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Comments on the recent changes in taxonomy of pygmy unicorns, with description of a new species of *Metopomystrum* from Brazil (Insecta, Tetrigidae, Cleostratini, Miriatrini)

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Abstract

The tribe Cleostratini Bolívar, 1887 *sensu* Storozhenko, 2016 does not represent a monophyletic taxon because it gathers various Tetrigidae genera with various types of horn and prolongation of frons or vertex. Prolongation of these structures is present in morphologically and biogeographically distant groups. We do not regard Miriatrini Cadena-Castañeda & Cardona, 2015 synonymous with Cleostratini because the genus *Miriatra* Bolívar, 1906 belongs to a group of genera distant from *Cleostratus* Stål, 1877. There is no adequate diagnosis for proposed groups of genera forming tribes Cleostratini or Miriatrini. Miriatrini **stat. resurr.** are monotypic and include only *Miriatra*, Cleostratini are monotypic as well. *Apteromystrum* Storozhenko, 2016 **syn. n.** is regarded synonymous with *Metopomystrum*, *M. apterum* **comb. resurr.**, *M. amazoniensis* **comb. resurr.** and *Miriatra brevifastigiata* (Cadena-Castañeda & Cardona, 2015), **comb. n.**

are not *Metopomystrum* member. Herein a new species of pygmy unicorn, *Metopomystrum muriciense* Silva & Skejo, **sp. n.**, is described from Atlantic Forest remnants in northeast of Brazil, collected on the Estação Serra do Ouro (municipality of Murici, Alagoas state). Distribution data, morphological characterization, and an identification key to *Metopomystrum* species are also presented.

Keywords
Apteromystrum, Atlantic Forest, fastigium, pygmy grasshopper, taxonomy

Introduction

Members of the family Tetrigidae are distributed all over the world (Hancock 1907), in almost all climatic zones except deserts and regional New Zealand (Rehn 1952, Tumbrinck 2014). Pygmy grasshoppers usually live close to water, decomposing soil and leaf litter (Hancock 1902). They are more active in warm temperatures and are extremely difficult to find because they move very slowly in the substrate (Ragge 1965). Currently, the family includes about 1900 species within about 280 genera within eight subfamilies Batrachideinae Bolívar, 1887, Cladonotinae Bolívar, 1887, Discotettiginae Hancock, 1907, Lophotettiginae Hancock, 1909, Metrodorinae Bolívar, 1887, Scelimeninae Bolívar, 1887, Tetriginae Rambur, 1838 and Tripetalocerinae Bolívar, 1887 (Cigliano et al. 2017).

The subfamily Metrodorinae is not a monophyletic, but polyphyletic group established for practical identification (Pavón-Gozalo et al. 2012). The subfamily was erected by Bolivar in 1887 with the following diagnostic characters: lateral lobes of the pronotum directed sidewards (in rare cases downwards, similarly to Tetriginae), obliquely truncated behind and very rarely bearing acute spines (similar to Scelimeninae). In 2015 Cadena-Castañeda and Cardona established the tribe Miriatrini to gather all the genera with prolonged fastigium of the vertex within the subfamily Metrodorinae. The tribe included two Neotropical genera *Metopomystrum* Günther, 1939 (five species) and *Miriatra* Bolívar, 1906 (four species), and nine more genera from other biogeographic regions, namely *Corystotettix* Günther, 1939 (Indonesia, one species); *Indomiriatra* Tinkham, 1939 (India, one species); *Procytettix* Bolívar, 1912 (Indian Ocean Islands, four species); *Rhynchotettix* Hancock, 1907 (Madagascar, two species); *Rhopalotettix* Hancock, 1910 (Asia and China, nine species); *Rostella* Hancock, 1913 (Asia, two species); *Spadotettix* Hancock, 1910 (India, Sri Lanka, China and Asia, five species); *Thibron* Rehn, 1939 (Africa, five species) and *Thyrsus* Bolívar, 1887 (Fiji and New Guinea, two species). The following characters are included in the Miriatrini diagnosis: long face; elevated vertex, exceeding length of scape and pedicel; ovoid eyes (in lateral view); narrow frontal costa with base connected to fastigium; pronotum dorsally flattened and elongated, as long as alae, lateral lobes of pronotum not expanded or with lateral spines (Cadena-Castañeda and Cardona 2015).

The subfamily Cleostratinae was established by Bolívar in 1887 as 'sectio Cleostratae' for a single genus *Cleostratus* Stål, 1877, unique among Tetrigidae in having antennal grooves and the median ocellus placed between the compound eyes and an extremely produced frons. Recently, Storozhenko (2016) transformed the subfamily Cleostratinae into the tribe Cleostratini and placed it within Metrodorinae subfamily. Storozhenko (2016) regards Miriatrini synonymous with Cleostratini. The tribe Cleostratini *sensu* Storozhenko now gathers the following genera: (1) *Apteromystrum* Storozhenko, 2016 (established for wingless *Metopomystrum*), (2) *Cleostratus*, (3) *Halmahera* Storozhenko, 2016, (4) *Indomiriatra*, (5) *Metopomystrum*, (6) *Miriatra*, (7) *Miriatroides* Zheng & Jiang, 2002, (8) *Procytettix*, (9) *Pseudomitraria* Hancock, 1907, (10) *Rhopalina* Tinkham (= *Corystotettix*), 1939, (11) *Rhopalotettix*, (12) *Rhynchotettix*, (13) *Rostella*, (14) *Spadotettix*, (15) *Thyrsus*, and (16) *Uvarovithyrsus* Storozhenko, 2016 (established for *Thyrsus* from New Guinea). All the genera are grouped together on the basis of a single character: presence of a horn-like structure on the head (frons or fastigium of vertex well developed and projected into long or relatively short protuberance directed forwards or upwards).

The genus of pygmy unicorns *Metopomystrum* Günther, 1939 (Günther 1939, pp. 270) is a South American genus that includes five species if old taxonomy is followed (e.g., Günther 1939; Cadena-Castañeda and Cardona 2015), namely (1) *M. amazoniensis* Cadena-Castañeda and Cardona, 2015; (2) *M. brevifastigiata* Cadena-Castañeda and Cardona, 2015; (3) *M. lilianae* Cadena-Castañeda and Cardona, 2015; (4) *M. pehlkei* Günther, 1939 and (5) *M. apterum* Günther, 1939. Storozhenko (2016) divided the genus into two genera, one consisting of winged species: *Metopomystrum* including *M. pehlkei* and *M. lilianae* and the other of wingless species: *Apteromystrum* including *A. amazoniensis* (Cadena-Castañeda and Cardona, 2015), *A. brevifastigiata* (Cadena-Castañeda and Cardona, 2015) and *A. apterum* (Günther, 1939).

Our aims are (1) to describe a new species of pygmy unicorn from Atlantic Forest in the state of Alagoas, Brazil, by providing distribution data, morphological characterization and an identification key for species of the genus, (2) to test if there are relevant differences between *Metopomystrum* and *Apteromystrum* regardless of the presence of wings and (3) to discuss taxonomic and evolutionary aspects of Cleostratinae, Cleostratini, and Miriatrini.

Materials and methods

Sampling and study area. The specimen of the new species of pygmy unicorn was collected by the "Biota de Orthoptera do Brasil" research group, 21–23 January 2013 at the Estação Serra do Ouro, municipality of Murici (state of Alagoas, Brazil) (coordinates 9°14.54'S, 35°50.2'W), with a pitfall trap containing ethanol fuel killing solution.

Microscopy and photography. External morphological characteristics were examined using a Zeiss Stemi 2000 stereomicroscope and photographed with Zeiss Stereo Discovery V20 stereomicroscope. Photographs were taken with the multidimensional acquisition function with AXIO VISION software, which allows capturing a series of pictures at different focal planes. The resulting images were then combined into a single picture using the Extended Focus Z function. The image plates were prepared in image editing software. Photographs of lateral and dorsal view of the holotype were taken, as well as more detailed photographs of important morphological characters (antennal segments, frontal costa, fastigium, vertex, maxillary palp, lateral lobes of the

Figure 1. Distribution map of *Metopomystrum* with *Miriatra brevifastigiata* comb. n., before Storozhenko (2016).

pronotum, sternomentum, abdomen (lateral and ventral profile), forelegs, hind femur, supranal plate, cerci, and subgenital plate.

Terminology. Morphological terminology follows Devriese (1996) and Tumbrinck (2014). Measurements and character description are based on Tumbrinck (2014).

Distribution map and depository of type specimen. Distribution map (Fig. 1) was produced with all available distribution records of the species of *Metopomystrum* (before Storozhenko, 2016). Geographical coordinates of localities were estimated using the information available in the literature (Table 1). The holotype of the new species is deposited in the Museu Nacional da Universidade Federal do Rio de Janeiro (**MNRJ**).

Table 1. Distribution data for hitherto described species of the genus *Metopomystrum*.

Species	Type series (holotype sex, locality, depository)	References
Metopomystrum amazoniensis comb. resurr.	1♀, Colombia: Amazonas, PNN Amacayacu (Universidad Distrital Francisco José de Caldas, Colección de Entomología y Aracnología, Bogota, Colombia)	Cadena-Castañeda and Cardona (2015)
Metopomystrum apterum comb. resurr.	1♂, Brazil Northeast: Bahia, Freire* (Museum für Naturkunde, Berlin, Germany)	Günther (1939)
Miriatra brevifastigiata comb. n.	1♂ (nymph), Colombia: Antioquia, Envigado (Universidad Distrital Francisco José de Caldas, Colección de Entomología y Aracnología, Bogota, Colombia)	Cadena-Castañeda and Cardona (2015)
Metopomystrum lilianae	1♂, Colombia, Colombia: Santander, Puerto Parra, Campo Capote, Borojó (Universidad Distrital Francisco José de Caldas, Colección de Entomología y Aracnología, Bogotá, Colombia)	
Metopomystrum pehlkei	1♂ Colombia: Tolima, Hacienda Pehlke, Städtisches Museum Stettin, Szczecin, Poland	

* We could not find any locality with this name in the state of Bahia (Brazil).

Results

Taxonomic comment on *Metopomystrum brevifastigiata*

The species *Metopomystrum brevifastigiata* Cadena-Castañeda and Cardona, 2015 is not member of *Metopomystrum* nor *Apteromystrum*, but its holotype represents a male nymph of *Miriatra* sp. The holotype of *M. brevifastigiata* lacks antegenicular teeth on the hind femora which implies that it is not an adult animal. Head and pronotal morphology is also rather different from *Metopomystrum* and *Apteromystrum* species and represents a typical set of characters defining *Miriatra*. Thus, the new combination *Miriatra brevifastigiata* (Cadena-Castañeda and Cardona, 2015) comb. n. should be used when referring to this specimen. This species is very close to *Miriatra producta* (Bolívar, 1887) and the differences should be checked when adults will be found.

Re-evaluation of diagnostic characters separating *Metopomystrum* and *Apteromystrum*

Storozhenko (2016) established the genus *Apteromystrum* and separated it from *Metopomystrum* on the basis of lack of the flying organs. Diagnosis is not exactly stated in the descriptive paper, but should be derived from the key. Thus, here we briefly compare main features of *Metopomystrum* and *Apteromystrum*, including characters of a new species that should be placed within *Apteromystrum* after Storozhenko's (2016) division into a winged (*Metopomystrum*) and an apterous group (*Apteromystrum*). From Storozhenko (2016) the diagnostic features of those genera are (after combination of characters from the key): ***Metopomystrum*** (after Storozhenko 2016, every character is shortened with M and number for discussion): (M1) antennal grooves situated in the level of the lower margin of the compound eyes or slightly above it; (M2) frontal ridge in lateral view with weak excision between the compound eyes;

(M3) median ocellus situated distinctly below the lower margin of the compound eyes; (M4) fastigium of the vertex long and produced forwards with pointed, triangular or broadly rounded apex, its length equal or greater than the length of an eye; (M5) median carina of the vertex absent, or if present weak; (M6, corresponds to A1) ventral and tegminal sinuses on the paranota well developed, tegmina and wings visible, wings reaching the apex of the posterior process of the pronotum; (M7) lower side of lateral lobes of the pronotum in dorsal view without spine; (M8) fore and mid femora without lobes on upper margin and (M9) ventral margins of femora straight or slightly undulated. *Apteromystrum* (after Storozhenko, every character is shortened with A and number for discussion): (A1, corresponds to M6) paranota only with ventral sinus, lacking tegminal sinus, tegmina and wings absent or not visible; (A2) fastigium of the vertex with continuous lateral margins; (A3, corresponds to M5) fastigium lacking median carina.

It is evident that comparison of *Metopomystrum* and the new genus *Apteromystrum* in Storozhenko (2016) is not completely satisfactory. For most of the diagnostic characters of *Metopomystrum* (M1, M2, M3, M4, M7, M8, M9) there is no comparison with corresponding characters of *Apteromystrum* and there are only three *Apteromystrum* characters, which is not satisfactory as generic diagnosis, because the main diagnostic character for *Apteromystrum* is the lack of visible flight organs (A1 contrary to M6), while A3 is the same as M5 and for A2 there is no comparison with *Metopomystrum*. Concerning diagnostic characters, there are no significant differences in morphology, except for lack of wings in *Apteromystrum*. However, apterous *A. amazoniensis* morphologically looks more similar to biogeographically closer *M. pehlkei* and *M. lilianae* than to *A. muriciense* Silva & Skejo, sp. n. and *A. apterum* from Brazil. Thus, we do not regard the division in two genera necessary but regard *Apteromystrum* Storozhenko, 2016, syn. n. synonymous with *Metopomystrum*. Here we provide a redescription and diagnosis of the genus.

Genus *Metopomystrum* Günther, 1939

= *Apteromystrum* Storozhenko, 2016, syn. n.

Type species. *Metopomystrum pehlkei* Günther, 1939 by original designation.

Composition and distribution. Five species, all in northern part of South America (Brazil, Colombia), namely (1) *M. amazoniensis* (Colombia: Amazonas), (2) *M. apterum* (Brazil: Bahia), (3) *M. lilianae* (Colombia: Santander), (4) *M. muriciense* Silva & Skejo, sp. n. (Brazil: Alagoas), and (5) *M. pehlkei* (Colombia: Tolima).

Revised generic description. *Head.* Frontal costa bifurcation situated above the paired lateral ocelli, between the compound eyes, so the frontal costa is long and evident before bifurcation, scutellum narrower than scapus, antennal grooves situated at the level of the lower margins of the compound eyes, paired lateral ocelli situated between the compound eyes, head and eyes exserted above pronotum, eyes protruding, so the vertex is not visible in lateral view, antennae 15-segmented, filiform, with cylindrical segments and smooth margins, fastigium narrower than the compound eyes, lateral carinae of the vertex continuous, not elevated, median carina of the vertex very weak, almost absent, anterior margin of the vertex rounded or acute, fastigium of the vertex projecting forwards and forming a horn longer than combined length of a compound eye and frontal costa above its bifurcation, dorsum of the horn with deep depression formed of joined fossulae, frontal ridge in lateral view with weak excision between the compound eyes.

Pronotum. slender in appearance, anterior margin truncated, prozonal carinae present, parallel or slightly diverging, extralateral carinae indistinct, median carina continuous from the anterior margin to the posterior apex, pronotal projections lacking, humeral angle wide, obliquely rounded, interhumeral carinae indistinct, interscapular area in winged species narrow with parallel margins, in wingless species as wide as mid femur, lateral area wider in wingless species, humero-apical, humeral and lateral carinae continuous, not armed or tuberculated, paranota triangular, lateral lobes of the pronotum directed slightly sidewards, with rounded apex lacking ventrolateral spine, dorsum of pronotum between the carinae smooth, pronotal apex truncated or acute.

Legs. Fore and mid femora not significantly compressed, fore femora with straight to slightly undulated dorsal and ventral margins, not armed with teeth or spines, mid femora not compressed, carinated above, with straight to slightly undulated dorsal and more undulated ventral margins, hind femora with smooth dorsal and ventral margins, dorsal margin with genicular and antigenicular teeth in hind knee, transverse ridges in the external surface well visible, not armed with lappets or spines, hind tibiae and tarsi not flattened or widened.

Revised generic diagnosis. From other genera previously assigned to Cleostratini or Miriatrini, and from all the South American Metrodorinae genera (*Allotettix* Hancock, 1899; *Amorphopus* Serville, 1838; *Chiriquia* Morse, 1900; *Cota* Bolívar, 1887; *Cotys* Bolívar, 1887; *Crimisus* Bolívar, 1887; *Eomorphopus* Hancock, 1900; *Hancockiella* Cadena-Castañeda & Cardona, 2015; *Metrodora* Bolívar, 1887; *Miriatra* Bolívar, 1906; *Otumba* Morse, 1900; *Platythorus* Morse, 1900; *Plesiotettix* Hancock, 1907; *Scabrotettix* Hancock, 1907 and *Trigonofemora* Hancock, 1906). The genus *Metopomystrum* can be separated by the following set of characters: head exserted above the pronotum, frontal costa long above the bifurcation, antennal grooves situated at the level of the lower margins of the compound eyes, antennae 15-segmented, filiform, paired lateral ocelli situated between the compound eyes, median carina of the vertex weak, indistinct, not projecting forwards and not compressed, fastigium of the vertex with deep depression, lateral carinae of the vertex continuous, pronotum flat, without projections and protuberances, lateral pronotal lobes directed sidewards, having rounded apices, femora without teeth or lappets, fore and mid femora not compressed and flattened.

New species description

Metopomystrum muriciense Silva & Skejo, sp. n.

http://zoobank.org/2415AEB8-097F-48C9-8064-7311E629BDCF
Figures 1–3

Specimen. Holotype 1♂, in alcohol. Original label: "Brasil, Alagoas, Murici, Estação Serra do Ouro (9°14.54'S, 35°50.2'W), 21–23/i/2013. C. Sperber e equipe leg." "[licença Sisbio n° 37717]" (MNRJ). Conservation status: left antenna broken.

Type locality. Brazil: Alagoas state, municipality of Murici, Estação Serra do Ouro, the holotype was caught in forest leaf litter [coordinates 9°14.54'S, 35°50.2'W].

Etymology. The species name refers to the municipality of Murici.

Diagnosis. This species can be distinguished from other species of *Metopomystrum* by the following set of characters: (i) long and acute fastigium, directed forwards, slightly upwards in its apex, (ii) forehead, genae and posthumeral spots in the pronotum yellowish, (iii) tegmina, alae and tegminal sinus absent, (iv) lateral lobes of the pronotum directed slightly sidewards, with rounded apex and yellowish band, (v) sternomentum necklace-shaped, brown with yellowish spots.

Comparative notes. The species can easily be separated from winged Colombian species (*M. lilianae* and *M. pehlkei*) by the horn morphology, fastigium having a rounded anterior margin in those species, while it is acute in *M. muriciense* Silva & Skejo, sp. n., and it is directed upwards in those species, while forwards in *M. muriciense* Silva & Skejo, sp. n. *Metopomystrum lilianae* and *M. pehlkei* are winged species, with visible tegmina, narrower than the maximum width of the mid femora, and tegminal sinus, hence narrow infrascapular area which is wide and evident in apterous *M. muriciense* Silva & Skejo, sp. n. From the apterous Colombian species *M. amazoniensis*, the new species can be separated by the straight horn, not directed upwards as in *M. amazoniensis*. However, the two species only share morphology of the anterior margin, laterally vertex being narrower in *M. muriciense* Silva & Skejo, sp. n. than in *M. amazoniensis*. The occipital area in *M. muriciense* Silva & Skejo, sp. n. is much longer than in Colombian species of the genus. The species is morphologically most similar to *M. apterum*, also from Brazil, with which it shares numerous morphological features, differing however in horn (projection of the fastigium of the vertex) direction-forwards and slightly upwards in *M. muriciense* Silva & Skejo, sp. n., while slightly downwards in *M. apterum*. In *M. muriciense* Silva & Skejo, sp. n. the vertex is narrower and more acute than in *M. apterum*.

Holotype description. ***Head.*** In lateral view (Figs 2C, 3A): occipital area elongated and granulated, head and compound eye insert exerted above the pronotal disc; vertex is not visible; fastigium of vertex and frontal carina forming long triangular horn with acute apex that is as long as the compound eye measured from its most frontal point to the apex; frontal carina not projecting; antennal groove situated slightly below the compound eye, almost at the level of its lower margin; palpi compressed, segments enlarging towards apex. In frontal view (Fig. 2A): frontal costa above the bifurcation long; frontal costa bifurcation placed between the compound eyes; scutellum very narrow; scapus

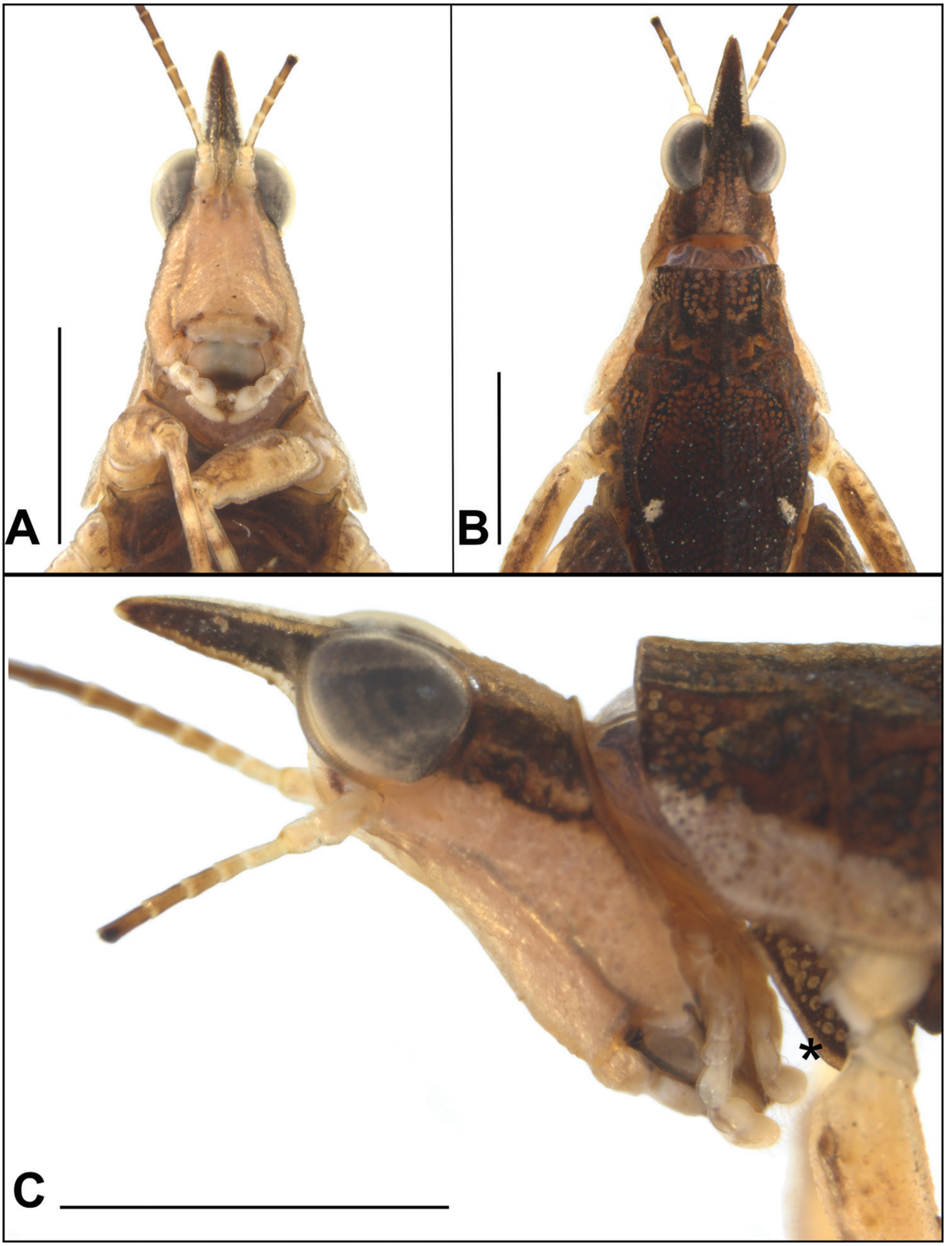

Figure 2. *Metopomystrum muriciense* Silva & Skejo, sp. n.: **A** Male holotype, head and portion of sternum, frontal view **B** head and portion of pronotum, dorsal view **C** head and portion of pronotum, lateral view (* sternomentum). Scale bars: 2.0 mm.

two times as wide as scutellum; antennae filiform with 15 antennomeres, segments elongated, cylindrical with smooth margins, paired lateral ocelli situated between the compound eyes, slightly below the frontal costa bifurcation; median ocellus placed in

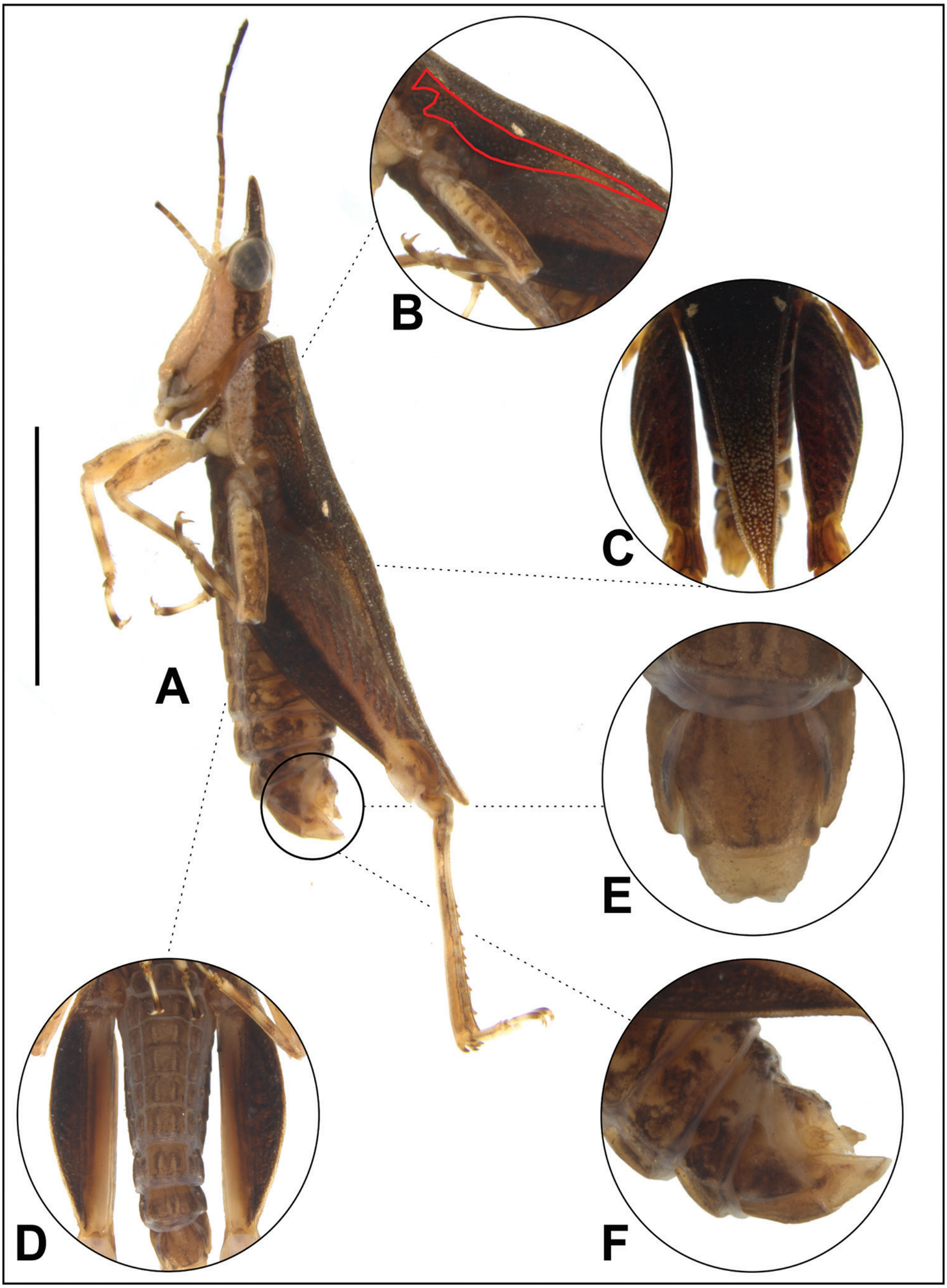

Figure 3. *Metopomystrum muriciense* Silva & Skejo, sp. n.: **A** Male holotype, habitus, lateral view **B** pronotum, lateral view, with infrascapular area marked in red lines **C** distal portion of pronotum with yellowish posthumeral spots and pronotum tip with serrate edge and many yellowish spots, dorsal view **D** abdomen and hind femur, ventral view **E** subgenital plate, dorsal view **F** terminalia, lateral view. Scale bar: 5.0 mm.

the end of facial carinae, in the place where frontal costa shallowly continues towards the clypeal triangle, of which carinae are also weak and not prominent, in the widest part; head slightly wider than the width between the lateral margins of the compound eyes. In dorsal view (Fig. 2B): vertex between the eyes as wide as a compound eye's horizontal diameter; fastigium of the vertex triangular, with acute apex; median carina of the vertex inconspicuous; fastigium lowest in the part of median carina, forming depression; occipital area 2× shorter than a compound eye's vertical diameter and granulated. *Coloration* (Figs 2A–C, 3A): fastigium of the vertex and vertex between the compound eyes dark brown; lateral area between frontal costa and lateral carinae of the vertex dark brown as well; median part of occipital area yellowish, with dark ornamentation; behind the eyes dark brown band with weaker pale brown and yellowish band inside; frons, clypeal triangle and gena pale yellowish; palpi pale; first four antennomeres almost white.

Pronotum. Brachypronotal (because of lack of wings it can be also regarded nanopronotal, organs of flight not visible), reaching abdominal apex. In lateral view (Figs 2C, 3A–B): median carina slightly undulated; prozonal carina visible, short, extralateral carina inconspicuous, visible as a few fine tubercles; ventral sinus absent, covered with infrascapular area; sulci between prozonal and humero-apical carina deep; paranota smooth, with few pits and tubercles, triangularly shaped (in typical way for non-Batrachideinae tetrigids); lateral lobe directed sidewards and truncated in apex; humero-apical carina connected to external lateral carina, which is parallel to median carina; infrascapular area wide, almost as wide as mid femur, with numerous shallow depressions (places where the chitinous layer is thinner, well visible by changing light under stereomicroscope); width of the infrascapular area decreasing towards apex; infrascapular area connected to narrow lateral area; internal lateral carina parallel to external lateral carina; apex of the pronotum directed upwards. In frontal view (Fig. 2A): shoulders not projected, lateral pronotal lobes directed downwards and sidewards. In dorsal view (Figs 2B, 3C): dorsum rich in fine granules, tubercles and small pits (shallow depressions in chitinous layer, look like holes, light permeable); anterior margin of the pronotum truncated, slightly inverted, prozonal carinae short, visible; angle between humero-apical and external lateral carinae obtusely rounded; median carina not strongly elevated, continuous; interhumeral carina indistinct; small posthumeral spots present; pronotum suddenly narrowed in the apex, its apex acute; lateral lobes with weak triangular ventrolateral projection with bluntly truncated apex, directed outwards and backwards. *Coloration*: dorsum brown, holes and granules being pale when enlightened; distal part of the disc, around apex, with numerous pale spots; ventral third of paranota with pale yellowish band; two posthumeral yellowish spots present, left rounded, while right triangular, smaller than observed in other Tetrigidae species.

Wings. Flightless species, tegmina and wing not visible, reduced and covered by infrascapular area of pronotum, not functional. (Note: to check if wings are present pronotum needs to be broken. We did not want to break the pronotum since there is only one specimen, the holotype). *Sternomentum* (Fig. 2C) [= modified prothoracic sternum]. Sternomentum collar-like, necklace shaped, well visible in lateral and ventral view, brown in color, ornamented with numerous yellowish spots of the same shape as pits on pronotal surface.

Legs (Figs 2A–B, 3A–D). *Fore legs:* fore femur approximately rounded in cross-section; dorsal margin carinated, dorsal carina made of fine tubercles, slightly undulated; ventral carina made of fine tubercles too, almost straight; fore femur widened in medial part, narrowed towards proximal and distal connection; distal part of the dorsal margin bearing a blunt tooth; fore tibia robust, slightly longer than fore femur; distal third of the inner margin equipped with four pairs of spines; proximal tarsal segment short, with three rounded pulvilli on its ventral surface; distal tarsal segment longer than the proximal, at its apex with two claws. *Mid legs:* femur with distinctly carinated dorsal and ventral margins; dorsal and ventral carinae of the mid femur visible in lateral view, not very prominent; dorsal and ventral margins finely tuberculated, slightly undulated to almost straight; mid tibia slightly shorter than the mid femur, robust, with small spines on its inner margin; proximal tarsal segment short, with angular pulvilli on ventral surface; distal segment four times as long as proximal, at its apex with claws. *Hind legs*: dorsal and ventral margins of hind femora finely granulated, without lappets or projections; genicular and antigenicular teeth small; clearly visible hind femur elongated and reaching slightly below the pronotal apex when extended; external surface finely granulate, with seven transverse ridges in its external surface (or more if short are counted towards the knee); dorso-external and ventro-external carinae of the hind femur without tubercles or projections, smooth, dorsal margin in dorsal view straight; ventral margin and inner ventral margin of the hind femora straight; tibial sulcus (= the depression on the ventral side of the hind femora in which the tibiae are put when the grasshopper is walking) half as wide as hind femora in ventral view; hind tibiae robust, shorter than hind femora with dorsal surface concave, ventral convex, dorsal surface with two rows of spines from its middle to the connection tarsus; inner margin with nine visible spines, outer with seven, on connection of tibia and tarsus there are 6 spines, three on each side; proximal segment of the hind tarsus with acute pulvilli; mid segment short; distal segment as long as proximal, having two claws in its apex. *Coloration*: fore femur yellowish, with small amount of darker areas in its dorsal part; fore tibia of the same colour as fore femur, with two dark rings, the distal one being broader and darker; proximal segment of fore tarsus dark; one half of the distal segment pale, the other part dark; claws yellowish with dark apex. Mid femur yellowish, with dorsal and distal part being dark and having four dark patches in external surface; mid tibia yellowish, with two dark rings, the distal one being broader and darker; proximal segment of the mid tarsus pale brown; distal segment with two thirds yellowish, apical third dark, claws yellowish with dark apex; ventral external area of the hind femur very dark; median external area lighter brown; dorsal area somewhat darker than median, but lighter than ventral; hind knee yellowish; hind tibia yellowish with brownish patches, not forming dark rings; proximal and mid segment of hind tarsi yellowish, apical part of the distal segment darker, rest of it yellowish; claws light with dark apex.

Abdomen (Figs 3A, 3D–F). Subgenital plate bilobate, with deep triangular incision; each lobe triangular with blunt apex; in lateral view subgenital plate with apex directed upwards; cerci short, robust, their basal part swollen and hirsute. *Coloration*: visible parts of dorsal sternites dark brown, similar to pronotum; upper lateral parts of the sternites light yellowish, from the middle to the connection with sternites ornamented with dark brown and yellowish patches; epiproct and cerci yellowish; subgenital plate light brown; sternites light brown and each of them ornamented with a pair of thin pale lines, having darker margins outside.

Female. Unknown.

Measuremens (all in mm). Body length from the tip of the fastigium projection to the end of the abdomen 10.8; fastigium length 1.03; vertical eye diameter 0.96; horizontal eye diameter 0.67; vertex width 0.41; pronotum length 8.12; pronotum lateral lobes maximal width 1.86; infrascapular area length 5.54; fore femur length 1.61; fore femur width 0.62; fore tibia length 1.63; mid femur length 1.99; mid femur width 0.59; mid tibia length 1.48; hind femur length 5.11; hind femur maximal width 1.67; hind tibia length 4.08; proximal hind tarsal segment length 0.51; mid hind tarsal segment length 0.04; distal hind tarsal segment length 0.50.

Key to the species of *Metopomystrum*

1 Fastigium of the vertex and frontal costa forming horn with rounded apex in dorsal view, in frontal and lateral view horn projecting above the eyes for more than one half of a compound eye height. Tegmina and wings visible and surpassing abdominal apex. [Colombia]..**2**

– Fastigium of the vertex and frontal costa forming horn with acute apex in dorsal view, in frontal and lateral view horn projecting above the eyes for less than one half of a compound eye height. Tegmina and wings not visible, infrascapular area visible in their place. **3**

2 Horn directed forwards and upwards at about 30° in relation to the vertex between the eyes and pronotal disc. Tegmina and pronotum unicoloured [Colombia: Tolima] .... ***Metopomystrum pehlkei* Günther, 1939**

– Horn directed strongly upwards at about 45° in relation to the vertex between the eyes and pronotal discus. Ventral margin of tegmina and dorsal margin of pronotum yellowish. [Colombia: Santander] ....***Metopomystrum lilianae* Cadena-Castañeda & Cardona, 2015**

3 Horn directed upwards, elevated in relation to pronotal disc for about one third of a compound eye height, in lateral view horn wide and with rounded apex, scutellum two times narrower than scapus, eyes in lateral view triangular. [Colombia: Amazonas].. ***Metopomystrum amazoniensis* Cadena-Castañeda & Cardona, 2015, comb. resurr.**

– Horn directed almost completely forwards, only slightly elevated above a compound eye, in lateral view horn thin and with triangular apex, scutellum three times narrower than scapus, eyes in lateral view rounded. [Brazil] **4**

4 Horn directed forwards, slightly upwards, vertex narrow and acute in dorsal and lateral view............. ***Metopomystrum muriciense* Silva & Skejo, sp. n.**

– Horn directed forwards, slightly downwards in its apex, vertex wider and more rounded in dorsal and lateral view.. ***Metopomystrum apterum* Günther, 1939 comb. resurr.**

Discussion

Taxonomic and biogeographic considerations on *Metopomystrum* species

Storozhenko's (2016) division of the genus into two genera is not advisable, because it is based mostly on presence or absence of tegmina and wings, so *Apteromystrum* syn. n. is regarded synonymous with *Metopomystrum* (*Metopomystrum apterum* comb. resurr. and *Metopomystrum amazoniensis* comb. resurr.). Holotype of *Miriatra brevifastigiata* comb. n. is likely a nymph of *Miriatra* close to *M. producta* (see Results-Taxonomic comment on *Metopomystrum brevifastigiata*).

Günther (1939) stated that *Metopomystrum* was similar to *Miriatra* Bolivar, 1906. We cannot confirm this statement since *Metopomystrum* is very different from *Miriatra* in vertex, pronotum and leg morphology, of slender appearance with weak elevations of pronotal carinae, while *Miriatra* has robust, *Chiriquia*-like appearance, with strong and tuberculated carinae and strong lateral lobes of the pronotum. Frontal projection is wide in *Metopomystrum*, much more similar in form to that in *Procytettix* Bolívar, 1912; *Rhopalotettix* Hancock, 1910 and *Rhynchotettix* Hancock, 1907. *Miriatra* Bolívar, 1906 is unique in having highly laterally compressed median carina of the vertex that is connected to frontal carina, together forming a horn. In pronotal and leg morphology *Miriatra* is similar to members of *Metrodora* Bolívar, 1887, *Cota* Bolívar, 1887, *Chiriquia* Morse, 1900 and *Otumba* Morse, 1900.

Within Miriatrini and Cleostratini, *Metopomystrum* is the only genus comprising winged and wingless species. The problem of division of genera by the presence or lack of wings is widespread in Tetrigoidea taxonomy (e.g., Bolívar 1887, Storozhenko 2016; see *Procytettix* in Bolívar 1912 and Rehn 1937). The species with short pronotum exhibit stronger carination, undulation, and tuberculation of its surface in comparison to species with longer pronotum (e.g., Rehn 1937, Tumbrinck 2014).

Metopomystrum muriciense Silva & Skejo, sp. n. is the only known species of the genus that has small posthumeral spots. *Metopomystrum* species have very diverse coloration and probably colour varies within a species. A lot of Tetrigidae species are known to have huge colour pattern variation within and among populations (e.g., Nabours 1929). Variation is a result of numerous factors, including genetics, epigenetics (Karlsson et al. 2009), habitat selection and environmental change (Hochkirch et al. 2008, Forsman et al. 2011), mating (Caesar et al. 2007), temperature effects, camouflage and predator avoidance (Ahnesjö and Forsman 2006, Karlsson and Forsman 2010, Tsurui et al. 2010).

Information on habitat and distributions are lacking for the majority of species of the family Tetrigidae. *Metopomystrum* is not exception. This genus was erected by Günther (1939), who described two species (*M. pehlkei* from Colombia and *M. apterum* comb. resurr. from Bahia). After almost eight decades without records Cadena-Castañeda and Cardona 2015 described three new species for Colombia, of which two are currently assigned to *Metopomystrum* (*M. lilianae* and *M. amazoniensis* comb. resurr.). The genus is not well documented and remains poorly known, all the species being described from only a few available individuals, and the variability remaining completely undocumented. Here we reviewed critically diagnostic characters that unite the reported species and specimens into one taxonomic unit. Even with the new species described herein from Alagoas, knowledge on *Metopomystrum* remains scarce.

The genus has a large gap in the known distribution between Colombia and Brazil (Fig. 1). Serious studies are needed to assess the complete distribution of these tropical rainforest species, to study them and to protect them because pygmy unicorns exhibit rare and interesting morphological features not seen in other tetrigids. We are sure that more species of this genus exist, but they could not be documented yet due to limited zoological expeditions focusing on pygmy grasshopper collection in their distribution areas. On the other hand, many tetrigids species have been described from the gap area, by several different authors from several different collections (e.g., Serville 1838, Walker 1871, Bolívar 1887, Hancock 1907, Bruner 1910), from northern Brazil (Pará): *Amorphopus notabilis* Serville, 1838; *Metrodora gibbinotus* (Bruner, 1910); *Metrodora uniformis* (Bruner, 1910); *Otumba basalis* Bruner, 1910 and *Paurotarsus ruficornis* (Walker, 1871). From Guyana: *Eomorphopus granulatus* Hancock, 1907; *Otumba lobata* Hancock, 1907 and from Surinam *Otumba concinna* (Bolívar, 1887). This can imply that *Metopomystrum* species occur in not so accessible areas and that they are not among the common species of South America.

Taxonomic comments on genera previously included in Miriatrini and Cleostratini

The group proposed by Cadena-Castañeda and Cardona (2015) and the group proposed by Storozhenko (2016), unifying Miriatrini and *Cleostratus* into Cleostratini, are not evolutionary units, but artificial groups gathering numerous genera with various morphology of fastigium, head, pronotum, and legs, with the single 'shared' character being the presence of a horn. Here we provide a brief overview of the diversity of horn morphology within Tetrigidae in groups that developed a long fastigium, frontal costa, or scutellum independently.

Africa and islands of the Indian Ocean: members of *Rhynchotettix* Hancock, 1907 (Madagascar, Metrodorinae) is unique genus in having toothed lateral lobes of the pronotum, directed outwards and forwards. *Pseudomitraria* has the frontal carina with part of the scutellum forming the horn, in a very unusual way.

Asia and Islands of SE Asia, Wallacea, Papua, and Oceania: *Rostella* Hancock, 1913 (Asia, Metrodorinae) resembles *Pseudomitraria* and *Metopomystrum* in the way the horn is formed in lateral view. However, *Rostella,* contrary to *Metopomystrum*, has a wide scutellum and is in pronotal morphology related to Metrodorinae and Scelimeninae (not Scelimenini) of Asia, such as *Spadotettix* Hancock, 1910; *Indomiriatra* Tinkham, 1939 and *Eucriotettix* Hebard, 1930. *Spadotettix* (India, SE Asia, Metrodorinae) does not have a produced vertex, its length usually being less than half of the eye height, as in *Tetrix subulata* (Linnaeus, 1758), among others. Morphologically, *Spadotettix* is more similar to *Indomiriatra*, formerly assigned to *Spadotettix*. *Indomiriatra* (India, Metrodorinae) and *Spadotettix* have a more produced vertex and stronger angles of the lateral lobes of the pronotum. Both genera are similar to certain members of *Coptotettix* Bolívar, 1887 (Tetriginae) and *Criotettix* Bolívar, 1887 (Scelimeninae), in broken median carina (discontinuous, with flattened parts) of the pronotum and with species with or without laterally projecting lobes, varying even within populations of one species *Indomiriatra provertex* could be regarded as a large species of *Spadotettix*. *Thyrsus* Bolívar, 1887 (Oceania) shares with *Birmana* Brunner von Wattenwyl, 1893 (Myanmar) and *Clinophaestus* Storozhenko, 2013 (Thailand) (last two Tripetalocerinae, Clinophaestini) interesting morphological characters-nymphs of all these genera have flattened antennal segments, the number of antennal segments is eleven, apical ones are reduced, the preapical, medial and sometimes the basal antennomeres are widened, and their hind-femora are very robust. *Thyrsus* is not related to Miriatrini in any sense, probably neither to *Cleostratus*. Members of the genus *Cleostratus* Stål, 1877 are unique in having the frons projecting as a horn, and the bifurcation of the frontal costa being above the compound eyes. Therefore it is left as single genus in Cleostratini since no other species of Tetrigidae exhibit a similar way in which the frons is projecting. Thus, Cleostratini, even monotypic, represent a more logical taxon than to group it with *Miriatra*.

Rhopalotettix, Pseudomitraria and *Spadotettix* are good examples that it is possible to find high variability of vertex prolongation among species of the same genus. This character is present in other Tetrigidae groups, like *Clinotettix* Bey-Bienko, 1933 (Tetriginae), whose members have a longer vertex than members of *Spadotettix*. Rehn (1938) concluded from examination of *Pseudomitraria* and *Miriatra* that the elongation of the fastigium represents a parallel specialization. Taxonomic considerations from Storozhenko (2016) should be re-evaluated. The main advantage of Storozhenko's (2016) monograph on Cleostratini is the amount of drawings, photos and catalogued data on Tetrigidae with a horn, but the main disadvantage is erecting a tribe for such a group and synonymizing Cleostratinae. We leave only *Miriatra* in Miriatrini, while we leave only *Cleostratus* in Cleostratini. Other genera remain without tribal placement within Metrodorinae, because solely based on horn morphology (modified fastigium, fastigium and frontal costa, or frontal costa, or frons with scutellum), genera previously unified within Miriatrini are rather diverse. A comprehensive revision is needed with numerous characters (cladistic approach, where comparison is possible among numerous characters in matrix) to provide well-founded basis for taxonomic acts.

We conclude (1) that Cleostratini and Miriatrini stat. ressur. are not synonymous, because *Cleostratus* and *Miriatra* belong to morphologically and biogeographically different pygmy grasshopper groups, despite both of them having a horn, (2) that a prolonged horn occurs in different evolutionary groups of pygmy grasshoppers, and (3) that a prolonged horn is not an adequate character useful in Tetrigidae suprageneric taxonomy.

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RESEARCH ARTICLE

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First record of *Thecturota tenuissima* Casey from Canada (Coleoptera, Staphylinidae, Aleocharinae)

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Abstract

Thecturota tenuissima Casey, is reported for the first time from Canada, based on records from Ontario and Quebec. It was originally described from Rhode Island, USA, and no other records of this species in North America were published since that time. The specimens from Canada were captured by car netting. We provide here a redescription of this species and never before published images of habitus, tergite, and sternite VIII of both sexes, median lobe of aedeagus and spermatheca. The features distinguishing *T. tenuissima* from *T. capito* Casey (=*pusio* (Casey)), the only other species reported in Canada, are provided and illustrated.

Keywords

Canada, new record, *Thecturota*, Aleocharinae, Staphylinidae, Coleoptera

Introduction

Thecturota Casey, is a genus of the tribe Homalotini Heer, with 5 valid species in the Nearctic region (Fenyes 1920). Two species, *T. ruficollis* Casey and *T. subtilior* (Bernhauer), occur in southwestern USA, Arizona, southern California, and Nevada. The remaining three valid species, *T. capito* Casey, *T. demissa* Casey, *T. tenuissima* Casey, are reported from central, eastern, and southern USA (Rhode Island, New York, Iowa, Indiana, Virginia, and Texas), and eastern Canada. We have examined the type specimens of the three eastern species. The objective of this paper is to publish a new Canadian record of *T. tenuissima* with redescription and images of body and genital structures and to provide a key for identification of the Canadian species. It is important to note that the shape of the spermatheca is the best criterion for separating species of this genus.

Materials and methods

All specimens in this study were dissected to examine the genital structures. Extracted genital structures were dehydrated in absolute alcohol, mounted in Canada balsam on celluloid micro-slides, and pinned with the specimen from which they originated. Images of the entire body and the genital structures were taken using an image processing system (Nikon SMZ 1500 stereoscopic microscope; Nikon Digital Camera DXM 1200F, and Adobe Photoshop software).

Morphological terminology mainly follows that used by Seevers (1978). The ventral side of the median lobe of the aedeagus is considered to be the side of the bulbus containing the foramen mediale, the entrance of the ductus ejaculatorius, and the adjacent ventral side of the tubus of the median lobe with the internal sac and its structures (this part is referred to as the parameral side in some recent publications); the opposite side is referred to as the dorsal part.

Depository/institutional abbreviations

LFC	Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, R. Martineau Insectarium, Quebec City, Quebec, Canada.
TSC	Tim Struyve collection, Leuvensesteenweg. 187, 2800 Mechelen, Belgium.
USNM	United States National Museum, Washington, D.C, USA.

Systematic treatments

Genus *Thecturota* Casey, 1893

Figs 1–15

Casey 1893, 1911, Seevers 1978, Ashe 2001

Diagnosis. Body slender, narrow, linear, small, length 1.0–1.7 mm; pubescence on pronotum and elytra directed laterad; head subquadrate with angular posterior tempora, as long and at least as wide as pronotum; eyes shorter than length of temples;

antennomeres V-X strongly transverse and slightly incrassate apically, pronotum small, subquadrate or 1.2 times as wide as long, broadest subapically, pubescence directed anteriad and laterad from midline of disc; elytra short, at suture about as long as pronotum or slightly longer; abdomen subparallel. Male tergite VIII truncate apically; tubus of median lobe of aedeagus simple in form, its venter arcuate; internal sac structures inconspicuous; spermatheca small, capsule subspherical with small or without apical invagination, stem very short.

Key to Canadian species of *Thecturota*

1 Male tergite VIII nearly two times as wide as long (Fig.4); male sternite VIII about one fourth wider than long (Fig. 5); spermatheca with capsule pitcher-shaped with narrow apical invagination (Fig. 8) ..... ***Thecturota capito*** **Casey**

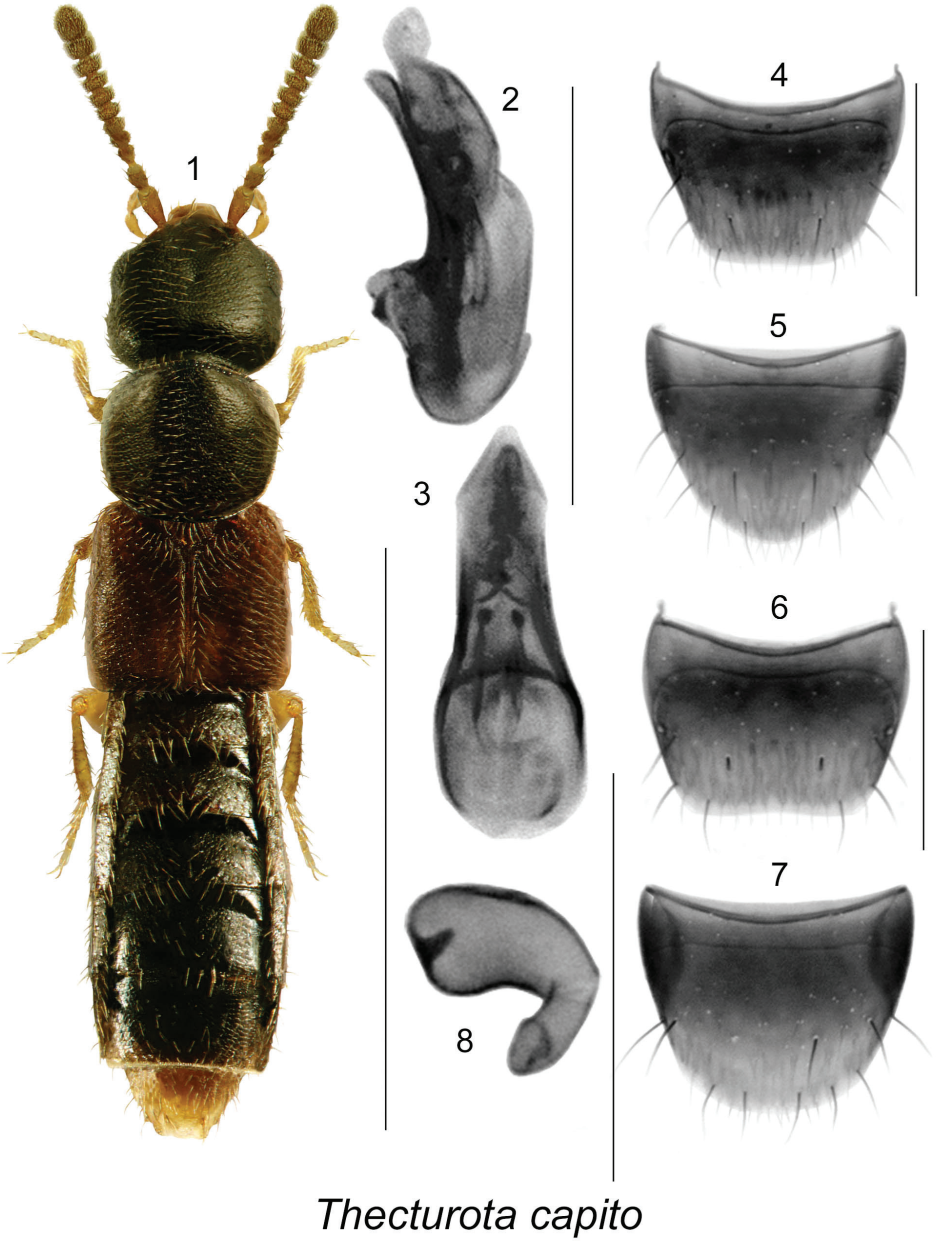
– Male tergite VIII nearly as wide as long (Fig. 11); male sternite VIII about as wide as long (Fig. 12; spermatheca with capsule subspherical lacking apical invagination (Fig.15) .... ***Thecturota tenuissima*** **Casey**

1. *Thecturota capito* Casey

Figs 1–8

Thecturota capito Casey, 1893: 358. Casey 1911, Fenyes 1920, Moore and Legner 1975, Seevers 1978, Brunke et al. 2012 (as *T. pusio* (Casey)).
Oligurota pusio Casey, 1893: 362. Brunke et al. 2012. Synonymized by Fenyes 1920.
Thecturota exigua Casey, 1894: 360. Synonymized by Fenyes 1920.
Thecturota histrio Casey, 1911: 210. Synonymized by Fenyes 1920.
Thecturota laticeps Casey, 1911: 208. Synonymized by Fenyes 1920.

Diagnosis. Body length 1.2–1.6 mm; body narrowly subparallel, linear, color variable: reddish brown with head and abdomen dark brown to piceous, or body piceous with reddish brown elytra, and yellowish-red legs, basal antennomeres and tip of abdomen; integument finely punctate; head subquadrate, larger than pronotum, with postocular area longer than diameter of eye, hind angles angular and rounded; antennomeres IV-X transverse and VI-X strongly transverse and about 3 times wider than long; pronotum broadest in apical third, narrow at base, pubescence directed laterad from midline of disc; elytra subparallel, at suture about as long as pronotum; abdomen subparallel, slightly broadening posterad. MALE: tergite VIII nearly two times as wide as long (Fig. 4); sternite VIII about one fourth wider than long (Fig. 5); median lobe of aedeagus with narrowly oval bulbus and subparallel tubus in dorsal view (Fig. 3); in lateral view tubus broadly arcuate ventrally, with apex narrow and rounded (Fig. 2). FEMALE: tergite VIII nearly two times as wide as long (Fig. 6); sternite VIII rounded apically (Fig. 7); spermatheca with large pitcher-shaped capsule and narrow apical invagination, stem very short (Fig. 8).



Figures 1–8. *Thecturota capito* Casey: **1** habitus in dorsal view **2** median lobe of aedeagus in lateral view **3** median lobe of aedeagus in dorsal view **4** male tergite VIII **5** male sternite VIII **6** female tergite VIII **7** female sternite VIII **8** spermatheca. Scale bars: 1 mm for habitus; 0.2 mm for remaining structures.

Distribution. Origin: Nearctic. **Canada**: **ON**. **USA**: IA, IN, TX, VA.

Collection and habitat data. Habitat: oak savanna from leaf, log, and grass litter. **Collecting period**: X. **Collecting method**: Berlese extraction of leaf, log, and grass litter. Live adults of this species were extremely slow-moving and the use of a Berlese funnel likely facilitated the capture of this minute beetle.

Comments. *Thecurota capito* Casey was recorded from Canada (ON) for the first time under a synonymic name *T. pusio* (Casey) by Brunke et al. (2012). Fenyes (1920) and Moore and Legner (1975) listed *T. pusio,* originally named as *Oligurota pusio* Casey 1893: 362, as a synonym of *T. capito* Casey 1893: 358. We overlooked this fact in Brunke et al. 2012, and now it is corrected. In the original description, Casey also mentioned specimens from AZ (Tucson).

2. *Thecurota tenuissima* Casey

Figs 9–15

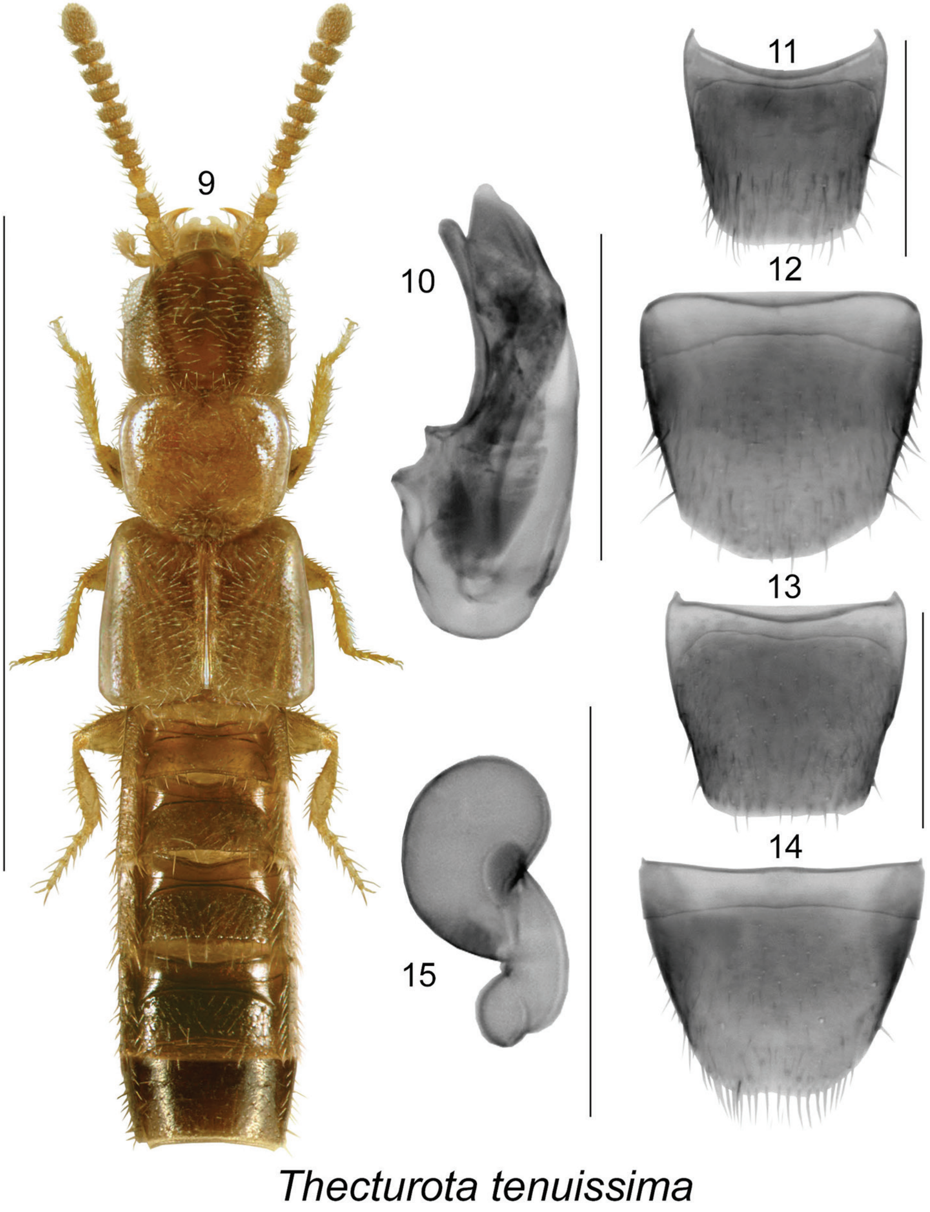
Thecurota tenuissima Casey, 1893: 358. Fenyes 1918, 1920, Moore and Legner 1975, Seevers 1978, Sikes 2004.

Diagnosis. Body length 1.5–1.7 mm; body narrowly subparallel, linear, yellowish brown with head, most of antennae, and apical part of abdomen dark brown to piceous, or body light brown with darker head and posterior abdomen or pronotum and elytra brown and remainder of the body dark brown to almost black; integument finely punctate; head subquadrate, larger than pronotum, with postocular area longer than diameter of eye, hind angles angular and rounded; antennomeres IV-X transverse and VI-X strongly transverse and about 2 times wider than long; pronotum broadest in apical third, narrow at base, pubescence directed laterad from midline of disc; elytra subparallel, at suture slightly longer than pronotum; abdomen subparallel, slightly broadening posterad. MALE: tergite VIII nearly as wide as long (Fig. 11); sternite VIII about as wide as long (Fig. 12); median lobe of aedeagus with tubus arcuate ventrally and narrow at apex in lateral view (Fig. 10). FEMALE: tergite VIII subquadrate (Fig. 13); sternite VIII rounded apically and in some specimens slightly emarginate medially (Fig. 14); spermatheca with subspherical capsule and without apical invagination, stem very short and sinuate (Fig. 15).

Distribution. Origin: Nearctic. **Canada**: **ON**, **QC**. **USA**: RI.

Collection and habitat data. Habitat: unspecified forests. **Collecting period**: VII. **Collecting method**: car netting.

New locality data. CANADA, **Quebec**: Oka, ~ 45.49°N, 74.01°W, 12.VII.2016, car netting, Tim Struyve (LFC, TSC) 1 male, 15 females; Saint-Joseph-du-Lac, ~ 45.53°N, 74.02°W, 11.VII.2016, car netting, Tim Struyve (LFC, TSC) 4 males, 1 female; Port Rowan, ~ 42.62°N, 80.53°W, car netting, Tim Struyve (LFC, TSC) 2 females. **Ontario**: Algonquin Provincial Park near Petawawa, ~ 45.87°N, 77.33°W, car netting, Tim Struyve (LFC, TSC) 1 male, 1 female.



Figures 9–16. *Thecturota tenuissima* Casey: **9** habitus in dorsal view **10** median lobe of aedeagus in lateral and dorsal view **11** male tergite VIII **12** male sternite VIII **13** female tergite VIII **14** female sternite VIII **15** spermatheca. Scale bars: 1 mm for habitus; 0.2 mm for remaining structures.

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Revision of *Hemiquedius* Casey (Staphylinidae, Staphylininae) and a review of beetles dependent on beavers and muskrats in North America

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Abstract

Based on newly discovered characters on the male genitalia, external morphology and an accumulation of ecological data, we revise the single member of the genus *Hemiquedius*. Two new species, *H. infinitus* Brunke & Smetana, **sp. n.** and *H. castoris* Brunke & Smetana, **sp. n.**, from eastern North America are described, and *H. ferox* (LeConte), restricted to peninsular Florida, is re-described. *Hemiquedius castoris* is strongly associated with the microhabitats provided by nest materials of the North American beaver and muskrat. A key to the three species of *Hemiquedius* is provided and diagnostic characters are illustrated. We also review the beetles known to be obligate associates of beavers and muskrats, and discuss the potential role of these keystone vertebrates in beetle evolution and distribution. Based on nest-associated beetles and their closest living relatives, beaver and muskrat lodges may extend distributions northward by moderating winters, promote sympatric speciation and act as refugia against extinction of lineages on a broader timescale. Further research into these potential impacts by ecologists and evolutionary biologists is encouraged.

Keywords

nidicoly, sympatric speciation, cryptic diversity, Nearctic, Staphylinini, Acylophorina

Introduction

The genus *Hemiquedius* (Fig. 1A) is endemic to North America and a member of the predaceous rove beetle subtribe Acylophorina (Staphylininae: Staphylinini) (Brunke et al. 2016). Currently, one widespread eastern species, *Hemiquedius ferox* (LeConte, 1878), is recognized that occurs from northern Ontario, south to eastern Texas, east to Florida and north to Nova Scotia (Smetana 1971a, 1978, 1990). It inhabits a wide variety of water-soaked decaying organic matter at the edges of forested and open wetlands and is consistently but sparingly collected by submerging this debris by 'treading' it under foot (see Smetana 1971a). Several specimens of *Hemiquedius* collected from beaver and muskrat houses were observed by Smetana (1971b) to differ from all others by their elytral setation but were not recognized as a separate species at that time due to limited material and a lack of other corroborating differences. Since then, an entire rove beetle assemblage has been discovered that is strongly associated with the nest materials of beaver and muskrat houses, including several species new to science (Campbell 1979, Hoebeke 1985, Smetana 1995). Most of these species were described relatively recently and were overlooked until beaver and muskrat nests were targeted for sampling.

Here we re-assess the taxonomic status of the ecologically specialized population of *Hemiquedius* and other putative species based on morphological characters and CO1 barcode data. Although ecosystem engineering by beavers is well known to positively impact populations of wetland fauna such as fish, birds, reptiles and invertebrates (Rosell et al. 2005), the promotion of invertebrate speciation by beavers is not well understood. Based on the diversity of lineages that have evolved specialized associations with beaver lodge-building activity, their impact on speciation may be significant and widespread. To facilitate future investigation of this phenomenon, we review the beetle species that appear to specialize on the microhabitat provided by beaver and muskrat houses.

Material and methods.

Specimens were examined from the following institutions:

BIO	Biodiversity Institute of Ontario, Guelph, Ontario, Canada (V. Levesque-Beaudin, J. deWaard)
CNC	Canadian National Collection of Insects Arachnids and Nematodes, Ontario, Canada
DEBU	University of Guelph Insect Collection, Ontario, Canada (S. Marshall)
MEM	Mississippi State University, Mississippi, U.S.A. (via S. Chatzimanolis, Chattanooga, Tennessee)
FMNH	Field Museum of Natural History, Illinois, U.S.A. (C. Maier, M. Thayer, A. Newton)
TAMU	Texas A&M University, Texas, U.S.A. (Karen Wright)

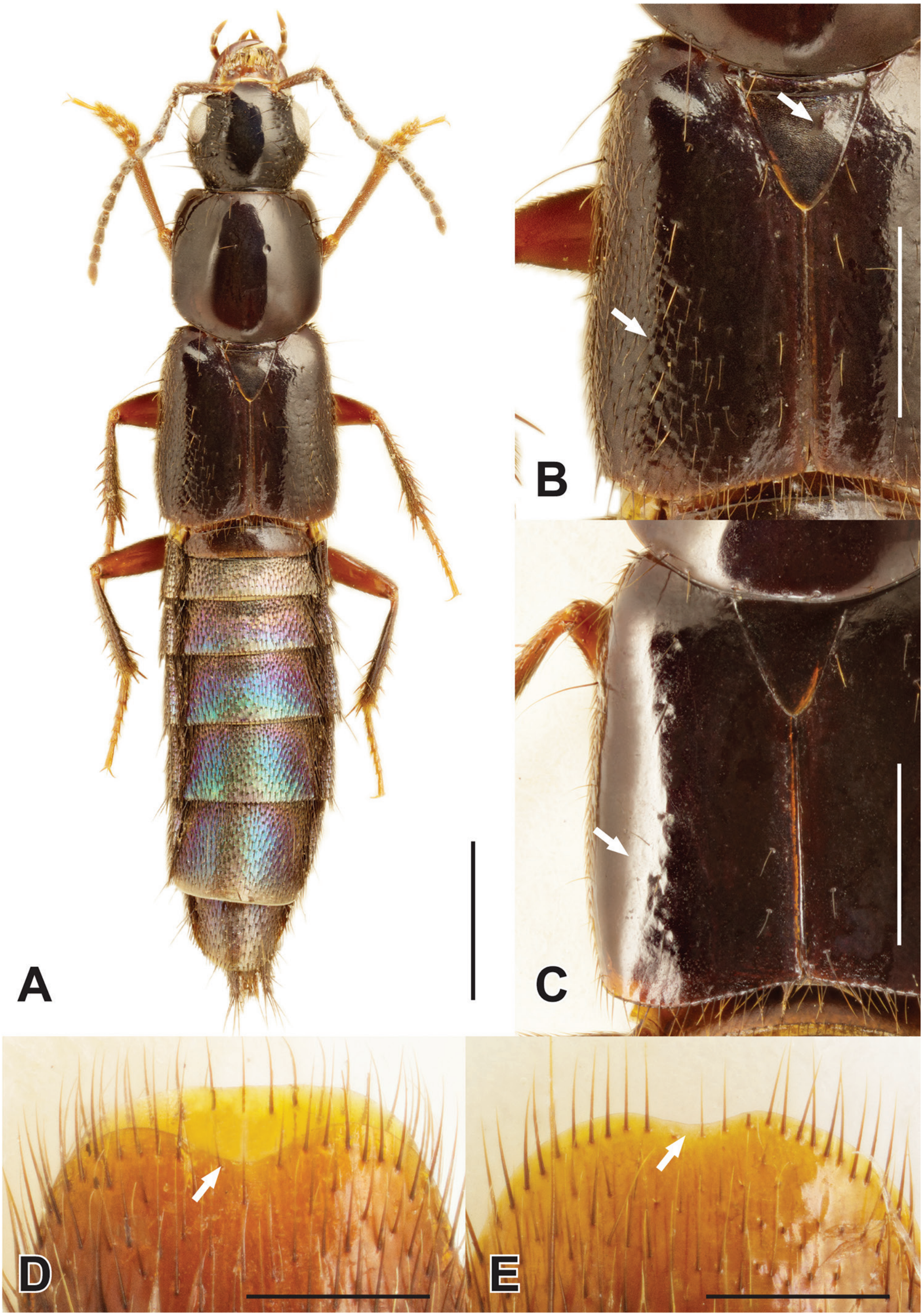

Figure 1. Habitus of *Hemiquedius castoris* Brunke and Smetana (**A**); *H. castoris*, elytra and scutellum (**B**); *H. infinitus* Brunke and Smetana, elytra and scutellum (**C**); *H. ferox* (Casey), male sternite VIII (**D**); *H. castoris*, male sternite VIII (**E**). Scale bars: 2 mm (**A**); 1 mm (**B–E**).

Microscopy, illustration, photography and mapping

All specimens were examined using a Nikon SMZ25 stereomicroscope. To allow for the routine dissection of the terminal abdominal segments (including the aedeagus), distilled water was applied directly to the tip of the abdomen using a fine paintbrush. As a precaution against DNA degradation, specimens examined in the present study were never subjected to high ambient humidity relaxing chambers or entirely submersed in water. Genitalia were washed with 70% alcohol and placed in glycerin for observation. Genitalia were placed in glycerin filled vials for long-term storage, which were pinned with their respective specimen.

Measurements were performed using the live measurement module in NIS Elements BR v4.5. Measurements were taken as listed below, but only proportional (HW/HL, PW/PL, EW/EL, ESut/PL, PW/HW) and forebody measurements were stated directly in descriptions due to variability in body size. Total body length is generally difficult to measure accurately in Staphylinidae due to the contractile nature of the abdomen. Abbreviations for measurements are as follows:

HL	Head Length, at middle, from the anterior margin of frons to the nuchal ridge.
HW	Head Width, the greatest width, including the eyes.
PL	Pronotum Length, at middle.
PW	Pronotum Width, greatest width.
EL	Elytral Length, greatest length taken from level of the anterior most large, lateral macroseta to apex of elytra. Its length approximates the length of the elytra not covered by the pronotum and therefore contributing to the forebody length.
EW	Elytral Width, greatest width.
ESut	Sutural Length, length of elytral suture.
Forebody	HL + PL + EL.

Line illustrations were performed in Adobe Illustrator CS6 based on photographs. Photomontage was accomplished using a motorized Nikon SMZ25 microscope and NIS Elements BR v4.5. Photos were processed in Adobe Photoshop CS6. Distribution maps were created using SimpleMappr (Shorthouse 2010). The graph of pronotum length versus width was created in Microsoft Excel and then modified in Adobe Illustrator. Regression lines were added in Excel but for qualitative purposes only.

Molecular data

Extraction, amplification and sequencing of the barcoding fragment of *CO1* was performed by the Biodiversity Institute of Ontario (**BIO**) (Guelph, Ontario, Canada). Sequences were uploaded to Barcode of Life Datasystems v4 (**BOLD**) (http://www.boldsystems.org) and those sequences deemed to be barcode compliant by BOLD were assigned BINs (Barcode Index Numbers, Ratnasingham and Hebert 2013) as tentative species hypotheses. Using the Taxon-ID tree tool in the workbench of BOLD, barcodes with BINs were visualized in a neighbor-joining tree using the BOLD aligner and Kimura-2 Parameter distances. The barcodes are available in BOLD as the published dataset DS-HEMIQUED. Novel sequences were uploaded to GenBank under the accession numbers: MF966147–MF966149.

Results

A revision of *Hemiquedius ferox* resulted in the recognition of three species: *H. infinitus* Brunke and Smetana, sp. n. and *H. castoris* Brunke and Smetana, sp. n., from eastern North America and *H. ferox* (LeConte), restricted to peninsular Florida. Although *H. infinitus* and *H. castoris* occur sympatrically, *H. castoris* is strongly associated with the nest material of North American beaver and muskrat, while *H. infinitus* occurs outside of this microhabitat, along the margins of various wetlands. A total of three DNA barcodes >500bp (barcode compliant) and two incomplete barcodes (176 and 306 bp) were generated from available dried specimens. An additional 3 specimens of *H. infinitus* were processed but failed to provide sequences, likely due to inadequate preservation. *Hemiquedius infinitus* and *H. castoris* were represented by 3 and 2 sequences, respectively, and both species were represented by barcodes >500bp that were assigned BINs. Their process IDs are given in the material examined section under the corresponding species. Although two BINs were identified by BOLD (BOLD:ABW6323 and BOLD:ACL9384), sequences did not cluster by the morphology and ecology-based species concepts proposed herein (tree not shown here). However, an OTU (operational taxonomic unit) cluster analysis of both compliant and incomplete barcode fragments in BOLD suggested only a single OTU (average distance = 0.94%, maximum distance = 2.78%). It is likely that, with additional barcode compliant sequences in the future, the two existing BINs will be synonymized into one. Molecular data were unavailable for *H. ferox* as DNA from three dried specimens failed to amplify.

Key to the species of *Hemiquedius* Casey

1 Elytral disc with fine setation laterally (Fig. 1B); entire scutellum with coarse and distinctly meshed microsculpture (Fig. 1B); usually collected from the nest wall material of occupied and recently abandoned beaver and muskrat houses, occasionally collected in adjacent wetland microhabitats or in flight traps; aedeagus as in Fig. 2C, D, F................. ***H. castoris* Brunke and Smetana, sp. n.**

– Elytral disc without fine setation (Fig. 1C); scutellum usually with only fragments of shallow microsculpture, never entirely covered (single specimen seen with only margins missing microsculpture); collected from a wide variety of wetland edge microhabitats but not known from beaver or muskrat houses; aedeagus as in Fig. 2A, B, E, G **2**

2 Male sternite VIII with distinct emargination (Fig. 1D); median lobe in parameral view with acute apex (Fig. 2A); paramere barely constricted at base (Fig. 2E); pronotum slightly longer than wide (Fig. 3C); peninsular Florida (Fig. 4).. ***H. ferox* (LeConte)**

– Male sternite VIII without or with slight emargination (Fig. 1E); median lobe with obtuse apex (Fig. 2C); paramere distinctly constricted at base (Fig. 2C, G); pronotum slightly wider than long (Fig. 3B); broadly distributed across eastern North America, not known from peninsular Florida (Fig. 4)............ .... ***H. infinitus* Brunke and Smetana, sp. n.**

Hemiquedius Casey, 1915

Hemiquedius Casey, 1915: 397, 399; Smetana 1971a (diagnosis, as 'Quediini'); Chatzimanolis et al. 2010 (as Staphylinini: Quediina); Brunke et al. 2016 (as Staphylinini: Acylophorina)

Diagnosis. *Hemiquedius* can be readily recognized as a member of the subtribe Acylophorina by its elongate, non-lobed and cylindrical mid and hind tarsomeres, and the empodial setae of the hind tarsus, which is distinctly longer than that of the foretarsus. Within the subtribe, *Hemiquedius* has a unique habitus (Fig. 1A) but is also distinguished by a combination of: foretibia without distinct spines; at least sutural half of elytron lacking regular, evenly distributed setae; antennae non-geniculate; pronotum roughly parallel-sided.

Hemiquedius ferox (LeConte, 1878)

Figs 1D, 2A, B, E, 3C, 4 map

Quedius ferox LeConte, 1878: 388
Hemiquedius ferox: Smetana 1971a

Type locality. Enterprise, Florida

Type material. The male lectotype of *Quedius ferox* designated by Smetana (1971a) is deposited in the MCZ (Museum of Comparative Zoology, Harvard University, Cambridge, United States) and was examined via photographs in the MCZ online type database (http://mczbase.mcz.harvard.edu/name/Quedius%20ferox). Based on the distribution of the lectotype (Enterprise, Florida), pronotum shape and the distinct emargination of male sternite VIII, the name *H. ferox* corresponds to the species restricted to peninsular Florida.

Other material. UNITED STATES: Florida: *Dade County*: 50 km SW Miami, Chekika State Rec. area, Grossman Hammock Forest, malaise-FIT, '66b', 15.XI.1985 to 24.II.1986, S. & J. Peck, 1 specimen with CNC656114 BOLD Proc ID CNC-

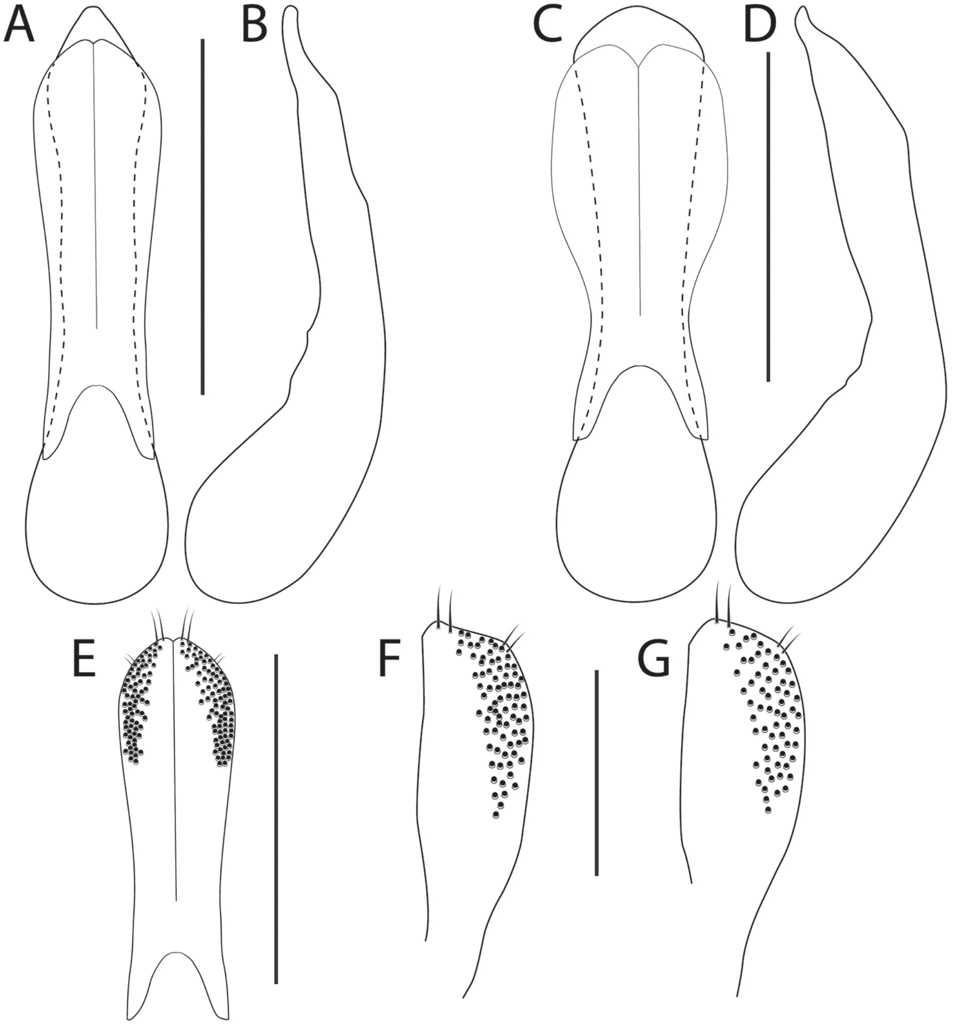

Figure 2. *Hemiquedius ferox* (Casey) (**A, B, E**); *H. infinitus* Brunke and Smetana (**C, D, G**); and *H. castoris* Brunke and Smetana (**F**). Aedeagus in parameral view (**A, C**), median lobe in lateral view (**B, D**), paramere (**E**), left portion of paramere with peg setae (**F, G**). Scale bars: 0.5 mm (**A–E**), 0.25 mm (**F–G**).

CT067-17 (21, CNC); same except 28.VII to 15.XI.1985 (6, CNC); same except 3.III to 28.IV.1985 (2, CNC); same except no date, CNC656113, BOLD Proc ID CNCCT066-17 (2, CNC); Everglades National Park, Mahogany Hammock, forest, UV light, 1.VIII.1981, S. Peck, (1, CNC); Everglades National Park, Long Pine Key, pinelands, malaise-FIT, 8.VI to 26.VIII.1986, S. & J. Peck, CNC656086, BOLD Proc ID CNCCJ3081-14 (1, CNC); Homestead, 28.II.1968, A. Smetana (1, CNC).

Diagnosis. *Hemiquedius ferox* can be distinguished by the distinct emargination of male sternite VIII (Fig. 1D), acute apex of the median lobe (Fig. 2A) and very slightly elongate pronotum (Fig. 3C). It is also the only species known from peninsular Florida.

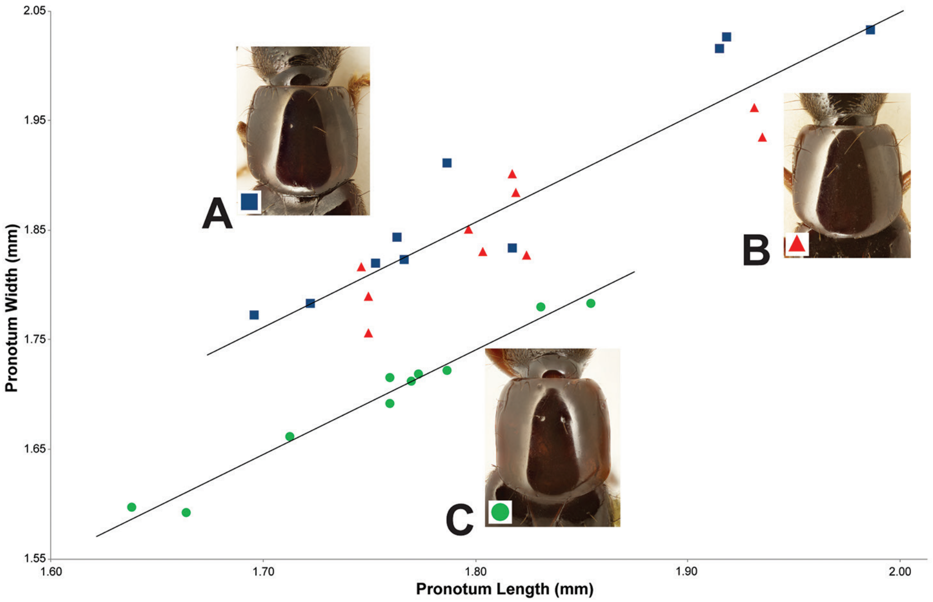

Figure 3. Pronotum shape in *Hemiquedius* species (n = 10, 5 of each sex): *Hemiquedius castoris* Brunke and Smetana (**A**); *H. infinitus* Brunke and Smetana (**B**) and *H. ferox* (Casey) (**C**).

Redescription. Measurements ♂ (n = 5): HW/HL 1.18–1.20; PW/PL 0.96–0.98; EW/EL 0.91–0.96; ESut/PL 0.69–0.77; PW/HW 1.21–1.25; forebody length 5.03–5.31 mm.

Measurements ♀ (n = 5): HW/HL 1.14–1.18; PW/PL 0.96–0.97; EW/EL 0.92–0.96; ESut/PL 0.72–0.74; PW/HW 1.24–1.28; forebody length 4.80–5.50 mm.

Coloration: body dark brown, pronotum sometimes moderately paler, dark reddish brown, abdomen with strong iridescence; palpi reddish brown; legs except coxae light reddish to reddish brown, paler than rest of body, coxae dark brown; antennae dark reddish brown, apical 1-2 segments slightly paler.

Head transverse, slightly more so in males, temples slightly smaller to slightly longer than eyes, middle of disc without punctures. Antennomeres elongate, antennomere 3 extremely elongate, segments decreasing in length to penultimate, which is slightly elongate.

Pronotum slightly longer than wide, weakly converging anteriad, disc without microsculpture, wider than head (Fig. 3C). Elytra broader and considerably shorter than pronotum at middle, fine, uniform setation restricted to epipleuron (as in Fig. 1C), disc with only a few sparse rows of setae, elytral disc without distinct microsculpture, scutellum at most with shallow fragments of meshed microsculpture, never entirely covered with a coarse mesh.

Abdominal tergites with pubescence moderately sparse, setae separated by far more than their diameter, especially sparse at middle of each disc.

Median lobe in lateral view narrowed to simple apex, which is deflexed ventrad at apical fifth (Fig. 2B); median lobe in parameral view with acute apex, expanded subapically (Fig. 2A); paramere in situ shorter than median lobe (Fig. 2A), broad and scarcely constricted at base, with small median incision, peg setae arranged in a pair of crescent-shaped fields (Fig. 2E); apical margin of male sternite VIII with distinct emargination (Fig. 1D); male tergite X triangular, with apex ranging from obtuse to slightly acute, not emarginate; male sternite IX with small but distinct and semi-circular emargination.

Female tergite X elongate triangular, with thin median extension that gradually extends from lateral margin in most specimens, shape overlapping with some specimens of *H. infinitus*.

Distribution. Figure 4. This species is currently known only from Dade and Volusia counties in peninsular Florida.

Bionomics. Specimens have been collected using FITs in hammock forests, 'pinelands', and one specimen came to a UV light. Two specimens were teneral (3.III to 28.IV, 15.XI to 24.II).

Comments. *Hemiquedius ferox* is distinguishable externally from other species of the genus by the slightly longer pronotum and the distinctly emarginate male sternite VIII.

Hemiquedius castoris Brunke & Smetana, sp. n.

http://zoobank.org/4CE9BE4C-693B-4077-93D6-A61C39726351

Figs 1A, B, E, 2F, 3A, 4 map

BINs (shared with *H. infinitus*). BOLD:ACL9384 + BOLD:ABW6323

Type locality. Gatineau Park, Outaouais region, Quebec, Canada.

Type material. Holotype (♂, CNC). "hutte à castor" [=beaver lodge] [small label] / Lac Fortune, Parc Gatineau, Qué, 15.VIII.1976, R. Sexton / CNC Coleo DNA Barcode voucher 00251682 / Barcode of Life, DNA voucher specimen, Sample ID CNC COLEO 00251682, BOLD Proc. ID: CNCCJ3033-14 [blue label].

Paratypes. (19 ♂ 17 ♀ CNC, 22♂ 19 ♀ DEBU): **CANADA: New Brunswick**: *Kent Co.*: Kouchibouguac National Park, 19.XI.1977, Campbell and Smetana, (5, CNC); same except S.J. Miller (1, CNC). **Ontario:** *Bruce Co.*: Stokes Bay, beaver lodge, 1.VI.2008, S.A. Marshall (1, DEBU); *Chatham-Kent Co.*: Rondeau Prov. Park, Marsh Trail, ex. muskrat nest in marsh, 4.VI.1985, A. Davies and J.M. Campbell, specimen CNC656084 with BOLD Proc ID CNCCJ3032-14 (8, CNC); *Kenora Distr.*: 4 mi E. Alcona, 18.VI.1973, Campbell and R. Perry (2, CNC); Ignace, 16.VI.1973, Campbell and Perry (1, CNC); 47 mi S. Pickle Lake, 22.VI.1979, Campbell and Perry (1, CNC); *Ottawa Reg.*, South March, ex. muskrat, 3.V.1969, A. Smetana, BOLD Proc ID CNCCJ3034-14 (1, CNC); Ottawa, Mer Bleue, 3.VII.1973, Smetana and Davies (1, CNC); *Thunder Bay Distr.*: 52 mi N Hurkett, Black Sturgeon Lake, 28.VI.1973, R. Perry and J. M. Campbell (1, CNC). **Quebec:** *Outaouais Reg.*: Gatineau Park, Lac Fortune, hutte à castor, 26.VIII.1976, R. Sexton (1, CNC, 5 DEBU); same except 27.VIII.1976 (1, DEBU); same except 21.VIII.1976 (5, DEBU); same except 29.VIII.1976 (1, CNC); same except 15.VIII.1976 (4, DEBU); same except 6.IX.1976 (1, DEBU) Gatineau Park, Blind

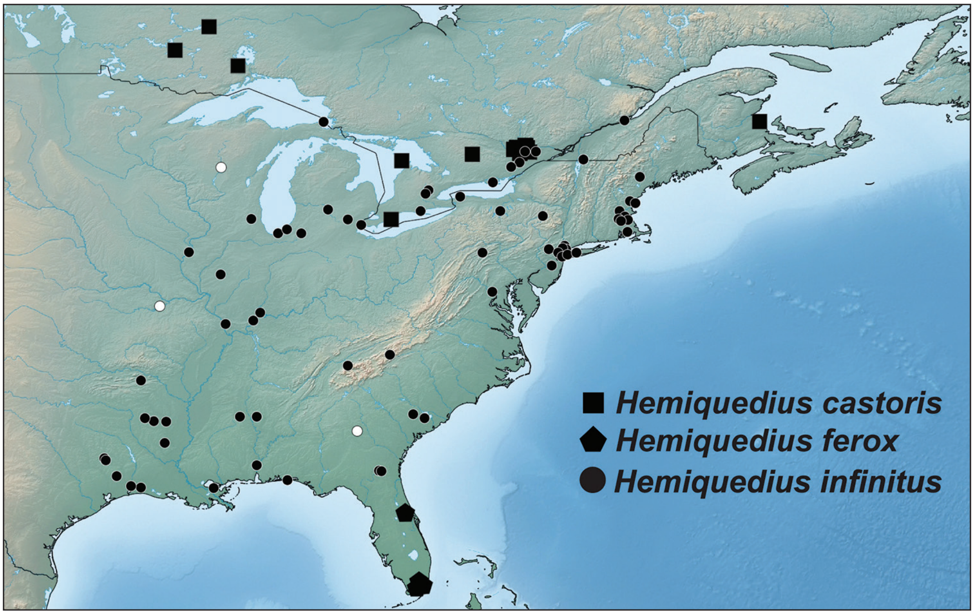

Figure 4. Distribution of *H. castoris* Brunke and Smetana, *Hemiquedius ferox* (Casey), and *H. infinitus* Brunke and Smetana. White markers indicate state only records (placed at the centre of each state) in the absence of more detailed data.

Lake, 8.VIII.1969, J. M. Campbell (7, CNC); same except 11.XI.1970, J.M. Campbell and S. Peck (2, CNC); Gatineau, Old Chelsea, hutte de castor, 4.IX.1976, J.F. Laundry (3, CNC); Gatineau Park, Old Chelsea, hutte castor, 26.VIII.1975, R. Sexton (1, DEBU); Gatineau Park, Hay Lake, ex. beaver lodge, 2.X.1976, Campbell and Sexton (1, CNC); Gatineau Park, Lac Hay, hutte à castor, 2.X.1976, R. Sexton (3, DEBU); Gatineau Park, Meech Lake, 8.XI.1967, (1, CNC); Gatineau Park, Lac Kidder, hutte à castor, 10.X.1976, R. Sexton (2, DEBU); Perkins, hutte à castor, 25.VIII.1976, R. Sexton (4, DEBU); Gatineau Park, Lac Holly, hutte à castor, 11.IX.1976, R. Sexton (3, DEBU); Val-des-Monts, Lac Clermont, hutte à castor, 26.VI.1976, R. Sexton (4, DEBU); same except 1.VII.1976 (1, DEBU); same except 28.VI.1976 (1, DEBU); same except 12.VI.1976 (3, DEBU); Quyon, Pontiac, hutte à castor, 5.IX.1976, R. Sexton (3, DEBU); St. Pierre de Wakefield, hutte castor, 11.XI.1975, R. Sexton (1, DEBU).

Diagnosis. *Hemiquedius castoris* can be easily distinguished by the setose lateral portions of the elytral disc (Fig. 1B) and the coarse meshed microsculpture on the entire surface of the scutellum (Fig. 1B). *Hemiquedius infinitus* and *H. castoris* cannot be distinguished by their CO1 barcodes.

Description. Measurements ♂ (n = 5): HW/HL 1.11–1.16; PW/PL 1.01–1.07; EW/EL 0.99–1.04; ESut/PL 0.71–0.77; PW/HW 1.21–1.26; forebody length 5.05–5.81 mm.

Measurements ♀ (n = 5): HW/HL 1.18–1.20; PW/PL 1.02–1.06; EW/EL 0.94–0.97; ESut/PL 0.74–0.77; PW/HW 1.23–1.26; forebody length 5.21–6.06 mm.

Similar to *Hemiquedius ferox* and differing only in the following: palpi and antennae slightly darker, dark brown to dark reddish brown; antennae on average slightly thinner and shorter in appearance, in most specimens antennomere 8 and 9 slightly less elongate; head slightly more transverse in females rather than males; pronotum slightly wider than long; elytral disc with dense fine setae on lateral portion, scutellum with distinct, transverse meshed microsculpture on entire surface; punctures on abdominal tergites slightly denser; median lobe narrowed to shorter apex, length and shape of narrow apical portion highly variable (as in Fig. 2D); median lobe in parameral view with obtuse apex (as in Fig. 2C); paramere more strongly constricted at base (as in Fig. 2C); paired lobe of paramere elongate relative to that of *H. infinitus* (Fig. 2F); apical margin of male sternite VIII without or with barely discernable emargination (Fig. 1E); female tergite X in most specimens with median extension broader at base and more strongly constricted from lateral margin.

Etymology. We describe this species in honor of Canada on its 150th birthday. Like its national animal, the North American Beaver, Canada promotes a diverse community within its greater environment. The species epithet refers to the close association of this rove beetle with beaver lodges.

Distribution. Figure 4. This species is currently known only in Canada from northern Ontario to New Brunswick but very likely occurs broadly across eastern North America where beavers and muskrats occur. Its distribution includes both the boreal and deciduous forest regions.

Bionomics. All specimens with collecting data have been taken from the nest material within beaver or muskrat lodges, some of which were abandoned for several years. Teneral specimens have been collected in August and September.

Comments. *Hemiquedius castoris* is most similar to the sympatric *H. infinitus* but can be easily distinguished based on the fine setation on the elytral disc. The genitalia of these two species are extremely similar and only differ by the shape of the paramere (Fig. 2F vs. 2G). It is interesting to note that all boreal records of *Hemiquedius* represent *H. castoris*. *Hemiquedius castoris* is not likely to be sympatric with *H. ferox* as its host, the North American Beaver, does not occur naturally in peninsular Florida (Peck 2007).

Hemiquedius infinitus **Brunke & Smetana, sp. n.**

http://zoobank.org/AC0C138A-ED2B-45D7-9C56-4505DDD5030C
Figs 1C, 2C,D,G, 3B, 4 map

BINs (shared with *H. castoris*). BOLD:ACL9384 + BOLD:ABW6323

Type Locality. 3 mi northwest of Orange, Orange County, Texas.

Type material. Holotype (♂, CNC). Tex. Orange Co., 3 mi NW Orange, 17.IV.1976, A. Smetana [dissected parts mounted on card].

Paratypes. (13 ♂ 17 ♀ CNC, 1 ♂ 4 ♀ DEBU, 1 sex? BIO, 1 ♀ TAMU, 1 ♀ MEM, 6 ♂ 7 ♀ FMNH): **CANADA: Ontario:** *Haldimand-Norfolk Region*: ~6 km W of St. Williams, Cronmiller prop., 42°40'21"N, 80°29'26"W, forest pools, 5.VII.2011,

A. Brunke, debu01149192, debu01146692 (2, DEBU); Backus Woods, north block, treading vernal pools, 42°40'7"N, 80°29'34"W, 23.IV.2011, Brunke and Marshall, debu00340010 (1, DEBU); Long Point, woodlot jct Hwys 24 & 59, leaf litter at very edge of temp pond, 21.IV.1973, H. Frania (1, CNC); *Lanark County*: 13 km S of Smith's Falls, 17.V.1981, J. M. Campbell (1, CNC); *Leeds and Grenville County*: 4 km N of Westport, 26.V.1981, A. Davies (1, CNC); *Ottawa Region*: Ottawa (1, CNC); 8 km N Limoges, Larose Forest, 45.388°N 75.228°W tread marshy vegetation around ponds, 81 m, 23.VI.2016, A. Brunke and A. Davies (1, CNC). *Prince Edward Co.*: Brimley, 28.IV.1946 (2, CNC); same except 8.V.1946 (1, CNC); same except 9.V.1943 (1, CNC); same except 12.V.1954 (1, CNC); same except 29.IX.1943 (1, CNC); same except 7.V.1933 (1, CNC); *Wellington Co.*: Conc. 11 and Hume Rd, 43.537 -80.134, 27.X.2010, P. Hebert, sample ID BIOUG01310-E07 (1, BIO); Guelph, 4.VI.1985, B. Longpre, (1, DEBU); Guelph, University Arboretum, cedar swamp, 18.IV.2009, A. Brunke, debu00305699 (1, DEBU); Rockwood (1, CNC). **Quebec**: *Communauté-Urbaine-de-Quebec*: Quebec, 2.X.1969, C. Chantal (1, FMNH); *Montérégie Reg.*: Philipsburg, 19.IX to 12.X.1972, Dondale and Redner (1, CNC).

United States: Alabama: *Mobile County*: Mt. Vernon, 20.III.1932, H. Dietrich (1, CNC). **Arkansas:** *Union County*: Backwaters of Grand Marais Lake, under debris, 9.VII.1974, R. G. Chenowith, CNC656112, BOLD Proc ID CNCCT065-17 (1 CNC), 10 mi S El Dorado, Little Cornie Bayou, treading, 20.V.1974 (1, FMNH). **Florida:** *Okaloosa County*: Fort Walton Beach, 18.III.1976, E.J. Kiteley (1, CNC). **Illinois**: *McHenry County*: Moraine Hills State Park, litter at log, 7.IV.1984, L.E. Watrous (1, FMNH); *Union County*: 1 mi E of Wolf Lake, 8.V.1976, A. Smetana, CNC656110, BOLD Proc ID CNCCT069-17 (2, CNC). **Indiana:** *Porter County*: Tremont, 14.IV.1938 (1, FMNH). **Louisiana:** state record only (1, FMNH). **Massachusetts:** *Middlesex County*: Sherborn, 26.VIII.1934, C.A. Frost (1, CNC); same except 16.X.1881 (1, CNC). **Michigan:** *Berrien County*: Warren Woods, Lakeside, 6.V.1969, W. Suter (1, FMNH). **Mississippi:** *Oktibbeha County*: Noxubee N.W. Refuge, 33.290 -88757, alpha-pinine baited Lindgren funnel, bottomland hardwood forest, 21-29.VII.2009, J.G. Hill & J. Seltzer (1, MEM). **New Jersey:** *Bergen County*: River Vale, 25.V.1980, P.J.D (1, CNC); *Sussex County*: Hopatcong (1, CNC); state record only, Schwarz (1, FMNH). **New York:** *Long Island*: Queens, 18.X.1924, F.M. Schott (1, CNC); *Richmond County*: Staten Island, Concord (1, CNC); *Seneca County*: Willard, V.1970, R. Lenczy (1, FMNH); *Westchester County*: Yonkers, 29.III.1941 (1, FMNH). **South Carolina:** *Dorchester County*: Francis Beidler Forest, 10 km NE Harleyville, bald cypress swamp, FIT, 1-9.V.1987, CNC656111, BOLD Proc ID CNCCT068-17 (1, CNC); *Orangeburg County*: Orangeburg, The Methodist Oaks, 33.419 -80.858, Berlese wet leaf litter in wetland, 27.III.2010, J. & S. Cornell (4, FMNH). **Texas:** *Houston County*: 11 mi E Ratcliff, 24.IV.1976, A. Smetana, CNC656109, BOLD Proc ID CNCCT064-17 (2, CNC); *Orange County*: 3 mi NW Orange, 17.IV.1976, A. Smetana, CNC656108, BOLD Proc ID CNCCT063-17 (1, CNC); *Trinity County*: 12 mi SW Lufkin, 22.IV.1976, A. Smetana (1, CNC); *Tyler Co.*: Kirby State Forest, 30.575 -94.417, ground level FIT, 9-30.III.2003, E. Riley (1, TAMU).

Diagnosis. *Hemiquedius infinitus* can be distinguished by a combination of the elytral disc without fine dense setae (Fig. 1C), pronotum with PW/PL ≥ 1.00 (Fig. 3B) and the indistinct or absent emargination of male sternite VIII (as in Fig. 1E). *Hemiquedius infinitus* and *H. castoris* cannot be distinguished by their CO1 barcodes.

Description. Measurements ♂ (n = 5): HW/HL 1.15–1.21; PW/PL 1.00–1.05; EW/EL 0.92–0.95; ESut/PL 0.72–0.79; PW/HW 1.19–1.27; forebody length 5.24–5.53 mm.

Measurements ♀ (n = 5): HW/HL 1.17–1.21; PW/PL 1.00–1.04; EW/EL 0.91–0.94; ESut/PL 0.75–0.77; PW/HW 1.21–1.27; forebody length 5.30–5.87 mm.

Extremely similar to *H. castoris* and differing only in the following: elytral disc without fine dense setae (Fig. 1C); scutellum with shallow microsculpture in small fragments or with, at most, entire disc except margins with shallow meshed microsculpture; head not sexually dimorphic; pronotum slightly more elongate on average (Fig. 3B); paramere more strongly constricted at base forming a more rounded lobe (Fig. 2G).

Etymology. The species epithet means unbounded in Latin and refers to the occurrence of this species in a variety of wetland habitats, though not inside the lodges of beavers or muskrats.

Distribution. Figure 4. This species is currently known from a wide area of eastern North America: southern Ontario and Quebec, south to the Florida panhandle, west to Texas and north to northern Michigan. Its distribution corresponds well with that of the eastern deciduous forest. All data from Smetana (1971a) can technically be associated with this species except two specimens from peninsular Florida and two from Quebec, with setose elytra.

Bionomics. Specimens have been collected from a variety of wetland edge habitats ranging from open eutrophic ponds to shaded vernal forest pools.

Comments. *Hemiquedius infinitus* is most similar to *H. castoris* but can be easily distinguished based on the lack of fine dense setae on the elytral disc. The genitalia of these two species are extremely similar, variable and only differ by the shape of the paramere. At present *H. infinitus* is not known to be sympatric with *H. ferox* but may overlap with it in northern Florida.

Discussion

Species and distributional limits in *Hemiquedius*

A taxonomic revision of *Hemiquedius ferox* revealed the existence of three distinct species: one known only from peninsular Florida and a pair of highly similar and sympatric eastern species that are thus far allopatric with the former. The eastern pair of species represent an unusual situation in Staphylinidae, where CO1 barcodes are not diagnostic and male genitalia are almost identical (*contra* Hendrich et al. 2014, von Beeren et al. 2016). However, non-overlapping differences in external morphology and ecology indicate that these two species are, possibly rather recently, reproductively isolated. Other examples of similar species that are not distinguishable by CO1 barcodes exist in the Coleoptera and an example was discovered by Grebennikov et al. (2017), who explored the longhorn beetle (Cerambycidae) fauna of the Russian Far East. Two species, separable by external morphology and host plant received the same BIN and were not reciprocally monophyletic in neighbor-joining trees (Grebennikov et al. 2017). An almost identical situation to *Hemiquedius* is known in the ground beetles (Carabidae) with *Pterostichus castor* Goulet & Bousquet, strictly associated with beaver lodges, and *Pterostichus ebeninus* Dejean occurring in various forested and unforested wetlands (Larochelle and Lariviere 2003). The species are at least partly sympatric in the northern U.S. and southern Ontario (Bousquet 2012). Male genitalia in these species are identical but there are consistent differences in external morphology, such as presence/absence of an iridescent sheen and shape of the pronotum (Goulet and Bousquet 1983). Copulation in *Pterostichus castor* was observed on the undersides of branches composing the surface of the lodge (Webster and DeMerchant 2012a). A preference for mating in or on the lodge surface may provide a mechanism for reproductive isolation and subsequent speciation in beaver-associated beetles.

The distribution of *Hemiquedius castoris* is certainly greater than that reported here. We expect this species to occur in at least Wisconsin to New England and across the maritime provinces of Canada. Beaver and muskrat lodges are poorly sampled and the presence of *H. castoris* in the boreal forest region makes it likely to be rather widely distributed across Canada. The North American Beaver and Muskrat do not occur in peninsular Florida (Banfield 1974) and *H. castoris* may be truly allopatric with *H. ferox*.

Obligate associations with beavers and muskrats in the Coleoptera

Thus far, eleven species of beetle are obligate associates of beaver and muskrat lodges in North America (Table 1). Representatives of the Carabidae, Leiodidae and Staphylinidae are known but the evolution of this association has occurred most frequently in the staphylinids. Most of these associates are predators within the lodge but the most extreme of them, the leiodids, are strongly modified for life as adult and larval ectoparasites of beavers, feeding on dead skin and wound exudates (as reviewed in Peck 2006, 2007). Beaver and muskrat lodges represent a stable and predictable microhabitat that is maintained year-round, and therefore are host to a diverse assemblage of obligate and, even more numerous, facultative associates among the beetles (*e.g.*, Bousquet 1985, Smetana 1995, Webster and DeMerchant 2012b). Unlike the other species of the genus and nearly all other Acylophorina, *H. castoris* is distributed north to the boreal forest of northwestern Ontario, possibly due to milder overwintering conditions within its host's lodge. A similar situation is known for the carabid *Atranus pubescens* (Dejean), which is strongly associated with beaver lodges in the northern part of its range but occurs in caves and deep litter in the southern United States (Bousquet 1985). In North America, the Holarctic rove beetle genus *Coprophilus* is represented by the non-native (western Palaearctic) *C. striatulus* (Fabricius), *C. sexualis* Leech, limited

Table 1. Obligate associations of beetles with the lodges of beavers and muskrats in North America.

Family	Subfamily	Species
Carabidae	Harpalinae	*Pterostichus castor* Goulet & Bousquet (Goulet and Bousquet 1983)
	Patrobinae	*Platypatrobus lacustris* Darlington (Larochelle and Lariviere 2003)
Leiodidae	Platypsyllinae	*Leptinillus validus* (Horn) (Peck 2007)
		Platypsyllus castoris Ritsema (Peck 2006)
Staphylinidae	Aleocharinae	*Aleodorus partitus* (LeConte) (Hoebeke 1985)
		Myrmecocephalus gatineauensis Hoebeke (Hoebeke 1985)
	Micropeplinae	*Micropeplus browni* Campbell (Campbell 1968)
	Oxytelinae	*Coprophilus castoris* Campbell (Campbell 1979)
	Staphylininae	*Gabrius vindex* Smetana (Smetana 1995)
		Hemiquedius castoris Brunke & Smetana, sp. n.
		Quedius campbelli Smetana (Smetana 1971a)

to a small range in the Pacific Northwest, and the obligate beaver-associate *Coprophilus castoris* Campbell in the northeast (Campbell 1979, Hoebeke 1995). *Coprophilus castoris* appears to be much more closely related to the Palaearctic species rather than the other native Canadian species and may be a relict in North America, surviving in a specialized and moderated niche. Therefore, another potential impact of beavers and muskrat lodges on biodiversity may be in the form of a stable refugium against extinction on a broader time scale. Although beavers and muskrats undoubtedly have a positive impact on invertebrate diversity at multiple spatial and taxonomic levels, the mechanisms involved in these interactions remain unexplored and untested by ecologists and evolutionary biologists. We hope that this review draws attention to this interesting phenomenon and the diverse community supported by the beaver, a charismatic national symbol of Canada.

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A revision of *Meladema* diving beetles (Coleoptera, Dytiscidae), with the description of a new species from the central Mediterranean based on molecules and morphology

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Abstract

Meladema Laporte, 1835 are relatively large, stream-dwelling diving beetles, distributed widely in the Western Palaearctic, from the Atlantic Islands to Turkey, and from southern France and the Balkans to the central Sahara. In addition to the three previously recognised taxa (*M. coriacea* Laporte, 1835, *M. imbricata* (Wollaston, 1871) and *M. lanio* (Fabricius, 1775)) we describe a new, cryptic, species from the central Mediterranean area, which can be distinguished from *M. coriacea* on both DNA sequence data and morphology, and provide a key to known species of the genus. Based on the study of genotyped material, both recent and archival, as well as the examination of a large number of museum specimens, we show that *M. lepidoptera* **sp. n.** occurs to the apparent exclusion of *M. coriacea* on Corsica, Sardinia and islands of the Tuscan Archipelago, but that both taxa are found in peninsular Italy, where they may occasionally hybridize. In the absence of the original type series, we designate a neotype for *M. coriacea*, and take the opportunity to designate a lectotype for *M. lanio*. Morphological variation in *Meladema* species is discussed, including that seen in known and presumed hybrids. Our study highlights the incomplete state of knowledge of Mediterranean biodiversity, even in relatively large, supposedly well-studied taxa.

Keywords

Systematics, integrative taxonomy, biogeography, cryptic species, freshwater, biodiversity, entomology

Introduction

Meladema Laporte, 1835 is a small genus of large diving beetles, found in streams in the Western Palaearctic, from the Canary Islands and Madeira, to western Turkey (Sharp 1882, Guignot 1932, Franciscolo 1979, Balke et al. 1989, Balke et al. 1990, Ribera et al. 2003, Darilmaz and Kiyak 2009, Touaylia et al. 2011, Sýkora et al. 2017). Species of the genus are particularly characteristic of deeper, (semi) permanent pools, and may often function as top predators in fishless streams on the Atlantic Islands, and in temporary Mediterranaean systems. At present the genus contains three species: the widespread *Meladema coriacea* Laporte, 1835, distributed from the Canary Islands to Turkey and ranging from southern France and the central Balkans south to the central Sahara, and two Atlantic Island endemics, *Meladema imbricata* (Wollaston, 1871) from the western Canary Islands and *Meladema lanio* (Fabricius, 1775) from the main island of Madeira.

Ribera et al. (2003) studied the phylogeny and phylogeography of *Meladema* using mitochondrial DNA sequences, and demonstrated that the genus contains four divergent mtDNA clades, two corresponding to the Atlantic Island species, the other two nesting within *M. coriacea*; specimens from the island of Corsica being highly divergent from all other material examined from the Canaries, Iberia, the Balearic Islands, southern France and North Africa. The two lineages within *M. coriacea* were thought to be morphologically identical, however, without apparent differences in characters habitually used in the species level-taxonomy of Dytiscidae, including male genitalia. Subsequently, Sýkora et al. (2017) surveyed both mitochondrial and nuclear DNA sequence variation across a wider range of localities, confirming the presence of these four genetic lineages, *M. coriacea* being divided (on both mitochondrial and nuclear markers) into a widespread clade, distributed from the Canary Islands to Turkey, and another clade, restricted in their analyses to Corsica, Sardinia and Montecristo (termed '*coriacea* CSM'). Molecular dating analyses suggested that *Meladema* originated in the Middle Miocene, approximately 14.4 million years ago (MYA; 95% CI 10-20 MYA), with all four extant lineages dating from the early Pleistocene ca. 1.2-1.5 MYA (Sýkora et al. 2017). Ribera et al. (2003) and Sýkora et al. (2017) refrained from describing '*coriacea* CSM' as a distinct species, despite its genetic divergence, since it was apparently morphologically identical to other populations of *M. coriacea*.

We have reexamined morphological variation in *Meladema* in the light of these recent molecular results, and demonstrate that whilst '*coriacea* CSM' cannot be distinguished from other *M. coriacea* using male genital anatomy, these two lineages can be separated reliably on the basis of differences in the elytral sculpture of both sexes. By studying a combination of newly genotyped specimens and extensive museum material, we show that '*coriacea* CSM', here described as *M. lepidoptera* sp. n., occurs on the Tyrrhenian Islands (Corsica, Sardinia, Elba, Montecristo) and on the Italian mainland, where it comes into contact with *M. coriacea*. Since the type series of *M. coriacea* could not be located, and is likely destroyed (Evenhuis 2012), we designate a neotype for this species in the interests of stability, using a genotyped specimen from southern France, where Laporte's material originated. We also take the opportunity to designate a lectotype for *M. lanio*, and discuss character variation in the genus, including that seen in known or presumed hybrid individuals from the Atlantic Islands and Italy. Our work highlights the incomplete state of knowledge of Mediterranean biodiversity, where even relatively large, well-known taxa can hide previously unrecognised species (see also Audisio et al. 2009, Zauli et al. 2016).

Materials and methods

Morphology

Specimens were studied with Leica MZ8 and M205C stereomicroscopes at x8–100, illuminated with a Fluopac FP1 flourescent light, or a swan-neck illuminator diffused using a tracing paper collar close to the specimen (to enable study of microsculpture). A wide range of morphological characters were initially compared across genotyped material of *M. coriacea* and *M. lepidoptera* sp. n., in the search for diagnostic features. These included dorsal and ventral sculpture of both sexes and secondary sexual characters (male and female genitalia and last abdominal ventrites, male tarsal modifications). Digital photographs were taken with a Canon EOS 500D camera with a Sigma 50mm f/2.8 EX DG macro lens, illuminated with two Fluopac FP1 flourescent lights (habitus photos) or with a Leica Z6 Apo macroscope, fitted with a 2x objective lens illuminated using a Leica LED5000 HDI dome illuminator to avoid shadow (all other features). Male and female genitalia were studied wet, temporarily mounted in alcohol-based hand sanitizer gel to stabilize their position during image stacking. Image stacks were produced by hand, and combined using Zerene Stacker software (www.zerenesystems.com). For scanning electron microscopy material was degreased for two days in 100% acetone and air-dried overnight at 60°C, before being mounted onto metal stubs using double-sided carbon conducting tape. Specimens were gold sputter coated using an Emitech K550 Coating Unit, then examined and photographed in a JEOL JSM6610LV Scanning Electron Microscope (SEM). Elytral sculpture was typically imaged at the shoulder and in the centre, close to the suture (Figure 1), these positions being chosen following initial screening described above.

The terminology to denote the orientation of male genitalia follows Miller and Nilsson (2003). Female reproductive tracts were prepared as follows: the last three abdominal segments were removed from ethanol preserved material and rehydrated for 10 min in distilled water. Terga were opened with dissecting scissors, and the whole abdomen macerated for 20 min in 10% aqueous potassium hydroxide at 30°C. The reproductive tract and associated sclerites were then removed from the abdomen and redigested in 10% potassium hydroxide at 30°C for a further 10 mins. Following this they were placed in 10% acetic acid for 1 min at room temperature, before being transferred to 70% ethanol prior to examination.

Exact label data for specimens are cited in quotation marks; separate quotes for the same specimen indicate separate labels. A double slash (//) indicates separate label lines. All descriptions are based on genotyped material unless otherwise stated.

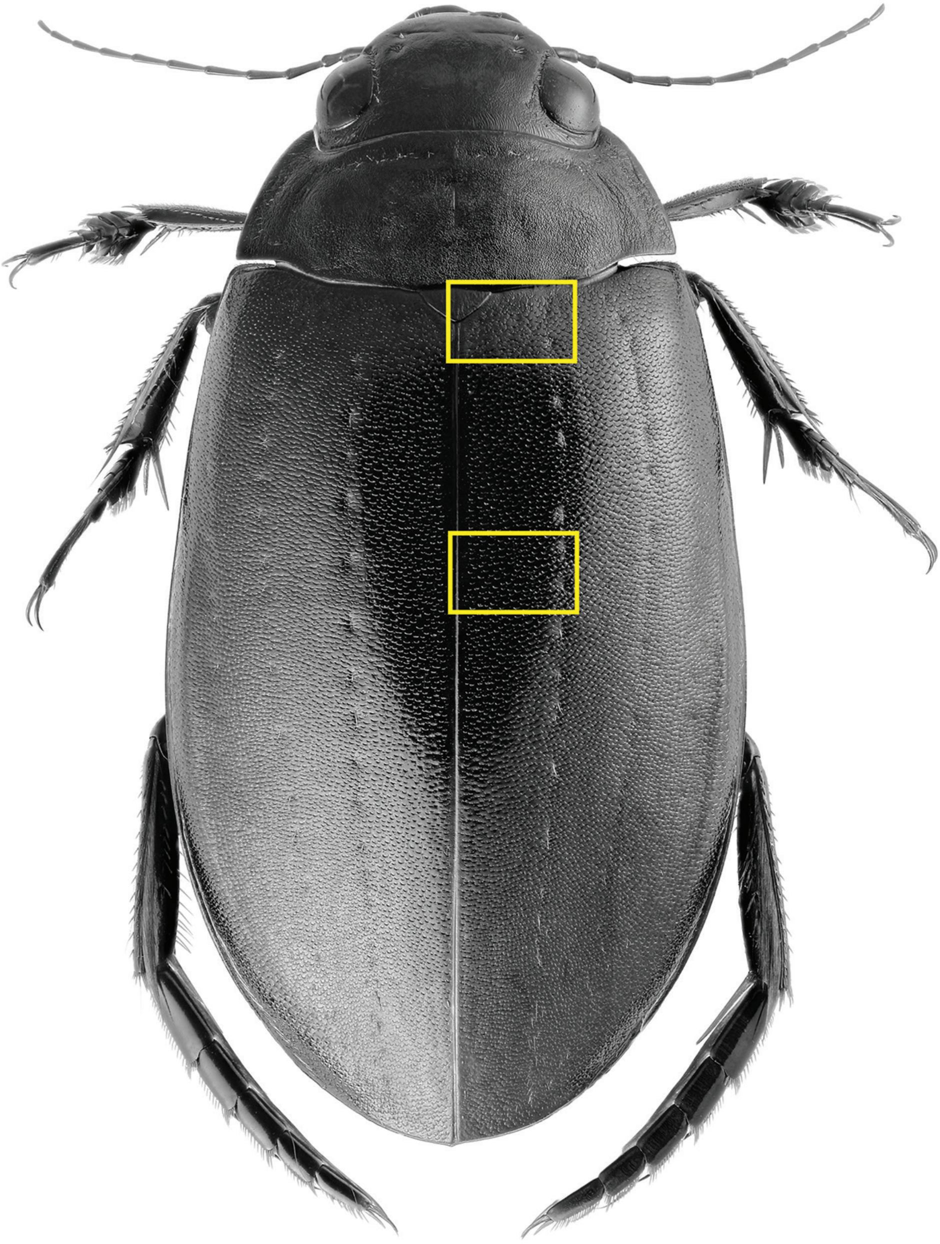

Figure 1. Dorsal view of *Meladema coriacea*, showing regions in which scanning electron and light micrographs of elytral sculpture were made.

Molecular data and analyses

We added newly sequenced specimens from mainland Italy, some Tyrrhenian islands and North Africa (Table 1) to the molecular dataset of Sýkora et al. (2017). DNA

Table 1. Specimens of *Meladema* used in genetic analyses, with DNA voucher, locality, collector and accession numbers of available sequences (newly obtained sequences in bold). The COI-3' sequence of specimen IBE-AN691 is of very low quality and was not submitted. Neotype of *M. coriacea* and holotype of *M. lepidoptera* sp. n. indicated with asterisks (all other specimens of *M. lepidoptera* sp. n. are paratypes). See text for full label data.

Taxon	Voucher	Country/ Island	Locality	Collector	COI-5' (barcode)	COI-3'	16S+tRNA-L +nad1	H3	WG
coriacea	IBE-AN691	Sicily	Bosco Ficuzzo	M.Toledo		x			
coriacea	IBE-AN739	Chad	Tibesti, Koudou	Bruneau de Miré				**LT898148**	
coriacea	IBE-DV291	Spain	Cáceres, PN Monfragüe	I.Ribera & P.Abellán	**LT898152**	LT602719	LT602827	LT602736	LT602782
coriacea	IBE-DV292	Spain	Huesca, Bco. de Bernués	I.Ribera & A.Cieslak	**LT898153**	LT602720	LT602828	LT602737	LT602783
coriacea	IBE-DV293	Spain	Girona, Port Bou	I.Ribera & A.Cieslak	**LT898154**	LT602721	LT602829	LT602738	LT602784
coriacea	IBE-DV294	Turkey	Izmir, Phoca	I.Ribera & A.Cieslak	**LT898155**	LT602722	LT602830	LT602739	LT602785
coriacea	IBE-RA1064	Malta	between Mosta and L-Imtarfa	A.Rudoy		LT602725	LT602833	LT602740	LT602786
coriacea	MNCN-AI104	Spain	Corbera d'Ebre, riu Gaia	I.Ribera		LT602727	LT602835	LT602743	LT602789
coriacea	MNCN-AI1095	Tenerife	Chamorga, Bco. Roque Bermejo	A.Castro		LT602730	LT602838	LT602744	LT602790
coriacea	MNCN-AI84	Tunisia	Cite el Morjne	M.G.París	**LT906387**	LT602726	LT602834	LT602745	LT602791
coriacea	MNCN-AI860	Spain	Castellón, Ballestar	I.Ribera		LT602728	LT602836	LT602746	LT602792
coriacea	MNCN-AI861	Spain	Castellón, Ballestar	I.Ribera		LT602729	LT602837		
coriacea	MNCN-HI4	Algeria	Oued Bagrat	S.Bouzid		LT602731	LT602839	LT602747	LT602793
coriacea	MNCN-HI6	Algeria	Aïn Damous	S.Bouzid		LT602732	LT602840	LT602748	LT602794
coriacea	NHM-IR47	Morocco	Taza, Tazzeka N.P.	I.Ribera				EF670124	
coriacea	NHM-IRM10a	Spain	Cádiz, Fancinas	I.Ribera		AF428215	AF428189		
coriacea	NHM-IRM11a	France	Var, La Londe-les-Maures	P.Ponel		AF428208	AF428189		
coriacea	NHM-IRM11b	France	Var, La Londe-les-Maures	P.Ponel		AF428209	AF428189	LT602749	LT602795
*coriacea**	NHM-IRM11c	France	Var, La Londe-les-Maures	P.Ponel		AF428207	AF428189		
coriacea	NHM-IRM13a	Spain	Murcia, Fte. Caputa	A.Millán		AF428218	AF428189	LT602753	LT602798
coriacea	NHM-IRM14a	Spain	Córdoba, Baena, Arroyo de las Beatas	M.Baena		AF428216	AF428190	LT602754	LT602799
coriacea	NHM-IRM14b	Spain	Córdoba, Baena, Arroyo de las Beatas	M.Baena		AF428216	AF428190		
coriacea	NHM-IRM14c	Spain	Córdoba, Baena, Arroyo de las Beatas	M.Baena		AF428217	AF428189		

Taxon	Voucher	Country/ Island	Locality	Collector	COI-5' (barcode)	COI-3'	16S+tRNA-L +nad1	H3	WG
coriacea	NHM-IRM18a	Tenerife	Bco. Del Infierno	D.T.Bilton		AF428222	AF428189	LT602757	LT602802
coriacea	NHM-IRM19a	Tenerife	Bco. De Masca	D.T.Bilton		AF428222	AF428189	LT602758	LT602803
coriacea	NHM-IRM19b	Tenerife	Bco. De Masca	D.T.Bilton		AF428222	AF428189	LT602759	LT602804
coriacea	NHM-IRM1a	Morocco	Taza, Tazzeka N.P.	I.Ribera		AF428212	AF428189	LT602760	LT602805
coriacea	NHM-IRM1c	Morocco	Taza, Tazzeka N.P.	I.Ribera		AF428213	AF428189		
coriacea	NHM-IRM20a	Gran Canaria	S. Nicolas de Tolentino, bco. Guy Guy grande	I.Ribera & A.Cieslak		AF428221	AF428189	LT602761	LT602806
coriacea	NHM-IRM21a	Morocco	Immouzèr-des-Ida-Outanane, Assif Tanit	I.Ribera & A.Cieslak		AF428214	AF428189	LT602762	LT602807
coriacea	NHM-IRM21b	Morocco	Immouzèr-des-Ida-Outanane, Assif Tanit	I.Ribera & A.Cieslak		AF428215	AF428189		
coriacea	NHM-IRM22a	Morocco	Tachokchte, Assif Siroua	I.Ribera & A.Cieslak		AF428216	AF428189	LT602763	LT602808
coriacea	NHM-IRM22b	Morocco	Tachokchte, Assif Siroua	I.Ribera & A.Cieslak		AF428216	AF428189		
coriacea	NHM-IRM23a	Mallorca	Mortixet, Te. Son March	I.Ribera & A.Cieslak		AF428219	AF428191	LT602764	LT602809
coriacea	NHM-IRM23b	Mallorca	Mortixet, Te. Son March	I.Ribera & A.Cieslak		AF428220	AF428189		
coriacea	NHM-IRM24a	Mallorca	Els Casals, Te. Son March	I.Ribera & A.Cieslak		AF428215	AF428189		
coriacea	NHM-IRM2a	Morocco	Anti Atlas, Oued Massa	I.Ribera		AF428210	AF428189		
coriacea	NHM-IRM2b	Morocco	Anti Atlas, Oued Massa	I.Ribera		AF428211		LT602765	LT602810
imbricata	NHM-IRM15a	Gomera	El Cedro	D.T.Bilton		AF428224	AF428192	LT602766	LT602811
imbricata	NHM-IRM15b	Gomera	El Cedro	D.T.Bilton		AF428225	AF428192	LT602767	LT602812
imbricata	NHM-IRM17a	Tenerife	Bco. del Río	D.T.Bilton	**KJ637881**	AF428228	KJ637898	KJ638011	
imbricata	NHM-IRM17b	Tenerife	Bco. del Río	D.T.Bilton		AF428230	AF428192	LT602768	LT602813
imbricata	NHM-IRM3a	Gomera	El Cedro	D.T.Bilton		AF428224	AF428192	LT602770	LT602815
imbricata	NHM-IRM4a	Gomera	El Cedro	D.T.Bilton		AF428224	AF428192	LT602771	LT602816
imbricata	NHM-IRM4b	Gomera	El Cedro	D.T.Bilton		AF428224	AF428192	LT602772	LT602817
imbricata	NHM-IRM5a	Tenerife	Bco. del Río	D.T.Bilton		AF428230	AF428192	LT602773	LT602818
imbricata	NHM-IRM5d	Tenerife	Bco. del Río	D.T.Bilton		AF428229			
imbricata	NHM-IRM6a	La Palma	Bco. del Hoyo Verde	D.T.Bilton		AF428227			
imbricata	NHM-IRM6b	La Palma	Bco. del Hoyo Verde	D.T.Bilton		AF428227	AF428192	LT602775	LT602820

Taxon	**Voucher**	**Country/ Island**	**Locality**	**Collector**	**COI-5' (barcode)**	**COI-3'**	**16S+tRNA-L +nad1**	**H3**	**WG**
imbricata	NHM-IRM6c	La Palma	Bco. del Hoyo Verde	D.T.Bilton		AF428227	AF428192	LT602776	LT602821
imbricata	NHM-IRM7a	La Palma	Bco. del Rio above Santa Cruz	D.T.Bilton		AF428226	AF428192		
lanio	IBE-DV298	Madeira	Canhas, Paul da Serra	A.Rudoy	**LT898156**	LT602733	LT602841	LT602777	LT602822
lanio	NHM-IRM8a	Madeira	Ribera dos Cedros	L.C.Kelly		AF428233	AF428194	LT602778	LT602823
lanio	NHM-IRM9a	Madeira	Levada das Faias	L.C.Kelly		AF428231	AF428194		
lanio	NHM-IRM9b	Madeira	Levada das Faias	L.C.Kelly		AF428232	AF428194	LT602779	LT602824
lepidoptera sp. n.	IBE-AN692	Elba	Pomonte, Fosco Barione	M.Toledo		**LT898157**			
lepidoptera sp. n.	IBE-AN693	Italy	Toscana, S. Luce	M.Toledo		**LT898158**		**LT898147**	
lepidoptera sp. n.	IBE-AN760	Italy	Monti della Tolfa	V.Buono	**LT898149**	**LT898159**			
lepidoptera sp. n.	IBE-DV289	Montecristo		R.Vila	**LT898150**	LT602717	LT602825	LT602734	LT602780
lepidoptera sp. n.	IBE-DV290	Montecristo		R.Vila	**LT898151**	LT602718	LT602826	LT602735	LT602781
lepidoptera sp. n.	IBE-RA18	Sardinia	Ogliastra, ca. 5 km WNW Tortoli	H.Fery & M.Toledo		LT602724	LT602832	LT602741	LT602787
lepidoptera sp. n.	IBE-RA5	Sardinia	Nuoro prov., Villagrande Strìsaili	H.Fery & M.Toledo		LT602723	LT602831	LT602742	LT602788
lepidoptera sp. n.	NHM-IRM12a	Corsica	Porto-Vecchio, l'Ospedale	I.Ribera & A.Cieslak	**LT906388**	AF428203			
lepidoptera sp. n.	NHM-IRM12b	Corsica	Ghisoni, road to Campannella	I.Ribera & A.Cieslak		AF428204	AF428187	LT602750	
lepidoptera sp. n.	NHM-IRM12c	Corsica	Cap Corse, Bettolacce	I.Ribera & A.Cieslak	**LT906389**	AF428205	AF428188	LT602751	LT602796
lepidoptera sp. n.	NHM-IRM12d	Corsica	Porto-Vecchio, l'Ospedale	I.Ribera & A.Cieslak	**LT906390**	AF428203	AF428187	LT602752	LT602797
lepidoptera sp. n.*	NHM-IRM12e	Corsica	Cap Corse, Bettolacce	I.Ribera & A.Cieslak		AF428206	AF428188		
lepidoptera sp. n.	NHM-IRM12f	Corsica	Cap Corse, Bettolacce	I.Ribera & A.Cieslak	**LT906391**	AF428207	AF428187		
lepidoptera sp. n.	NHM-IRM12g	Corsica	Porto-Vecchio, l'Ospedale	I.Ribera & A.Cieslak		AF428203	AF428187		
coriaceaximbricata	NHM-IRM16a	Tenerife	Bco. del Río	D.T.Bilton		AF428223	AF428192	LT602755	LT602800
coriaceaximbricata	NHM-IRM16b	Tenerife	Bco. del Río	D.T.Bilton		AF428223	AF428192	LT602756	LT602801
imbricataxcoriacea	NHM-IRM5b	Tenerife	Bco. del Río	D.T.Bilton		AF428222	AF428189		
imbricataxcoriacea	NHM-IRM5c	Tenerife	Bco. del Río	D.T.Bilton		AF428222	AF428189	LT602774	LT602819
imbricataxcoriacea	NHM-IRM17c	Tenerife	Bco. del Río	D.T.Bilton		AF428222	AF428189	LT602769	LT602814

Table 2. Primers used for amplification and sequencing. In brackets, length of the amplified fragment.

Gene	Primer	Sequence	Reference
COI-3’	Jerry (5’)	CAACATTTATTTTGATTTTTTGG	Simon et al. (1994)
(826)	Pat (3’)	TCCAATGCACTAATCTGCCATATTA	Simon et al. (1994)
	Chy (5’)	T(A/T)GTAGCCCA(T/C)TTTCATTA(T/C)GT	Ribera et al. (2010)
	Tom (3’)	AC(A/G)TAATGAAA(A/G)TGGGCTAC(T/A)A	Ribera et al. (2010)
COI-5’	LepF1b	ATTCAACCAATCATAAAGATATTGGAAC	Dincă et al. (2017)
(658)	LepR1	TAAACTTCTGGATGTCCAAAAAATCA	Hebert et al. (2003)
H3	H3aF (5’)	ATGGCTCGTACCAAGCAGACRCG	Colgan et al. (1998)
(327)	H3aR (3’)	ATATCCTTRGGCATRATRGTGAC	Colgan et al. (1998)

was extracted non-destructively with commercial kits (“DNeasy Tissue Kit”, Qiagen GmbH, Hilden, Germany) following the manufacturer’s instructions. DNA extractions are retained in the collections of the Institut de Biologia Evolutiva, Barcelona (IBE). Fresh specimens were extracted following the methods detailed in Sýkora et al. (2017). Dry preserved specimens were first soaked for 1 h in a 10% SDS solution at 35°C. Following this, the beetle was carefully removed from its mount or pin, placed in a new, sterile petri-dish containing ultrapure water, and the genitalia and associated tissues removed with watchmaker’s forceps. All specimen manipulation was conducted in a fume hood, in a laboratory which never handles DNA samples. Forceps were dipped in 100% ethanol and flamed between samples, and fresh vinyl gloves were worn to handle each beetle. Following tissue extraction, the specimen was air dried and remounted. DNA extractions and amplifications of tissues from dry or badly preserved specimens were conducted under a fume hood, with filter tips and fresh primer and chemical aliquotes for each specimen, to prevent contamination. Following DNA extraction, genital structures were mounted beside the specimen, or on a card on the same pin.

We amplified fragments of the Cytochrome Oxidase Subunit 1 mitochondrial gene (5’ end, COI-5’, and 3’ end, COI-3’) and an internal fragment of the nuclear gene Histone 3 (H3) (see Table 2 and Sýkora et al. (2017) for details on primers used and PCR cycling conditions). Attempts to amplifly additional gene fragments used in Sýkora et al. (2017) from dry material were not succesful (see Results below). New sequences have been deposited in Gen Bank with accession numbers LT898147–LT898159 and and LT906387–LT906391 (Table 1).

To place newly sequenced specimens in a phylogenetic context we included them in a matrix with the COI data from Sýkora et al. (2017), and analysed it with a fast Maximum Likelihood heuristic algorithm in RAxML-HPC2 in the CIPRES Science Gateway (Miller et al. 2010), using a single partition with a GTR+G evolutionary model and assessing node support with 100 pseudoreplicates of a rapid bootstrapping algorithm (Stamatakis et al. 2008).

Abbreviations

BMNH	Natural History Museum, London, UK
CBF	Collection H. Bussler, Freising, Germany
CBP	Collection D.T. Bilton, Plymouth, UK
CFA	Collection G.N. Foster, Ayr, UK (to be deposited in Hunterian Museum, Glasgow University, Glasgow, UK)
CTP	Collection M. Toledo, Parma, Italy
CVR	Collection V. Volpe, Roma, Italy
IBE	Institut de Biologia Evolutiva, Barcelona, Spain
ISNB	Institut royal des Sciences naturelles de Belgique, Brussels, Belgium
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain
MNHN	Muséum national d'Histoire naturelle, Paris, France
NMW	Naturhistorisches Museum, Wien, Austria
ZSM	Zoologische Staatssammlung, München, Germany
TL	Total length, front of head to elytral apices
EL	Elytral length
MW	Maximum width, elytra
HW	Handwriting

Results

We obtained enough sequence data from the COI gene to allow an unambiguous phylogenetic placement of two specimens from mainland Italy (Toscana and Lazio, DNA vouchers IBE-AN693 and IBE-AN760 respectively; Table 1) and one from Elba (IBE-AN692). We also obtained partial COI data from one specimen from Sicily (IBE-AN691) allowing its identity to be established and nuclear (H3) data from one specimen from the Tibesti, in Chad (IBE-739), which included diagnostic positions allowing some discrimination, but not an unambiguous species identification. We could not obtain any sequences from two of the dry specimens extracted, IBE-AN694 (mainland Italy, Campania) and IBE-AN740 (Chad, Tibesti).

In the RAxML analysis with the COI-3' marker the two sequenced specimens from mainland Italy and the one from Elba were clearly clustered with other specimens from Corsica, Sardinia and Montecristo, with strong bootstrap support (Figure 2). Although only a limited number of specimens were sequenced for the COI-5' fragment (Table 1), there was also a clear segregation of *M. coriacea*/*lepidoptera* sp. n. haplotypes into two groups, fully congruent with that seen with the COI-3' fragment.

For the Sicilian specimen (IBE-AN691) it was only possible to obtain a low quality partial sequence for the reverse primer of the 3' end of the COI gene (ca. 664 nucleotides, primer Jerry, see Table 2). Of the six diagnostic positions separating *M. coriacea* from *M. lepidoptera* sp. n. in this gene fragment, four were apparently *M. coriacea* and

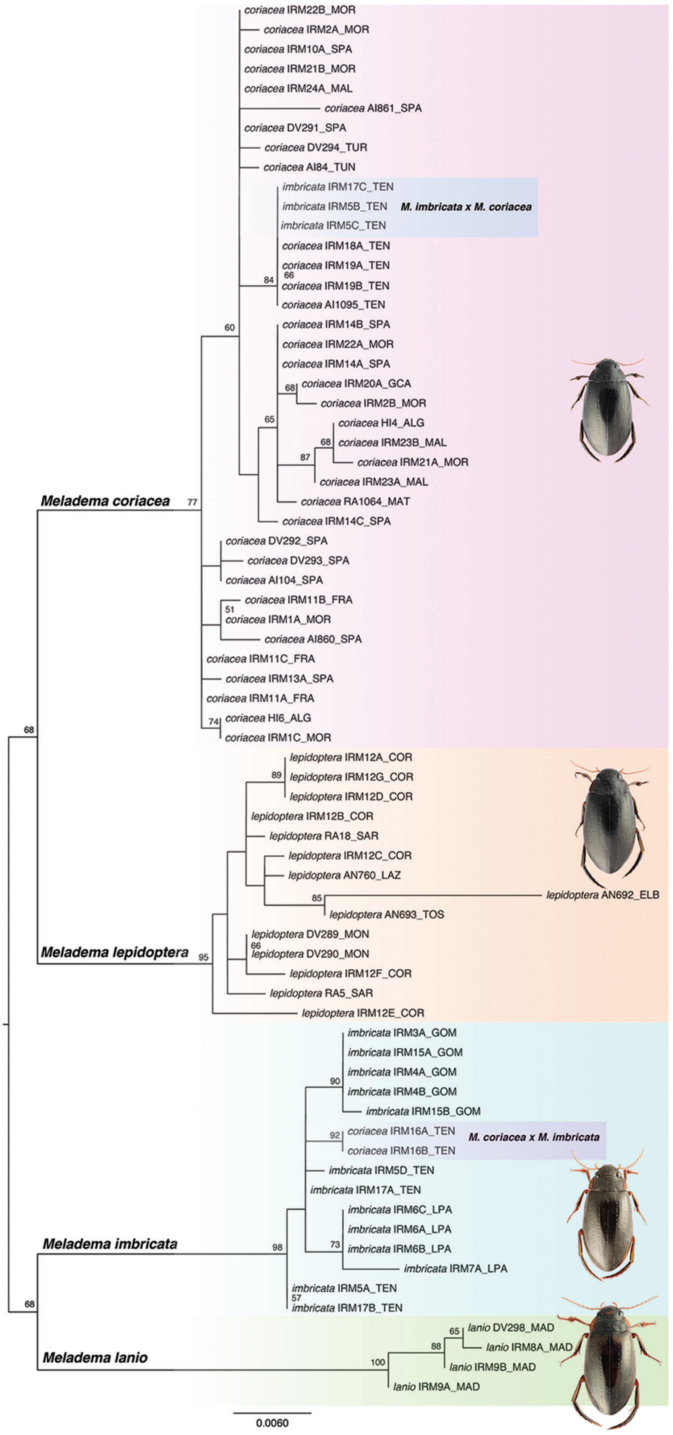

Figure 2. Phylogram obtained from analysis of the COI-3' fragment in RAxML. Numbers on nodes, bootstrap support values. See Table 1 for specimen and locality codes. Habituses correspond to those in Figure 3.

two *M. lepidoptera* sp. n. This specimen had been previously unambiguously assigned to *M. coriacea* on external morphology.

We obtained the H3 sequence from one of the specimens from the Tibesti (AN739, Table 1), although it was not possible to sequence any other markers from this specimen. The H3 sequence was identical to the sequence of all *M. coriacea* + *lepidoptera* sp. n. and different from *M. imbricata* and *M. lanio* in the single diagnostic position in this gene fragment (see Sýkora et al. 2017).

Taxonomy

Meladema Laporte, 1835

Meladema Laporte, 1835:98, gender feminine; type species: *Meladema coriacea* Laporte, 1835:98, by monotypy; conserved in ICZN Opinion 1725 (ICZN 1993). *Scutopterus* Dejean, 1833:54, unavailable name, rejected in Opinion 1725 (ICZN 1993).

Diagnosis. Adults can be recognised within the Colymbetinae on the following combination of characters: pronotal beading absent; protibiae only weakly emarginate basoventrally; prosternal process medially rounded; anterior margin of metaventrite deeply incised for reception of prosternal process; metatarsomeres I-IV distinctly sinuate apically, with apicolateral lobes and metatarsal claws subequal in length, outer approximately two-thirds length of inner (Miller and Bergsten 2016). The sculpture of the elytra referred to by Miller and Bergsten (2016) is not a constant generic character of *Meladema* (see below). Larvae of two species (*M. coriacea* and *M. lanio*) have been described to date (Bertrand 1928, 1932a, 1932b, Falkenström 1938, Nilsson and Hilsenhoff 1991, Alarie and Hughes 2006). First instar larvae of *Meladema* can be distinguished from most other genera of Colymbetinae on: Additional setae present on dorsal margin of femur; short, spine-like mesofemoral seta FE5; additional setae on both ventral and dorsal margins of tibiae and relatively large size (Alarie and Hughes 2006). They can be separated from *Bunites* Spangler, 1972 on details of the setation of the coxae and abdominal segment 8 (Michat 2005). Third instar larvae are characterized by: relatively large size (head length > 4.40 mm cf. < 3.50 mm in other described Colymbetinae); urogomphus more elongate (> 1.7× dorsal length of last abdominal segment cf. < 1.5×); large number of secondary setae on legs and the presence of predominantly short and spine-like setae on outer and elongate setae with hair-like secondary setae along inner margin of urogomphus (see Alarie and Hughes 2006).

Description. Compound eyes large, rounded, laterally somewhat protruding (Figure 3); anterior margin distinctly emarginate. Antennae long, slender, all segments elongate; segment 2 least so, 2.5× longer than broad; all other segments > 3× longer than broad; all segments broadening distally. Antennal insertions invisible dorsally, adjacent to anterior margins of compound eyes, below lateral margins of frons. Anterior margin of clypeus arcuate; anterior angles obtuse, weakly rounded. Clypeus with strongly transverse anterolateral foveae, each occupying approximately 0.25× length of anterior margin. Foveae shallow posteriorly, deep and abrupt anteriorly; furnished with stiff whitish or golden-yellow setae. Anterior margin of labrum with broad, semicircular emargination; central 0.4 furnished with stiff, close-set setae. Labium transverse, broadest anteriorly; anterior margin with brush of fine, close, elongate setae; lateral setae approximately 2× length of those at centre. Labial palpomeres elongate, particularly palpomere 2. Palpomere 3 with raised medial and apical tubercles ventrally, furnished with stout setae. Palpomere 3 expanded to apex, curved, convex ventrally and concave dorsally. Maxillary palpomere 1 slightly elongate; palpomeres 2–4 increasingly so. Palpomere 4 swollen, inner face almost straight, outer strongly curved; with setae on internal and ventral faces towards apex. Mentum setose anterolaterally; excavated in centre, with longitudinal ridges laterally. Pronotum strongly transverse, somewhat thickened laterally; without distinct lateral bead (Figure 3). Anterior angles acute, furnished with bunch of stiff, golden setae; posterior angles obtusely rounded. Anterior margin broadly arcuate around centre; posterior margin sinuate laterally or almost straight (Figure 3). Elytra elongate, broadest close to or behind middle (Figures 3, 4), with strong lateral bead; apices conjointly rounded. Each elytron with three rows of serial punctures (Figure 3). Each puncture of rows bearing 1–5 stout, recumbent to erect setae (e.g. Figures 3, 9, 10). Elytra of at least some individuals of all species with transverse, crescentic striolae (e.g. Figures 5, 6, 25, 26). Prosternum arched to tectiform; prosternal process lanceolate, bordered laterally, apex acuminately rounded. Metaventrite projecting anteriorly between mesocoxae; projection with elongate median groove to receive prosternal process; groove with marked central ridge, widening anteriorly. Discrimen and metacoxal suture strong, deep. Metacoxal lines strongly marked; metacoxal processes broadly rounded. Abdominal pleurite 2 without transverse ridges. Abdominal ventrites 2–6 with semicircular foveae laterally. Abdominal ventrite 6 with curved lateral wrinkles (Figures 11, 15).

Male. Foretarsi (Figure 12) with segments 1–3 strongly expanded and transverse, bearing four distinct rows of large articulo-setae ventrally; two on segment 1, one each on segments 2–3. Articulo-setal field bordered by dense, stiff, elongate, curved, hooked, golden setae. Segment 4 transverse; approximately 0.6–0.8 width of segment 3; with fields of stout, elongate setae of varying size laterally, inner setae curved anteriorly. Segment 5 elongate, with stout, elongate spines of varying size ventrally, close to lateral margins; basal spines curved interiorly. Foretarsal claws (Figures 12, 13) elongate, subequal, curved. Mesotarsi (Figure 12) with segments 1–3 expanded, transverse, bearing four distinct rows of large articulo-setae ventrally; two on segment 1, one each on segments 2–3. Articulo-setal field bordered by dense, stiff, elongate, curved, hooked, golden setae. Segment 4 elongate, with two rows of short, stout, stiff curved spines. Segment 5 strongly elongate, with two rows of stout spines ventrally, close to lateral margins. Mesotarsal claws elongate, subequal, curved. Abdominal ventrite 6 with weakly emarginated apex (Figure 11). Median lobe of aedeagus (Figure 14) elongate, strongly curved dorsally, with narrowly acuminate apex; lateral margins with transverse wrinkles in basal half; sinuate laterally towards apex in ventral view. Parameres (Figure 14) elongate, with dense setal fringe along internal margin, continued around apex, with scattered setae along external margin.

Female. Fore and mesotarsi simple, with ambulatory spines and setae only. Abdominal ventrite 6 (Figure 15) with bluntly pointed apex. Reproductive tract (Figure 16) with large, sclerotised bursa, with transverse corrugations and an elongate bursal gland; gland reddish in fresh material. Spermatheca elongate, fertilization and spermathecal ducts closely aligned, both relatively short. Gonocoxae (Figure 16) stout, elongate, with dense setation over entire surface and distinct apical penicil of setae. Laterotergites (Figure 16) elongate, with medial articulation. Gonocoxosternites (Figure 16) with bluntly pointed, setose apices. Female tract and genital structures do not appear to differ significantly between species and are not discussed further.

Remarks. Both molecular and morphological data suggest a close relationship between *Meladema* and the Nearctic *Hoperius* Fall, 1927 and *Neoscutopterus* J. Balfour-Browne, 1943 (Morinière et al. 2015, 2016, Miller and Bergsten 2014). Female genital tract anatomy, here described for the first time, is similar to that described and figured for *Neoscutopterus* (Miller 2001).

Meladema coriacea Laporte, 1835

Figures 3A, 4A, 5A, 6A, 7A, C, 8A, C, 9, 10, 11A, 12A, E 13A, 14A, 15A, 16, 17, 18D, 19, 20A–N, 23, 25C

Scutopterus coriaceus Dejean, 1833: 54, nomen nudum.
Meladema coriacea Laporte, 1835: 98 (partim); Sharp 1882: 631 (partim); Guignot 1932: 655 (partim); Gschwendtner 1936: 41 (partim); Guignot 1961: 769 (partim); Guéorguiev 1987: 127 (partim); Machado 1987: 60 (partim); Franciscolo 1979: 617 (partim);
Colymbetes coriaceus (Laporte, 1835): Aubé 1836: 94; Aubé 1838: 220 (partim); Wollaston 1865: 67 (partim).
Scutopterus coriaceus (Laporte, 1835): Wollaston 1871: 221 (partim).
Meladema coriaceum Laporte, 1835: Branden 1885: 95 (partim).

Notes. Of these earlier works, only Aubé (1836) provides sufficient detail to demonstrate that he is referring to *M. coriacea* as redefined below. His description states: "entièrement couvertes de petites impressions demi-circulaires, plus profondes à la partie convexe; en avant elles sont assez bien isolées; en arrière elles sont un peu confondues", details which allow the separation of *M. coriacea* from *M. lepidoptera* sp. n. (see below).

Laporte's original description (1835) could refer to either *M. coricaea* as redefined here, or *M. lepidoptera* sp. n., the only reference to the unique elytral sculpture of these beetles being "corps couvert de points très serrés, presque chagriné". As discussed by Evenhuis (2012), attempts to locate types of material described by Laporte between 1828 and 1840 have almost always proved fruitless, and it is generally assumed that this material is lost or destroyed. It seems Laporte donated his early collection (pre-1840 material) to the forerunner of the Smithsonian Institution in January 1842, and that these collections have been lost in a subsequent fire (Evenhuis 2012). As with

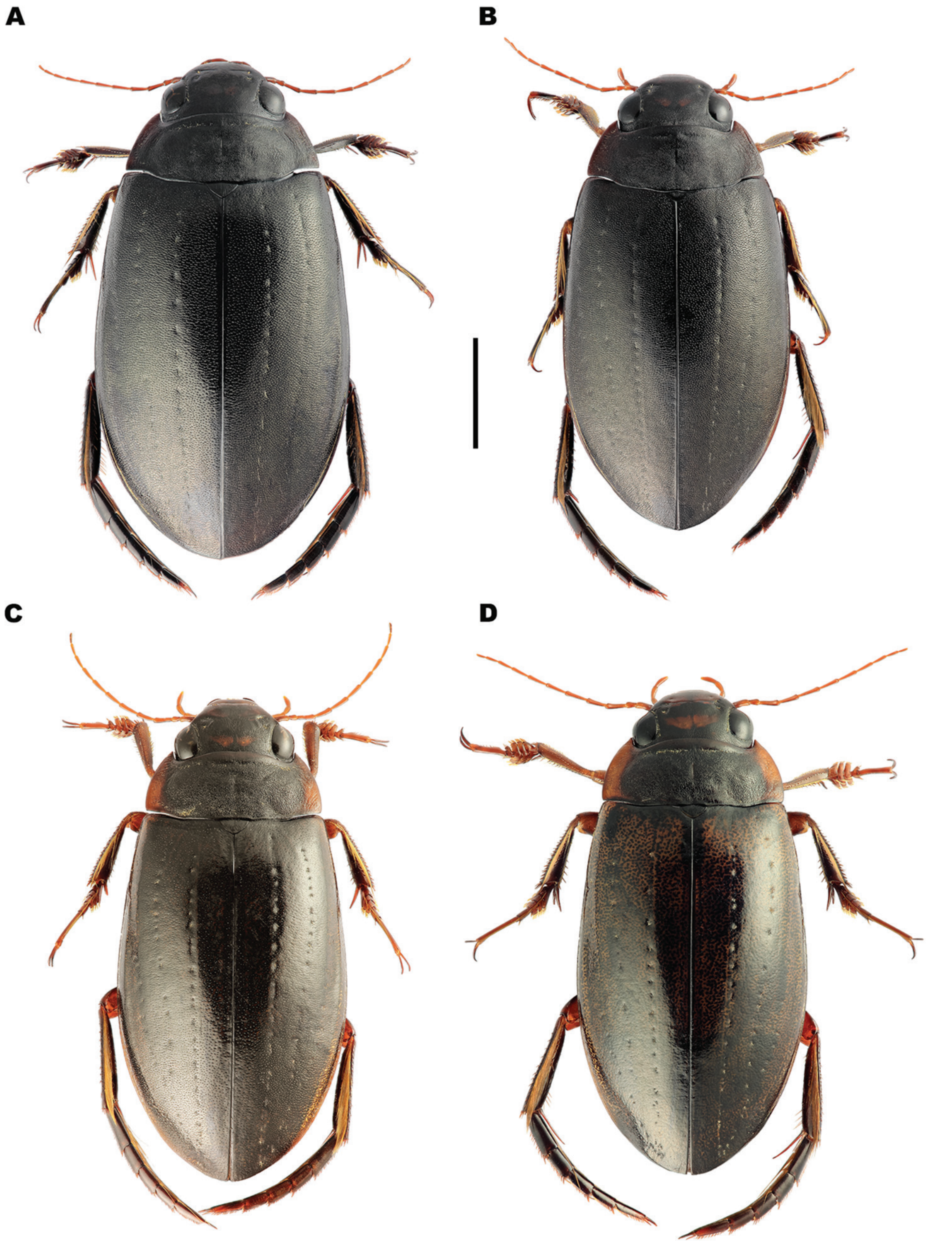

Figure 3. Dorsal habitus of *Meladema* species males. **A** *M. coriacea*, Spain, Cáceres, nr. Plasencia **B** *M. lepidoptera* sp. n., Corsica, Francardo **C** *M. imbricata*, La Gomera, El Cedro **D** *M. lanio*, Madeira, Rabacal. Scale bar = 5 mm.

other Laporte taxa, our attempts to locate the original type series of *M coriacea* have failed, no specimens being present in MNHN, despite Guignot (1961) suggesting that they may be located in this institution, nor in the BMNH or Melbourne Museum, Australia (S. Hinckley *pers. comm.*), the other two locations known to house some Laporte types (Sharp 1901, Horn et al. 1990). As a consequence, and in accordance with article 75.3 of the ICZN (1999), we here designate a neotype for *M. coriacea*, in order to establish its taxonomic identity and precise usage of the name. Laporte's original description cites "Midi de la France", a term used to describe a large part of the south of the country (not the centre, as suggested by Nilsson and Hájek, 2017a). All material we have genotyped, or examined, from southern France to date belongs to this same taxon.

Type locality. "Midi de la France".

Type material. Neotype ♀ (herein designated): "24/viii/2006 FRANCE Var// La Londe-les-Maures,// Vallon de Valcros, Les// Gaouby (ruines), pools in// Maravenne Torrent, 45m// P. Ponel leg." "43°09'45.74"N 9°15'38.82"E" "DNA Voucher// NHM-IRM11C" "*Meladema coriacea*// Laporte, 1835// NEOTYPE// D T Bilton & I Ribera des. 2017" (NMW). Dry card mounted, tissue sample in ethanol and DNA aliquote, both with same data, retained in IBE. Sequence data from the neotype has been deposited in GenBank with accession numbers AF428207 (COI-3') and AF428189 (16S ribosomal RNA).

Additional material examined (genotyped specimens). Algeria: 1 ♂ "24/viii/2006 ALGERIA// Aïn Damous 36 25.350N// 07 51.367E 523m V67// S. Bouzid leg." "Meladema// coriacea Laporte// Fery det. 2007" "DNA voucher// MNCN-HI6" (IBE); 1 ♀ "24/iii/2006 ALGERIA// Oued Bagrat V28// S. Bouzid leg." "Meladema// coriacea Laporte// Fery det. 2007" "DNA voucher// MNCN-HI4" (IBE). **Chad:** 1 ♀ "KOUDOU// VERS 2000 m.// 17 XI 49" "TIBESTI// MASSIF KOUSSI// PH. DE MIRÉ" "MUSÉUM PARIS" [blue label] "DNA voucher// IBE-AN739" (MNHN). **France, mainland:** 1 ♀ "24/viii/2006 FRANCE Var// La Londe-les-Maures,// Vallon de Valcros, Les// Gaouby (ruines), pools in// Maravenne Torrent, 45m// P. Ponel leg." "Meladema coriaceum// FRANCE, Dept. du Var.// La Londe-les-Maures,// Vallon de Valcros,// Les Gaouby (ruines),// pools in Maravenne// torrent, alto 45 m// 5 ix 99 P. Ponel" [HW] "DNA Voucher// NHM-IRM11A" (IBE); 1 ♀ "24/viii/2006 FRANCE Var// La Londe-les-Maures,// Vallon de Valcros, Les// Gaouby (ruines), pools in// Maravenne Torrent, 45m// P. Ponel leg." "DNA Voucher// NHM-IRM11B" (IBE). **Italy, Sicily:** 1 ♂ "SICILIA – PA// Bosco Ficuzzo// im beraio// 29.VII.88 le. M. ROMANO" [im beraio & date HW] "DNA voucher// IBE-AN691" (CTP). **Malta:** 1 ♀ "23/iv/2013 MALTA// between Mosta and L-Imtarfa// stony stream 35 53 60N// 14 24 14E A. Rudoy leg." "DNA voucher IBE-RA1064" (IBE). **Morocco:** 1 ♂ "17/vii/1997 MOROCCO// Tazzeka Nat. Park/ 4, ca.// 4 km tras desvío Cedral// I. Ribera leg." "DNA voucher// NHM--IRM1A" (IBE); 1 ♂ "17/vii/1997 MOROCCO// Tazzeka Nat. Park/ 4, ca.// 4 km tras desvío Cedral// I. Ribera leg." "DNA voucher// NHM-IRM1C" (IBE); 1 ♂ "2i/vii/1997 MOROCCO// Anti-Atlas, Oued Massa// I. Ribera leg." "DNA voucher// NHM-IRM2A" (IBE); 1 ♂ "2i/vii/1997 MOROCCO// Anti-Atlas, Oued Massa// I. Ribera leg." "DNA voucher// NHM-IRM2B" (IBE); 1 ex. "4 MOROCCO Taza 22.3.2008// mountain stream in Tazzeka N.P.// 1448m N34°03'09.2" W4°10'27.0"//

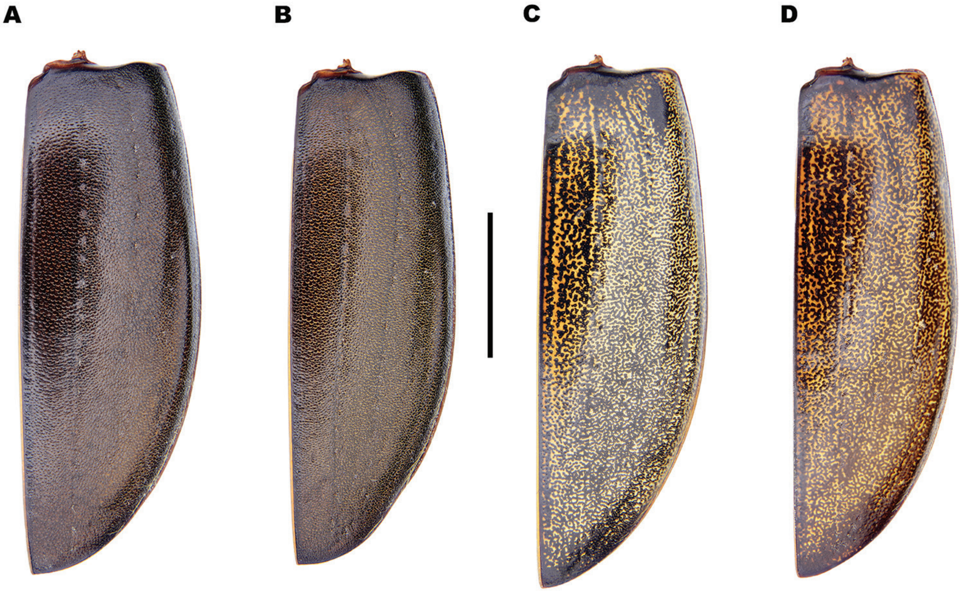

Figure 4. *Meladema* species males, colour pattern of isolated elytra (DNA voucher codes, where applicable). **A** *M. coriacea*, Spain, Murcia, Fte. Caputa **B** *M. lepidoptera* sp. n., Corsica, Cap Corse (NHM-IRM12F) **C** *M. imbricata*, La Gomera, El Cedro (NHM-IRM3A) **D** *M. lanio*, Madeira, Ribeira dos Cedros (NHM-IRM8A). Scale bar = 5 mm.

Ribera, Hernando & Aguilera leg." "DNA Voucher// NHM-IR47" (IBE); 1 ex. "58 MOROCCO 19.4.2001// 30°47'507"N 7°31'351"W// Tachokchte: Assif Siroua// c.1500 m I.Ribera & A.Cieslak leg." "DNA Voucher// NHM-IRM22a" (IBE); 1 ex. "58 MOROCCO 19.4.2001// 30°47'507"N 7°31'351"W// Tachokchte: Assif Siroua// c.1500 m I.Ribera & A.Cieslak leg." "DNA Voucher// NHM-IRM22b" (IBE); 1 ex. "60 MOROCCO 21.4.2001// 30°39'456"N 9°21'134"W// Immouzèr-des-Ida--Outanane// Assif Tanit, 550 m I. Ribera & A. Cieslak" "DNA Voucher// NHM--IRM21a" (IBE); 1 ex. "60 MOROCCO 21.4.2001// 30°39'456"N 9°21'134"W// Immouzèr-des-Ida-Outanane// Assif Tanit, 550 m I. Ribera & A. Cieslak" "DNA Voucher// NHM-IRM21b" (IBE). **Spain, mainland:** 1 ♂, "1 ES Girona, Port Bou// Cami de la Riera, 28.6.2013// 42°25'34.5"N 3°8'9.3"E// 65m I.Ribera & A.Cieslak leg." "DNA Voucher// IBE-DV293" (IBE); 1 ex. "Tarragona// Corbera d'Ebre// r. Gaia 10.1.2004 I.Ribera" "DNA Voucher// MNCN-AI104"(IBE); 1 ♂, "3 ES Huesca 6km S Bernués// Bco. de Bernués 6.9.2013// 42°26'38"N 0°36'51"W// 690m I.Ribera & A.Cieslak leg" "DNA Voucher// IBE-DV292" (IBE); 1 ex. "1 ES Castellón, Ballestar// r. Sénia, pools upstr. reservoir// 500m N40°41'41" E0°13'25.5"// I. Ribera leg. 2.6.2006" "DNA Voucher// MNCN-AI860" (IBE); 1 ex. "1 ES Castellón, Ballestar// r. Sénia, pools upstr. reservoir// 500m N40°41'41" E0°13'25.5"// I. Ribera leg. 2.6.2006" "DNA Voucher// MNCN-AI861" (IBE); 1 ♂ "8 ES Cáceres, PN Monfragüe// Arroyo de Trasierra, G. del Fraile// N39°50'07.2" W6°06'02.6"

317m// I.Ribera & P.Abellán leg. 13.6.2008" "DNA Voucher// IBE-DV291" (IBE); 1 ♂ "19/ix/1999 SPAIN Murcia// Fte. Caputa, Rio Mula// A. Millán leg." "DNA voucher NHM-IRM13a" (IBE); 1 ♂ "29/ix/1999 SPAIN Cordoba// Baena, Arroyo de las Beatas// 36 37 00N 04 20 00W// M. Baena leg." "DNA voucher// NHM-IRM14A" (IBE); 1 ♀ "29/ix/1999 SPAIN Cordoba// Baena, Arroyo de las Beatas// 36 37 00N 04 20 00W// M. Baena leg." "CORDOBA 9.99// M. BAENA" "DNA voucher// NHM-IRM14B" (IBE); 1 ♂ "29/ix/1999 SPAIN Cordoba// Baena, Arroyo de las Beatas// 36 37 00N 04 20 00W// M. Baena leg." "DNA voucher// NHM-IRM14C" (IBE); 1 ♀ "26/vii/1998 SPAIN Cadiz// Facinas// I. Ribera leg." "CADIZ 98// 10a" [HW] "DNA voucher// NHM-IRM10A" (IBE). **Spain, Mallorca:** 1 ex. "4 MALLORCA Mortixet// Rd. C710 tributary Te. Son March// I.Ribera & A.Cieslak 12.11.2000" DNA Voucher// NHM-IRM23a" (IBE); 1 ex. "4 MALLORCA Mortixet// Rd. C710 tributary Te. Son March// I.Ribera & A.Cieslak 12.11.2000" DNA Voucher// NHM-IRM23b" (IBE); 1 ex. "5 MALLORCA Els Casals// Rd. C710 Te. Son March// I.Ribera & A.Cieslak 12.11.2000" "DNA Voucher// NHM-IRM24a" (IBE). **Spain, Canary Islands:** 1 ex. "2 Gran Canaria 14.4.2001// S. Nicolas de Tolentino// Risco: bco. Guy Guy grande// I.Ribera & A.Cieslak leg." "DNA Voucher// NHM-IRM20a" (IBE); 1 ♀ "12/i/2000 Tenerife// Bco. Infierno 900m// coriacea" "DNA voucher// NHM-IRM18a" (CBP); 1 ♂ "14/i/2000 SPAIN Tenerife// Bco. de Masca// D. T. Bilton leg." "DNA voucher// NHM-IRM19A" (CBP); 1 ♂ "14/i/2000 SPAIN Tenerife// Bco. de Masca// D. T. Bilton leg." "DNA voucher// NHM-IRM19B" (CBP); 1 ex. "Tenerife, Chamorga// Bco. Roque Bermejo// 20.7.2006 A. Castro" "DNA Voucher// MNCN-AI1095" (IBE). **Tunisia:** 1 ♀ "13/iii/2005 TUNISIA// Cite el Morjne// 36 56 17.1N 8 47 29.8E// A. Castro leg." "Cite-el-Morjene// N36°56'17.1// E8°47'29.8// 13-03-2005" reverse "Meladema" [HW] "MNCN AI-84// DNA spare ex." [HW] "DNA voucher// MNCN-AI84" (IBE). **Turkey:** 1 ♀ "26/vii/2014 TURKEY Izmir// 6 km E of Phoca, head of// reservoir 38 39 37.3N// 26 49 23.9E 40m// I. Ribera & A Cieslak leg." "TR 15" [HW] "DNA voucher// IBE-DV294" (IBE). All with "*Meladema// coriacea* Laporte, 1835// D T Bilton [or I Ribera] det. 2017".

Additional material examined (non-genotyped specimens). Algeria: 8 ♂♂, 15 ♀♀ "Algerie// Yakouren// J Dayren// VI.VII. 1909" "MUSÉUM PARIS// 1952// COLL R OBERTHUR" [blue label] (MNHN); 1 ♂, 1 ♀ "Algerie// Yakouren// J Dayren// VI.VII. 1909" "MUSÉUM PARIS// 1952// COLL R OBERTHUR" [blue label] "Meladema// coriaceum// Cast.// de. M. Brancucci '82" [Latin name, describer & '82 HW] (MNHN); 1 ♀ "Algerie// Yakouren// J Dayren// VI.VII. 1909" "MUSÉUM PARIS// 1952// COLL R OBERTHUR" [blue label] "Meladema// coriacea// Cast." [HW] (MNHN); 1 ♀ "Meladema// coriaceum// O. Kaïrous, Mouz.// 8 avríl 06" [HW] "MUSÉUM PARIS// Coll. P. de Peyerimhoff// 1950" (MNHN); 1 ♀ "O. Kaïrous// mouzaïa// 8 avríl 06" [HW] "MUSÉUM PARIS// Coll. P. de Peyerimhoff// 1950" (MNHN); 1 ♂ "Meladema// coriaceum// Djurdj. 9" [HW] "MUSÉUM PARIS// Coll. P. de Peyerimhoff// 1950" (MNHN); 1 ♂ "Djurdjura// 14.VIII.1947" [HW] "MUSÉUM PARIS// Coll. P. de Peyerimhoff// 1950" (MNHN);

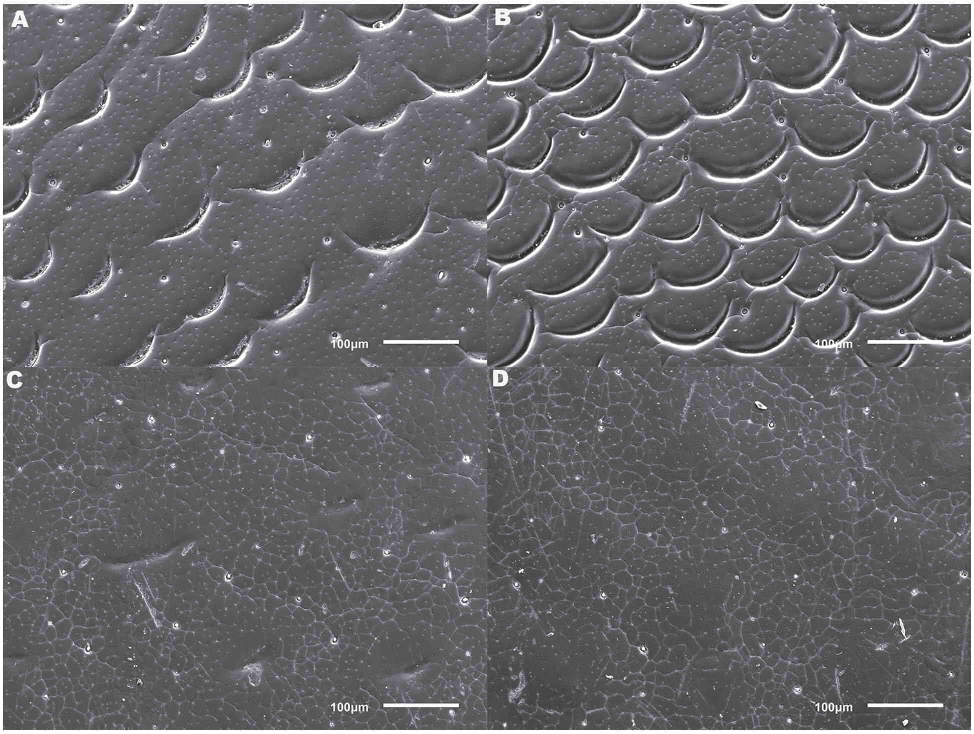

Figure 5. *Meladema* species males, elytral shoulder sculpture SEMs (DNA voucher codes, where applicable). **A** *M. coricaea*, Spain, Murcia, Fte. Caputa **B** *M. lepidoptera* sp. n., Corsica, Cap Corse (NHM-IRM12F) **C** *M. imbricata*, La Gomera, El Cedro (NHM-IRM3A) **D** *M. lanio*, Madeira, Ribeira dos Cedros (NHM-IRM8A).

1 ♀ “Aïn Takrarat// Mouzaïa// 28.VII.1934” [HW] “MUSÉUM PARIS// Coll. P. de Peyerimhoff// 1950” (MNHN); 1 ♂ “Oued In Dalay// Kouddu// Hoggar// 19.3.1925” [HW] “MUSÉUM PARIS// Coll. P. de Peyerimhoff// 1950” (MNHN); 1 ♂, 1 ♀ “Aguelmane// Sekkarasen// Hoggar 206// 29.3.1928” [HW] “MISSION DU// HOGGAR// FÉVRIER-MAI// 1928” “MUSÉUM PARIS// Coll. P. de Peyerimhoff// 1950” (MNHN); 1 ♂ “Oued Tinikert// Mt. Oudan, 1160// 16 avril 1928” [HW] “MISSION DU// HOGGAR// FÉVRIER-MAI// 1928” “MUSÉUM PARIS// Coll. P. de Peyerimhoff// 1950” (MNHN); 1 ♀ “Tassili des Ajjers// Gta. de Tikkal// 24 mars 1961” [HW] “MUSÉUM PARIS// Coll. P. de Peyerimhoff// 1950” (MNHN); 1 ♂ [green circle, illegible HW] “Meladema// coriaceum// Bône” [HW] (ISNB); 1 ♂ “C. coriaceus// Alger” [HW] “G. C. Champion Coll.// B. M. 1927-409” (BMNH); 1 ♂ “27// 95” “Setif.// Algerien” [HW] “Meladema// coriacea Lap.// det. H. Shaverdo 2015” [Latin name, describer & 15 HW] (NMW). **Chad:** 1 ♂ “KOUDOU// VERS 2000 m.// 17 XI 49” “TIBESTI// MASSIF KOUSSI// PH. DE MIRÉ” “Meladema// coriaceum Cast.// C. Legros det.” [Latin name & describer HW] (MNHN); 2 ♀♀ “KOUDOU// VERS 2000 m.// 17 XI 49” “TIBESTI// MASSIF KOUSSI// PH. DE MIRÉ” (MNHM); 1 ♀ “Bassin de Gorrom// 2500m.// 24 déc. 1958” “TIBESTI//

Emi Koussi// Bruneau de Miré" "DNA voucher// IBE-AN740" [not possible to amplify any DNA sequences] (MNHN); 1 ♀ "Tibesti// S. O du Kohoz// 2000m// 6. XI.49 Miré" [HW] "MUSÉUM PARIS// Coll. P. de Peyerimhoff// 1950" (MNHN). **France, mainland:** 1 ♂, 1 ♀ "S. France,// Cerbere.// C. Thomas &// R. L. Pocock.// 1900-215.// 18.IV.00" [date HW] (BMNH); 1 ♂ "S. France,// Cerbere.// C. Thomas &// R. L. Pocock.// 1900-215.// 18.IV.00" [date HW] "Scutopterus// coriaceus Aub," [HW] (BMNH); 1 ♀ "S. France,// Cerbere.// C. Thomas &// R. L. Pocock.// 1900-215.// 18.IV.00" [date HW] "Meladema// coriacea Cast.// C. R. Smith det. 1982" [Latin name, describer & 2 HW] (BMNH); 1 ♂, 3 ♀♀ " BANYULS// PYR. OR.// 12.8.1950" [12.8. HW] "BACHUFER" (NMW); 2 ♂♂, 1 ♀ "Banyuls s. Mer// 17.25 – V – 1951// F. G. Overlaet" "R, Mouchamps det.// Meladema coriacea Cast." [Latin name & describer HW] (ISNB); 1 ♂, 2 ♀♀ "Banyuls s. Mer// 17.25 – V – 1951// F. G. Overlaet" (ISNB); 1 ♂, 1 ♀ "21.8.84 France// Pyr. Or., ung. Banyuls// Bach Fery leg." [HW] "Mel.// coriacea// Cast. Fery det." [HW] (NMW); 1 ♂ "meladema// coriaceum" [HW] "Foix" [HW] "Coll. E. Dongé// Le Moult vendit" (ISNB); 1 ♂ "AVEYRON FR.// ST. ROME CERN.// VII-VIII 1940" "Coll. R. Van Dorsselaer" (ISNB); 1 ♀ "Provence" "Coll. P. Boppe// Le Moult vendit" (ISNB); 3 ♀♀ "France. 10.10.55.// Provence.// leg. Weygoldt." reverse "Coriaceum// Budberg" [HW] (NMW); 1 ♂ "Carcassonne// L. GAVOY" "♂" "MELADEMA// CORIACEUM// LAP." (ISNB); 1 ♀ "Carcassonne// Aude" [HW] "Ex. Coll. Bettinger" (ISNB); 1 ♀ "Toulon." [HW] "Gallia// mer." "Collectio// Kaufmann" (NMW); 1 ♂, 2 ♀♀ "Toulon// S. Frankreich" reverse "A// 7598" [HW] (NMW); 1 ♂, 1 ♀ "Gard" [HW] "ex coll R P David// ex coll Peres Jesuites// (le moult vendit)" (ISNB); 1 ♂ "La Sauzette" "Meladema// coriaceum" [HW] (ISNB); 1 ♂ "St. Etienne Valléefranc. de// s// Rogerie" [HW – Villefranche de Rougerie?] "Coll. A. Fauvel" "Coriacea// Lap." [HW] (ISNB); 1 ♂ "CAUX// HERAULT// IX 1928" [IX & 8 HW] "Collection// Dr. Guignot" "♂" "Guignot det// MELADEMA// coriacea Cast." [Latin name & describer HW] (ISNB); 1 ♂ "CAUX// HERAULT// IX 1928" [8 HW] "♂" "MUSÉUM PARIS// 1960// Coll F. Guignot" "coriacea Cast." [HW] (MNHN); 2 ♀♀ "CAUX// HERAULT// IX 1928" [8 HW] "♀" "MUSÉUM PARIS// 1960// Coll F. Guignot" (MNHN); 2 ♂♂ "neffies// HERAULT// H. LAVAGNE" [neffies HW] "Coriaceum" [HW] "Ex Coll. Bettinger" (ISNB); 1 ♀ "St GUILHEM// HERAULT// H. LAVAGNE" "Coriaceum" [HW] "Ex. Coll. Bettinger" (ISNB); 1 ♀ "Meladema// coriaceum" [HW] "Montpellier// (Hérault)" [HW] "Coll. E. Dongé// Le Moult vendit" (ISNB); 1 ♀ "Béziers// (He^{lt}.)" [HW] "Coll. E. Dongé// Le Moult vendit" (ISNB); 2 ♂♂ "Lozère" [HW] "Meladema// coriaceum" [HW] "Coll. E. Dongé// Le Moult vendit" (ISNB); 2 ♂♂ "Lozère" [small, circular brown label, no text] "Coll. Odier.// B. M. 1921-288" (BMNH); 1 ♀ "♀// 5188" [HW] "Coll. R. I. Sc. N. B.// France Marseille// Coll. Fairmaire// Coll. L. Pandellé" [Marseille & Coll. Fairmaire HW] "Coll. A. Fauvel// (ex. coll. Pandellé)// Meladema// coriacea Lap.// R.I.Sc.N.B. 17.819" [Latin name & describer HW] (ISNB); 1 ♀ "♀" [HW] "Coll. R. I. Sc. N. B.// France Marseille// Coll. Fairmaire// Coll. L. Pandellé" [Marseille & Coll. Fairmaire HW] "Coll. A. Fauvel// (ex. coll. Pandellé)// Meladema// coriacea Lap.// R.I.Sc.N.B.

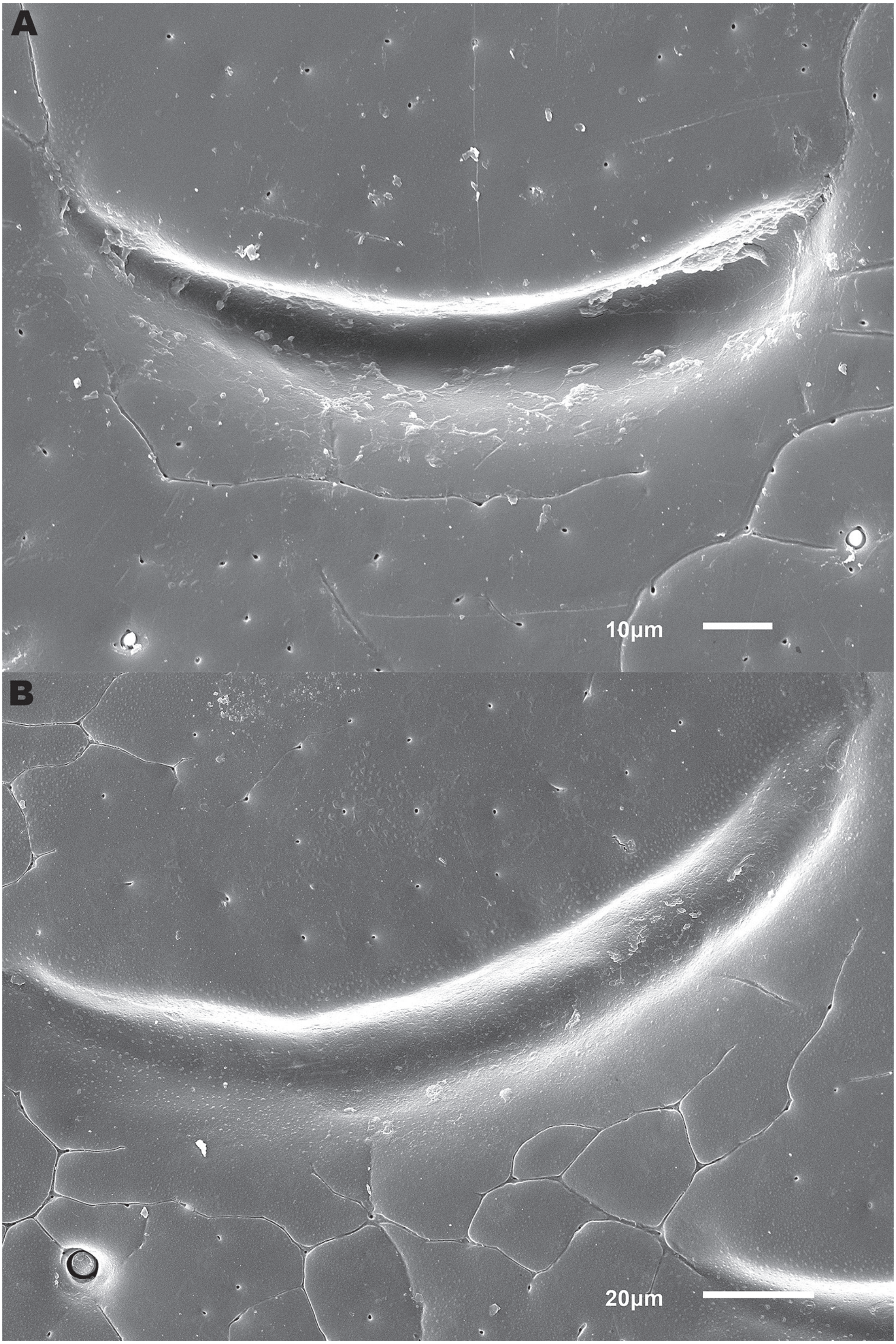

Figure 6. Details of elytral shoulder sculpture SEMs (DNA voucher codes where applicable). **A** *M. coriacea*, Spain, Murcia, Fte. Caputa **B** *M. lepidoptera* sp. n., Corsica, Cap Corse (NHM-IRM12F).

17.819" [Latin name & describer HW] (ISNB); 1 ♂ "♂// 5188" [HW] "Coll. R. I. Sc. N. B.// France Marseille// Coll. Fairmaire// Coll. L. Pandellé" [Marseille & Coll. Fairmaire HW] "Coll. A. Fauvel// (ex. coll. Pandellé)// Meladema// coriacea Lap.// R.I.Sc.N.B. 17.819" [Latin name & describer HW] (ISNB); 1 ♂ "♂// 5188" [HW] "Coll. R. I. Sc. N. B.// France Marseille// Coll. Fairmaire// Coll. L. Pandellé" [Marseille & Coll. Fairmaire HW] "Coll. A. Fauvel// (ex. coll. Pandellé)// Meladema// coriacea Lap.// R.I.Sc.N.B. 17.819" [Latin name & describer HW] "Colymbetes Clairville// coriaceus, Hoffm.// Marseilles" [HW] (ISNB); 6 ♂♂, 2 ♀♀ "St Cyr// Ravindu// Degoutant" [HW] (MNHN); 1 ♀ "Le Beausset.// Octobre" "Meladema// coriaceum Lap." [HW] (NMW); 1 ♀ "Le Beausset.// Mol. de Boissy" (NMW); 1 ♀ "M. coriaceum" [HW] "M. de Boissy// Le Beausset Var" [HW] (NMW); 1 ♀ "Rhonetal// mont. ol. Maures// östl. Aixen Provence" [HW] "M. J. MAURES// Det. VI/81//511" [HW] (NMW); 1 ♂, 1 ♀ "Nice" [HW] "coll. P. J. Roeflofs" (ISNB); 1 ♀ "Gallia merid// Agay (Var)// 15 Juli 14// W. Liebmann// Arnstadt" [15 HW] (NMW); 2 ♂♂ "Gallia merid// Agay (Var)// 15 Juli 14// W. Liebmann// Arnstadt" [15 HW] "Collectio// Paganetti" (NMW); 1 ♂, 1 ♀ "St. Maxime// Var// G. Audran" [HW] "R. Mus. Hist. Nat.// Belg. I.G. 14.406" (ISNB); 1 ♀ "Hyères" [HW] "coll. A. Fauvel" (ISNB); 1 ♂ "Nyons" [HW] "Colymbetes// coriaceus// 22" [HW] "coll. Delgrange" (ISNB); 1 ♀ "Colymbetes// coriaceus// Capt. P. Bauret" [HW] "Trinité-Victor// Juillet 1942" [HW] (ISNB); 1 ♂ "Colymbetes// coriaceus// Lap." [HW] "Oct. 46// Le Laghet// Trinite Victor" [HW] (ISNB); 1 ♀ "Colymbetes// coriaceus// Lap." [HW] "October 1945// Le Laghet// Trinité Victor" [HW] (ISNB); 1 ♂ "Cavalaire" [HW] "f. 532 Coll.//Dr. Mouchamps" [32 HW] "Pavel Riha leg.// MELADEMA// coriacea Cast." [Latin name & describer HW] (ISNB); 3 ♀♀ "261// 131" [blue, circular label, HW] reverse "Savoy" [HW] (BMNH); 1 ♂ "[illegible]// Coll. Chevrolat// Det. Sharp 82." [HW] "3306" "Colymbetes// coriaceus// Ex Aubé 220,// Gall. mer." [HW] (ISNB); 1 ♂ "Gallia m." (NMW); 1 ♂ "8367" [blue-green label, HW] "Gallia" [HW] "Fry Coll.// 1905-100" (BMNH); 1 ♀ "Gallia" [HW] "Fry Coll.// 1905-100" (BMNH); 1 ♀ "Colymbetes// coriaceus. Hoffm.// Gehin France" [HW] (BMNH); 1 ♀ "Coriaceus// Gallia" [blue label, HW] "Sharp Coll.// 1905-31." (BMNH); 1 ♀ "Gallia 10" "Coll. Liepolt" (ISNB); 1 ♂ "coriaceus Lap.// Gallia// Bien Bacher" [HW] "c. Epplsh.// Steind. d." (NMW). **Greece, mainland:** 1 ♂ "Attica// Dr. Kinper" [HW] "Collect.// Hausser" (NMW); 1 ♀ "Attica// Dr. Kinper" [HW] "punctulatus" [HW] "Collect.// Hausser" (NMW). **Greece, Aegina:** 1 ♀ "Griechenland// Aegina// F. Werner, 13 V. 37" [Aegina & 13 HW] (NMW). **Greece, Amorgos:** 1 ♀ "Graecia, KYKL.// Amorgos// P. Velensky lgt.// 13.-16.5.1984" "Coll.// HENDRICH// Berlin" (ZSM); 1 ♀ "Graecia, KYKL.// Amorgos// 13.-16.5.1984// P. Velensky lgt." "Coll.// HENDRICH// Berlin" (ZSM). **Greece, Chios:** 1 ♀ "GR: Chios// Mai 1980// lg. Bilak, Kritscher" (NMW). **Greece, Corfu:** 1 ♂, 1 ♀ "GREECE: NE Corfu (GR3)// ca. 1.5 km W Zigos// 200 m a.s.l., 19.VII.08// leg. M. A. Jäch" "small shallow residual// pool in river bed// 39°43'44.4"N// 19°46'38.3"E" "Meladema// coriacea Laporte// Fery det. 2010" (NMW); 1 ♂, 2 ♀♀ "28/v/2017 Greece Corfu// nr. Zigos 233 m// 39 43 40.6N 19 46 41.0E// C R Turner leg." (CBP). **Greece, Ios:** 1 ♂ "Kykladen// Ios, Buch

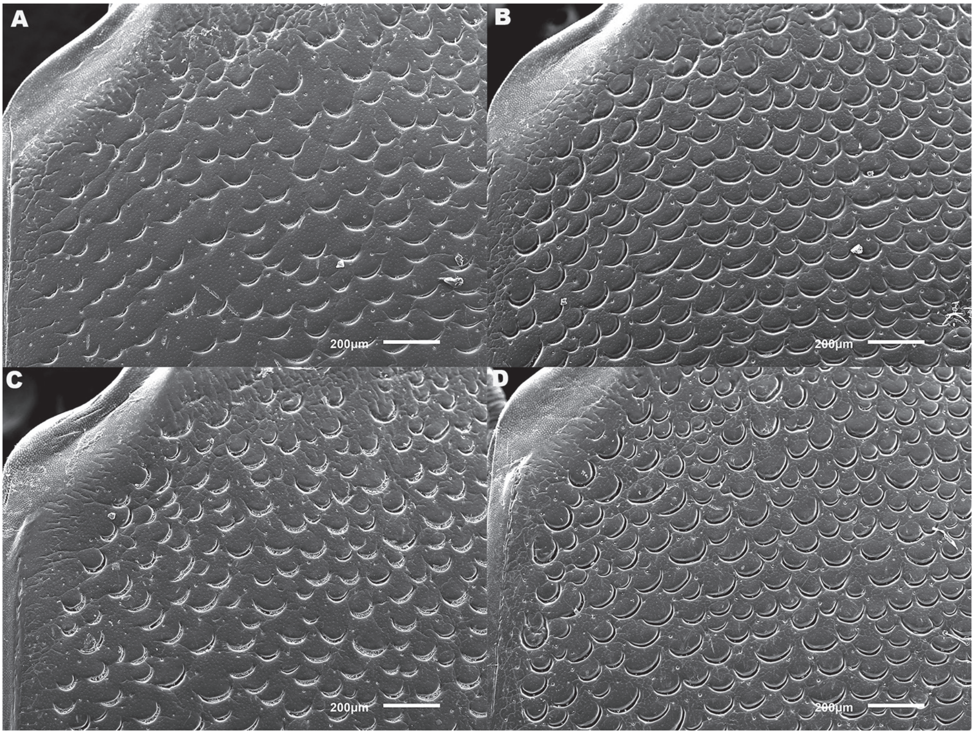

Figure 7. *Meladema* species elytral shoulder sculpture SEMs (DNA voucher codes where applicable). **A** *M. coriacea*, male, Spain, Murcia, Fte. Caputa **B** *M. lepidoptera* sp. n., male, Corsica, Cap Corse (NHM-IRM12F) **C** *M. coriacea*, female, Spain, Murcia, Fte. Caputa **D** *M. lepidoptera* sp. n., female, Corsica, Porto-Vecchio (NHM-IRM12A).

von// Milopotamos" "leg. Schönmann// 9. April 1981" [first 9 HW] (NMW); 1 ♀ "Kykladen// Ios, Buch von// Milopotamos" "leg. Schönmann// 8. April 1981" [first 8 HW] (NMW). **Greece, Kithira:** 1 ♀ "GR-Kithira (4)// Arlemonas 8.V.76// leg. Malicky" "Melaema// coriacea Cast.// det. Wewalka 76" [HW] (NMW). **Greece, Milos:** 3 ♂♂, 1 ♀ "GR-MILOS 19.9.90// 1km E. Sider ianos.// leg. M. Jäch (5)" (NMW). **Greece, Naxos:** 1 ♀ "GR-Naxos V.1988// leg. Bilak// et Kritscher" (NMW); 2 ♀♀ "GR-Naxos (13)// Potamia 26.V.76// leg. Malicky" (NMW). **Greece, Poros:** 1 ♂ "GR-Poros (2)// Kampos 17.V.74// leg. Malicky" (NMW). **Greece, other:** 1 ♀ "Griechenland// Kylhima// F. Werner, 26.V.37" [Kylhima & 26 HW] (NMW); 1 ♂ "Greece// Merlin Coll.// 96-275" (BMNH); 1 ♂ "Greece// Merlin Coll.// 96-275" "Spec. nov.// Hymettus" [pink label, HW] "Received with// this name// from Merlin// C. O. W." [Merlin HW] (BMNH); 1 ♂ "Graecia" "Meladema// coriaceus" [HW] "Coll. Plason" (NMW). **Italy, mainland:** 1 ♂ "Grotta di// Pastena// Italie merid." [HW] "Meladema// coriacea Cast." [HW] "Brit. Mus.// 1963-344." (BMNH); 1 ♂, 2 ♀♀ "Meladema// coriaceum" [HW] "Italie" [HW] "Coll. E. Dongé// Le Moult vendit" (ISNB); 1 ♂ "Coriaceus// Italia F" [HW] "R. Mouchamps det.// Meladema// coricaea Cast." [Latin name & describer HW] (NMW); 1 ♀ "Meladema// coriaceum"

[HW] “Calabre” [HW] “Coll. E. Dongé// Le Moult vendit” (ISNB); 1 ♀ “Gerace, Calab.// Paganetti” “Collectio// Paganetti” (NMW); 1 ♀ “Gerace, Calab.// Paganetti” “Collectio// Paganetti” “Meladema// coriaceum” [HW](NMW). **Italy, Pontine Islands:** 2 ♂♂, 3 ♀♀ “Ins. Pont. - @ nos// auf Tamanis// 12-4-57// Dr. Eckerlein leg. [HW] (NMW). **Italy, Sicily:** 1 ♂ “Madricia// Ragusa” [HW] “3306” (ISNB); 1 ♀ “Monts Madonie 74” “E. Ragusa” (BMNH); 1 ♀ “Castelbueno// Ragusa” [HW] “3307” (ISNB); 2 ♂♂, 1 ♀ “Sicil.” “Collectio// Kaufmann” (NMW); 1 ♀ [circular label, black margin, no text] “Sicilia” [HW] “alte// Sammlung” (ZSM); 1 ♀ “Sic.” “Sammlung// C. Müller” (ZSM); 1 ♀ “Italia: Sicilia – PA// MTE. Maganoce// 900 M. Ü. N.” [HW] (ZSM). **Malta:** 2 ♀♀ “Prof. Barthet// Malta” “29.8.25// Malta” [HW] “R.L.S.N.B.//I.G. 17.619” (ISNB); 1 ♀ “Malta” [HW] “Ex. Coll. Bettinger” (ISNB); 1 ♂ “Malta” “G.C. Champion Coll.// B. M. 1929-409” “Meladema// coriaceum Lap.// Malta” [HW] (BMNH); 1 ♂ “Buskett Gdns.// Malta// 12.XII.55.// G. V. P. Sewell” [HW] “Meladema// coriacea Cast// C. R. Smith det. 182” [Latin name, describer & 2 HW] (BMNH); 1 ♂ “MALTA// Chadwick Lakes// Mars ‘85// D. Johnson” [HW] (NMW). **Morocco:** 1 ♂, 1 ♀ “Tachdirt// Marocco// Schwingenschuss” [HW] “Coll. Liepolt” (ISNB); 7 ♂♂, 5 ♀♀ “Maroc: Azrou// 6-12-vii-1934 (1350m)// A. Ball 56 M 22” “R. Mus. Hist. Nat.// Belg. I.G. 10.417” “A. Ball det. 1935// Meladema// coriacea Cast.” [1935, Latin name & describer HW] (ISNB); 1 ♀ “Middle Atlas Mts// Oviduane// 2,000ft.” “MOROCCO:// K. Chapman &// J.W.S. Pringle.// B.M. 1934-554” ‘MELADEMA// coriacea// Laporte” [HW] “det. J. Hajek// xi. 2008” (BMNH); 4 ♂♂, 4 ♀♀ “Middle Atlas Mts// Oviduane// 2,000ft.” “MOROCCO:// K. Chapman &// J.W.S. Pringle.// B.M. 1934-554” (BMNH); 1 ♂ “Middle Atlas Mts// Oviduane// 2,000ft.” “MOROCCO:// K. Chapman &// J.W.S. Pringle.// B.M. 1934-554” “Oum en Rhio Aug 20th// large beetle 400” [folded, HW, 400 in a box] (BMNH); 1 ♀ “MOROCCO// Dayet Ifrah (lake)// 16 km. E.N.E. Ifrane// 28.V.1961.” [all except Morocco HW] “1334// P. N. Lawrence// B. M. 1961-328” [HW] (BMNH); 1 ♀ “MOROCCO// Great Atlas Mts.// Ijoukak. 3,900ft.// 3.vi.1936” [3 HW] “K. H. Chapman// & G. A. Bisset.// B. M. 1936-527.” (BMNH); 1 ♀ “S. MORROCCO// TIZI-N-BACHKOUM env.// 25.4.1995// P. Prüdek leg.” “Coll.// HENDRICH// Berlin” “Meladema// coriacea// Cast.// HENDRICH det. 1996” [name & describer HW] (ZSM); 1 ♂ “Imi n’ Ouaka// 1500m.” “Maroc// 1-15 Sept.” “♂” “♂” “MUSÉUM PARIS// 1960// Coll F. Guignot” (MNHN); 2 exx. “71 MOROCCO 8.4.2007// Tizi-n’Rechou, Kerrouchèn// stream on rock N pass, rd. 3437// 1570m N32°48'22.1" W5°16'13.9"// Aguilera Hernando & Ribera leg.” (IBE); 1 ♀ “99 MOROCCO Chefchauen// 13.2.2015 afl. Oued Laou 150m// 35°17'57.0"N 5°12'55.5"W// Ribera, Millán & Velasco leg.” (IBE); 1♂, 1♀ “Morocco// Âit-Iftene// 29, Oued Ait-Baha// 220797 Ribera, Aguilera, Hernando, Millán” (IBE); 1♂, 1♀ “Morocco// Sidi-Ibrahim// 17, 77.5 km S Guercif// 150797 Ribera, Aguilera, Hernando, Millán” (IBE); 1 ex. “MOROCCO Haut Atlas// NE Tizi-n-Test, 1710m No.18// 30°54'12N 08°18'39W// 30.12.2002 V.Assing & P.Wunderle” (IBE). **Portugal, mainland:** 1 ♂ “Portugal// Oliveira” [HW] “3306” (ISNB); 3 ♀♀ “Portugal// Oliveira” [HW] “3307” (ISNB); 1 ♀ “Portugal// Oliveira” [HW] “♀” (ISNB); 1 ♂

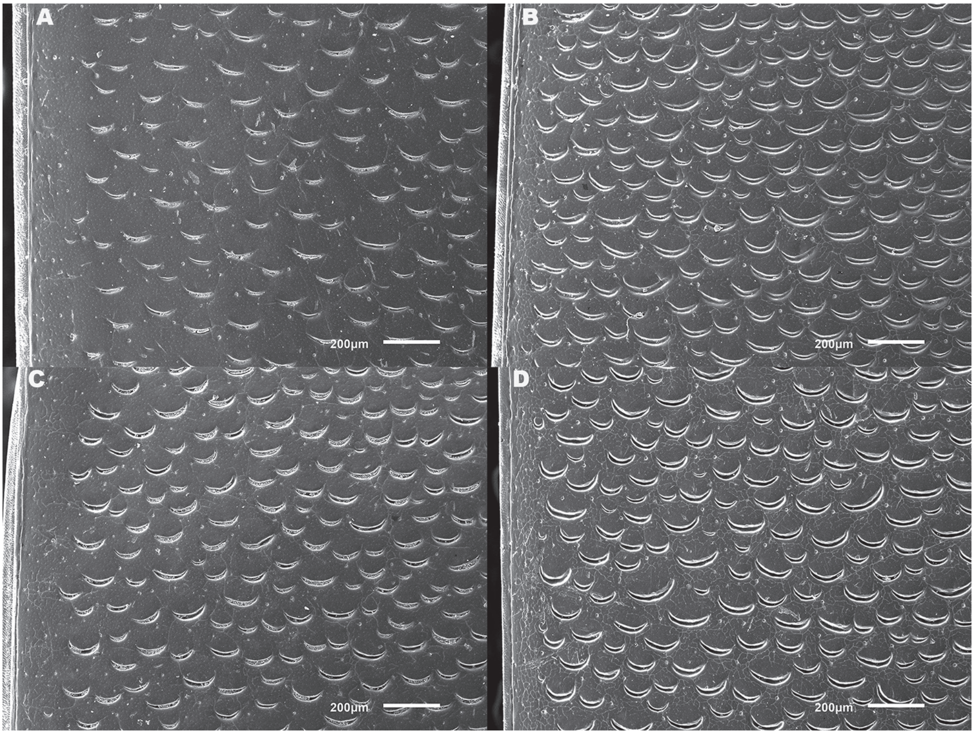

Figure 8. *Meladema* species elytral middle sculpture SEMs (DNA voucher codes where applicable). **A** *M. coriacea*, male, Spain, Murcia, Fte. Caputa **B** *M. lepidoptera* sp. n., male, Corsica, Cap Corse (NHM-IRM12F) **C** *M. coriacea*, female, Spain, Murcia, Fte. Caputa **D** *M. lepidoptera* sp. n., female, Corsica, Porto-Vecchio (NHM-IRM12A).

"Portugal// Oliveira" [HW] (ISNB); 8 ♂♂, 10 ♀♀ "PORTUGAL:// Serra do Malhao.// 8.v.1966// J. Abraham &// M. E. Bacchus.// B. M. 1966-296" "M. E. Bacchus// B. M. 1966-296" (BMNH); 1 ♀ "PORTUGAL:// Algarve. Rio Seco.// 250m ca. 10km.// W. Barranco de// Velho. 10.v.1966." (BMNH); 1 ♀ "PORTUGAL:// Algarve. Rio Seco.// 250m ca. 10km.// W. Barranco de// Velho. 10.v.1966." "Meladema// coriacea cast.// J. Balfour-Browne det.// xii. 1972" (Latin name, describer & 72 HW) (BMNH); 1 ♀ "5/v/93 Portugal// Viana do Castelo// Serra do Minho// stream @ ca. 700m// D. T. Bilton leg." [HW] (CBP); 1 ♀ "PORTUGAL: Traz os Montes// Carrazeda de Anciais// 745m., 7.viii.1966" "slow weedy// stream" "Brit. Mus.// 1973-562" "Meladema// coriacea Cast.// J. Balfour-Browne det.// IX 1969" [Latin name, describer, IX & last 9 HW] (BMNH). **Spain, mainland:** 1 ♂, 2 ♀♀ "Cataluna// Vall. x-42// Español" [HW] "R. Mouchamps det 1948// MELADEMA// coriacea Cast." [8, Latin name & describer HW] (ISNB); 2 ♂♂ "Vallvidrera// Barcelona// VIII.1948// Español" [HW] "R. Mouchamps det.// Meladema// coriacea Cast." [Latin name & describer HW] (ISNB); 2 exx. "Barcelona// Montseny d'Amunt// Riachuelo: remanso// 290988 I. Ribera" (IBE); 1 ♂ "Girona// Capmany// Estanys: alberca// 041189 I.Ribera" (IBE); 3 ♂♂, 1 ♀ "Girona// Capmany// Estanys: alberca// 110389 I.Ribera"

(IBE); 4 ♂♂, 3 ♀♀ "Girona// Capmany// Estanys: alberca// 281090 I. Ribera" (IBE); 6 ♂♂, 3 ♀♀ "Girona// Capmany// Estanys: alberca// 251190 I. Ribera" (IBE); 4 ♂♂, 3 ♀♀ "Girona// Capmany// Estanys: alberca// 120191 I.Ribera" (IBE); 2 ♀ "Girona// Capmany// Estanys: alberca// 171294 I. Ribera & P. Aguilera" (IBE);1 ♂ "Girona// Capmany// Estanys: alberca// 100994 I.Ribera & P.Aguilera" (IBE); 2 exx. "1 GIR La Junquera 4.x.2014// estanys de Capmany: alberca// 42°24'20.5"N 2°54'8.0"E// 188m I. & B.Ribera leg." (IBE); 1 ♂ "Girona// Capmany// Querafumat: abrevadero 1// 251190 I. Ribera" (IBE); 2 ♂♂, 1 ♀ "2 ES Girona, Port Bou// Cami de la Riera, 10.5.2012// N42°25'38.2" E3°08'13.4"// 81m I.Ribera & A.Cieslak leg." (IBE); 2 ♂♂, 2 ♀♀ "Girona// Sta. Pau// Rio Ser: remanso 1b// 260890 I. Ribera" (IBE); 1 ♀ "Girona// Sta. Pau// Rio Ser: remanso 2// 260890 I. Ribera" (IBE); 2 ♂♂, 1 ♀ "1 ES Girona, Port Bou// Cami de la Riera, 28.6.2013// 42°25'34.5"N 3°8'9.3"E// 65m I. Ribera & A.Cieslak leg." (IBE); 1 ex. "Tarragona// Vila-rodona// Jardín: alberca// 110985 M.Galán" (IBE); 1 ex. "Tarragona// Vila-rodona// Jardín: alberca// 201085 I.Ribera" (IBE); 2 ♂♂, 2 ♀♀ "16/v/1994// SPAIN Tarragona// stream 2km SW of// Esblada D. T. Bilton leg." (CBP); 1 ♂, 3 ♀♀ "3 ES Huesca 6km S Bernués// Bco. de Bernués 6.9.2013// 42°26'38"N 0°36'51"W// 690m I.Ribera & A.Cieslak leg" (IBE); 3 exx. "1 ES Castellón, Ballestar// r. Sénia, pools upstr. reservoir// 500m N40°41'41" E0°13'25.5"// I. Ribera leg. 2.6.2006" (IBE); 1 ♂, "Teruel// Calaceite// Riu Matarranya// 240794 I.Ribera & P.Aguilera" (IBE); 1 ♂, 1 ♀ "19/ix/1999 SPAIN Murcia// Fte. Caputa, Rio Mula// A. Millán leg." (IBE); 1 ♂ "19/ix/1999 SPAIN Murcia// Fte. Caputa, Rio Mula// A. Millán leg." "Fte Caputa// R. Mula 19-9-99// A. Mellado" [HW] (IBE); 1 ♂ "19: SPAIN: CACERES:// 21 km S of Aldeanuo// del Camino: granite// stream 18 April 1985" (CBP); 1 ♂, 1 ♀ "12/v/1990 SPAIN Cáceres// stream with pools 7km N of// Plasencia on N630 road" (CBP); 2 ♀♀ "27/iv/1993// Spain Extremadura// Cáceres stream by N630// 15km N of Plasencia" (CBP); 1 ex. "3 ES Cáceres, PN Monfragüe// Arroyo de Malvecino// N39°51'04.0" W6°02'22.3" 284m// I.Ribera & P.Abellán leg. 12.6.2008" (IBE); 1 ♀ "SPAIN: Cordoba.// Posadas – Villaviciosa Rd.// 20 Km N. of Posadas// Arroyo Calderas. 500m.// 14.V.1967" "Meladema coriacea// CAST. I. RIBERA det 1990" [HW] (BMNH); 1 ♂ "MALAGA// H. Clark.// May 1856" "Fry Coll.// 1905-100" (BMNH); 2 ♀♀ "MALAGA// H. Clark.// May 1856" (BMNH); 1 ex. "1 ESP. Malaga 3.1.03// Villanueva del Trabuco// r. Guadalhorce, cta. MA156// I.Ribera & A.Cieslak leg." (IBE); 1 ♂, 1 ♀ "Almería// Tabernas// Rbla. de Tabernas: charca 1// 110597 I.Ribera & A.Millán" (IBE); 1 ♂ "Nerja" [HW] (MNHN); 1 ♂ "24/iv/1993// Spain Andalucia Cadiz// Drying stream by N340// 28km N of Tarifa" (CBP); 1 ♀ "17: SPAIN: HUELVA: 1 km// S. of Santa Ollala del// Cala: weedy stream:// 18 April 1985// R.B. Angus & G.N. Foster" "Meladema corac" [HW] (BMNH); 2 ♂♂, 1 ♀ "17: SPAIN: HUELVA: 1 km// S. of Santa Ollala del// Cala: weedy stream:// 18 April 1985// R.B. Angus & G.N. Foster" "R. B. Angus// BMNH(E) 2010-22" (BMNH); 1 ♂, 1 ♀ "Hispania" [HW] "Meladema// Lap.// coriacea// Cast." [HW, genus name on green label, glued on top of original] "Coll. Martin// Le Moult vendit" (ISNB); 1 ♂, 1 ♀ "Hispan" [HW] "Fry Coll.// 1905-100" (BMNH); 1 ♂ "Hispa// nia" [HW] "57.// 107." [blue, circular label, HW]

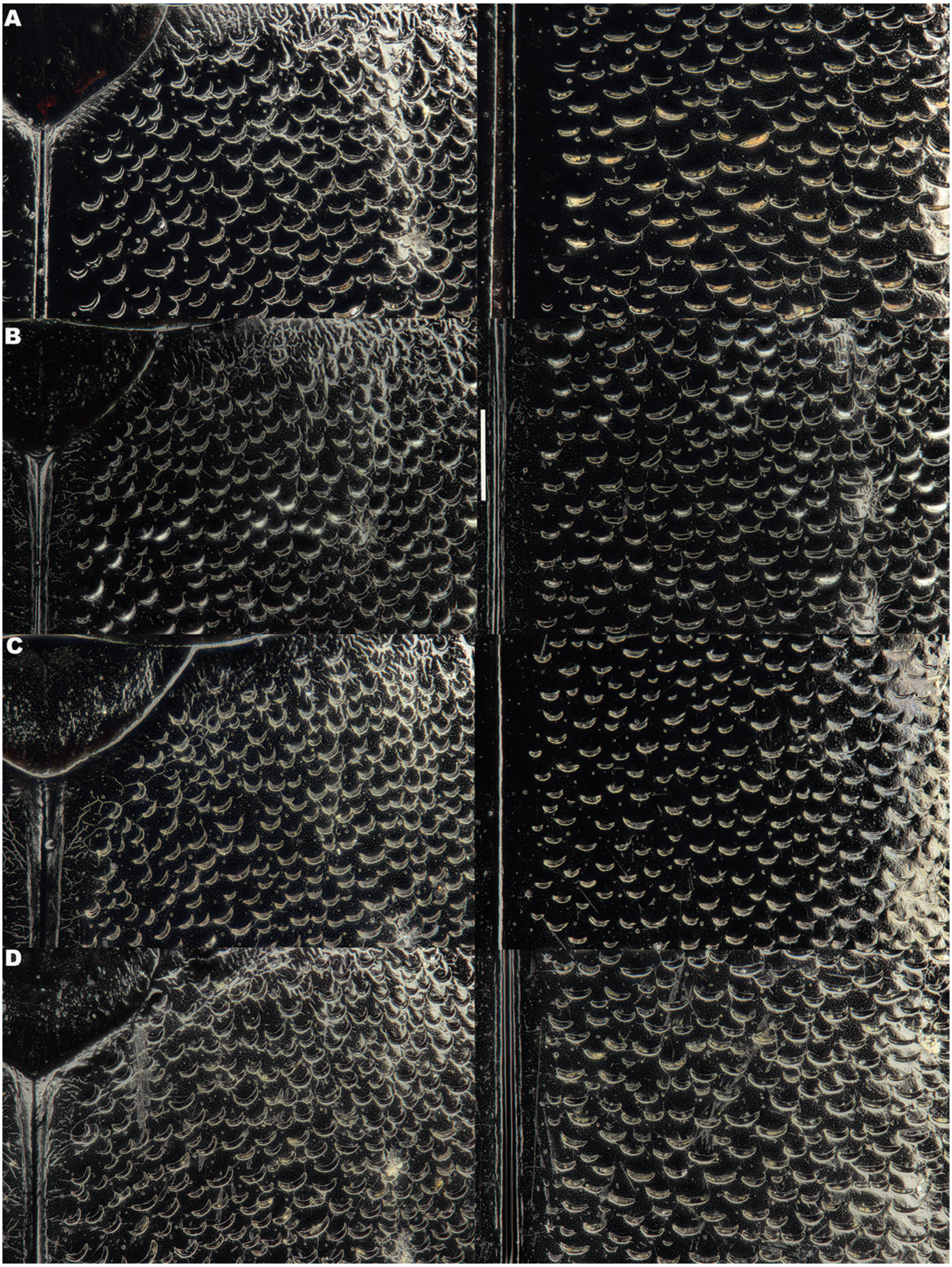

Figure 9. *Meladema coriacea* female elytral sculpture; shoulder and middle left and right, respectively (DNA voucher codes). **A** neotype, France, Var, La-Londe-les-Maures (NHM-IRM11C) **B** Spain, Córdoba, Baena (NHM-IRM14B) **C** Morocco, Tazzeka (NHM-IRM1A) **D** Algeria, Oued Bagrat (MNCN-HI4). Scale bar = 0.5 mm.

(BMNH). **Spain, Mallorca:** 2 exx. “1 Mallorca, Lloseta 13.5.2007// te. des Estorall, potabilizadora// 170m N39°43'49.7" E2°50'04.6"// I.Ribera & A.Cieslak leg.” (IBE); 1 ♂, 1 ♀ “2 Mallorca, Bunyola 13.5.2007// te. de Bunyola, Ma 2100 pk 5.5// 455m N39°43'24.7" E2°43'15.7"// I.Ribera & A.Cieslak leg.” (IBE) ; 1 ♂ “Inca, Majorca.// March.// O. Thomas &// R. I. Pocock.// 1900-215” (BMNH). **Spain, Canary Islands:** 2 ♀♀ “Canary Is.// Gran Canaria,// Sta Brigida.// 5.ix.1927.// E. Appenhagen.// B. M. 1928-20” [5 & ix HW] (BMNH); 1 ♂ “Canary Is.// Gran Canaria,// Sta Brigida.// 5.ix.1927.// E. Appenhagen.// B. M. 1928-20” [5 & ix HW] “Colymbetes// coriaceus, Cast.// 5-9-27.// 206” [HW] (BMNH); 1 ♀ “CANARY IS.// Gran Canaria// 29.xii.92-11.i.93” “Bco de// Ayagaures// ca 100 m.” [HW] “P. M. Hammond// B. M. 1993-11” “coriaceus” [HW] (BMNH); 1 ♂ “Barranco de// Temise près Haria// (Lanzarote) 2” [HW] “coll. A. Fauvel” (ISNB); 1 ♀ “Colymbetes// coriaceus Hoffm.// Bajamar XI. 1909” [HW] “Le Moult vend.” (ISNB); 1 ♂ “Teneriffa// geibelez” [HW] “DON// P DUPUIS” (ISNB); 1 ♀ “Colymbetes Clairv.// 203 coriaceus Lap.// 6 ex Teneriffe 1904 (Prevost):Elliott Coll.” [HW, folded] “Claude Morley// Collection// B.M. 1952-159” “Meladema// coriacea Cast.// C. R. Smith det. 1982” [Latin name, describer & 2 HW] (BMNH); 2 ♂♂, 1 ♀ “Claude Morley// Collection// B.M. 1952-159” [part of same series as previous] (BMNH); 1 ♂ “Claude Morley// Collection// B.M. 1952-159” “Meladema// coriacea Cast.// C. R. Smith det. 1982” [Latin name, describer & 2 HW] [part of same series as previous] (BMNH); 2 ♂♂, 2 ♀♀ “Canary Is.// Teneriffe,// Guajonje,// 17.iii.1927// E. Appenhagen” [Guajonje & date HW] (BMNH); 1 ♀ “Canary Is.// Teneriffe,// Guajonje,// 17.iii.1927// E. Appenhagen” [Guajonje & date HW] “Colymbetes// coriaceus, Lap.// G. J. Arrow det.” [Latin name & describer HW] (BMNH); 1 ♂ “Tenerife// Barr. Bufadno” [HW] “6.2.1949// Fernandez” [6, 2 & last 9 HW] “Brit. Mus.// 1951-318” “Meladema// coriaceum Lap.// Harald Lindb. det” [Latin name & describer HW] (BMNH); 1 ♂ “ES: Tenerife// Masca 12 April// 1991 AN Nilsson” “Meladema coriacea// Laporte, 1835// Det AN Nilsson 1991” (CBP); 1 ♂ “April 1998 SPAIN// Islas Canarias Tenerife// Bco. del Infierno Pools// D.T. Bilton leg.” (CBP); 1 ♂, 1 ♀ “April 1998 SPAIN// Islas Canarias Tenerife// Bco. de Masca Pools// D.T. Bilton leg.” (CBP); 1 ♀ “29/xi/97 Tenerife// Anaga Massif – stream// @ Iguana D.T. Bilton” [HW] (CBP); 1 ♀ “CANARIES” “Coll. R. Van Dorsselaer” (ISNB); 1 ♀ “Canary Is.// 1903 (Prevost)// coll. Elliott . 36” [HW] “Claude Morley// Collection// B.M. 1952-159” (BMNH). **Tunisia:** 3 ♀♀ “TUN.: 3.8.91(7)// Beni Melir SE// A. Draham, Schödl” (NMW). **Turkey:** 1 ♀ “Asia min. occ.// Izmir (H. Mudja)// 20 m. St. 71// 8-V-’31 (Orch.)” “Reg. Mus. Hist. Nat.// Belg. I.G. 9642” “A. Ball det. 1935// Meladema// coriacea Cast.” [1935, Latin name & describer HW] (ISNB). **Without locality data:** 1 ♂ “Coll Abcedal” [HW] “Colymbetes// coriaceus” [HW] “R.I.Sc.N.B. 21.418// Coll. P. de Moffarts” “Meladema// coriaceum// Lap.” [green label, HW] (ISNB); 1 ♂ “Coll Abcedal” [HW] “Coll. P. de Moffarts” (ISNB); 1 ♀ “Meladema// coriaceum// Coll. Hevon” [HW] “Ex coll. Bettinger” (ISNB); 1 ♂ “121” “Meladema// coriaceum” [HW] “Ex. Coll. Bettinger” (ISNB); 1 ♂ “ex coll R P David// ex coll Peres Jesuites// (Le Moult vendit)” “coriaceus Cast.// Region mediterranee” [HW] (ISNB); 1 ♂ “Coll. P. Boppe// Le

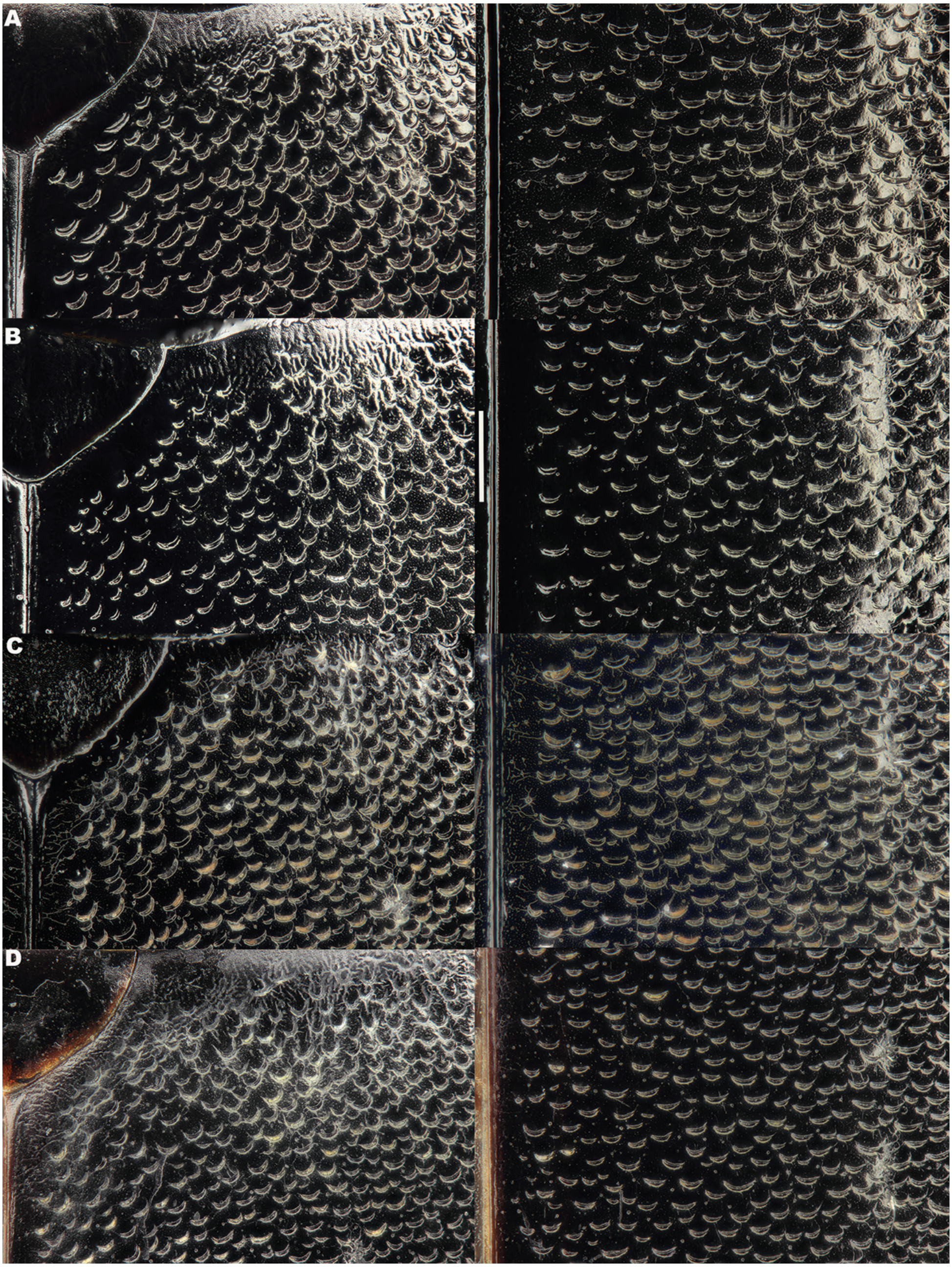

Figure 10. *Meladema coriacea* elytral sculpture; shoulder and middle left and right, respectively (DNA voucher codes). **A** Female, Turkey, Izmir (IBE-DV294) **B** male, Spain, Córdoba, Baena (NHM-IRM14A) **C** male, Morocco, Oued Massa (NHM-IRM2A) **D** male, Algeria, Aïn Damous (MNCN-HI6). Scale bar = 0.5 mm.

Moult vendit" "Meladema// coriaceum// Cast." [HW] (ISNB); 1 ♂ "Meladema// coriaceum" [HW] "Coll. E. Dongé// Le Moult vendit" (ISNB); 1 ♂ "H Guyon" [HW] "Coll. E. Traizet// Le Moult vendit" (ISNB); 7 ♂♂, 4 ♀♀ "coll. A. Fauvel" (ISNB); 1 ♂ "coll. Delgrange" (ISNB); 1 ♂ "G. C. Champion Coll.// B. M. 1927-409" (BMNH); 1 ♀ "Coll. Odier.// B. M. 1921-288" (BMNH); 2 ♀♀ [small, circular brown label, no text] "Coll. Odier.// B. M. 1921-288" (BMNH); 1 ♂ "Alono-// dorsar" [? HW] "Meladema// coriacea" [HW] (BMNH); 1 ♂ "Europa// B. Heyne" [HW] (BMNH); 1 ♂ "coriaceus Lap." [folded, HW] (BMNH); 1 ♂ "Dytiscus coriaceus// no. in list. 19." [HW] reverse "Presented by// Signor Passerini" [name HW] (BMNH); 1 ♂ "1911" [round label, HW] (BMNH). All with "*Meladema// coriacea* Laporte, 1835// D T Bilton [or I Ribera] det. 2017".

Description. *Size*: Neotype TL = 22.66 mm; EL = 16.90 mm; MW = 11.52 mm. Other material examined TL = 18.56–23.17 mm; EL = 14.34–16.90 mm; MW = 8.45–11.14 mm.

Colour. Dorsum dark reddish brown to black (Figure 3A); lateral margins of pronotum, labrum and anterior half of clypeus somewhat paler, sometimes with diffuse lateral maculae. Elytra unicolorous, without distinct mottling even when lifted (Figure 4A). Head with a pair of oval, reddish yellow medial interocular patches, slightly elongated apicolaterally. Antennae and maxillary and labial palpi reddish yellow. Legs dark reddish brown to black with golden yellow setae; large spines somewhat paler. Venter reddish brown to black; gula, meso and metacoxae and trochanters paler.

Head. Labrum shining, with moderate to coarse, sparse punctures. Reticulation absent in apical half, becoming increasingly more evident basally, here forming weakly impressed, transverse meshes. Clypeus and anterior half of frons shining, doubly punctate, without reticulation and with very close, fine and very sparse, coarse punctures. Coarse punctures approximately 5–8x diameter of fine; without visible reticulation. Paired epicranial foveae, one immediately behind the other, on each side of frons, close to lateral margins and immediately behind lateral remnants of frontoclypeal suture. Anterior epicranial foveae transverse, posterior slightly elongate oval; both with cluster of stout, yellow recumbent to decumbent setae. Areas between anterior and posterior foveae with coarse wrinkles. Posterior frons with open, elongate, wrinkled reticulation, especially alongside lateral margins of compound eyes and onto vertex; meshes tumid, with rugose appearance. Internal and posterior borders of compound eyes distinct, raised relative to level of adjacent cuticle. Lateral margins bordered by distinct narrow channel; deeper anteriorly than posteriorly and continuing behind posterior margin of eye onto vertex. Channel with dense punctures, bearing long, stiff, yellow recumbent to decumbent setae.

Pronotum. Posterior margin strongly sinuate laterally (Figure 3A). Surface somewhat shining, strongly rugose. Reticulation meshes large, open, almost isodiametric and relatively flat either side of mid-line on disc; smaller, tumid and more uneven in size and shape towards all margins. Transverse irregular row of medium punctures bearing long, yellow recumbent to decumbent setae 1/5 behind anterior pronotal margin; interrupted briefly in centre, continuing inside lateral margins and inside lateral third

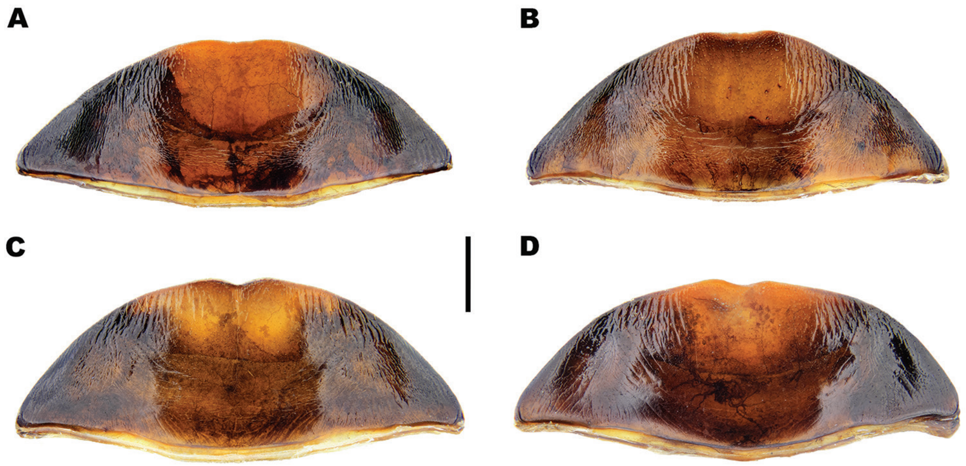

Figure 11. *Meladema* species males, abdominal ventrite 6 (DNA voucher codes where applicable). **A** *M. coricaea*, Spain, Murcia, Fte. Caputa **B** *M. lepidoptera* sp. n., Corsica, Cap Corse (NHM-IRM12F) **C** *M. imbricata*, La Gomera, El Cedro (NHM-IRM3A) **D** *M. lanio*, Madeira, Ribeira dos Cedros (NHM-IRM8A). Scale bar = 1 mm.

of posterior margin. Centre of disc with elongate, narrow, slit-like fovea, sometimes partially interrupted in mid-length. Lateral margins slightly raised, shining, without rugose sculpture and with fine, scattered punctures.

Elytra. Somewhat shining, with dense, transverse, crescentic striolae (Figures 5A, 6A) giving a scaly appearance (Figure 3A). Striolae less dense anteriorly and medially, here mostly distinctly separated from each other laterally (e.g. Figures 5A, 7A, C, 8A, C, 9, 10). Size of crescentic striolae variable, especially on disc close to suture (e.g. Figures 9, 10). Crescentic striolae becoming denser and somewhat continuous laterally and posteriorly (Figure 3A). Surface between crescentic striolae (Figures 5A, 6A) doubly punctate, with very fine, close punctures and medium, very sparse punctures (the latter bearing short, peg-like setae); also with fine, obsolete, open reticulation, usually more evident in apical two thirds, and more evident in some specimens than others; sometimes apparently absent. Puncture rows well-marked, continuous almost to elytral apices; punctures shallower posteriorly than anteriorly.

Venter. Prementum shining, tumid in centre, with fine and medium, sparse punctures. Mentum shining; central projection with shallow median emargination. Lateral lobes with medium, sparse punctures, and scattered, whitish recumbent to decumbent setae. Submentum shining, with transverse wrinkles centrally, and elongate wrinkles laterally. Central 1/4 with medium, sparse punctures bearing long, white-yellowish, erect setae. Gula shining, with sparse, shallow, transverse wrinkles; patch of medium-coarse punctures posterolaterally. Genae shining, with obsolete, open, elongate reticulation. Prosternum shining, with irregular transverse ridges laterally. Strongly arched in centre and with fine, moderate to close punctures laterally, bearing long, white-yellowish, recumbent to erect setae; punctures and setae extending in a sparse, irregular row onto process, just below arch. Process lanceolate, tectiform; apex acuminately rounded. Centre of prosternum and process with double punctation of very fine, moderate and medium, very sparse punctures. Pronotal hypomeron shining, impunctate. Elytral epipleurs shining, with fine wrinkles; irregular puncture row close to internal margin, from centre to close to apex; punctures bearing fine, whitish, erect setae. Metaventrite shining, central portion with sparse, transverse scratches and fine to very fine, sparse to very sparse punctures; not clearly forming two size classes. Metaventral process strongly reticulate, with transverse, rugose meshes and traces of fine, sparse punctures; small, central patch at base with very small reticulation meshes. Metaventral process relatively broad; apex acuminate and upturned slightly anterolaterally. Metacoxal lines almost reaching anterior border of metacoxae; shallow and interrupted in anterior 1/5. Internal laminae of metacoxae shining, sculpture as on centre of metaventrite. Metacoxal lobes sculptured as internal laminae, strongly rounded, with irregular, elongate field of medium to coarse punctures close to lateral margins, bearing fine, white, recumbent to erect setae. External laminae of metacoxae shining, smooth close to process, but with strong reticulation elsewhere; reticulation meshes very elongate posteromedially, to transverse anteriorly. Abdominal ventrites shining. Ventrites 3–5 with cluster of golden, erect setae anteromedially. Ventrite 1 with elongate reticulation throughout. Ventrite 2 with similar reticulation; absent close to centre. Ventrite 3 with elongate reticulation laterally, becoming transverse close to smooth central 1/5. Reticulation of ventrites 4 and 5 restricted to lateral third and with superimposed elongate furrows. Ventrites 2–5 doubly punctate; very fine, moderate and fine, sparse to very sparse punctures; punctures most evident in areas without reticulation. Ventrites 3–5 with transverse irregular row of long, yellowish, recumbent to decumbent setae laterally. Ventrite 6 (Figure 11A) with very fine, moderate punctures and medium to coarse, sparse to moderate punctures; punctures coarser close to apex. Elongate, semicircular wrinkles and channels apicolaterally. Some punctures in channels bearing elongate, whitish, erect setae.

Male. Foretarsi (Figure 12A) with articulo-setal counts as follows (base to apex): row 1, 7; row 2, 8–10; row 3, 8–10; row 4, 6-8. Number of setae in rows may differ from right to left tarsus in same beetle. Curved, golden setae bordering articulo-setal field dense, particularly basally. Foretarsal claws (Figures 12A, 13A) elongate, curved; interior margin straight or somewhat raised in basal two thirds, strongly curved in apical third. Mesotarsi (Figure 12E) with articulo-setal counts as follows (base to apex): row 1, 7–8; row 2, 8; row 3, 7; row 4, 4 (2 clusters of 2, situated laterally). Curved, golden setae bordering articulo-setal field dense, particularly basally. Mesotarsal claws (Figure 12E) elongate, strongly curved. Abdominal ventrite 6 (Figure 11A) with apex rounded, with very shallow median emargination. Median lobe asymmetrical (Figure 14A), sinuation weak, approximately 1/5–1/4 from apex; ventral margin of apical portion relatively straight in lateral view. Parameres (Figure 14A) with basal portion of inner margin relatively evenly curved; outer and inner margins almost straight over apical two thirds.

Female. As male, except for simple fore and mesotarsi, differently shaped abdominal ventrite 6 (with bluntly pointed apex, Figure 15A). The density of crescentic strio-

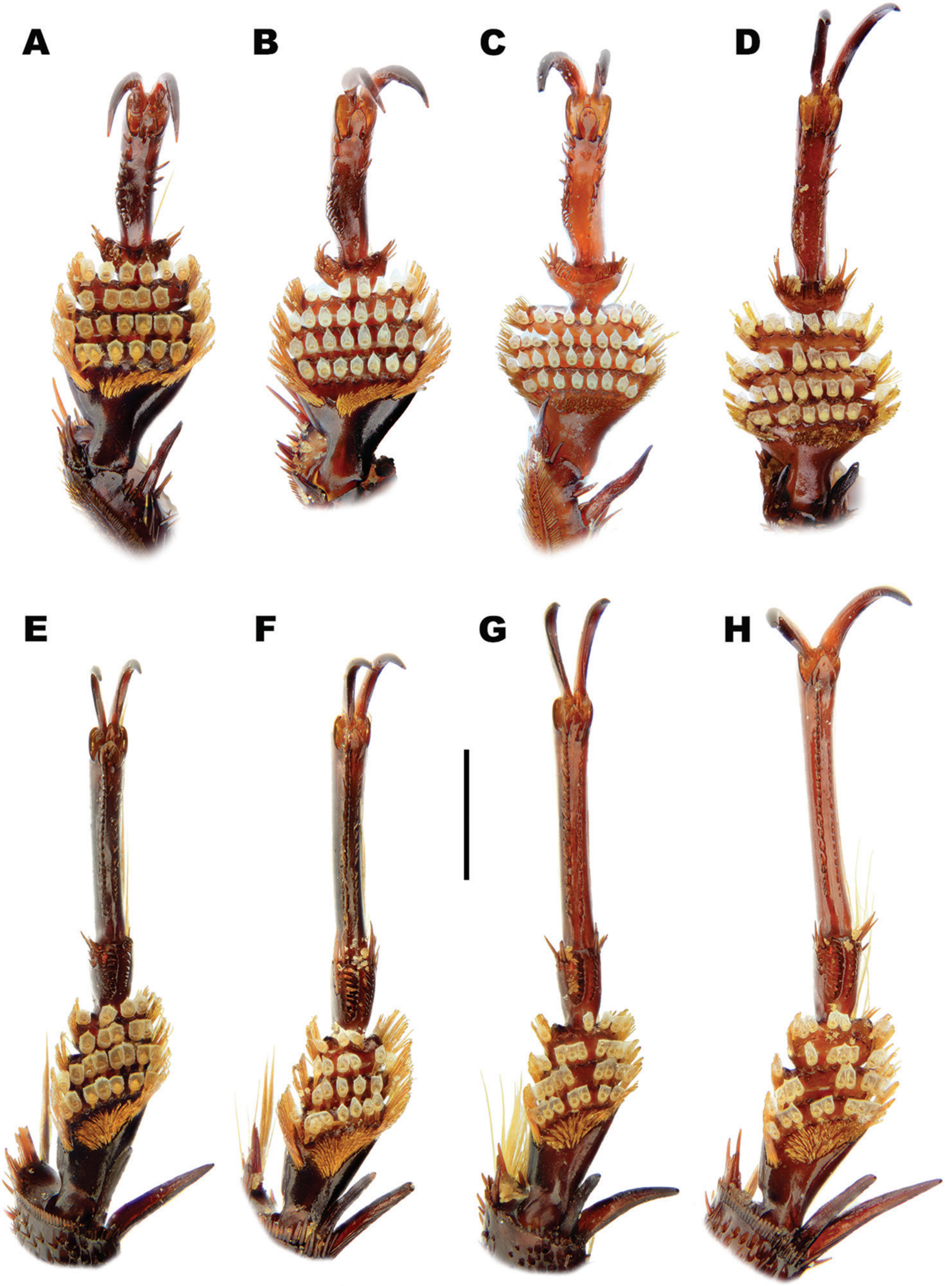

Figure 12. *Meladema* species males, fore (**A–D**) and mesotarsi (**E–H**), ventral view (DNA voucher codes where applicable). **A, E** *M. coriacea* Spain, Cáceres, nr. Plasencia **B, F** *M. lepidoptera* sp. n. holotype, Corsica, Cap Corse (NHM-IRM12E) **C, G** *M. imbricata*, La Gomera, El Cedro (NMH-IRM3A) **D, H** *M. lanio*, Madeira, Rabacal. Scale bar = 1 mm.

lae on the elytra does not differ consistently between sexes, contrary to the statement of Balfour-Browne (1948).

Variation. Variation is evident in a number of characters. The size and density of the crescentic striolae on the elytra differs between individuals (e.g. Figures 5A, 7A, C, 8A, C, 9, 10, 17, 18D, 19), and shows some geographical structure. Specimens of both sexes from the Iberian Peninsula (e.g. Figures 7A, C, 8A, C, 9B, 10B) have relatively sparse crescentic striolae, with individual striolae relatively small in size, features also seen in most specimens from the Balkans and Anatolia (e.g. Figure 10A). Some specimens from France, North Africa and southern Italy (e.g. Figures 9D, 10C, D, 19) have slightly denser striolae, with some of these slightly larger. Specimens from massifs in the central Sahara (Hoggar and Tassili n'Ajjer (Algeria), Tibesti (Chad)) have very dense crescentic striolae (Figure 17). In these beetles the striolae are relatively small and strongly curved, giving a distinctly tuberculate appearance to the elytra, even close to the shoulders. In no cases do the elytral striolae approach the condition seen in *M. lepidoptera* sp. n., however (see below). The degree of curvature of male foretarsal claws differs between individuals, even within the same population. Some specimens have claws which are shorter, and broader at their apices that in Figure 13A, these almost certainly being older insects, whose claws have become worn down during life. The size and shape of the median lobe also varies slightly between individuals and populations (e.g. Figure 20). Specimens from North Africa, for example, (Figure 20H–K) have narrower apical portions, whilst the largest median lobes are seen in Greek animals (Figure 20M–N).

Differential diagnosis. Morphologically, this species is almost identical to *M. lepidoptera* sp. n., something which has prevented the latter's formal description until now. The two species can be reliably separated only on details of their elytral sculpture, *M. coriacea* having smaller, less dense crescentic striolae than *M. lepidoptera* sp. n., this being particularly evident at the elytral base, close to the scutellum, and in the middle, close to the suture (see Figure 1 and e.g. Figures 7A, C, 8A, C, 9, 10 vs. 7B, D, 8B, D, 21, 22). In *M. coriacea*, the striolae are largely well separated from each other in both regions (see comment by Aubé 1836, quoted above) whereas in *M. lepidoptera* sp. n. they are typically much more contiguous (see below). In the mid-elytra of *M. coriacea* there is also typically a distinct gap between the elytral suture and the first crescentic striolae (see e.g. Figure 8A, C), whereas in *M. lepidoptera* sp. n. the striolae begin much closer to the suture (e.g. Figure 8B, D). Whilst there is some variation, as illustrated in the figures, these features appear consistent throughout the wide geographical range of *M. coriacea*. Other characters, including male genitalia, claws, and the shape and sculpture of abdominal ventrite 6 in both sexes, do not differ consistently between the two species, there being as much intraspecific as interspecific variation.

The genetic differences between *M. coriacea* and *M. lepidoptera* sp. n. are well defined and comparable to those seen between *M. imbricata* and *M. lanio*, although mostly seen in mitochondrial markers (Sýkora et al. 2017). Of the two nuclear markers sequenced, H3 was identical in *M. coriacea* and *M. lepidoptera* sp. n. (but differ-

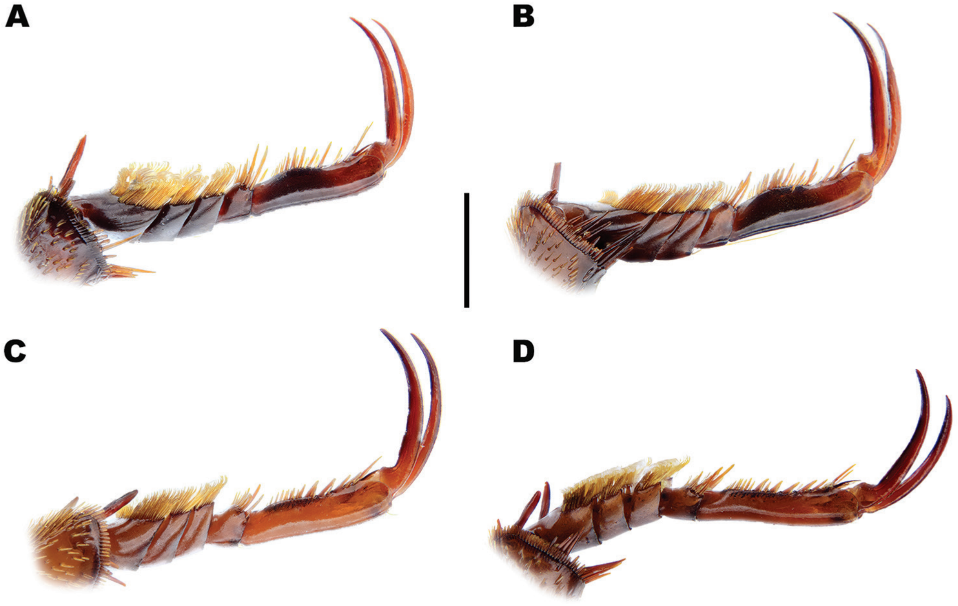

Figure 13. *Meladema* species males, fore tarsal claws, lateral view (DNA voucher codes where applicable). **A** *M. coriacea* Spain, Cáceres, nr. Plasencia **B** *M. lepidoptera* sp. n. holotype, Corsica, Cap Corse (NHM-IRM12E) **C** *M. imbricata*, La Gomera, El Cedro (NMH-IRM3A) **D** *M. lanio*, Madeira, Rabacal. Scale bar = 1 mm.

ent from *M. lanio* and *M. imbricata*), only wingless having some diagnostic positions separating the two species (see Sýkora et al. 2017).

Distribution. Even as redefined here, this is by far the most widespread species of the genus, distributed from the Canary Islands to Turkey, and south to massifs of the central Sahara (Figure 23). We have examined material from all countries from which this species has been reported, with the exception of Bulgaria (Guéorguiev 1987). Despite being listed from Lybia in the Palaearctic and World Catalogues of Dytiscidae (Nilsson and Hájek 2017a, 2017b), all Saharan records which we have traced emanate from Algeria and Chad. As discussed by Sýkora et al. (2017), basal splits within the *M. coriacea* lineage apparently took place in north-west Africa, with subsequent range expansion across the western Mediterranean, and several apparently independent, recent, colonisations of the Canary Islands from Morocco. The most easterly specimens included in genetic analyses (from Malta and Izmir, Turkey) were more closely related to beetles from north Africa than those from Iberia or southern France, suggesting that colonisation of the eastern part of the species range occurred via dispersal from Algeria/Tunsia, likely through Malta, Sicily and southern Italy. Genotyped individuals have been studied from throughout the wide range of *M. coriacea*, as well as a large number of additional non-genotyped specimens (Figure 23). The exact limits of *M. coriacea* in the Italian Peninsula remain unclear, and can only be resolved through combined genetic and morphological study of additional, fresh material. It is apparent, however, that *M. coriacea* is present in at least Sicily and that *M. lepidoptera* sp. n. occurs in the north and centre of the peninsula (Toscana and Lazio – as confirmed from genotyped specimens). Beetles morphologically intermediate between *M. coriacea* and *M. lepidoptera* sp. n. have been seen from Apulia and Campania (Figure 18B, C), suggesting possible hybridization between the two species where their ranges come into contact. Such a process is already established to have occurred between *M. coriacea* and *M. imbricata* on Tenerife (see below and Ribera et al. 2003). *Meladema coriacea* is a species typical of seasonally fluctuating or intermittent Mediterranean stream systems, being particularly characteristic of localities with winter-spring flow, which dry down to pools in summer. It is associated with drier and more seasonally variable conditions than other species of the genus, something which may have facilitated its range expansion (Sýkora et al. 2017).

Meladema lepidoptera sp. n.

http://zoobank.org/C28258E3-0B86-4983-AB52-7C1301A4A24A

Figures 3B, 4B, 5B, 6B, 7B, D, 8B, D, 11B, 12B, F, 13B, 14B, 15B, 18A, 20O–U, 21, 22, 23

Type locality. France, Corsica, Cap Corse, stream nr. Bettolacce, 42°58'2.4"N 9°24'42.4"E.

Type material (genotyped specimens only). Holotype ♂: “11 FR Corsica 21.ix.1999// Cap Corse: Bettolacce// 42°58'2.4"N 9°24'42.4"E 250m// I.Ribera & A. Cieslak leg.” “DNA voucher// NHM-IRM12E” “*Meladema lepidoptera*// Bilton & Ribera, 2017//HOLOTYPE” (NMW). Dry card mounted, tissue samples and DNA aliquotes, with same data, in IBE. Sequence data from the holotype has been deposited in GenBank with accession numbers AF428206 (COI-3’) and AF428188 (16S ribosomal RNA). **Paratypes (13):** 1 ♂ “11 FR Corsica 21.ix.1999// Cap Corse: Bettolacce// 42°58'2.4"N 9°24'42.4"E 250m// I.Ribera & A. Cieslak leg.”“DNA voucher// NHM-IRM12F” (NMW); 1 ♀ “11 FR Corsica 21.ix.1999// Cap Corse: Bettolacce// 42°58'2.4"N 9°24'42.4"E 250m// I.Ribera & A. Cieslak leg.” “DNA voucher// NHM-IRM12C” (BMNH); 1 ♀ “5 FR Corsica 19.ix.1999// Porto-Vecchio, l’Ospedale// 41°39'13.7"N 9°12'41.0"E 690m// I.Ribera & A. Cieslak leg.” “DNA voucher// NHM-IRM12A” (CBP); 1 ♀ “5 FR Corsica 19.ix.1999// Porto-Vecchio, l’Ospedale// 41°39'13.7"N 9°12'41.0"E 690m// I.Ribera & A. Cieslak leg.” “DNA voucher// NHM-IRM12D” (MNHN); 1 ♀ “5 FR Corsica 19.ix.1999// Porto-Vecchio, l’Ospedale// 41°39'13.7"N 9°12'41.0"E 690m// I.Ribera & A. Cieslak leg.” “DNA Voucher// NHM-IRM12g” (IBE); 1 ♀ “9 FR Corsica 19.ix.1999// Ghisoni, road to Campannella// 42°4'8.7"N 9°11'6.0"E 830m// I.Ribera & A. Cieslak leg.” “DNA Voucher// NHM-IRM12b” (IBE); 1 ♂ “Toscana (PI) S. Luce// ‘Boso’ de Castagni, s tr. s.// Luce-Castellina Marittima// 3.X.2007 leg. M. Toledo” “DNA voucher// IBE-AN693” (CTP); 1 ♀ “April 2015 Italy Monti della Tolfa// Rio Ippovia della Cicugnola// (pozze ruscellamento)// 42°4'26.27"N 11°56'12.25"E// V. Buono leg.”

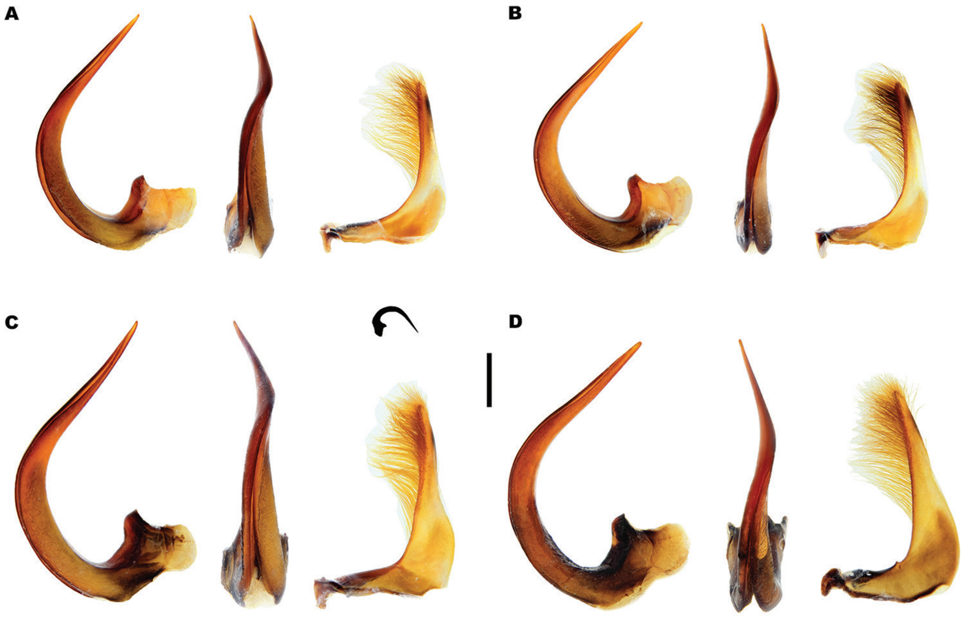

Figure 14. *Meladema* species male genitalia. Median lobe, lateral and ventral view; paramere (DNA voucher codes where applicable). **A** *M. coriacea* Spain, Cáceres, nr. Plasencia **B** *M. lepidoptera* sp. n. holotype, Corsica, Cap Corse (NHM-IRM12E) **C** *M. imbricata*, La Gomera, El Cedro (NMH-IRM3A) **D** *M. lanio*, Madeira, Rabacal. Silhouette indicates orientation of median lobe for imaging in ventral view. Scale bar = 1 mm.

"DNA voucher// IBE-AN760" (CVR); 1 ♂ "I. D'ELBA – POMONTE// Fosso BARIONE// m 250-300// 29.V.94 TOLEDO LGT." [HW] "DNA voucher// IBE-AN692" (CTP); 1 ♂ "3/vi/2014 ITALY Montecristo// 42.334N 10.308E 260m// R. Vila leg." "DNA voucher// IBE-DV289" (IBE); 1 ♂ "3/vi/2014 ITALY Montecristo// 42.334N 10.308E 260m// R. Vila leg." "DNA voucher// IBE-DV290" (ISNB); 1 ♂ "27/v/2009 ITALY Sardinia// Nuoro prov.(Ogliastra historical region)// brook 562m ESE Villagrande Strìsaili (WNW Tortoli)// 39.95084N 9.51912E H. Fery & M. Toledo leg." "DNA voucher// IBE-RA5" (MNCN); 1 ♀ "27.5.2009 Italy, Sardinia// Ogliastra prov., ca. 5 km// WNW Tortoli, (on road// Tortoli – Villagrande Stris.)" "39.93982N 9.59280E// ca 80m, brook// Fery & Toledo leg." "DNA voucher// IBE-RA18" (MNCN). Each with red label "*Meladema lepidoptera*// Bilton & Ribera, 2017//PARATYPE". All dry card mounted, tissue samples and DNA aliquotes, with same data, in IBE.

Additional material examined (non-genotyped specimens). France, Corsica: 2 ♂♂, 1 ♀ "11/iv/1993// Corsica Francardo// Mediterranean stream// D. T. Bilton leg." (CBP); 1 ♀ "Calvi// 29.VIII." "Pietra// Maggiore" "KORSIKA// VIII.1955" "Meladema// coriacea Cast.// M/ Balke det. 1990" [Latin name, describer & 90 HW] (NMW); 1 ♂, 2 ♀♀ "12.4.79 Korsika// Pinito, ca 700m// Bach" [HW] reverse "Fery leg." "Mel.// coriacea// Cast." [HW] (NMW); 1 ♀ "12.4.79 Korsika// Pinito, ca 700m// Bach" [HW] reverse "Fery leg." "Mel.// coriacea// Cast." [HW] "coll. Shaverdo" (NMW); 1

♀ “Korsika// 7.80” [HW] “Meladema// coriacea Cast.// M. Balke 1990” [Latin name, describer & 90 HW] (NMW); 1 ♂ “Corse” [HW] “Reveliere” [yellow, square label, HW] “Coriaceus// Corsica” [HW] “C. Epplsh.// Steind. d.” (NMW); 1 ♂ “Corsica” (NMW); 1 ♀ “12.4.79 Korsika// Pinito, ca. 700m// Bach” [HW] “Mel.// coriacea// Cast.” [HW] “Coll.// HENDRICH// Berlin” (ZSM). **Italy, Sardinia:** 5 ♂♂, 3 ♀♀ “Sardinia (CA) Dolianova// Rio Flumini 30.VI.91// leg. Meloni” (CBP, CTP); 3 ♂♂, 1 ♀ “SARDINIEN// Bosa// 24.5-24.6.//1963, Budberg” reverse “Meladema// coriaceum Lap.” [HW] (NMW); 1 ♀ “coll. Win-// gelmüller” “coriaceum Lap.// Sardinien” [HW] (NMW); 1 ♂ “Villasimius// Sard. m. 19.9.59// E. Jünger” [19 HW] “A7598// coricae Cast.// det. K. Hoch 1959” [number, Latin name, describer & 9 HW] (ZSM); 1 ♀ “Sardegna// Lode// 28.7.79// S. Gottwalt” [HW] “coll.//HENDRICH// Berlin” (ZSM); 2 ♀♀ “Sardinien: bei Nuvafus,// 09.IX.1978” “Meladema// coriacea// Cast.” [HW] “entnommen// 1 Exempl.” [HW] “Sardinien// S. Nuvafus// 9.9.78” [HW] (ZSM); 1 ♂, 1 ♀ “Sardinien: S Monte// Limbara. Tempio, 650m,// 28.VIII.1978” “Meladema// coriacea// Cast.” [HW] “Entnommen// 1 Exempl.” [HW] “Sardinien// Südl. Monte. Liombara// Tempio 650m// 28.8.78” [HW] “Fuss Monte// Limbara 650m// 28.8.78” [HW] (ZSM); 1 ♀ “Sardinien: Lagoatto di// Flumendosa, Villanova// Strisaili, 05.IX.1978” “Meladema// coriacea// Cast.” [HW] “Sardinien// Lagoatto di Flumendosa// Villanova Strisaili// 5.9.1978” [HW] (ZSM); 6 ♂♂, 3 ♀♀ “Meladema// coriacea Cast.// Italien/ Sardinien// Giara di Gesturi// - 9.1980// Coll./ leg.// Burmeister” “Sardinien// Giara di Gesturi// 9.1980// leg. Burmeister” [HW] “Meladema// coriacea// Cast.” [HW] (ZSM); 1 ♂ “Meladema// coriacea Cast.// Italien/ Sardinien// b. Tempio// Bergbach am// Monte Limbarra// - 9.1980// Coll./ leg.// Burmeister” “Sardinien// b. Tempio// Bergbach am// Monte Limbarra// 9. 1980” [HW] “Meladema// coriacea// Cast.” [HW] (ZSM); 2 ♂♂, 2 ♀♀ “Meladema// coriacea Cast.// Italien/ Sardinien// Pass b. Genne// Cruxi// 1.9.1980// Coll./ leg.// Burmeister” “Sardinien// Pass b. Genne Cruxi// 10. [circled]// leg. Burmeister” [HW] (ZSM); 2 ♀♀ “Meladema// coriacea Cast.// Italien/ Sardinien// b. Nuragus// (Viehtränke)// 3.9.1980// Coll./ leg.// Burmeister” “Sardinien// b. Nuragus// Viehtränke// 3.9.1980 23. [circled]// leg. Burmeister” [HW] “Meladema// coriacea// Cast.” [HW] (ZSM); 1 ♂ “Meladema// coriacea Cast.// Italien/ Sardinien// b. Tempio// Bergbach// b. Mnte Limbarra// - 9.1980// Coll./ leg.// Burmeister” “Sardinien// b. Tempio, Bergbach// b. Monte Limbarra// 9/1980 39. [circled]// leg. Burmeister” [HW] ‘Meladema// coriacea// Cast.” [HW] (ZSM); 1 ♂ “Glasgow University// HUNTERIAN MUSEUM// ex. coll. G.N. Foster” “Sardinia 32T UTH// 04602/44750// S of Mont Minerva// G N Foster 16.10.2006” (CFA); 1 ♀ “27.5.2009 Italy, Sardinia// Ogliastra prov., ca. 5 km// WNW Tortoli, (on road// Tortoli – Villagrande Stris.)” “39.93982N 9.59280E// ca 80m, brook// Fery & Toledo leg.” (IBE). 1 ♂ “9 Sardinia, Calangianus 11.iv.2017// stream, way to Pascaredda tomb// 40°54'35.6"N 9°10'12.8"E 435m// I.Ribera & A.Cieslak leg.” (IBE); **Italy, Elba:** 1 ♂ [no head] “Ins. Elba// 1908// Paganetti” (NMW); 2 ♂♂ “Elba: bei Marciana, Bach in// Kastanienwald, 17.IX.1975,// leg.: Schmalfuss” “17.9.75 Elba, bei Murciana// Bach in Kastanienwald// Schmalfuss leg.” [HW] “Meladema// coriaceum// Lap.” [HW] “Meladema coriacea Cast.” [HW] (ZSM). **Italy, mainland:** 5 ♂♂, 3 ♀♀

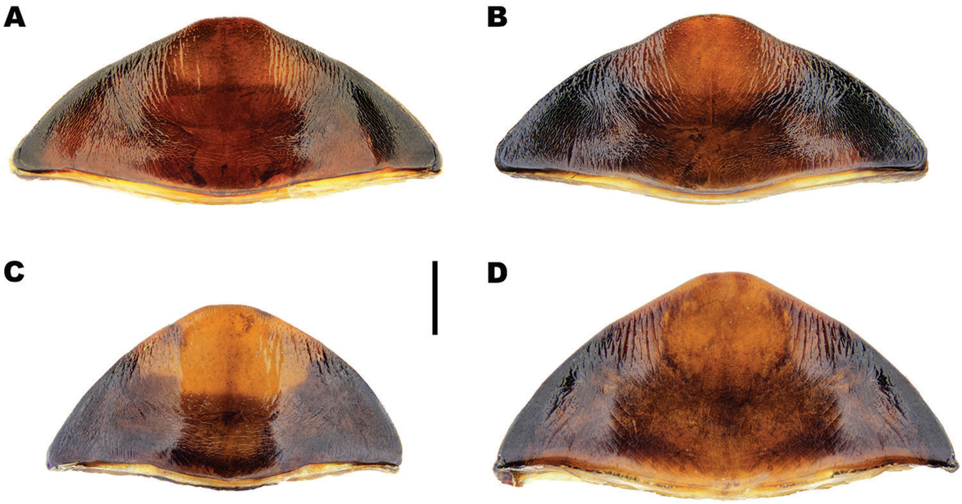

Figure 15. *Meladema* species females, abdominal ventrite 6 (DNA voucher codes where applicable). **A** *M. coricaea*, Spain, Murcia, Fte. Caputa **B** *M. lepidoptera* sp. n., Corsica, Cap Corse (NHM-IRM12C) **C** *M. imbricata*, La Palma, Bco. Hoyo Verde **D** *M. lanio*, Madeira, Ribeira dos Cedros (NHM-IRM9A). Scale bar = 1 mm.

"Levante,// Liguria, Italy." "Coll. Odier.// B.M. 1921-288." (BMNH); 1 ♂, 1 ♀ "Levante,// Liguria, Italy." "Coll. Odier.// B.M. 1921-288." "Meladema// coriacea Cast// C.R. Smith det. 1982" [Latin name, describer & 2 HW] (BMNH); 1 ♀ "ITALY: Liguria.//Torr. 2km W. of Pogli,// trib. of Torr. Arroscia, nr. Albenga, 7.iv.1958// J. Balfour-Browne." "Brit. Mus.// 1960-482." [482 HW] "Meladema// coriacea Cast// C.R. Smith det. 1982" [Latin name, describer & 2 HW] (BMNH); 3 ♂♂, 1 ♀ "Italia// Ruta// 2-6. VII.95// A. Fiori" [HW, A. Fiori printed] (NMW); 1 ♀ "coriaceus// Toscana// V. Heyden" [HW] "c. Epplsh.// Steind. d." (NMW); 1 ♂ "S. gimignano// Sienna → Florenz// 3.8.36 Eiselt" [HW] "Meladema// coriaceum" [HW] (NMW); 1 ♂ "San Gimignano// IX 36 EISELT" "Meladema// coriaceum Lap." [HW] (NMW); 1 ♀ "San Gimignano// IX 36 EISELT" (NMW); 1 ♂ "Nervi// 27.III.05" [HW] (ZSM); 2 ♀♀ "Italia// 26.3.05" [date HW] "Nervi" (ZSM); 1 ♀ "Italien// 11.xii.05" [HW] "♀" "Samml. A.// Zimmermann" (ZSM); 1 ♀ [small, circular brown label, no text] "Pisa" [HW] "alte// Sammlung" (ZSM); 1 ♀ "Italia: Umbria, NE Gosparini,// 550m, dry stream, 09.IX.2015// 43°14'31.73"N, 12°6'19.69"E,// leg. Komarek, Beutel (TM7)" "Meladema// coriacea Lap.// det. H. Shaverdo 2016" [Latin name, describer & 16 HW] (NMW). **Without locality data:** 1 ♀ [small, circular brown label, no text] "Coll. Odier.// B.M. 1921-288." (BMNH); 1 ♀ "coriaceus" [HW] "E Coll.// Curtis" [HW] (BMNH); 1 ♂ "40// 4 2// 2135" [round label, HW] (BMNH). All with "*Meladema lepidoptera*// Bilton & Ribera// D T Bilton [or I Ribera] det. 2017".

Description. *Size*: Holotype TL = 20.74 mm; EL = 15.74 mm; MW = 10.50 mm. Other material examined TL = 19.20–20.99 mm; EL = 14.98–16.38 mm; MW = 9.73–11.39 mm.

Colour. Dorsum dark reddish brown to black (Figure 3B); lateral margins of pronotum, labrum and anterior half of clypeus somewhat paler, sometimes with diffuse lateral maculae. Elytra unicolorous, without distinct mottling even when lifted (Figure 4B). Head with a pair of oval, reddish yellow medial interocular patches, slightly elongated apicolaterally. Antennae and maxillary and labial palpi reddish yellow. Legs dark reddish brown to black with golden yellow setae; large spines somewhat paler. Venter reddish brown to black; gula, meso and metacoxae and trochanters paler.

Head. Labrum shining, with moderate to coarse, sparse punctures. Reticulation absent in apical half, becoming increasingly more evident basally, here forming weakly impressed, transverse meshes. Clypeus and anterior half of frons shining, doubly punctate, without reticulation and with very close, fine and very sparse, coarse punctures. Coarse punctures approximately 5–8x diameter of fine; without visible reticulation. Paired epicranial foveae, one immediately behind the other, on each side of frons, close to lateral margins and immediately behind lateral remnants of frontoclypeal suture. Anterior epicranial foveae transverse, posterior slightly elongate oval; both with cluster of stout, yellow recumbent to decumbent setae. Areas between anterior and posterior foveae with coarse wrinkles. Posterior frons with open, elongate, wrinkled reticulation, especially alongside lateral margins of compound eyes and onto vertex; meshes tumid, with rugose appearance. Internal and posterior borders of compound eyes distinct, raised relative to level of adjacent cuticle. Lateral margins bordered by distinct narrow channel; deeper anteriorly than posteriorly and continuing behind posterior margin of eye onto vertex. Channel with dense punctures, bearing long, stiff, yellow recumbent to decumbent setae.

Pronotum. Posterior margin strongly sinuate laterally (Figure 3B). Surface somewhat shining, strongly rugose. Reticulation meshes large, open, almost isodiametric and relatively flat either side of mid-line on disc; smaller, tumid and more uneven in size and shape towards all margins. Transverse irregular row of medium punctures bearing long, yellow recumbent to decumbent setae 1/5 behind anterior pronotal margin; interrupted briefly in centre, continuing inside lateral margins and inside lateral third of posterior margin. Centre of disc with elongate, narrow, slit-like fovea, sometimes partially interrupted in mid-length. Lateral margins slightly raised, shining, without rugose sculpture and with fine, scattered punctures.

Elytra. Somewhat shining, with dense, transverse, sometimes contiguous, crescentic striolae, giving a very scaly appearance (Figure 3B). Striolae relatively dense throughout, frequently contacting each other laterally on shoulder close to suture (e.g. Figures 5B, 7B, 18A, 21, 22, and relatively dense in mid-elytra close to suture (e.g. Figures 7D, 8D, 18A, 21, 22)). Size of crescentic striolae relatively large, both in shoulder and mid-elytral regions (e.g. Figures 7B, D, 8B, D, 18A, 21, 22). Crescentic striolae becoming denser and somewhat continuous laterally and posteriorly. Surface between crescentic striolae (Figures 5B, 6B) doubly punctate, with very fine, close punctures and medium, very sparse punctures (the latter bearing short, peg-like setae); also with fine, obsolete, open reticulation, usually more evident in apical two thirds, and more evident in some specimens than others. Puncture rows well-marked, continuous almost to elytral apices; punctures shallower posteriorly than anteriorly.

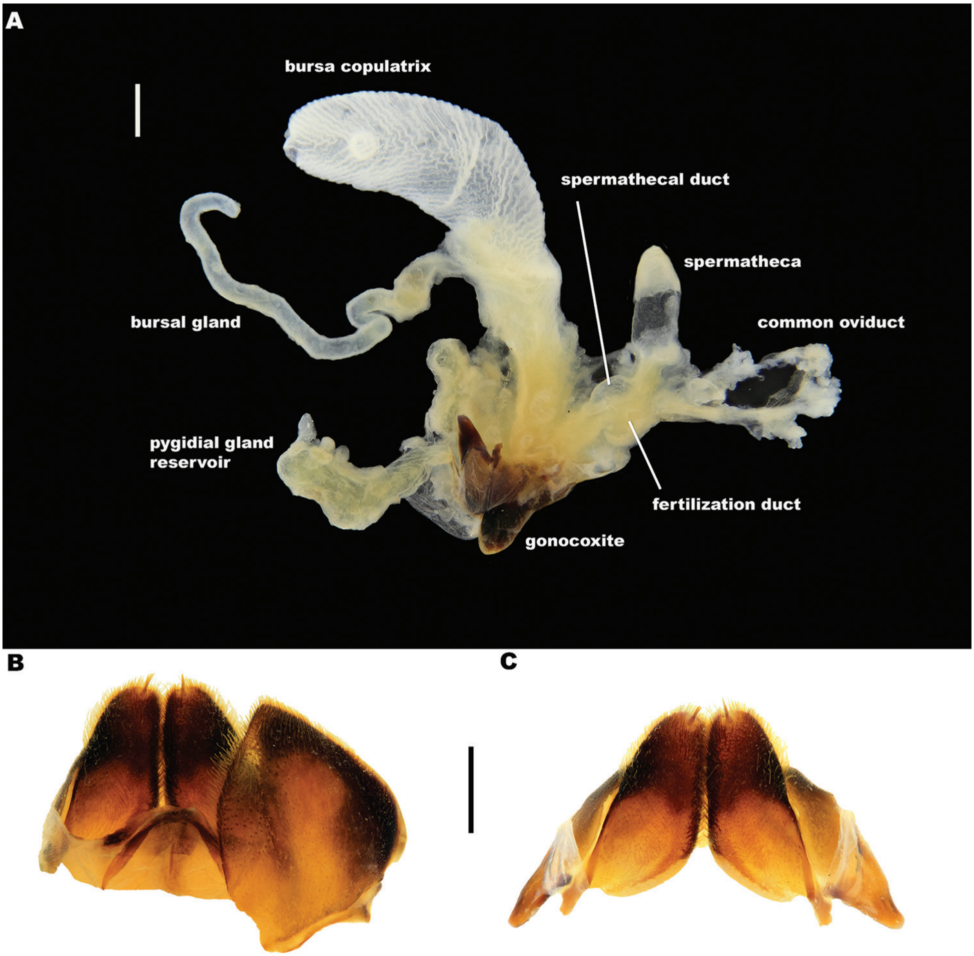

Figure 16. *Meladema coriacea*, Var, France, La-Londe-les-Maures, female reproductive tract and genitalia (DNA voucher codes). **A** reproductive tract anatomy (NHM-IRM11A) **B** gonocoxae and gonocoxosternite (left gonocoxosternite removed) (NHM-IRM11B) **C** gonocoxae with laterotergites expanded (NHM-IRM11B). Scale bars = 1 mm.

Venter. Prementum shining, tumid in centre, with fine and medium, sparse punctures. Mentum shining; central projection with shallow median emargination. Lateral lobes with medium, sparse punctures, and scattered, whitish recumbent to decumbent setae. Submentum shining, with transverse wrinkles centrally, and elongate wrinkles laterally. Central 1/4 with medium, sparse punctures bearing long, white-yellowish, erect setae. Gula shining, with sparse, shallow, transverse wrinkles; patch of medium-coarse punctures posterolaterally. Genae shining, with obsolete, open, elongate reticulation. Prosternum shining, with irregular transverse ridges laterally. Strongly arched in centre and with fine, moderate to close punctures laterally, bearing long, white-yellowish, recumbent to erect setae; punctures and setae extending in a sparse, irregular row onto process, just below arch. Process lanceolate, tectiform; apex acuminately rounded. Centre of prosternum and process with double punctation of very fine, moderate and medium, very sparse punctures. Pronotal hypomeron shining, impunctate. Elytral epipleurs shining, with fine wrinkles; irregular puncture row close to internal margin, from centre to close to apex; punctures bearing fine, whitish, erect setae. Metaventrite shining, central portion with sparse, transverse scratches and fine to very fine, sparse to very sparse punctures; not clearly forming two size classes. Metaventral process strongly reticulate, with transverse, rugose meshes and traces of fine, sparse punctures; with small central patch of reticulation with very small meshes. Metaventral process relatively broad; apex acuminate and upturned slightly anterolaterally. Metacoxal lines almost reaching anterior border of metacoxae; shallow and interrupted in anterior 1/5. Internal laminae of metacoxae shining, sculpture as on centre of metaventrite. Metacoxal lobes sculptured as internal laminae, strongly rounded, with irregular, elongate field of medium to coarse punctures close to lateral margins, bearing fine, white, recumbent to erect setae. External laminae of metacoxae shining, smooth close to process, but with strong reticulation elsewhere; reticulation meshes very elongate posteromedially, to transverse anteriorly. Abdominal ventrites shining. Ventrites 3–5 with cluster of golden, erect setae anteromedially. Ventrite 1 with elongate reticulation throughout. Ventrite 2 with similar reticulation; absent close to centre. Ventrite 3 with elongate reticulation laterally, becoming transverse close to smooth central 1/5. Reticulation of ventrites 4 and 5 restricted to lateral third and with superimposed elongate furrows. Ventrites 2–5 doubly punctate; very fine, moderate and fine, sparse to very sparse punctures; punctures most evident in areas without reticulation. Ventrites 3–5 with transverse irregular row of long, yellowish, recumbent to decumbent setae laterally. Ventrite 6 (Figure 11B) with very fine, moderate punctures and medium to coarse, sparse to moderate punctures; punctures coarser close to apex. Elongate, semicircular wrinkles and channels apicolaterally. Some punctures in channels bearing elongate, whitish, erect setae.

Male. Foretarsi (Figure 12B) with articulo-setal counts as follows (base to apex): row 1, 7; row 2, 8–10; row 3, 8–10; row 4, 6–8. Number of setae in rows may differ from right to left tarsus in same beetle. Curved, golden setae bordering articulo-setal field dense, particularly basally. Foretarsal claws (Figures 12B, 13B) elongate, curved; interior margin straight or somewhat raised in basal two thirds, strongly curved in apical third. Mesotarsi (Figure 12F) with articulo-setal counts as follows (base to apex): row 1, 7–8; row 2, 8; row 3, 7; row 4, 4 (2 clusters of 2, situated laterally). Curved, golden setae bordering articulo-setal field dense, particularly basally. Mesotarsal claws (Figure 12F) elongate, strongly curved. Abdominal ventrite 6 (Figure 11B) with apex rounded, with very shallow median emargination. Median lobe asymmetrical (Figure 14B), sinuation weak, approximately 1/5–1/4 from apex; ventral margin of apical portion relatively straight in lateral view. Parameres (Figure 14B) with basal portion of inner margin relatively evenly curved; outer and inner margins almost straight over apical two thirds.

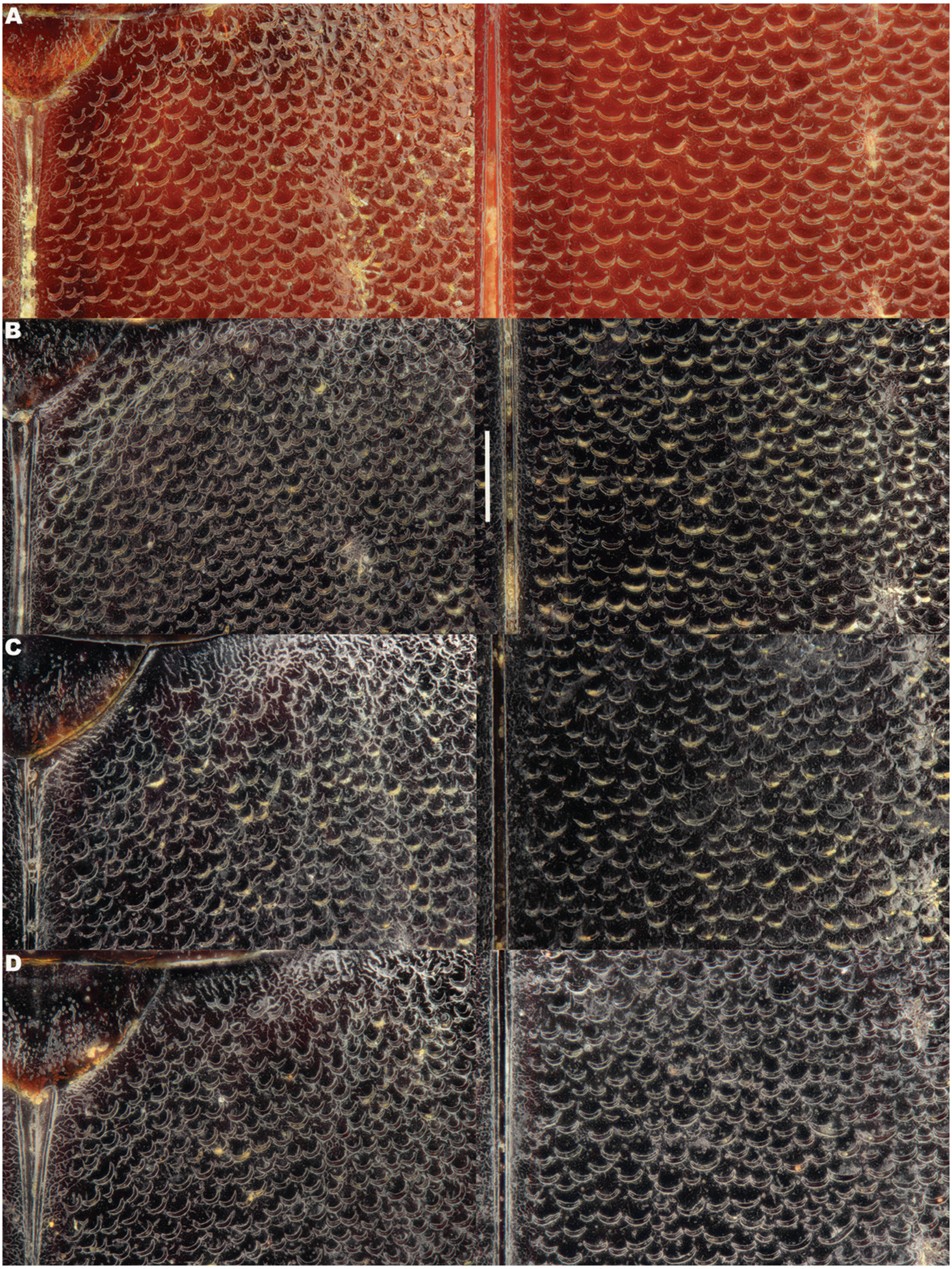

Figure 17. *Meladema coriacea*, Sahara, elytral sculpture; shoulder and middle left and right, respectively. **A** male, Chad, Tibesti, Koudou **B** female, Chad, Tibesti, Bassin de Gorrom **C** male, Algeria, Hoggar, Aguelmanne **D** female, Algeria, Hoggar, Aguelmanne. Scale bar = 0.5 mm.

Female. As male, except for simple fore and mesotarsi, differently shaped abdominal ventrite 6 (with bluntly pointed apex - Figure 15B). As with *M. coriacea*, no consistent differences between males and females are evident in terms of elytral sculpture.

Variation. The size and density of the crescentic striolae on the elytra differs somewhat between individuals and localities (Figures 5B, 7B, D, 8B, D, 18A, 21, 22), these being relatively dense in mainland Italy, Corsica and the Tuscan archipelago, and less so in most Sardinian specimens (e.g. Figure 22). The combination of size and density of these striolae is always greater than seen in *M. coriacea*, however (see above). The degree of curvature of male foretarsal claws differs between individuals, as in *M. coriacea*, as does the size and shape of the median lobe (e.g. Figure 20O–U).

Differential diagnosis. Morphologically almost identical to *M. coriacea* (see above). Only distinguishable on the size, shape and density of crescentic striolae on the elytra, which give *M. lepidoptera* sp. n. a very scaly appearance, evident even at relatively low magnification (e.g. Figure 3A vs. 3B). See above for genetic differences between this species and *M. coriacea*.

Etymology. From the ancient Greek "lepidos" (λεπὶδος, scale, but also referring to roof tiles) and "pteron" (πτερόν, wing). The specific epithet is a noun in the nominative plural.

Distribution. On the basis of current data, found on Corsica and Sardinia, islands of the Tuscan Archipelago (Elba, Montecristo) and parts of peninsular Italy, from Liguria to Umbria (Figure 23). *M. lepidoptera* sp. n. is apparently the only species of the genus found on Corsica, Sardinia, Elba and Montecristo (past records of *M. coriacea* from these islands - e.g. Poggi 1976, Franciscolo 1979, Dettner 2007 - almost certainly referring to this species), but co-occurs with *M. coriacea* in the Italian peninsula. The exact limits of the distribution of the two species in peninsular Italy remain unclear (see above), but there is morphological evidence suggesting hybridization where they meet, at least in the south (see below). The contact zone between the two species in the north appears to be situated on the Mediterranean coast, somewhere close to the French-Italian border, but to date no intermediate specimens have been seen from this area. Clearly future work, using both genetic and morphological approaches, would be illuminating in understanding the location and dynamics of these contact zones. As with other extant *Meladema* lineages, this species appears to have originated in the early Pleistocene, colonisation of the Tyrrhenean islands occurring long after the Messinian Salinity Crisis (Ribera et al. 2003, Sýkora et al. 2017). Sýkora et al. (2017) suggest that *M. lepidoptera* sp. n. may have originated following the colonization of the Tyrrhenian islands, a hypothesis which should be tested in the future through genetic study of more individuals from peninsular Italy. Sýkora et al. (2017) additionally suggest that this species is characteristic of sites with lower seasonality than is typical for *M. coriacea*, based on MaxEnt modelling. They note that many of the peninsular Italian localities (obtained from the literature) included in their analyses (from which specimens were not studied) fitted into the climatic space occupied by *M. lepidoptera* sp. n. (as '*coriacea*

Figure 18. *Meladema* species, Italy, male elytral sculpture; shoulder and middle left and right, respectively (DNA voucher codes, where applicable). **A** *M. lepidoptera* sp. n., Liguria, Levante **B** intermediate specimen, Campania, S. Michele (IBE-AN694) **C** intermediate specimen, Apulia, Vieste **D** *M. coriacea*, Lazio, Grotta di Pastena. Scale bar = 0.5 mm.

CSM'), not surprising given our finding that this species does indeed occur on the Italian mainland. Clearly it would be interesting to repeat Sýkora et al.'s (2017) analyses in the future, once the range limits of these taxa are better established. On the basis of current evidence, this species occurs in similar habitats to those occupied by *M. coriacea*, although the two taxa have not been detected to date in the same locality.

Meladema imbricata **(Wollaston, 1871)**

Figures 3C, 4C, 5C, 11C, 12C, G, 13C, 14C, 15C, 23, 24A, 25D, F

Scutopterus imbricatus Wollaston, 1871: 220.
Meladema imbricata (Wollaston, 1871): Sharp 1882: 824; Régimbart 1895: 184; Machado 1987: 58; Balke et al. 1990: 364.
Meladema lanio ab. *imbricata* (Wollaston, 1871): Gcshwendtner 1936: 42.
Meladema imbricatum Branden, 1885: 95.
Meladema lanio f. *imbricata* Sanfilippo, 1966: 49.

Type locality. "Madeira" [mislabelled].

Type material (BMNH). Holotype ♀ (Figure 24A): "Scutopterus// imbricatus, Woll" [HW] Scutopterus// imbricatus Woll// M.E.Bacchus det 1977// HOLOTYPE" [Latin name, describer & last 7 HW] "Holo-// type" [small, circular label, red margin] "Meladema// imbricata (Woll.)// M. Balke det. 1989" [Latin name, describer & 89 HW] (dry pinned, BMNH, Wollaston Collection).

Note that as discussed by Machado (1987), the type specimen must have been mislabelled, as this species is now known to be endemic to the Canary Islands.

Additional material examined (genotyped specimens). Spain, Canary Islands. 1 ♂ "1998 SPAIN Islas Canarias// La Gomera// El Cedro – stream in laurysilva// D. T. Bilton leg." "M. IMBRICATA" [HW] "G4 Mel// below G3" [HW] "DNA voucher// NHM-IRM3A" (IBE); 1 ♂ "1998 SPAIN Islas Canarias// La Gomera// El Cedro – stream in laurysilva// D. T. Bilton leg." "M. IMBRICATA" [HW] "G1 Mel" [HW] "DNA voucher// NHM-IRM4A" (IBE); 1 ♂ "1998 SPAIN Islas Canarias// La Gomera// El Cedro – stream in laurysilva// D. T. Bilton leg." "DNA voucher// NHM-IRM4b" (IBE); 1 ♀ "15/i/2000 SPAIN Islas Canarias// La Gomera// El Cedro// D. T. Bilton leg." "DNA voucher// NHM-IRM15A" (CBP); 1 ♂ "15/i/2000 SPAIN Islas Canarias// La Gomera// El Cedro// D. T. Bilton leg." "DNA voucher// NHM-IRM15B" (CBP); 1 ♂ "April 1999 SPAIN// Islas Canarias La Palma// Bco. Hoyo Verde Caldera de// Taburiente D. T. Bilton leg." "DNA voucher// NHM-IRM6A" (CBP); 1 ♀ "April 1999 SPAIN// Islas Canarias La Palma// Bco. Hoyo Verde Caldera de// Taburiente D. T. Bilton leg." "DNA voucher// NHM-IRM6B" (CBP); 1 ♀ "April 1999 SPAIN// Islas Canarias La Palma// Bco. Hoyo Verde Caldera de// Taburiente D. T. Bilton leg." "DNA voucher// NHM-IRM6C" (CBP); 1 ♂ "April 1998 SPAIN//

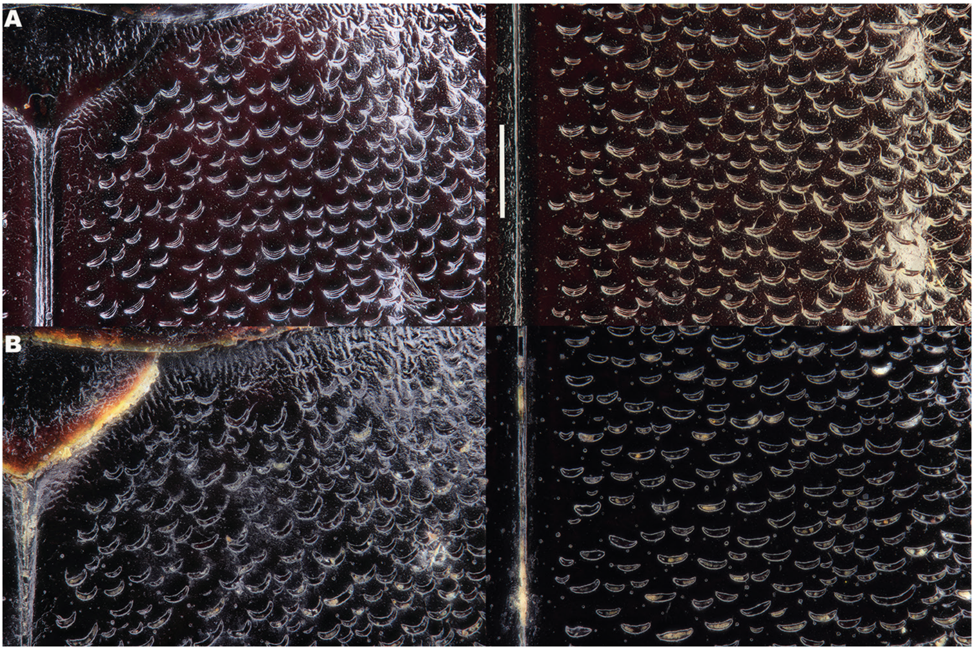

Figure 19. *Meladema coriacea*, Italy, Sicily elytral sculpture; shoulder and middle left and right, respectively (DNA voucher codes, where applicable). **A** male, Bosco Ficuzzo (IBE-AN691) **B** female, Monte Maganoce. Scale bar = 0.5 mm.

Islas Canarias La Palma// Bco. del Rio upper reaches in// Laurisylva D. T. Bilton leg." "DNA voucher// NHM-IRM7A" (CBP); 1 ♂ "1998 SPAIN Islas Canarias// Tenerife// Barranco del Río 1,600m// D. T. Bilton leg." "M. IMBRICATA" [HW] "T7// Mel." [HW] "DNA voucher// NMH-IRM5A" (IBE); 1 ♂ "1998 SPAIN Islas Canarias// Tenerife// Barranco del Río 1,600m// D. T. Bilton leg." "DNA voucher// NMH-IRM5D" (IBE); 1 ♂ "13/i/2000 SPAIN Islas Canarias// Tenerife// Barranco del Rio 1,600m// D. T. Bilton leg." "DNA voucher// NHM-IRM17A" (CBP); 1 ♀ "13/i/2000 SPAIN Islas Canarias// Tenerife// Barranco del Rio 1,600m// D. T. Bilton leg." "DNA voucher// NHM-IRM17B" (CBP). All with "*Meladema imbricata*// (Wollaston, 1871)// D T Bilton [or I Ribera] det. 2017".

Additional material examined (non-genotyped specimens). Spain, Canary Islands. 1 ♂ "April 1998 SPAIN// Islas Canarias la Gomera// El Cedro stream in Garajonay// laurisylva D. T. Bilton leg." (CBP); 1 ♀ "April 1998 SPAIN// Islas Canarias La Palma// Bco. del Río upper reaches in// Laurisylva D. T. Bilton leg." (CBP); 1 ♂ "Islas Canarias: Tene-// rife, 9.-10.vi. 1989// Bco. del Río 1100m.// Balke & Hendrich leg." "Meladema// imbricata// M. Balke det 2011" "M. Balke// BMNH(E) 2013-119" (BMNH); 1 ♂ "I. Canarias/ Tenerife// Bco. del Rio, 1400m// 9.-10.6.1989, Bach// Balke/ Hendrich, leg." "Meladema// imbricata Woll.// HENDRICH det. 1995" [Latin name & describer HW] (CBP); 2 ♂♂, 2 ♀♀ "9.-10.6.89 Islas Canarias// Tenerife, Barranco// del Rio, ca. 1000m// Balke, Hendrich, Fery leg." [HW] "Meladema// imbricata// Woll.// Fery det. 89" [HW] (CBF); 2 ♂♂, 1 ♀ "ESP. Tenerife// Bco. del Río 1600m// 2.xi.1991 AN Nilsson" "Meladema imbricata// (Wollaston, 1871)// Det. AN Nilsson 1991" (CBP); 1 ♂ "April 1998 SPAIN// Islas Canarias Tenerife// Bco. del Río Upper// Reaches D. T. Bilton leg" (CBP). All with "*Meladema// imbricata* (Wollaston, 1871)// D T Bilton [or I Ribera] det. 2017".

Description (based on all material examined). *Size*: Holotype TL = 22.13 mm; EL = 15.79 mm; MW = 10.22 mm. Other material examined TL = 18.05–21.38 mm; EL = 13.57–15.62 mm; MW = 8.83–9.98 mm.

Colour. Dorsum (Figure 3C), dark reddish brown to yellow. Labrum yellowish; clypeus yellowish except central 1/4 red to blackish, connected to dark pigmentation on frons. Frons with transverse pale strip anterolaterally, adjacent to pale parts of clypeus, otherwise dark reddish brown. Medial, paired interocular patches on frons yellow; strongly transverse apicolaterally, almost reaching channel around interior margin of compound eye. Pronotum dark reddish brown on disc; narrowly reddish along anterior margin; lateral margins broadly yellowish to pale red. Elytra yellowish brown, with black irrorations; pattern much more clearly visible when lifted (Figure 4C). Legs yellowish brown to black; posterior tibiae and tarsi darkest. Antennae and maxillary and labial palpi yellowish to reddish. Venter reddish brown; prementum and posterior genae yellow; mentum and submentum reddish. Pronotal hypomeron and shoulder, outer portion of elytral epipleurs and apex of metacoxal process yellowish.

Head. Labrum shining, with medium to fine, sparse punctures. Reticulation absent anteriorly, clearly evident in posterior half, here fine and composed of small, isodiametric to slightly transverse meshes. Clypeus weakly shining, with medium to fine, sparse punctures and traces of very fine, shallow, close punctures. Frons weakly shining, entire surface with coarse, open reticulation, becoming stronger and more evident posteriorly. Meshes transverse to isodiametric apically and medially, strongly elongate posteriorly and onto vertex. Paired epicranial foveae on anterior frons, one immediately behind the other. Anterior foveae transverse, posterior foveae elongate oval. Foveae all strongly reticulate; anterior and posterior foveae linked by reticulated channel. Internal and posterior borders of compound eyes distinct, raised relative to level of adjacent cuticle. Lateral margins bordered by distinct narrow channel; deeper anteriorly than posteriorly and continuing behind posterior margin of eye onto vertex. Channel with dense punctures, bearing long, stiff, yellow recumbent to decumbent setae.

Pronotum. Posterior margin weakly sinuate laterally (Figure 3C). Surface somewhat shining, strongly rugose. Reticulation meshes large, open, flat and with varying sizes and orientations. Transverse irregular row of medium punctures bearing long, yellow recumbent to decumbent setae 1/5 behind anterior pronotal margin; interrupted briefly in centre, obscured by reticulation inside lateral margins but continuing inside lateral third of posterior margin. Reticulation weak and obsolete anterior to transverse row, surface here clearly doubly punctate, with very fine, dense and medium, sparse to very sparse punctures. Scattered medium punctures visible elsewhere, amongst meshes of reticulation. Centre of disc with traces elongate, narrow, slit-like fovea, typically obscured by reticulation, but traceable as an elongate reticulation chan-

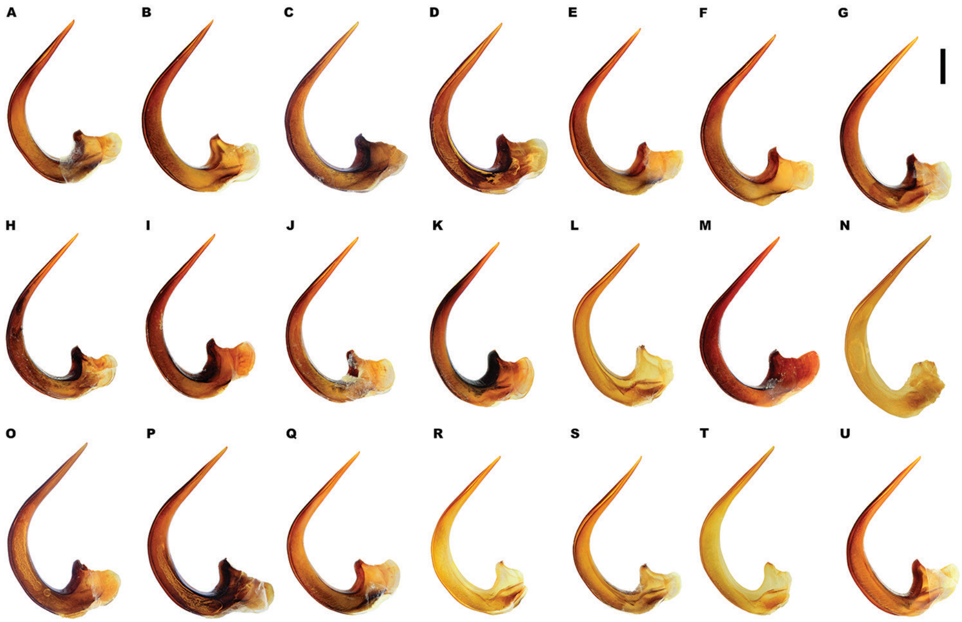

Figure 20. *Meladema* species, variation in male median lobes, lateral view. **A–N** *M. coriacea*; **O–U** *M. lepidoptera* sp. n. (DNA voucher codes, where applicable). **A** Spain, Huesca, Bernués (IBE-DV292) **B** Spain, Girona, Port Bou (IBE-DV-293) **C** Spain, Tarragona, Esblada **D** Spain, Cáceres, nr. Plasencia **E** Spain, Murcia, Fte. Caputa (NHM-IRM13) **F** Spain, Córdoba, Baena (NHM-IRM14C) **G** Tenerife, Chamorga (MNCN-AI1095) **H** Morocco, Oued Massa (NHM-IRM2A) **I** Morocco, Tazekka (NHM-IRM1C) **J** Morocco, Sidi-Ibrahim (NHM-IR7) **K** Algeria, Aïn Damous (MNCN-HI6) **L** Italy, Sicily, Bosco Ficuzzo (IBE-AN691) **M** Greece, Poros, Kampos **N** Greece, Ios **O–P** Corsica, Francardo **Q** holotype, Corsica, Cap Corse (NHM-IRM12E) **R** Italy, Montecristo (IBE-DV289) **S** Sardinia, Villagrande Strìsaili (IBE-RA5) **T** Italy, Elba, Pomonte (IBE-AN692) **U** Italy, Tuscany, S. Luce (IBE-AN693). Scale bar = 1 mm.

nel. Lateral margins slightly raised, shining, without rugose sculpture and with fine, scattered punctures.

Elytra. Shining, with short, transverse, usually straight or weakly curved crescentic striolae of varying sizes and density (Figures 5C, 25D, F). Striolae shallow and moderate on shoulder and anterior disc, widely separated; becoming closer, larger and more curved posteriorly. Posterior third of elytra with an almost scaly appearance (Figure 3C); striolae here almost touching each other laterally. Surface between crescentic striolae doubly punctate and reticulate (Figure 5C); with very fine, close and medium, sparse to very sparse punctures (the latter bearing short, peg-like setae). Reticulation fine, somewhat obsolete, meshes isodiametric; more evident in posterior half, sometimes obscuring very fine punctation. Puncture rows well-marked, continuous almost to elytral apices; punctures shallower posteriorly than anteriorly.

Venter. Prementum shining, tumid in centre, with fine and medium, sparse punctures. Mentum shining; central projection with shallow median emargination. Lateral lobes with very fine, close punctures, scattered, whitish recumbent to decumbent setae and longitudinal wrinkles. Submentum shining, with transverse wrinkles. Central 1/4 with medium, sparse punctures bearing long, white-yellowish, erect setae. Gula shining, with sparse, shallow, transverse wrinkles; patch of medium-coarse punctures posterolaterally. Genae shining, strongly reticulate; meshes transverse anteriorly and posteriorly, almost isodiametric in centre. Prosternum shining, with weak, low irregular transverse ridges laterally. Arched in centre and with fine, moderate to close punctures laterally, bearing long, white-yellowish, recumbent to erect setae; punctures and setae extending in an irregular row onto process, just below arch. Process lanceolate, arched; apex acuminately rounded. Centre of prosternum and process with double punctation of very fine, close to very close and medium, sparse to moderate punctures. Pronotal hypomeron shining, impunctate. Elytral epipleurs shining, with fine wrinkles; irregular puncture row close to internal margin, from centre to close to apex, punctures bearing fine, whitish, erect setae. Metaventrite shining, central portion with reticulation reduced to sparse, transverse scratches and very fine, close and fine to medium, sparse punctures. Metaventral process strongly reticulate, with transverse to elongate, rugose meshes and traces of fine, sparse punctures; small central area with reticulation of very small meshes. Metaventral process relatively broad; apex acuminate and upturned slightly anterolaterally. Metacoxal lines not reaching anterior border of metacoxae, disappearing approx 1/10 from margin. Internal laminae of metacoxae shining, sculpture as on centre of metaventrite. Metacoxal lobes sculptured as internal laminae, strongly rounded, with irregular, elongate field of medium to coarse punctures close to lateral margins, bearing fine, white, recumbent to erect setae. External laminae of metacoxae shining, smooth close to process, but with strong reticulation elsewhere; reticulation meshes very elongate posteromedially, to transverse anteriorly. Abdominal ventrites shining. Ventrites 3–5 with cluster of golden, erect setae anteromedially. Ventrite 1 with elongate reticulation throughout. Ventrite 2 with similar reticulation; absent close to centre. Ventrite 3 with elongate reticulation laterally, becoming transverse close to smooth central 1/5. Reticulation of ventrites 4 and 5 restricted to lateral third and with superimposed elongate furrows. Ventrites 2–5 doubly punctate; very fine, moderate and fine, sparse to very sparse punctures; punctures most evident in areas without reticulation. Ventrites 3–5 with transverse irregular row of long, yellowish, recumbent to decumbent setae laterally. Ventrite 6 (Figure 11C) with very fine, moderate punctures and medium to coarse, sparse to moderate punctures; punctures coarser close to apex. Elongate, semicircular wrinkles and channels apicolaterally and centrally; apicolateral sculpture extending basally around central portion of ventrite. Some punctures in channels bearing elongate, whitish, erect setae.

Male. Foretarsi (Figure 12C) with articulo-setal counts as follows (base to apex): row 1, 8; row 2, 10; row 3, 10; row 4, 8. Curved, golden setae bordering articulo-setal field dense, particularly basally. Foretarsal claws (Figures 12C, 13C) elongate, curved. Mesotarsi (Figure 12G) with articulo-setal counts as follows (base to apex): row 1, 8; row 2, 9–10; row 3, 8–9; row 4, 7 (2 clusters, 4 on inner side, 3 on outer side, situated laterally). Curved, golden setae bordering articulo-setal field relatively dense, especially

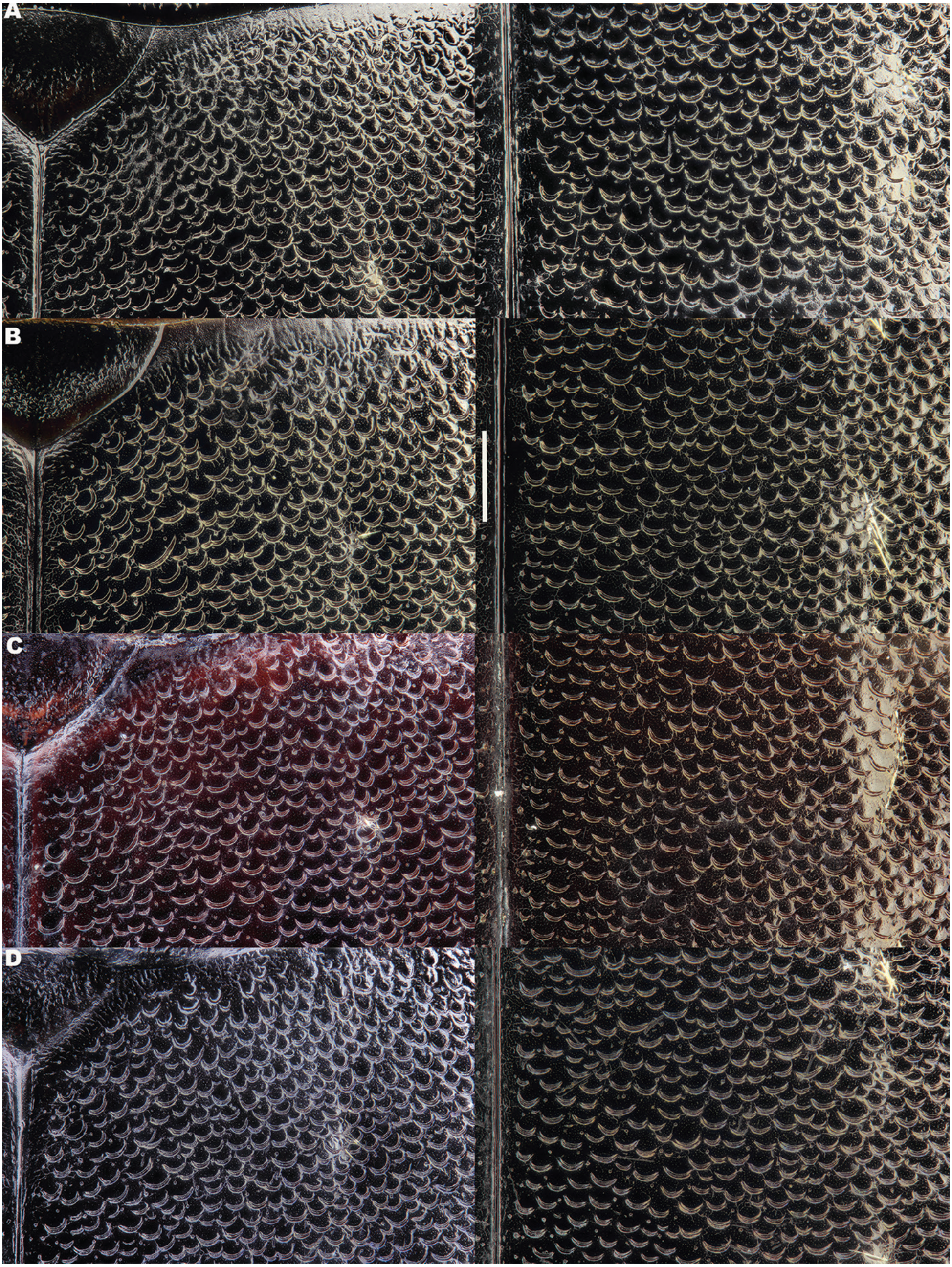

Figure 21. *Meladema lepidoptera* sp. n. elytral sculpture (males); shoulder and middle left and right, respectively (DNA voucher codes). **A** holotype male, Corsica, Cap Corse (NHM-IRM12E) **B** Italy, Montecristo (IBE-DV289) **C** Italy, Elba, Pomonte (IBE-AN692) **D** Italy, Tuscany, S. Luce (IBE-AN693). Scale bar = 0.5 mm.

basally. Mesotarsal claws (Figure 12G) elongate, curved. Abdominal ventrite 6 (Figure 11C) with apex rounded, with well-marked median emargination. Median lobe asymmetrical (Figure 14C), sinuation strong, approximately 1/4–1/3 from apex; ventral margin of apical portion weakly concave in lateral view. Parameres (Figure 14C) with inner margin almost right-angled at base; outer and inner margins undulated slightly.

Female. As male, except for simple fore and mesotarsi and differently shaped abdominal ventrite 6 (with bluntly pointed apex - Figure 15C).

Variation. The size and density of the crescentic striolae on the elytra differs somewhat between individuals and localities (e.g. Figure 25D, F). At least some of this variation may be due to hybridization with *M. coriacea* (see below), making the extent to which this is truly intraspecific unclear. On La Palma, however, an island with no known populations of *M. coriacea*, and no genetic evidence of hybridization, the crescentic striolae are relatively very large and dense in some females (Figure 25F), approaching the situation seen in some females of *M. lanio* (see below).

Differential diagnosis. Morphologically somewhat intermediate between *M. coriacea*/*M. lepidoptera* sp. n. and *M. lanio*. From *M. coriacea* and *M. lepidoptera* sp. n. *M. imbricata* can be distinguished on its different dorsal colouration, particularly the strongly mottled elytra, with much smaller, sparser crescentic striolae, as well as the less strongly sinuate posterior pronotal margin, details of the male genitalia (median lobe with sinuation further away from apex, with concave ventral margin in lateral view) and the last abdominal ventrites of both sexes. The habitus of *M. imbricata* is also typically more elongate than either of the above species (Figure 3). There are also additional minor differences in dorsal and ventral sculpture, as described above. With the exception of some females (see below), *M. imbricata* can be separated from *M. lanio* on the presence of crescentic striolae on the elytra. The male genitalia of the two species are also different, the sinuation of the median lobe of *M. lanio* occurring further from the apex than *M. imbricata* (see Figure 14C, D). *M. imbricata* also differs from all individuals of *M. lanio* in its less elongate habitus (Figure 3) and the much stronger sculpture of the metacoxae and abdominal ventrites.

Distribution. Endemic to the western Canary Islands (Figure 23), being erroneously reported from Madeira in the original description, as discussed by Machado (1987). We have only seen material from a single locality on Tenerife (upper reaches of Barranco del Río), one on La Gomera (El Cedro, in the laurel forest of Garajonay National Park), and two streams on La Palma (Barranco del Río and Barranco Hoyo Verde, situated on opposite sides of the Caldera de Taburiente). Lüderitz et al. (2010) report the species from one additional locality each on La Gomera and Tenerife, although the Tenerife locality (Barranco del Infierno, 500 m) has been visited by DTB in the early 2000s, when it contained only *M. coriacea*, as reported by Malmqvist et al. (1995). Additionally, neither of these records are mentioned by Lüderitz et al. (2016), casting some doubt on both of them. The number of permanent stream systems on the Canary Islands has declined seriously in recent decades, as a result of unsustain-

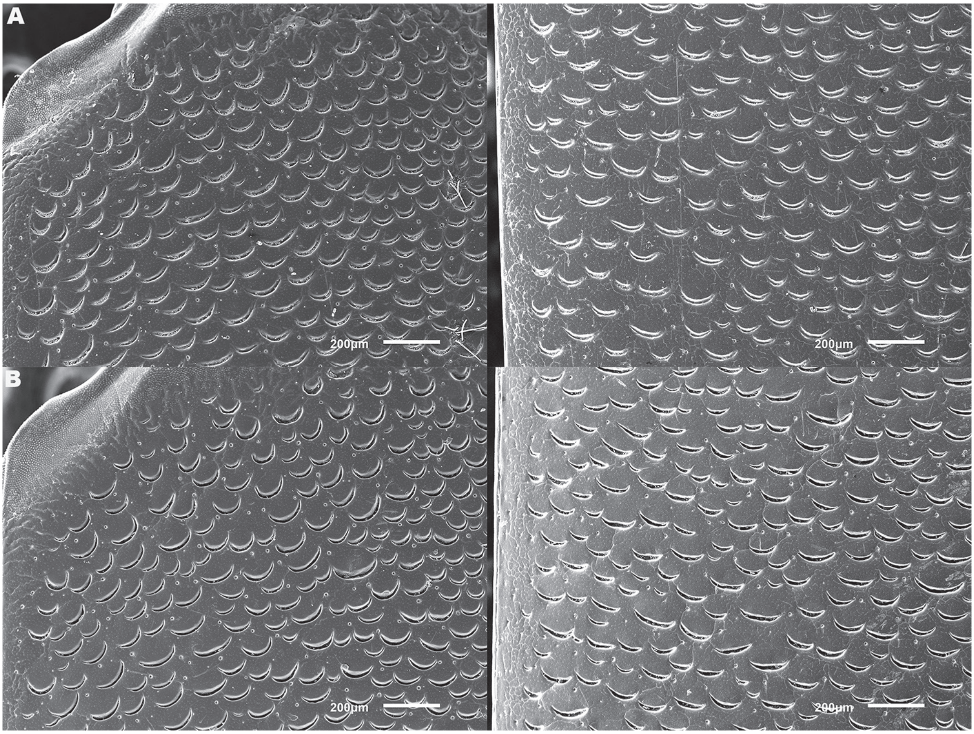

Figure 22. *Meladema lepidoptera* sp. n., Sardinia, elytral sculpture SEMs; shoulder and middle left and right, respectively (DNA voucher codes). **A** male, Villagrande Strìsaili (IBE-RA5) **B** female, Tortoli (IBE-RA18).

able water use. Streams have been variously diverted, piped, dammed, and negatively affected by abstraction directly from aquifers (Malmqvist et al. 1993, 1995, Kelly et al. 2002, Lüderitz et al. 2010, 2016). As a consequence, *M. imbricata*, which appears to be restricted to permanent reaches at relatively high altitude, particularly in forested regions, is very rare, being listed as Critically Endangered (1Ac) in the IUCN Red List (Foster 1996a). The species is also potentially threatened by hybridization with *M. coriacea* (see Ribera et al. 2003 and below), a process which may be further facilitated by ongoing climate change favouring the expansion of this more eurytopic species. Lüderitz et al. (2016) suggest that *M. imbricata* may have disappeared from the El Cedro stream on La Gomera recently, apparently being replaced by *M. coriacea* between 2006 and 2013. It is not clear, however, whether the same stream reaches were sampled on these two occasions. Work establishing the current status of this species in the Canary Islands is clearly a conservation priority.

Meladema lanio (Fabricius, 1775)

Figures 3D, 4D, 5D, 11D, 12D, H, 13D, 14D, 15D, 23, 24B, 26.

Dytiscus lanio Fabricius, 1775: 231.

Colymbetes lowei Gray, 1831: 284.

Scutopterus lanio (Fabricius, 1775): Dejean 1833: 61; Wollaston 1871: 221.

Colymbetes lanio (Fabricius, 1775): Aubé 1838: 221; Wollaston 1854: 82; Wollaston 1865:68.

Meladema lanio (Fabricius, 1775): Sharp 1882: 632; Régimbart 1895: 184; Gschwedntner, 1936: 42; Falkenstöm 1938: 15; Guignot 1961: 770; Balke and Hendrich 1989: 71.

Type locality. "Maderae aquis"

Type material (BMNH). Lectotype ♀ (herein designated, Figure 24B): "Dytiscus lanio// Fab. Entom. p. 231. n. 8." [Latin name & 231. n. 8. HW] "*Dytiscus lanio*// Fabricius, 1775// LECTOTYPE// DT Bilton & I Ribera des. 2017" (dry pinned, BMNH, Banks Collection). Supposed syntypes comprise the above specimen and one other female, located in the Zoological Museum, University of Copenhagen (Zimsen, 1964; A. Solodovnikov, *pers. comm.*). Sree Selvantharan and Aslak Hansen have kindly communicated a photo of the Copenhagen specimen labelled as *lanio* (both on its pin, and above it in the cabinet). This is in fact a species of *Cybister*.

Additional material examined (genotyped specimens). Portugal, Madeira: 1 ♂ "vi/1998 PORTUGAL Madeira// Ribeira dos Cedros// L. C. Kelly leg." "M3 Hand// Coleoptera" [HW] "Meladema// lanio" [HW] "DNA voucher// NHM-IRM8A" (IBE); 1 ♀ "vi/1998 PORTUGAL Madeira// Levada das Faias// L. C. Kelly leg." "M2 handsearch// Coleoptera" [HW] "Meladema// lanio" [HW] "DNA voucher// NHM--IRM9A" (IBE); 1 ♀ "vi/1998 PORTUGAL Madeira// Levada das Faias// L. C. Kelly leg." "DNA voucher// NHM-IRM9B" (IBE); 1 ♂ "Madeira, Canhas// lado sur de Paul da Serra// 1398 m 32°44'36"N 17°05'56"W// charca sobre arroyo de pietras// 19.7.2011 A. Rudoy leg." "DNA Voucher// IBE-DV298" (IBE). All with "*Melademal*// *lanio* (Fabricius, 1775)// D T Bilton [or I Ribera] det. 2017"

Additional material examined (non-genotyped specimens). Portugal, Madeira: 1 ♀ "pouzo" [HW] "var. squamata" [HW] "passage à la m.// imbricatum Woll." [HW] (ISNB); 1 ♀ "Madeira// 90.32." [HW] (BMNH); 1 ♀ "Madeira// 90.32." [HW] "Colymbetes// lanio// Fabr." [HW] (BMNH); 1 ♀ "Madeira" reverse "48// 99" [small, circular label, HW] "Colymbetes// lanio Fabr.// Madeira" [HW] (BMNH); 1 ♀ "Madeira" reverse "48// 99" [small, circular label, HW] (BMNH); 1 ♂ "Sharp Coll.// 1905-313." "Dytiscus lanio Fab.// (Scutopterus Woll. Meladema D. S.)// Madeira T. V. Wollaston" [HW] (BMNH); 2 ♂♂, 2 ♀♀ "Madeira// in Fauvel" [HW] "Coll. Odier.// B. M. 1921-288" (BMNH); 3 ♂♂, 3 ♀♀ "MADEIRA// Ribeira da St.// Luzia// 24.VIII.1964// E. W. Classey" [HW] "Brit. Mus.// 1968-48." [8-48 HW] (BMNH); 3 ♂♂, 3 ♀♀ "MADEIRA:// Ribeira de St. Martinho// 13.VIII.1966// E. W. Classey" [HW] "Brit. Mus.// 1966-446" [6-446 HW] (BMNH); 6 ♂♂, 4 ♀♀ "MADEIRA:// Ribeiro de St.// Martinho// 13.VIII.1966// E. W. Classey" [HW] "Brit. Mus.// 1968-48." [8-48 HW] (BMNH); 1 ♂, 2 ♀♀ "MADEIRA:// Ribeira da Abilheira// 19/VIII/1966// E. W. Classey" [HW] (BMNH); 2 ♂♂ "23/iii/1995 MADEIRA// Ribera on 103 below// Poiso & Monte ca.// 900m D. T. Bilton leg." (CBP);

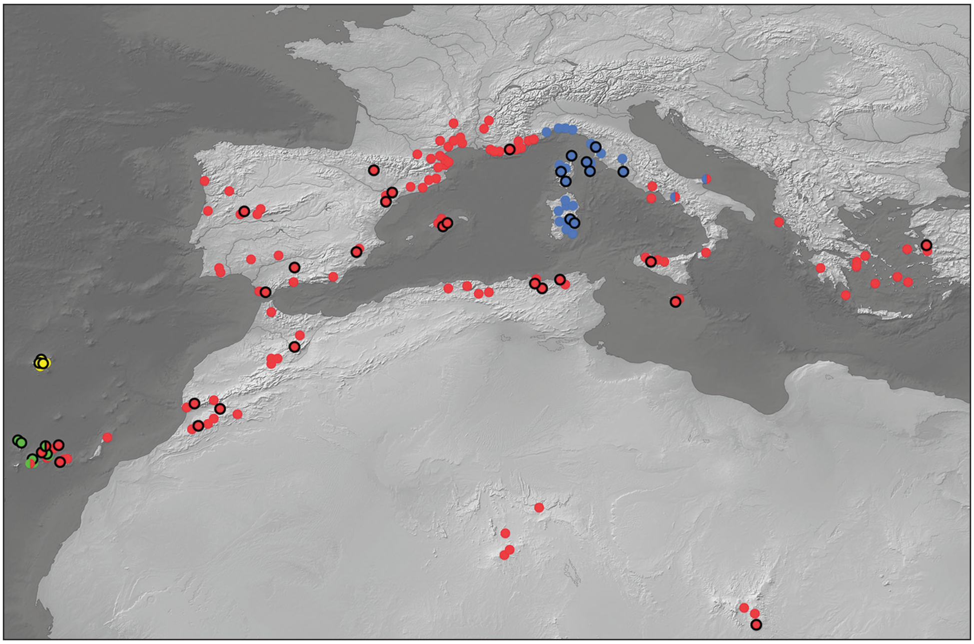

Figure 23. *Meladema* distribution, material examined. Symbols with black border show locations of genotyped specimens. Symbol colours as follows: *M. coriacea* – red; *M. lepidoptera* sp. n. – blue; *M. imbricata* – green; *M. lanio* – yellow. Bicoloured symbols, hybrid or morphologically intermediate individuals.

2 ♂♂, 1 ♀ "March 2001 MADEIRA// Levada @ Rabacal// D. T. Bilton leg." (CBP); 1 ♂ "Madeira 1.-4.8.86// 1kn nördl. Poiso// Quellarn d. R. Frio// leg. Balke// Hendrich" "COLL.// HENDRICH// BERLIN" "Meladema// lanio F." [HW] (CBP); 3 ♂♂, 3 ♀♀ "Madeira 8 Anchadas da Cruz// 932 m 32°48'35"N 17°17'47"W// charca de arroyo// 4.07.15 A. Rudoy leg." (IBE); 1 ♂ "Madeira, Canhas// lado sur de Paul da Serra// 1398 m 32°44'36"N 17°05'56"W// charca sobre arroyo de pietras// 19.7.2011 A. Rudoy leg." (IBE); 1 ♂ "lanio Fab." [HW] (BMNH); 1 ♂ "40// 4 2// 2156" [small, circular label, HW] (BMNH); 1 ♂ "40// 4 2// 2157" [small, circular label, HW] "C. Lanio Fabr." (BMNH); 2 ♂♂, 2 ♀♀ without labels (BMNH, Wollaston Collection); 1 ♂ "Meladema// lanio// Fauvel 1897// Madère" [HW] "MUSÉUM PARIS// Coll. P. de Peyerimhoff// 1950" (MNHN); 1 ♂ "MUSÉUM PARIS// Coll. P. de Peyerimhoff// 1950" (MNHN). All with "*Meladema lanio*// (Fabricius, 1775)// D T Bilton [or I Ribera] det. 2017".

Description (based on all material examined). *Size*: Lectotype TL = 20.30 mm; EL = 16.30 mm; MW = 10.18 mm. Other material examined TL = 17.40–21.12 mm; EL = 12.67–15.36 mm; MW = 8.70–10.50 mm.

Colour. Dorsum (Figure 3D), dark reddish brown to yellow. Labrum yellowish, red anterolaterally in some specimens; clypeus yellowish except central ca. 1/6 red to blackish, connected to dark pigmentation on frons. Frons with transverse pale strip anterolaterally, adjacent to pale parts of clypeus, otherwise dark reddish brown. Me-

Figure 24. *Meladema* type labels and specimens *in situ*. **A** *M. imbricata*, holotype, BMNH, Wollaston Collection **B** *M. lanio* lectotpe, BMNH, Banks Collection.

dial, paired interocular patches on frons yellow; strongly transverse apicolaterally, almost reaching channel around interior margin of compound eye; confluent in centre in some specimens. Pronotum dark reddish brown on disc; narrowly reddish along anterior margin; lateral margins broadly yellowish. Elytra yellowish brown to greenish brown, with black irrorations; pattern visible without being lifted, but more evident when done so (Figures 3D, 4D). Legs yellowish brown to black; posterior tibiae and tarsi darkest. Antennae and maxillary and labial palpi yellowish to reddish. Venter reddish brown; prementum yellow; posterior genae, mentum and submentum reddish. Pronotal hypomeron and shoulder and outer portion of elytral epipleurs yellowish.

Head. Labrum shining, with medium to fine, sparse punctures. Reticulation absent anteriorly, clearly evident in posterior half, here fine and composed of small, isodiametric to transverse meshes. Clypeus weakly shining, with medium to fine, sparse punctures and traces of very fine, shallow, close punctures. Frons weakly shining, entire surface with, open reticulation; weak in front of interocular patches, becoming stronger and more evident posteriorly. Meshes transverse to isodiametric apically and medially, strongly elongate posteriorly and onto vertex. Paired epicranial foveae on anterior frons, one immediately behind the other. Anterior foveae transverse, posterior foveae elongate oval. Foveae reticulate; anterior and posterior foveae linked by reticulated channel. Internal and posterior borders of compound eyes distinct, raised relative to level of adjacent cuticle. Lateral margins bordered by distinct narrow chan-

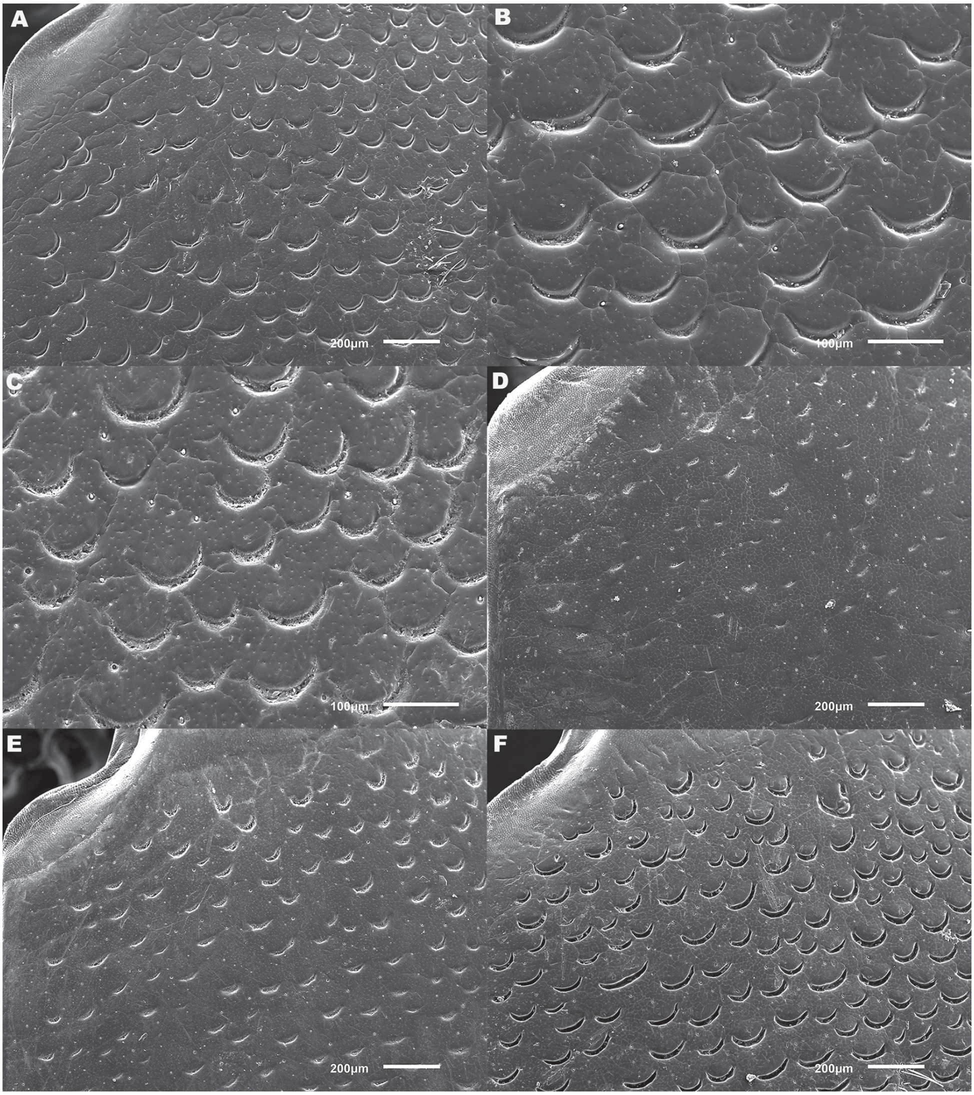

Figure 25. *Meladema* species, Canary Islands, elytral shoulder sculpture SEMs **A–E** males **F** female (DNA voucher codes where applicable). **A–B** *M. coriacea* x *imbricata* hybrid, Tenerife, Bco. del Río 600 m (NHM-IRM16A) **C** *M. coriacea*, Tenerife, Bco. de Masca (NHM-IRM19A) **D** *M. imbricata*, La Gomera, El Cedro (NHM-IRM3A) **E** *M. imbricata* x *coriacea* hybrid, Tenerife, Bco. del Río 1,600 m (NHM-IRM5B) **F** *M. imbricata*, La Palma, Bco. Hoyo Verde.

nel; deeper anteriorly than posteriorly and continuing behind posterior margin of eye onto vertex. Channel with dense punctures, bearing long, stiff, yellow recumbent to decumbent setae.

Pronotum. Posterior margin weakly sinuate laterally (Figure 3D). Surface somewhat shining, strongly rugose. Reticulation meshes large, open, flat and with varying sizes and orientations. Transverse irregular row of medium punctures bearing long, yellow recumbent to decumbent setae 1/5 behind anterior pronotal margin; interrupted

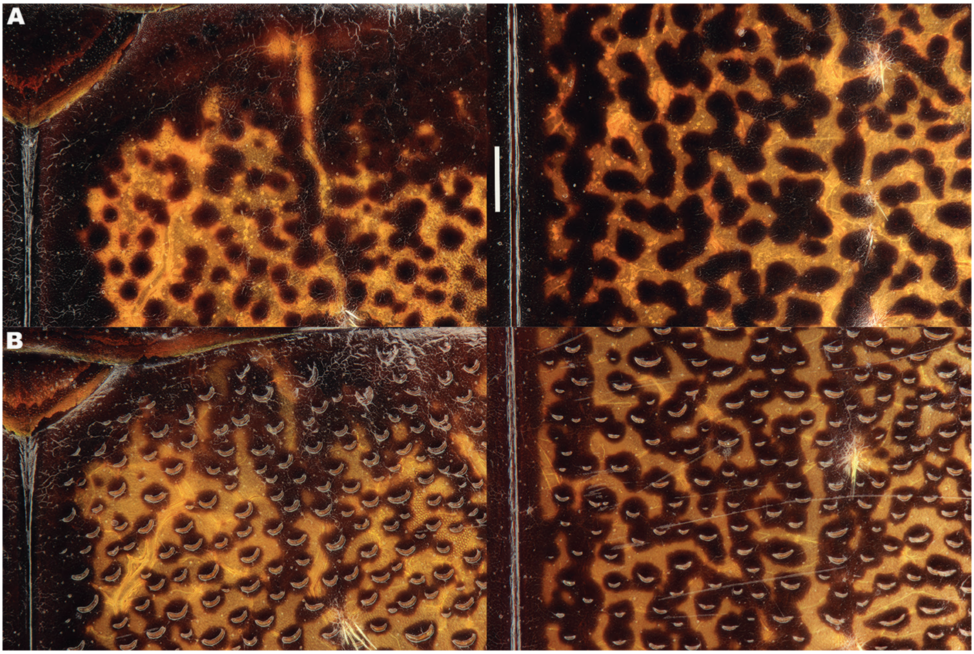

Figure 26. *Meladema lanio*, Madeira, Ribeira da St. Luzia, female elytral sculpture; shoulder and middle left and right, respectively. **A** specimen without and **B** specimen with crescentic striolae. Scale bar = 0.5 mm.

briefly in centre, obscured by reticulation inside lateral margins but continuing inside lateral third of posterior margin. Reticulation weak and obsolete anterior to transverse row, surface here clearly double punctate, with very fine, dense and medium, sparse to very sparse punctures. Scattered medium punctures visible elsewhere, amongst meshes of microreticulation. Centre of disc with elongate, narrow, slit-like fovea, partly obscured by reticulation in some specimens, but then traceable as an elongate reticulation channel. Lateral margins slightly raised, shining, without rugose sculpture and with fine, scattered punctures.

Elytra. Shining, without crescentic striolae (except in some females – see below). Surface doubly punctate and reticulate (Figure 5D); with very fine, close and fine to medium, sparse punctures (the latter bearing short, peg-like setae). Reticulation fine, somewhat obsolete, meshes isodiametric; sometimes obscuring very fine punctation. Surface weakly tuberculate towards sides and apex, particularly in posterior third (see Figure 3D). Puncture rows well-marked, continuous almost to elytral apices; punctures shallower posteriorly than anteriorly.

Venter. Prementum shining, tumid in centre, with fine and medium, sparse punctures. Mentum shining; central projection with shallow median emargination. Lateral lobes with medium, sparse punctures, and scattered, whitish recumbent to decumbent setae. Submentum shining, with transverse wrinkles centrally, and elongate wrinkles laterally. Central 1/4 with medium, sparse punctures bearing long, white-yellowish, erect setae. Gula shining, with sparse, shallow, transverse wrinkles; patch of medium-coarse punctures posterolaterally. Genae shining, with obsolete, open, elongate reticu-

Figure 27. *Meladema* hybrid males, Tenerife, Bco. del Río; isolated elytron, fore and midtarsus, median lobe (lateral and ventral views) and abdominal ventrite 6, respectively (DNA voucher codes). **A** *M. coriacea* x *imbricata*, 600 m (NHM-IRM16A) **B** *M. imbricata* x *coriacea*, 1,600 m (NHM-IRM5B). Scale bars as follows: elytra 5 mm; tarsi, abdominal ventrites, median lobes 1 mm.

lation. Prosternum shining, with weak, low, irregular transverse ridges laterally. Arched in centre and with fine, moderate to close punctures laterally, bearing long, white-yellowish, recumbent to erect setae; punctures and setae extending in an irregular row onto process, just below arch. Process lanceolate, arched; apex acuminately rounded. Centre of prosternum and process with double punctation of very fine, close to very close and medium, sparse to moderate punctures. Pronotal hypomeron shining, impunctate. Elytral epipleurs shining, with fine wrinkles; irregular puncture row close to internal margin, from centre to close to apex, punctures bearing fine, whitish, erect setae. Metaventrite shining, central portion with reticulation reduced to sparse, transverse scratches and very fine, close and fine to medium, sparse punctures. Metaventral process strongly reticulate, with transverse to elongate, rugose meshes and traces of fine, sparse punctures. Metaventral process relatively broad; apex acuminate and upturned slightly anterolaterally. Metacoxal lines not reaching anterior border of metacoxae, disappearing approx 1/10 from margin. Internal laminae of metacoxae shining, sculpture as on centre of metaventrite. Metacoxal lobes sculptured as internal laminae, strongly rounded, with irregular, elongate field of medium to coarse punctures close to lateral margins, bearing fine, white, recumbent to erect setae. External laminae of metacoxae shining, smooth close to process, and with obsolete reticulation elsewhere; without distinct meshes, wrinkled, elongate around anterior and posterior margins; doubly ounctate, with very fine, close and fine, very sparse punctures. Abdominal ventrites shining. Ventrites 3–5 with cluster of golden, erect setae anteromedially. Ventrite 1 with weak reticulation of elongate scratches throughout. Ventrite 2 with similar reticulation; absent close to centre. Ventrite 3 and 4 with scratches restricted to lateral 1/3. Ventrites 2–5 doubly punctate; very fine, moderate and fine, sparse to very sparse punctures; punctures most evident in areas without reticulation. Ventrites 3–5 with transverse irregular row of long, yellowish, recumbent to decumbent setae laterally. Ventrite 6 (Figure 11D) with very fine, moderate punctures and medium to coarse, sparse to moderate punctures; punctures coarser close to apex. Elongate, semicircular wrinkles and channels apicolaterally and centrally; apicolateral sculpture extending basally around central portion of ventrite. Some punctures in channels bearing elongate, whitish, erect setae.

Male. Foretarsi (Figure 12D) with articulo-setal counts as follows (base to apex): row 1, 8–9; row 2, 10; row 3, 10; row 4, 8. Number of setae in rows may differ from right to left tarsus in same beetle. Curved, golden setae bordering articulo-setal field relatively sparse, particularly laterally. Foretarsal claws (Figures 12D, 13D) elongate, curved. Mesotarsi (Figure 12H) with articulo-setal counts as follows (base to apex): row 1, 7–8; row 2, 8; row 3, 8; row 4, 6 (2 clusters of 3, situated laterally). Curved, golden setae bordering articulo-setal field relatively sparse, especially laterally. Mesotarsal claws (Figure 12H) elongate, curved. Abdominal ventrite 6 (Figure 11D) with apex rounded, with well-marked median emargination. Median lobe (Figure 14D) asymmetrical, sinuation strong, approximately 1/3–0.35 from apex; ventral margin of apical portion relatively straight in lateral view. Parameres (Figure 14D) with inner margin almost right-angled at base, with distinct small projection; outer margin undulated slightly; inner straight.

Female. As male, except for simple fore and mesotarsi, and differently shaped abdominal ventrite 6 (with bluntly pointed apex - Figure 15D).

Variation. Males and females generally have identical sculpture on the elytra. Two females studied, one from Ribeira da St. Luzia (Figure 26B, BMNH) and one from "pouzo" (ISNB) have distinct crescentic striolae, as have been observed in female *M. imbricata* from La Palma (see above). Females sculptured in this manner appear to be relatively rare, the only other occurrences of this form we can find being mentioned by Aubé (1838), who had seen a female with this sculpture (see also Sharp 1882) and Falkenström (1938). Such females may be mistaken for *M. imbricata*, as was the case with the ISNB animal listed above.

Differential diagnosis. Closest to *M. imbricata*; for diagnostic characters see under that species.

Distribution. Restricted to the main island of Madeira (Figure 23), where it is relatively widely distributed in permanent streams, particularly in remnant laurel forests in the mountains. Can also be found in man-made levada systems. Much more abundant on Madeira than *M. imbricata* on the Canaries, but still listed as Vulnerable (B1 + 2b) on the IUCN Red List (Foster 1996b), reflecting its very small global range.

Identification key for *Meladema* species

1 Dorsum predominantly dark brown to black, unicolourous (Figure 3A, B); reddish in tenerals (e.g. Figure 17A, 18C, D). Sinuation of posterior margin of pronotum relatively strong (Figure 3A, B). Elytra with crescentic striolae relatively large and dense (Figure 5A, B). Median lobe with apical sinuation weak and relatively close to apex (Figure 14A, B) **2**

– Dorsum not unicolourous, with elytra distinctly mottled and pronotum with distinct paler margins (Figure 3C, D). Sinuation of posterior margin of pronotum relatively weak (Figure 3C, D). Elytra with crescentic striolae usually small or absent (Figure 5C, D). Median lobe with apical sinuation stronger, situated further from apex (Figure 14C, D) **3**

2 Crescentic striolae on elytra relatively small and sparse, particularly on shoulder and on disc close to suture; most striolae not contiguous laterally with neighbours (Figures 5A, 7A, C, 8A, C, 9, 10), giving a less scaly appearance overall (Figure 3A). If striolae denser (specimens from central Sahara only), striolae relatively small (Figure 17) .... ***M. coriacea* Laporte, 1835**

– Crescentic striolae on elytra relatively larger and denser, particularly on shoulder and on disc close to suture (Figures 5B, 7B, D, 8B, D, 18A, 21, 22), giving a strongly scaly appearance overall (Figure 3B). Many striolae contiguous laterally, especially anteriorly..***lepidoptera* sp. n.**

3 Elytra weakly shining, with (typically small) crescentic striolae in all specimens (Figures 5C, 25D, F). Habitus less elongate (Figure 3C). Elytral colour pattern less evident until lifted (Figures 3C, 4C); paler markings on head less extensive (Figure 3C). Median lobe with sinuation strong, approximately 1/4–1/3 from apex (Figure 14C)...............***M. imbricata* (Wollaston, 1871)**

– Elytra strongly shining, without crescentic striolae in most specimens (Figures 5D, 26). Habitus relatively elongate (Figure 3D). Elytral colour pattern more evident, even without being lifted (Figures 3D, 4D); paler markings on head more extensive (Figure 3D). Median lobe with sinuation strong, approximately 1/3–0.35 from apex (Figure 14D) ....***M. lanio* (Fabricius, 1775)**

Discussion

It is almost 15 years since it was first recognised that central Mediterranean populations of *Meladema* were genetically divergent from those elsewhere (Ribera et al. 2003). A combination of limited geographical sampling of genotyped individuals, and the apparent absence of diagnostic morphological characters have, however, prevented this lineage from being formally described until now. As with many arthropods, closely related dytiscid species typically are identified most reliably on features of the male genitalia (see e.g. Miller and Bergsten 2016). In these *Meladema*, whilst there is some variation in male genital anatomy, this is of no value in separating *M. coriacea* and *M. lepidoptera* sp. n.; these cryptic species (*sensu* Bickford et al. 2006) instead being diagnosable on subtle, but consistent, differences in elytral sculpture. Our study demonstrates how a combination of mitochondrial and nuclear genetic data is required to make sense of such variation, and highlights the importance of retaining reference material of genotyped individuals for future study. Our work also highlights our limited understanding of freshwater biodiversity in Mediterranean systems, where further undetected but genetically divergent cryptic species with (almost) identical morphologies are likely to occur, particularly in less well studied lineages.

As noted above, *Meladema* specimens from central Saharan mountains (Hoggar, Tassili n'Ajjer, Tibesti) have an elytral sculpture unlike any other material examined. In the absence of more comprehensive genetic data, we treat these beetles here under the widespread *M. coriacea*, but they may represent an additional lineage within the genus. Whilst the Sahara probably originated on closure of the Tethys seaway ca. 7 million years ago (Zhang et al. 2014), the relative extent of desertic conditions has fluctuated considerably since this time, 'Green Sahara' periods with extensive vegetation and wetlands being relatively frequent (e.g. Drake et al. 2011, Larrasoaña et al. 2013, Tierney et al. 2017), most recently until around 6,000 BP. Present-day oases in the Sahara support a biota containing a mix of Ethiopian and Palaearctic elements (e.g. Bruneau de Miré and Quézel 1961, Brito et al. 2011, Habel et al. 2013), with isolated populations of a number of aquatic insects, including *Meladema* (Peyerimhoff 1931, Bruneau de Miré and Legros 1963), and some apparent endemics (e.g. Fery and Bouzid 2016). The role of North Africa as a differentiation and speciation centre during the Plio-Pleistocene is increasingly recognised (Husemann et al. 2014) and it is possible that the Green Sahara and its massifs were also important in this process. Genetic studies of *Meladema* and other water beetle populations from these areas would clearly prove illuminating in the future.

Intermediate specimens and natural hybridization in Meladema

As shown by Ribera et al. (2003), DNA sequence data strongly suggest that *M. coriacea* and *M. imbricata* hybridize in areas where they come into contact on Tenerife. In Barranco del Río, on the south side of the Teide caldera, *coriacea* and *imbricata*-like beetles co-occur, although apparently not in the same stream reach. Specimens identified as *M. coriacea* from 600 m, in a reach with intermittent flow and semi-permanent pools surrounded by xerophytic vegetation, had mtDNA haplotypes characteristic of *M. imbricata* (hereafter referred to as *M. coriacea* x *imbricata* – see Figure 2). Further up the same stream, at 1,600 m, in a reach with permanent flow surrounded by pine forest, two of the four genotyped specimens identified as *M. imbricata* had *M. coriacea* mtDNA (hereafter referred to as *M. imbricata* x *coriacea* – see Figure 2). In contrast to mitochondrial DNA, the nuclear markers (fragments of Histone 3 and Wingless) of hybrid specimens correspond to the species they most resemble on external morphology (see Fig. S1 in Sýkora et al. 2017). However, detailed morphological study of these specimens reveals that despite appearing most like one or other species they show some intermediate characteristics, further supporting the hypothesis of their hybrid origin. *M. coriacea* x *imbricata* specimens from 600 m show a number of features suggestive of introgression (see Figures 25A–B, 27), including partial mottling of the elytra (more clearly visible when lifted, as in Figure 27A), a more distinct pale margin to the pronotum, more elongate segment 5 on the fore and mesotarsi, and median lobe with sinuation somewhat further from the apex (Figure 27A). These beetles have articulo-setal counts (base to apex) as follows. Foretarsi: row 1, 7; row 2, 9; row 3, 8; row 4, 6. Mesotarsi: row 1, 7; row 2, 8; row 3, 6; row 4, 5 (2 clusters, 3 on inner side, 2 on outer side, situated laterally). Specimens of *M. imbricata* x *coriacea* from 1,600 m have similar median lobes to the above and somewhat larger crescentic striolae on the elytra (Figure 25E) than most *M. imbricata* seen from elsewhere (the exception being some La Palma females noted above), but are otherwise very close to male *M. imbricata* collected elsewhere in the Canary Islands, albeit with lower articulo-setal counts (base to apex, as follows). Foretarsi: row 1, 7; row 2, 9; row 3, 8; row 4, 7. Mesotarsi: row 1, 8; row 2, 9; row 3, 8; row 4, 5 (2 clusters, 3 on each side, situated laterally). As well as these genotyped individuals, beetles with similar morphology to the *M. coriacea* x *imbricata* hybrids referred to above have also been seen from La Gomera. All specimens examined of apparently hybrid origin are listed below.

Whilst we do not have genetic data to confirm their status, we have seen *Meladema* material from mainland Italy which also suggests that hybridization occurs between *M. coriacea* and *M. lepidoptera* sp. n. in areas where they come into contact. Specimens with elytral sculpture intermediate between the two species (Figure 18B, C) have been seen from Apulia and Campania (see below). Given the fact that *M. coriacea* and *M. imbricata* hybridize on the Canary Islands it seems likely that these beetles also represent individuals of mixed ancestry. The precise geographical limits of *M. coriacea* and *M. lepidoptera* sp. n. in the Italian Peninsula remain unclear, but it is likely that a similar contact zone, with hybridization, may occur (or have occurred) in coastal regions of the Alpi Marittimi, an area where, like much of Mediterranean France, recent coastal development has destroyed many historical *Meladema* localities. Further genetic sampling of Italian *Meladema* is clearly required to confirm this hypothesis.

Hybridization between different *Meladema* taxa is perhaps facilitated by the relatively uniform nature of their genitalia and secondary sexual characteristics (see above).

Compared to most dytiscid genera, the male genitalia of *Meladema* species are remarkably similar, particularly the median lobes. *M. coriacea* and *M. imbricata*, for example can be readily distinguished on a suite of external characters, but have median lobes which differ only slightly from each other. In the case of *M. coriacea* and *M. lepidoptera* sp. n., the median lobes are apparently identical in all aspects, as noted above. Despite evidence suggesting some hybridization, we retain these taxa as separate species since they are diagnosible on a suite of both molecular and morphological characters, and appear to remain distinct, suggesting limited gene exchange (Coyne and Orr 2004, DeQueiroz 2007).

Hybrid/intermediate specimens examined are as follows: ***M. coriacea* x *imbricata* hybrids.** Genotyped specimens: 1 ♂ "13/v/2000 SPAIN Tenerife// Bco. del Río 600m// D. T. Bilton leg." "DNA voucher// NHM-IRM16A" (CBP); 1 ♂ "13/v/2000 SPAIN Tenerife// Bco. del Río 600m// D. T. Bilton leg." "DNA voucher// NHM-IRM16B" (CBP). Other specimens: 7 ♂♂ "Meladema// hybr. ♂// det. H. Bußler" [Meladema hybr. & ♂ HW] "La Gomera 1.4.94// Bco. de las Hoyas// leg. H Bußler" (CBF); 15 ♀♀ "Meladema// hybr. ♀// det. H. Bußler" [Meladema hybr. & ♀ HW] "La Gomera 1.4.94// Bco. de las Hoyas// leg. H Bußler" (CBF). ***M. imbricata* x *coriacea* hybrids.** Genotyped specimens: 1 ♂ "1998 SPAIN Islas Canarias// Tenerife// Barranco del Río 1,600m// D. T. Bilton leg." "DNA voucher// NMH-IRM5B" (IBE); 1 ♂ "1998 SPAIN Islas Canarias// Tenerife// Barranco del Río 1,600m// D. T. Bilton leg." "DNA voucher// NMH-IRM5C" (IBE); 1 ♂ "1998 SPAIN Islas Canarias// Tenerife// Barranco del Río 1,600m// D. T. Bilton leg." "DNA voucher// NMH-IRM17C" (CBP). **Intermediates between *coriacea* and *lepidoptera* sp. n:** 1 ♂ "Apulien 10.-20.5.65// Vieste.// Budberg" [Vieste HW] (NMW); 1 ♂ "CAMPANIA// S. Michele P.-AV// IX-1996// leg. Pertuzziello I." "DNA voucher// IBE-AN694" [not possible to amplify any DNA sequences] (CTP).

Veiwed more widely, our study highlights the fact that our fundamental knowledge of biodiversity remains limited, even in the case of comparatively large taxa, in relatively well-studied regions of the world. If we are to understand the origins of such diversity, and how best to protect it in the future, we clearly need accurate taxonomies, which integrative approaches, such as those adopted here, are perhaps best able to supply.

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RESEARCH ARTICLE

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Two new species of the *Phanaeus endymion* species group (Coleoptera, Scarabaeidae, Scarabaeinae)

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Abstract

Phanaeus bravoensis **sp. n.** is described from the coniferous-oak forests in the state of Guerrero, and *P. huichol* **sp. n.** from coniferous-oak forests and cloud forests in Jalisco and Nayarit. The new species are closely related to *P. halffterorum* and *P. zoque* respectively. Morphological trait combination, geographic distribution, and trophic habits show important differences among the studied species. A distribution map and an updated key to separate the species are included.

Resumen

Describimos a *Phanaeus bravoensis* **sp. n.** proveniente de los bosques de coníferas y encino del estado de Guerrero, y a *P. huichol* **sp. n.** de los bosques de coníferas y encino y bosques de niebla de Jalisco y Nayarit. Las nuevas especies están cercanamente relacionadas con *P. halffterorum* y *P. zoque*, respectivamente. Las combinaciones de caracteres morfológicos, áreas de distribución geográfica y los hábitos alimenticios muestran diferencias importantes entre las especies estudiadas. Incluimos un mapa de distribución y una clave actualizada para separar a las especies.

Keywords

Dung beetle, Mexican Transition Zone, mycophagy, Phanaeini, Sierra Madre del Sur, Trans-Mexican Volcanic Belt

Palabras clave

Micofagia, escarabajos del estiércol, Phanaeini, Sierra Madre del Sur, Sistema Volcánico Transversal, Zona de Transición Mexicana

Introduction

Phanaeus Macleay, 1819 is a new world genus of dung beetles that presents a bright metallic coloration and a pronounced sexual dimorphism (males with large cephalic horns and striking pronotal projections) (Edmonds 2006). *Phanaeus* includes at least 55 valid species and 12 species groups. Several studies of *Phanaeus* have been published in recent years, including major reviews (Edmonds 1994, Arnaud 2002, Edmonds and Zídek 2012). As a consequence, there is a broad knowledge of the geographical distribution of *Phanaeus*, and it is considered a Neotropical taxon of South American origin. The subgenerus *Phanaeus* s. str. probably colonized the Mexican Transition Zone during the Miocene, where it diversified and expanded northward into the U.S.A. The subgenus *Notiophanaeus*, however, radiated and expanded in South America and one species group arrived to the Mexican Transition Zone prior to closure of the Panama land bridge: the *endymion* species group (Halffter and Morrone 2017).

The *Phanaeus endymion* species group brings together five closely related Mesoamerican species: *Phanaeus endymion* Harold, 1863, *P. halffterorum* Edmonds, 1979, *P. pyrois* Bates, 1887, *P. zapotecus* Edmonds, 2006 and *P. zoque* Moctezuma & Halffter, 2017 (Moctezuma and Halffter 2017), in addition to the two new species described here. *Phanaeus halffterorum* was described with 17 individuals from Estado de Mexico and one male from Guerrero. Edmonds (1979) included among the features of *P. halffterorum* a strong acute tooth in the middle of anterior margin of pronotum (a character present even in the smallest individuals), with the exception of the Guerrero specimen. We studied the *P. halffterorum* type series and new specimens collected in Guerrero, and we have concluded that the *halffterorum* population from Guerrero represents a new species, which is described in this work. *Phanaeus endymion* is a tropical species that appeared to present a disjunct population in temperate forests from the Mexican Pacific slope of the Trans-Mexican Volcanic Belt (Edmonds 1994, Edmonds and Zídek 2012). In this study, we also recognize these "*endymion*" Pacific slope populations as a new species, which is closely related to *P. zoque*.

Methods

The studied specimens are deposited in the following collections:

CEMT	Seção de Entomologia da Coleção Zoológica, Departamento de Biologia e Zoologia, Universidade Federal de Mato Grosso, Cuiabá, MG, BRA
CNIN	Colección Nacional de Insectos, Instituto de Biología, Universidad Nacional Autónoma de México, México City, MX
IEXA	Colección Entomológica, Instituto de Ecología, A. C., Xalapa, Ver., MX
TAMU	Texas A&M University Insect Collection, TX, USA
FSCA	Florida State Collection of Arthropods, Gainesville, FL, USA
CDINECOL	C Deloya Collection - Instituto de Ecología, A. C., Xalapa, Ver., MX

JLSHC	JL Sánchez-Huerta Collection, Xalapa, Veracruz, MX
MXAL	MA Morón Collection, Xalapa, Veracruz, MX
VMC	V Moctezuma Collection, Xalapa, Veracruz, MX

For this study, the phylogenetic species concept is used (Wheeler and Platnick 2000), which defines species as the smallest aggregation of populations diagnosable by a unique combination of character states. Type specimens bear determination labels printed with black ink on acid-free red paper. The aedeagus and internal sac were prepared as outlined by Marchisio and Zunino (2012) and Moctezuma and Halffter (2017). All measurements and pictures (z-stack image capture method) were taken using a Leica Z16APOA stereomicroscope and the fabricant software.

Taxonomy

Phanaeus halffterorum Edmonds, 1979

Figs 1–4

Phanaeus halffterorum: Edmonds (1979: 99; *partim*), Halffter and Edmonds (1982: 88–89), Anduaga and Halffter (1991: 157), Delgado-Castillo et al. (1993: 125), Edmonds (1994: 39–43, 101), Anduaga (2000: 125, 130), Arnaud (2002: 95–96), Edmonds (2003: 61, 65), Edmonds (2006: 31, 34, 36), Ceballos et al. (2009: 397), Edmonds and Zídek (2012: 3, 5, 12, 52, 54), Deloya et al. (2014: 77), Moctezuma and Halffter (2017: 52, 54–55), Lizardo et al. (in press).

Type material examined (5 ♂♂, 2 ♀♀)**.** Paratypes (TAMU): 2 ♂♂, 2 ♀♀ labeled "MEXICO: Mexico, 5 km E Temascaltepec, Real de Arriba, 2200 m, 10-VII-1976, Fungus, oak-pine forest, W.D. Edmonds, P. Reyes, B. Kohlmann cols."; 2 ♂♂ labeled "MEXICO: Mexico, 8 km W Temascaltepec, 2360 m, 11-VII-76, Fungus in pine-oak forest, W.D. Edmonds, P. Reyes and B. Kohlmann cols."; 1 ♂ labeled "Real de Arriba, Dist. Temascaltepec, Edo. Mex., VII-1932, 6300 ft, Mexico D.F., Hinton Coll. B.M.1939-583".

Distribution and ecology. This species is known from the environs of Temascaltepec, State of Mexico (Fig. 5), and inhabits pine-oak forests from 2200–2360 m. a.s.l. *Phanaeus halffterorum* is considered a mycetophagous species (Edmonds 1979, 1994, Halffter and Edmonds 1982).

Phanaeus bravoensis sp. n.

http://zoobank.org/41BF39B8-9D18-4275-9A1A-01BA830C3867

Figs 6–10

Phanaeus halffterorum: Edmonds (1979: 99; *partim*), Arnaud (2002: 95–96), Edmonds (2003: 61, 65), Edmonds (2006: 31, 34, 36), Deloya et al. (2013: 90–92), Deloya

Figure 1. *Phanaeus halffterorum* major male, dorsal view (paratype).

Figure 2. *Phanaeus halffterorum* major male, lateral view (paratype).

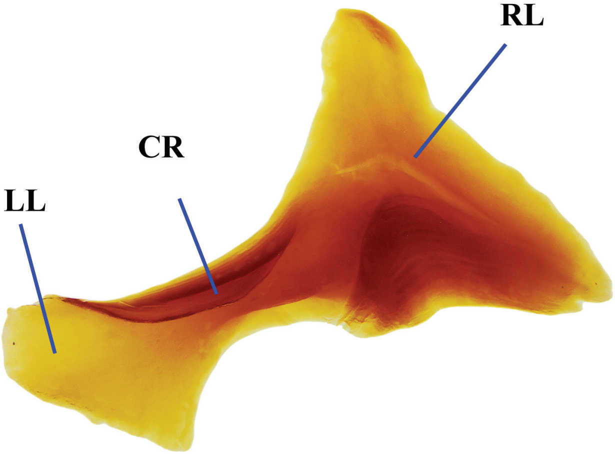

Figure 3. Lamella copulatrix of *Phanaeus halffterorum* (paratype). Abbreviations: LL: left lobe, CR: central ridge, RL: right lobe.

Figure 4. *Phanaeus halffterorum* female, dorsal view (paratype).

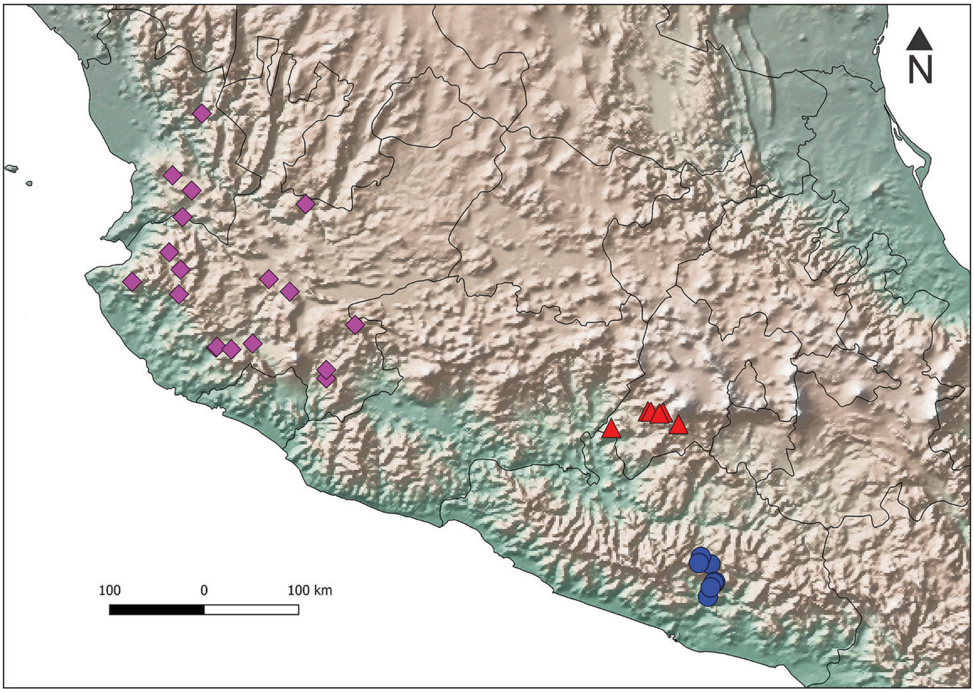

Figure 5. Distribution of *Phanaeus halffterorum* (red triangle), *P. bravoensis* sp. n. (blue circle) and *P. huichol* sp. n. (purple diamonds).

et al. (2014: 77, 206), Edmonds (1994: 39–43, 101), Edmonds and Zídek (2012: 3, 5, 12, 52, 54), Moctezuma and Halffter (2017: 52, 54–55), Lizardo et al. (in press). *Non halffterorum* Edmonds, 1979.

Type material (17 ♂♂, 13 ♀♀)**.** Holotype major male pinned with genitalia in microvial (Figs 6-8): "MEXICO: Guerrero, Chilpancingo de los Bravo, entre Amojileca-Xocomanatlán, V-XI/2014, 17°33'41.17"N, 99°36'59.95"W, necrotrampa, bosque de encino-pino, 1860 m, Ernesto L. Huicochea col.". Paratypes: 5 ♂♂, 1 ♀ same data as holotype; 5 ♂♂, 2 ♀♀ labeled "MEXICO: Guerrero, Chilpancingo, Amojileca, 434559 mE, 1941772 nM, 1772 msnm, bosque de *Quercus*-coníferas, 27/VI/2014, NTP, E. López-Huicochea Col."; 2 ♂♂, 3 ♀♀ *ídem* except "03/XI/2014"; 4 ♀♀ *ídem* except "1860 msnm, 10/X/2014"; 2 ♂♂ labeled "MEXICO: Guerrero, Chilpancingo, Xocomanatlán, 432832 mE, 1938117 mN, 2100 msnm, bosque de coníferas-*Quercus*, 10/VIII/2014, NTP, E. López-Huicochea Col."; 1 ♀ *ídem* except "04/IX/2014"; 1 ♂, 2♀♀ labeled "MEXICO: Guerrero, Chilpancingo, La Cimaroa, Ejido Amojileca, 431911 mE, 1939239 mN, 2150 msnm, bosque de Quercus magnolifolia, 10/VIII/2014, NTP, E. López-Huicochea Col."; "; 2 ♂♂ labeled "MEXICO: Guerrero, Chilpancingo, Acahuizotla, 28/06/2008 – 31/07/2008, veg. encino-pino, sitio 4, NTP IV, Madora Astudillo M col.".

Type deposition. Holotype 1 ♂ IEXA; paratypes: 1 ♂ TAMU; 1 ♂ JLSHC; 2 ♂♂, 1 ♀ VMC; 12 ♂♂, 12 ♀♀ temporally deposited in CDINECOL (12 paratypes will be permanently deposited in CNIN and 12 paratypes in FSCA).

Diagnosis. Pronotal granulate sculpturing; major male lacks a tooth in the middle of anterior pronotal margin, pronotal triangle sides curved (Figs 6, 7); sutural margin of each elytron upturned to form a sharp ridge, which is progressively more elevated posteriorly and prolonged into a small, sharp tooth at apical angle; lamella copulatrix as in Fig. 8.

Description. Holotype length 17.8 mm, width at bases of elytra 9.8 mm. **Head:** Clypeus black with metallic green bright, anterior margin weakly bidentate. Genae metallic green with granular rough sculpturing. Frons with a black cephalic horn, curved posteriorly over pronotum; lateral region of frons is metallic green and weakly rough with no evident punctures. **Pronotum:** Triangular pronotal disc with lateral fossae and dark metallic green coloring, flattened with lateral undulations. Lateral lines of pronotal disc recurved. Granulate sculpturing without punctuation. Posterior pronotal angles very salient, directed posterolaterally and slightly upturned apically. Basal fossae rounded but weakly impressed. **Elytra:** Striae fine, black colored, with small but well defined and regularly separated punctures, shagreened rough sculpturing. Interstriae of opaque appearance, dark metallic green coloring, weakly flattened, with shagreened sculpturing, small weakly impressed punctures and transverse roughness more evident on the first three interstriae. Sutural margin of each elytron forms a sharp ridge, which is elevated posteriorly and prolonged into a small tooth at the apical angle. **Pygidium:** Metallic dark green, glabrous, with weakly impressed small punctures and shagreened rough sculpturing. **Protibia:** Quadridentate with apical spur. **Aedeagus:** Similar to that of the *P. endymion* species group. Lamella copulatrix as Fig. 8.

Variation. Minor male (Fig. 9): Similar to major male, except the cephalic horn smaller or completely reduced to a frontal carina, posterolateral angles of pronotum reduced to small tubercles located on the central part of pronotum and lesser transverse roughness on the interstriae. The tooth on the elytra sutural margin is reduced. **Female (Fig. 10):** As male except head black with green reflections in frons and genae, cephalic carina trituberculate with middle tubercle more elevated, pronotal sculpturing regularly reticular, most of pronotal disk dull black with a well-impressed coarse midline over posterior half of pronotum, pronotal process trituberculate, with the middle tubercle more elevated. **Size of paratypes.** Mean length 15.5 mm (13.3–17.1 mm), mean width 8 mm (6.8–9 mm).

Etymology. Bravo + *ensis*. Bravo refers to type locality, Chilpancingo de los Bravo.

Remarks. *Phanaeus bravoensis* is easily distinguished from the closely related *P. halffterorum* by geographic distribution and morphological characters: *P. bravoensis* major male lacks a tooth in the middle of anterior pronotal margin and its pronotal triangle sides are curved (Figs 6, 7), whereas these are straight on *P. halffterorum* (Figs 1, 2). Differences are observed between the lamella copulatrix (more developed left lobe in *P. halffterorum*, strongly developed central ridge and right lobe in *P. bravoensis*; Figs 3, 8) and shape of female pronotum. In *P. bravoensis* mayor female

Figure 6. *Phanaeus bravoensis* sp. n. major male, dorsal view (holotype).

Figure 7. *Phanaeus bravoensis* sp. n. major male, lateral view (holotype).

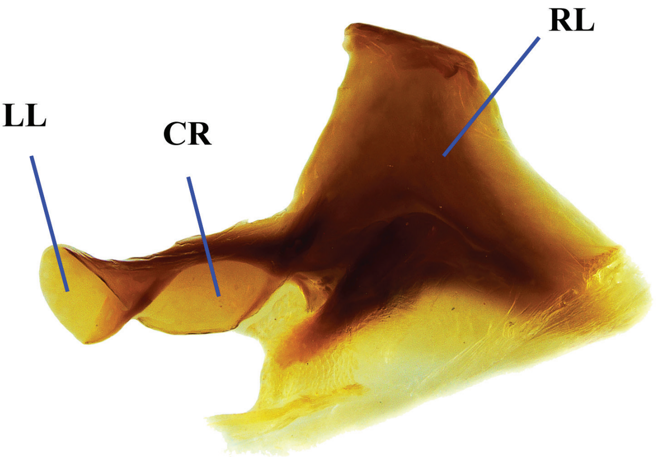

Figure 8. Lamella copulatrix of *Phanaeus bravoensis* sp. n. (holotype). Abbreviations: LL: left lobe, CR: central ridge, RL: right lobe.

Figure 9. *Phanaeus bravoensis* sp. n. minor male, dorsal view (paratype).

Figure 10. *Phanaeus bravoensis* sp. n. female, dorsal view (paratype).

pronotal midline is stronger impressed; pronotal tubercles are located in similar position and of equal size in *P. halffterorum*, while pronotal central tubercle is in anterior position and bigger than lateral tubercles in *P. bravoensis* (Figs 4, 10).

Type locality. MEXICO, Guerrero, Chilpancingo de los Bravo.

Distribution and Ecology. This species occurs in the Sierra Madre del Sur, Guerrero (Fig. 5), in coniferous-oak forest between 750–2150 m. a.s.l. Specimens have been collected with carrion and dung baited pitfall traps, and attracted to light. Therefore, *P. bravoensis* seems to be copronecrophagous (Edmonds 1994, Deloya et al. 2013, 2014).

Phanaeus huichol **sp. n.**

http://zoobank.org/EAAACC06-DAD3-4BB3-8790-97A5F96E20F5

Figs 11–16, 18

Phanaeus endymion: Edmonds (1994: 39–44, 101; *partim*), Arnaud (2002: 94–95), Edmonds (2003: 61, 65), Quiroz-Rocha et al. (2008: 29, 33, 34, 36, 37), Edmonds and Zídek (2012: 1, 3, 5-8, 12, 13, 52, 53), Moctezuma and Halffter (2017: 47, 52-55), Lizardo et al. (in press). *Non endymion* Harold, 1863.

Type material (12 ♂♂, 8 ♀♀)**.** Holotype major male pinned with genitalia in microvial (Figs 11, 12): "MEXICO: Jalisco, 3 mi. NE Mazamitla, VII-12-1982, in moist cow dung, Fred G. Andrews col." Paratypes: 1 ♂, 1 ♀ labeled "MEXICO, Jalisco, Sierra de Talpa (CT), 1470 m, 11/13-VIII-2010, Nogueira col."; 2 ♂♂ labeled "MEXICO, Jalisco, Mpio. Talpa de Allende, 20°13'03.4"N, 104°45'58.8"W, 1655 m, 18–22.vii.09, fungi, WD Edmonds & P. Reyes cols."; 1 ♂, 1 ♀ labeled "MEXICO, Jalisco, S. Manantlán, 1650 m, 18-20/VII/95, G. Nogueira col."; 1 ♂, 1 ♀ labeled "MEXICO, Jalisco, Mixtlán, 1758 m, 13-VIII-2012, G. Nogueira col."; 1 ♂, 1 ♀ labeled "JA: hwy 200, 21 mi S Puerto Vallarta, vii-9,10-84, 2310', ex fungi, S McCleve, P. Jump cols."; 1 ♀ labeled "MEX, Jal., 4200', 10mi SW Autlán, IX.19.71, A. Newton col."; 1 ♂ labeled "MEXICO: Jalisco, Autlán, Puerto los Mazos, Bosque de galería, 1580m, Necrotrampa, x.2000, H. Bustos col"; 1 ♀ *ídem* except "Encino caducifolio, 1480m, xi.2000"; 1 ♂ labeled "MEXICO: Jalisco, Zapopan, Los Guayaboa (La Guayaba?), BEpert, 1600m, 8.vii.1995, NTP-80, G. Quiroz y J.L. Navarrete cols."; 1 ♀ *ídem* except "8.vii-4.viii.1994"; 1 ♀ *ídem* except "14.ix-15.x.1994, pulpo, G. Quiroz y J.L. Navarrete cols."; 1 ♂ labeled "MEXICO: Nayarit, Sierra el Nayar, July 1994, Guillermo Nogueira lgt."; 1 ♂ labeled "MEXICO, Nayarit, Sierra del Nayar, Chapalilla, 1280 m, 17-VII-94, coprotr. G. Nogueira col."; 1 ♂ *ídem* except "17.xii.1994".

Type deposition. Holotype 1 ♂ and six paratypes (4 ♂♂, 2 ♀♀) TAMU; rest of paratypes as follows: 1 ♂, 1 ♀ MXAL; 2 ♂♂, 1 ♀ VMC; 1 ♂, 1 ♀ JLSHC, 3 ♂♂, 3 ♀♀ CEMT.

Diagnosis. Dorsum metallic green; anterior margin of pronotum projected upwards; acute posterolateral angles of pronotum (Fig. 11); anterior metasternal angle almost right angled but with rounded apex in lateral view (Fig. 16); lateral metasternal angles evanescent (Fig. 18); lamella copulatrix as in Fig. 12.

Description. Holotype length 17.6 mm, width at base of elytra 9.8 mm. **Head:** Clypeus dark brown with bright metallic green, anterior margin bidentate. Genae metallic green with granular sculpturing. Frons with a black cephalic horn, curved posteriorly over pronotum; lateral region of frons is metallic green weakly rough with coarse and weakly impressed punctures. **Pronotum:** Triangular pronotal disc with lateral fossae and metallic olive green coloring, flattened with lateral undulations. Lateral lines of pronotal disc not impressed. Sculpturing shagreened without punctures. Anterior pronotal angles wide and rounded. Posterior pronotal angles sa-

Figure 11. *Phanaeus huichol* sp. n. major male, dorsal view (holotype).

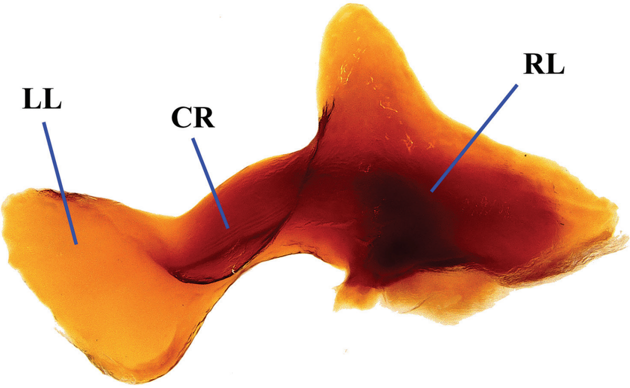

Figure 12. Lamella copulatrix of *Phanaeus huichol* sp. n. (holotype). Abbreviations: LL: left lobe, CR: central ridge, RL: right lobe.

Figure 13. *Phanaeus huichol* sp. n. minor male, dorsal view (paratype).

lient, directed laterally and weakly upturned apically. Basal fossae weakly impressed. Two lateral carinas are impressed near to pronotal apex. **Elytra:** Striae black-green colored, shagreened with small well-spaced punctures and weakly rough sculpturing. Interstriae strongly impressed with small punctures. **Pygidium:** Metallic olive green, with well-impressed punctures and shagreened rough sculpturing. **Protibia:** Quadridentate with apical spur. **Aedeagus:** Similar to that of *P. endymion* species group. Lamella copulatrix as Fig 12.

Variation. This species shows variation in color, being olive green or dark green with blue reflections. **Minor male (Fig. 13):** Similar to major male, except the cephalic horn smaller and the posterolateral angles of pronotum reduced. **Female (Figs 14, 15):**

Figure 14. *Phanaeus huichol* sp. n. female, dorsal view (paratype).

As male except head black with green reflections in frons and genae, cephalic carina trituberculate, pronotal sculpturing shagreened, most of pronotal disk dull black, pronotal process trituberculate. **Size of paratypes.** Mean length 17.5 mm (16–18.7 mm), mean width 9.4 mm (8.7–9.8 mm).

Etymology. The name of the new species refers to the Huichol ethnic group, which inhabits part of the geographic region where the type series was collected.

Remarks. *Phanaeus huichol* is easily distinguished from the closely related *P. zoque* by its geographic distribution and morphological characters: *Phanaeus huichol* male shows two elongate and weak tumescences near to pronotal apex, while *P. zoque* presents two strong tubercles; the anterior lateral angles of the pronotum

Figure 15. *Phanaeus huichol* sp. n. female, frontal view (paratype).

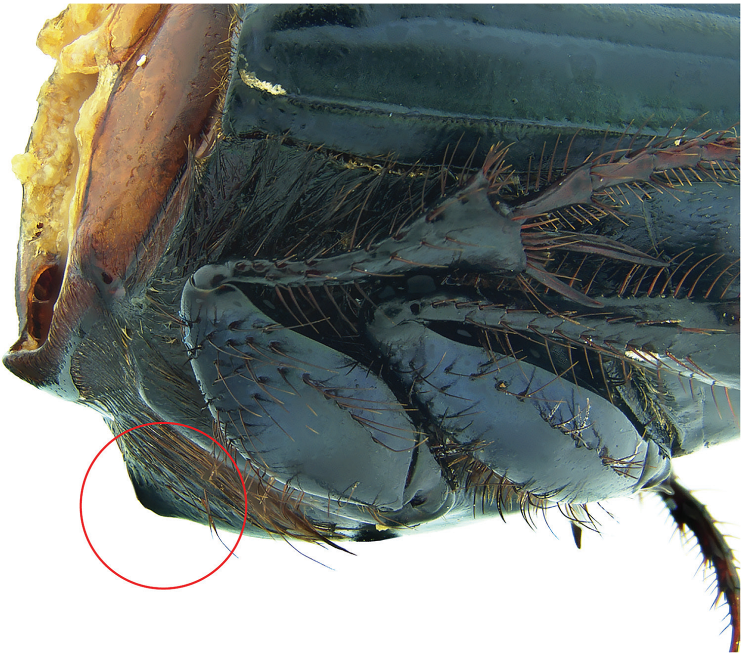

Figure 16. *Phanaeus huichol* sp. n. anterior metasternal angle pointed out with a red circle, lateral view (paratype).

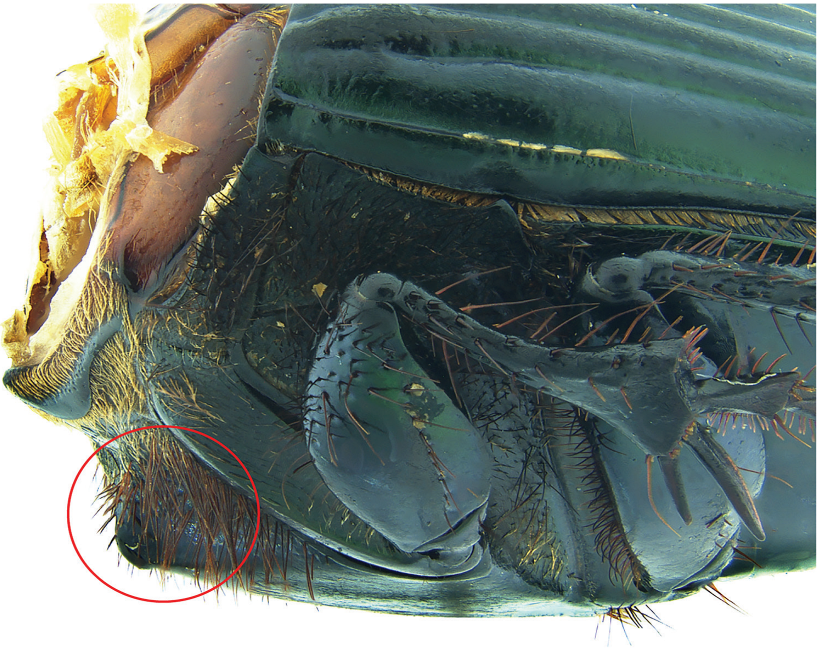

Figure 17. *Phanaeus zoque* anterior metasternal angle pointed out with a red circle, lateral view (paratype).

of *P. huichol* are wider and more rounded than those of *P. zoque*. Major females of *P. huichol* show tridentate pronotal projections with teeth of similar size (Fig. 15), while in the *P. zoque* major female the middle dent resembles a carina, with smaller lateral teeth. In both males and females of *P. huichol* the anterior metasternal angle is obtuse in lateral view (Fig. 16), whereas in *P. zoque* this is almost right-angled but with a rounded apex (Fig. 17). Anterior metasternal angles are notably less angular in *P. huichol* (Fig. 18), while they are more evident in *P. zoque* (Fig. 19). Differences in angulation are also evident in other ventral sternites (lateral meso-metasternal angles evanescent in *P. huichol*, those angles well defined and slightly curved in *P. zoque*). *Phanaeus huichol* is restricted to the Pacific slope of Mexico (Jalisco and Nayarit), while *P. zoque* is found in the Mexican southeast (Oaxaca and Chiapas).

Type locality. MEXICO, Jalisco, Mazamitla.

Distribution and Ecology. This species occurs in the Sierra Occidental of Jalisco and the Sierra del Nayar (Nayarit), in coniferous-oak forests, cloud forests and riparian forests, between 700–1760 m a.s.l. This species seems to be generalist, since specimens have been collected with carrion, dung and fungus.

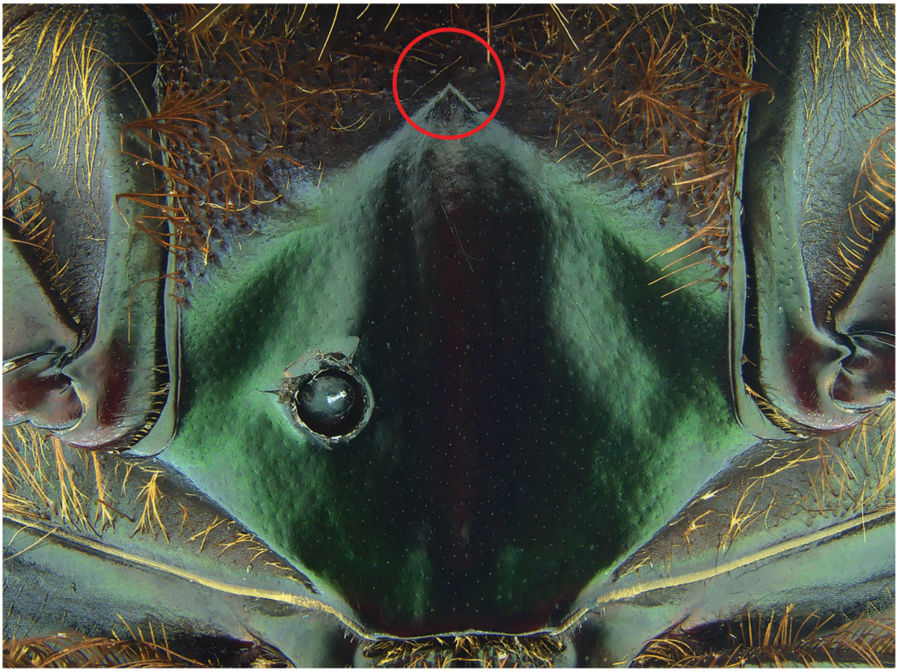

Figure 18. *Phanaeus huichol* sp. n. metasternum (paratype). The anterior metasternal angle is indicated with a red circle.

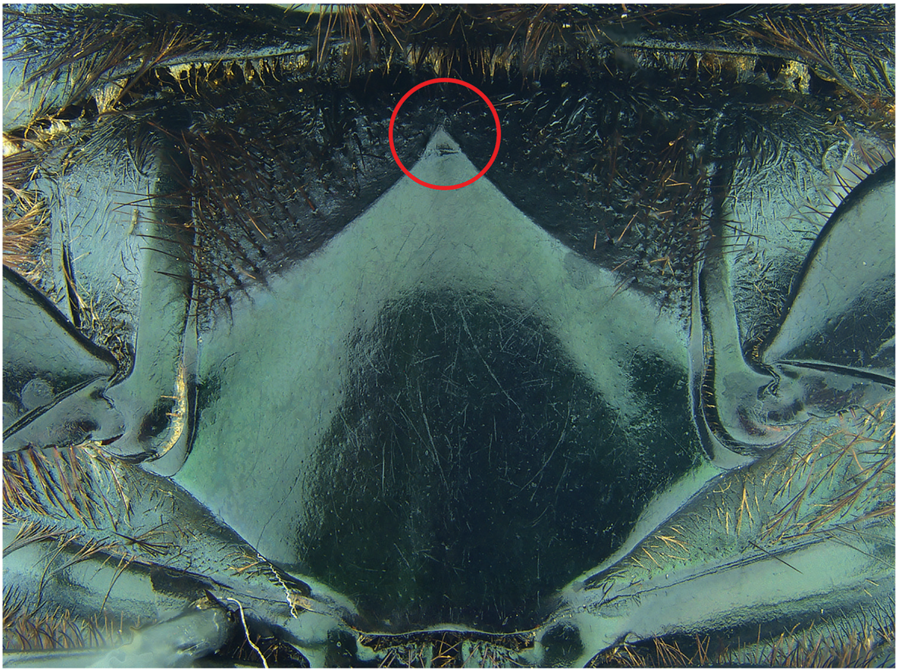

Figure 19. *Phanaeus zoque* metasternum (paratype). The anterior metasternal angle is indicated with a red circle.

Key to the *Phanaeus endymion* species group (modified from Edmonds and Zídek 2012 and Moctezuma and Halffter 2017).

1 Sutural margin of each elytron upturned to form a sharp ridge, which is progressively more elevated posteriorly and prolonged into a small, sharp tooth at apical angle; elytral margin slightly excised adjacent to this tooth............**2**

– Sutural margin of elytra simple. Color and distribution variable **3**

2 Major male with a tooth in the middle of anterior pronotal margin, pronotal triangle sides straight (Figs 1, 2). Lamella copulatrix as in Fig. 3. South-western Mexico State (Estado de México) ....***P. halffterorum***

– Major male lacks a tooth in the middle of anterior pronotal margin, pronotal triangle sides curved (Figs 6, 7). Lamella copulatrix as in Fig. 8. Sierra Madre del Sur of central Guerrero... ***P. bravoensis* sp. n.**

3 Triangular pronotal disk of male evenly and densely but finely granulate (×10), granules in most specimens larger and becoming squamose along lateral margins of disk and extending onto posterolateral angles (when distinctly developed); sides of pronotum roughened (×10), lacking distinct punctures except behind lateral fossae. Female pronotum minutely roughened, evenly, distinctly punctate (×10), punctures becoming smaller dorsally but not disappearing altogether; disk impressed medially as a distinct furrow visible to unaided eye, extending forward from posterior margin to near middle of disk. Puebla-Oaxaca Mountain System and Sierra Madre del Sur of south-central Oaxaca..............***P. zapotecus***

– Pronotal disk of male either lacking distinct granulation, or, if granules present, these are minute and restricted along lateral margins of disk; sides of pronotum smooth, minutely punctate. Female pronotum (fig. 140) smooth, punctures (×50) fine and usually restricted to sides; median furrow lacking or at most indicated by fine, scarcely visible line...**4**

4 Elytral interstriae distinctly flattened and uniformly dull (more convex and shiny in some Central American populations); striae not strongly impressed basally, anterior ends in most specimens bearing deep punctures rather than large fossae. Male: Pronotal disk dull, velvety smooth medially, finely asperate, brighter laterally. Female: Pronotum evenly convex, lacking anteromedial concavity even in largest specimens, bearing three round, smooth tubercles in transverse line near anterior margin. Head and pronotum largely highly shiny metallic red to nearly completely dull black with metallic red restricted to ridges and isolated areas on anterior part of pronotum; elytra dull to weakly shiny black; pygidium usually metallic red medially, green peripherally, in some completely red or green. Southern Nicaragua through Central America into western Colombia and Ecuador..***P. pyrois***

– Elytral interstriae evenly convex and glossy midlongitudinally; striae impressed basally as distinct fossae. Male: Pronotal disk velvety smooth medially, finely aspirate laterally and sometimes also medially. Female: Pronotum with anteromedial concavity bounded anteriorly by a raised U- or V-shaped ridge **5**

5 Dorsum dark blue or shiny green; in few specimens shiny green with strong yellow reflections. Anterior margin of pronotum projected forwards. Relatively rounded posterolateral angles of pronotum. Internal sack of aedeagus and lamella copulatrix as in Moctezuma and Halffter (2017; Fig. 16). Southwestern Mexico to Honduras .... ***P. endymion***

– Dorsum metallic green. Anterior margin of pronotum projected upwards. Acute posterolateral angles of pronotum **6**

6 Anterior metasternal angle obtuse in lateral view (Fig. 17). Lateral metasternal angles well defined and slightly curved (Fig. 19). Few specimens olive green with golden/reddish reflections. Internal sack of aedeagus and lamella copulatrix as in Moctezuma and Halffter (2017; Fig. 15). Eastern Oaxaca and western Chiapas .... ***P. zoque***

– Anterior metasternal angle almost right angled but with rounded apex in lateral view (Fig. 16). Lateral metasternal angles evanescent (Fig. 18). Lamella copulatrix as in Fig. 12. Jalisco and Nayarit......................... ***P. huichol* sp. n.**

Discussion

Notwithstanding the fact that a review and new key are required for the *endymion* species group, we have found no reason to delay publication of this new species. We do not include a new key to separate the *endymion* species group. As an alternative, however, we modified the keys presented by former studies (Edmonds and Zídek 2012, Moctezuma and Halffter 2017). We also considered species distribution, ecology, and trophic preferences as additional criteria to separate the new species.

Phanaeus bravoensis and *P. halffterorum* exhibit unique combinations of character states in the external morphology and in the sclerites of the internal sack of the aedeagus, and these character combinations are sufficient to consider them as distinct species (Wheeler and Platnick 2000). *Phanaeus bravoensis* and *P. halffterorum* seem to be closely related species, because of similarity in the granular pronotal microsculpture, pronotum shape and the apical tooth in the base of the elytra.

Phanaeus bravoensis and *P. halffterorum* occupy distinct ecological niches. They both inhabit coniferous-oak forests, but *P. halffterorum* is a mycetophagous specialist while *P. bravoensis* is attracted to dung and carrion (Edmonds 1979, 1994, 2003, Deloya et al. 2014). Both species are geographically isolated and endemic to small montane areas. *Phanaeus bravoensis* is restricted to the Sierra Madre del Sur (750-2150 m. a.s.l.) in the surroundings of Chilpancingo de Los Bravo, while *P. halffterorum* has been reported from the mid highlands of the central region of the Trans-Mexican Volcanic Belt (2200-2360 m. a.s.l.), in the surroundings of Temascaltepec. Arnaud (2002) mentioned that *P. halffterorum* is located in the “Federal District”, but this location is doubtful and the name could have been confused with State of Mexico (Estado de México). Climatic conditions where these species are found differ, being tropical or sub-tropical for *P. bravensis* and temperate for *P.*

halffterorum. Lizardo et al. (in press) states that potential distribution modeling of species could not be performed using localities of *P. halffterorum* from the State of Mexico and Guerrero simultaneously, probably because of the lack of information and/or taxonomical/geographical errors. We agree with the view of Lizardo et al. (in press) and have therefore included additional localities and corrected the taxonomical issue that involved *P. halffterorum*.

Vicariance is likely the process that led the radiation of *P. bravoensis* and *P. halffterorum*. Aridification of the Balsas Valley during the Pleistocene could have isolated the populations of a common ancestor (Edmonds 1994). This hypothesis considers a relatively recent origin of this species within the *endymion* species group. We consider the possibility that *P. bravoensis*, *P. halffterorum* and *P. zapotecus* represent a phyletic line within the *endymion* species group, characterized by the presence of a granular pronotal microsculpture. Molecular phylogenetic studies are required to confirm or refute our hypothesis on the vicariant origin of *P. bravoensis*, the geological period of divergence and the existence of the lineage *bravoensis-halffterorum-zapotecus*.

Phanaeus huichol has been traditionally confused with *P. endymion*, a noteworthy fact considering the number of important reviews that have been published in recent years (Edmonds 1994, Arnaud 2002, Edmonds and Zídek 2012). Species potential distribution modeling clearly demonstrates a geographical segregation among *P. huichol*, *P. endymion* and *P. zoque* (Lizardo et al. in press). This new species seems to be closely related to the recently described *P. zoque* in size, coloring and habitat preference, but there are clear differences in external and genital morphology. On the other hand, an important disjunction exists between the distributions of both species: they are separated by ≈900 km of distance, including the presence of important biogeographic barriers (i.e., the Tehuantepec Isthmus, the Sierra Madre del Sur and the Balsas Valley). *Phanaeus huichol* could represent a relatively ancient colonization by the *P. endymion* species group in the Central Pacific region of Mexico, that drove a later isolation of this species in the westernmost areas of the Trans-Mexican Volcanic Belt.

While both species prefer pine-oak forests, *P. huichol* also inhabits cloud forests, while *P. zoque* has not been collected despite intensive sampling effort in cloud forests of Los Chimalapas (Moctezuma and Halffter 2017). Trophic habits of *P. huichol* are well known, being a generalist species attracted to different kinds of dung, carrion, and fungus, while *P. zoque* has been collected only on dung (Quiroz-Rocha et al. 2008, Moctezuma and Halffter 2017). Feeding habits of *P. huichol* could be related to xeric conditions during dry season, when dung becomes an extremely ephemeral resource that rapidly loses humidity and dietary quality, and additional food sources are required (Halffter and Edmonds 1982, Moctezuma et al. 2016). Elevation tolerance of these species seems to overlap and they are endemic to montane areas, although the altitudinal range of *P. huichol* is greater: *P. huichol* is found between 700-1760 m. a.s.l., while *P. zoque* inhabits between 918-1325 m. a.s.l.

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Supplementary material 1

Table of localities

Authors: Victor Moctezuma, José Luis Sánchez-Huerta, Gonzalo Halffter

Data type: occurrence

Link: https://doi.org/10.3897/zookeys.702.14728.suppl1

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First checklist of the fruit flies of Morocco, including new records (Diptera, Tephritidae)

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Abstract

The first checklist of the Tephritidae of Morocco, containing 59 species, is presented here. Out of 38 species collected during the present project, three (*Campiglossa martii* (Becker, 1908), *Tephritis divisa* (Rondani, 1871), and *Terellia* sp. near *longicauda*) present new records for North Africa, and ten (*Carpomya incompleta* (Becker, 1903), *Chaetorellia conjuncta* (Becker, 1913), *Chetostoma curvinerve* Rondani, 1856, *Dacus frontalis* (Becker, 1922), *D. longistylus* (Wiedemann, 1830), *Dioxyna sororcula* (Wiedemann, 1830), *Ensina sonchi* (Linnaeus, 1767), *Myopites inulaedyssentericae* Blot, 1827, *M. stylatus* Fabricius, 1794, and *Tephritis vespertina* (Loew, 1844)) are new for Morocco.

Keywords

Anti Atlas, Beni Snassen, High Atlas, Middle Atlas, North Africa, Rif, Sahara

Introduction

Tephritidae is one of the largest families of the acalyptrate Diptera, and more than 4300 valid species are known in the world (Norrbom 2004). Prior to this study, the Tephritid fauna of Morocco has not been the subject of focused research. Only few studies from North Africa were devoted to the fruit flies (e.g., Tunisia, Arambourg and Soria 1961; Algeria, Hering 1937; Morocco, Algeria and Tunisia, Heřman and Dirlbek 2006). Some new species were described from Algeria (Dirlbek and Dirlbekova 1976; Hendel 1927; Hering 1938; Séguy 1934a) and Morocco (Becker and Stein 1913; Séguy 1930, 1941).

The Tephritidae of Morocco have been also published upon among some Diptera studies (Wiedemann 1824; Becker and Stein 1913; Séguy (1930, 1934b, 1941, 1949, 1953). Faunal records from all relevant publications have been registered in the Catalogue of the Tephritidae of the World (Norrhbom et al. 1999). A total of 46 species have been previously recorded from Morocco. New findings increase the number of fruit flies known from Morocco to 59.

The material reported in the present article was mostly collected in Morocco between 2013–2016 in 99 field expeditions over mountainous areas (Rif, Beni Snassen (eastern Morocco), Middle Atlas, Anti Atlas) and the arid area of Morocco (Sahara). Thirty-eight species of Tephritidae were identified from this material, of which ten species are new to Morocco, and three species are new to North Africa. One of the main achievements of this project is the first checklist of Tephritidae from Morocco, containing 59 species, which is presented here.

Materials and methods

Collecting methods

A total of 924 specimens of Tephritidae were collected by sweeping nets and malaise traps, or reared from flower heads or fruits of plants, examined, and preserved in 70% ethanol. When terminalia were necessary to confirm species identity, they were prepared by boiling the abdomen in 10% KOH for 20 minutes at 95°C and preserved in glycerine. Species were recognised according to the identification keys of Hendel (1927), Freidberg and Kugler (1989), White and Elson-Harris (1992), Merz (1994), Korneyev and White (1992, 2000). The systematic classification is based on White and Elson-Harris (1992), Norrbom et al. (1999), White et al. (2000) and White and Goodger (2009).

A list of 99 sampling sites, with coordinates and altitudes, is given in Table 2, and the locations of the sites are shown in Map 1, elaborated using the logiciel GisArc (Geographic Information System, version 9.3). All the specimens are deposited in the collection of Diptera of the Department of Biology, Faculty of Sciences, University Abdelmalek Essaâdi, Tétouan.

The following checklist summarizes the species inventory presently known from Morocco, and their worldwide distribution.

Table 1. Species (in alphabetical order) of Tephritidae known from North Africa.

Species	Morocco	**Algeria**	**Tunisia**	**Libya**	**Egypt**
Acanthiophilus helianthi (Rossi, 1794)	X*	X	X		
Aciura coryli Rossi, 1794	X				X
Bactrocera cucurbitae (Coquillett, 1899)					X
Bactrocera oleae Rossi, 1790	X**				X
Bactrocera zonata Saunders, 1842				X	
Campiglossa hofferi (Dirlbek & Dirlbekova, 1976)		X			
Campiglossa martii (Becker, 1908)	X****				
Campiglossa producta Loew, 1844	X*	X	X		
Capitites ramulosa (Loew, 1844)	X	X			X
Capparimyia savastani (Martelli, 1911)	X	X	X	X	X
Carpomya incompleta (Becker, 1903)	X***				X
Carpomya pardalina (Bigot, 1891)					X
Ceratitis capitata (Wiedemann, 1824)	X*	X	X	X	X
Chaetorellia conjuncta (Becker, 1913)	X***				X
Chaetorellia hestia (Hering, 1937)	X**	X			
Chaetorellia succinea Costa, 1844	X				X
Chaetostomella cylindrica Robineau-Desvoidy, 1830	X	X	X		
Chetostoma curvinerve Rondani, 1856	X***	X?	X?	X?	X?
Dacus annulatus (Becker, 1903)					X
Dacus ciliatus (Loew, 1862)					X
Dacus frontalis (Becker, 1922)	X***	X		X	X
Dacus longistylus (Wiedemann, 1830)	X***			X	X
Dacus semisphaereus (Becker, 1903)					X
Dacus sexmaculatus (Walker, 1871)					X
Desmella conyzae (Frauenfeld, 1857)					X
Desmella rostellata (Séguy, 1941)	X				
Dioxyna bidentis (Robineau-Desvoidy, 1830)	X ?	X?	X?	X?	X?
Dioxyna sororcula (Wiedemann, 1830)	X***	X	X		
Ensina sonchi (Linnaeus, 1830)	X***	X			
Euaresta bullans (Wiedemann, 1830)	X*	X	X		
Euarestella iphionae (Efflatoun, 1924)					X
Euarestella kugleri (Freidberg, 1974)					X
Euarestella pninae (Freidberg, 1981)					X
Euleia heraclei (Linnaeus, 1758)	X**	X			
Euleia marmorea (Fabricius, 1805)	X				
Goniurellia lacerata (Becker, 1913)					X
Goniurellia longicauda (Freidberg, 1980)	X**	X	X	X	X
Goniurellia persignata (Freidberg, 1980)	X*				X
Goniurellia spinifera (Freidberg, 1980)					X
Hyalotephritis planiscutellata (Becker, 1903)					X
Hypenidium graecum (Loew, 1862)	X				
Katonaia aida (Hering, 1938)					X
Metasphenisca gracilipes (Loew, 1862)					X
Metasphenisca haematopoda (Bezzi, 1924)					X
Metasphenisca negeviana (Freidberg, 1974)					X

Species	Morocco	**Algeria**	**Tunisia**	**Libya**	**Egypt**
Myopites apicatus (Freidberg, 1979)	X				
Myopites boghariensis (Séguy, 1934)		X			
Myopites cypriacus Hering, 1938	X				
Myopites inulaedyssentericae Blot, 1827	X***	X			
Myopites stylatus Fabricius, 1794	X***	X	X?	X?	X?
Myopites variofasciatus (Becker, 1903)					X
Neoceratitis efflatouni (Hendel, 1931)					X
Notomma mutilum Bezzi, 1923					X
Oedaspis daphnea (Séguy, 1930)	X				
Oedaspis farinosa (Hendel, 1927)		X			
Oedaspis fissa Loew, 1862		X			
Oedaspis multifasciata (Hering, 1937)	X	X			
Oedaspis trotteriana (Bezzi, 1913)	X	X		X	X
Oedaspis villeneuvei (Bezzi, 1913)		X		X	X
Oxyaciura tibialis Robineau-Desvoidy 1830	X*				
Oxyna superflava (Freidberg, 1974)	X				X
Paradesis augur (Frauenfeld, 1857)		X	X		X
Parasphenicus debskii (Efflatoun, 1924)					X
Schistopterum moebiusi (Becker, 1903)					X
Spathulina acroleuca (Schiner, 1868)					X
Spathulina sicula (Rondani, 1856)	X*		X		
Sphaeniscus filiolus (Loew, 1869)	X**				X
Sphenella marginata (Fallen, 1814)	X*				X
Tephritis bimaculata (Freidberg, 1981)					X
Tephritis dioscurea Loew, 1856	X				
Tephritis divisa (Rondani, 1871)	X****				
Tephritis formosa (Loew, 1844)	X**				
Tephritis jabeliae (Freidberg, 1981)					X
Tephritis leontodontis De Géer, 1776	X	X?	X?	X?	X?
Tephritis matricariae (Loew, 1844)	X*				X
Tephritis nigricauda Loew 1856	X**	X			X
Tephritis postica (Loew, 1844)	X**	X	X		
Tephritis praecox (Loew, 1844)	X**	X			
Tephritis pulchra Loew, 1844	X	X			
Tephritis simplex (Loew, 1844)	X	X	X		
Tephritis stictica Loew, 1862	X				
Tephritis spreta (Loew, 1861)					X
Tephritis theryi (Séguy, 1930)	X				
Tephritis truncata (Loew, 1844)			X		
Tephritis vespertina (Loew, 1844)	X***		X		
Tephritomyia lauta (Loew, 1869)	X**		X		X
Terellia colon Meigen, 1826	X	?	X	?	?
Terellia fuscicornis (Loew, 1844)	X	X?	X?	X?	X?
Terellia longicauda Meigen, 1838	X				
Terellia luteola (Wiedemann, 1830)			X		X
Terellia oasis (Hering, 1938)		X			

Species	Morocco	**Algeria**	**Tunisia**	**Libya**	**Egypt**
Terellia serratulae (Linnaeus, 1758)	X*	X	X		
Terellia sp. near *longicauda*	X****				
Terellia vectensis Collin, 1937		X			
Terellia virens (Loew, 1846)	X**		X		
Trupanea amoena (Frauenfeld, 1857)	X**		X		
Trupanea guimari (Becker, 1908)	X**	X			
Trupanea pseudoamoena (Freidberg, 1974)					X
Trupanea repleta (Bezzi, 1918)					X
Trupanea stellata (Fuesslin, 1775)	X**		X		
Urelliosoma desertorum (Efflatoun, 1924)					X
Urelliosoma pulcherrimum (Efflatoun, 1924)		X	X		X
Urophora calcitrapae (White & Korneyev, 1989)					X
Urophora mauritanica (Macquart, 1851)	X**	X		X	
Urophora pauperata Zaitzev, 1945					X
Urophora phaeocera (Hering, 1961)					X
Urophora quadrifasciata (Meigen, 1826)	X	X	X		
Urophora quadrifasciata algerica (Hering, 1941)		X	X		
Urophora solstitialis Linnaeus 1758	X	X	X		

X****: new species for North Africa; X***: new species for Morocco; X**: new species for one or more of the geographic regions of Morocco; X*: species known from Morocco and collected by the authors; ?: species considered, in the literature, present in North Africa without specifying country.

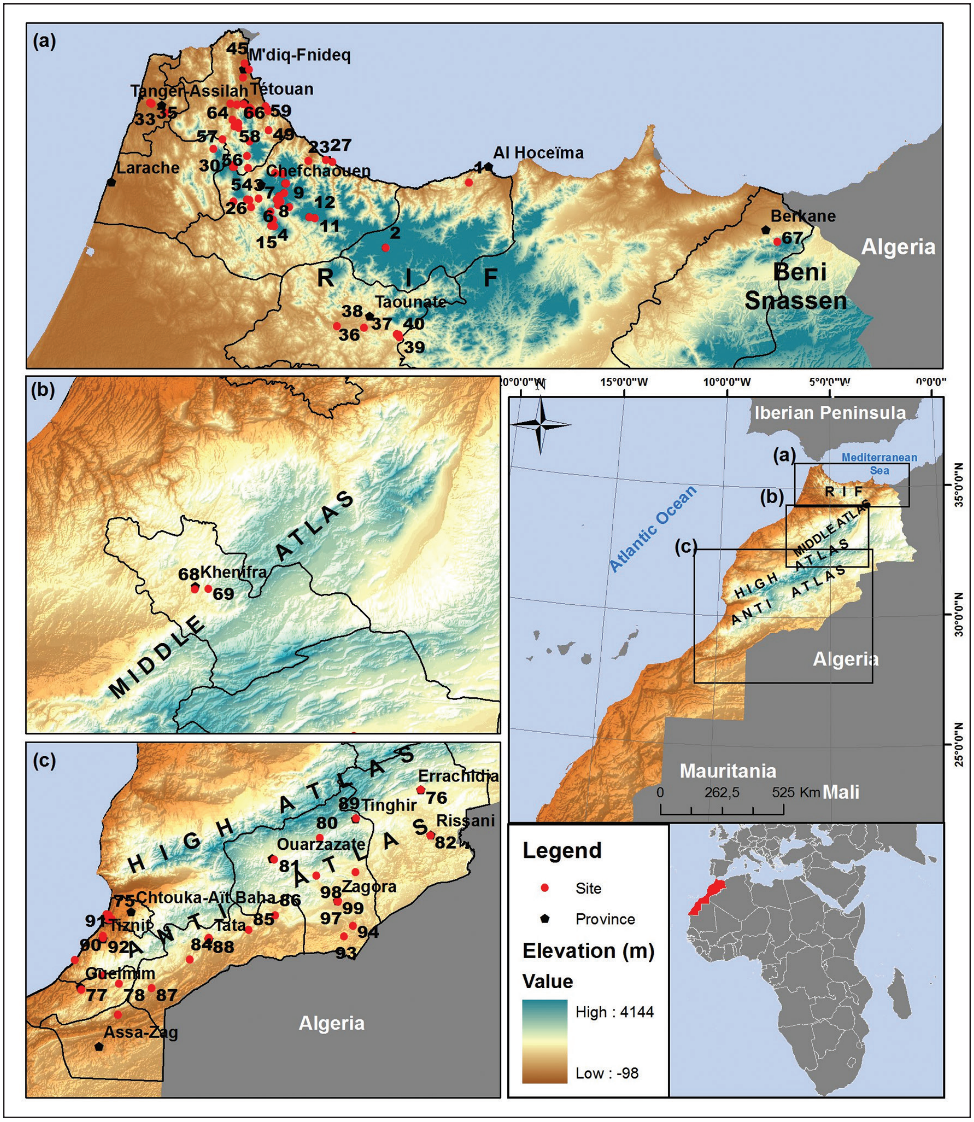
Table 2. Sampling sites (in alphabetical order) harboring the species collected in Morocco with localities, geographical coordinates, and altitudes.

Province	Station	Locality	Altitude (m)	Geographical coordinates
Rif				
Al Hoceïma	1. Affluent Tarmast	Parc National d'Al Hoceïma	168	N35°10.666', W004°03.088'
	2. Oued Azila	Azila, Jbel Tidghine	1601	N34°52.028', W004°32.609'
Chefchaouen	3. Aïn Afersiw	Mezine	746	N35°05.945' ,W005°20.439'
	4. Aïn El Ma Bared	Bouzthate	1267	N35°00.333', W005°12.105'
	5. Aïn El Malâab	Parc National Talassemtane	1278	N35°05.509', W005°09.443'
	6. Aïn El Maounzil	Parc National Talassemtane	1106	N35°04.577', W005°10.406'
	7. Aïn Tiouila	Parc National Talassemtane	1502	N35°07.194', W005°09.978'
	8. Bab El Karne	Tamakoute	1248	N34°58.510', W005°11.838'
	9. Cascade Chrafate	Chrafate	820	N35°03.997', W005°06.434'
	10. Daya Afrate	Tanaqoub	600	N35°05.634', W005°26.028'
	11. Daya El Ânassar	Bab Berred	1183	N35°00.788', W004°57.419'
	12. Daya El Birdiyel	Ânasar	1300	N35°01.089', W004°59.477'
	13. Douar Abou Boubnar (Marabout Sidi Gile)	Parc National Talassemtane	1247	N35°10.812', W005°07.500'

Chefchaouen	14. Douar Ouslaf	Parc National Talassemtane	625	N35°13.787', W005°11.376'
	15. Douar Tamakoute	Tamakoute	1089	N34°58.609', W005°12.743'
	16. Maison forestière	Parc National Talassemtane	1674	N35°08.076', W005°08.262'
	17. Mizoghar	El Khizana	1005	N35°02.725', W005°12.969'
	18. Oued Abou Bnar	Parc National Talassemtane	1260	N35°10.854', W005°07.840'
	19. Oued Derdara	Derdara	400	N35°06.484', W005°17.147'
	20. Oued El Kanar	Stehate	50	N35°17.233', W004°59.639'
	21. Oued El Kelâa	Akchour	510	N35°13.514', W005°08.553'
	22. Oued Jbara	Tanaqoub	600	N35°05.634', W005°26.028'
	23. Oued Jnane Niche	Jnane Niche	36	N35°17.019', W004°51.233'
	24. Oued Majjou	Village Majjou	799	N35°06.186', W005°10.935'
	25. Oued Mezine	Mezine	778	N35°06.104', W005°21.177'
	26. Oued Sidi Ben Sâada	Derdara	220	N35°03.921', W005°19.895'
	27. Oued Sidi Yahya Aârab	Sidi Yahya Aârab	62	N35°17.545', W004°53.503'
Larache	28. Affluent Oued Amsemlil	Jbel Bouhachem	1130	N35°15.657', W005°26.159'
	29. Daya Mtahen	Jbel Bouhachem	966	N35°16.195', W005°26.158'
	30. Daya Tazia	Route Moulay Abdessalam	721	N35°20.814', W005°33.139'
	31. Oued Tkaraâ	Jbel Bouhachem	959	N35°16.063', W005°25.829'
M'diq-Fnideq	32. Ksar Rimal	Kabila	11	N35°43.806', W005°20.509'
Tanger-Assilah	33. Daya Aïn Jdioui	Aïn Jdioui	5	N35°34.074', W005°55.499'
	34. Daya El Hajjami	Barrage 9 Avril	21	N35°31.306', W005°50.263'
	35. Oued Aïn Jdioui (Touaret)	Aïn Jdioui	2	N35°33.768', W005°55.002'
Taounate	36. Aïn Boharroch	Aïn Aïcha	234	N34°29.049', W004°40.442'
	37. Dhar Sbagh Mâasra	Khemis Hoara	396	N34°26.977', W004°28.972'
	38. El Hajria	Sahel Botaher	184	N34°29.496', W004°49.886'
	39. Koudia El Aouinate	Douar Kda	403	N34°26.170', W004°28.167'
	40. Lâazaba	Khemis Hoara	357	N34°26.820', W004°28.408'
Tétouan	41. Aïn El Âakba Larbaâ	Mokdassene	95	N35°31.328', W005°19.012'
	42. Barrage Nakhla	Zinat	240	N35°26.954', W005°24.326'
	43. Barrage Smir	Bouzaghlale (M'diq)	20	N35°41.491', W005°22.673'
	44. Daya Amsemlil	Jbel Bouhachem	1059	N35°15.596', W005°25.917'
	45. Daya Jbel Zemzem	Jbel Zemzem	216	N35°45.457', W005°22.189'
	46. Douar Dacheryène	Dacheryène	132	N35°33.863', W005°27.162'
	47. Douar Kitane	Kitane	52	N35°32.412', W005°20.393'
	48. Douar Taghbaloute	Larbaa Beni Hassen	379	N35°15.323', W005°20.887'
	49. Douar Tizga	Amsa	516	N35°26.237', W005°13.694'
	50. El Haouta	Kitane	52	N35°32.230', W005°20.166'
	51. El Malâab	Kitane	75	N35°32.348', W005°20.290'
	52. Jumb Kitane	Kitane	38	N35°32.759', W005°20.420'
	53. Oued Achekrade	Douar Aouzighen	642	N35°22.931', W005°20.364'
	54. Oued Al Mizzine	Mezine	790	N35°06.143', W005°21.272'
	55. Oued Amsa	Amsa	11	N35°31.926', W005°13.747'

Tétouan	56. Oued Boumarouil	Larbaa Beni Hassen	551	N35°18.733', W005°21.271'
	57. Oued El Hamma	Beni Ydder	200	N35°23.532', W005°30.051'
	58. Oued El Kebir	Route Vers Beni Yedder	89	N35°27.351', W005°25.796'
	59. Oued Halila	Azla	3	N35°33.137', W005°14.678'
	60. Oued Maâza (Âachira)	Kitane	15	N35°32.596', W005°20.350'
	61. Oued Maâza (Tarik El Ouasâa)	Kitane	39	N35°32.237', W005°19.891'
	62. Oued Martil	Mhannech 2	9	N35°33.693', W005°22.510'
	63. Oued Martil (Tamouda)	Tamouda	8	N35°33.627', W005°24.799'
	64. Oued Sahel	Ben Karrich	40	N35°29.238', W005°26.352'
	65. Oued Zarka	Zarka	128	N35°31.211', W005°20.477'
	66. Oued Zinat	Zinat	190	N35°28.207', W005°24.224'
Beni Snassen (Eastern Morocco)				
Berkane	67. Oued Beni Ouaklane	Beni Snassen	630	N34°51.581', W002°15.180'
Middle Atlas				
Khénifra	68. Oued Oum Er Rbia	Farra	826	N32°55.358', W005°40.390'
	69. Sensla	Arougo	1111	N32°55.387', W005°34.081'
Anti Atlas				
Assa zag	70. Oued Assa	Assa	306	N28°36.507', W009°25.800'
Chtouka-Aït Baha	71. Avant Sidi Binzarne	Massa	10	N30°03.144', W009°39.067'
	72. Centre Sidi Ouassay	Massa	41	N30°03.387', W009°41.249'
	73. Douar Sidi Abou	Massa	55	N29°59.322', W009°35.627'
	74. Environs Massa	Massa	24	N29°59.353', W009°38.708'
	75. Oued Massa (Pont Aghbalou)	Massa	2	N30°02.007', W009°38.768'
Errachidia	76. Oued Ziz (Pont Errachidia)	Oued Ziz	1026	N31°56.253', W004°25.455'
Guelmim	77. Msidira	El Filaha	257	N28°56.865', W010°02.979'
	78. Oued Sayad	Taghjijt	568	N29°03.784', W009°26.027'
	79. Oued Tisla	Bouizakarne	613	N29°09.908', W009°43.280'
Ouarzazate	80. Douar Zaouia	Kelâa M'gouna	1238	N31°14.275', W006°08.169'
	81. Oued Ouarzazate	Ouarzazate	1135	N30°54.917', W006°54.187'
Rissani	82. Ksibat Elhdeb	Rissani	770	N31°16.494', W004°16.310'
Tata	83. Douar Tighrimt	Tighrimt	706	N29°45.742', W007°58.521'
	84. Douar Zaouiet	Akka	554	N29°26.485', W008°16.535'
	85. Imzine	Tissint	566	N29°53.415', W007°18.928'
	86. Oued Foum Ziguid (Douar Ouaiftoute)	Foum Ziguid	665	N30°06.786', W006°52.639'
	87. Oued Tamanarne	Foum El Hisn	480	N29°00.941', W008°53.588'
	88. Oued Tata	Tata	277	N29°45.348', W007°58.690'
Tinghir	89. Oued Tinghir	Douar Ihertane	1280	N31°31.366', W005°31.677'
Tiznit	90. Airport Sidi Ifni	Sidi Ifni	51	N29°22.654', W010°10.711'
	91. Atbane	Tiznit	191	N29°44.388', W009°43.740'
	92. Route Bab El Khemis	Tiznit	225	N29°42.647', W009°43.702'

Zagora	93. Aït Aissa O Brahim	Mhamid El Ghizlane	556	N29°48.948', W005°43.676'
	94. Douar Rggaga	Tagonite	614	N29°57.874', W005°34.532'
	95. Isdaoun	Tazzarine	852	N30°44.748', W005°32.194'
	96. Jnane Makadir	Zagora	726	N30°19.209', W005°50.498'
	97. Kasbah Asma	Amzrou	718	N30°19.015', W005°50.016'
	98. Oued Drâa (Ikhf Mezrou)	Zagora	872	N30°41.466', W006°11.405'
	99. Oued Drâa (Tahtah)	Zagora	718	N30°19.665', W005°49.813'



Map 1. Map showing all collecting sites in Morocco.

Results

Faunistic records

Family TEPHRITIDAE (Newman, 1834)
Subfamily DACINAE (Loew, 1862)
Tribe CERATITIDINI Bezzi, 1910
Genus *CAPPARIMYIA* Bezzi, 1920

***Capparimyia savastani* Martelli, 1911**

Literature records. Morocco, Anti Atlas: Tiznit (Séguy 1953).

World distribution. Algeria, Tunisia, Libya, Egypt, Italy, Greece, Malta, Israel, Oman, France, Yemen and Pakistan (Freidberg and Kugler 1989, Norrbom et al. 1999, Donati and Belcari 2003, De Meyer and Freidberg 2005, Miranda et al. 2008, Papachristos et al. 2009).

Genus *CERATITIS* MacLeay, 1829

***Ceratitis capitata* (Wiedemann, 1824)**

Literature records. Morocco, Rif: Tangier (Becker and Stein 1913), High Atlas (Séguy 1930), Ouadj-Ouli-Mohamed, env. Settat, Insgane (De Meyer 2000).

New records. Morocco, Rif: Douar Kitane, 4♂♂, 4♀♀, 23-IX-2014- 4♂♂, 24-IX-2014- 4♂♂, 3♀♀, 25-IX-2014- 1♂, 2♀♀, 27-IX-2014- 1♂, 3♀♀, 02-X-2014- 4♂♂, 1♀, 27-VII-2015 (reared); El Haouta, 1♂, 1♀, 20-IX-2014 (net sweeping)- 5♂♂, 11♀♀, 02-X-2014 (reared); Jumb Kitane, 4♂♂, 7♀♀, 30-VI-2015. Middle Atlas: Sensla, 1♀, 14-VII-2016 (net sweeping). Anti Atlas: Environs Massa, 1♀, 11-V-2015; Oued Massa (Pont Aghbalou), 2♂♂, 12-V-2015; Douar Sidi Abou, 23♂♂, 34♀♀, 13-V-2015; Douar Tighrimt, 1♂, 29-V-2015; Douar Zaouia, 1♂, 11-VI-2015 (net sweeping).

Host plants. A highly polyphagous species, including the infestation of fruits of *Ficus carrica* L., *Prunus armeniaca* L., *Prunus persica* L., and *Pyrus communis* L. from which the recorded specimens were reared, and *Argania spinosa* L. (Fig. 1) from which our specimens were collected by sweep-netting.

World distribution. Algeria, Tunisia, Libya, Egypt, Angola, Burundi, Cameroon, Congo, Ghana, Guinea, Kenya, Madagascar, Mozambique, Nigeria, South Africa, Seychelles Is, St Helena I., Tanzania, Benin, Burkino Faso, Cape Verde Is, Ethiopia, Gabon, Ivory Coast, Liberia, Malawi, Mali, Mauritius I., Niger, Reunion I., São Tomé I., Senegal, Sudan, Togo, Uganda, Zimbabwe, South Europe, Middle East, Neotropics, West Australia, Hawaii (Norrbom et al 1999, De Meyer 2000, De Meyer et al. 2013).

Figure 1. *Argania spinosa* L. host plant of *Ceratitis capitata*.

Tribe DACINI Loew, 1862
Genus *BACTROCERA* Macquart, 1835
Subgenus *Bactrocera* Macquart, 1835

Bactrocera oleae (Rossi, 1790)

Literature record. Morocco, Rif: Tangier (Becker and Stein 1913). First record for the Middle and Anti Atlas.

New records. Rif: El Haouta, 1♂, 30-I-2014 (net sweeping); Oued Maâza (Tarik El Ouasâa), 5♂♂, 1♀ 18-III-2015 (reared); Cascade Chrafate, 1♂, 28-IV-2015 (net sweeping); Koudia El Aouinate, 3♂♂, 6♀♀, 12-XII-2015 (net sweeping); Lâazaba, 2♂♂, 12-XII-2015 (net sweeping); Dhar Sbagh Mâasra, 2♂♂, 12-XII-2015 (net sweeping); El Hajria, 1♀, 13-XII-2015 (net sweeping). Middle Atlas: Sensla, 1♂, 1♀, 14-VII-2016 (net sweeping). Anti Atlas: Route Bab El Khemis, 2♂♂, 2♀♀, 14-V-2015 (net sweeping).

Host plant. Fruits of *Olea europea* L. from which the specimens were both reared and collected by sweep-netting.

World distribution. Mediterranean region, Eritrea, Ethiopia, Kenya, Angola, Lesotho, Namibia, South Africa, Sudan, Greece, Italy, Portugal, Spain, Madeira, Canary Islands, North Africa, Israel, Lebanon, Jordan, Réunion, Saudi Arabia, Syria, Turkey, Caucasus, Pakistan, nw. India, USA, Mexico (Séguy 1930, Munro 1984, White and Hancock 1997, Norrbom et al. 1999, Copeland et al. 2004, White 2006).

Genus *DACUS* Fabricius, 1805

Dacus frontalis (Becker, 1922)

New records. Morocco, Anti Atlas: Oued Foum Ziguid (Douar Ouaiftoute), 1♂, 2♀♀, 01-VI-2015 (net sweeping); Oued Drâa (Ikhf Mezrou), 1♂, 1♀, 06-VI-2015 (net sweeping); Isdaoun, 2♂♂, 3♀♀, 07-VI-2015 (net sweeping). First record for Morocco.

World distribution. Algeria, Libya, Egypt, Angola, Benin, Botswana, Cape Verde Is., Congo, Eritrea, Kenya, Lesotho, Namibia, Saudi Arabia, South Africa, Sudan, Tanzania, Yemen, Zimbabwe (White 2006, White and Goodger 2009, De Meyer et al. 2013).

Dacus longistylus (Wiedemann, 1830)

New records. Morocco, Anti Atlas: Oued Tata, 1♀, 29-V-2015 (net sweeping); Douar Tighrimt, 1♂, 29-V-2015 (net sweeping); Oued Foum Ziguid (Douar Ouaiftoute), 31♂♂, 12♀♀, 01-VI-2015 (net sweeping). First record for Morocco.

Host plant. *Calotropis* L. (Fig. 2) from which the specimens were collected by sweep-netting.

World distribution. Libya, Egypt, Benin, Cameroon, Chad, Eritrea, Ethiopia, Kenya, Mali, Mauritania, Niger, Nigeria, Oman, Saudi Arabia, Senegal, Somalia, Sudan, Tanzania, Uganda, Yemen (White and Hancock 1997, White 2006, White and Goodger 2009, De Meyer et al. 2013).

Subfamily TEPHRITINAE (Newman, 1834)
Tribe DITHRYCINI Hendel, 1927
Subtribe OEDASPIDINA Hering, 1947
Genus *OEDASPIS* Loew, 1862

Oedaspis daphnea (Séguy 1930)

Literature records. Morocco, Middle Atlas: El Mers (Séguy 1930, Foote 1984, Norrbom et al. 1999).

World distribution.

Comments. The species was described from Morocco and never recorded since; we did not examine the type material.

Figure 2. *Calotropis procera* L., host plant of *Dacus longistylus*.

Oedaspis multifasciata (Loew, 1850)

Literature records. Morocco, Middle Atlas: Itzer (Séguy 1953).

World distribution. Spain, France, Germany, Italy, Croatia, Austria, Ukraine (Korneyev 2002).

Oedaspis trotteriana (Bezzi, 1913)

Literature records. Morocco (Ribera and Blasco-Zumeta 1998).

World distribution. Algeria, Libya, Egypt, Israel (Ribera and Blasco-Zumeta 1998, Norrbom et al. 1999).

Tribe MYOPITINI Hendel, 1927
Genus *MYOPITES* Blot, 1827

Myopites inulaedyssentericae Blot, 1827

New record. Morocco, Rif: Affluent Tarmast, 1♂, 26-IV-2013; Aïn Afersiw, 1♀, 11-VI-2013 (net sweeping). First record for Morocco.

World distribution. Algeria, Great Britain, Estonia, France, Germany, Italy, Poland, Russia, Spain, Switzerland, Ukraine, Balkans, central Europe (Evstigneev 2011).

Myopites stylatus Fabricius, 1794

New record. Morocco, Rif: Affluent Tarmast, 1♀, 26-VI-2013; Oued El Hamma, 1♂, 25-IV-2014; El Haouta, 1♂, 18-VI-2014 (net sweeping). First record for Morocco.

World distribution. North Africa, southern Europe, Israel, Spain, Albania, (Zimsen 1964, Freidberg and Kugler 1989, Norrbom et al 1999, Merz 2001, Korneyev 2003).

Genus *UROPHORA* Robineau-Desvoidy, 1830

Subgenus *Urophora* Robineau-Desvoidy, 1830

= *Euribia* Meigen, 1800

Urophora sp. near *congrua*

Literature records. Morocco, Anti Atlas: Taroudant (Séguy 1941).

World distribution. France, South Germany, Austria (Norrbom et al, 1999).

Comments. The presence of *Urophora congrua* Loew, 1862 in Morocco is obviously a misidentification of another *Urophora* (Personal communication with Valery Korneyev). The literature records and the world distribution given above are those of *U. congrua* and therefore do not necessarily represent the true information for the species that occurs in Morocco

Urophora mauritanica (Macquart, 1851)

Literature records. Morocco, High Atlas: Imi N'Takandout, Dar Kaid M'tougui (Séguy 1930), Ito (White and Korneyev 1989). First record for the Anti Atlas.

New records. Morocco, Anti Atlas: Airport Sidi Ifni, 1♀, 17-V-2015; Oued Tata, 5♂♂, 29-V-2015 (net sweeping); Oued Tata, 12♂♂, 8♀♀, 06-VI-2015 (reared); Douar Tighrimt, 3♂♂, 29-V-2015; Imzine, 3♂♂, 1♀, 30-V-2015; Jnane Makadir, 1♀, 03-VI-2015; Oued Ouarzazate, 2♂♂, 12-VI-2015 (net sweeping)- 25♂♂, 14♀♀, 28-VI-2015- 7♂♂, 2♀♀, 01-VII-2015 (reared).

Host plant. *Centaurea calcitrapa* L. (Fig. 3) from which the specimens were reared.

World distribution. Algeria, Libya, Albania, Azerbaijan, Bulgaria, Cyprus, Czech Rep., France, Greece, Iran, Israel, Italy, Jordan, Kazakhstan, Lebanon, Macedonia, Malta, Moldova, Russia, Spain, Tajikistan, Turkey, Turkmenistan, Ukraine, Uzbekistan

Figure 3. *Centaurea calcitrapa* L., host plant of *Urophora mauritanica*, *Chaetorellia conjuncta* and *Terellia virens*.

(White and Korneyev 1989, Korneyev and White 1996, 1999, Norrbom et al. 1999, Gharali et al. 2005, Khaghaninia and Gharajedaghi 2012).

Urophora quadrifasciata (Meigen, 1826)

Literature records. Morocco (Séguy 1930).

World distribution. South to North Africa, Europe, Kazakstan, Iran, North America, Australia (Norrbom et al. 1999, Heřman and Dirlbek 2006).

Urophora solstitialis Linnaeus, 1758

Literature record. Morocco, High Atlas: Haute Reraya (Séguy 1930).

World distribution. Tunisia, Great Britain, Eastern Scandianvia to Kazakhstan, China, France, Italy, Switzerland, Turkey, Iran, Armenia, Moldova, Poland, Russia, Ukraine, North America, Australia, New Zealand (Korneyev and White 1999, Heřman and Dirlbek 2006, Evstigneev 2011).

Tribe Noeetini (Norrbom & Korneyev, 1999)
Genus *ENSINA* Robineau-Desvoidy, 1830

Ensina sonchi (Linnaeus, 1767)

New records. Morocco, Rif: Ksar Rimal, 5♂♂, 2♀♀, 05-VI-2013- Douar Tizga, 1♂, 25-VI-2014- Oued El Kebir, 1♀, 31-V-2015. Middle Atlas: Sensla, 1♂, 14-VII-2016 (net sweeping). Anti Atlas: Oued Massa (Pont Aghbalou), 1♀, 12-V-2015 (net sweeping); Centre Sidi Ouassay, 1♂, 12-V-2015; Aïn Boharroch, 1♀, 13-XII-2015; Atbane, 1♀, 14-V-2015; Oued Tamanarne, 1♂, 26-V-2015; Oued Drâa (Tahtah), 6♂♂, 7♀♀, 03-VI-2015; Jnane Makadir, 3♂♂, 1♀, 03-VI-2015; Kasbah Asma, 16♂♂, 13♀♀, 04-VI-2015 (net sweeping)- 7♂♂, 13♀♀, 10-VI-2015 (reared); Aït Aissa O Brahim, 1♀, 05-VI-2015; Oued Ziz (Pont Errachidia), 2♂♂, 2♀♀, 09-VI-2015; Oued Ouarzazate, 4♂♂, 2♀♀, 12-VI-2015 (net sweeping). First record for Morocco.

Host plants. Flower heads of *Hypochaeris radicata* L. (Fig. 4) from which the specimens were reared.

World distribution. South to North Africa, Great Britain, Scandinavia, Andorra, Czech Rep., France, Germany, Iran, Poland, Portugal, Spain, Sweden, Switzerland,


2015/06/04

Figure 4. *Hypochaeris* sp., host plant of *Ensina sonchi*.

Turkey, Ukraine, Saudi Arabia, Japan, Korea, India, Ethiopia, Taiwan, Philippines, Hawaii (White and Elson-Harris 1992, Merz and Dawah 2005, Heřman and Dirlbek 2006, Gharajedaghi et al. 2012).

Genus *HYPENIDIUM* Loew, 1862

Hypenidium graecum (Loew, 1862)

= *Stephanaciura bipartita* Séguy, 1930

Literature records. Morocco, Middle Atlas: Taffert (Séguy 1930, Norrbom et al. 1999).

World distribution. Bosnia, Greece, Hungary, Israel, Italy, Portugal, Spain, Ukraine (Korneyev et al. 2011).

Tribe TEPHRELLINI Hendel, 1927
Subtribe TEPHRELLINA Hendel, 1927
Genus *ACIURA* Robineau-Desvoidy, 1830

Aciura coryli (Rossi, 1794)

= *Aciura powelli* (Séguy, 1930)

Literature records. Morocco, Middle Atlas: Azrou (Séguy 1930), Korifla (Séguy 1953).

World distribution. North Africa, Spain and southern France to southern Ukraine, Canary Islands, Esrael, Syria (Korneyev and Dirlbek 2000).

Genus *OXYACIURA* Hendel, 1927

Oxyaciura tibialis (Robineau-Desvoidy, 1830)

Literature records. Morocco, Rif: Tangier (Becker and Stein 1913), Sker (Séguy 1930).

New sites. Morocco, Rif: Daya El Birdiyel, 1♂, 27-VI-2013; Oued Azila, 1♂, 27-VI-2013; Maison forestière, 1♂, 17-VI-2014; Oued Maâza (Tarik El Ouasâa), 1♂, 18-IV-2015 (net sweeping).

World distribution. North Africa, Canary Islands, Cape Verde Islands, Madeira, Spain, China, Iran, Israel, Kazakhstan, Saudi Arabia, Syria, United Arab Emirates, Afghanistan, Ethiopia (Merz 1992, 2008, Korneyev and Dirlbek 2000, Merz and Dawah 2005, Gharajedaghi et al. 2012).

Genus *SPHAENISCUS* Becker, 1908

Sphaeniscus filiolus (Loew, 1869)

= *Spheniscomyia aegyptiaca* (Efflatoun, 1924)

Literature records. Morocco, Anti Atlas: Goulimine (Séguy 1930, 1949). First record for the Rif.

New records. Morocco, Rif: Affluent Tarmast, 1♂, 26-VI-2013; Oued Maâza (Tarik El Ouasâa), 2♂♂, 1♀, 19-VI-2014 (net sweeping).

World distribution. Egypt, Spain, Canary Islands, Cape Verde Islands, Israel, Ethiopia (Séguy 1930, 1949; Merz 1992, 2001).

Tribe TEPHRITINI Macquart, 1835

Genus *ACANTHIOPHILUS* Becker, 1908

Acanthiophilus helianthi (Rossi, 1794)

Literature records. Morocco, Rif: around Tangier (Becker and Stein 1913, Séguy 1930), Middle Atlas (Séguy 1930), Anti Atlas: Goulimine, Foum el Hassan, Alnif, Tarfaia, Boufarik (Séguy 1949).

New sites. Morocco, Rif: Oued Zinat, 1♀, 27-IV-2012; Ksar Rimal, 1♀, 10-V-2013; Oued Derdara, 1♀, 24-V-2013; Affluent Tarmast, 1♂, 26-VI-2013; Daya El Birdiyel, 1♀, 27-VI-2013; Oued Azila, 1♂, 27-VI-2013; Daya Jbel Zemzem, 1♂, 23-IV-2014; Oued Boumarouil, 2♂♂, 1♀, 10-V-2014; Douar Abou Boubnar (Marabout Sidi Gile), 1♀, 18-V-2014; El Haouta, 1♂, 18-VI-2014; Oued Maâza (Tarik El Ouasâa), 1♀, 19-VI-2014- 1♀, 18-IV-2015; Douar Tizga, 1♂, 25-VI-2014; Daya Afrate, 1♀, 18-IV-2015; Oued Mezine, 1♂, 18-IV-2015; Aïn El Malâab, 1♂, 1♀, 21-IV-2015; Oued Jnane Niche, 1♀, 25-IV-2015. Middle Atlas: Oued Oum Er Rbia, 1♂, 14-VII-2016. Anti Atlas: Centre Sidi Ouassay, 1♂, 2♀♀, 12-V-2015; Avant Sidi Binzarne, 1♀, 12-V-2015; Route Bab El Khemis, 1♂, 1♀, 14-V-2015; Airport Sidi Ifni, 22♂♂, 22♀♀, 17-V-2015; Oued Tisla, 1♀, 24-V-2015; Oued Sayad, 1♀, 25-V-2015; Oued Tamanarne, 1♂, 1♀, 26-V-2015; Oued Foum Ziguid (Douar Ouaiftoute), 1♂, 1♀, 01-VI-2015; Jnane Makadir, 2♂♂, 4♀♀, 03-VI-2015; Douar Rggaga, 1♀, 05-VI-2015; Oued Tinghir, 1♂, 1♀, 11-VI-2015; Oued Ouarzazate, 12♂♂, 6♀♀, 12-VI-2015 (net sweeping).

World distribution. Algeria, Tunisia, Albania, Andorra, Austria, Balearic Is., Belgium, Great Britain, Bulgaria, Corsica, Cyprus, Czech Rep., France, Germany, Greece, Hungary, Italy, Malta, Moldova, Netherlands, Norway, Poland, Portugal, Romania, Russia, Sardinia, Sicily, Slovakia, Spain, Switzerland, Ukraine, Turkey, Central Asia, Mongolia, China, Madeira, Canary Islands, Ethiopia, Kenya, Sudan, Afghanistan, Iran, Israel, Kazakhstan, Kyrgyzstan, Lebanon, Saudi Arabia, United Arab Emirates, Syria, India, Nepal, Pakistan, Thailand (Séguy 1930, Merz and Korneyev 2004, Heřman and Dirlbek 2006, David and Ramani 2011, Merz 2011).

Genus *CAMPIGLOSSA* Rondani, 1870

Campiglossa martii (Becker, 1908)

= *Oxyna martii* Becker, 1908

New records. North Africa, Morocco, Rif: Oued El Kebir, 1♀, 31-V-2014 (net sweeping). Anti Atlas: Centre Sidi Ouassay, 1♂, 12-V-2015 (net sweeping). First record for Morocco and North Africa.

World distribution. Canary Islands (Frey 1958a), Cape Verde Islands (Frey 1958b), Spain (Merz 1992).

Campiglossa producta Loew, 1844

= *Paroxyna tessellata* Hendel, 1927

Literature records. Morocco, Rif: Tangier and its surroundings, (Becker and Stein 1913, Séguy 1930), High Atlas (Séguy 1930).

New sites. Morocco, Rif: Oued Al Mizzine, 1♀, 11-VI-2013; Aïn El Malâab, 1♂, 17-V-2014; Daya El Hajjami, 1♂, 28-III-2015 (net sweeping).

World distribution. Algeria, Tunisia, Great Britain, Finland, Netherlands, Poland, Portugal, Spain, Switzerland, Madeira, Canary Islands, Turkey, Syria, Jordan, Iran, Israel, Iraq, Afghanistan, Central Asia, India, China, Thailand, Vietnam, Korea, Japan (Korneyev and Dirlbek 2000, Hancock and McGuire 2002, Korneyev 2004, Heřman and Dirlbek 2006, Mohamadzade Namin and Nozari 2011).

Genus *CAPITITES* Foote & Freidberg, 1981

Capitites ramulosa (Loew, 1844)

Literature records. Morocco, Middle Atlas: Forest of Timelilt (Séguy 1941). High Atlas: Tizi n'Test, Imdress, Taroudant (Séguy 1941), Foum El Hassan, Akka, Agdz, Alnif (Séguy 1949).

World distribution. Algeria, Tunisia, Egypt, Greece, Portugal, Spain, Cyprus, Syria, Israel, Iraq, Canary Islands, Cape Verde Islands (Séguy 1930, Freidberg and Kugler 1989, Merz 1992, Norrbom et al. 1999, Korneyev and Dirlbek 2000).

Genus *DESMELLA* Munro, 1957

Desmella rostellata (Séguy, 1941)

= *Paroxyna rostellata* (Séguy, 1941)

Literature record. Morocco, Anti Atlas: Agadir (Séguy 1941).

Genus *DIOXYNA* Frey, 1945

Dioxyna sororcula (Wiedemann, 1830)

New records. Morocco, Rif: Ksar Rimal, 2♂♂, 19-V-2013- 1♂, 2♀♀, 26-V-2013; Oued Jnane Niche, 2♀♀, 14-VI-2013; Oued Halila, 1♂, 05-XI-2013; Oued Zarka, 7♂♂, 1♀, 14-XI-2013; Oued Martil, 1♂, 1♀, 13-XII-2013; Oued Amsa, 1♀, 19-XII-2013; Oued Sahel, 1♂, 05-IV-2014; Daya Jbel Zemzem, 1♂, 17-IV-2014; Oued Majjou, 2♂♂, 10-V-2014; Dhar Sbagh Mâasra, 1♀, 12-XII-2015; Douar Kitane, 15♂♂, 5♀♀, 14-XI-2013- 1♂, 2♀♀, 13-III-2014- 1♀, 17-III-2014- 2♂♂, 1♀, 10-IV-2014- 5♂♂, 13♀♀, 02-V-2014- 26♂♂, 14♀♀, 23-I-2016 (net sweeping). First record for Morocco.

World distribution. Algeria, Tunisia, South Africa, Madeira, Canary Islands, Spain, Saudi Arabia, Yemen, India, West Bengal, Nepal, Thailand, China, Korea, Japan, Taiwan, Botswana, Namibia, Zambia, Zimbabwe, Australia, New Caledonia, Western Samoa, Niue, Cook Is., French Polynesia, Fiji, Hawaii (Hancock and McGuire 2001, Norrbom and Hancock 2004, Merz and Dawah 2005, David and Ramani 2011).

Genus *EUARESTA* Loew, 1873

Euaresta bullans (Wiedemann, 1830)

Literature records. Morocco, Anti Atlas: Tiznit, Sidi-Moussa-d'Aglou (Heřman and Dirlbek 2006).

New site. Morocco, Anti Atlas: Msidira, 2♂♂, 1♀, 18-V-2015 (net sweeping).

World distribution. Algeria, Tunisia, South Africa, Argentina, Bolivia, Chile, Peru, Uruguay, California, Arizona, Bulgaria, France, Greece, Hungary, Iran, Israel, Italy, Macedonia, Moldova, Russia, Slovakia, Spain, Turkey, Ukraine, Australia (Herman and Dirlbek 2006, Khaghaninia and Gharajedaghi 2012).

Genus *GONIURELLIA* Hendel, 1927

Goniurellia longicauda (Freidberg, 1980)

Literature records. Morocco, Middle Atlas: Tizi s'Tkrine, Forest of Azrou (Séguy 1930, Freidberg 1980), High Atlas: Taroudant (Séguy 1953, Freidberg 1980). Anti Atlas: Edehby Ouarzazate (Pârvu et al. 2006).

New sites. Morocco, Anti Atlas: Airport Sidi Ifni, 4♂♂, 17-V-2015; Oued Tisla, 6♂♂, 9♀♀, 24-V-2015; Oued Tamanarne, 1♂, 26-V-2015; Douar Zaouiet, 1♂, 27-V-2015; Oued Tata, 1♀, 29-V-2015; Douar Tighrimt, 1♀, 29-V-2015; Ksibat Elhdeb, 2♂♂, 07-VI-2015; Oued Ziz (Pont Errachidia), 1♀, 09-VI-2015; Oued Ouarzazate, 2♂♂, 12-VI-2015 (net sweeping).

World distribution. Algeria, Tunisia, Libya, Egypt, France, Canary Islands, Cape Verde Islands, Iran, Iraq, Israel, Saudi Arabia, Syria, Turkey, United Arab Emirates, Kenya (Freidberg 1980, Freidberg and Kugler 1989, Merz 1992, Norrbom et al. 1999, 2008, Korneyev and Dirlbek 2000, Al Dhafer et al. 2012).

Goniurellia persignata Freidberg, 1980

Literature records. Morocco, Eastern region: Defilia, nr. Figuig (Freidberg 1980). Anti Atlas: Tiffoultoute (Norrbom et al. 1999, Heřman and Dirlbek 2006).

New records. Morocco, Rif: Dhar Sbagh Mâasra, 1♀, 12-XII-2015. Anti Atlas: Douar Zaouiet, 1♂, 27-V-2015; Oued Ouarzazate, 1♂, 12-VI-2015 (net sweeping). First record for the Rif.

World distribution. Egypt, China, Crete, Cyprus, Ethiopia, Israel, Saudi Arabia, Sri Lanka, Turkmenistan, Namibia? (Freidberg 1980, Norrbom et al. 1999, Hancock et al. 2001, Merz and Dawah 2005, Herman and Dirlbek 2006).

Genus *SPATHULINA* Rondani, 1856

Spathulina sicula (Rondani, 1856)

Literature records. Morocco (Séguy 1930).

New site. Morocco, Rif: Barrage Smir, 1♂, 27-IV-2014 (net sweeping).

World distribution. Spain, Portugal, Italy, Israel, Canary Is. (Norrbom et al. 1999).

Genus *SPHENELLA* Robineau-Desvoidy, 1830

Sphenella marginata (Fallén, 1814)

Literature records. Morocco, Rif: around Tangier (Becker and Stein 1913, Séguy 1930).

New sites. Morocco, Rif: Affluent Tarmast, 1♂, 26-VI-2013; Daya Jbel Zemzem, 5♂♂, 2♀♀, 23-IV-2014; El Malâab, 1♂, 02-II-2015; Oued Maâza (Âachira), 1♀, 10-III-2015; Daya Aïn Jdioui, 1♀, 28-III-2015; Oued Majjou, 1♀, 09-IV-2015; Daya Afrate, 1♂, 1♀, 18-IV-2015 (net sweeping).

World distribution. Egypt, South Africa, Czech Rep., Poland, Portugal, Spain, Sweden, Switzerland, Ukraine, Russia, Madeira, Afghanistan, Canary Islands, China, Iran, Israel, Kazakhstan, Saudi Arabia, Turkey, Turkmenistan, Eritrea, Kenya, Lesotho, Mozambique (Gharajedaghi et al. 2012).

Genus *TEPHRITIS* (Latreille, 1804)

Tephritis dioscurea Loew, 1856

Literature records. Morocco, Middle Atlas: El Hajeb (Séguy 1930).

World distribution. Sweden, France, Hungary, Austria, Germany, Switzerland, Russia, Estonia, Latvia, Lithuania, Ukraine, Moldova, Azerbaijan, Armenia, Georgia, Kazakhstan, Turkey, Iran (Foote 1984, Merz 1994, Thompson 1998, Kütük 2005, Zarghani et al. 2010).

Tephritis divisa (Rondani, 1871)

New record. Morocco, Rif: Daya Amsemlil, 1♀, 01-XI-2014 (net sweeping). First record for Morocco and North Africa.

World distribution. Croatia, France, Greece, Israel, Italy, Near East Asia, Spain, Switzerland, Turkey and Ukraine (Norrbom 1999, Korneyev 2003, Merz and Korneyev 2004, Kütük 2005).

Tephritis formosa (Loew, 1844)

Literature record. Morocco, High Atlas: Asni (Séguy 1930).

New records. Morocco, Rif: Oued Abou Bnar, 1♂, 18-V-2014; Oued Sidi Ben Sâada, 1♂, 30-V-2014; Oued Achekrade, 1♂, 31-V-2014; Oued El Kanar, 1♀, 25-IV-2015 (net sweeping). First record for the Rif.

World distribution. Caucasus, Israel, Persia, Russia, Ukraine, Moldova, Azerbaijan, Georgia, Armenia, England, Switzerland, Germany, Iran, Turkey, China (Hendel 1927, Dirlbek and Dirlbek 1971, Giray 1979, Foote 1984, White 1988, Freidberg and Kugler 1989, Merz 1994, Wang 1998).

Tephritis leontodontis De Géer, 1776

Literature record. Morocco (Séguy 1930).

World distribution. Austria, Albania, Belgium, Bulgaria, United Kingdom, Estonia, Ireland, Spain, Italy, Latvia, Lithuania, Netherlands, Germany, Norway, Poland, Russian Federation, Romania, Slovakia, Hungary, Ukraine, Finland, France, United Kingdom, Czech Republic, Sweden, Switzerland (Korneyev 2016).

Tephritis matricariae Loew, 1844

Literature records. Morocco (Séguy 1930).

New sites. Morocco, Rif: Affluent Oued Amsemlil, 1♂, 30-V-2013; El Haouta, 1♀, 30-I-2014; Daya Jbel Zemzem, 1♂, 23-IV-2014; Daya Amsemlil, 1♂, 01-XI-2014; Oued El Hamma, 1♀, 24-IV-2015 (net sweeping).

World distribution. Algeria, Tunisia, Libya, Egypt, England, Netherlands, Austria, Andorra, Greece, Portugal, Spain, Switzerland, Turkey, Iran (Norrbom et al. 1999, Merz 2001, Mohamadzade Namin et al. 2010a).

Tephritis nigricauda Loew, 1856

Literature records. Morocco: Berrechid (Séguy 1930). First record for the Rif.

New sites. Daya Jbel Zemzem, 2♂♂, 23-IV-2014; Oued Maâza (Tarik El Ouasâa), 1♂, 18-IV-2015; Aïn El Maounzil, 1♂, 21-IV-2015; Daya Tazia, 1♀, 24-IV-2015; Daya Amsemlil, 1♀, 27-V-2015; Douar Tamakoute, 1♂, 1♀, 25-XII-2015 (net sweeping).

World distribution. Algeria, Egypt, Poland, Portugal, Spain, Iran, Iraq, Jordan, Russia, Syria (Korneyev and Dirlbek 2000, Merz 2001, Gharajedaghi et al. 2012).

Tephritis postica (Loew, 1844)

Literature records. Morocco, Middle Atlas: Volubilis (Heřman and Dirlbek 2006). First record for the Anti Atlas.

New records. Anti Atlas: Ksibat Elhdeb, 1♀, 07-VI-2015 (net sweeping)- 1♂, 1♀, 23-VI-2015- 1♂, 1♀, 26-VI-2015- 1♂, 1♀, 28-VI-2015 (reared); Oued Tinghir, 1♂, 11-VI-2015 (net sweeping).

Figure 5. *Onopordum acanthium* L. host plant of *Tephritis postica*.

Host plant. Flower heads of *Onopordum acanthium* L. (Fig. 5) from which the specimens were reared.

World distribution. Algeria, Tunisia, Spain, France, Czech Rep., Georgia, Germany, Hungary, Poland, Slovakia, Ukraine, Russia, Turkey, Kazakhstan, Kyrgyzstan, China, Iran, Israel, Lebanon (Séguy 1934a, Richter 1970, Merz 1994, 2001, Wang 1998, Klasa 2001, Heřman and Dirlbek 2006, Zarghani et al. 2010, Gharajedaghi et al. 2012, Hancock 2013).

Tephritis praecox (Loew, 1844)

Literature records. Morocco, Rif: Tangier (Heřman and Dirlbek 2006). Middle Atlas: Tizi s'Tkrine (Séguy 1930), Ifrane-Azrou National Park (Heřman and Dirlbek 2006). First record for eastern Morocco.

New sites. Morocco, Rif: Daya El Ânassar, 2♂♂, 24-V-2013; Daya Amsemlil, 1♀, 30-V-2013; Affluent Oued Amsemlil, 1♀, 30-V-2013; Douar Dacheryène, 1♀, 04-IV-2014; Douar Taghbaloute, 1♂, 05-IV-2014; Barrage Nakhla, 1♂, 05-IV-2014; Oued Sahel, 2♂♂, 05-IV-2014; Daya Jbel Zemzem, 4♂♂, 2♀♀, 17-IV-2014- 1♂, 23-IV-2014; Douar Kitane, 1♂, 19-IV-2014; Oued El Hamma, 1♂, 25-IV-2014; Oued El Kebir, 2♂♂, 2♀♀, 25-IV-2014; Aïn El Ma Bared, 1♂, 06-V-2014; Aïn El Malâab, 1♂, 1♀, 17-V-2014; Douar Abou Boubnar (Marabout Sidi Gile), 1♀, 18-V-2014; Maison forestière, 1♂, 1♀, 17-VI-2014; Douar Tizga, 1♀, 25-VI-2014; Oued Aïn Jdioui (Touaret), 1♀, 28-III-2015;

Daya Afrate, 1♂, 18-IV-2015; Oued Jbara, 1♂, 18-IV-2015; Aïn El Malâab, 1♂, 21-IV-2015; Aïn El Maounzil, 11♂♂, 8♀♀, 21-IV-2015; Daya Tazia, 1♂, 24-IV-2015; Oued Jnane Niche, 5♂♂, 4♀♀, 25-IV-2015; Oued Majjou, 1♀, 27-IV-2015; Aïn Tiouila, 1♂, 02-V-2015; Daya Mtahen, 1♂, 1♀, 07-V-2015; Lâazaba, 3♂♂, 1♀, 12-XII-2015; Dhar Sbagh Mâasra, 1♂, 3♀♀, 12-XII-2015; El Hajria, 1♀, 13-XII-2015; Aïn Boharroch, 1♂, 13-XII-2015; Douar Tamakout, 1♀, 25-XII-2015; Douar Ouslaf, 1♂, 2♀♀, 26-XII-2015 (net sweeping). Beni Snassen (Eastern Morocco): Oued Beni Ouaklane, 1♂, 24-XI-2014.

World distribution. Algeria, Spain, Portugal, Switzerland, Great Britain, Austria, Hungary, Madeira, Canary Islands, Syria, Iran, Israel, Iraq, Afghanistan (Séguy 1930, Norrbom et al. 1999, Korneyev and Dirlbek 2000, Smit 2006, Heřman and Dirlbek 2006, Zarghani et al. 2010, Gharajedaghi et al. 2012).

Tephritis pulchra Loew, 1844

Literature records. Morocco (Séguy 1930).

World distribution. North Africa, France, Spain, Austria, Hungary, Italy, Greece, Poland, Iran, Turkey, China (Norrbom et al. 1999, Merz 2001, Freidberg and Kütük 2002, Mohamadzade Namin and Nozari 2011).

Tephritis simplex Loew, 1844

Literature records. Morocco (Séguy 1930).

World distribution. Algeria, Tunisia, Spain, Portugal, Crete, Turkey, Israel (Norrbom et al. 1999, Merz 2001).

Tephritis stictica Loew, 1862

Literature records. Morocco: Rabat (Séguy 1930).

World distribution. Algeria (Séguy 1930), southern Europe (Norrbom et al. 1999).

Tephritis theryi (Séguy 1930)

Literature records. Morocco, High Atlas: Asni (Séguy 1930, Norrbom et al. 1999).

Tephritis vespertina (Loew, 1844)

New record. Morocco, Rif: Daya Mtahen, 1♀, 27-V-2015; Dhar Sbagh Mâasra, 1♂, 1♀, 12-XII-2015 (net sweeping). First record for Morocco.

World distribution. South to North Africa, Andorra, Germany, Hungary, Poland, Portugal, Spain, Switzerland, Ukraine, Turkey (Merz 2001, Hendel 1927, Foote 1984, Norrbom et al. 1999, Merz 1994, Kütük and Özgür 2003).

Genus *TEPHRITOMYIA* Hendel, 1927

Tephritomyia lauta (Loew, 1869)

Literature records. Morocco, High Atlas: Tachdirt (Séguy 1930); Tizi-n-Tichka (Morgulis 2015). First record for the Rif.

New records. Morocco, Rif: Daya El Birdiyel, 1♂, 27-VI-2013; Daya Amsemlil, 1♀, 01-XI-2014; Lâazaba, 1♂, 12-XII-2105. Anti Atlas: Msidira, 1♂, 18-V-2015; Oued Ouarzazate, 1♂, 6♀♀, 12-VI-2015 (net sweeping).

World distribution. Tunisia, Egypt, Cyprus, Greece, Iran, Iraq, Israel, Lebanon, Syria, Turkey (Freidberg and Kugler 1989, Norrbom et al. 1999, Korneyev and Dirlbek 2000, Mohamadzade Namin and Nozari 2011, Morgulis 2015).

Genus *TRUPANEA* (Schrank, 1795)

Trupanea amoena (Frauenfeld, 1857)

Literature records. Morocco, Middle Atlas: Aïn Leuh (Séguy 1930). First record for the Rif.

New records. Morocco, Rif: Ksar Rimal, 1♂, 05-VI-2013; Oued Jnane niche, 1♂, 14-VI-2013; Affluent Tarmast, 2♀♀, 26-VI-2013; Oued Martil (Tamouda), 1♀, 13-VII-2013; Oued Amsa, 1♂, 13-XII-2013; Oued El Hamma, 2♂♂, 1♀, 25-IV-2014; Oued Boumarouil, 1♀, 10-V-2014; Oued Sidi Yahya Aârab, 1♂, 25-IV-2015; Aïn Tiouila, 1♂, 02-V-2015. Anti Atlas: Oued Massa (Pont Aghbalou), 1♂, 12-V-2015; Centre Sidi Ouassay, 1♂, 12-V-2015; Avant Sidi Binzarne, 2♂♂, 1♀, 12-V-2015; Oued Tisla, 2♀♀, 24-V-2015; Douar Tighrimt, 1♂, 29-V-2015; Oued Draa (Tahtah), 1♂, 03-VI-2015; Jnane Makadir, 1♂, 03-VI-2015; Douar Rggaga, 1♀, 05-VI-2015; Aït Aissa O Brahim, 1♂, 05-VI-2015; Oued Drâa (Ikhf Mezrou), 1♂, 06-VI-2015; Isdaoun, 1♂, 07-VI-2015; Ksibat Elhdeb, 1♀, 07-VI-2015; Oued Tinghir, 2♂♂, 11-VI-2015 (net sweeping).

World distribution. North Africa, Canary Islands, Ceylon, Ethiopia, England, Germany, India, Iran, Israel, Middle Asia, Middle and North Europe, Netherlands, Philippines, Saudi Arabia, Switzerland, Taiwan, Turkey, United Arab Emirates (Hendel 1927, Séguy 1930, Giray 1969, Foote 1984, White 1988, Freidberg and Kugler 1989, Merz 1994, Merz and Korneyev 2004, Merz and Dawah 2005, Merz 2008, Mohamadzade Namin et al. 2010b).

Trupanea guimari (Becker, 1908)

Literature records. Morocco, Middle Atlas: Tizi s'Tkrine, Forest of Azrou (Séguy 1930). High Atlas: Tenfecht (Séguy 1930). First record for the Anti Atlas.

New records. Morocco, Anti Atlas: Centre Sidi Ouassay, 4♂♂, 12-V-2015; Msidira, 1♂, 18-V-2015; Jnane Makadir, 2♂♂, 1♀, 03-VI-2015; Aït Aissa O Brahim, 1♂, 1♀, 05-VI-2015; Ksibat Elhdeb, 1♀, 07-VI-2015 (net sweeping).

World distribution. Algeria, Spain, Canary Islands, Cape Verde Islands (Merz 1992, 1999).

Trupanea stellata (Fuessly, 1775)

Literature records. Morocco, Middle Atlas: Forest of Timelilt (Séguy 1930), Anti Atlas: Goulimine (Séguy 1949). First record for the Rif.

New records. Morocco, Rif: Mizoghar, 1♀, 06-V-2014; Oued Maâza (Tarik El Ouasâa), 1♂, 19-VI-2014; Daya Afrate, 1♀, 18-IV-2015; Aïn El Malâab, 1♀, 21-IV-2015; Oued Tkaraâ, 1♀, 07-V-2015. Anti Atlas: Centre Sidi Ouassay, 1♀, 12-V-2015 (net sweeping).

World distribution. Tunisia, Andorra, Armenia, British Isles, Scandinavia, Czech Rep., Madeira, Poland, Spain, Switzerland, Turkey, Ukraine, Mongolia, China, Canary Islands, Iraq, Israel, Saudi Arabia, United Arab Emirates, Iran, India (Norrbom et al. 1999, Heřman and Dirlbek 2006, David and Ramani 2011, Gharajedaghi et al. 2012, Merz 2011).

Tribe TERELLINI Hendel, 1927

Genus *CHAETORELLIA* Hendel, 1927

Chaetorellia conjuncta (Becker, 1912)

New records. Morocco, Anti Atlas: Airport Sidi Ifni, 5♂♂, 5♀♀, 17-V-2015; Oued Assa: 3♂♂, 2♀♀, 21-V-2015; Oued Sayad, 1♂, 25-V-2015; Oued Foum Ziguid (Douar Ouaiftoute), 1♀, 01-VI-2015; Ksibat Elhdeb, 1♂, 07-VI-2015; Oued Ziz (Pont Errachidia), 1♀, 09-VI-2015 (net sweeping)- 1♀, 12-VI-2015- 3♂♂, 23-VI-2015 (reared); Oued Ouarzazate, 4♂♂, 2♀♀, 12-VI-2015 (net sweeping)- 1♂, 28-VI-2015- 1♂, 1♀, 01-VII-2015 (reared). First record for Morocco.

Host plants. Flower heads of *Centaurea calcitrapa* L. from which the specimens were reared.

World distribution. Egypt, Afghanistan, Albania, Caucasus, Cyprus, Greece, Hungary, Iraq, Iran, Israel, Jordan, Kazakhstan, Lebanon, Pakistan, Syria, Turkey (White and Marquardt 1989, Norrbom et al. 1999, Korneyev and Dirlbek 2000, Merz 2000).

Chaetorellia hestia Hering, 1937

Literature record. Morocco, High Atlas: Essaouira (Séguy 1930). First record for the Anti Atlas.

New record. Morocco, Anti Atlas: Centre Sidi Ouassay, 2♂♂, 12-V-2015 (net sweeping).

World distribution. Algeria, France, Spain, Italy (Séguy 1930, White and Marquardt 1989, Norrbom et al. 1999).

Genus *TERELLIA* Robineau-Desvoidy, 1830

Terellia colon Meigen, 1826

Literature records. Morocco (Séguy 1930).

World distribution. North Africa, Austria, Azerbaijan, Belgium, Great Britain, Crete, Czech Republic, Denmark, Dodecanese Islands, France, Germany, Georgia, Greece, Hungary, Israel, Italy, Kazakhstan, Kyrgyzstan, Lithuania, Moldova, North Aegean Islands, Poland, Romania, Russia, Sicily, Slovakia, Spain, Sweden, Switzerland, West Siberia, Tajikistan, Netherlands, Turkmenistan, Turkey, Ukraine, Uzbekistan (Foote 1984, Norrbom et al. 1999, Kütük and Özgür 2003, Özgür and Kütük 2003, Merz and Korneyev 2004, Heřman and Dirlbek 2006).

Terellia fuscicornis (Loew, 1844)

Literature records. Morocco (Séguy 1930).

World distribution. North Africa, Crete, Cyprus, France, Greece, Italy, Madeira, Malta, Sardinia, Sicily, Spain, Iran, Israel, Lebanon, Turkey, California, Scotland (Norrbom et al. 1999, Merz 2001, Whittington 2002, Kütük and Yaran 2011, Mohamadzade Namin 2011).

Terellia longicauda (Meigen, 1838)

Literature records. Morocco, High Atlas: Tizi n'Test, Middle Atlas: Aïn Leuh (Séguy 1930, 1934b).

World distribution. Albania, Austria, Great Britain, Bulgaria, Czech Republic, Cyprus, France, Germany, Hungary, Italy, Near East, Poland, Russia, Slovakia, Spain, Switzerland, Ukraine, Turkey (Kütük 2003, Merz and Korneyev 2004).

Figure 6. *Cynara cardunculus* L. host plant of *Terellia* sp. near *longicauda*.

Terellia sp. near *longicauda*

New record. Morocco, Rif: Douar Kitane, 4♂♂, 10-VIII-2016- 2♂♂, 3♀♀, 11-VIII-2016- 1♂, 3♀♀, 12-VIII-2016- 1♀, 13-VIII-2016 (reared). First record for Morocco and North Africa.

Host plants. Flower heads of *Cynara cardunculus* L. (Fig. 6) from which the specimens were reared.

World distribution. Spain, Canary Islands (Merz 1992).

Comments. This is an undescribed, cryptic species of the *Terellia serratulae* L. complex known to infest *Cynara cardunculus* L. in Spain and the Canary Islands. The *serratula* group contains cryptic species, a situation that needs to be resolved, and for which a molecular approach should be adopted (Valery Korneyev, pers. comm.).

Terellia serratulae (Linnaeus, 1758)

Literature records. Morocco, Rif: Tangier (Wiedemann 1824, Becker and Stein 1913).

New sites. Morocco, Rif: Daya Jbel Zemzem, 1♀, 23-IV-2014; Oued Maâza (Tarik El Ouasâa), 2♂♂, 1♀, 18-VI-2014 (net sweeping).

World distribution. Algeria, Tunisia, Albania, Andorra, Armenia, Austria, Azerbaijan, Balearic Islands, Belgium, Great Britain, Bulgaria, China, Corsica, Crete, Cyprus, Czech Rep., Denmark, Finland, France, Georgia, Germany, Greece, Iran, Iraq, Ireland, Israel, Italy, Kazakhstan, Korea, Lebanon, Malta, Moldova, Mongolia, Netherlands, Norway, Poland, Portugal, Romania, Russia, Sardinia, Sicily, Slovakia, Spain, Sweden, Switzerland, Syria, Turkey, Ukraine (Korneyev and Dirlbek 2000, Han and Kwon 2000, Merz 2001, Heřman and Dirlbek 2006, Kütük and Yaran 2011, Khaghaninia et al. 2012).

Terellia virens (Loew, 1846)

Literature records. Morocco, High Atlas: Jbel Ayachi (White 1989), Tizi-n-Talrhemt (Korneyev et al. 2013). First record for the Anti Atlas.

New record. Morocco, Anti Atlas: Airport Sidi Ifni, 2♂♂, 17-V-2015; Oued Ouarzazate, 5♂♂, 12-VI-2015 (net sweeping)- 1♀, 01-VII-2015 (reared).

Host plants. Flower heads of *Centaurea calcitrapa* L. from which the specimens were reared.

World distribution. Tunisia, Albania, Afghanistan, Austria, Bulgaria, Corsica, Czech Rep., France, Germany, Greece, Hungary, Iran, Iraq, Israel, Italy, Jordan, Kazakhstan, Moldova, Netherlands, Poland, Romania, Russia, Serbia, Sicily, Slovakia, Spain, Switzerland, Turkey, Ukraine, USA (Séguy 1930, Kütük and Yaran 2011, Gharajedaghi et al. 2012, Korneyev et al. 2013).

Subfamily TRYPETINAE (Robineau-Desvoidy, 1830)
Tribe CARPOMYINI Korneyev, 1995
Subtribe CARPOMYINA Norrbom, 1989
Genus *CARPOMYA* Costa, 1854

Carpomya incompleta (Becker, 1903)

New record. Morocco, Anti Atlas: Douar Zaouia, 1♂, 1♀, 11-VI-2015 (net sweeping). First record for Morocco.

World distribution. Italy, Egypt, Ethiopia, Iraq, Israel, Saudi Arabia, Sudan, United Arab Emirates, Burkina Faso, Kenya (Norrbom et al. 1999, Merz 2011, Copeland 2009, Tankoano et al. 2012).

Tribe TRYPETINI Loew, 1861
Subtribe CHETOSTOMATINA
Genus *CHETOSTOMA* Rondani, 1856

Chetostoma curvinerve Rondani, 1856

New record. Morocco, Rif: Oued El Kelâa, 1♂, 18-XII-2015; Bab El Karne, 1♀, 25-XII-2015 (net sweeping). First record for Morocco.

World distribution. North Africa, Austria, Great Britain, Italy, Netherlands, Portugal, Spain, Switzerland, Uzbekistan, Iran, Israel (Norrbom et al., 1999, Mohamadzade Namin et al. 2010).

Subtribe TRYPETINA Loew, 1861

Genus *EULEIA* Walker, 1835

Euleia heraclei (Linnaeus, 1758)

Literature records. Morocco, Gharb plain: Sidi Slimane (Séguy 1953). First records for the Rif.

New record. Morocco, Rif: Oued Boumarouil, 1♂, 10-V-2014; Aïn El Âakba Larbaâ, 1♂, 18-IV-2015 (net sweeping).

World distribution. Algeria, Madeira, Great Britain, Czech Rep., Estonia, Latvia, Moldova, Poland, Romania, Russia, Spain, Switzerland, Ukraine, Afghanistan, Armenia, Azerbaijan, Georgia, Iran, Israel, Kazakhstan, Kyrgyzstan, Tadjikistan, Turkey, Turkmenistan, Uzbekistan, Japan (Norrbom et al. 1999, Heřman and Dirlbek 2006, Gilasian and Merz 2008).

Euleia marmorea (Fabricius, 1805)

Literature records. Morocco, Rif: Tangier (Séguy 1930, Zimsen 1964).

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