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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

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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, Francischolo 1979, Balke et al. 1989, Balke et al. 1990, Ribera et al. 2003, Darilmaz and Kiyak 2009, Touaylia et al. 2011, Šýkora 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 Mediterranean 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, Šýkora 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 (Šýkora et al. 2017). Ribera et al. (2003) and Šýkora 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 Tyrrehenian 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 lecto-
type 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 fluorescent 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 fluorescent 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 Šýkora 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.

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A revision of *Meladema* diving beetles (Coleoptera, Dytiscidae)...

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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 amplify additional gene fragments used in Sýkora et al. (2017) from dry material were not successful (see Results below). New sequences have been deposited in Gen Bank with accession numbers LT898147–LT898159 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).

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

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A revision of *Meladema* diving beetles (*Coleoptera, Dytiscidae*)...

**Abbreviations**

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**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.
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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


**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; metatarsomerers 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). They can be separated from *Bunites* Spangler, 1972 on details of the setation of the coxae and abdominal segment 8 (Michar 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 trans-
verse 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 palpmores elongate, particularly palpmore 2. Palpmore 3 with raised medial and apical tubercles ventrally, furnished with stout setae. Palpmore 3 expanded to apex, curved, convex ventrally and concave dorsally. Maxillary palpmore 1 slightly elongate; palpmores 2–4 increasingly so. Palpmore 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 acuminate rounded. Metaventrite projecting anteriorly between mesocoxae; projection with elongate median groove to receive prosternal process; groove with marked central ridge, widening anteriorly. Discrmen 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. Gonocoexae (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).

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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).
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: “entièremment 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. coriacea 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,
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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).


Figure 4. *Meladema* species males, colour pattern of isolated elytra (DNA voucher codes, where applicable). A *M. coriacea*, Spain, Murcia, Fre. 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.
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Figure 5. *Meladema* species males, 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)

C. *M. imbricata*, La Gomera, El Cedro (NHM-IRM3A)

D. *M. lanio*, Madeira, Ribeira dos Cedros (NHM-IRM8A).


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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).
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Figure 7. Meladema species elytral shoulder sculpture SEMs (DNA voucher codes where applicable). A M. coriacea, male, Spain, Murcia, Fre. Caputa B M. lepidoptera sp. n., male, Corsica, Cap Corse (NHM-IRM12F) C M. coriacea, female, Spain, Murcia, Fre. Caputa D M. lepidoptera sp. n., female, Corsica, Porto-Vecchio (NHM-IRM12A).
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Italy, Pontine Islands: 2 ♂, 3 ♀ “Ins. Pont. - @ nos// auf Tamanis// 12-4-57// Dr. Eckerlein leg.


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).

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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.
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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-HI16). Scale bar = 0.5 mm.
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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 punctuation 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 acuminated 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 contiguously (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 (Guéorguiév 1987). Despite being listed from Libya 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/Tunisia, 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,
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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

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

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.


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.


**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” (λεπίδος, 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 Tyrrhenian 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.
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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)


*Scutopterus imbricatus* Wollaston, 1871: 220.


*Meladema imbricatum* Branden, 1885: 95.


**Type locality.** “Madeira” [mislabelled].


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.

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.


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**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 apicilaterally, 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. 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-

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, 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, Monte Cristo (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-
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)

*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.

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.


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. imbri cata* – green; *M. lanio* – yellow. Bicoloured symbols, hybrid or morphologically intermediate individuals.


**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-
dial, paired interoculr 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 interoculr 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 24. Meladema type labels and specimens in situ. A. M. imbricata, holotype, BMNH, Wollaston Collection B. M. lanio lectotype, BMNH, Banks Collection.
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
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-
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

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.
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...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. Metaventraceous 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 punctate, 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. 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, 10; 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 fe-
males 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 un-
der 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 for-
est 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 pro-
notum 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. Crescentic striolae on elytra relatively small and sparse, particularly on shoul-
der 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

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

5. Elytra weakly shining, with (typically small) crescentic striolae in all speci-
mens (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)

6. 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’Ajjjer, 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 Pliocene-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 × 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 × 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 × 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 × 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 × 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 diagnosable on a suite of both molecular and morphological characters, and appear to remain distinct, suggesting limited gene exchange (Coyne and Orr 2004, DeQueiroz 2007).


Viewed 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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