of the tribe Helopini. Pp. 295–302. In: HÁJEK J. & BEZDĚK J. (eds): Insect biodiversity of the Socotra Archipelago. *Acta Entomologica Musei Nationalis Pragae* **52 (Supplementum 2)**: i–vi + 1–557.
- PURCHART L. & SCHAWALLER W. 2012: A new species of the genus *Corticeus* Piller et Mitterpacher, 1783 (Coleoptera: Tenebrionidae) from Socotra. Pp. 315–322. In: HÁJEK J. & BEZDĚK J. (eds): Insect biodiversity of the Socotra Archipelago. *Acta Entomologica Musei Nationalis Pragae* **52 (Supplementum 2)**: i–vi + 1–557.
- RAGUSA E. 1898: Catalogo ragionato dei coleotteri di Sicilia. II. *Naturalista Siciliano, Nuova Serie* **2** [1897–1897]: 105–130.
- REICHARDT A. N. 1936: *Zhuki-chernotelki triby Opatrini palearkticheskoy oblasti. Revision des opatrinés (Coleoptera Tenebrionidae) de la région paléarctique. Tableaux analytiques de la Faune de l'URSS* **19**. Nauka, Moskva, Leningrad, 224 pp.
- REITTER E. 1904: Bestimmung-Tabelle der Tenebrioniden-Unterfamilien: Lachnogyini, Akidini, Pedinini, Opatrini und Trachyscelini aus Europa und den angrenzenden Ländern. *Verhandlungen des Naturforschenden Vereins in Brünn* **42**: 25–189.
- ROTTENBERG A. VON 1871: Beiträge zur Coleopteren-Fauna von Sicilien. *Berliner Entomologische Zeitschrift* **14** [1870]: 235–260, pl. 2.
- SAHLBERG J. R. 1913: Coleoptera mediterranea orientalis quae in Aegypto, Palestina, Syria, Caramania collegunt John Sahlberg et Unio Saalas. *Öfversigt af Finska Vetenskaps-Societetens Förhandlingar, A. Matematik och Naturvetenskaper* **55(19)** [1912–1913]: 1–282.
- SCHAWALLER W. 2004: New species and records of Tenebrionidae (Coleoptera) from the Socotra Archipelago. *Fauna of Arabia* **20**: 439–458.
- SCHAWALLER W. & PURCHART L. 2012: *Nanocaecus hlavaci* gen. et sp. nov. – first record of the tribe Gnathiini (Coleoptera: Tenebrionidae: Diaperinae) from the Socotra Archipelago. Pp. 303–314. In: HÁJEK J. & BEZDĚK J. (eds): Insect biodiversity of the Socotra Archipelago. *Acta Entomologica Musei Nationalis Pragae* **52 (Supplementum 2)**: i–vi + 1–557.
- SEIDLITZ G. C. M. VON 1891: Gattungen. Pp. 129–160. Arten. Pp. 549–914. In: *Fauna Transsylvanica. Die Käfer (Coleoptera) Siebenbürgens*. Hartungsche Verlagsdruckerei, Königsberg, [12] + lvi + 192 + 914 pp., 1 pl. [issued in parts: pp. i–xl, Gattungen 1–48, Arten 1–240 in 1888; pp. xli–lvi, Gattungen 49–128, Arten 241–544 in 1889; pp. xlix–lvi, Gattungen 129–192, Arten 545–914 in 1891].

- SEIDLITZ G. C. M. VON 1898: Erste Abteilung. Coleoptera. Fünfter Band. Zweite Hälfte. Zweite Lieferung. Bogen 20 bis 43 [Pp. 305–680, Nachtrag, Lagriidae, Melandryidae]. In: KIESENWETTER H. & SEIDLITZ G. C. M. VON (eds): *Naturgeschichte der Insecten Deutschlands*. Nicolaische Verlags-Buchhandlung, Berlin, 1206 pp.
- SOLDATI L. 2009: *The Darkling Beetles (Coleoptera: Tenebrionidae) of Qatar*. Natura optima dux Foundation, Warszawa, 101 pp + XVII plates.
- TSCHINKEL W. R. & DOYEN J. T. 1980: Comparative anatomy of the defensive glands, ovipositors and female genital tubes of tenebrionid beetles (Coleoptera). *International Journal of Insect Morphology and Embryology* 9: 321–368.
- WATERHOUSE C. O. 1881: On the coleopterous insects collected by Prof. Bailey Balfour in the island Socotra. *Proceedings of the Zoological Society of London* 1881: 469–478.
- WOLLASTON T. V. 1861: On certain Coleoptera from the Island of St. Vincent. *Annals and Magazine of Natural History* 7: 197–206, 246–253.
- WOLLASTON T. V. 1864: *Catalogue of the Coleopterous insects of the Canaries in the Collection of the British Museum*. Taylor and Francis, London, xiii + 648 pp.
- WOLLASTON T. V. 1865: *Coleoptera Atlantidum, being an enumeration of the Coleopterous Insects of the Madeiras, Salvages, and Canaries*. John van Voorst, London, xlvii + 526 + 140 (Appendix) pp. + 1 map.
- WOLLASTON T. V. 1867: *Coleoptera Hesperidum, being an enumeration of the Coleopterous insects of the Cape Verde Archipelago*. John van Voorst, London, xxxix + 285 pp.

Appendix 1

Analysed distributional data of *Clitobius* in CSV format

Positions marked with asterisk were included in the ecological niche modeling (Fig. 4).

Species name, Country, Locality, Latitude, Longitude, Reference

C. cribricollis, Ethiopia, Abyssinie, x, x, Allard 1882 (not georeferenced)

C. cribricollis, Yemen, Kamaran Island, 15.3537, 42.59436, Kaszab 1982

C. cribricollis, Somalia, near the border of Hiran and Benadir, 2.187248, 45.323200, Koch 1960

C. endroediorum, South Africa, Elands Bay, -32.31401, 18.34413, Ferrer 2001

C. endroediorum, South Africa, Hondeklip Bay, -30.31531, 17.27171, Ferrer 2001

C. endroediorum, South Africa, 15 km West of Garies, -30.56223, 17.98905, Ferrer 2001

C. endroediorum, Namibia, Okakuejo, -19.179110, 15.918108, Ferrer 2001

C. endroediorum, Namibia, Namutoni, -18.808476, 16.939001, Ferrer 2004

C. grandis, Djibouti, Ambouli, 11.59, 43.1225, Ardoin 1979

C. grandis, Somalia, El Bur, 4.683760, 46.619969, Koch 1960

C. grandis, Somalia, Eil, 7.981168, 49.816679, Koch 1960

C. grandis, Somalia, Hordio, 10.563750, 51.133274, Koch 1960

C. kochi, Somalia, Jowhar, 2.783333, 45.5, Ferrer 1995

C. oblongiusculus, Algeria, Biskra, 34.85038, 5.72805, Fairmaire 1875, *

C. oblongiusculus, Egypt, Halwan, 29.84144, 31.30084, Andres 1913, *

C. oblongiusculus, Saudi Arabia, Abqaiq, 25.9371, 49.67761, Johnson 1989, *

C. oblongiusculus, Saudi Arabia, Udhailiyah Camp, 25.133333, 49.3, Johnson 1989, *

C. oblongiusculus, Saudi Arabia, Harad, 24.1485, 49.0577, Johnson 1989, *

C. oblongiusculus, Saudi Arabia, Hofuf, 25.36457, 49.56532, Kaszab 1982

C. oblongiusculus, Saudi Arabia, Qurayyah, 27.48055, 47.87371, Johnson 1989, *

C. oblongiusculus, Qatar, Trainah, 24.766667, 51.21388888888889, Soldati 2009, *

C. oblongiusculus, Qatar, Umsht Island, 25.294726, 51.645931, Soldati 2009

C. oblongiusculus, Qatar, Nakhlat al Oraiq area, 25.105706, 51.164889, Soldati 2009

C. oblongiusculus, Qatar, Al Zubarah, 25.976967, 51.045358, Soldati 2009, *

C. oblongiusculus, Qatar, Rawdat al Faras, 25.804585, 51.347057, Soldati 2009 (see also Ardoin 1972), *

C. oblongiusculus, Cyprus, Akrotiri, 34.60088, 32.95536, Grimm 1991, *

C. oblongiusculus, Cyprus, Larnaka, 34.92291, 33.6233, Grimm 1991, *

C. oblongiusculus, Iran, Qeshem Island, 26.9113889, 55.74444444444445, Grimm 2015

C. oblongiusculus, Iran, Qeshem Island, 26.9117222, 55.74627777777778, Grimm 2015

C. oblongiusculus, Iran, Pahel, 26.9824167, 55.64075, Grimm 2015, *

C. oblongiusculus, Iran, Bandar Abbas, 27.1841389, 56.39413888888889, Grimm 2015, *

- C. oblongiusculus, Morocco, Aouinet Torkoz, 28.4842, -9.85104, Kocher 1958, *
- C. oblongiusculus, Egypt, Wadi an-Natrun, 30.583333, 30.333333, Alfieri 1976, *
- C. oblongiusculus, Egypt, Bahariya, 28.351489, 28.862375, Alfieri 1976, *
- C. oblongiusculus, Egypt, Antonius Monastery, 28.923889, 32.35, Alfieri 1976, *
- C. oblongiusculus, Egypt, Al Jaghbub, 29.68333, 24.71667, Gridelli 1930, *
- C. oblongiusculus, Iraq, Amara, 31.99406, 47.15745, Blair 1925, *
- C. oblongiusculus, Iraq, Khatuniyah, 35.34241, 44.00687, Holdhaus 1919, *
- C. oblongiusculus, Western Sahara, Laayoune, 27.153611, -13.203333, Espanol 1967
- C. oblongiusculus, Western Sahara, Al Aiun, 27.1418, -13.18797, Espanol 1946, *
- C. oblongiusculus, Egypt, Cairo, 30.05, 31.233333, Allard 1882
- C. oblongiusculus, Egypt, 14 km S Taba, 29.487028, 34.876043, Lillig & Pavliček 2003, *
- C. oblongiusculus, Egypt, 10 km N Nuweiba, 29.04681, 34.6634, Lillig & Pavliček 2003, *
- C. oblongiusculus, Egypt, Dhahab, 28.50098, 34.51338, Lillig & Pavliček 2003, *
- C. oblongiusculus, Egypt, Sharm el Sheik, 27.91582, 34.32995, Lillig & Pavliček 2003, *
- C. oblongiusculus, Egypt, Gebel Helal, 30.653236, 34.028926, Alfieri 1976, *
- C. oblongiusculus, Egypt, El Arish, 31.131826, 33.802644, Alfieri 1976, *
- C. oblongiusculus, Egypt, Tor, 28.24168, 33.6222, Koch 1935, *
- C. oblongiusculus, Egypt, Wadi eth-Thal, 29.14902, 33.04946, Peyerimhoff 1907, *
- C. oblongiusculus, Tajikistan, Tigrovaya Balka State Nature, 37.195209, 68.419466, Carl 1991, *
- C. oblongiusculus, Azerbaijan, Sabirabad district, 40.48.6, Abdurakhmanov & Nabozhenko 2011, *
- C. oblongiusculus, Azerbaijan, Apsheron Peninsula, 40.463667, 49.957581, Abdurakhmanov & Nabozhenko 2011, *
- C. oblongiusculus, Libya, Ajwilah, 29.133335, 21.449999, Gridelli 1933, *
- C. oblongiusculus, Libya, Gialo, 29.033334, 21.533332, Gridelli 1933
- C. oblongiusculus, Cambodia, Battambang, 13.10271, 103.19822, Allard 1891
- C. oblongiusculus, Saudi Arabia, Hejaz, 24.49764, 38.50654, Fairmaire 1879b, *
- C. oblongiusculus, Sudan, Faras, 22.2, 31.46667, Ardoin 1972, *
- C. oblongiusculus, Western Sahara, x, x, x, Espanol 1967 (not georeferenced)
- C. oblongiusculus, Chad, Borkou, 18.10639, 18.52833, Pierre, 1961 (ssp. borkouensis), *
- C. oblongiusculus, Egypt, Sharm el Sheik, 27.954059, 34.381988, New Data (SMNS)
- C. oblongiusculus, Syria, Maskanah, 35.964209, 38.032393, New Data (SMNS)
- C. oblongiusculus, Tajikistan, Tigrovja Bal. Reservat, 37.266667, 68.466667, New Data (SMNS)
- C. oblongiusculus, Jordan, Dead Sea - Hot Springs, 31.599658, 35.610470, New Data (SMNS)
- C. oblongiusculus, Israel, Einot Taukim Reserve - Ein Fashka, 31.7144, 35.4533, New Data (SMNS)
- C. oblongiusculus, Saudi Arabia, Riyadh - Wadi Hanifa, 24.801466, 46.7618, New Data (SMNS)
- C. oblongiusculus, Iran, Hormozgan Province - Pahel, 27.016589, 55.744176, New Data (SMNS)
- C. omanicus, Oman, Wadi Ain, 17.016669, 54.783334, New data
- C. ovatus, Malta, Marsaskala, 35.862064, 14.554158, Mifsud & Scupola 1998
- C. ovatus, Malta, Balluta, 35.913569, 14.493162, Mifsud & Scupola 1998, *
- C. ovatus, Malta, Qolla I-Bajda, 36.076903, 14.248437, Mifsud & Scupola 1998
- C. ovatus, Malta, Qbajjar, 36.07778, 14.25028, Mifsud & Scupola 1998
- C. ovatus, Cape Verde, Ribeira Pombas, 17.152685, -25.026956, Espanol & Lindberg 1963, *
- C. ovatus, Cape Verde, Mindelo, 16.882881, -24.983449, Espanol & Lindberg 1963
- C. ovatus, Cape Verde, Ribeira Jukiao, 16.864073, -24.984241, Espanol & Lindberg 1963, *
- C. ovatus, Cape Verde, Ponta do Norte, 16.8854, -22.9197, Espanol & Lindberg 1963
- C. ovatus, Cape Verde, Ponta de Joao d'Évora, 16.9223, -24.9618, Espanol & Lindberg 1963
- C. ovatus, Cape Verde, Salinas, 15.13333, -23.25, Espanol & Lindberg 1963
- C. ovatus, Cape Verde, Santa Maria, 16.6, -22.9, Espanol & Lindberg 1963
- C. ovatus, Cape Verde, Pedra da Lume, 16.763, -22.895, Espanol & Lindberg 1963
- C. ovatus, Cape Verde, Monte Grande, 16.82083, -22.91, Espanol & Lindberg 1963
- C. ovatus, Cape Verde, Ribeira Feijoal, 16.75, -22.9, Espanol & Lindberg 1963, *
- C. ovatus, Cape Verde, Sal Rei, 16.18333, -22.91667, Espanol & Lindberg 1963
- C. ovatus, Cape Verde, Ribeira da Lagoa, 15.25, -23.66667, Espanol & Lindberg 1963
- C. ovatus, Cape Verde, Morrinho, 15.26667, -23.23333, Espanol & Lindberg 1963
- C. ovatus, Cape Verde, Praia, 14.93152, -23.51254, Espanol & Lindberg 1963, *
- C. ovatus, Cape Verde, Lagoa, 15.13333, -23.15, Espanol & Lindberg 1963, *
- C. ovatus, Bengale, "Le Bengale", 24.88, Mulsant & Rey 1859
- C. ovatus, Italy, Lampedusa, 35.504444, 12.609722, Focarile 1969, *
- C. ovatus, Chad, Lake Chad, 13.25, 14, Kaszab 1963, *
- C. ovatus, Spain, Gran Canaria, 27.96667, -15.6, Grimm 1995, *
- C. ovatus, Spain, Fuerteventura (Las Salinas), 28.36329, -13.87405, Grimm 1995
- C. ovatus, Spain, Fuerteventura (Puerto del Rosario), 28.533333, -13.866667, Grimm 1995
- C. ovatus, Spain, Tenerife, 28.316667, -16.566667, Grimm 1995, *
- C. ovatus, Spain, Lobos, 28.748636, -13.822861, Grimm 1995
- C. ovatus, Spain, Lanzarote (La Santa), 29.10696, -13.66761, Grimm 1995
- C. ovatus, Spain, Lanzarote (Salinas del Rio), 29.217132, -13.491299, Grimm 1995, *
- C. ovatus, Spain, Gran Canaria (Las Palmas), 28.130679, -15.438244, Español 1962
- C. ovatus, Spain, Gran Canaria (Galdar), 28.149415, -15.649358, Español 1962

- C. ovatus, Spain, Gran Canaria (Arguineguin), 27.761683, -15.680764, Español 1962
 C. ovatus, Spain, Gran Canaria (Maspalomas), 27.760026, -15.585479, Wollastone 1864
 C. ovatus, Spain, Tenerife (El Médano), 28.048304, -16.538401, Español 1962
 C. ovatus, Spain, Tenerife (Los Cristianos), 28.053026, -16.712177, Español 1962
 C. ovatus, Spain, Fuerteventura (Corralejo), 28.727783, -13.868034, Español 1962, *
 C. ovatus, Spain, Fuerteventura (Chilegua), 28.255314, -14.176321, Español 1962
 C. ovatus, Spain, Fuerteventura (El Jable), 28.153984, -14.274329, Español 1962, *
 C. ovatus, Spain, Lobos, 28.746615, -13.818686, Español 1962
 C. ovatus, Spain, Lanzarote (Las Salinas), 28.93932, -13.82067, Español 1962
 C. ovatus, Morocco, Essaouira, 31.513056, -9.769722, Faucheux 2011, *
 C. ovatus, Namibia, Kubis, -19.93333, 17.53333, Gebien 1920, *
 C. ovatus, Namibia, Lüderitz, -26.64806, 15.15944, Gebien 1920, *
 C. ovatus, Namibia, Rehoboth, -23.317, 17.09, Gebien 1920, *
 C. ovatus, Namibia, Swakopmund, -22.68333, 14.53333, Gebien 1920, *
 C. ovatus, Namibia, Lüderitz, -26.150029, 16.350011, Ferrer 2004, *
 C. ovatus, Namibia, Halali (Etosha National Park), -19.017978, 16.482329, Ferrer 2004, *
 C. ovatus, Namibia, Epupa Falls (Kunene), -16.999764, 13.250966, Ferrer 2004, *
 C. ovatus, Chad, Borkou, 17.9167, 19.1167, Ardoin 1963
 C. ovatus, Senegal, Kayar, 14.916063, -17.116927, Ardoin 1971, *
 C. ovatus, Senegal, x, x, x, Erichson 1843 (not georeferenced)
 C. ovatus, Morocco, Uad Buchini, 29.53105, -10.04743, Espanol 1946
 C. ovatus, Morocco, Sidi Ifni, 29.37975, -10.17299, Espanol 1946, *
 C. ovatus, Western Sahara, Al Aiun, 27.1418, -13.18797, Espanol 1946, *
 C. ovatus, Italy, Syracuse, 37.083333, 15.283333, Rottenberg 1870, *
 C. ovatus, Italy, Pachino, 36.71522, 15.09019, Marcuzzi, 1970
 C. ovatus, Italy, Porto Palo, 37.57671, 12.90595, Aliquo & Leo 1999, *
 C. ovatus, Italy, Pantano Cuba, 36.706455, 15.027734, Aliquo & Leo 1999, *
 C. ovatus, Italy, Marza, 36.695891, 14.962427, Aliquo & Leo 1999
 C. ovatus, Morocco, Mogador, 31.5125, -9.77, Escalera 1914, *
 C. ovatus, Morocco, Mazagan, 33.231949, -8.515923, Escalera 1914, *
 C. ovatus, Italy, Torre San Teodoro, 37.908097, 12.462911, Aliquo & Soldati 2010
 C. ovatus, Italy, Tindari, 38.142413, 15.044830, Aliquo & Soldati 2010, *
 C. ovatus, Botswana, lac N'Gami, -20.5, 22.66667, Fairmaire 1888, *
 C. ovatus, Spain, Gran Canaria (Isleta), 28.16365, -15.41751, Lindberg 1962
 C. ovatus, Libya, Benghazi, 32.11486, 20.06859, Gridelli 1933, *
 C. ovatus, Libya, Tagiura, 32.88167, 13.35056, Gridelli 1933, *
 C. ovatus, Morocco, Oualidia, 32.73372, -9.03059, Espanol 1967, *
 C. ovatus, Morocco, Tamri, 30.695843, -9.829765, Espanol 1967, *
 C. ovatus, Morocco, Ait Melloul, 30.34164, -9.50356, Espanol 1967, *
 C. ovatus, Morocco, Mirleft, 29.578130, -10.032265, Espanol 1967
 C. ovatus, Morocco, El Khebita, 28.02, -12.38, Espanol 1967, *
 C. ovatus, Morocco, "Foum Oued Noun", x, x, x, Espanol 1967 (not georeferenced)
 C. ovatus, Morocco, "Bedousa, pr. Safi", x, x, x, Espanol 1967 (not georeferenced)
 C. ovatus, Cape Verde Islands, Boa Vista, 16.08333, -22.83333, Gridelli 1954, *
 C. ovatus, Egypt, El Tor, 28.24168, 33.6222, Kneucker & Andres 1920, *
 C. ovatus, Egypt, 'Uyun Musa, 29.86667, 32.65, Kneucker & Andres 1920, *
 C. ovatus, Sudan, Port Sudan, 19.61745, 37.21644, Ebner 1923, *
 C. ovatus, Tunisia, x, x, x, Desbrochers des Loges 1898 (not georeferenced)
 C. ovatus, South Africa, Richtersveld NP - Paradyskloof, -33.964270, 18.853706, New Data (SMNS)
 C. ovatus, Botswana, road Nato to Gweta, -20.102887, 25.649, New Data (SMNS)
 C. ovatus, Namibia, Lüderitz, -26.647094, 15.182115, New Data (SMNS)
 C. obesus, Yemen, Hadibo, 12.647507, 54.019426, Koch 1970
 C. obesus, Yemen, Samha, 12.157858, 53.036302, Schawaller 2004
 C. obesus, Somalia, Karin, 10.98415, 49.21792, Koch 1960
 C. obesus, Yemen, Halla, 12.55, 54.45166666666667, New data
 C. obesus, Yemen, Samha, 12.15, 53.05, New data
 C. obesus, Yemen, Deiqub, 12.384230, 54.015491, New data
 C. obesus, Yemen, Gubbah, 12.607479, 53.784391, New data
 C. obesus, Yemen, Samha Island, 12.173203, 53.015326, New data
 C. obesus, Yemen, Hadibo, 12.64881, 54.01895, New data
 C. stronglyloides, Namibia, Zambezi Region, -17.5, 24.266667, Fairmaire 1892, 1894