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Taxonomy of West-Palaearctic *Lampromeloe* (Coleoptera: Meloidae) with the description of a new species

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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.

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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-Miguéns *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 Palaearctic 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.

Lampromeloe cavensis is widespread around the Mediterranean basin, ranging from Portugal and Morocco in the West to Iran in the East (Bologna 1991, 1994, 2020; Ghahari & Campos-Soldini 2019). *Lampromeloe variegatus* presents an even wider distribution with two subspecies recognized, *L. v. variegatus* extended throughout Eurasia (from the Iberian Peninsula to East Siberia and northeastern China) and northwestern Africa (Cros 1941; Bologna 1991, 1994, 2008, 2020; Ruiz & Ávila 1994), and *L. v. mandzhuricus* (Pliginskij, 1930) restricted to the Chinese province of Heilongjiang (Pliginskij 1930; Bologna 2008, 2020).

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 Gyllenhal, 1810 based on molecular data found two distinct lineages within

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 García-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-landmark 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

ECWP	=	Emirates Center for WildLife Propagation, Missour, Morocco
MCNB	=	Museu de Ciències Naturals de Barcelona, Barcelona, Spain
MNB	=	Museum für Naturkunde, Berlin, Germany
MNCN-CSIC	=	Museo Nacional de Ciencias Naturales, Madrid, Spain

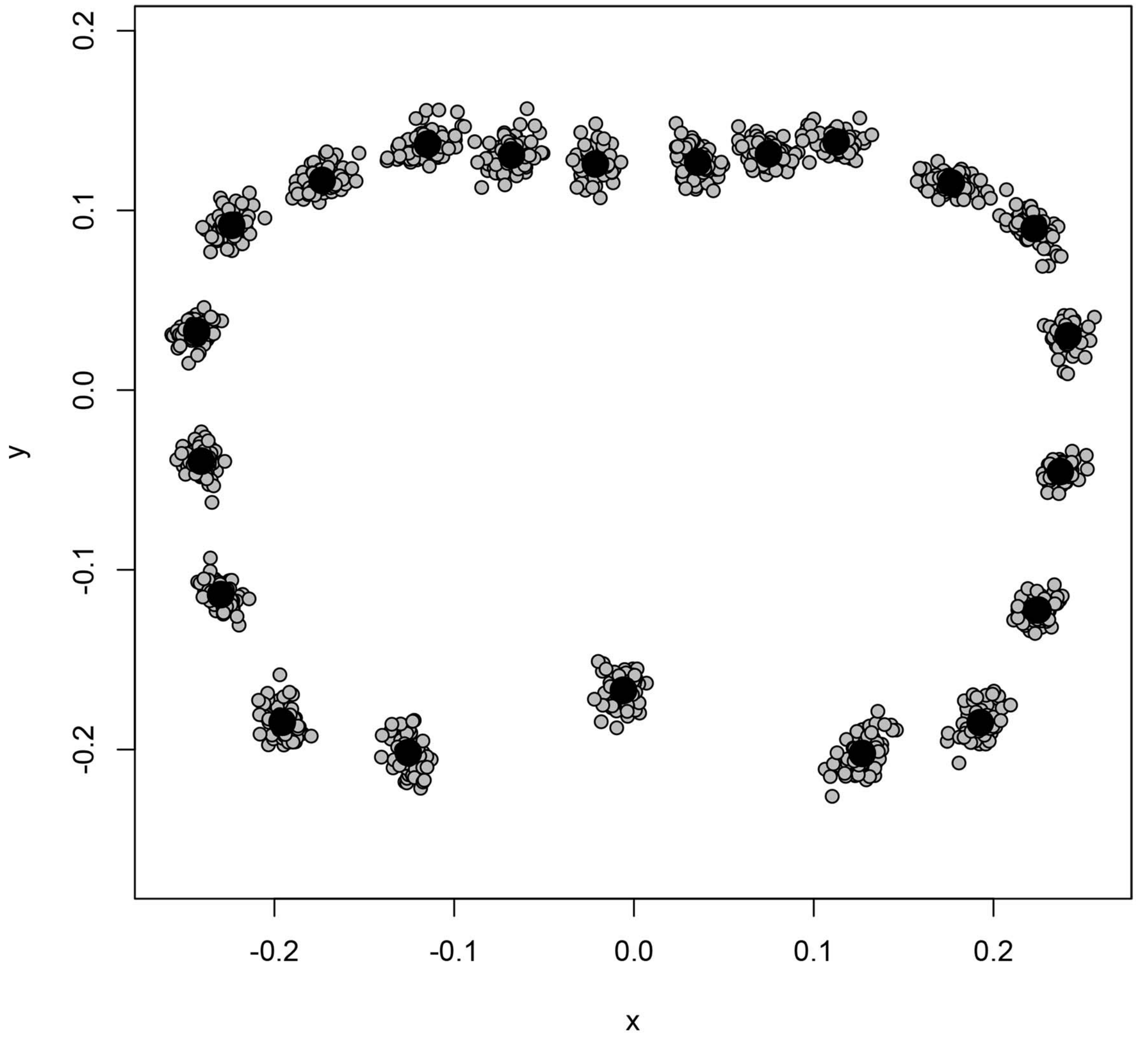

Fig. 1. Landmark configurations of the 74 specimens examined of *Lampromeloe* Reitter, 1911 after generalized Procrustes superimposition analysis. For each landmark, the black dot indicates the average shape, and grey dots represent the locations of each specimen.

DNA extraction, sequencing, sequence alignment, and phylogenetic analyses

The molecular study includes a total of 19 samples of *Lampromeloe*: 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_2O, 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 10×10^6 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.

Species	Locality	Voucher number	CoxI	16S	CAD
L. variegatus	Spain: Salamanca: 5 km NW of Palencia de Negrilla	mel 04076	ON454990		
L. variegatus	Spain: Salamanca: 4 km NW of Palencia de Negrilla	mel 04078	ON454992		
L. variegatus	Spain: Salamanca: Palencia de Negrilla	mel 05013	ON454989	ON455125	
L. variegatus	Spain: Salamanca: 5 km W of Palencia de Negrilla	mel 05014	ON454993	ON455126	
L. variegatus	Spain: Salamanca: 5 km W of Palencia de Negrilla	mel 05015	MW158203	MW158034	
L. variegatus	Spain: Salamanca: 2 km NW of Tardáguila	mel 05016	ON454995		
L. variegatus	Spain: Salamanca: 6 km SW of Topas	mel 05017	ON454991		
L. variegatus	Spain: Ávila: Fuente el Sauz	mel 11003	ON454994	ON455127	
L. variegatus	Hungary: Komárom-Esztergom: Vèrtesszölös	mel 81068	MW158204	MW158035	OQ872386
L. cavensis	Morocco: Casablanca-Settat: Mohammedia	mel 06011	MW158201	MW158032	
L. cavensis	Morocco: Casablanca-Settat: Mohammedia	mel 06012	ON454984	ON455122	
L. cavensis	Spain: Jaén: Linares	mel 81029	ON454986	ON455124	
L. cavensis	Morocco: Casablanca-Settat: Ben Slimane-el Hadida	mel 81043	ON454985	ON455123	
L. cavensis	Morocco: Casablanca-Settat: Ben Slimane-el Hadida	mel 81044	ON454987		
L. cavensis	Morocco: Casablanca-Settat: Ben Slimane-el Hadida	mel 81045	ON454988		
L. cavensis	Morocco: Guelmim-Oued Noun: Sidi Ifni	ASV2210			OQ872385
L. pantherinus sp. nov.	Morocco: Marrakesh-Safi: 5.5 km NE of Aguelmouse, Tizi n'Tichka, High Atlas	mel 81010	MW158202	MW158033	
L. pantherinus sp. nov.	Morocco: Marrakesh-Safi: 2 km N of Aguelmouse, Tizi n'Tichka, High Atlas	mel 81011	ON454996		
L. pantherinus sp. nov.	Morocco: Fez-Mequinez: Aïn Zelfane: Jbel Tsiwant	ASV2100	ON454997	ON455128	OQ872384

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.

SPAIN – **Andalucía: Sevilla** • 9 exx.; Zapater leg.; MNCN_Ent 76618, 255397 to 255400, 255429, 255430, 255440, 255441. – **Granada** • 1 ex.; Granada; Apr. 1901; M. Escalera leg.; MNCN_Ent 255405 • 1 ex.; Granada; M. Escalera leg.; MNCN_Ent 255404 • 1 ex.; Granada; MNCN_Ent 255406 • 1 ex.; Limones; MNCN_Ent 255407. – **Huelva** • 1 ex.; La Palma; Antonio leg.; MNCN_Ent 255408. – **Jaén** • 1 ex.; Baeza; MNCN_Ent 255409 • 4 ex.; Baeza; Dantin leg.; MNCN_Ent 255410 to 255413 • 1 ex.; Sierra de Cazorla; Dantin leg.; MNCN_Ent 255414. – **Málaga** • 2 exx.; Torremolinos; J. Ardois leg.; MNCN_Ent 255431, 255432 • 1 ex.; Vivero; Vazquez leg.; MNCN_Ent 255433. – **Almería** • 1 ex.; Jan. 1926; M. Escalera leg.; MNCN_Ent 255401 • 1 ex.; Las Casillas de Atochares; 30 Mar. 2008; E. Recuero and C. Settani leg.; MNCN_Ent 255451. – **Cádiz** • 2 exx.; Jérez; 1916; Fernández leg; MNCN_Ent 255402, 255403 • 1 ex.; E. Pons leg.; MNCN_Ent 76616. – **Murcia** • 3 exx.; Cartagena; Sánchez Gómez leg.; MNCN_Ent 255434 to 255436 • 2 exx; Cartagena; M. Escalera leg.; MNCN_Ent 255437, 255438 • 1 ex.; Mazarrón; M. Escalera leg.; MNCN_Ent 255439. – **Comunidad Valenciana: Valencia** • 5 exx.; Benifayó; R. Aguilar leg.; MNCN_Ent 255444 to 255448 • 1 ex.; Alcira; Moróder leg.; MNCN_Ent 255443 • 1 ex.; 1886; Botanic Garden of Valencia; MNCN_Ent 255449. – **Comunidad de Madrid: Madrid** • 10 exx.; Madrid; C. Bolívar leg.; MNCN_Ent 255419 to 255428 • 1 ex.; Aranjuez; F. Arias leg.; MNCN_Ent 255415 • 1 ex.; Vía Vallecas; Lauffer leg.; MNCN_Ent 255418 • 1 ex.; Vía Vallecas; G. Carrasco leg.; MNCN_Ent 255417 • 1 ex; Cerro Grande, Vallecas; F. Bonet leg.; MNCN_Ent 255416. – **Castilla la Mancha: Albacete** • 1 ex.; Elche de la Sierra; MNCN_Ent 255450. – **Toledo** • 1 ex.; Cebolla; Naceiro leg.; MNCN_Ent 255442. – **Balearic Islands: Mallorca** • 1 ex.; Aranda leg.; MNCN_Ent 76617. – **Ceuta** • 1 ex.; Benítez; 15 Dec. 1952; Ferrer Andreu leg.; MNCN_Ent 255452. – **Melilla** • 6 exx.; Dec. 1909; Arias leg.; MNCN_Ent 255266, 255268 to 255273 • 1 ex.; Rostrogordo; Feb. 1948; F. Codina leg.; MNCN_Ent 255276 • 1 ex.; Sidi-Guariach; Feb. 1950; F. Codina leg.; MNCN_Ent 255277 • 2 exx.; Sidi-Guariach; Dec. 1949; F. Codina leg.; MNCN_Ent 255278, 255279 • 1 ex.; Sidi-Guariach; Jan. 1950; F. Codina leg.; MNCN_Ent 255280.

Ethanol preserved specimens
MOROCCO – **Casablanca-Settat** • 3 exx.; El Jadida; 3 Feb. 2006; M. García-París and A. Machordom leg.; mel 81043 to mel 81045; MNCN • 2 exx.; Mohamedia; mel 06011, mel 06012; MNCN. – **Marrakech-**

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.; Montalbanejo; 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-París leg.; MNCN_Ent 31488 • 1 ex.; Negrilla; C. Escribano leg.; MNCN_Ent 31498 • 1 ex.; Palencia de Negrilla; 21 Apr. 2005; M. García-París 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.; Vèrtesszölös; 5 Apr. 2008; L. Somai and J. Nèdli leg.; mel 81068; MNCN.

SPAIN – **Castilla y León: Salamanca** • 1 ex.; 5 km W of Palencia de Negrilla; 8 May 2004; M. García-París leg.; mel 04076; MNCN • 3 exx.; 5 km W of Palencia de Negrilla; 16 Apr. 2005; M. García-París leg.; mel 05013 to mel 05015; MNCN • 1 ex.; 4 km W of Palencia de Negrilla; 8 May 2004; M. García-París leg; mel 04078; MNCN • 1 ex.; Tardáguila; 16 Apr. 2005; M. García-París leg.; mel 05016; MNCN • 1 ex.; Naharros de Valdunciel; 14 Apr. 2013; F.A. Montes leg.; MNCN • 1 ex.; Fuente Sauz; 31 Mar. 2011; F.A. Montes leg; mel 11003; MNCN • 1 ex.; 6 km SO of Topas; 16 Apr. 2005; M. García-París leg.; mel 05017; MNCN.

Phylogenetic relationships within Lampromeloe

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

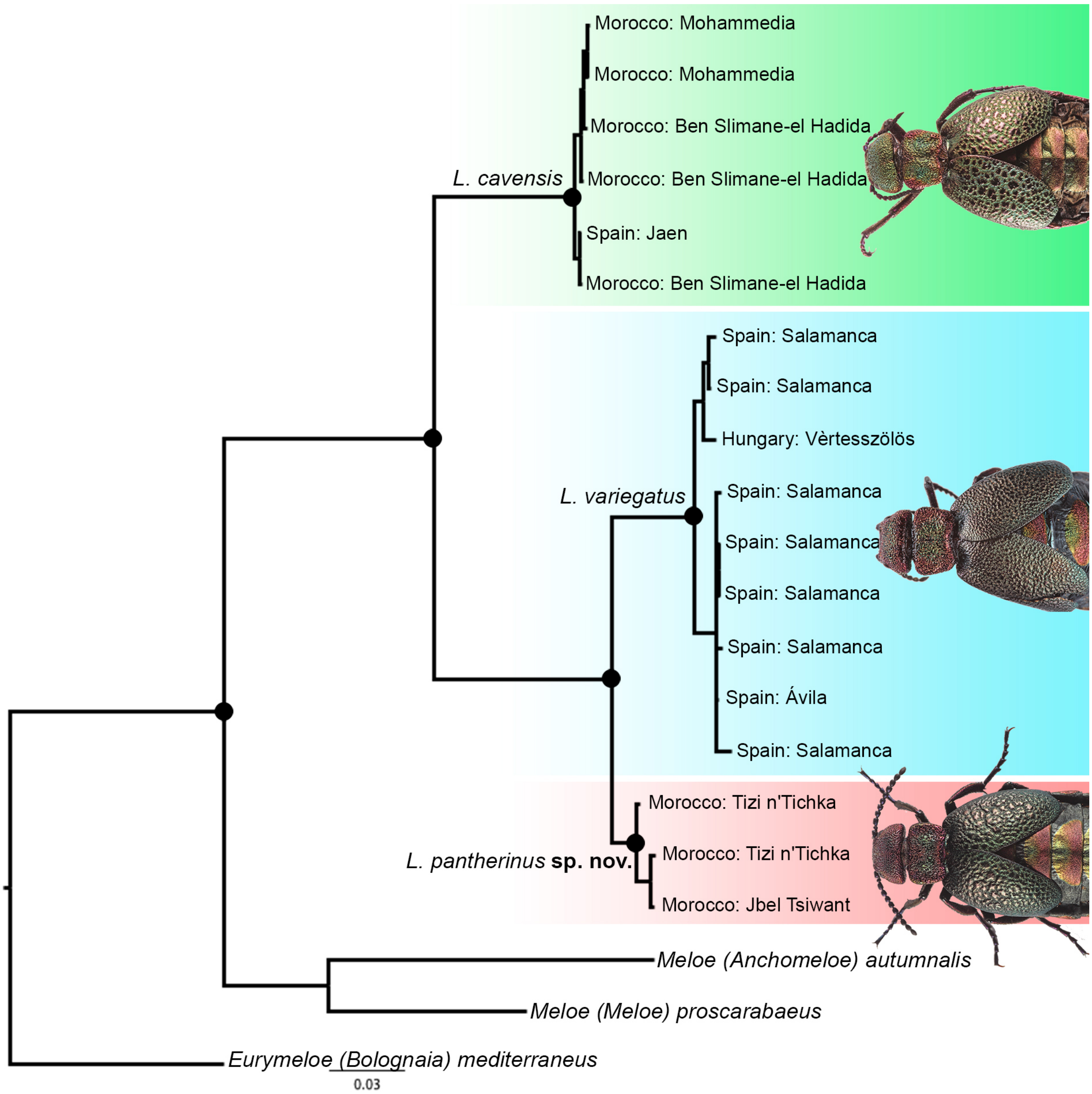

Fig. 2. Bayesian phylogenetic relationships based on mtDNA (*COI* and 16S) of the genus *Lampromeloe* Reitter, 1911. High bayesian posterior probabilities (>98%) are denoted by a dot on each corresponding node.

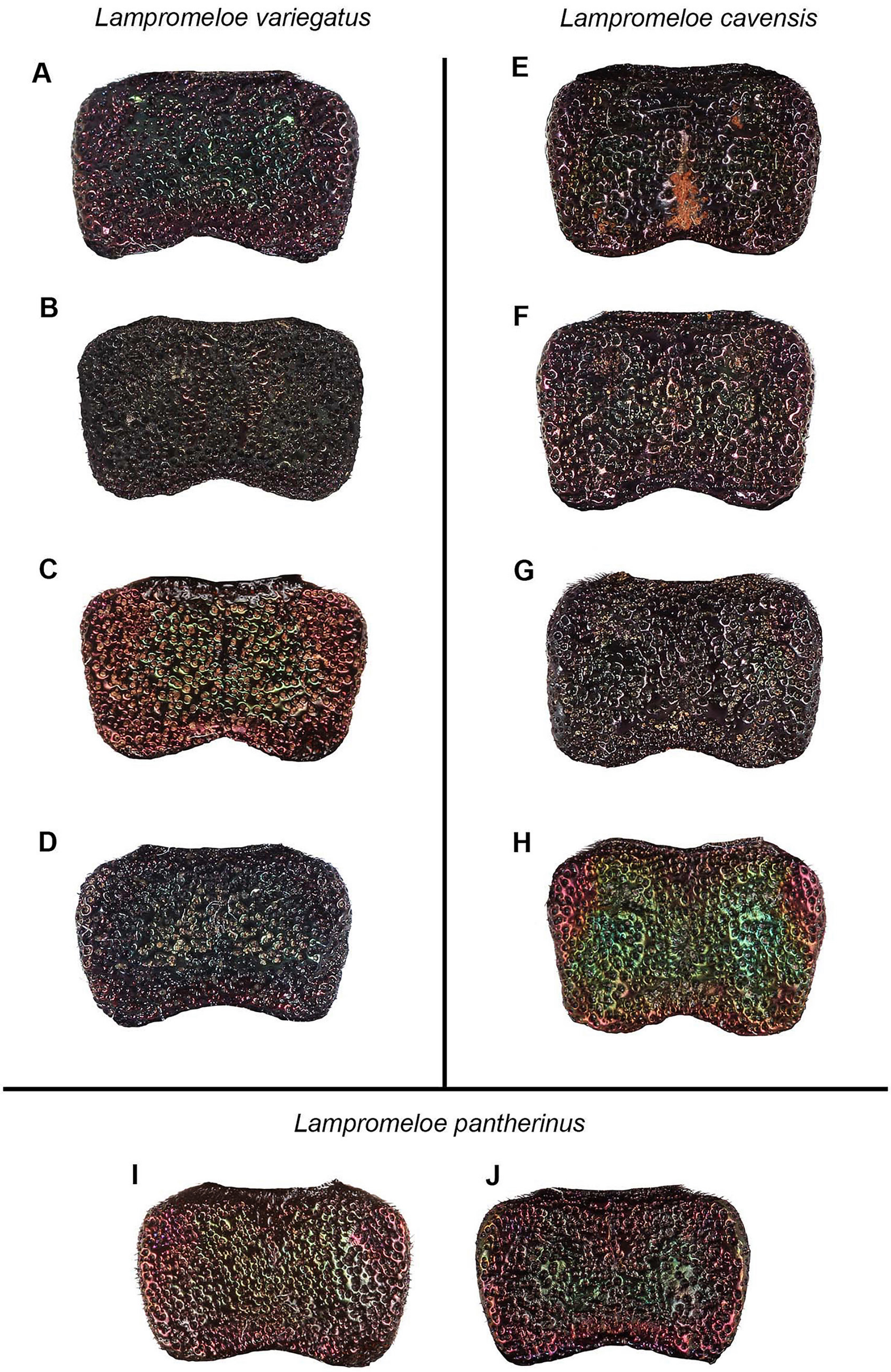

Fig. 3. Dorsal view of the pronotum. **A–D**. *Lampromeloe variegatus* (Donovan, 1793). **E–H**. *L. cavensis* (Petagna, 1819). **I–J**. *L. pantherinus* sp. nov. **A**. Tardáguila, Salamanca (Spain). **B**. Palencia de Negrilla, Salamanca (Spain). **C**. Fuente el Sauz, Ávila (Spain). **D**. Naharros de Valdeunciel, Salamanca (Spain). **E**. Ben Slimane (Morocco). **F–G**. Essaouira, Moulay Bouzerktoun (Morocco). **H**. Linares, Jaén (Spain). **I**. Holotype, ♂ (MNCN_Ent 325513) from Tizi n'Tichka (Morocco). **J**. Paratype, ♂ (MNCN_Ent 325515) from El Hajeb, Fès-Meknès region (Morocco). Photographs by AS-V.

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 Meloidae Gyllenhal, 1810
Genus *Lampromeloe* Reitter, 1911

Lampromeloe pantherinus sp. nov.

urn:lsid:zoobank.org:act:53F43B51-16B2-4B96-82C2-98BB583AD42E
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

MOROCCO • ♂; "2 km north of Aguelmouse, Tizi n'Tichka, High Atlas, Morocco, 31°16'25''N 7°22'41''W, 2180 m, 21-II-2010, M. García-París leg. // mel 81011 // MNCN_Ent 325513 // Holotypus *Lampromeloe pantherinus* Sánchez-Vialas, López-Estrada, Ruiz & García-París des. 2023" [white label, printed]; MNCN_Ent 325513. Preserved in absolute ethanol, stored in the Entomological collection of the MNCN-CSIC.

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.

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 semierect setae. Clypeus-frontal 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

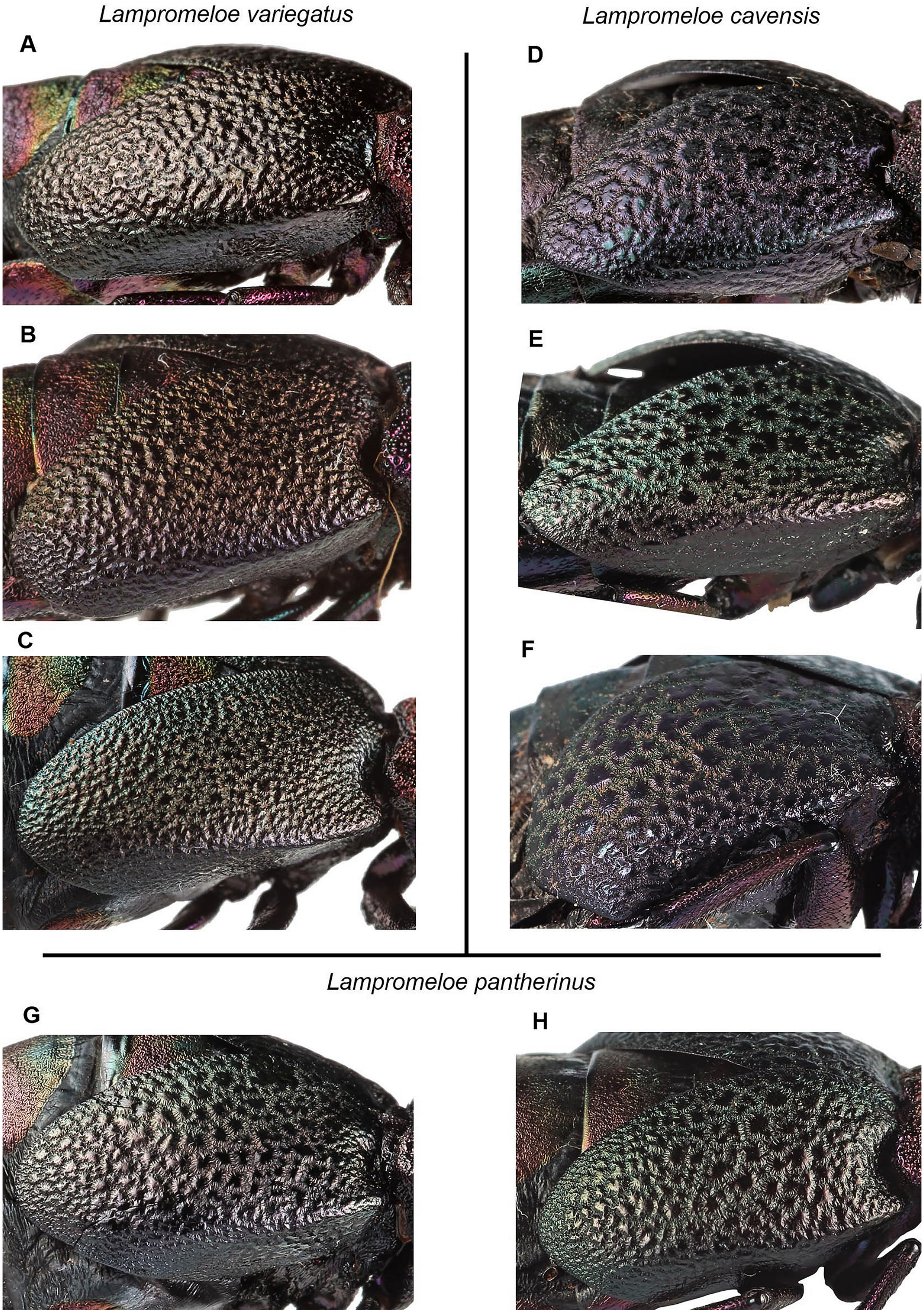

Fig. 4. Lateral view of the elytra. **A–C**. *Lampromeloe variegatus* (Donovan, 1793). **D–F**. *L. cavensis* (Petagna, 1819). **G–H**. *L. pantherinus* sp. nov. **A**. Vértesszőlős (Hungary). **B**. Topas, Salamanca (Spain). **C**. Fuente el Sauz, Ávila (Spain). **D**. Mohamedia (Morocco). **E**. Linares, Jaén (Spain). **F**. Ben Slimane (Morocco). **G**. Holotype, ♂ (MNCN_Ent 325513) from Tizi n'Tichka (Morocco). **H**. Paratype, ♂ (MNCN_Ent 325515) from El Hajeb (Morocco). Photographs by AS-V.

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 puncturation 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. Metafemur longer than metatibia (metafemur: 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 puncturation, 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). Gonostyli 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 ventrite 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

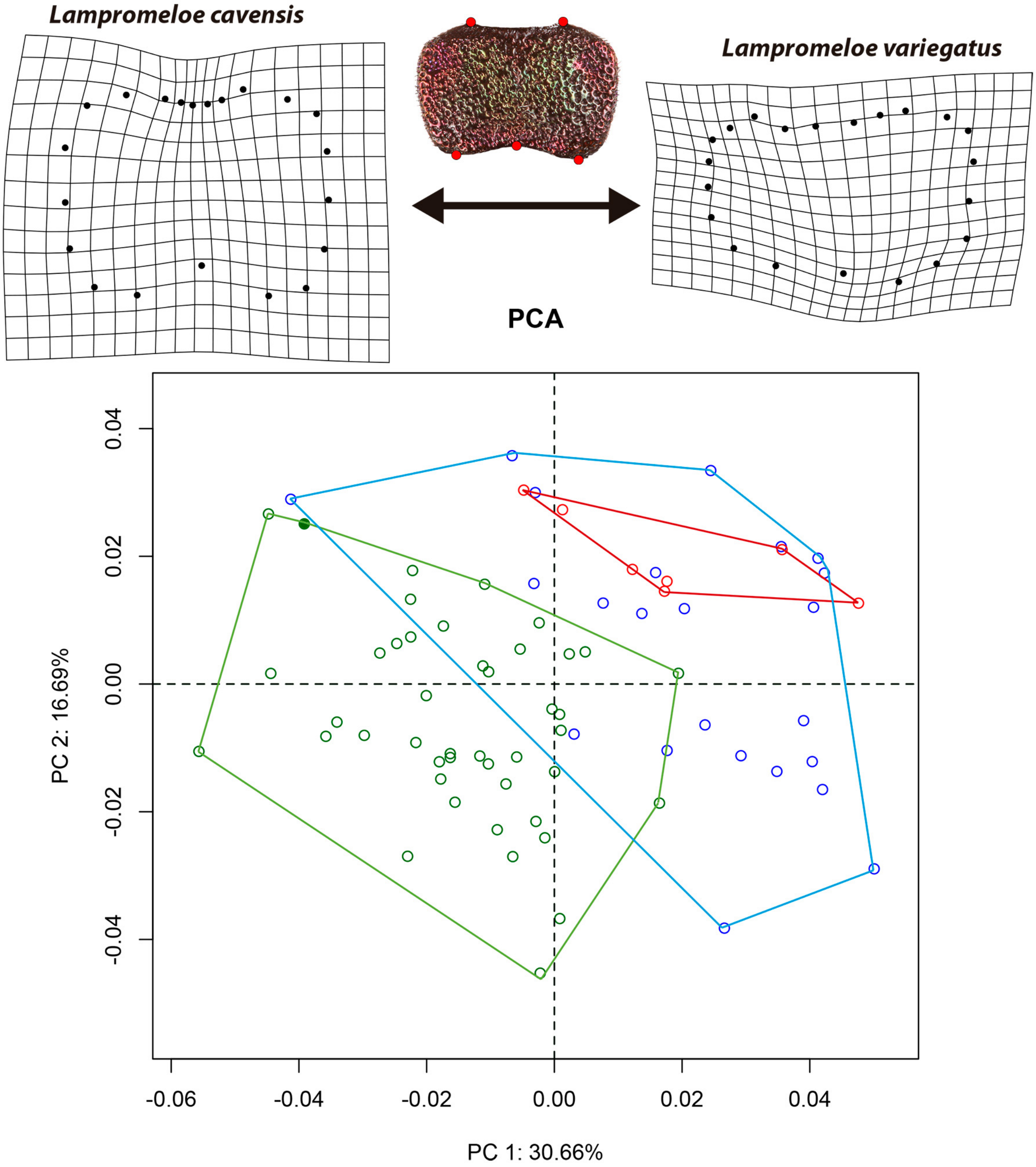

Fig. 6. Upper central: selected landmarks (red dots) in the pronotum (dorsal side) used in this study. Upper sides: deformation grids showing extremes of shape variation represented by *L. cavensis* (Petagna, 1819) (left) and *L. variegatus* (Donovan, 1793) (right). Below: Principal Component Analysis 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*

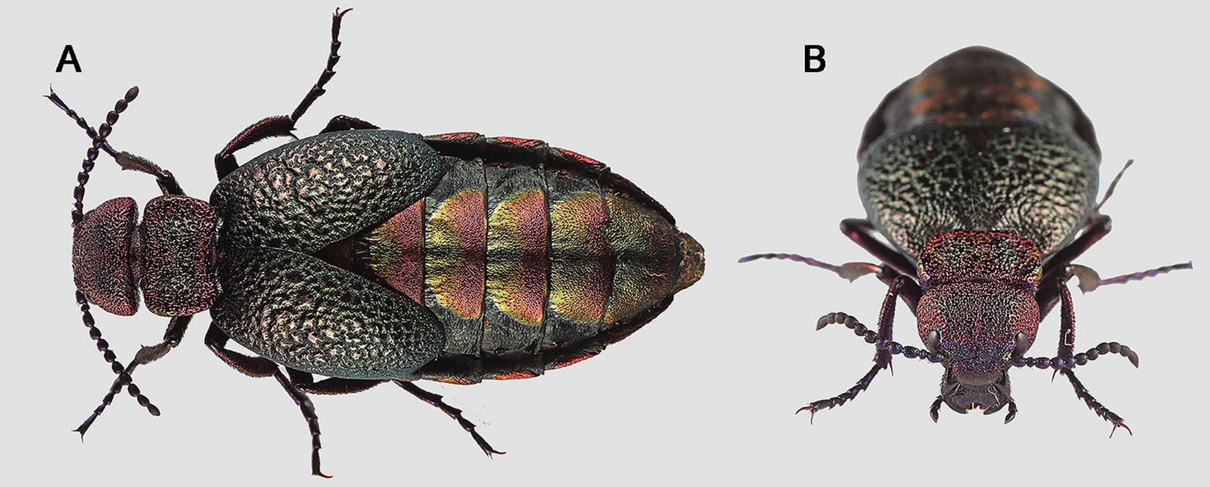

Fig. 7. *Lampromeloe pantherinus* sp. nov., paratype, ♂ (MNCN_Ent 325515) from El Hajeb, Morocco. **A**. Dorsal view. **B**. Frontal view. Photographs by AS-V.

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

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

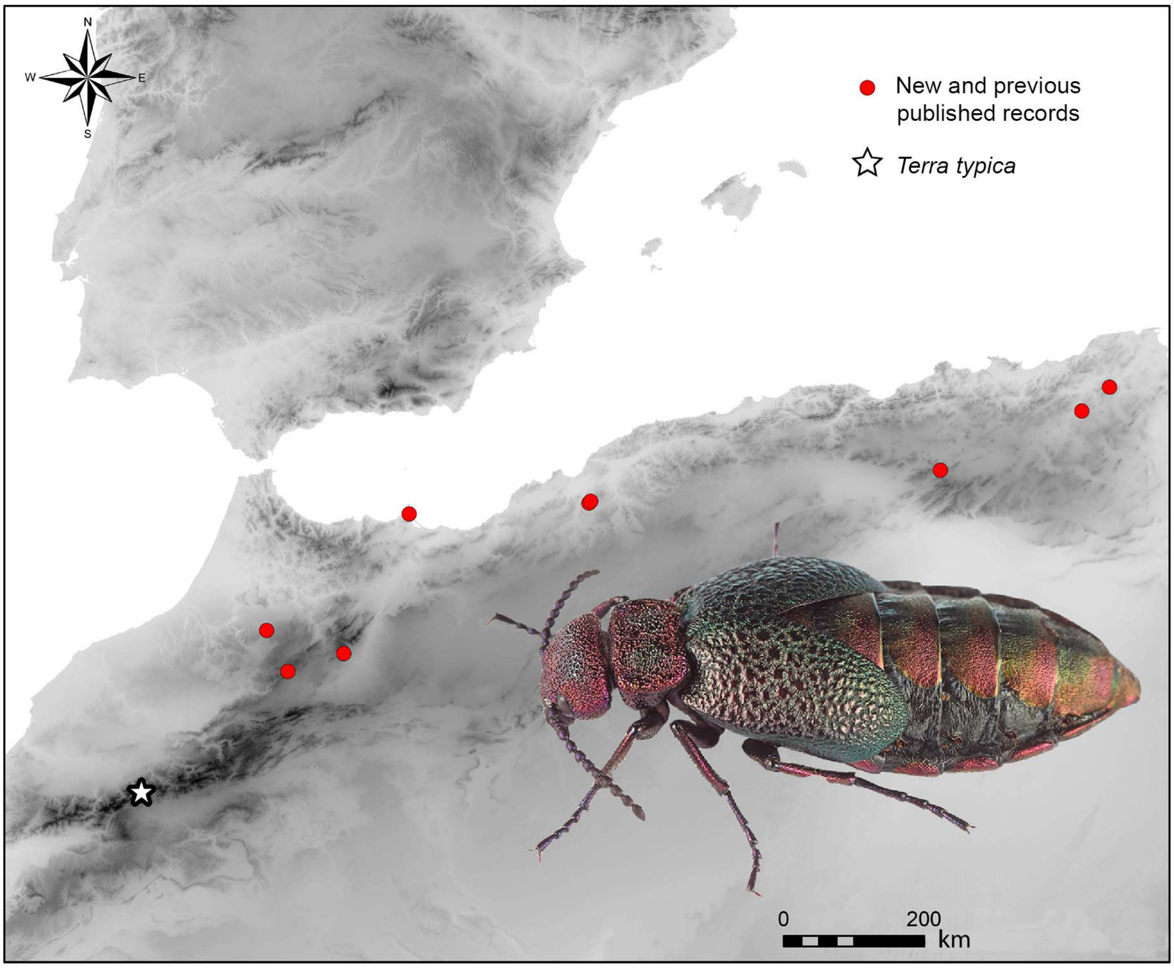

Fig. 9. Distribution of *Lampromeloe pantherinus* sp. nov. Known records and type locality are depicted by red dots and a white star, respectively.

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

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

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 purpurascens Germar, 1836: 12. Terra typica: "Turcia".
Meloe sardous Gené, 1836: 38. Terra typica: "In Sardinia australiori...".
Meloe aenea Laporte, 1840: 278. Terra typica: "Espagne".
Meloe latreillei Reiche in Marseul, 1867: 89 (replacement name for *M. aeneus* Laporte, 1840, non *Meloe aeneus* Tauscher, 1812).
Meloe specularis Gredler, 1877: 518. Terra typica: "Gondokoro" (doubtful assignment).
? *Meloe stellata* Pliginskij, 1923: 143. Terra typica: "Persia: Arabistan".

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

Lampromeloe pantherinus Sánchez-Vialas, López-Estrada, Ruiz & García-París 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; García-París & Ruiz 2011). Although *L. variegatus* and *L. pantherinus* overlap in climatic requirements, and are geographically close, only separated by a known distance of

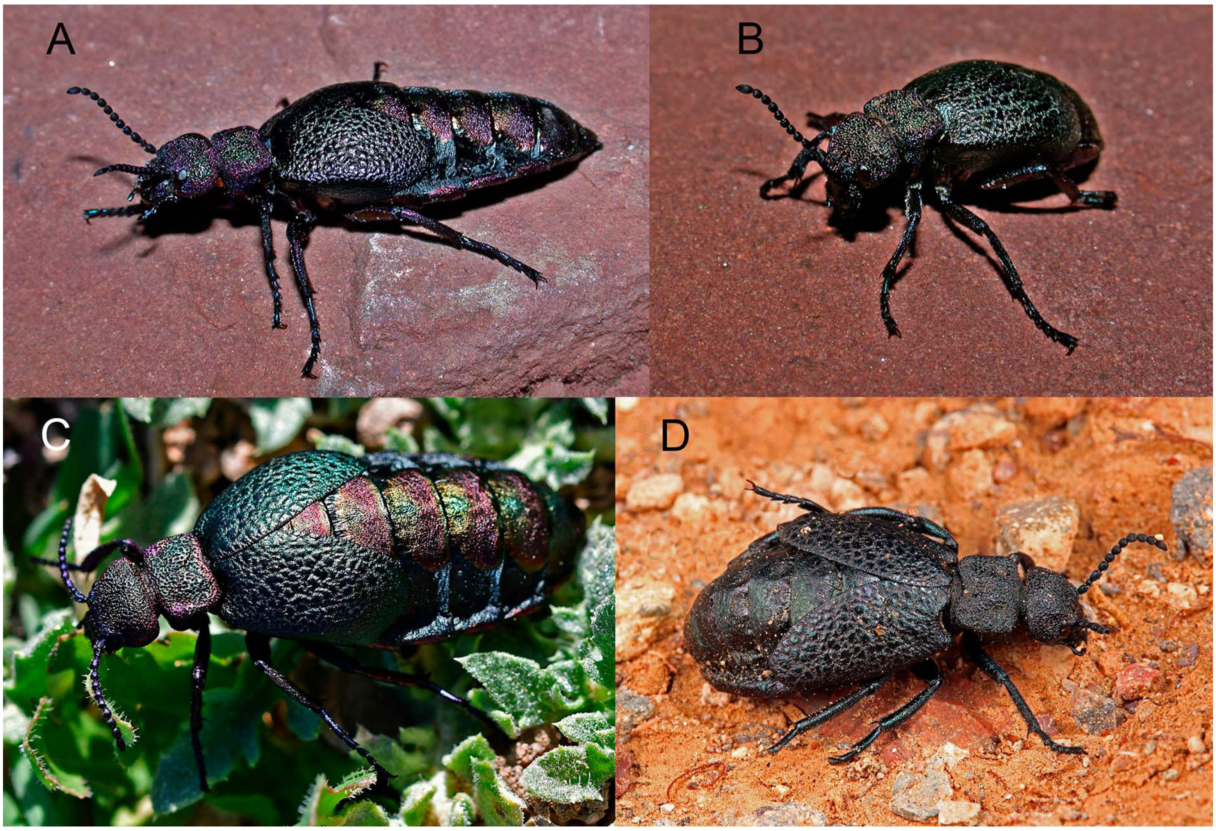

Fig. 11. Habitus of Moroccan living specimens of *Lampromeloe.* **A–C**. *L. pantherinus* sp. nov. **D**. *L. cavensis* (Petagna, 1819). **A–B**. Holotype, ♂ (MNCN_Ent 325513) and paratype, ♂ (MNCN_Ent 325514) from Tizi n'Tichka. **C**. Paratype (ECWP 24078) from Jbel Tsiwant. **D**. Sidi Ifni. Photographs 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 *Lampromeloe* 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 (Rodríguez-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 *Lampromeloe*, *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 *Lampromeloe stellatus* is currently considered a synonym of *L. cavensis* (Bologna 1991, 2008, 2020; Ghahari & Campos-Soldini 2019), the absence of molecular data together with the finding of a first instar larva of an unknown species of *Lampromeloe* 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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References

Aksentjev S.I. 1988. A catalogue of the genus-group taxa of the beetle family Meloidae (Coleoptera). *Entomologicheskoye Obozreniye* 67: 569–582. [In Russian.] [English translation published in *Entomological Review* 68 (3): 11–26.]

Arntzen J.W. & Hedlund L. 1990. Fecundity of the newts *Triturus cristatus*, *T. marmoratus* and their natural hybrids in relation to species coexistence. *Ecography* 13 (4): 325–332. https://doi.org/10.1111/j.1600-0587.1990.tb00625.x

Aulagnier S., Cuzin F. & Thévenot M. 2017. *Mammifères sauvages du Maroc. Peuplement, Repartition, Écologie.* Société française pour l'Étude et la Protection des Mammifères, Paris.

Barata M., Perera A., Martínez-Freiría F. & Harris D.J. 2012. Cryptic diversity within the Moroccan endemic day geckos *Quedenfeldtia* (Squamata: Gekkonidae): a multidisciplinary approach using genetic, morphological and ecological data. *Biological Journal of the Linnean Society* 106 (4): 828–850. https://doi.org/10.1111/j.1095-8312.2012.01903.x

Baudi F. 1878. Europaeae et circummediterraneae Faunae Heteromerum specierum, quae Comes Dejean in suo Catalogo, editio 3ª, consignavit, exejusden collectione in R. Taurinensi Musaeo asservata, cum auctorum hodierne recepta denominatione collatio. Pars sexta. *Deutsche Entomologische Zeitschrift* 22 (2): 337–376. Available from https://www.biodiversitylibrary.org/page/31169796 [accessed 13 Nov. 2023].

Benabid A. 1985. Les écosystèmes forestiers, préforestiers et presteppiques du Maroc: diversité, répartition biogéographique et problèmes posés par leur aménagement. *Forêt méditerranéenne* 7: 53–64.

Black S.A., Fellous A., Yamaguchi N. & Roberts D.L. 2013. Examining the extinction of the Barbary lion and its implications for felid conservation. *PLoS ONE* 8 (4): e60174. https://doi.org/10.1371/journal.pone.0060174

Bologna M.A. 1991. *Fauna de Italia. XXVIII. Coleoptera Meloidae*. Edizioni Calderini, Bologna.

Bologna M.A. 1994. I Meloidae della Grecia (Coleoptera). *Fragmenta Entomologica* 25 Supplemento: 1–119.

Bologna M.A. 2008. Meloidae. *In*: Löbl I. & Smetana A. (eds) *Catalogue of Palaearctic Coleoptera. Vol. 5. Tenebrionoidea*: 370–412. Apollo Books, Stenstrup.

Bologna M.A. 2020. Meloidae. *In*: Iwan D. & Löbl I. (eds) *Catalogue of Palaearctic Coleoptera. Vol. 5. Tenebrionoidea*: 500–562. Revised and updated 2nd Edition. Brill, Leiden.

Brito D. 2010. Overcoming the Linnean shortfall: data deficiency and biological survey priorities. *Basic and Applied Ecology* 11 (8): 709–713. https://doi.org/10.1016/j.baae.2010.09.007

Brown R.P., Suárez N.M. & Pestano J. 2002. The Atlas mountains as a biogeographical divide in North-West Africa: evidence from mtDNA evolution in the Agamid lizard *Agama impalearis*. *Molecular Phylogenetics and Evolution* 24 (2): 324–332. https://doi.org/10.1016/s1055-7903(02)00218-x

Casal-López M., Perea S., Yahyaoui A. & Doadrio I. 2015. Taxonomic review of the genus *Luciobarbus* Haeckel, 1843 (Actinopterygii, Cyprinidae) from Northwestern Morocco with the description of three new species. *Graellsia* 71 (2): e027. https://doi.org/10.3989/graellsia.2015.v71.135

Chatzimanolis S. 2014. Phylogeny of xanthopygine rove beetles (Coleoptera) based on six molecular loci. *Systematic Entomology* 39: 141–149. https://doi.org/10.1111/syen.12040

Cros A. 1929. Notes sur les larves primaires des Meloidae (3e Série). *Annales de la Société entomologique de France* 98: 193–222.

Cros A. 1941. Le *Meloe variegatus* Donovan. Sa présence dans le Nord de l'Afrique. Sa biologie. *EOS, Revista española de Entomología* 17: 313–334.
Available from http://hdl.handle.net/10261/147963 [accessed 13 Nov. 2023].

deMenocal P.B. 1995. Plio-Pleistocene African climate. *Science* 270: 53–59.
https://doi.org/10.1126/science.270.5233.5

deMenocal P.B. 2004. African climate change and faunal evolution during the Pliocene-Pleistocene. *Earth and Planetary Science Letters* 220 (1): 3–24. https://doi.org/10.1016/S0012-821X(04)00003-2

de Queiroz K. 1998. The general lineage, concept of species, species criteria, and the process of speciation. *In*: Howard D.J. & Berlocher S.H. (eds) *Endless Forms: Species and Speciation*: 57–75. Oxford University Press, Oxford, UK.

Di Giulio A., Carosi M., Khodaparast R. & Bologna M.A. 2014. Morphology of a new blister beetle (Coleoptera, Meloidae) larval type challenges the evolutionary trends of phoresy-related characters in the genus *Meloe*. *Entomologia* 2 (164): 69–79. https://doi.org/10.4081/entomologia.2014.164

Doadrio I., Perea S. & Yahyaoui A. 2015. Two new species of Atlantic trout (Actinopterygii, Salmonidae) from Morocco. *Graellsia* 71 (2): e031. https://doi.org/10.3989/graellsia.2015.v71.142

Doadrio I., Casal-López M., Perea S. & Yahyaoui A. 2016. Taxonomy of rheophilic *Luciobarbus* Haeckel, 1842 (Actinopterygii, Cyprinidae) from Morocco with the description of two new species. *Graellsia* 72 (1): e039. https://doi.org/10.3989/graellsia.2016.v72.153

Doadrio I., Araujo R. & Sánchez Almazán J.I. (eds) 2019. *Las Colecciones del Museo Nacional de Ciencias Naturales: Investigación y Patrimonio*. Consejo Superior de Investigaciones Científicas, Madrid.

Donovan E. 1793. *The Natural History of the British Insects; Explaining them in their Several States, with the Period of their Transformations, their Food, Oeconomy, &c. Together with the History of such Minute Insects as Require Investigations by the Microscope. The whole Illustrated by Coloured Figures Designed and Executed from Living Specimens. Vol. II.* Printed for the author and for F. and C. Rivington, London. https://doi.org/10.5962/bhl.title.39400

Folmer O., Black M., Hoeh W., Lutz R. & Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299.

Froufe E., Sousa P., Alves P.C. & Harris D.J. 2008. Genetic diversity within *Scorpio maurus* (Scorpiones: Scorpionidae) from Morocco: preliminary evidence based on CO1 mitochondrial DNA sequences. *Biologia* 63: 1157–1160. https://doi.org/10.2478/s11756-008-0176-y

García-París M. & Ruiz J.L. 2011. *Meloe* (*Lampromeloe*) *variegatus* Donovan, 1793. *In*: Verdú J.R., Numa C. & Galante E. (eds) *Atlas y Libro Rojo de los Invertebrados de España (Especies Vulnerables)*: 295–302. Dirección General de Medio Natural y Política Forestal, Ministerio de Medio Ambiente y Medio Rural y Marino.

García-París M., Good D.A., Parra-Olea G. & Wake D.B. 2000. Biodiversity of Costa Rican salamanders: implications of high levels of genetic differentiation and phylogeographic structure for species formation. *Proceedings of the National Academy of Sciences* 97 (4): 1640–1647.
https://doi.org/10.1073/pnas.97.4.1640

García-París M., Trotta-Moreu N. & Capote L. 2006. Estado de conocimiento actual y problemas de conservación de los Meloidae (Coleoptera) de la Comunidad de Madrid. *Graellsia* 62: 333–370.
https://doi.org/10.3989/graellsia.2006.v62.iExtra.123

García-París M., Ruiz J.L. & Alonso-Zarazaga M.A. 2010. Catálogo sinonímico de los táxones ibero-baleares de la familia Meloidae (Coloeptera). *Graellsia* 66: 165–212.
https://doi.org/10.3989/graellsia.2010.v66.018

Gené G. 1836. De quibusdam Insectis Sardiniae novisaut minus cognitis. Fasciculus I. *Memoralia Regiae Scientarum Academiae Taurinensis* 39: 1–39. https://doi.org/10.5962/bhl.title.8156

Germar E.F. 1836. *Fauna Insectorum Europae*. Fasciculus XVI. Car. Aug. Kummelii, Halle [Halae].

Ghahari H. & Campos Soldini M.P. 2019. An annotated catalogue of blister-beetles (Coleoptera: Tenebrionoidea: Meloidae) of Iran. *Entomofauna* 40/1 (5): 59–138.

Gómez A. & Lunt D.H. 2007. Refugia within refugia: patterns of phylogeographic concordance in the Iberian Peninsula. *In*: Weiss S. & Ferranz N. (eds) *Phylogeography of Southern European Refugia*: 155–188. Springer, Dordrecht.

Gómez F., Beauchamp W. & Barazangi M. 2000. Role of the Atlas Mountains (northwest Africa) within the African-Eurasian plate-boundary zone. *Geology* 28 (9): 775–778.
https://doi.org/10.1130/0091-7613(2000)28<775:ROTAMN>2.0.CO;2

González-Miguéns R., Nozal E., Jiménez-Ruiz Y., Más-Peinado P., Ghanavi H. & García-París M. 2020. Speciation patterns in the *Forficula auricularia* species complex: cryptic and not so cryptic taxa across the western Palaearctic region. *Zoological Journal of the Linnean Society* 190 (3): 788–823.
https://doi.org/10.1093/zoolinnean/zlaa070

Gower J.C. 1975. Generalized procrustes analysis. *Psychometrika* 40: 33–50.
https://doi.org/10.1007/BF02291478

Gredler I.V.M. 1877. Zur Käfer-Fauna Central-Afrikas. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* 27: 501–522.
Available from https://www.biodiversitylibrary.org/page/26709348 [accessed 14 Nov. 2023].

Grixti J.C., Wong L.T., Cameron S.A. & Favret C. 2009. Decline of bumble bees (*Bombus*) in the North American Midwest. *Biological Conservation* 142 (1): 75–84.
https://doi.org/10.1016/j.biocon.2008.09.027

Gyllenhal L. 1810. *Insecta Suecica descripta, Classis I, Coleoptera sive Eleutherata*. Tomi I, Pars II. F.J. Leverentz, Scaris. https://doi.org/10.5962/bhl.title.8767

Hewitt G.M. 2011. Mediterranean Peninsulas: the evolution of hotspots. *In*: Zachos F.E. & Habel J.C. (eds) *Biodiversity Hotspots*: 123–148. Springer, Amsterdam.
https://doi.org/10.1007/978-3-642-20992-5_7

International Union for Conservation of Nature and Natural Resources (IUCN) 2001. *IUCN Red List Categories and Criteria: Version 3.1*. IUCN Species Survival Commision, Gland, Switzerland and Cambridge, UK. Available from https://portals.iucn.org/library/node/7977 [accessed 13 Dec. 2023].

Jaskuła R. 2015. The Maghreb – one more important biodiversity hot spot for tiger beetle fauna (Coleoptera, Carabidae, Cicindelinae) in the Mediterranean region. *ZooKeys* 482: 35–53.
https://doi.org/10.3897/zookeys.482.8831

Kaliontzopoulou A., Pinho C., Harris D.J. & Carretero M.A. 2011. When cryptic diversity blurs the picture: a cautionary tale from Iberian and North African *Podarcis* wall lizards. *Biological Journal of the Linnean Society* 103 (4): 779–800. https://doi.org/10.1111/j.1095-8312.2011.01703.x

Katoh K. & Toh H. 2008. Recent developments in the MAFFT multiple sequence alignment program. *Briefings in Bioinformatics* 9: 286–298. https://doi.org/10.1093/bib/bbn013

Kocher L. 1956. Catalogue commenté des Coléoptères du Maroc. V. Héteromères (Tenebrionides excepts). *Travaux de l'Institut scientifique chérifien (Série Zoologie)* 10: 1–107.

Korba J., Opatova V., Calatayud-Mascarell A., Enguídanos A., Bellvert A., Adrián S., Sánchez-Vialas A. & Arnedo M.A. 2022. Systematics and phylogeography of Western Mediterranean tarantulas (Araneae: Theraphosidae). *Zoological Journal of the Linnean Society* 196 (2): 845–884. https://doi.org/10.1093/zoolinnean/zlac042

Lansari A., Vences M., Hauswaldt S., Hendrix R., Donaire D., Bouazza A., Joger U., El Mouden E.A. & Slimani T. 2015. The Atlas Massif separates a northern and a southern mitochondrial haplotype group of North African water frogs *Pelophylax saharicus* (Anura: Ranidae) in Morocco. *Amphibia-Reptilia* 36 (4): 437–443. https://doi.org/10.1163/15685381-00003015

Laporte M.L.F. 1840. Histoire naturelle des insectes coléoptères. *In*: *Histoire naturelle des Animaux articulés. Annelides, Crustacés, Arachnides, Myriapodes et Insectes*. Vol. II. Duménil, Paris. https://doi.org/10.5962/bhl.title.47104

Larson E.L., White T.A., Ross C.L. & Harrison R.G. 2014. Gene flow and the maintenance of species boundaries. *Molecular Ecology* 23 (7): 1668–1678. https://doi.org/10.1111/mec.12601

Le Houérou H.N. 1989. Classification écoclimatique des zones arides (S.I.) de l'Afrique du Nord. *Ecologia Mediterranea* 15: 95–144.

Linnaeus C. 1758. *Systema Naturae per Regna tria Naturae, secundum Classes, Ordines, Genera, Species, cum characteribus, differentiis, synonymis, locis*. Ed. X. Vol. I. L. Salvii, Stockholm [Holmiae]. https://doi.org/10.5962/bhl.title.542

López-Estrada E.K., Sánchez-Vialas A., Manzanilla J., Piñango C., Ruiz J.L. & García-París M. 2022. An overview of the taxonomy and geographic distribution of Venezuelan *Epicauta* (Coleoptera: Meloidae). *Annales Zoologici* 72: 9–47. https://doi.org/10.3161/00034541ANZ2022.72.1.002

Machordom A., Araujo R., Erpenbeck D. & Ramos M.A. 2003. Phylogeography and conservation genetics of endangered European Margaritiferidae (Bivalvia: Unionoidea). *Biological Journal of the Linnean Society* 78: 235–252. https://doi.org/10.1046/j.1095-8312.2003.00158.x

Maddison W.P. & Maddison D.R. 2016. Mesquite: a modular system for evolutionary analysis. Version 3.04. Available from http://www.mesquiteproject.org [accessed 14 Nov. 2023].

Malcolm J.R., Liu C., Neilson R.P., Hansen L. & Hannah L.E.E. 2006. Global warming and extinctions of endemic species from biodiversity hotspots. *Conservation Biology* 20 (2): 538–548. https://doi.org/10.1111/j.1523-1739.2006.00364.x

Marsham T. 1802. *Coleoptera Britannica, sistens Insecta Coleoptera Britanniae indigena secundum methodum Linnaeanam disposita*. White, London. https://doi.org/10.5962/bhl.title.65388

Más-Peinado P., Buckley D., Ruiz J.L. & García-París M. 2018. Recurrent diversification patterns and taxonomic complexity in morphologically conservative ancient lineages of *Pimelia* (Coleoptera: Tenebrionidae). *Systematic Entomology* 43: 522–548. https://doi.org/10.1111/syen.12291

Metallinou M., Červenka J., Crochet P.A., Kratochvíl L., Wilms T., Geniez P., Shobrak M.Y., Brito J.C. & Carranza S. 2015. Species on the rocks: systematics and biogeography of the rock-dwelling

Ptyodactylus geckos (Squamata: Phyllodactylidae) in North Africa and Arabia. *Molecular Phylogenetics and Evolution* 85: 208–220. https://doi.org/10.1016/j.ympev.2015.02.010

Miralles A., Geniez P., Beddek M., Aranda D.M., Brito J.C., Leblois R. & Crochet P.A. 2020. Morphology and multilocus phylogeny of the Spiny-footed Lizard (*Acanthodactylus erythrurus*) complex reveal two new mountain species from the Moroccan Atlas. *Zootaxa* 4747 (2): 302–326. https://doi.org/10.11646/zootaxa.4747.2.4

Müller G. 1925. Sulle *Meloë* europee del grupo *rugosus*. *Studi Entomologici, Raccolta lavori entomologia sistematica* 1 (1): 21–25.

Myers N., Mittermeier R.A., Mittermeier C.G., Da Fonseca G.A. & Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403 (6772): 853–858. https://doi.org/10.1038/35002501

Olsen A.M. & Westneat M.W. 2015. StereoMorph: an R package for the collection of 3D landmarks and curves using a stereo camera set-up. *Methods in Ecology and Evolution* 6 (3): 351–356. https://doi.org/10.1111/2041-210X.12326

Pardo Alcaide A. 1950. *Contribución al Conocimiento de la Fauna Entomológica Marroquí. III*. Instituto General Franco, Publicaciones fuera de serie, Tetuán.

Percino-Daniel N., Buckley D. & García-París M. 2013. Pharmacological properties of blister beetles (Coleoptera: Meloidae) promoted their integration into the cultural heritage of native rural Spain as inferred by vernacular names diversity, traditions, and mitochondrial DNA. *Journal of Ethnopharmacology* 147: 570–583. https://doi.org/10.1016/j.jep.2013.03.037

Pérez-Moreno I., San Martín A.F. & Recalde J.I. 2003. Aportaciones corológicas y faunísticas sobre meloidos ibéricos (Coleoptera: Meloidae). *Boletín de la Sociedad entomológica aragonesa* 33: 195–217.

Petagna L. 1819. Memoria su di alcuni insetti del Regno di Napoli. *Memorie delle Accademia delle Scienze, Classe de Fisica e di Storia Naturale di Napoli* 1: 19–40.

Pleguezuelos J.M., Brito J.C., Fahd S., Feriche M., Mateo J.A., Moreno-Rueda G., Reques R. & Santos X. 2010. Setting conservation priorities for the Moroccan herpetofauna: the utility of regional red lists. *Oryx* 44 (4): 501–508. https://doi.org/10.1017/S0030605310000992

Pliginskij V.G. 1923. Espèces nouvelles des Coléoptères paléarctiques. *Revue russe d'Entomologie* [*Russkoe Entomologiceskoe Obozrenie*] 18: 141–143.

Pliginskij V.G. 1930. Zwei neue Meloiden-Formen (Coleoptera). *Revue russe d'Entomologie* [*Russkoe Entomologiceskoe Obozrenie*] 24: 109–110.

Prieto M., García-París M. & Masó G. 2016. La colección ibero-balear de Meloidae Gyllenhal, 1810 (Coleoptera, Tenebrionoidea) del Museu de Ciències Naturals de Barcelona. *Arxius de Miscel·lània Zoològica* 1: 117–216. https://doi.org/10.32800/amz.2016.14.0117

R Core Team 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.R-project.org/ [accessed 13 Nov. 2023].

Rankou H., Culham A., Jury S.L. & Christenhusz M.J. 2013. The endemic flora of Morocco. *Phytotaxa* 78 (1): 1–69. https://doi.org/10.11646/phytotaxa.78.1.1

Reiche L.J. 1867. *Meloe* Latreillei. *In*: Marseul S.A. de (ed.). *Catalogus Coleopterorum Europae et Confinium*. *L'Abeille, Journal d'Entomologie* 4: 1–131.

Reitter E. 1895. *Bestimmungs-Tabellen der europaïschen Coleopteren Meloidae. I Theil: Meloini. Vol. 32.* Verlag des Verfassers, Paskau.

Reitter E. 1911. *Fauna Germanica. Die Käfer des Deutschen Reiches. Nach der analytischen Methode bearbeitet. 3*. Lutz, Stuttgart.

Rodríguez-Flores P.C., Jiménez-Ruiz Y., Forró L., Vörös J. & García-París M. 2017. Non-congruent geographic patterns of genetic divergence across European species of *Branchinecta* (Anostraca: Branchinectidae). *Hydrobiologia* 801: 47–57. https://doi.org/10.1007/s10750-017-3266-4

Ronquist F., Teslenko M., van der Mark P., Ayres D.L., Darling A., Höhna S., Larget B., Liu L., Suchard L.A & Huelsenbeck J.P. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61 (3): 539–542. https://doi.org/10.1093/sysbio/sys029

Rosado D., Rato C., Salvi D. & Harris D.J. 2017. Evolutionary history of the Morocco lizard-fingered geckos of the *Saurodactylus brosseti* complex. *Evolutionary Biology* 44 (3): 386–400. https://doi.org/10.1007/s11692-017-9417-8

Ruiz J.L. & Ávila J.M. 1994. *Meloe* (*Lampromeloe*) *variegatus* Donovan, 1793 en el Medio Atlas marroquí (Coleoptera: Meloidae). *Boletín de la Asociación española de Entomología* 18 (3–4): 104.

Sánchez-Vialas A., García-París M., Ruiz J.L. & Recuero E. 2020. Patterns of morphological diversification in giant *Berberomeloe* blister beetles (Coleoptera: Meloidae) reveal an unexpected taxonomic diversity concordant with mtDNA phylogenetic structure. *Zoological Journal of the Linnean Society* 189 (4): 1249–1312. https://doi.org/10.1093/zoolinnean/zlz164

Sánchez-Vialas A., Recuero E., Jiménez-Ruiz Y., Ruiz J.L., Marí-Mena N. & García-París M. 2021. Phylogeny of Meloini blister beetles (Coleoptera, Meloidae) and patterns of island colonization in the Western Palaearctic. *Zoologica Scripta* 50 (3): 358–375. https://doi.org/10.1111/zsc.12474

Salvador R.B. & Cunha C.M. 2020. Natural history collections and the future legacy of ecological research. *Oecologia* 192 (3): 641–646. https://doi.org/10.1007/s00442-020-04620-0

Salvi D., Perera A., Sampaio F.L., Carranza S. & Harris D.J. 2018. Underground cryptic speciation within the Maghreb: multilocus phylogeography sheds light on the diversification of the checkerboard worm lizard *Trogonophis wiegmanni*. *Molecular Phylogenetics and Evolution* 120: 118–128. https://doi.org/10.1016/j.ympev.2017.11.013

Sars G.O. 1867. *Histoire naturelle des Crustacés d'eau douce de Norvège*. C. Johnsen, Oslo [Christiania].

Selander R.B. 1966. A classification of the genera and higher taxa of the Meloid subfamily Eleticinae (Coleoptera). *Canadian Entomologist* 98: 449–481. https://doi.org/10.4039/Ent98449-5

Simon C., Frat F., Beckenbach A., Crespi B., Liu H. & Flook P. 1994. Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America* 87: 651–701. https://doi.org/10.1093/aesa/87.6.651

Sousa P., Froufe E., Harris D.J., Alves P.C. & van der Meijden A. 2011. Genetic diversity of Maghrebian *Hottentotta* (Scorpiones: Buthidae) scorpions based on CO1: new insights on the genus phylogeny and distribution. *African Invertebrates* 52 (1): 135–143. https://doi.org/10.5733/afin.052.0106

Suarez A.V. & Tsutsui N.D. 2004. The value of museum collections for research and society. *BioScience* 54 (1): 66–74. https://doi.org/10.1641/0006-3568(2004)054[0066:TVOMCF]2.0.CO;2

Ursenbacher S., Carlsson M., Helfer V., Tegelström H. & Fumagalli L. 2006. Phylogeography and Pleistocene refugia of the adder (*Vipera berus*) as inferred from mitochondrial DNA sequence data. *Molecular Ecology* 15 (11): 3425–3437. https://doi.org/10.1111/j.1365-294X.2006.03031.x

Waters J.M., Fraser C.I. & Hewitt G.M. 2013. Founder takes all: density-dependent processes structure biodiversity. *Trends in Ecology & Evolution* 28 (2): 78–85. https://doi.org/10.1016/j.tree.2012.08.024

Wiens J., Parra-Olea G., García-París M. & Wake D.B. 2007. Phylogenetic history underlies elevational biodiversity patterns in tropical salamanders. *Proceedings of the Royal Society of London B* 274: 919–928. https://doi.org/10.1098/rspb.2006.0301

Wiley E.O. 1978. The evolutionary species concept reconsidered. *Systematic Zoology* 27: 17–26. https://doi.org/10.2307/2412809

Wiley E.O. & Mayden R.L. 2000. A critique from the evolutionary species concept perspective. *In*: Wheeler Q.D. & Meier R. (eds) *Species Concepts and Phylogenetic Theory: A Debate*. Columbia University Press.

Zhang Z., Ramstein G., Schuster M., Li C., Contoux C. & Yan Q. 2014. Aridification of the Sahara desert caused by Tethys Sea shrinkage during the Late Miocene. *Nature* 513 (7518): 401–404. https://doi.org/10.1038/nature13705

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