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Documenting tenebrionid diversity: progress on *Blaps* Fabricius (Coleoptera, Tenebrionidae, Tenebrioninae, Blaptini) systematics, with the description of five new species

Laurent SOLDATI [1,*], Fabien L. CONDAMINE [2], Anne-Laure CLAMENS [3] & Gael J. KERGOAT [4,*]

[1,2,3,4] INRA – UMR 1062 CBGP (INRA, IRD, CIRAD, Montpellier SupAgro), 755 Avenue du Campus Agropolis, 34988 Montferrier-sur-Lez, France.
[2] CNRS – UMR 5554 Institut des Sciences de l'Evolution (Université de Montpellier), Place Eugène Bataillon, 34095 Montpellier, France.

[*] Corresponding authors: laurent.soldati@inra.fr (LS) and gael.kergoat@inra.fr (GJK)
[2] Email: fabien.condamine@gmail.com
[3] Email: anne-laure.clamens@inra.fr

[1] urn:lsid:zoobank.org:author:B1795703-9439-4572-BC41-C01171062B7D
[2] urn:lsid:zoobank.org:author:27BF116A-15A1-4D4C-A259-B5D9059A578C
[3] urn:lsid:zoobank.org:author:D0ABC503-75A3-4DB4-9409-6F308124A1E1
[4] urn:lsid:zoobank.org:author:2F61F799-F919-42CA-927B-3712DB88AD04

Abstract. With about 250 species, the genus *Blaps* Fabricius, 1775 is one of the most diverse genera of darkling beetles (Coleoptera: Tenebrionidae: Tenebrioninae: Blaptini: Blaptina). In this study, we provide new insights on the evolutionary relationships of *Blaps* species using a combined molecular and morphological dataset encompassing 69 distinct *Blaps* species and subspecies (105 specimens in total, all belonging to the subgenus *Blaps*), four other representatives of the tribe Blaptini (from the subtribes Gnaptorina, Gnaptorinina and Prosodina) and 12 outgroup species. Five new species of *Blaps* are also described within the subgenus *Blaps*: *B. effeminata* sp. nov. from Libya, *B. intermedia* sp. nov. from Morocco, *B. maldesi* sp. nov. from Algeria, *B. nitiduloides* sp. nov. from Algeria and Tunisia and *B. teocchii* sp. nov. from Tunisia. The results of the phylogenetic analyses indicate that the genus *Blaps* is likely paraphyletic; the two highlighted clades are morphologically distinct and correspond to groups previously referred to as sections (I and II) within the subgenus *Blaps*. This suggests the need for more phylogenetic studies in order to clarify the status of the various genera and subgenera belonging to the tribe Blaptini.

Keywords. *Blaps*, molecular phylogenetics, morphology, taxonomy, Tenebrionidae.

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Introduction

The species-rich darkling beetle family (Coleoptera: Tenebrionidae) encompasses ca 20 000 described species worldwide (Ślipiński *et al*. 2011). The family currently consists of nine subfamilies, 96 tribes and 2300 genera (Matthews *et al.* 2010), some of which are highly diverse (e.g., the genus *Strongylium* Kirby, 1819 encompasses more than 1000 species). One of these species-rich genera is *Blaps* Fabricius, 1775, which belongs to the tribe Blaptini Leach, 1815 within the polyphyletic subfamily Tenebrioninae Latreille, 1802 (Kergoat *et al.* 2014a, 2014b). The tribe Blaptini consists of about 500 species, divided into five subtribes and 28 genera (Medvedev 2001, 2007; Medvedev & Merkl 2002). Half of the tribe's species diversity is made up by the genus *Blaps* (ca 250 species; Löbl *et al.* 2008: 219–228), which belongs to the subtribe Blaptina Leach, 1815. Interestingly, new species of *Blaps* are regularly described, even from well-prospected areas such as Spain (Martinez Fernández 2010; Castro Tovar 2014). Most species of *Blaps* (i.e., 230) are from the subgenus *Blaps* Fabricius, 1775, whereas the remaining species are found in the subgenera *Arenoblaps* Medvedev, 1999, *Dineria* Motschulsky, 1860 and *Prosoblapsia* Skopin & Kaszab, 1978 (Löbl *et al.* 2008). All these subgenera represent conspicuous elements of Western and Central Asian beetle biodiversity; because these areas encompass the highest level of species and genus diversity within Blaptini, they are generally considered as the tribe's centre of origin and diversification (Medvedev 2000; Condamine *et al.* 2013). Representatives of the subgenus *Blaps* have the largest area of distribution as they are also found in the Mediterranean Basin (Condamine *et al.* 2011, 2013). Within the subgenus *Blaps*, two distinct groups – referred to as sections by Seidlitz (1893) – have been recognized on the basis of specific morphological features (Solier 1848; Allard 1880, 1881, 1882; Seidlitz 1893; Gebien 1937). Recent phylogenetic analyses relying on either morphological only datasets (Condamine *et al*. 2011) or molecular and morphological datasets (Condamine *et al*. 2013) tend to support the hypothesis that both groups constitute monophyletic sister groups.

All species of *Blaps* are flightless and well adapted to semi-arid and arid environments because of several specific behavioural and morphological adaptations (Condamine *et al.* 2011). Subspecies of *Blaps* are generally morphologically well differentiated and may constitute species of their own (Ardoin 1973; Soldati 1994; Soldati *et al.* 2009; Condamine *et al.* 2011), as underlined by recent molecular phylogenetic analyses (Condamine *et al.* 2013). Previous biogeographical analyses found that geological events played an important role in their evolutionary history (Condamine *et al.* 2013). Because of their flightless habit, species of *Blaps* have limited dispersal abilities; in the context of the Mediterranean Basin, both the topographical and environmental heterogeneity, and the geographic isolation of many mountainous areas made them very prone to allopatric speciation (vicariance). This complex biogeographic context parallels the convoluted history of the taxonomy of Blaptini where numerous taxa have been alternatively treated as species or subspecies.

In this study, we conduct phylogenetic analyses relying on the largest dataset ever assembled for the subgenus *Blaps* (105 specimens belonging to 69 distinct species and subspecies are included), which includes three species that were not sampled in the study of Condamine *et al.* (2013). In contrast with the 2013 study, this dataset also includes four representatives of other Blaptini genera (*Gnaptor* Brullé, 1832, *Gnaptorina* Reitter, 1887 and *Prosodes* Eschscholtz, 1829), which belong to the subtribes Gnaptorina Medvedev, 2001 (genus *Gnaptor*), Gnaptorinina Medvedev, 2001 (genus *Gnaptorina*) and Prosodina Skopin, 1960 (genus *Prosodes*). To root the tree, we used 12 tenebrionid species as outgroups (Table 1). For this study, we assess the phylogenetic relationships of the subgenus *Blaps*, and we also include the description of five new species of *Blaps* from the Mediterranean Basin.

Table 1. Taxon sampling. For each species and subspecies, the avialability of morphological data (the 'Morpho.' column) and the number of sequenced specimens are indicated. Additional taxonomic information for species of *Blaps* is also provided (section and species group for members of section I). [continued on next page]

Species/subspecies	Morpho.	# of seq. specimens	Section	Species group
Blaps alternans Brullé, 1938	yes	1	I	*alternans*
Blaps inflata Allard, 1880	yes	2	I	*alternans*
Blaps maroccana Seidlitz, 1893	yes	2	I	*alternans*
Blaps ovipennis Seidlitz, 1893	yes	1	I	*alternans*
Blaps quedenfeldtii Seidlitz, 1893	yes	3	I	*alternans*
Blaps antennalis Allard, 1880	yes	0	I	*alternans*
Blaps tingitana Allard, 1880	yes	1	I	*alternans*
Blaps bifurcata mirei Gridelli, 1952	yes	1	I	*bifurcata*
Blaps bifurcata strauchii Reiche, 1861	yes	3	I	*bifurcata*
Blaps superstitiosa Erichson, 1841	yes	1	I	*bifurcata*
Blaps cognata Solier, 1848	yes	1	I	*cordicollis*
Blaps cordicollis Solier, 1848	yes	0	I	*cordicollis*
Blaps judaeorum Miller, 1858	yes	1	I	*cordicollis*
Blaps kaifensis Seidlitz, 1893	yes	0	I	*cordicollis*
Blaps kollarii Seidlitz, 1893	yes	2	I	*cordicollis*
Blaps appendiculata Motschulsky, 1851	yes	2	I	*emondi*
Blaps binominata Escalera, 1914	yes	1	I	*emondi*
Blaps debdouensis Obenberger, 1914	yes	2	I	*emondi*
Blaps emondi Solier, 1848	yes	2	I	*emondi*
Blaps intermedia Soldati sp. nov.	yes	2	I	*emondi*
Blaps maldesi Soldati sp. nov.	yes	1	I	*emondi*
Blaps nitiduloides Soldati sp. nov.	yes	1	I	*emondi*
Blaps prodigiosa Erichson, 1841	yes	2	I	*emondi*
Blaps teocchii Soldati sp. nov.	yes	0	I	*emondi*
Blaps approximans Seidlitz, 1893	yes	2	I	*gigas*
Blaps divergens Fairmaire, 1875	yes	1	I	*gigas*
Blaps doderoi Schuster, 1922	yes	2	I	*gigas*
Blaps effeminata Soldati sp. nov.	yes	3	I	*gigas*
Blaps gigas Linnaeus, 1767	yes	4	I	*gigas*
Blaps haberti Peyerimhoff, 1943	yes	1	I	*gigas*
Blaps nefrauensis nefrauensis Seidlitz, 1893	yes	1	I	*gigas*
Blaps nefrauensis vespertina Koch, 1937	yes	2	I	*gigas*
Blaps polychresta Forskål, 1775	yes	1	I	*gigas*
Blaps taeniolata Ménétriés, 1832	yes	2	I	*gigas*
Blaps wiedemannii Solier, 1848	yes	1	I	*gigas*
Blaps bedeli Chatanay, 1914	yes	0	I	*lusitanica*
Blaps hispanica Solier, 1848	yes	1	I	*lusitanica*
Blaps lusitanica Herbst, 1799	yes	1	I	*lusitanica*

Table 1. [continued from previous page; continued on next page]

Species/subspecies	Morpho.	# of seq. specimens	Section	Species group
Blaps torressalai Español, 1961	yes	0	I	*lusitanica*
Blaps tichyi Martínez Fernández, 2010	no	1	I	*lusitanica*
Blaps waltlii Seidlitz, 1893	yes	1	I	*lusitanica*
Blaps magica Erichson, 1841	yes	0	I	*magica*
Blaps plana Solier, 1848	yes	3	I	*magica*
Blaps murati Peyerimhoff, 1943	yes	0	I	*murati*
Blaps nitens barbara Solier, 1848	yes	2	I	*nitens*
Blaps nitens brachyura Küster, 1848	yes	1	I	*nitens*
Blaps nitens medvedevi Soldati *et al.*, 2009	yes	2	I	*nitens*
Blaps nitens mercatii Canzoneri, 1969	yes	1	I	*nitens*
Blaps nitens nitens Laporte, 1840	yes	3	I	*nitens*
Blaps nitens requieni Solier, 1848	yes	1	I	*nitens*
Blaps sulcifera Seidlitz, 1893	yes	2	I	*nitens*
Blaps megalatlantica Koch, 1945	yes	2	I	*peyerimhoffi*
Blaps pauliani Koch, 1945	yes	1	I	*peyerimhoffi*
Blaps peyerimhoffi Koch, 1945	yes	2	I	*peyerimhoffi*
Blaps pinguis Allard, 1880	yes	1	I	*pinguis*
Blaps propheta fiorii Español, 1967	yes	1	I	*propheta*
Blaps propheta propheta Reiche, 1861	yes	2	I	*propheta*
Blaps pubescens Allard, 1880	yes	3	I	*propheta*
Blaps ruhmeri Seidlitz, 1893	yes	1	I	*propheta*
Blaps tripolitanica Karsch, 1881	yes	2	I	*propheta*
Blaps dentitibia Reitter, 1889	no	1	II	–
Blaps femoralis medusula Skopin, 1964	no	1	II	–
Blaps gibba Laporte de Castelnau, 1840	no	1	II	–
Blaps inflata Allard, 1880	no	1	II	–
Blaps jeannei Ferrer & Soldati, 1999	yes	1	II	–
Blaps lethifera Marsham, 1802	yes	1	II	–
Blaps mucronata Latreille, 1804	yes	1	II	–
Blaps plana Solier, 1848	no	1	II	–
Blaps rugosa Gebler, 1825	no	1	II	–
Blaps tibialis Reiche & Saulcy, 1857	no	1	II	–
Gnaptor prolixus Fairmaire, 1866	no	1	–	–
Gnaptor spinimanus Pallas, 1781	yes	1	–	–
Gnaptorina cylindricollis Reitter, 1889	no	1	–	–
Prosodes jakowlewi Semenov, 1894	yes	1	–	–
Accanthopus velikensis Piller & Mitterpacher, 1783	no	1	–	–
Dendarus coarcticollis Mulsant, 1854	no	1	–	–
Helops caeruleus Linnaeus, 1758	no	1	–	–
Helops rossii Germar, 1817	no	1	–	–

Table 1. [continued from previous page]

Species/subspecies	Morpho.	# of seq. specimens	Section	Species group
Nalassus dryadophilus Mulsant, 1854	no	1	–	–
Nalassus harpaloides Küster, 1850	no	1	–	–
Platydema sp.	no	1	–	–
Scaurus atratus Fabricius, 1775	no	1	–	–
Scaurus striatus Fabricius, 1792	no	1	–	–
Scaurus uncinus Forster, 1771	no	1	–	–
Uloma artensis Perroud, 1864	no	1	–	–
Uloma rufa Piller & Mitterpacher, 1783	no	1	–	–

Material and methods

Taxon sampling and morphological study

Most specimens were acquired during field missions or through loans (see Condamine *et al.* 2011, 2013 for more details). Collected insects were identified by comparison with types and specimens housed in the following museums and private collections:

HNHM = Hungarian Natural History Museum, Budapest, Hungary
MCG = Museo Civico di Genova, Genova, Italy
MHNL = Muséum d'Histoire naturelle de Lyon, Lyon, France
MNHN = Muséum national d'Histoire naturelle, Paris, France
CMF = Collection of J.C. Martínez Fernández, Murcia, Spain
CS = Collection of L. Soldati, Clapiers, France
CT = Collection of V. Tichý, Trebon, Czech Republic

Holotypes of the new species were deposited in the MNHN, whereas paratypes were deposited in HNHM, MCG, MNHN, CMF, CS and CT. Photographs of specimens were taken using a Canon EOS 450D digital single-lens reflex camera fitted with an EF-S 60 mm macro lens. Photographs of male aedeagi were taken using EntoVision multifocus system.

In the Material examined sections, literal quotes from labels are placed within quotation marks.

Morphological dataset

The morphological dataset corresponds to the one published in the study of Condamine *et al*. (2011, see Appendix). This dataset consists of 47 morphological characters that have been scored for 62 species and subspecies of *Blaps* plus two other members of the tribe Blaptini (*Gnaptor spinimanus* (Pallas, 1781) and *Prosodes jakowlewi* Semenov, 1894). It is based on the examination of more than 2500 specimens; all characters are discrete, and multistate characters were treated as unordered (the annotated dataset is deposited in MorphoBank, homology of phenotypes over the web, under project number 2341, available from http://dx.doi.org/10.7934/P2341; see also http://morphobank.org/index.php).

Molecular dataset

The molecular dataset is based on that presented in the study of Condamine *et al*. (2013). The sampling for the tribe Blaptini is more comprehensive in the present study as it includes sequence data for five new species of *Blaps* and four other members of the tribe (see details below). It consists of four mitochondrial gene fragments: cytochrome oxidase I (COI), cytochrome b (Cytb), ribosomal 12S RNA (12S), and ribosomal 16S RNA (16S) (see Condamine *et al*. 2013 for the list of primers). Additional sequences were also obtained for five species (*Blaps pinguis* Allard, 1880, *B. tichyi* Martínez, 2010, *Gnaptor prolixus* Fairmaire, 1866, *G. spinimanus* and *Prosodes jakowlewi*) following the protocols described in Condamine *et al*. (2013). Newly generated PCR products were processed by Genoscope (France); all corresponding sequences were deposited in GenBank (see Appendix for accession numbers). In addition, we also used sequences available on GenBank for four species (*Blaps dentitibia* Reitter, 1889, *B. femoralis medusula* Skopin, 1964, *B. rugosa* Gebler, 1825 and *Gnaptorina cylindricollis* Reitter, 1889). In total, 112 specimens (96 of *Blaps*, four other representatives of the Blaptini tribe and 12 outgroup species) were included in the molecular dataset, with a total of 2011 aligned characters.

Phylogenetic analyses

Bayesian inference was used to infer phylogenetic relationships from a dataset combining the morphological and molecular matrices. This combined dataset encompasses 121 individuals (105 members of the genus *Blaps*, four other representatives of the Blaptini tribe and 12 outgroup species), of which nine are only included based on morphological characters. To improve the phylogenetic accuracy, we carried out partitioned analyses (Nylander *et al.* 2004). Partitions and substitution models for the molecular subset of the matrix were determined using PartitionFinder v. 1.1.1 (Lanfear *et al.* 2012). The Bayesian information criterion (BIC) was used for both partition and model selection (Ripplinger & Sullivan 2008). Based on the BIC results we used five partitions for the molecular subset (Table 2). For the morphological data subset, we used an evolutionary model analogous to the JC69 model, except that it has a variable number of states (one-parameter Markov k-state model; Lewis 2001). Bayesian inference analyses were then carried out using MrBayes v. 3.2.6 (Ronquist *et al.* 2012). We conducted two independent runs with four MCMC (one cold and three incrementally heated) that ran for 50 million generations, with trees sampled every 5000 generations. A conservative burn-in of 25% was then applied after checking for stability on the log-likelihood curves and the split-frequencies of the runs. Support of nodes for MrBayes analyses was provided by clade posterior probabilities (PP) as directly estimated from the majority-rule consensus topology. Nodes supported by PP ≥ 0.95 were considered strongly supported following Erixon *et al.* (2003).

Results

Taxonomic descriptions

Class Hexapoda Blainville, 1816
Order Coleoptera Linnaeus, 1758
Family Tenebrionidae Latreille, 1802

Blaps Fabricius, 1775

Blaps effeminata Soldati sp. nov.
urn:lsid:zoobank.org:act:1D90B029-4826-4525-9A59-22B6B0A91806
Fig. 1A–I

Etymology

The name of this species refers to the lack of abdominal hair tufts in males.

Material examined

Holotype

LIBYA: ♂, "Tombe a Nord di Cirene / Cirenaica, 27.IV.1967, G. Dellacasa & P. Maifredi / Museo Civico di Genova / *Blaps polychresta* ssp. *effeminata* Soldati, Holotype" (MCG).

Table 2. Results of PartitionFinder analyses, based on the BIC.

Partitions	Models
#1: COI_pos1, Cytb_pos1	GTR + G
#2: COI_pos2	GTR + G
#3: COI_pos3, Cytb_pos3	GTR + G
#4: Cytb_pos2	GTR + G
#5: 12S, 16S	GTR + G

Allotype

LIBYA: ♀, "Tombe a Nord di Cirene / Cirenaica, 27.IV.1967, G. Dellacasa & P. Maifredi / Museo Civico di Genova / *Blaps polychresta* ssp. *effeminata* Soldati, Allotype" (MCG).

Paratypes

LIBYA: 17 spec., "Cirene, Cir. 7.6.1936 R.e C. Koch" (HNHM); 16 spec., same data as holotype and allotype (MCG); 1 ♂, "18.IV.1968, Apollonia, Cirenaïque, Libye, D. Seiler leg." (CS); 2 ♂♂, "Cyrenaika, Cirene, Wohlb. 4.34" (CS); 1 ♀, "Tombe a Nord di Cirene / Cirenaica, 27.IV.1967, G. Dellacasa & P. Maifredi" (CS).

Other material (13 specimens, HNHM; 8 specimens, MCG)

LIBYA: Cyrene, E Libya, (HNHM); Sho-Hat (HNHM); Al Baida, 32°38.047′ N, 21°47.425′ E (MCG); Al Qubbah, Cyrene, Marsa (Tobruch) (MCG); Uadi el Magrum, E Libya, 15 km W of Tobruch (MCG); Uadi Pescara, E Libya, 16 km W of Tobruch (MCG).

Description

Length: 26.0–43.0 mm; width: 12.0–15.0 mm. Dull black. Oval-oblong, elongated (Fig. 1A–C). Elytra costulated. Upper surface covered with very fine and sparse punctures, progressively denser from elytra to head.

HEAD. Clypeus arcuately emarginated, with lateral angles protruding frontwards, clypeo-labial membrane slightly visible. Clypeo-frontal suture reduced to thin, superficially engraved glossy line. Middle of frons (disc) with faint, generally obliterated, transverse depression. Mentum transverse, punctate, with anterior third sloping toward anterior edge. Gula microshagreened, dull. Labium triangularly emarginated in middle of front edge.

ANTENNAE. Long and slender, reaching pronotal base when directed backwards (Fig. 1D).

PRONOTUM. Broadest in its middle, sides more strongly narrowed toward base than forward, not or barely sinuous before posterior angles and arcuately narrowed frontwards. Anterior angles rounded. Posterior angles blunt. External rim fine, complete on lateral margins, but obliterated in middle of front edge and base. Disc convex. Punctation fine, uniform. Carina of anterior foramen of pronotum thick and neck-shaped below. Episternum of prosternum wrinkled near coxae and lighter toward margins. Prosternal apophysis oblique or steep and upright towards apex, S-shaped, just behind anterior coxae, then shortly denticulate in middle at apex.

ELYTRA. Ovoid, broadest around its middle, flat on disc. Upper surface leathery and covered with extremely fine and sparse punctures. Elytra costulate. Each elytron bearing 10 costae, alternate ones (3-5-7-9) slightly higher than others. Pseudopleural carina only visible on anterior half (in ♂♂ and ♀♀) from above, because of transversal convexity of elytra. Caudal extension at apex of elytra (mucro) measuring between 2.0 and 4.0 mm. Seen from above, right, parallel: deep suture flanked by two thick,

Fig. 1. *Blaps effeminata* Soldati sp. nov. **A**. ♂, habitus (dorsal view). **B**. ♂, habitus (lateral view). **C**. ♂, habitus (ventral view). **D**. ♂, left antenna (dorsal view). **E**. ♂, mucro (dorsal view). **F**. ♂, mucro (lateral view). **G**. ♀, mucro (dorsal view). **H**. ♂, aedeagus (ventral view). **I**. ♂, aedeagus (lateral view). Scale bars: A–C = 10 mm; D = 5 mm; E–G = 2 mm; H–I = 3 mm.

transversely wrinkled ribs, which end in acute angular gap (Fig. 1E). In lateral view, mucro narrow, elongated, progressively narrowed to apex (Fig. 1F) and often bent upwards. Below, mucro groove-shaped, with external edges blurred and bottom transversally wrinkled.

Abdomen. Ventrites heavily wrinkled-punctate; anal ventrite finely and densely punctate, transversally impressed on disc, external rim complete and fine.

Legs. Long and slender. Protibiae with internal face sinuous, external one straight in males; similar but less pronounced in females. Outer and posterior face of protibiae and posterior face of mesotibiae superficially grooved. Mesotibiae almost straight. Tarsi long, slender.

Sexual dimorphism. In males, no tuft of bristles between ventrites 1 and 2, and presence of light callosity near base of intercoxal process of ventrite 1. This callosity reduced to short transverse strip, with some longitudinal and oblique folds on front side, and coarse transversal wrinkles behind. In lateral view posterior declivity of elytra steeper in females. Mucro longer in males (3.5–4.0 mm) than in females (2.0–2.5 mm) (Fig. 1E, G). In males, rear edges of median and especially hind tibiae strongly denticulated**.** In males, metatibiae straight and flat on inner face; less pronounced in females.

Aedeagus. Parameres widely open, subcordiform, on sternal face (Fig. 1H) with apex triangular. In lateral view (Fig. 1I), parameres very thick and parallel, then abruptly narrowed at apex.

Bionomics

Most known specimens were collected in antique ruins between April and October.

Distribution

Libya. This species appears to be endemic to the eastern part of Libya (formerly known as Cyrenaica).

Remarks

This species belongs to the *Blaps gigas* species group (*sensu* Condamine *et al.* 2011). It is morphologically close to *Blaps polychresta* Forskål, 1775 from Egypt, from which it differs by: (i) its stronger elytral costulation, especially on the disc; (ii) the absence of the abdominal hair tuft in males (between ventrites 1 and 2); (iii) in males, the presence of a very reduced abdominal callosity located near the base of the intercoxal process of ventrite 1.

In Eastern Libya, *Blaps effeminata* sp. nov. can also be confounded with other species of *Blaps* with costulate elytra, namely *B. bifurcata* Solier, 1848, *B. doderoi* Schuster, 1922, *B. nitens laportei* Ardoin, 1973, *B. rhumeri* Seidlitz, 1893, *B. sulcifera* Seidlitz, 1893 and *B. wiedemannii* Solier, 1848. In *Blaps bifurcata*, *B. nitens laportei*, *B. rhumeri* and *B. sulcifera*, the mentum is longitudinaly impressed in the middle, with the front edge emarginated. In *Blaps doderoi* and *B. wiedemannii*, the antennae are shorter (reaching only ¾ of pronotal length when directed backwards), the abdominal ventrites are much less densely punctuated, the mucro is shorter and much less narrow, the male abdominal callosity is high and rearward, and males exhibit a yellow hair tuft between ventrites 1 and 2.

Blaps intermedia Soldati sp. nov.
urn:lsid:zoobank.org:act:EC3407F9-8A76-4296-AEC5-DFDA9F06CDE1
Fig. 2A–I

Etymology

The name of this species refers to the fact that it looks like a morphological intermediary between *Blaps appendiculata* Motschulsky, 1851 and *B. debdouensis* Obenberger, 1914.

Material examined

Holotype

MOROCCO: ♂, "4.IV.1996, Arhbalou, Moyen Atlas, Maroc, P. Jolivet leg. / Museum Paris coll. P. Ardoin 1978 / *Blaps* ssp. *intermedia* m. Soldati det. 1996 / *Blaps intermedia* m. n. sp., L. Soldati 2015, HOLOTYPE" (MNHN).

Paratypes

MOROCCO: 1 ♂, "Marocco, Moyen Atlas 6.04.1958 Leg. L. Kocher / Coll. N. Skopin / *appendiculata* Motsch. 1975 N. Skopin det. / *Blaps appendiculata canalicauda* subsp. n. / *Blaps emondi intermedia* n. ssp. PARATYPE" (HNHM); 2 ♂♂, "Dj. Hebbri 18.IV.1926 / Coll. Dr. G. Audéoud" (HNHM); 2 ♂♂, "El Hajeb 19.IV.1926" (HNHM); 1 ♂, "Moyen Atlas, route P21 bif.r.3206 21.7.69 / Marokko O. Stemmler / *Blaps tingitana* All. Dr. Z. Kaszab det. 1973" (HNHM); 3 ♂♂, same data as holotype (MNHN); 1 ♂, "14.V.1969, Azrou, Moyen Atlas, Durand" (MNHN); 1 ♂, "20.IV.1965, Almis du Guigou p. Boulemane, Moyen Atlas, P. Jolivet" (MHNH); 1 ♂, "Azrou" (MNHN); 1 ♂, "20.IV.1965, Boulemane, Moyen Atlas, P. Jolivet" (MNHN); 1 ♂, "29.V.1968, 1800 m, Djebel Hebri, Moyen Atlas, Maroc, D. Seiler" (MNHN); 1 ♂, "Moyen Atlas, 1960 m, Djebel Hebri, Maroc, 30.IV.1970" (MNHN); 1 ♂, "Timhadit, 1900 m, Alluaud 1881" (MNHN); 1 ♂, 1 ♀, "rte entre Ajabou et Azrou (stat° 21, 1900 m, 33°15′ N / 05°14′ WW)" (MHNL); 1 ♂, "Aknoul 11/10/1936" (CS); 1 ♂, 2 ♀♀, "Jbel Tichtrar, Moy. Atl. 6.1973, Maroc, H. Fongond" (CS); 1 ♂, "Tizi Abekhnanes, Jbel Tichtrar, Maroc Moy. Atl. 27.VI.1973, H. Fongond" (CS); 1 ♂, "Forêt de Jaaba 11 km W. Ifrane Moyen Atlas Maroc 30.V.08" (CT); 1 ♂, "Maroc m 2000, Moyen Atlas, Aguelmame Sidi Ali, 20.VI.1998, P. Leo" (CMF); 1 ♀, "Aguelm. Sidi Ali,Moy. Alt., Maroc, 6.IV.1980, H. Fongond" (CMF).

Other material (50 specimens, MNHN)

MOROCCO: Aknoul, Almis du Guigou, Azerzou (SE of Khenifra) (MNHN); Azrou, Arhbalou-n-Serdane, Bekrite, 1950 m (Middle Atlas) (MNHN); Berkane (MNHN); Dayet Ifrah (MNHN); El Hadjeb (MNHN); Ifrane (MNHN); Zaouïa de l'Oued Ifrane (MNHN); Djebel Hebri (MNHN); Guercif (MNHN); Mechrâ Safsaf (near Berkane) (MNHN); Taza (MNHN); Tendrara (MNHN); Timhadit, Zad, 2100 m (MNHN).

Description

Length: 32.0–42.0 mm; width: 12.0–16.0 mm. Dull black. Oval-oblong, elongated (Fig. 2A–C). Upper surface covered with very fine and sparse punctures, progressively denser from elytra to head.

Head. Clypeus arcuately emarginate, with lateral angles protruding frontwards, clypeo-labial membrane not visible. Clypeo-frontal suture reduced to thin, superficially engraved glossy line. Middle of frons (disc) with faint, generally obliterated, transverse depression. Mentum transverse, punctate and slightly impressed in middle of anterior edge. Gula microshagreened, dull. Labium triangularly emarginated in middle of front edge.

Antennae. Medium size, reaching at most ¾ of pronotal length when directed backwards (Fig. 2D).

Pronotum. Broadest in its middle, sides distinctly sinuated before posterior angles and arcuatly narrowed frontwards. Anterior angles rounded. Posterior angles sub-right and blunt. External rim fine, complete on lateral margins, but obliterated in middle of front edge and base. Disc convex. Punctuation fine, uniform. Carina of pronotum anterior foramen thick and neck-shaped below. Episternum of prosternum shallowly wrinkled near coxae and obliterate toward margins. Prosternal apophysis vertically bent just behind anterior coxae, then very slightly denticulate in middle at apex.

Elytra. Ovoid, broadest around its middle, flat on disc. Upper surface leathery, covered with extremely fine and sparse punctures. Pseudopleural carina only visible from above because of tranversal convexity

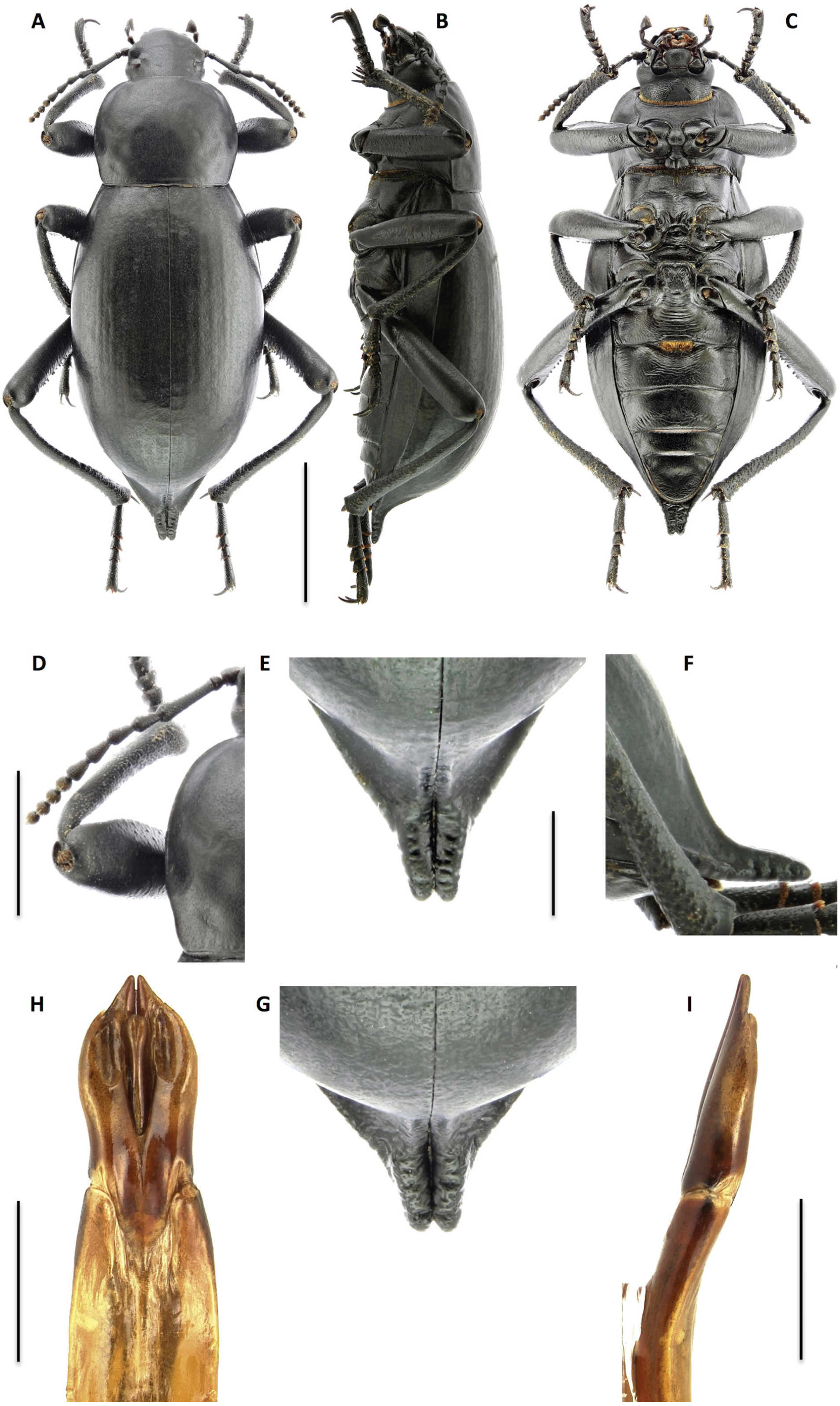

Fig. 2. *Blaps intermedia* Soldati sp. nov. **A**. ♂, habitus (dorsal view). **B**. ♂, habitus (lateral view). **C**. ♂, habitus (ventral view). **D**. ♂, left antenna (dorsal view). **E**. ♂, mucro (dorsal view). **F**. ♂, mucro (lateral view). **G**. ♀, mucro (dorsal view). **H**. ♂, aedeagus (ventral view). **I**. ♂. aedeagus (lateral view). Scale bars: A–C = 10 mm; D = 5 mm; E–I = 2 mm.

of elytra. Caudal extension at apex of elytra (mucro) measuring between 1.5 and 3.5 mm. Seen from above, mucro triangularly narrowed; deep suture flanked by two thick, coarsely transversely wrinkled ribs, converging toward apex, which ends in acute angular gap (Fig. 2E). In lateral view, mucro regularly narrowed up to apex, with lower face sub-horizontal (Fig. 2F); below, regularly but not deeply excavated, with sharp external edges and bottom transversally wrinkled.

Abdomen. Ventrites wrinkled-punctate; anal ventrite finely punctate, denser along external rim, external rim complete and fine.

Legs. Mesotibiae curved. Inner face of pro-and mesotibiae superficially grooved.

Sexual dimorphism. Yellow tuft of bristles between ventrites 1 and 2, and strong callosity between middle and front edge of intercoxal process of ventrite 1. Callosity directed backwards, bifid on top (when not eroded), with some longitudinal and oblique folds on front side, and coarse, transversal wrinkles hindwards. Pseudopleural carina of elytra only visible on anterior half in males, visible on anterior third in females. In lateral view, posterior declivity of elytra steep in males and subvertical in females. Mucro longer in males (2.0–3.5 mm) than in females (1.5–2.0 mm) (Fig. 2E, G). Male protibiae slightly flexuous; straight in females. In males, rear edges of median and especially hind tibiae strongly denticulate**.** Male metatibiae flexuous and shallowly emarginated on inner face; female metatibiae straight and simple.

Aedeagus. Parameres open on sternal face (Fig. 2H), with apex acuminate. In lateral view (Fig. 2I), parameres thick and convex at base, then narrowed almost in straight line up to apex.

Bionomics

The examined material was collected between April and October.

Distribution

Morocco: Middle Atlas mountain range and further north, up to the surroundings of Taza and Aknoul.

Remarks

This species belongs to the *Blaps emondi* species group (*sensu* Condamine *et al.* 2011). *Blaps intermedia* sp. nov. is morphologically very close to *B. debdouensis*, and the aedeagus is the most reliable character to the two species: in *B. intermedia* sp. nov. the parameres are more extended laterally and appear inflated, whereas they are parallel and gutter-shaped in *B. debdouensis*. However, it is worth underlining that the aedeagus is often distorted by dehydration because of the very thin lateral tegument of the parameres. In the case of isolated females, the geographic distribution is a good criterion to distinguish females of *Blaps intermedia* sp. nov. from females of *B. debdouensis*.

Blaps maldesi Soldati sp. nov.
urn:lsid:zoobank.org:act:ECAD95F0-9469-4AA3-824D-960F20F3DD15
Fig. 3A–I

Etymology

This species is named in honor of Jean-Michel Maldes, friend and colleague, entomologist at the CIRAD, specialist in Asilidae (Diptera), who discovered this new species of *Blaps* while prospecting in the Aures mountain range.

Material examined

Holotype

ALGERIA: ♂, "Algérie, M^if^ Aurès, S'Gag, 1900 m, 19.VI.1981 / ALGERIE J. M. MALDES / *Blaps maldesi* m. n. sp., L. Soldati 2015, HOLOTYPE" (MNHN).

Allotype

ALGERIA: ♀, "S'Gag, 2000 m, Ras Gueddelane, M^{if} des Aurès, 18.VI.1981 / ALGERIE J. M. MALDES / *Blaps maldesi* m. n. sp., L. Soldati 2015" (MNHN).

Paratype

ALGERIA: 1 ♂, "Sgag (Aurès) / *Blaps maldesi* m. n. sp., L. Soldati 2015, PARATYPE" (CS).

Description

Length: 29.0–35.0 mm; width: 10.0–15.0 mm. Dull to semi-gloss black. Oval-oblong (Fig. 3A–C). Upper surface covered with very fine and sparse punctures, denser on head and pronotum.

Head. Clypeus arcuately emarginated, with lateral angles right and protruding frontwards, leaving clypeo-labial membrane partially visible. Clypeo-frontal suture reduced to thin, superficially engraved gloss line. Middle of frons (disc) with faint transverse depression. Mentum transverse, punctate and slightly impressed in middle of anterior edge. Gula microshagreened, matte. Labium deeply notched in middle of front edge.

Antennae. Medium size, not reaching pronotal base when directed backwards (Fig. 3D).

Pronotum. Broadest in its middle, sides narrowed almost in straight line posteriorly, sinuated before posterior angles and arcuately narrowed toward front. Anterior angles rounded. Posterior angles obtuse and blunt. External rim fine, complete on lateral margins, but briefly obliterated in middle of front edge and base. Disc quite convex. Punctation fine, uniform. Carina of anterior foramen of pronotum thick and neck-shaped below. Episternum of prosternum wrinkled near coxae and obliterate toward sides. Prosternal apophysis vertically bent just behind anterior coxae, then flat and non-protruding posteriorly.

Elytra. Ovoid, broadest around its middle, flat on disc. Upper surface leathery and covered with extremely fine and sparse punctures. Pseudopleural carina only visible on anterior half from above because of transversal convexity of elytra. Caudal extension at apex of elytra (mucro) measuring less than 2.0 mm. Deep suture of mucro flanked by two thick, coarsely transversely wrinkled ribs, converging toward apex, apex ends in narrow apical gap (Fig. 3E). In lateral view, mucro regularly sloping up to apex (Fig. 3F). Below, mucro regularly excavated, with sharp external edges and bottom transversally wrinkled.

Abdomen. Ventrites wrinkled-punctate; anal ventrite densely punctate, especially along external rim, external rim complete and quite thick. In one case (paratype), external rim of anal ventrite shortly interrupted in middle of apex.

Legs. Protibiae long and flexuous, especially in males. Mesotibiae curved. Inner face of pro- and mesotibiae widely grooved. Tarsi elongated; claws long. Hind tarsi approximately as long as one half of length of corresponding tibiae.

Sexual dimorphism. Yellow tuft of bristles between ventrites 1 and 2, and a callosity in middle of intercoxal process of ventrite 1. Callosity directed backwards, with some oblique folds on front side. Elytra slightly larger than pronotum in males. In lateral view, posterior declivity of elytra steep in males and subvertical in females. Mucro longer in males (1.5–2.0 mm) than in females (0.5 mm) (Fig. 3E, G). Seem from above, mucro triangularly narrowed in males and acuminate in females. Rear edges of median and especially hind tibiae strongly denticulate in males. Male metatibiae flexuous and shallowly emarginated on inner face; female metatibiae straight and simple.

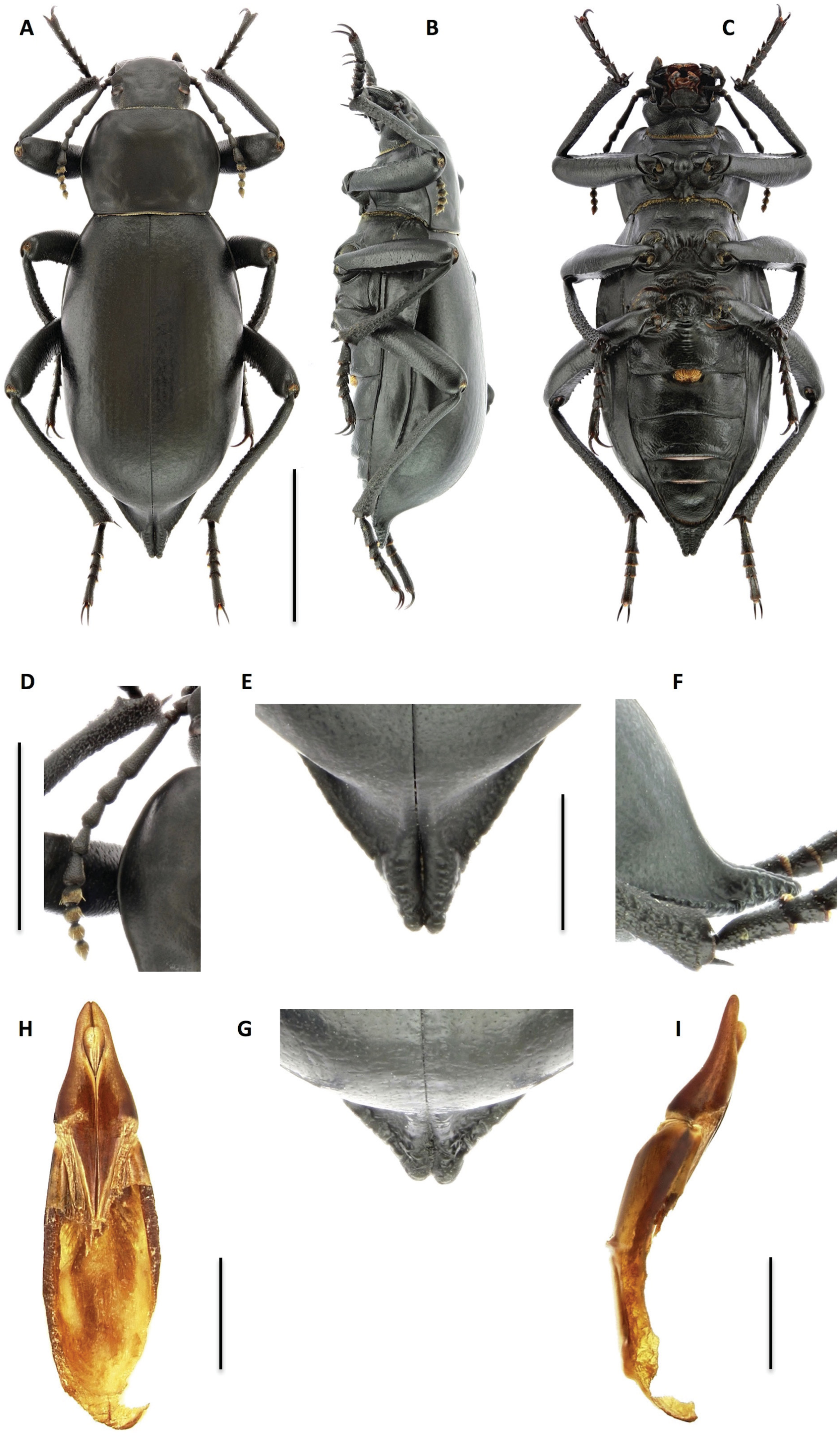

Fig. 3. *Blaps maldesi* Soldati sp. nov. **A**. ♂, habitus (dorsal view). **B**. ♂, habitus (lateral view). **C**. ♂, habitus (ventral view). **D**. ♂, left antenna (dorsal view). **E**. ♂, mucro (dorsal view). **F**. ♂, mucro (lateral view). **G**. ♀, mucro (dorsal view). **H**. ♂, aedeagus (ventral view). **I**. ♂, aedeagus (lateral view). Scale bars: A–C = 10 mm; D = 5 mm; E–G = 2 mm; H–I = 1 mm.

Aedeagus. Parameres bottleneck-shaped on sternal face (Fig. 3H), with apex acuminate. In lateral view (Fig. 3I), parameres thick and convex at base, then narrowed almost in a straight line up to apex.

Bionomics

The three known specimens were taken in the cedar forest of S'Gag (Algeria).

Distribution

Algeria. This species is currently known only from the type locality of S'Gag in the Aurès region.

Remarks

This species belongs to the *Blaps emondi* species group (*sensu* Condamine *et al.* 2011). It is morphologically most similar to *B. teocchii* sp. nov. from Tunisia. *Blaps maldesi* sp. nov. is most clearly separated from *B. teocchii* sp. nov. by having shorter antennae and tarsi, a wider pronotum and by the presence of a tuft of yellow bristles between abdominal ventrites 1 and 2. Until now, these two species have passed unnoticed in the collections because they superficially look like small specimens of other species of the *emondi* group, especially when the specimens are prepared in the old-fashioned way, with the legs tucked under the body. Compared to other species in the *emondi* group, these two species are characterized by the following combination of characters: slender legs; long and flexuous fore-tibiae, with inferior face distinctly grooved; tarsi long; and bottleneck-shaped parameres of aedeagus.

Blaps nitiduloides Soldati sp. nov.

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Fig. 4A–I

Etymology

The name of this species refers to its resemblance to *Blaps emondi* var. *nitidula* Solier, 1848.

Material examined

Holotype

TUNISIA: ♂, "27.IV.1964, Maktar, TUNISIE, Besnard réc. / MUSEUM PARIS COLL. P. ARDOIN 1978 / *Blaps binominata* Esc. = *caudigera* Allard P. ARDOIN DET. 1977 / *Blaps nitiduloides* m. n. sp. L. Soldati 2015, HOLOTYPE" (MNHN).

Allotype

TUNISIA: ♀, "Tunis / MUSEUM PARIS COLL. L. BEDEL 1922 / *Blaps nitiduloides* m. n. sp. L. Soldati 2015, ALLOTYPE" (MNHN).

Paratypes

ALGERIA: 1 ♂, "Aïn Beida, Constantinois, ALGERIE" (MNHN).

TUNISIA: 1 ♂, 1 ♀, "Tunis 9.IX.26 J. Briel" (MNHN); 1 ♂, "27.IV.1964, Maktar, TUNISIE, Besnard réc." (MNHN); 1 ♂, "Carthage, Tunisie, 10.IX.26, Briel" (MNHN); 1 ♂, 1 ♀, "MUSEUM PARIS TUNIS Belvédère A. WEISS 1902" (MNHN); 1 ♂, "Teboursouk, Tunisie" (MNHN); 1 ♂, "Hadger El Aioun (Tunisie) DE VAULOGER" (MNHN); 1 ♂, "Sbeitla, De Vauloger" (MNHN); 1 ♀, "Tunis: Gassa (91 Augos) / *Edmondi* / Sammlung J. Daniel / *Blaps* ♀ ? *torretassoi* Koch i. l. 1977 N. Skopin det." (HNHM); 1 ♂, "Tunisie, Teboursouk" (CS); 1 ♂, "Tunis" (CS); 1 ♂, "Tunisie, Sousse, 10.IV.1997, M. Martinez leg." (CS); 1 ♀, "27.IV.1964, Maktar, TUNISIE, Besnard réc." (CS); 1 ♂, 1 ♀, "Tunisia NE, Hammam-Lif, 3–4.IV.1999, lgt. M. Kalabza" (CT); 1 ♀, "Tunisia NW, 20 km N Beja, 19.4.2001, LGT. M. Halada" (CT).

Other material (3 specimens, MNHN)
ALGERIA: Constantine (Khenichela), Mt Tebessa, 1100 m (MNHN).

TUNISIA: Carthago, Radès (MNHN).

Description

Length: 33.0–42.0 mm; width: 12.5–16.0 mm. Semi-gloss black (Fig. 4A–C). Upper surface covered with extremely fine, sparse and superficial punctures.

Head. Covered with fine punctation, more pronounced than on rest of upper body surface. Punctation becomes even denser on clypeus. Clypeus arcuately emarginated, with anterior angles right and protruding frontwards, leaving clypeo-labial membrane partially visible. Clypeo-frontal suture reduced to thin, brilliant line. In middle of frons, just behind eyes, two shallow, circular depressions, sometimes joined by short transverse depression. Mentum transverse, densely and coarsely punctate. Gula microshagreened, matte. Labium deeply notched in middle of front edge.

Antennae (Fig. 4D). Short, barely reaching basal third of pronotum when directed backwards. Antennomeres 4–7 particularly short and thick.

Pronotum. Usually weakly transverse, not wider than long, broadest at or just behind its middle. Disc slightly convex. Sides regularly arcuate, except at posterior angles. Posterior angles obtuse and blunt. Anterior angles rounded. External rim complete on lateral margins, but obliterated in middle of front edge and base. Punctation extremely fine, sometimes barely visible. Carina of anterior foramen of pronotum very thick and neck-shaped. Episternum of prosternum superficially wrinkled. Prosternal apophysis vertically bent just after anterior coxae, then flat and generally non-protruding posteriorly.

Elytra. Ovoid, broadest around its middle. Upper surface smooth and covered with extremely fine and sparse punctures; background integument shining. Pseudopleural carina just visible on anterior half from above because of transversal convexity of elytra. Posterior declivity of elytra steep in lateral view. Mucro at apex of elytra measuring between 2.0 and 5.0 mm. Seen from above, deep suture flanked by two thick, coarsely transversely striated ribs, converging in curve toward apex, apex ending in deep and narrow apical gap (Fig. 4E). In lateral view, mucro thick on ¾ of its length, then abruptly sloping toward apex (Fig. 4F). Basin-shaped below, with bottom coarsely striated transversely.

Abdomen. Ventrites wrinkled; anal ventrite punctate, with light depression on disc, external rim complete.

Legs. Quite short and stout. Protibiae slightly curved. Tarsi short.

Sexual dimorphism. No tuft of bristles between ventrites 1 and 2, but strong callosity present in middle of intercoxal process of ventrite 1 in males. Mucro longer in males (2.5–5.0 mm) than in females (2.0–2.2 mm) (Fig. 4E, G). Male mesotibiae curved, slightly grooved on upper face. Male posterior tibiae flexuous and shallowly emarginated in middle of inner side, straight and simple in females.

Aedeagus. On sternal face (Fig. 4H), parameres open, subparallel for ⅘ of their length, then triangularly narrowed at apex. In lateral view (Fig. 4I), parameres first subparallel for 9/10 of their length, then obliquely truncated and end in a point.

Bionomics

The examined material was collected between April and September.

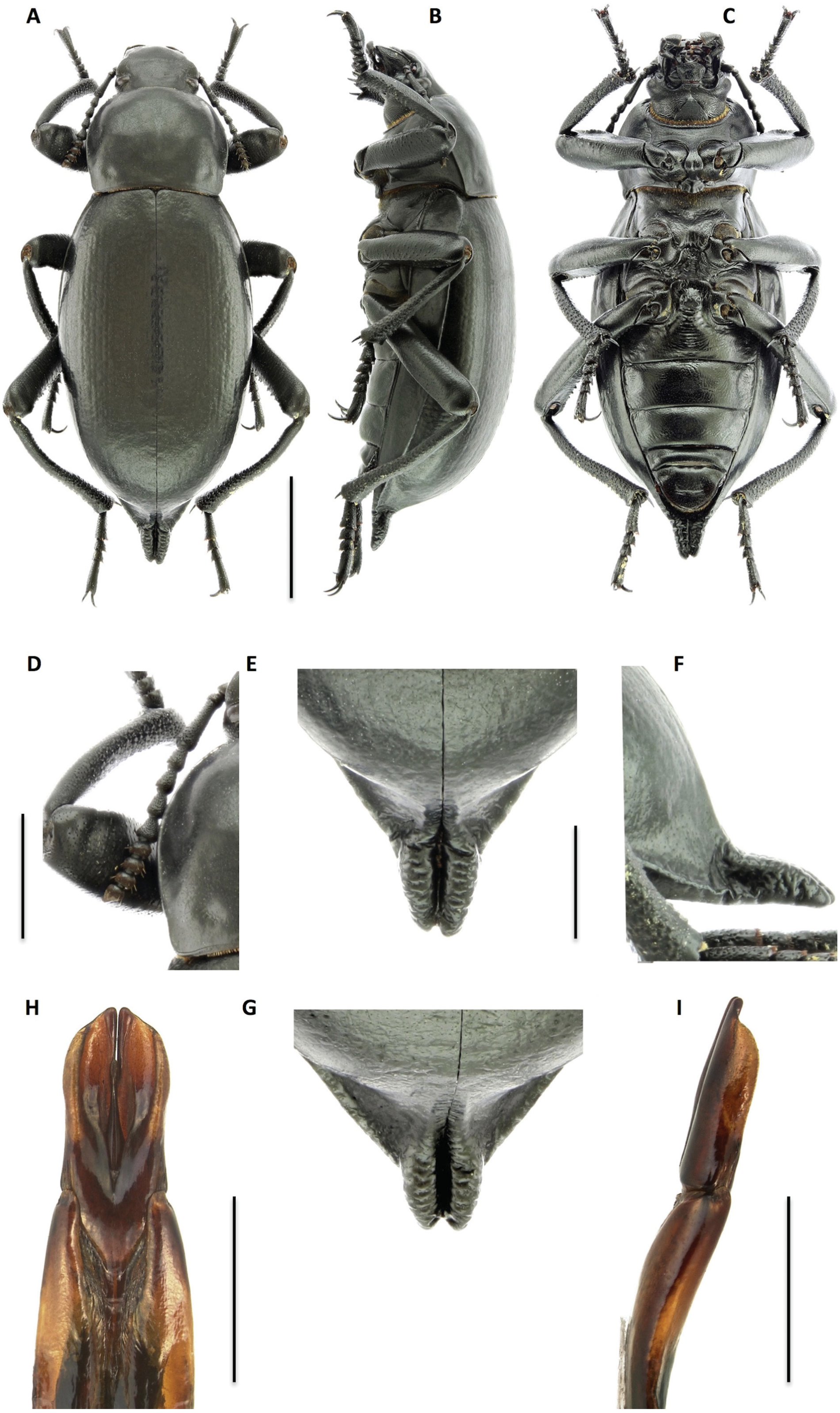

Fig. 4. *Blaps nitiduloides* Soldati sp. nov. **A**. ♂, habitus (dorsal view). **B**. ♂, habitus (lateral view). **C**. ♂, habitus (ventral view). **D**. ♂, left antenna (dorsal view). **E**. ♂, mucro (dorsal view). **F**. ♂, mucro (lateral view). **G**. ♀, mucro (dorsal view). **H**. ♂, aedeagus (ventral view). **I**. ♂, aedeagus (lateral view). Scale bars: A–C = 10 mm; D = 5 mm; E–I = 2 mm.

Distribution

Algeria and Tunisia. This species is currently only known from Tunisia and the Constantine region of Algeria.

Remarks

This species belongs to the *Blaps emondi* species group (*sensu* Condamine *et al.* 2011). It is morphologically related to *B. emondi* Solier, 1848 and *B. binominata* Escalera, 1914. In *B. binominata* the characteristic mucro is very broad and parallel, with a strong apical gap at a right angle. The male of *B. emondi* exhibits a tuft of yellow bristles between ventrites 1 and 2, and the abdominal callosity is located near the front edge of the intercoxal process of ventrite 1. It is also worth highlighting that *Blaps nitiduloides* sp. nov. is not found in sympatry with either *B. binominata* or *B. emondi*; the latter occurs in central and western Algeria, north of the 'Hauts Plateaux', and northeastern Morocco, whereas the distribution of *B. binominata* extends from the Oran region to the northeast of Morocco and the Spanish enclave of Melilla.

Blaps teocchii Soldati sp. nov.

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Fig. 5A–I

Etymology

This species is named in honour of Pierre Teocchi, cerambycid specialist, to whom one of us (L. Soldati) owes having become an entomologist.

Material examined

Holotype

TUNISIA: ♂, "Zaghouan, 20–22.V.1995, M. Ouda leg. / *Blaps teocchii* m. n. sp. L. Soldati 2015, HOLOTYPE" (MNHN).

Allotype

TUNISIA: ♀, same data as holotype (MNHN).

Paratypes

TUNISIA: 1 ♂, same data as holotype (CS); 1 ♂, same data as holotype (CT).

Description

Length: 31.0–33.0 mm; width: 11.0–13.0 mm. Semi-gloss black. Oval-oblong (Fig. 5A–C). Upper surface covered with very fine, sparse and superficial punctures, denser on head and pronotum.

Head. Clypeus arcuately emarginated, with lateral angles right and protruding frontwards, leaving clypeo-labial membrane partially visible. Clypeo-frontal suture reduced to thin gloss line. Middle of frons (disc) with faint transverse depression. Mentum transverse, coarsely punctate and slightly impressed in middle of anterior edge. Gula microshagreened, matte. Labium deeply notched in middle of front edge.

Antennae. Slender, barely reaching pronotal base when directed backwards (Fig. 5D).

Pronotum. Broadest in its middle, with sides narrowed almost in straight line posteriorly and arcuately towards front. Anterior angles rounded. Posterior angles obtuse and blunt. External rim fine, complete on lateral margins but obliterated in middle of front edge and base. Disc slightly convex. Punctation fine, uniform, as on head. Carina of anterior foramen of pronotum thick and neck-shaped below. Episternum

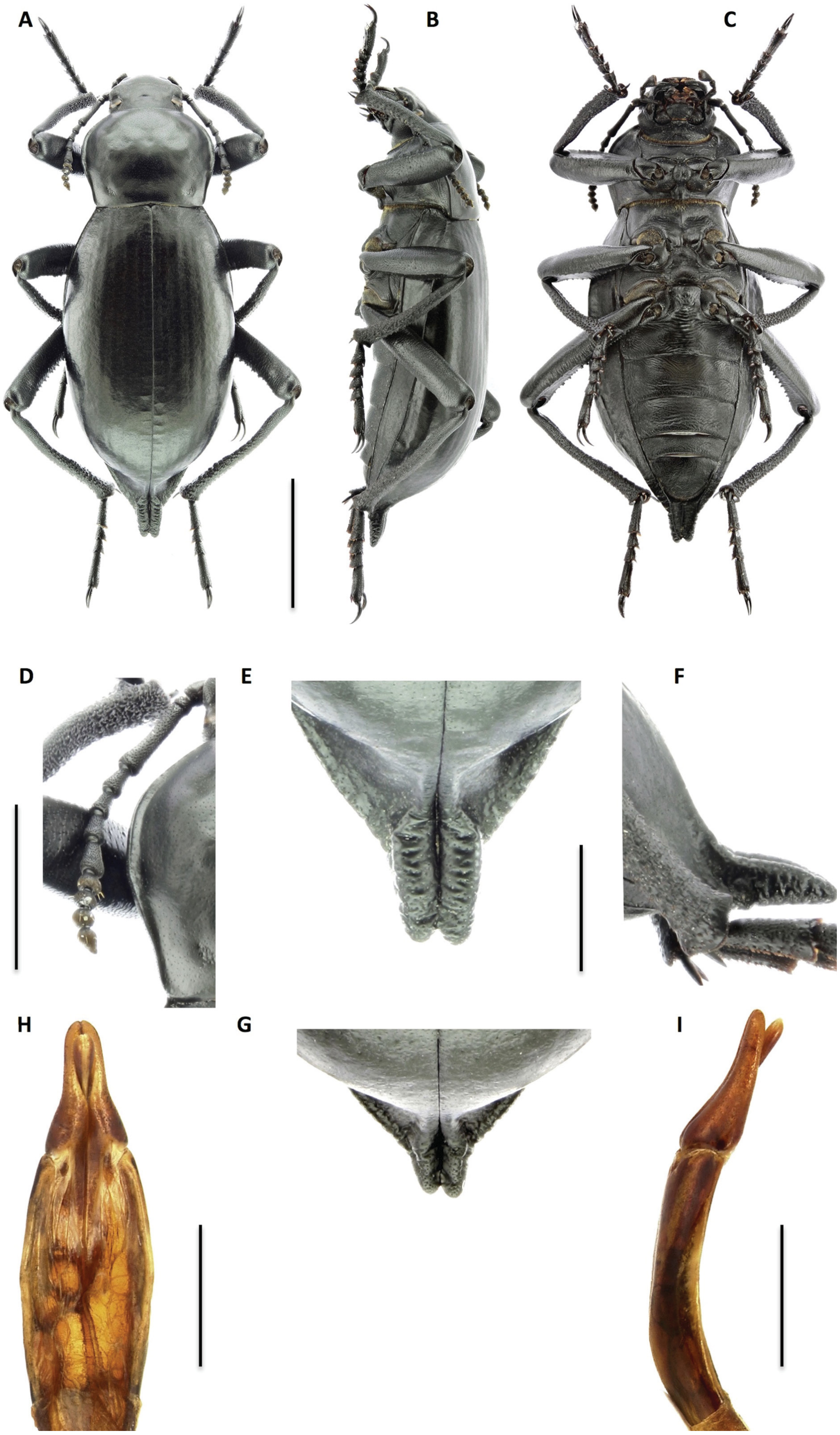

Fig. 5. *Blaps teocchii* Soldati sp. nov. **A**. ♂, habitus (dorsal view). **B**. ♂, habitus (lateral view). **C**. ♂, habitus (ventral view). **D**. ♂, left antenna (dorsal view). **E**. ♂, mucro (dorsal view). **F**. ♂, mucro (lateral view). **G**. ♀, mucro (dorsal view). **H**. ♂, aedeagus (ventral view). **I**. ♂, aedeagus (lateral view). Scale bars: A–C = 10 mm; D = 5 mm; E–G = 2 mm; H–I = 1.5 mm.

of prosternum superficially wrinkled. Prosternal apophysis vertically bent just behind anterior coxae, then flat and non-protruding posteriorly.

Elytra. Ovoid, broadest around its middle, depressed on disc. Upper surface smooth and covered with very fine and sparse punctures; background integument semi-gloss. Caudal extension at apex of elytra (mucro) measuring between 1.0 and 2.5 mm. Seen from above, mucro almost subparallel; deep suture flanked by two thick, coarsely transversely wrinkled ribs, slightly converging toward apex, apex ending in narrow apical gap (Fig. 5E). In lateral view, mucro regularly sloping up to apex (Fig. 5F). Seen from below, mucro regularly excavated, with sharp external edges and bottom transversally wrinkled.

Abdomen. Ventrites wrinkled-punctate; anal ventrite densely punctate, with external rim complete and quite thick.

Legs. Protibiae long and flexuous. Mesotibiae curved. Inner face of pro- and mesotibiae widely grooved. Tarsi elongated and stout; claws long. Hind tarsi as long as ¾ of length of corresponding tibiae.

Sexual dimorphism. No yellow tuft of bristles between ventrites 1 and 2, but strong callosity present between middle and anterior ridge of intercoxal process of ventrite 1 and directed backwards, with some oblique folds on front side. Elytra slightly larger than pronotum in males. Pseudopleural carina only visible on anterior half from above in males, or on anterior third in females, because of transversal convexity of elytra. In lateral view, posterior declivity of elytra steeper in females. Mucro longer in males (2.5 mm) than in females (1.0 mm) (Fig. 5E, G). Rear edges of median and especially hind tibiae strongly denticulate in males. Male metatibiae flexuous and shallowly emarginated on inner face at middle third; straight and simple in females.

Aedeagus. Parameres bottleneck-shaped on sternal face (Fig. 5H), with apex acuminate. In lateral view (Fig. 5I), parameres thick and convex at base, then narrowed almost in straight line up to apex.

Bionomics

Unknown.

Distribution

Tunisia. So far known only from the type locality of Zaghouan in Tunisia.

Remarks

This species belongs to the *Blaps emondi* species group (*sensu* Condamine *et al.* 2011). It is morphologically very similar to *B. maldesi* sp. nov. from Tunisia (see above for more information).

Phylogenetics analyses

Overall, the phylogenetic analyses resulted in a relatively well-supported tree (70.8% and 43.3% of nodes supported by PP ≥ 0.50 and 0.95, respectively; see Fig. 6). Nodal support was usually low (PP < 0.50) for the terminal parts of the tree encompassing taxa for which only morphological information was available (but see also *Blaps magica* Erichson, 1841 and *B. antennalis* Allard, 1880).

The monophyly of the tribe Blaptini was recovered with strong support (PP = 0.96). Of particular interest is the fact that the genus *Blaps* is not monophyletic in our phylogenetic reconstruction, due to the placement of the four other members of the Blaptini tribe. The latter are recovered in a weakly supported clade (PP = 0.49) sister to a large, well-supported clade (PP = 0.95) that encompasses all sampled representatives of the subgenus *Blaps* belonging to section I. For their part, all sampled members of the subgenus *Blaps* belonging to section II are recovered in a weakly supported clade (PP = 0.31), which

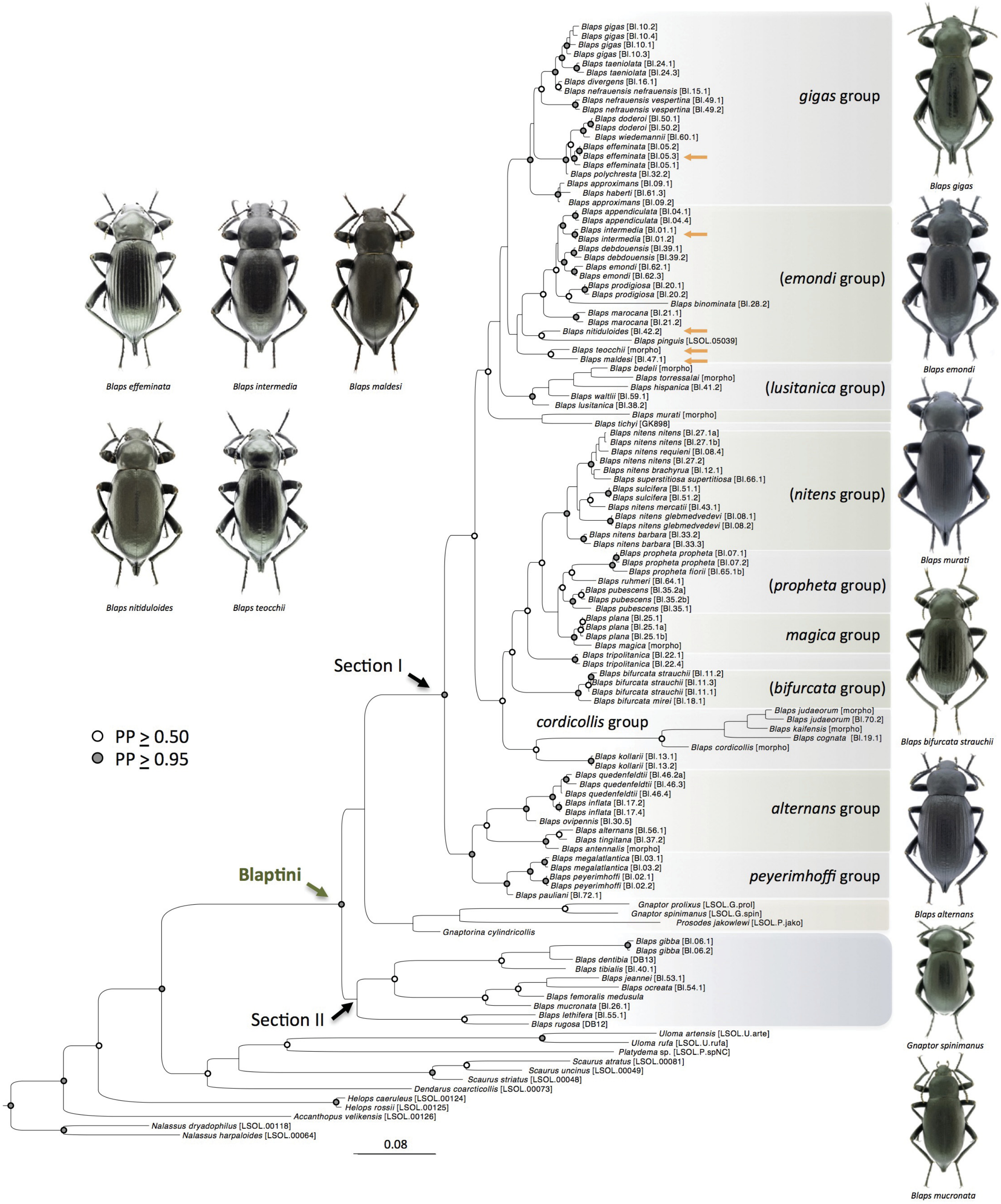

Fig. 6. Bayesian maximum consensus tree resulting from the analysis of the combined molecular and morphological dataset carried out with MrBayes. Support of nodes is indicated using empty circles (for PP ≥ 0.50) and filled circles for PP ≥ 0.95). Species groups for *Blaps* belonging to section I are highlighted using transparent coloured frames. Paraphyletic species groups are highlighted using bracketed names; orange arrows are also used to highlight the placement of the five new species. For illustrative purposes, the habitus of some adults are figured on the right side of the figure; on the left upper side, the habitus of the five new species are also presented (all photographs were taken by L. Soldati).

is sister to all other sampled Blaptini. Within section I of subgenus *Blaps*, half of the species groups (considering only groups for which we have more than one sampled representative) are recovered monophyletic, namely the species groups *alternans*, *cordicollis*, *gigas*, *magica* and *peyerimhoffi*. All species and subspecies for which several representatives are included are recovered monophyletic, with the noticeable exceptions of *Blaps approximans* Seidlitz, 1893 (due to the placement of an individual of *B. haberti* Peyerimhoff, 1943) and *B. nitens nitens* Laporte, 1840 (due to the placement of an individual of *B. nitens requieni* Solier, 1848). Regarding the placement of the new species, it is worth underlining that although *Blaps intermedia* sp. nov. is morphologically very similar to *B. debdouensis*, it is more closely related to *B. appendiculata*, while *B. debdouensis* is more closely related to *B. emondi*.

Discussion

The moderate support for our phylogenetic reconstruction can likely be accounted for by the amount of missing data in our dataset, especially given the fact that no molecular data was available for nine taxa. The low rate of PCR success results from the fact that we mostly processed specimens collected more than 10 years ago (PCR failed for more than 50 specimens). Because numerous species of interest are distributed in areas that are now hardly accessible, we think that future phylogenetic studies on species of *Blaps* (especially for the species that are distributed in Northern Africa) will require the intensive use of museomics approaches (see, e.g., Tin *et al*. 2014; Kanda *et al*. 2015).

Though the inferred basal phylogenetic relationships within sampled representatives of the tribe Blaptini are not well supported overall (for instance, the sampled *Blaps* from section II are recovered monophyletic, but with weak support), the inferred paraphyly of the genus is likely not artefactual. Indeed, its possible paraphyletic status does not come as a surprise given the taxonomic history of the tribe Blaptini, where numerous species were originally described in the genus *Blaps,* including species that are now assigned to genera belonging to other subtribes (Löbl *et al.* 2008). As a result, the subtribe Blaptina is possibly also paraphyletic, as it encompasses two clades (one for the sampled representatives of section I and one for the sampled representatives of section II of the subgenus *Blap*s) that are separated by representatives of three distinct subtribes of Blaptini. Obviously, because two of the three basal nodes are weakly supported, these results should be taken cautiously and highlight the need for more molecular data and a denser sampling for the tribe Blaptini. Since the subtribe Blaptina currently consists of 11 genera, our results emphasize the need for phylogenetic studies with a more comprehensive sampling at the genus level in order to properly redefine the higher systematics of the tribe Blaptini.

Within section I of subgenus *Blaps*, our results highlight the paraphyletic nature of several species groups. In contrast with the results of Condamine *et al.* (2013), in this study the *alternans* group is recovered monophyletic, while the *propheta* group is recovered paraphyletic due to the placement of individuals of *B. tripolitanica* Karsch, 1881. This paraphyly is likely artefactual, and it is only moderately supported in our analyses (PP = 0.63 and 0.72 for the nodes leading to the other representatives of the *propheta* group). The discrepancies between the two studies probably result from the inclusion of additional taxa and molecular data, in combination with the use of more thorough partitioning strategies. In our study, the *lusitanica* species group is also recovered paraphyletic as a result of the inclusion of a representative of *B. tichyi* Martínez Fernández, 2010. With reference to the latter, we think that the position of *Blaps tichyi* (sister to *B. murati* Peyerimhoff, 1943) is also artefactual because of the lack of character overlap between the two taxa (no molecular data is available for *B. murati* and, conversely, no morphological data is available for *B. tichyi*). Regarding the remaining three paraphyletic species groups (*bifurcata*, *emondi* and *nitens*), our results stress the need for a reappraisal of the boundaries of several species groups. For instance, the inclusion of *Blaps superstitiosa* Erichson, 1841 within the *nitens* group is to be considered as being based on the results of the molecular analyses, despite the fact that this species does not share the unique synapomorphy of the group (i.e., a straight posterior tibia). Similarly, the inclusion of *Blaps maroccana* Seidlitz, 1893 and *B. pinguis* Allard, 1880 as members of the *emondi* group might be warranted, but will require redefining the combination of character states that describe/delineate the clade.

At the species level our phylogenetic framework allows us to discuss the placement of the five newly described species, four of which belong to the *emondi* group. In the case of *Blaps intermedia* sp. nov., the results of the phylogenetic analyses support our view of considering this taxon as a distinct species within the *emondi* group, not directly related to *B. debdouensis*. The placement of *Blaps nitiduloides* sp. nov. (clustered with *B. pinguis*) came as a surprise, because this species is morphologically most similar to *B. binominata* and *B. emondi*; we cannot exclude that this position is artefactual, especially given the fact that it is only weakly supported (PP = 0.79). Regarding *Blaps maldesi* sp. nov. and *B. teocchii* sp. nov., both species are clustered together as sister to all remaining members of the *emondi* group (plus the only representative of the *pinguis* group); this placement is not surprising given that both species share unique combinations of character states (see above). Within the *gigas* group, *Blaps effeminata* sp. nov. is recovered as sister to a clade encompassing *B. doderoi* and *B. wiedemannii*, while being morphologically closer to *B. polychresta*; that being said, the corresponding node is only weakly supported (PP = 0.69).

Our results also provide further evidence to support the hypothesis that most subspecies of *Blaps* correspond to distinct valid species; this is especially the case for the subspecies that do not cluster together in the phylogenetic tree, such as *B. nefrauensis nefrauensis* Seidlitz, 1893 and *B. nefrauensis vespertina* Koch, 1937, or for the subspecies of *B. nitens*, which do not constitute a monophyletic group due to the placement of individuals of *B. sulcifera* and *B. superstitiosa*. To advance on this issue, more morphological and molecular studies, as well as the sequencing of additional specimens, are definitely required.

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Appendix. Accession numbers; outgroup species are listed after species of Blaptini.

Species	Voucher	Country	GenBank accession no.			
			COI	*Cytb*	12S	16S
Blaps alternans Brullé, 1938	Bl.56.1	Canary Islands	–	KC160330	KC160416	–
Blaps appendiculata Motschulsky, 1851	Bl.04.1	Morocco	KC160220	KC160278	–	–
Blaps appendiculata Motschulsky, 1851	Bl.04.4	Morocco	KC160221	–	KC160354	–
Blaps approximans Seidlitz, 1893	Bl.09.1	Tunisia	–	KC160286	KC160364	KC160432
Blaps approximans Seidlitz, 1893	Bl.09.2	Algeria	–	KC160287	KC160365	KC160433
Blaps bifurcata mirei Gridelli, 1952	Bl.18.1	Mali	–	KC160298	KC160380	–
Blaps bifurcata strauchii Reiche, 1861	Bl.11.1	Tunisia	KC160230	KC160290	KC160370	KC160435
Blaps bifurcata strauchii Reiche, 1861	Bl.11.2	Algeria	KC160231	KC160291	KC160371	KC160436
Blaps bifurcata strauchii Reiche, 1861	Bl.11.3	Libya	KC160232	KC160292	KC160372	KC160437
Blaps binominata Escalera, 1914	Bl.28.2	Morocco	–	KC699929	–	–
Blaps cognata Solier, 1848	Bl.19.1	Sudan	–	KC699930	–	–
Blaps debdouensis Obenberger, 1914	Bl.39.1	Morocco	KC160247	–	KC160400	–
Blaps debdouensis Obenberger, 1914	Bl.39.2	Morocco	KC160248	KC160316	KC160401	–
Blaps dentitibia Reitter, 1889	DB13	China	–	EU250308	–	–
Blaps divergens Fairmaire, 1975	Bl.16.1	Tunisia	KC160235	–	KC160377	KC160439
Blaps doderoi Schuster, 1922	Bl.50.1	Libya	–	KC160324	–	–
Blaps doderoi Schuster, 1922	Bl.50.2	Libya	–	KC160325	KC160410	–
Blaps effeminata Soldati sp. nov.	Bl.05.1	Libya	KC160222	KC160279	KC160355	–
Blaps effeminata Soldati sp. nov.	Bl.05.2	Libya	KC160223	KC160280	KC160356	–
Blaps effeminata Soldati sp. nov.	Bl.05.3	Libya	KC160224	KC160281	KC160357	–
Blaps emondi Solier, 1848	Bl.62.1	Morocco	KC160260	–	KC160418	–
Blaps emondi Solier, 1848	Bl.62.3	Morocco	KC160261	KC160333	KC160419	KC160448
Blaps femoralis medusula Skopin, 1964	–	China	–	–	–	AY663883
Blaps gibba Laporte de Castelnau, 1840	Bl.06.1	France	KC160225	–	KC160358	KC160430
Blaps gibba Laporte de Castelnau, 1840	Bl.06.2	France	KC160226	–	KC160359	KC160431
Blaps gigas Linnaeus, 1767	Bl.10.1	Tunisia	–	–	KC160366	–
Blaps gigas Linnaeus, 1767	Bl.10.2	Spain	–	–	KC160367	–

Species	Voucher	Country	GenBank accession no.			
			COI	*Cytb*	12S	16S
Blaps gigas Linnaeus, 1767	Bl.10.3	France	KC160229	KC160288	KC160368	KC160434
Blaps gigas Linnaeus, 1767	Bl.10.4	Italy	–	KC160289	KC160369	–
Blaps haberti Peyerimhoff, 1943	Bl.61.3	Algeria	–	KC160332	–	–
Blaps hispanica Solier, 1848	Bl.41.2	Spain	–	KC699931	–	–
Blaps inflata Allard, 1880	Bl.17.2	Morocco	–	KC160296	KC160378	–
Blaps inflata Allard, 1880	Bl.17.4	Morocco	–	KC160297	KC160379	–
Blaps intermedia Soldati sp. nov.	Bl.01.1	Morocco	KC160215	KC160274	KC160348	KC160425
Blaps intermedia Soldati sp. nov.	Bl.01.2	Morocco	KC160216	KC160275	KC160349	KC160427
Blaps jeannei Ferrer & Soldati, 1999	Bl.53.1	Turkey	KC160258	–	KC160413	–
Blaps judaeorum Miller, 1858	Bl.70.2	Syria	–	KC699932	–	–
Blaps kollarii Seidlitz, 1893	Bl.13.1	Qatar	KC160233	KC160293	KC160374	–
Blaps kollarii Seidlitz, 1893	Bl.13.2	Saudi Arabia	–	KC160294	KC160375	–
Blaps lethifera Marsham, 1802	Bl.55.1	Ukraine	KC160259	KC160329	KC160415	–
Blaps lusitanica Herbst, 1799	Bl.38.2	Spain	KC160246	–	–	–
Blaps maldesi Soldati sp. nov.	Bl.47.1	Algeria	KC160253	–	KC160407	–
Blaps maroccana Seidlitz, 1893	Bl.21.1	Morocco	KC160238	KC160301	KC160383	KC160442
Blaps maroccana Seidlitz, 1893	Bl.21.2	Algeria	KC160239	KC160302	KC160384	–
Blaps megalatlantica Koch, 1945	Bl.03.1	Morocco	KC160219	KC160277	KC160352	–
Blaps megalatlantica Koch, 1945	Bl.03.2	Morocco	–	–	KC160353	–
Blaps mucronata Latreille, 1804	Bl.26.1	Romania	–	KC160307	KC160392	–
Blaps nefrauensis nefrauensis Seidlitz, 1893	Bl.15.1	Tunisia	KC160234	KC160295	KC160376	KC160438
Blaps nefrauensis vespertina Koch, 1937	Bl.49.1	Libya	KC160254	KC160322	KC160408	–
Blaps nefrauensis vespertina Koch, 1937	Bl.49.2	Libya	KC160255	KC160323	KC160409	–
Blaps nitens barbara Solier, 1848	Bl.33.2	Libya	–	–	KC160396	–
Blaps nitens barbara Solier, 1848	Bl.33.3	Libya	–	–	KC160397	KC160444
Blaps nitens brachyura Küster, 1848	Bl.12.1	Spain	–	–	KC160373	–
Blaps nitens medvedevi Soldati *et al.*, 2009	Bl.08.1	Morocco	–	KC160284	KC160362	–
Blaps nitens medvedevi Soldati *et al.*, 2009	Bl.08.2	Morocco	–	KC160285	KC160363	–
Blaps nitens mercatii Canzoneri, 1969	Bl.43.1	Italy	KC160251	KC160318	KC160404	–

Species	Voucher	Country	GenBank accession no.			
			COI	***Cytb***	**12S**	**16S**
Blaps nitens nitens Laporte, 1840	Bl.27.1a	Algeria	–	KC160308	–	–
Blaps nitens nitens Laporte, 1840	Bl.27.1b	Algeria	–	KC160309	–	–
Blaps nitens nitens Laporte, 1840	Bl.27.2	Morocco	KC160242	KC160310	KC160393	–
Blaps nitens requieni Solier, 1848	Bl.08.4	Morocco	–	–	KC699928	–
Blaps nitiduloides Soldati sp. nov.	Bl.42.2	Tunisia	KC160250	KC160317	KC160403	–
Blaps ocreata Allard, 1880	Bl.54.1	Turkey	–	KC160328	KC160414	–
Blaps ovipennis Seidlitz, 1893	Bl.30.5	Morocco	–	–	KC160395	–
Blaps pauliani Koch, 1945	Bl.72.1	Morocco	KC160264	–	–	–
Blaps peyerimhoffi Koch, 1945	Bl.02.1	Morocco	KC160217	KC160276	KC160350	KC160428
Blaps peyerimhoffi Koch, 1945	Bl.02.2	Morocco	KC160218	–	KC160351	KC160429
Blaps pinguis Allard, 1880	LSOL.05039	Morocco	KX398844	–	–	–
Blaps plana Solier, 1848	Bl.25.1	Tunisia	KC160241	KC160304	KC160389	KC160443
Blaps plana Solier, 1848	Bl.25.1a	Tunisia	–	KC160305	KC160390	–
Blaps plana Solier, 1848	Bl.25.1b	Tunisia	–	KC160306	KC160391	–
Blaps polychresta Forskal, 1775	Bl.32.2	Egypt	–	KC160312	–	–
Blaps prodigiosa Erichson, 1841	Bl.20.1	Morocco	KC160236	KC160299	KC160381	KC160440
Blaps prodigiosa Erichson, 1841	Bl.20.2	Morocco	KC160237	KC160300	KC160382	KC160441
Blaps propheta fiorii Español, 1967	Bl.65.1b	Libya	KC160263	KC160334	–	–
Blaps propheta propheta Reiche, 1861	Bl.07.1	Libya	KC160227	KC160282	KC160360	–
Blaps propheta propheta Reiche, 1861	Bl.07.2	Libya	KC160228	KC160283	KC160361	–
Blaps pubescens Allard, 1880	Bl.35.1	Tunisia	KC160244	KC160313	–	KC160445
Blaps pubescens Allard, 1880	Bl.35.2a	Morocco	–	–	KC160398	–
Blaps pubescens Allard, 1880	Bl.35.2b	Morocco	KC160245	KC160314	KC160399	KC160446
Blaps quedenfeldtii Seidlitz, 1893	Bl.46.2a	Morocco	–	KC160319	–	–
Blaps quedenfeldtii Seidlitz, 1893	Bl.46.3	Morocco	–	KC160320	KC160405	–
Blaps quedenfeldtii Seidlitz, 1893	Bl.46.4	Morocco	KC160252	KC160321	KC160406	KC160447
Blaps rugosa Gebler, 1825	DB12	China	–	EU250307	–	–
Blaps ruhmeri Seidlitz, 1893	Bl.64.1	Libya	KC160262	–	KC160420	–

Species	Voucher	Country	GenBank accession no.			
			COI	***Cytb***	**12S**	**16S**
Blaps sulcifera Seidlitz, 1893	Bl.51.1	Libya	KC160256	KC160326	KC160411	–
Blaps sulcifera Seidlitz, 1893	Bl.51.2	Libya	KC160257	KC160327	KC160412	–
Blaps superstitiosa Erichson, 1841	Bl.66.1	Algeria	–	KC160335	KC160421	–
Blaps taeniolata Ménétriés, 1832	Bl.24.1	Cyprus	–	KC160303	KC160387	–
Blaps taeniolata Ménétriés, 1832	Bl.24.3	Iraq	–	–	KC160388	–
Blaps tibialis Reiche & Saulcy, 1857	Bl.40.1	Greece	KC160249	–	KC160402	–
Blaps tichyi Martínez Fernández, 2010	GK898	Spain	KX398845	KX398841	–	–
Blaps tingitana Allard, 1880	Bl.37.2	Morocco	–	KC160315	–	–
Blaps tripolitanica Karsch, 1881	Bl.22.1	Libya	–	–	KC160385	–
Blaps tripolitanica Karsch, 1881	Bl.22.4	Libya	KC160240	–	KC160386	–
Blaps waltlii Seidlitz, 1893	Bl.59.1	Spain	–	KC160331	–	–
Blaps wiedemannii Solier, 1848	Bl.60.1	Libya	–	–	KC160417	–
Gnaptor prolixus Fairmaire, 1866	LSOL.G.prol	Turkey	–	–	KX398838	–
Gnaptor spinimanus Pallas, 1781	LSOL.G.spin	Romania	–	KX398842	KX398839	–
Gnaptorina cylindricollis Reitter, 1889	–	China	–	–	–	AY663871
Prosodes jakowlewi Semenov, 1894	LSOL.P.jako	Iran	KX398846	KX398843	KX398840	–
Accanthopus velikensis Piller & Mitterpacher, 1783	LSOL.00126	France	–	KC160266	KC160338	–
Dendarus coarcticollis Mulsant, 1854	LSOL.00073	France	–	KC160265	KC160337	–
Helops caeruleus Linnaeus, 1758	LSOL.00124	France	–	–	KC160339	–
Helops rossii Germar, 1817	LSOL.00125	France	–	KC160267	KC160340	–
Nalassus dryadophilus Mulsant, 1854	LSOL.00118	France	–	KC160268	KC160341	–
Nalassus harpaloides Küster, 1850	LSOL.00064	France	–	KC160269	KC160342	–
Platydema sp.	LSOL.P.spNC	New Caledonia	–	–	KC160336	–
Scaurus atratus Fabricius, 1775	LSOL.00081	France	–	KC160270	KC160343	–
Scaurus striatus Fabricius, 1792	LSOL.00048	France	–	KC160271	KC160344	–
Scaurus uncinus Forster, 1771	LSOL.00049	France	–	KC160272	KC160345	–
Uloma artensis Perroud, 1864	LSOL.U.arte	New Caledonia	–	KC160273	KC160346	KC160423
Uloma rufa Piller & Mitterpacher, 1783	LSOL.U.rufa	France	–	–	KC160347	KC160424