Abstract. Widely distributed phoretic blister beetles usually display unstructured geographic patterns of genetic diversity within species, resulting from recurrent long-dispersal events across their range. To investigate the extent of this pattern in the phoretic genus *Lampromeloe*, and particularly in western Mediterranean and European populations of *L. variegatus*, we performed: (1) a phylogeographic analysis based on fragments of the mitochondrial genes COI and 16S, and (2) a morphological revision based on qualitative and morphometric traits. Two allopatric lineages were recovered within *L. variegatus*, one distributed across Europe and the other in North Africa. These lineages are readily distinguishable based on morphological traits. We conclude that these lineages constitute two diagnosable evolutionary units and, consequently, we describe the North African populations as a new species, *Lampromeloe pantherinus* sp. nov. The new species is closely related to *L. variegatus*, from which it differs mainly by the elytral macrosculpture and by the shape of male genitalia. The elytral macrosculpture of *L. pantherinus* is somewhat similar to that of *L. cavensis*, a species widely distributed in the lowlands of the Mediterranean Basin. However, these two non-sister species can be distinguished by the morphology and macrosculpture of the pronotum and by the shape of the male genitalia.

Keywords. Atlas Mountains, North Africa, blister beetles, taxonomy, geometric morphometrics.
Introduction

The Mediterranean Basin offered long-term opportunities for diversification, which resulted into its current high levels of biodiversity (Myers et al. 2000; Gómez & Lunt 2007). Among the key factors influencing the evolution of regional biotas are topographic heterogeneity (García-París et al. 2000; Wiens et al. 2007), climatic shifts (Gómez & Lunt 2007), and palaeogeology (Hewitt 2011; Más-Peinado et al. 2018). One of the most species-rich regions in North Africa is the western Maghreb (Pleguezuelos et al. 2010; Rankou et al. 2013; Jaskuła 2015). Despite being relatively well studied, this region is not exempt from the Linnean shortfall (see Brito 2010), a global problem for biodiversity conservation derived from the lack of taxonomic knowledge (López-Estrada et al. 2022). In the last decades, several phylogenetic and phylogeographic studies across the Maghreb unveiled the existence of a remarkable overlooked portion of diversity (e.g., Froufe et al. 2008; Kaliontzopoulou et al. 2011; Sousa et al. 2011; Barata et al. 2012; Casal-López et al. 2015; Doadrio et al. 2015, 2016; Metallinou et al. 2015; Rosado et al. 2017; Salvi et al. 2018; González-Miguëns et al. 2020; Miralles et al. 2020). The uplifting of the Atlas Mountains has been invoked to explain diversification patterns in different taxa, either from vicariance events that led to allopatric differentiation or by providing new ecological opportunities for diversification (Brown et al. 2002; Lansari et al. 2015; Rosado et al. 2017). However, there is another set of widespread Maghrebian taxa whose diversification seems not to be directly derived from the Atlas uplift (Salvi et al. 2018; Sánchez-Vialas et al. 2020). This seems to be the case for the genus Lampromeloe Reitter, 1911 (Coleoptera: Meloidae: Meloini).

Phoretic blister beetles of the genus Lampromeloe (type species: Meloe variegatus Donovan, 1793, by subsequent designation of Aksentjev 1988: 574) was originally described as a subgenus of Meloe Linnaeus, 1758 (Reitter 1911: 388) and treated as such until its recent rise to generic level by Sánchez-Vialas et al. (2021). It currently consists of two widely distributed and well-recognized species over great part of the Palaeartic region, *L. variegatus* and *L. cavensis* (Petagna, 1819) (Bologna 1991, 2020). However, a third taxon, *Meloe stellata* Pliginskij, 1923, described from “Persia, Arabistan” (= Lorestan, Iran) (Pliginskij 1923) was generally considered as a possible synonym of *L. cavensis* (e.g., Bologna 1991, 2008, 2020; García-París et al. 2010; Ghahari & Campos-Soldini 2019), but according to Di Giulio et al. (2014) a revision of the type material is necessary to clarify its taxonomic status. Larvae of Lampromeloe are well characterized by a combination of singular traits such as the presence of nine lanceolate spines directed forward, located in the fronto-clypeal medial anterior region, and mandibles ventrally denticulate, which are apparently morphological specializations for phoresy (Cros 1929, 1941; Bologna 1991; Di Giulio et al. 2014). Also, Di Giulio et al. (2014) noted the existence of a morphologically singular larva of Lampromeloe from Iran distinguishable from that of *L. variegatus* and *L. cavensis*, hypothesizing that an additional new species could be discovered in the future.


In the Western part of the Mediterranean region, *L. variegatus* is a very rare species (García-París & Ruiz 2011) that inhabits mainly the northern half of the Iberian Peninsula, with a few old records in the south (Pérez-Moreno et al. 2003; Prieto et al. 2016), and North Africa where it has only been recorded in eight localities, from northern Tunisia to western Morocco (Cros 1941; Pardo Alcaide 1950; Kocher 1956; Bologna 1991; Ruiz & Ávila 1994; Sánchez-Vialas et al. 2021). Previous studies of phylogenetic relationships of Meloini Gyllenhaal, 1810 based on molecular data found two distinct lineages within
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*L. variegatus*, one represented by the northern African populations (Moroccan Atlas, mainly) and the other by the European ones (including samples from the Iberian Peninsula and central Europe), which diverged from each other around 4 Ma ago (Sánchez-Vialas et al. 2021).

In this work, we aim to determine whether the two lineages found within *L. variegatus* represent different evolutionary and taxonomic units. Specifically, we: (1) analyse two mitochondrial fragments for newly studied specimens of *Lampromeloe* from Spain, central Europe and Morocco, and a fragment of the nuclear gene CAD for one specimen of each geographic provenance, and (2) perform a morphological study of specimens from different lineages through morphometric analysis and qualitative-based re-examination. We conclude that the North African populations previously treated as *Lampromeloe variegatus* (or *L.* aff. *variegatus*) represent an overlooked new species, which is herein described and named as *L. pantherinus* sp. nov.

Materials and methods

Morphological study

The material of *Lampromeloe* used in the morphological study is listed below in the examined material section (except the specimens from Museu de Ciències Naturals de Barcelona, detailed in Prieto et al. 2016), and was partially reviewed by Garcia-París et al. (2006) and García-París & Ruiz (2011). Regarding the specimens from the Museo Nacional de Ciencias Naturales (Madrid, Spain), we have included the individual code of the entomology collection of each specimen studied. The specimens of *L. pantherinus* sp. nov. designated as type material, a total of 6 (holotype and 5 paratypes), as well as the additional material studied from this new species, are listed in the species description (see Taxonomic account). Additional abbreviations: ex/x = exemplar/s.

Dry-mounted and ethanol-preserved specimens were examined under a stereo microscope for the morphological study. The assignment of the studied specimens to species was carried out according to the differential characters provided by Bologna (1991). Qualitative morphological traits previously recognized as diagnostic within *Lampromeloe* (see Bologna 1991) were revised, mainly the macrosculpture and shape of the pronotum, the integumentary sculpture of the elytra, and the male genitalia structure. Male specimens were rehydrated prior to the extraction of their genital pieces, which were subsequently mounted on a piece of cardboard using dimethylhydantoin formaldehyde resin (DMHF) and pinned adjacent to their respective specimen. The genitalia of the male holotype of the new species (ethanol-preserved) was extracted without rehydrating the specimen to avoid damaging the tissues, so that it may be used for future DNA studies. Measurements were taken using a micrometer that was coupled to one of the eyepieces. Digital pictures of live, dry-mounted specimens and male genital pieces were taken with a reflex camera (Canon 77D) fitted with a macro-lens and two external flashes. To describe the various parts of the male genitalia we used the terminology provided by Selander (1966). The distribution map of the new species was produced using QGIS ver. 3.8.

Because pronotum shape and structure has been used as one of the main traits to identify species of *Lampromeloe* (Bologna 1991), we studied its shape using geometric morphometric (GM) analysis. Digital images of the dorsal side of the pronotum were obtained using a reflex camera coupled with a macro lens. A total of 74 adult specimens (43 *L. cavensis*, 1 *L. stellatus*, 23 *L. variegatus*, and 7 *L. pantherinus* sp. nov.), dried or ethanol preserved, were photographed. A combination of five anatomical landmarks and 16 sliding semi-landmarks were used to quantify shape variation of the pronotum (Fig. 1). Landmarks were placed in homologous structures, whereas semi-landmarks were equidistantly placed between them (Korba et al. 2022). Landmarks and semi-landmarks were digitized using the R package “StereoMorph” ver. 1.6.2 (Olsen & Westneat 2015) in the free use program R ver. 3.6.0 (R Core Team 2021). The coordinates (X, Y) obtained from landmark and semi-landing
digitization were transformed into new coordinates by generalized Procrustes analysis (Gower 1975). Mean shapes were then calculated for each species and visualized using principal component analysis (PCA) on the coordinates projected into the linear tangent space using the function `gm.prcomp`. The first two principal components were used to visualize the pronotum shape variation.

**Institutional abbreviations**

<table>
<thead>
<tr>
<th>Institution</th>
<th>Full Name</th>
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<tbody>
<tr>
<td>ECWP</td>
<td>Emirates Center for WildLife Propagation, Missour, Morocco</td>
</tr>
<tr>
<td>MCNB</td>
<td>Museu de Ciències Naturals de Barcelona, Barcelona, Spain</td>
</tr>
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<td>MNB</td>
<td>Museum für Naturkunde, Berlin, Germany</td>
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<tr>
<td>MNCN-CSIC</td>
<td>Museo Nacional de Ciencias Naturales, Madrid, Spain</td>
</tr>
</tbody>
</table>

**Fig. 1.** Landmark configurations of the 74 specimens examined of *Lampronoloe* Reitter, 1911 after generalized Procrustes superimposition analysis. For each landmark, the black dot indicates the average shape, and grey dots represent the locations of each specimen.
DNA extraction, sequencing, sequence alignment, and phylogenetic analyses

The molecular study includes a total of 19 samples of *Lampronoloe*: seven *L. cavensis* from Morocco and Spain; nine *L. variegatus* from northern Spain and Hungary; and the other three *L. pantherinus* sp. nov. from western High Atlas and northeastern Middle Atlas (Table 1).

Tissue samples were extracted from the coxae of specimens preserved in absolute ethanol stored at -20°C. Genomic DNA was extracted using the Qiagen DNeasy extraction kit (Qiagen, Valencia, CA, USA).

Polymerase Chain Reaction (PCR) was used to amplify fragments of two mitochondrial regions: 658 base pairs (bp) of the mitochondrial region of Cytochrome Oxidase I (*COI*) (for 14 specimens) using the set of primers LCO 1490 (Folmer et al. 1994) and COI-H (Machordom et al. 2003), and 789 bp of 16S ribosomal RNA (16S) (for 7 specimens) using the set of primers 16S-AR and 16S-ND1 (Simon et al. 1994). An additional fragment (599 bp) of the nuclear CAD using the set of primers CD821F and CD1098R (Chatzimanolis 2014) was amplified for three specimens of *L. variegatus* from Hungary, *L. pantherinus* sp. nov. from Morocco, and *L. cavensis* from Spain. Polymerase chain reactions were performed in 25 µl, including 23 µl of the PCR mix, including 17.5 µl of H$_2$O, 2.5 µl of a reaction buffer with MgCl$_2$ (2 mm), 1 µl of dNTP (10 mm), 0.8 µl of MgCl$_2$ (50 mm), 0.5 µl of each primer (10 mM), 0.4 µl of Taq polymerase (Biotools, 5 U/mL) and 2 µl of specimen DNA. PCR conditions for *COI*: 5 min at 95°C, 40 cycles with a denaturing temperature of 94°C (45 s), annealing at 42°C (45 s) and extension at 72°C (1 min) with a final single extra extension step at 72°C for 10 min; for *16S*: 5 min at 94°, 35 cycles with a denaturing temperature of 94° (30 s), annealing at 42°C (30 s) and extension at 72°C (45 s) with a final single extra extension step at 72°C for 10 min. PCR products were checked in 1 % agarose gel and products with expected length were directly sequenced at Macrogen Inc. (Macrogen Europe, Madrid, Spain).

All sequences were compiled using Sequencher ver. 4.9 to assemble and to edit the sequence contigs, and aligned with MAFFT (Katoh & Toh 2008). DNA sequences were visually checked in Mesquite ver. 3.04 (Maddison & Maddison 2016) to refine the final alignments. We included as outgroup three additional species of the tribe Meloini: *Eurymeloe mediterraneus* (Müller, 1925), *Meloe* (*Meloe*) *proscarabaeus* Linnaeus, 1758 and *Meloe* (*Anchomeloe*) *autumnalis* Olivier, 1797, obtained from Sánchez-Vialas et al. (2021). New sequences are deposited in GenBank (Table 1).

Phylogenetic analyses were carried out under a Bayesian Inference framework conducted with MrBayes ver. 3.2.3 (Ronquist et al. 2012) with two partitions of the data set (one for each gene fragment). Analyses started with a randomly generated tree and were run four Metropolis coupled Monte Carlo Markov chains for $10 \times 10^6$ generations and sampling every 1000. We discarded 25% of the obtained trees as burn-in, and generated 50% consensus tree in MrBayes. We explored the substitution model space setting the option lset nst to mixed rates and to invgamma (Percino-Daniel et al. 2013). Posterior clade probabilities (BPP) were used to assess nodal support.

Species concept

For taxonomic decisions we have adopted the evolutionary species concept (Wiley 1978; de Queiroz 1998; Wiley & Mayden 2000), considering the species as a separately evolving lineage, that maintain its identity from other such lineages and which has its own evolutionary tendencies and historical fate (Wiley 1978). Under this concept, reciprocal monophyly and congruence across molecular data sets are important lines of evidence for species delimitation.
Table 1. Species identities, collecting localities, voucher numbers and GenBank accession numbers for the samples of *Lampromeloe* Reitter, 1911 analysed in this study.

<table>
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<th>Species</th>
<th>Locality</th>
<th>Voucher number</th>
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<th>16S</th>
<th>CAD</th>
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<td>ON455125</td>
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</table>
Results

Examined material

We studied a total of 149 specimens of the genus Lampromeloe. Among these, 125 specimens [consisting of 86 L. cavensis, 32 L. variegatus, and seven L. pantherinus sp. nov.; of these last, five partially constitute the type series (the holotype and four paratypes) and the other two are additional examined material] are held at the Entomological Collection of the MNCN-CSIC, two specimens (one of L. cavensis and one paratype of L. pantherinus sp. nov.) at the entomological collection of the ECWP, 17 specimens (16 of L. cavensis, one of L. variegatus), housed at the MCNB, which are listed in Prieto et al. (2016), and five syntypes of Meloe stellata [a possible synonym of L. cavensis (Bologna 1991)], preserved in the MNB. Specimens were preserved dry (131 specimens) and in absolute ethanol (18 specimens).

The examined material of each currently recognized species of the genus Lampromeloe is listed below, including type material (syntypes) of Meloe stellata, until now considered synonym of L. cavensis, but whose taxonomic status requires further molecular studies (see discussion).

Lampromeloe cavensis (n = 87)

Dry preserved specimens (excluding material listed in Prieto et al. 2016)

MOROCCO – Guelmim-Oued Noun • 1 ex.; Tiliuin (= Ifni); Dec. 1934; F. Escalera leg.; MNCN_Ent 255285. – Casablanca-Settat • 1 ex.; Casablanca; 29 Jan. 1985; F. De la Torre leg.; MNCN_Ent 165015. – Marrakech-Safi: Marrakech • 6 exx.; Jan. 1907; Escalera leg.; MNCN_Ent 255267, 255274, 255275, 255281 to 255283. – Oriental: Nador • 1 ex.; Monte Gurugú, Haddu. – Draa-Tafilalet • 1 ex.; Anezal; 30°43’25.7″ N, 7°16′47.2″ W; ECWP.

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Lampromeloe cavensis (n = 87)
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Safi: Marrakech • 1 ex.; Essaouira, Carretera Essaouira-Mulay Bouzerktoun; 31°35′46.5” N, 9°39′48.7” W; 137 m a.s.l.; 14 Mar. 2013; M. García-París and N. Percino leg; MNCN.

SPAIN – Andalucía: Jaén • 1 ex.; Linares; mel 81029; MNCN.

Type material of *Meloe stellata* (n = 5)

Dry preserved specimens

IRAN – Arabistan • 5 exx; Persia; 2 Apr. 1904; Zarudny leg.; MNB [syntypes of *Meloe stellata* chosen among the 20 preserved at MNB, labelled: “Pers. (= Persia) / 2. IV. 1904 / Zarudny” (label originally Cyrillic). The rest of the syntypes (originally described from 27 specimens) are lost or deposited at the Zoological Institute St. Petersburg (Bernd Jaeger pers. com.).

*Lampromeloe variegatus* (n= 32)

Dry preserved specimens

PORTUGAL – Estremadura • 1 ex.; Espichel; Lauffer leg.; MNCN_Ent 31482.

SPAIN – Asturias • 1 ex.; Puerto Pajares; A. Kricheldorff leg.; MNCN_Ent 31489. – Castilla la Mancha: Cuenca • 2 exx.; Carrascosa; Escalera leg.; MNCN_Ent 31478, 31480 • 1 ex.; Cuenca; Castro leg.; MNCN_Ent 31490 • 1 ex.; Cuenca; Senén leg.; MNCN_Ent 31486 • 2 exx.; Montalbanelo; Escalera leg.; MNCN_Ent 31479, 31483 • 1 ex.; Osa de la Vega; Escalera leg.; MNCN_Ent 31484 • 1 ex.; Saelices; Escalera leg.; MNCN_Ent 31481. – Guadalajara • 1 ex.; Casa de Uceda; MNCN_Ent 31495. – Castilla y León: Salamanca • 1 ex.; 5 km NO of Palencia de Negrilla; 8 May 2004; M. García-Paris leg.; MNCN_Ent 31488 • 1 ex.; Negrilla; C. Escrribano leg.; MNCN_Ent 31498 • 1 ex.; Palencia de Negrilla; 21 Apr. 2005; M. García-Paris leg.; MNCN_Ent 32641 • 1 ex.; Retortillo; Escalera leg.; MNCN_Ent 31487 • 1 ex.; Salamanca; MNCN_Ent 31492. – Soria • 1 ex.; Losana; Escalera leg.; MNCN_Ent 31496 • 1 ex.; Soria; MNCN_Ent 31494. – La Rioja • 1 ex.; San Felices, Logroño; J. Ardois leg.; MNCN_Ent 31497. – Comunidad de Madrid: Madrid • 1 ex.; Madrid; MNCN_Ent 31491 • 1 ex.; Rozas P.R.; Lauffer leg.; MNCN_Ent 31485. – Province not indicated • 1 ex.; Hispania; A. Kricheldorff leg.; MNCN_Ent 31493.

Ethanol preserved specimens

HUNGARY – Komárom-Esztergom • 1 ex.; Vértesszőlős; 5 Apr. 2008; L. Somai and J. Nédli leg.; mel 81068; MNCN.

PHYSIOGENETIC RELATIONSHIPS WITHIN LAMPROMEOLOE

The final alignment consisted of 1447 bp of the concatenated dataset of COI and 16S. The Bayesian hypothesis strongly supports the reciprocal monophyly between *L. variegatus* from Europe and *L. pantherinus* sp. nov. from Morocco (BPP = 1) that together form a clade sister to *L. cavensis* (BPP = 1) (Fig. 2). The CAD gene fragments of the analysed specimens of *L. variegatus* and *L. pantherinus* differ by two base substitutions from each other, and by eight minimum mutations with respect to specimens of *L. cavensis*. Intraspecific genetic distance (COI dataset) of the three analysed samples of *L. pantherinus* ranges between 0.3% and 1%, whereas between *L. pantherinus* and *L. variegatus* (n = 9) varies from
4.9 to 6.2%. The specimens of *L. pantherinus* from Jbel Tsiwant and from Tizi n’Tichka, separated by around 390 km, are very similar genetically between them (0.3–1%), and so are the geographically distant populations of *L. variegatus* from the Iberian Peninsula and Central Europe (0.7–2.9%) or those of *L. cavensis* from the Iberian Peninsula and Morocco (0.1–0.8%).

**Morphological results**

The pronotal macro-sculpture of *L. cavensis* and *L. variegatus* aligns with Bologna’s (1991) redescription of each species. The North African specimens of *L. pantherinus* sp. nov. present a macro-sculpture of the pronotum similar to the European *L. variegatus*, lacking the characteristic longitudinal depressions.

![Bayesian phylogenetic relationships based on mtDNA (COI and 16S) of the genus Lamproroe (Coleoptera) from North Africa](image)

**Fig. 2.** Bayesian phylogenetic relationships based on mtDNA (COI and 16S) of the genus Lamproroe (Coleoptera) from North Africa. High bayesian posterior probabilities (>98%) are denoted by a dot on each corresponding node.
of *L. cavensis* (Fig. 3). *Lampromeloe variegatus* and *L. pantherinus* show a relatively rounded subtle depression on the fore sides of pronotum (Fig. 3).

The examined specimens of *L. pantherinus* sp. nov. from Morocco and Algeria (Batna, Aures Mountains) show an elytral sculpture made up by relatively wide and glossy areolas separated by rugose and radiate spaces. The reviewed specimens of *L. cavensis* also present wide and glossy elytral areolas, generally slightly larger than in *L. pantherinus* (Fig. 4). By contrast, the studied specimens of *L. variegatus* present a completely different elytral macro-sculpture formed by reduced areolas or tubercles, giving a corrugated aspect to the elytral surface (Bologna 1991).

The male genitalia of *L. pantherinus* (Fig. 5A) presents a gonocoxal plate slightly enlarged in the middle, wider but shorter than parameres on dorsal view, whereas in *L. variegatus* (Fig. 5B) and *L. cavensis* the gonocoxal plate is more elongated and narrower in dorsal view and longer in lateral view than in *L. pantherinus*. Gonostyli in *L. pantherinus* are narrow and markedly converging towards the apex, with their distal portions on either side of the apical notch, narrow, long, and converging (Fig. 5A). By contrast, the distal portion of gonostyli is shorter and wider in *L. variegatus* (Fig. 5B) and *L. cavensis*. The ventral hooks of the aedeagus are more separated from each other in *L. pantherinus*, and they are closer to the apex in *L. pantherinus* and *L. variegatus* than in *L. cavensis*.

We calculated the morphometric space of the pronotum shape using the information from the first two principal components. The PC1 and PC2 accounted for 30.66% and 16.69% of the variability, respectively. Pronotum shape partly overlaps between *L. cavensis* and *L. variegatus*, but it clearly separates *L. pantherinus* sp. nov. from *L. cavensis*. However, the specimens of *L. pantherinus* are included within the variability of *L. variegatus* (Fig. 6). The general pronotum appearance of *L. pantherinus* closely resembles that of *L. variegatus*, being more transversal than in *L. cavensis* and the syntypes of *M. stellata*.

**Taxonomic results**

Our study shows that the Northern African populations previously treated as *L. variegatus* (or as *L. aff. variegatus*) (Ruiz & Ávila 1994; Sánchez-Vialas et al. 2021) differ consistently from *L. variegatus* and represent a clearly differentiated species (see comparisons below).

Due to the absence of available names for North African populations in the synonymic list of *L. variegatus* (e.g., García-París et al. 2010; Bologna 2020), the distinctive Maghrebian lineage of *Lampromeloe* requires a new name.

**Description of a new species of Lampromeloe Reitter, 1911**

Class Insecta Linnaeus, 1758  
Order Coleoptera Linnaeus, 1758  
Family Meloideae Gyllenhal, 1810  
Genus *Lampromeloe* Reitter, 1911

*Lampromeloe pantherinus* sp. nov.  
Figs 3I–J, 4G–H, 5A, 7, 9, 11A–C

**Diagnosis**

*Lampromeloe pantherinus* sp. nov. can be differentiated from the other species of *Lampromeloe* by the following combination of characters: elytra with medium-sized and glossy areolas, which are separated by a rugose and radiate space; pronotum lacking the median longitudinal depression, transverse, similar
to *L. variegatus*; male genitalia with gonostyli narrow, markedly converging towards the apex in dorsal view and wide in lateral view, with the apical notch deep, gonocoxal plate distinctly wide and short in dorsal view, and aedeagus with ventral hooks straight (not curved), directed posteriorly and well separated from each other.

**Etymology**

The specific epithet *pantherinus* (adjective, ‘panther-like’) refers to the areolar pattern of the elytra, somewhat reminiscent of the fur pattern of a leopard, *Panthera pardus* (Linnaeus, 1758), a species on the verge of extinction (if not already extinct) in Morocco (Aulagnier *et al.* 2017). Our intention with the species name is to remember the last known wild Barbary lion, *Panthera leo leo* (Linnaeus, 1758), which was shot in 1942 near Tizi n’Tichka (Black *et al.* 2013), the type locality of the newly described *Lampromeloe*.

**Type material**

**Holotype**


**Paratypes**

MOROCCO • 1 ♂; “2 km north of Tizi n’Tichka, High Atlas, Morocco, 31°18’30’’N 7°22’17’’W, 2088 m, 21-II-2010, M. García-París leg. // MNCN_Ent 325514 // mel 81010” [white label, printed; preserved in absolute ethanol]; MNCN_Ent 325514 • 1 ♂; “El Hajeb, Azrou, Morocco, 33°38’14.71’’N-5°22’22.6’’W, 1231 m, 12-III-2018, K. López-Estrada, E. Recuero and M. Gª-París leg. // MNCN_Ent 325515” [white label, printed; preserved in absolute ethanol]; MNCN_Ent 325515 (Fig. 7) • 1 ♀; “Aguelmane de Sidi Ali, Medio Atlas, Marruecos, 33°04’N-5°00’W, 2050 m, 30-III-1993, M. Tierno de Figueroa leg. [white label, printed] // MNCN_Ent 324812 [bluish grey label, printed]”; MNCN_Ent 324812 [preserved dried] • 1 ♀; “Tizi n’Tichka, Alto Atlas, Marruecos, 8-IV-1992, J.L. Ruiz leg. [white label, printed] // MNCN_Ent 324813 [bluish grey label, printed]”; MNCN_Ent 324813 [preserved dried] • 1 ♂; “20/02/2021, Jbel Tsiwant, 33.32998/-4.06199, G. Liénart, T. Dieuleveut, A. François // 1929 m, steppe à alfas et buis au bord d’un oued, 24078” [two beige labels, printed and handwritten; preserved dry]; ECWP.

All paratypes labelled: “Lampromeloe pantherinus Sánchez-Vialas, López-Estrada, Ruiz & García-París des. 2023” [white labels in ethanol preserved specimens and red labels in dry preserved specimens, all printed].

**Additional material studied**

ALGERIA – Batna • 1 ex.; Batna [“Batna, Buen” // Meloe purpurascens]; MNCN_Ent 255286 (dry preserved) • 1 ex.; Batna [“Batna, Buen”]; MNCN_Ent 255287 (dry preserved).

**Description**

**Adult male** (holotype, MNCN_Ent 325513)

**Measurements.** Total body length: 33 mm. Length from frons to posterior margin of elytra: 18 mm. Maximum body width (at level of last third of elytra): 12 mm.

**Appearance.** General appearance robust. Voluminous and elongated abdomen. Reduced, convex, and basally imbricated elytra; functional wings absent.
SÁNCHEZ-VIALAS A. et al., A new species of Lampromeloe (Coleoptera) from North Africa

**Colouration.** Tegument mostly metallic green, shiny, with purplish, dark greenish and blackish hues (same as in paratype in Fig. 7). Head and pronotum dark-purple, with greenish central area; elytra darker, with very dark purple, almost blackish areolas and very dark greenish hues between areolas; appendages dark purple; abdomen dorsally black, with each of sclerotized tergal areas (both on dorsal and ventral surfaces) two-coloured, greenish anteriorly and purple posteriorly; abdominal ventrites dark greenish with purple highlights. Tibial spines and tarsal claws brownish. Setation black over the body, short and very sparse on dorsal areas of head, thorax and abdomen, denser and longer in the ventral region of thorax and abdomen.

**Head.** Voluminous, slightly wider than pronotum (maximum width, in frontal view: 6 mm), broadly trapezoidal, almost flat in frontal surface, with wide and rounded temples, and weakly depressed longitudinal area behind eyes. Head surface densely punctured; punctures rounded, deeply marked, close to each other, mostly confluent and homogeneously distributed, from large to medium-sized; very short longitudinal midline weakly impressed from middle half of frons to fronto-clypeal suture. Eyes relatively small, kidney-shaped and weakly swollen, barely emarginated at level of antennal insertions, with upper and lower lobes of similar size; minimum interorbital distance: 3.6 mm. Frons and temple mostly glabrous, with very short seta on each puncture and longer setae on upper margin of antennal insertion; back of head bearing moderately long and semi-erect setae. Clypeus-fronto suture marked, arcuate. Clypeus flat, sub-rectangular, transverse (2.5 mm wide, 1.3 mm long); clypeal punctures medium-sized, close to each other, absent in distal region, turning brown coloured; clypeal setation made up of long setae, following puncture pattern in which they are inserted, directed forward. Clypeus-labrum suture almost straight. Labrum transverse (2.3 mm wide, 1.7 mm long), broadly emarginated in distal middle with small punctures; setae longer and widest in lobes, following puncture pattern, oriented forward and towards centre. Mandibles robust, longitudinally concave on outer side and notched at distal margin, basally pilose. Maxillary and labial palpi unmodified. Maxillary palps elongated; palpomere I very short, wide, subcylindrical (0.1 mm long, 0.2 mm wide), almost hidden by mentum; II longer, sub-troncoconical (0.6 mm long, 0.2 wide); III short, sub-cylindrical (0.6 mm long, 0.3 mm wide); IV sub-trapezoidal (0.7 mm long, 0.3 wide), widest, apically truncate, with narrow excavation along distal margin, which is brown coloured. Labial palpi with palpomere I very short, sub-cylindrical (0.09 mm long, 0.1 mm wide); II longer, troncoconical (0.2 mm long, 0.1 mm wide); III sub-trapezoidal (0.3 mm long, 0.15 mm wide); IV sub-trapezoidal (0.4 mm long, 0.2 mm wide), truncate at apex.

**Antennae.** Length: 7.7 mm, made up of 11 antennomeres, robust, moniliform, relatively short, not reaching the pronotum base when extended backward, with very short, decumbent black setae on segments I–VII, hardly noticeable among the rest antennomeres; antennomere I enlarged forward, sub-cylindrical (1 mm long); II very short, sub-globose (0.4 mm long); III (1 mm long) cylindrical slightly dilated apically; IV–X (0.6 mm long) similar in shape, sub-cylindrical, but IX and X slenderer; XI (1 mm long) sub-conical, narrowed forward, with a blunt tip.

**Pronotum.** Sub-rectangular, transverse (3.5 mm long, 6 mm wide), lateral margins slightly converge backwards, with lateral angles broadly rounded; anterior margin slightly curved and base concavely emarginated (Fig. 3I). Pronotal surface with three shallow depressed areas: wide and weak hemi-elliptical basal depression extending to second third and two oval-shaped depressions, with diffuse boundaries, next to antero-lateral margins. Pronotum densely and homogeneously punctured, similar to those on head; punctures large, circular and deep, close to each other, mostly confluent and forming subrugose pattern. Dorsal surface of pronotum almost glabrous in appearance, with very short, almost indistinct isolated seta in each puncture; anterior margin showing narrow band with numerous, moderately long setae. Mesonotum covered by pronotum, barely visible, showing only posterior margin. Metanotum completely covered by elytra. Prosternum very narrow, arcuate. Mesosternum relatively wide and transverse (width: 4 mm; length in middle: 1 mm); anterior margin marked and broadly arched, with
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small triangular prolongation backwards, ending in rounded tip extending to level of fore quarter of mesocoxae; surface with relatively large punctures (intermediate in size between those of pronotum and coxae) and long and diffuse oblique wrinkles; setation relatively dense consisting of long and semierect black setae, following puncture pattern in which they are inserted. Metasternum subtrapezoidal, wide, covered by mesocoxae, deep and closely notched in middle of posterior margin, between metacoxae.

**ELYTRA.** Reduced and convex, imbricated basally (right over left), longer than pronotum (11 mm long), strongly divergent posteriorly and reaching posterior e.g., of second tergum, covering first tergum almost completely; tegument glabrous, with sculpture based on medium-sized and glossy areolas, separated by micro-rugose narrow spaces between each other (Fig. 4G).

**LEGS.** Robust, surface with punctuation relatively fine and shallow, dense in the tibiae and scarcer in the femurs, covered by relatively dense setation, consisting of black, decumbent and relatively long setae, denser on tibiae. Holotype lacks middle and posterior left legs, and right tarsal claws. Metatibia longer than metatibia (metatibia: 6.5 mm long, 2 mm wide; metatibia: 5.4 mm long, 1.3 mm wide). Length (in mm) of pro-, meso- and metafemur as follows: 5.9, 6.1 and 6.5. Length (in mm) of pro-, meso- and metatibia as follows: 4.9, 5.1 and 5.4. Length (in mm) of the tarsomeres as follow (claws excluded): protarsus (4.9) (I: 1.5; II: 0.8; III: 0.8; IV: 0.7; V: 1.1), mesotarsus (mesotarsomere V is lacking in both legs) (I: 1.9 mm; II: 1; III: 0.8; IV 0.8; V: lacking), and metatarsus (6.3) (I: 3; II: 1; III: 0.8; IV: 1.5). Protibiae with two similar spurs, slender and straight; mesotibiae with inner spur slightly wider than outer; metatibial spurs dissimilar: outer spur spoon-shaped, inner spur similar to those of fore- and mesotibiae but little wider at base. Coxae dense and finely punctured, with dense setation, somewhat longer than that of femurs. Ventral pads of pro-, meso-, and meta- tarsus consisting on dense, short and thick tuft of semi-erected setae. Claws smooth, curved, with lower lobe slightly smaller.

**ABDOMEN.** Voluminous (maximum width: 12 mm at level of third abdominal segment). First tergite partly covered by elytra. Tergites with wide and well-sclerotized central semi-circular plate, metallic green in anterior half, turning purple in posterior; integumentary surface subcorrugated, with numerous small, fine wrinkles, longitudinally and obliquely arranged, and small, scattered, poorly printed punctures. Dorsal surface of abdomen almost glabrous, with sparse and very short setae on sclerotized plates. Distal margin of last tergite with dense short setae. Lateral areas of tergites, where spiracles are located, membranous and glabrous. Ventrites entirely sclerotized, with dense punctuation, made up of small, subcontiguous and relatively well marked rough punctures, that give them a subcorrugated appearance; setation dense, homogeneously dispersed, constituted by decumbent black setae, similar in length to that of femurs. Last ventrite markedly notched at apex.

**MALE GENITALIA (Fig. 5A).** With gonoforceps brownish; moderately elongated (4 mm long). Gonocoxal plate slightly enlarged in middle, wider but shorter than parameres on dorsal view (1.6 mm long, 1.7 mm wide). Gonostylus longer than wide (2.4 mm), sub-cylindrical, with short series of very small punctures followed by some hardly noticeable small setae on dorsal view; in lateral view, shape of gonostyli wide and ending on very wide rounded tip of parameral lobes. Distal portion of gonostyli separated by short longitudinal notch, and distantly convergent in dorsal view; apices rounded. Aedeagus long (2.3 mm), robust, flattened, truncate at apex, with two hooks, close to each other, similar in size but distal one slightly shorter and relatively close to apex. Hooks straight and directed posteriorly (as opposed and curved in L. variegatus). Uncus visible (Fig. 5A).

**Female**

Similar to male, but with last abdominal ventricle rounded and not emarginated in posterior margin, and with slightly shorter antennae.
Fig. 5. Male genitalia, from left to right: dorsal and lateral view of the tegmen, and lateral view of the aedeagus. A. *Lampromeloe pantherinus* sp. nov., holotype (MNCN_Ent 325513). B. *L. variegatus* (Donovan, 1793) from Salamanca, Palencia de Negrilla (MNCN_Ent 375546). Photographs by AS-V. Scale bar = 1 mm.
Variability

Body length (frons to posterior border of elytra) variable: 13.2–18 mm (mean: 15.65; n = 6); maximum width: 9.4–14.2 mm (mean: 11.61; n = 6); pronotum length: 2.8–3.5 mm (mean: 3.14; n = 6); pronotum maximum width: 4.85–6 mm (mean: 5.30; n = 6); head maximum width: 4.7–6.1 mm (mean: 5.37; n = 6); elytra length: 6.2–11.1 mm (mean: 9.30 mm; n = 6). There is a little morphological variability.

Fig. 6. Upper central: selected landmarks (red dots) in the pronotum (dorsal side) used in this study. Upper sides: deformation grids showing extremes of shape variation represented by *L. cavensis* (Petagna, 1819) (left) and *L. variegatus* (Donovan, 1793) (right). Below: Principal Component Analysis of pronotum shape among the three species of *Lampromeloe* Reitter, 1911. Empty red dots represent specimens of *L. pantherinus* sp. nov., empty blue dots *L. variegatus*, and empty green dots *L. cavensis*. 
between the studied specimens (Figs 3–4, 6–7), such as the extension of both dark purple and green metallic hues over the head and pronotum (Fig. 3). The variability of the pronotum shape is shown in Fig. 6.

Comparisons

Lampromeloe pantherinus sp. nov. can be diagnosed from its sister species L. variegatus by the medium-sized and glossy elytral areolas, which are separated by a rugose and radiate space (similar to L. cavensis, but in general with closer and smaller areolas in L. pantherinus), whereas in L. variegatus it is formed by very small areolas or tubercles, shiny only on top (Fig. 4). Pronotum of L. pantherinus (Figs 3, 6) similar to L. variegatus; no differences were found in the GM analysis (Fig. 6). Male genitalia show significant differences between these species: gonostyli are narrower and more converging towards the apex in L. pantherinus, with their distal portions on either side of the apical notch (which is shorter and wider in L. variegatus; Fig. 5B), narrower, longer, and markedly more converging in L. pantherinus; the gonocoxal plate clearly more elongated and narrow in dorsal view in L. variegatus; and the aedeagus with ventral hooks more robust and closer to each other and to the apex in the latter species (Fig. 5).

Lampromeloe pantherinus sp. nov. differs from L. cavensis in the morphology and macro-sculpture of the pronotum, markedly more transverse in L. pantherinus (similar to L. variegatus), lacking the marked entire median longitudinal depression characteristic of L. cavensis (Fig. 2). It also differs from L. cavensis in the smaller size of the punctures over the head and pronotum, the usually smaller areolas in L. pantherinus, and in the male genitalia, with gonostyli wider in dorsal and lateral view and gonocoxal plate distinctly wider and shorter in L. pantherinus, distal hooks of the aedeagus more separated from each other and closer to the apex in L. pantherinus (see Fig. 5, and Bologna 1991: 368, fig. 128e–f).

According to the original description, L. variegatus mandzhuricus is characterized by the body colouration and the pronotum shape (Pliginskij 1930). Lampromeloe pantherinus sp. nov. and L. v. variegatus present green hues in the central areas of the head and pronotum, which are totally cupreous or reddish in L. v. mandzhuricus. The pronotum macrosculpture in L. v. mandzhuricus differs from that of L. v. variegatus and L. pantherinus since it includes a deep mid-longitudinal depression in the first, much shallower in the other two taxa. In addition, L. pantherinus presents well-marked lateral depressions, especially in the anterior half of the pronotum, which are absent in L. v. mandzhuricus. Lampromeloe
pantherinus can also be differentiated from L. v. mandzhuricus by the elytral macrosculpture, which in L. v. mandzhuricus is similar to that of L. v. variegatus.

*Lampromeloe stellatus* (Fig. 8) is morphologically similar to *L. cavensis*. Thus, most of the aforementioned diagnostic traits used to differentiate *L. pantherinus* sp. nov. from *L. cavensis* are also valid for distinguishing from *L. stellatus* (morphology and macro-sculpture of the pronotum, size of punctures over the head and pronotum, and size of the elytral areolas).

It is necessary to study in detail the central Italian populations of *L. variegatus* (very scarce if not extinct; see Bologna 1991: 367) to elucidate their taxonomic assignment, since specimens from these populations show an elytral sculpture pattern similar to that of *L. pantherinus*.

**Geographic distribution and notes on natural history and conservation**

*Lampromeloe pantherinus* sp. nov. has been found, to date, in the Atlas Mountains and adjacent areas (Northwestern Africa). Despite its relatively wide range, it is only known from scattered localities in Morocco, Algeria and Tunisia (Fig. 9), usually in high or medium altitude regions. Known records of the species are detailed in Table 2. The geographic range of this species remains tentative at this stage, as new studies are required to clarify the taxonomic status of the central Italian populations of *L. variegatus* (see Bologna 1991).

*Lampromeloe pantherinus* sp. nov. inhabits different types of open habitats (alpine grasslands, agricultural fields and forest edges) mostly on calcareous soils, from wetland surroundings with peatbog formations and close to forests of *Cedrus atlantica* (Endl.) Manetti ex Carrière, as at Aguelman Sidi-Ali (Middle Atlas) (Ruiz & Ávila 1994, sub *L. variegatus*) to drier and abruptly changing landscapes at Tizi

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**Fig. 8. Meloe stellata** Pliginskij, 1923, syntype (MNB). Photograph by AS-V.
n’Tichka (M. García-París and J.L. Ruiz pers. obs.) (Fig. 10) and Jbel Tsiwant (A. François pers. com.). The ombrotype of its geographic area of occupancy varies from sub-humid to humid, at bioclimatic levels from Meso- to Mountainous-Mediterranean (Benabid 1985; Le Houérou 1989).

Biological aspects of this species are expected to be similar to *L. variegatus* (Bologna 1991). The observations described by Cros (1941) for North African *Meloe variegatus* should be referred to *L. pantherinus* sp. nov. Adults are found from February to April, during day time (Fig. 11). Two specimens of the type series (MNCN_Ent 325513 and MNCN_Ent 325514) were found under shrubs of *Erinacea anthyllis* Link in the second half of February in Tizi n’Tichka; the paratype MNCN_Ent 325515 from El Hajeb (Central Middle Atlas) was found walking on an open grassland, near a ploughed field close to the road, in March; and the single specimen from Jbel Tsiwant (northeastern Middle Atlas) (ECWP 24078) (Table 2) was found on 20 February 2021 in a steppe on the margin of a dry river, dominated by *Stipa* L. However, adult activity seems to be related to altitudinal gradients and likely extends from February to the end of April or May in higher areas.

*Lampromeloe pantherinus* sp. nov. seems to be mainly associated with the montane climatic conditions prevailing in the medium-highlands of Morocco, Algeria, and Tunisia. Therefore, it could be considered
Nevertheless, the extreme scarcity of historical data including bibliographic records and specimens preserved in collections (that represent a useful tool to detect historical changes in the conservation status of taxa; e.g., Suarez & Tsutsui 2004; Grixti et al. 2009; Doadrio et al. 2019; Salvador & Cunha 2020), impedes the inference of population trends or variations in its area of occupancy (sensu IUCN 2001). However, the pronounced decline reported for other species of the genus, at least in the Iberian Peninsula, even with regional extinction events (García-París et al. 2006; García-París & Ruiz 2011; Prieto et al. 2016), and its smaller and possibly fragmented geographic range, suggest that L. pantherinus requires a detailed evaluation to determine its vulnerability to extinction. In any case, it is necessary to increase the prospective effort to determine its current area of occupancy, which is essential to carry out an evaluation of its threat status in accordance with the IUCN (2001) generalized use criteria.

Table 2. Known localities of Lampromeloe pantherinus sp. nov. Approximate geographic coordinates, altitude and annual precipitation compiled from bibliographic sources are also provided.

<table>
<thead>
<tr>
<th>Locality</th>
<th>Geographic coordinates</th>
<th>Altitude</th>
<th>Annual average rainfall</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Algeria: Mascara to Saint-Hippolyte (= Ain Toudman)</td>
<td>35°25’09.67″ N, 00°08’14.46″ E</td>
<td>666 m a.s.l.</td>
<td>181 mm</td>
<td>Cros 1941</td>
</tr>
<tr>
<td>Algeria: Saint-Hippolyte (= Ain Toudman) to Sidi Daho</td>
<td>35°26’32.28″ N, 00°10’09.45″ E</td>
<td>706 m a.s.l.</td>
<td>181 mm</td>
<td>Cros 1941</td>
</tr>
<tr>
<td>Algeria: Bab Ali</td>
<td>35°24’01″ N, 00°08’09″ E</td>
<td>614 m a.s.l.</td>
<td>181 mm</td>
<td>Cros 1941</td>
</tr>
<tr>
<td>Algeria: Batna</td>
<td>35°34’04.91″ N, 06°11’55.32″ E</td>
<td>1060 m a.s.l.</td>
<td>496 mm</td>
<td>This work</td>
</tr>
<tr>
<td>Tunisia: Le Kef</td>
<td>36°10’38.43″ N, 08°43’17.20″ E</td>
<td>600 m a.s.l.</td>
<td>348 mm</td>
<td>Cros 1941</td>
</tr>
<tr>
<td>Tunisia: Teboursouk</td>
<td>36°27’11.38″ N, 09°14’52.18″ E</td>
<td>500 m a.s.l.</td>
<td>572 mm</td>
<td>Bologna 1991</td>
</tr>
<tr>
<td>Morocco: Aguelmane Sidi-Ali, Middle Atlas</td>
<td>33°03’56.26″ N, 04°59’59.26″ W</td>
<td>2050 m a.s.l.</td>
<td>430 mm</td>
<td>Ruiz &amp; Ávila 1994</td>
</tr>
<tr>
<td>Morocco: Tizi n’Tichka, High Atlas</td>
<td>31°16’25.00″ N, 07°22’41.00″ W</td>
<td>2180 m a.s.l.</td>
<td>207 mm</td>
<td>This work</td>
</tr>
<tr>
<td>Morocco: Tizi n’Tichka, High Atlas</td>
<td>31°18’30.00″ N, 07°22’17.00″ W</td>
<td>2088 m a.s.l.</td>
<td>207 mm</td>
<td>Sánchez-Vialas et al. 2021</td>
</tr>
<tr>
<td>Morocco: El Hajeb, N Middle Atlas</td>
<td>33°38’14.70″ N, 05°22’22.25″ W</td>
<td>1230 m a.s.l.</td>
<td>128 mm</td>
<td>This work</td>
</tr>
<tr>
<td>Morocco: Jbel Tsiwant, Middle Atlas</td>
<td>33°19’47.09″ N, 04°03’43.02″ W</td>
<td>1929 m a.s.l.</td>
<td>294 mm</td>
<td>This work</td>
</tr>
<tr>
<td>Spain: Melilla, Rostrogordo</td>
<td>35°18’16.81″ N, 02°57’45.00″ W</td>
<td>65 m a.s.l.</td>
<td>393 mm</td>
<td>Pardo Alcaide 1950</td>
</tr>
</tbody>
</table>

a candidate for threatened species within the current global warming scenario (Malcolm et al. 2006). Nevertheless, the extreme scarcity of historical data including bibliographic records and specimens preserved in collections (that represent a useful tool to detect historical changes in the conservation status of taxa; e.g., Suarez & Tsutsui 2004; Grixti et al. 2009; Doadrio et al. 2019; Salvador & Cunha 2020), impedes the inference of population trends or variations in its area of occupancy (sensu IUCN 2001). However, the pronounced decline reported for other species of the genus, at least in the Iberian Peninsula, even with regional extinction events (García-París et al. 2006; García-París & Ruiz 2011; Prieto et al. 2016), and its smaller and possibly fragmented geographic range, suggest that L. pantherinus requires a detailed evaluation to determine its vulnerability to extinction. In any case, it is necessary to increase the prospective effort to determine its current area of occupancy, which is essential to carry out an evaluation of its threat status in accordance with the IUCN (2001) generalized use criteria.
Synonymy list of Lampromeloe

**Lampromeloe cavensis** (Petagna, 1819)

*Meloe cavensis* Petagna, 1819: 40. Terra typica: “... nella Cava, ... nella Collina vulgarmente detta Rotolo”.


*Meloe sardous* Gené, 1836: 38. Terra typica: “In Sardinia australiori...”.


*Meloe latreilli* Reiche in Marseul, 1867: 89 (replacement name for *M. aeneus* Laporte, 1840, non *Meloe aeneus* Tauscher, 1812).


**Lampromeloe pantherinus** Sánchez-Vialas, López-Estrada, Ruiz & García-Paris sp. nov.

*Lampromeloe pantherinus* Sánchez-Vialas, López-Estrada, Ruiz & Garcia-Paris sp. nov. Terra typica: “2 km north of Aguelmouse, Tizi n’Tichka, High Atlas, Morocco, 31°16’25”N, 7°22’41”W, 2180 m”.

**Lampromeloe variegatus** (Donovan, 1793)

*Lampromeloe variegatus variegatus* (Donovan, 1793)

*Meloe variegatus* Donovan, 1793: 81. Terra typica: “... distant parts of Kent, ...”.

Fig. 10. Surroundings of Tizi n’Tichka, Morocco. Type locality of *Lampromeloe pantherinus* sp. nov. Photograph by MG-P.
Meloe scabrosus Marsham, 1802: 483. Terra typica: not stated, but according the title of the work should be “Britannia”.
Meloe scabrosa Laporte, 1840: 278. Terra typica: “… le midi de l’Europe et même aux environs de Paris”.
Meloe variegatus var. cupreus Baudi, 1878: 354. Terra typica: “Hisp.”.
Meloe variegatus var. areolatus Reitter, 1895: 8. Terra typica: “Kaukasus: Araxesthal”.

Lampromeloe variegatus mandzhuricus (Pliginskij, 1930)
Meloe variegatus mandzhuricus Pliginskij, 1930: 110. Terra typica: “Manschurei, Charbin”.

Discussion
Phoretic blister beetles are known to disperse over long distances, including recurrent overseas dispersal events. For example, the Strait of Gibraltar (which separates the Iberian Peninsula from North Africa) has been crossed in relatively recent times by Eurymeloe mediterraneus (Müller, 1925) and by L. cavensis (Sánchez-Vialas et al. 2021). Lampromeloe variegatus and L. pantherinus sp. nov. present wide distribution ranges, especially L. variegatus, which extends across most of the Palaearctic, approximately 9000 km between the most distant populations (Heilongjiang, China, in the East and Salamanca, Spain, in the West; Garcia-Paris & Ruiz 2011). Although L. variegatus and L. pantherinus overlap in climatic requirements, and are geographically close, only separated by a known distance of

Fig. 11. Habitus of Moroccan living specimens of Lampromeloe. A–C. L. pantherinus sp. nov.
D. L. cavensis (Petagna, 1819). A–B. Holotype, ♂ (MNCN_Ent 325513) and paratype, ♀ (MNCN_Ent 325514) from Tizi n’Tichka. C. Paratype (ECWP 24078) from Jbel Tsiwant. D. Sidi Ifni. Photographs by MG-P (A–B), A. François (C), and AS-V (D).
480 km, their ranges remain allopatric, without detected evidence of discordances between nuclear and mtDNA markers nor gene flow between them.

However, phoresis in Lampro meloe can potentially drive genetic exchange across geographically distant populations. Cytochrome oxidase I similarity between distantly located Iberian and Hungarian populations, paralleled to recent findings in Anostraca G.O. Sars, 1867 (Rodriguez-Flores et al. 2017), suggests that a fast range expansion of L. variegatus across Eurasia took place recently, probably during more favourable climatic periods in the Pleistocene, following the ice retreat from the steppe areas (Ursenbacher et al. 2006), where the optimal conditions for this species now occur (Bologna 1991). In this sense, if L. variegatus is able to experience a fast range expansion at large geographic scales, how could L. variegatus and L. pantherinus sp. nov. remain allopatric? Some hypotheses on this subject can be debated. A first one is that these species did not undergo oversea dispersal and remained geographically isolated since their divergence. This hypothesis is unlikely because according to our genetic data, another species of Lampro meloe, L. cavensis, was able to cross the Strait in recent times (Sánchez-Vialas et al. 2021). Possible alternatives involve recurrent dispersal events of L. variegatus and L. pantherinus across the Mediterranean Sea. If reproductive isolation between them was fully completed, a process of competitive exclusion could be expected, resulting in the prevalence of L. pantherinus in Northern Africa and L. variegatus in Europe. However, if reproductive isolation was not so strong, the putative genetic exchange (not detected by us) following punctuated colonization events could be diluted by population density processes (Waters et al. 2013) or hybrid unfitness (Arntzen & Hedlund 1990; Larson et al. 2014). Waters et al. (2013) proposed a principle of spatial biodiversity structuration based on what they called “founder takes all” (first populations in colonizing territories), in which density-dependent processes play a key role. Within this framework, populations can expand their range into territories unoccupied by similar congenerics or conspecifics; however, if the territories are already occupied, population density processes prevent colonization by latecomers (Waters et al. 2013). This could be the case for L. variegatus and L. pantherinus, which have expanded their ranges widely across Eurasia and North Africa, respectively, but have been unable to colonize territories already occupied by either of them.

The Atlas Mountains where L. pantherinus sp. nov. is largely present, occupy a vast area in the Maghreb, extending from Morocco to Tunisia through Algeria, with a maximum of 4167 m of altitude (Jbel Toubkal, Morocco). This mountain system arose as a consequence of a tectonic uplift around the mid to late Miocene (Gómez et al. 2000). As suggested by Sánchez-Vialas et al. (2021), the split between L. pantherinus and L. variegatus took place around the Pliocene (4.1 Ma, 95% HDP: 2–6.9 Ma), after the uplift of the Atlas Mountains. This period was characterized by drastic changes in habitat conformations (e.g., spreading of grasslands and open fields) influenced by a cooler and drier climate (deMenocal 1995; Zhang et al. 2014). In North Africa, the Pliocene aridification strongly shaped the distribution and evolution of many taxa (deMenocal 2004; Rosado et al. 2017), which could be the case for L. pantherinus, currently limited to the main mountain range and its surroundings where adequate ecological conditions persist.

Future studies should focus on elucidating the taxonomic placement of the central Italian populations of L. variegatus, which as noted by Bologna (1991: 367), show an elytral sculpture similar to that of L. pantherinus sp. nov. Similarly, the Asian populations of L. variegatus, including those of L. variegatus mandzhuricus, are in need of revision. Although Lampro meloe stellatus is currently considered a synonym of L. cavensis (Bologna 1991, 2008, 2020; Gahari & Campos-Soldini 2019), the absence of molecular data together with the finding of a first instar larva of an unknown species of Lampro meloe from Iran (Di Giulio et al. 2014), precisely the country where the terra typica of L. stellatus is located, leave its taxonomic status uncertain.
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