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Phylogeny of Meloini blister beetles (Coleoptera, Meloidae) and patterns of island colonization in the Western Palaearctic

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Abstract

Flightless, phoretic insects of the tribe Meloini include several widespread species able to inhabit both mainland and oceanic and continental islands. Relationships between phoretic and non-phoretic species of Meloini are unclear, precluding broad evolutionary and biogeographic analyses within the group. We provide a robust molecular phylogenetic framework for Meloini, with finer sampling in the Western Palaearctic, by analysing two nuclear (*Wg*, 18S) and two mtDNA (*cox1*, 16S) gene fragments of 24 species representing eight subgenera of *Meloe* and *Physomeloe*. Our phylogenetic analyses revealed that *Meloe*, as currently recognized, is paraphyletic. Our phylogenetic hypothesis clarifies several controversial relationships within the group. We provide a new taxonomic framework that better reflects the evolutionary relationships of the group by raising to genus all previously considered subgenera: *Afromeloe* Schmidt, 1913, *Alveomeloe* Pripisnova, 1987, *Chiromeloe* Reitter, 1911, *Desertimeloe* Kaszab, 1964, *Eurymeloe* Reitter, 1911, *Lampromeloe* Reitter, 1911, *Lasiomeloe* Reitter, 1911, *Listromeloe* Reitter, 1911, *Meloegonius* Reitter, 1911, *Mesomeloe* Reitter, 1911, *Meloenellus* Reitter, 1911, *Micromeloe* Reitter, 1911, *Taphromeloe* Reitter, 1911 and *Treiodous* Dugès, 1869; while *Anchomeloe* Iablokoff-Khnzorian, 1983, is recovered as subgenus of *Meloe*. In addition, we conducted an extensive intraspecific sampling for four phoretic taxa (*Meloe proscarabaeus*, *Meloe autumnalis*, *Eurymeloe mediterraneus* and *Eurymeloe tuccia*) and used mtDNA phylogeographic analyses to unveil patterns of overseas dispersal. Our phylogeographic analyses revealed a high level of geographically unstructured haplotype diversity within taxa, suggesting that transmarine dispersal events have occurred multiple times along the evolutionary history of phoretic species of blister beetles. Larval phoresy may explain the existence of idiosyncratic biogeographic and phylogeographic patterns in these flightless organisms.

KEYWORDS

Island colonization, overseas dispersal, palaearctic, phoresy, phylogeography, taxonomy

1 | INTRODUCTION

Island colonization and transoceanic dispersal are usually considered rare phenomena in terrestrial, non-flying animal groups, although the development of molecular phylogenetic techniques, including reliable methods to estimate lineage divergence dates, indicate a higher prevalence of transmarine dispersal events than traditionally thought (De Queiroz, 2005; Emerson, 2002; Sauer, 1969). In these cases, and given their overseas dispersal limitations, island populations usually remain isolated, which is reflected in the eventual differentiation of endemic evolutionary lineages and species (Gillespie & Roderick, 2002). A particular group of recognized successful long-distance dispersers are phoretic insects, some of which are non-flying species, such as the flightless blister beetles of the genus *Meloe* Linnaeus, 1758 (Coleoptera, Meloidae, Meloini). These beetles have been able to disperse overseas and effectively colonize islands, probably as first-instar larvae (triungulin) by travelling on flying bees (Apoidea) (Bologna, 1991; Bologna & Marangoni, 1990; Bologna & Pinto, 2001, 2002). They represent a particularly interesting case study: host bee populations must be settled on the island prior to any effective blister beetle colonization. *Meloe* species are, thus, not incipient colonizers but second wave invaders.

A set of geographic discontinuities in the Western Palaearctic (including the Canary Islands, the Balearic Islands and the continental gap between south-western Europe and north-western Africa) provides an ideal scenario for the study of transcontinental and island colonization by phoretic beetles. The volcanic Canary Islands, a well-studied oceanic archipelago, are separated from north-western Africa by a minimum distance of 110 km and from south-western Europe by about 1,000 km. By contrast, the Balearic Islands are separated from continental Europe by a minimum distance of 80 km and from north-western Africa by about 230 km. Additionally, dispersal of terrestrial organisms between Europe and Africa across the 14 km wide Strait of Gibraltar has been repeatedly reported (e.g. Gutiérrez-Rodríguez et al., 2017; Mas-Peinado et al., 2018; Recuero et al., 2007). Based exclusively on distribution records (Bologna & Marangoni, 1990), it seems that the colonization of the Canary or the Balearic Islands from continental Africa or Europe, and transcontinental dispersal across the Strait of Gibraltar, was possible for different lineages (species) along the evolutionary history of *Meloe*. Several species of *Meloe* inhabit different combinations of the four geographic units, for instance, the Canary Islands and continental Africa or continental Europe, or the Balearic Islands and continental Europe, without any evident intraspecific morphological differentiation (Bologna, 1991, 1994; Ruiz et al., 2010). However, other *Meloe* species show some degree of morphological differentiation across these geographic units, and some lineages are even morphologically diagnosable and endemic to one of these geographic units (Pardo Alcaide, 1951; Bologna, 1988, 1991, 1994, 2008; Ruiz & García-París, 2009, 2015; García-París et al., 2010). This array of possibilities allows for multiple comparisons across continental-island or transcontinental populations. Within this complex scenario, a multiscale phylogenetic/phylogeographic approach opens for the possibility of studying if observed patterns are the result of repeated colonization events, or alternatively, product of a single invasion followed by subsequent diversification. In addition, by identifying different levels of population isolation among lineages and species, we can evaluate the temporal framework and dispersal pattern of individual colonization events (Ribera et al., 2003).

Shared ancestry between a colonizer and its original source is necessary in order to determine the time elapsed since their isolation from one another (Emerson, 2002; Sanmartín et al., 2008). Intercontinental comparisons of genetic divergences, therefore, can only be made between sister species or among intraspecific lineages. *Meloe* is a highly diversified group of phoretic beetles comprised of around 155 species across 16 subgenera with a mainly Holarctic distribution (Bologna, 1991, 2008, 2020a; Bologna & Pinto, 2002; Pinto & Bologna, 1999). Hypotheses on the phylogenetic relationships among subgenera have not yet been proposed, and the taxonomic status of several subgenera remains controversial.

Mainly on the basis of larval morphology, Selander (1985, 1991) proposed a genus level characterization for some of the subgenera of *Meloe*, including *Lampromeloe* Reitter, 1911, *Afromeloe* Schmidt, 1913 and *Eurymeloe* Reitter, 1911. However, the generic treatment of these taxa was not followed by subsequent authors, who instead retained them as subgenera within a broad *Meloe sensu lato* (Bologna & Pinto, 1992; Bologna, 2008, 2020a). A deep revision of the systematics and internal phylogenetic structure of this group is needed in order to resolve relationships among the highly differentiated subgenera of *Meloe*, and their relationships with the closely related genus *Physomeloe* Reitter, 1911. *Physomeloe* includes a single non-phoretic species endemic to the Iberian Peninsula, *P. corallifer* (Germar, 1818). *Physomeloe* was initially described as a subgenus within *Meloe* (Reitter, 1911), but because of its non-phoretic larval characters, it was elevated to genus and transferred to the tribe Lyttini (Bologna & Aloisi, 1994). Later, it was transferred again to Meloini based on molecular data (Bologna et al., 2008).

Selander (1985, 1991), followed by Pinto and Bologna (1999), included tentatively in the tribe Meloini four poorly diversified New World genera: *Epispasta* Selander, 1960, *Lyttomeloe* Denier, 1920, *Spastomeloe* Selander, 1985 and *Spastonyx* Selander, 1954. But recent phylogenetic and anatomical works (Bologna & Pinto, 2001; Bologna & Di Giulio, 2011), demonstrated that the inclusion of these North and South American genera within the tribe Meloini was based only on homoplastic larval traits related to phoresy, and therefore unreliable to depict a monophyletic assemblage (Bologna & Pinto, 1992; Pinto & Bologna, 1999). Bologna and Pinto (2001: Appendix 7) removed the four American genera from the tribe, and as a result, the tribe Meloini was until the present work formed by two genera: the widespread and species rich genus *Meloe s. l.*, and the monotypic *Physomeloe* (the assignment of *Oreomeloe* Tan, 1981, to Meloini is very doubtful according to Bologna & Pinto, 2002 and Bologna, 2020a).

In this work, we propose a new molecular phylogenetic hypothesis on the relationships among lineages within *Meloe*, and conduct extensive phylogeographic analyses in four geographically widespread phoretic taxa to unveil patterns and timing of overseas dispersal. Our phylogeographic analyses revealed a high level of geographically unstructured haplotype diversity across taxa with a widespread distribution, suggesting that transmarine dispersal events have occurred multiple times along the evolutionary history of phoretic blister beetles. The main objectives are (1) to provide a first molecular phylogenetic reconstruction including multiple lineages within the genus *Meloe*, (2) to determine the timing of intraspecific colonization of islands or nearby continents in order to identify patterns and/or periods of high colonization success and (3) to discuss, in light of the newly proposed taxonomic framework, the relevance of some morphological characters that have been used previously to characterize lineages.

2 | MATERIAL AND METHODS

2.1 | Sampling and sequencing

A total of 163 ethanol-preserved specimens, corresponding to 23 species of *Meloe s. l.* (including 8 of the 16 currently recognized subgenera; see Bologna, 2008, 2020a; Bologna & Pinto, 2002) from the Western Palaearctic region (i.e. North Africa, Iberian, Italian and Arabian peninsulas, Central Europe and the Canary and Balearic Islands) and Central America (Figure 1; Table S1; geographic coordinates of sampling localities are shown in Table S2), were used for multilocus phylogenetic analyses (57 specimens) and phylogeographic analyses (108 specimens). We also included samples of *Physomeloe*, the only other genus included in the tribe Meloini. Additional representatives of the subfamily Meloinae were used as related outgroups for the phylogenetic analyses: *Cordylospasta fulleri* Horn, 1875 and *Phodaga alticeps* LeConte, 1858 (Eupomphini); and *Lytta vesicatoria* Linnaeus, 1758 (Lyttini). Polymerase chain reaction (PCR) was used to amplify fragments of two mitochondrial regions, cytochrome c oxidase I (*cox1*; 658 base pairs) and 16S ribosomal RNA (16S; 792 bp), and two nuclear regions, *Wingless* (*Wg*; 526 bp) and 18S ribosomal RNA (18S; 942 bp). We used the following set of primers: LCO1490 (Folmer et al., 1994) and COI-H (Machordom et al., 2003) for *cox1*; 16S-AR and 16S-ND1 (Simon et al., 1994) for 16S; wg1MP-F3 and wg1MP-R3 (Angelini & Jockusch, 2008) for *Wg*; 18Sai and 18Sbi (Whiting et al., 1997) for 18S. PCRs were performed in a total volume of 25 µl and included 17.5 µl of H_2O, 2.5 µl of a reaction buffer with $MgCl_2$ (3 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 DNA polymerase (1 unit, BioTools) and 2 µl of template DNA. The thermocycling conditions consisted of an initial step of denaturation at 96 ºC for 5 min (*cox1*, *Wg*, 18S) or for 3 min (16S) followed by 40 cycles of denaturation at 94 ºC for 30 s (*cox1*, 16S, 18S) or 1 min (*Wg*), annealing at 42 ºC for 45 s (*cox1*), 44 ºC for 1 min (16S), 48 ºC for 1 min (*Wg*) or 50 ºC for 45 s (18S), and extension at 72 ºC for 1 min (*cox1*, 16S, *Wg*) or 90 s (18S), and a final elongation step at 72 ºC for 5 min (*cox1*) or 10 min (16S, *Wg*, 18S). PCR products were checked on 1% agarose gels, and the products of expected length were directly sequenced at Macrogen Inc (Macrogen Europe).

2.2 | Sequence alignment, phylogenetic and coalescent analyses

Sequences were revised using Sequencher v.4.9 (Gene Code Corporation) and aligned with MAFFT (Katoh & Toh, 2008). Final alignments were visually inspected with Mesquite v.3.04 (http://mesquiteproject.org). Partition Finder v.1.1 (Lanfear et al., 2012) was used to determine the partition scheme and substitution models that best fitted the data. A total number of three datasets were constructed for the different analyses.

Phylogenetic analyses were carried out both under Bayesian inference (BI) and Maximum Likelihood (ML) methods using a concatenated dataset (2,917 bp) that included nuclear and mitochondrial gene fragments of 23 *Meloe* species (57 specimens) plus outgroups (Table S1). The BI analysis was conducted in MrBayes v.3.2.3 (Ronquist et al., 2012). Two partition schemes were assessed using four (*cox1*, 16S, *Wg* and 18S) or eight character sets (considering codon positions for *cox1* and *Wg*). Analyses consisted of two simultaneous runs of $10x10^6$ generations each, sampling every 1,000 generations. The consensus tree was generated in MrBayes with a 25% burnin, and posterior probabilities were used to assess nodal support. The ML analysis was carried out using the web server IQ-TREE (Nguyen et al., 2015) and the best fitting models for each partition selected by the same program. Branch support analysis was conducted with 1,000 ultrafast bootstrap replicates (Hoang et al., 2018).

Estimates of time to the most recent common ancestor (TMRCA) were obtained using BEAST v1.10.4 (Drummond et al., 2012) and the combined dataset with a partition scheme by gene. A molecular clock was calibrated using a Miocene fossil of *Meloe* (*Meloe*) *dominicanus* Poinar, 2009 to fix the minimum age of a clade including all studied members of

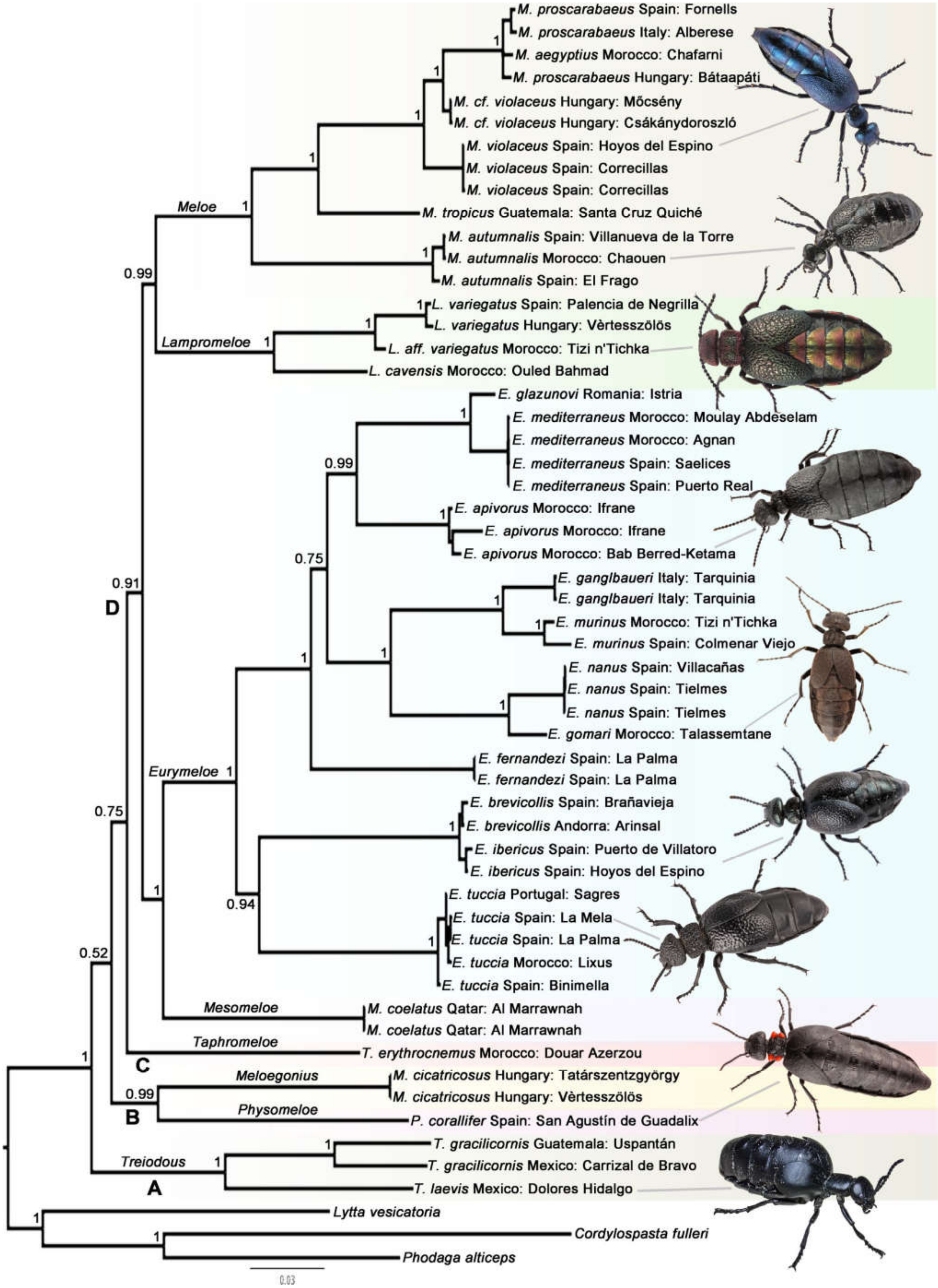
M. proscarabaeus Spain: Fornells
M. proscarabaeus Italy: Alberese
M. aegyptius Morocco: Chafarni
M. proscarabaeus Hungary: Bátaapáti
M. cf. violaceus Hungary: Mőcsény
M. cf. violaceus Hungary: Csákánydoroszló
M. violaceus Spain: Hoyos del Espino
M. violaceus Spain: Correcillas
M. violaceus Spain: Correcillas
M. tropicus Guatemala: Santa Cruz Quiché
M. autumnalis Spain: Villanueva de la Torre
M. autumnalis Morocco: Chaouen
M. autumnalis Spain: El Frago
Meloe
Lampromeloe
L. variegatus Spain: Palencia de Negrilla
L. variegatus Hungary: Vèrtesszölös
L. aff. variegatus Morocco: Tizi n'Tichka
L. cavensis Morocco: Ouled Bahmad
E. glazunovi Romania: Istria
E. mediterraneus Morocco: Moulay Abdeselam
E. mediterraneus Morocco: Agnan
E. mediterraneus Spain: Saelices
E. mediterraneus Spain: Puerto Real
E. apivorus Morocco: Ifrane
E. apivorus Morocco: Ifrane
E. apivorus Morocco: Bab Berred-Ketama
E. ganglbaueri Italy: Tarquinia
E. ganglbaueri Italy: Tarquinia
E. murinus Morocco: Tizi n'Tichka
E. murinus Spain: Colmenar Viejo
E. nanus Spain: Villacañas
E. nanus Spain: Tielmes
E. nanus Spain: Tielmes
E. gomari Morocco: Talassemtane
E. fernandezi Spain: La Palma
E. fernandezi Spain: La Palma
Eurymeloe
E. brevicollis Spain: Brañavieja
E. brevicollis Andorra: Arinsal
E. ibericus Spain: Puerto de Villatoro
E. ibericus Spain: Hoyos del Espino
E. tuccia Portugal: Sagres
E. tuccia Spain: La Mela
E. tuccia Spain: La Palma
E. tuccia Morocco: Lixus
E. tuccia Spain: Binimella
Mesomeloe
M. coelatus Qatar: Al Marrawnah
M. coelatus Qatar: Al Marrawnah
Taphromeloe
T. erythrocnemus Morocco: Douar Azerzou
Meloegonius
M. cicatricosus Hungary: Tatárszentgyörgy
M. cicatricosus Hungary: Vèrtesszölös
Physomeloe
P. corallifer Spain: San Agustín de Guadalix
Treiodous
T. gracilicornis Guatemala: Uspantán
T. gracilicornis Mexico: Carrizal de Bravo
T. laevis Mexico: Dolores Hidalgo
Lytta vesicatoria
Cordylospasta fulleri
Phodaga alticeps
A
B
C
D
0.99
0.91
0.75
0.52
0.99
0.75
0.94
0.99
1
0.03

FIGURE 1 Bayesian phylogenetic tree based on the combined dataset (*cox1*, 16S, 18S, *Wg*) for representatives of 23 species of *Meloe s. l.* plus *Physomeloe*. Species and clade names correspond to the new classification adopted in this work. Numbers at nodes represent the posterior probabilities of clades. The different background colours represent genera as recognized according to the results of the present study. The taxonomic identity of the specimens shown on the right is indicated by a grey line to their respective species name

the subgenus *Meloe* (Iturralde-Vinent & MacPhee, 1996; Poinar, 2009) (lognormal distribution, $M = 17.5$, $SD = 0.54$, off-set = 10, meanInRealSpace = true). Substitution rates previously estimated for tenebrionid beetles (Papadopoulou et al., 2010) were used in the analyses. We ran three independent analyses for $100x10^6$ generations each, sampling every 10×10^3 generations, using a lognormal relaxed clock and a 'Birth-Dead Incomplete Sampling' tree prior (Stadler, 2009). We assessed effective sample sizes (ESS) in Tracer v1.5. The maximum clade credibility (MCC) tree was summarized using TreeAnnotator with a 25% burnin.

Haplotype networks were built with minimum spanning networks as implemented in PopArt v1.7 (Leigh & Bryant, 2015). For this analysis, a second dataset was used that included *cox1* sequences from a set of species co-occurring in the Iberian and Tingitanian peninsulas and the Canary and/or Balearic Islands: *Meloe proscarabaeus* Linnaeus, 1758 ($n = 35$), *Meloe autumnalis* Olivier, 1797 ($n = 12$), *Eurymeloe mediterraneus* (Müller, 1925) ($n = 44$) and *Eurymeloe tuccia* (Rossi, 1790) ($n = 29$) (Table S1).

To infer past trends in effective population size, the demographic histories of some species were reconstructed by Bayesian skyline plot (BSP) analyses, as implemented in BEAST v1.10.4 (Drummond et al., 2012). A third dataset, which included partial mitochondrial *cox1* and 16S sequences was used for these analyses for the following species: *M. autumnalis*, *M. proscarabaeus*, *E. mediterraneus*, *E. tuccia* and *P. corallifer*. The selection of these taxa relies on (1) the number of available samples (more than 6 samples; see Supplementary Table 1) and (2) natural history: non-phoretic *Physomeloe* versus phoretic in the other species; autumn adult phenology in *M. autumnalis* versus spring phenology in the other species. BSP analyses were run for 300×10^6 generations, sampling every 30×10^3, under a lognormal relaxed clock and a Bayesian Skyline tree prior. We assessed ESS in Tracer v1.5 using a 25% burnin to build the BSPs.

3 | RESULTS

3.1 | Phylogenetic relationships and TMRCA estimates

Both BI and ML analyses produced almost the same tree topologies. Consequently, only the BI is herein discussed, while the ML tree is shown in Figure S1. Equivalent topologies obtained using alternative partition schemes in MrBayes and BEAST (Figures 1 and 2, respectively) show several inconsistencies with respect to current taxonomic classifications. Clade A (BPP = 1) includes the Central American species of *Treiodous* Dugès, 1869; clade B (BPP = 0.99) groups *Physomeloe* and *Meloegonius* Reitter, 1911; clade C is represented by *Taphromeloe* Reiter, 1911 and clade D (BPP = 0.91) groups the other previously described subgenera plus *Meloe autumnalis*, which was previously considered as a Palaearctic representative of the subgenus *Treiodous* (Bologna, 1991, 2008). Clade D consists of two strongly supported subclades, one that includes *Lampromeloe* and *Meloe* plus *M. autumnalis* (BPP = 0.99) and another that includes *Mesomeloe* Reitter, 1911 and *Eurymeloe* plus the only species of the subgenus *Coelomeloe* Reitter, 1911 (*E. tuccia*) (BPP = 1). Representatives of the subgenus *Meloe*, together with *M. autumnalis*, also form a highly supported subclade (BPP = 1). The *Meloe* subclade includes the European species *M. proscarabaeus* and *M. violaceus* and the Central American species *M. tropicus*. The subclade *Lampromeloe* includes the only two currently recognized species of the subgenus. The only studied species of *Mesomeloe* (*M. coelatus*) comprises a divergent subclade within the larger D clade. The subclade including *Eurymeloe* and *Coleomeloe* (BPP = 1) is internally structured, with *Coelomeloe* (*E. tuccia*) nested within *Eurymeloe*, thus breaking the monophyly of the subgenus *Eurymeloe*. The two taxa studied of the *Eurymeloe brevicollis* (Panzer, 1793) species group, *E. brevicollis* and *E. ibericus* Reitter, 1895, form a clade with *E. tuccia* (*Coelomeloe*) (BPP = 0.94). This clade is the sister group to the studied representatives of the *Eurymeloe rugosus* species group (Bologna, 1988) (BPP = 1).

Within the *E. rugosus* species group, *Eurymeloe fernandezi* (Pardo Alcaide, 1951), which is endemic to the Canary Islands, is the sister species to all the other species (BPP = 1). The *E. rugosus* species group cluster as follows: (a) *E. gomari* (Ruiz & García-París, 2009) and *E. nanus* (Lucas, 1849) (BPP = 1) as the sister group to *E. murinus* (Brandt & Erichson, 1832) and *E. ganglbaueri* (Apfelbeck, 1905) (BPP = 1) and (b) *E. glazunovi* (Plignskij, 1910) and *E. mediterraneus* (Müller, 1925) (BPP = 1) as the sister group to *E. apivorus* (Reitter, 1911) (BPP = 0.99).

Estimated TMRCAs (median and 95% HPD) are shown in Figure 2. The origin of the former concept of *Meloe* plus *Physomeloe* lineage is estimated around 41.3 Ma, during the late Eocene to early Oligocene (95% HPD: 28.18–56.58). At the intraspecific level, the TMRCA of the *E. tuccia* populations (insular ones from the Balearic and Canary Islands and continental ones from the Iberian Peninsula and North

TABLE 1 Taxonomic rearrangement of the tribe Meloini (Coleoptera, Meloidae) including all genera, subgenera and species, according to the new classification adopted in this work. New combinations are indicated for the taxa included in genera that changed their status, except those already changed in Selander (1985) and Koçak and Kemal (2010)

Genera	Type species	General Distribution	Species composition
Afromeloe Schmidt, 1913	*Meloe angulatus* Leach, 1815 by subsequent designation (Aksentjev, 1988)	Afrotropical region, Arabic Peninsula	*A. adisabebae* (Pliginskij, 1935) **comb. nov**., *A. angulatus* (Leach, 1815) **comb. nov**., *A. atrocyaneus* (Fairmaire, 1887) **comb. nov**., *A. caffer* (Péringuey, 1886) **comb. nov**., *A. chevrolati* (Coquerel, 1851) **comb. nov**., *A. lefevrei* (Guérin-Méneville, 1849) **comb. nov**., *A. meridianus* (Peringuey, 1892) **comb. nov**., *A. sanaanus* (Borchmann, 1938) **comb. nov**., *A. seineri* (Schmidt, 1913) **comb. nov**., *A. trapeziderus* (Gahan, 1903) **comb. nov**., *A. ukinganus* (Schmidt, 1913) **comb. nov**.
= *Submeloegonius* Pliginskij, 1935	*Meloe adisabebae* Pliginskij, 1935 by monotypy		
Alveomeloe Pripisnova, 1987 **stat. nov**.	*Meloe tadzhikistanicus* Pripisnova, 1987 by original designation	Central Asia (Tajikistan)	*A. babatagicus* (Pripisnova, 1987) **comb. nov**., *A. tadzhikistanicus* (Pripisnova, 1987) **comb. nov**.
Chiromeloe Reitter, 1911 **stat. nov**.	*Meloe nigropilosellus* Reitter, 1900 by monotypy	Central Asia (Uzbekistan)	*C. nigropilosellus* (Reitter, 1900) **comb. nov**.
Desertimeloe Kaszab, 1964 **stat. nov**.	*Meloe centripubens* Reitter, 1897 by original designation	China (Gansu, Xinjiang), Mongolia	*D. alashana* (Kaszab, 1964) **comb. nov**., *D. centripubens* (Reitter, 1897) **comb. nov**.
Eurymeloe Reitter, 1911	*Meloe brevicollis* Panzer, 1793 by subsequent designation (Pinto & Selander, 1970)	Mainly Palaearctic	*E. aeneus* (Tauscher, 1812) **comb. nov**., *E. affinis* (Lucas, 1847) **comb. nov**. [subspecies: *E. a. affinis* (Lucas, 1847), *E. a. schatzmayri* (Bologna, 1988) **comb. nov**.], *E. aleuticus* (Borchmann, 1942) **comb. nov**., *E. apivorus* (Reitter, 1895) **comb. nov**., *E. appenninicus* (Bologna, 1988) **comb. nov**., *E. asperatus* (Tarn, 1981) **comb. nov**., *E. austrinus* (Wollaston, 1854) **comb. nov**., *E. brevicollis* (Panzer, 1793) [subspecies: *E. b. brevicollis* (Panzer, 1793), *E. b. algiricus* (Escherich, 1890) **comb. nov**., *E. b. curticornis* (Martínez de la Escalera, 1914) **comb. nov**., *E. b. mistaniensis* (Aksentjev, 1985) **comb. nov**.], *E. baamarani* (Ruiz & García-París, 2015) **comb. nov**., *E. baudii* (Leoni, 1907) **comb. nov**., *E. baudueri* (Grenier, 1863) **comb. nov**., *E. corvinus* (Marseul, 1877), *E. crosi* (Peyerimhoff, 1926) **comb. nov**., *E. curticollis* (Kraatz, 1882) **comb. nov**., *E. escherichi* (Reitter, 1889) **comb. nov**., *E. fernandezi* (Pardo Alcaide, 1951) **comb. nov**., *E. flavicomus* (Wollaston, 1854) **comb. nov**., *E. frontalis* (Reitter, 1905) **comb. nov**., *E. gaberti* (Reitter, 1907) **comb. nov**., *E. ganglbaueri* (Apfelbeck, 1905) **comb. nov**., *E. glazunovi* (Pliginskij, 1910) **comb. nov**., *E. gomari* (Ruiz & García-París, 2009) **comb. nov**., *E. heptapotamicus* (Pliginskij, 1910) **comb. nov**., *E. ibericus* (Reitter, 1895) **comb. nov**., *E. kandaharicus* (Kaszab, 1958) **comb. nov**., *E. laevipennis* (Brandt & Erichson, 1832) **comb. nov**., *E. lederi* (Reitter, 1895) **comb. nov**., *E. lobicollis* (Fairmaire, 1891) **comb. nov**., *E. luctuosus* (Brandt & Erichson, 1832) **comb. nov**., *E. mandli* (Borchmann, 1942) **comb. nov**., *E. mathiesseni* (Reitter, 1905) **comb. nov**., *E. mediterraneus* (Müller, 1925) **comb. nov**., *E. murinus* (Brandt and Erichson, 1832), *E. nanus* (Lucas, 1847) **comb. nov**., *E. omanicus* (Kaszab, 1983) **comb. nov**., *E. pallidicolor* (Martínez de la Escalera, 1909) **comb. nov**., *E. primaeveris* (Kaszab, 1958) **comb. nov**., *E. primulus* (Semenow, 1903) **comb. nov**., *E. pubifer* (Heyden, 1887) **comb. nov**., *E. punjabensis* (Kaszab, 1958) **comb. nov**., *E. pusio* (Wellman, 1910) **comb. nov**., *E. rugosus* (Marsham, 1802), *E. saharensis* (Chobaut, 1898) **comb. nov**., *E. sarmaticus* (Shapovalov, 2012) **comb. nov**., *E. scabriusculus* (Brandt & Erichson, 1832) **comb. nov**., *E. schmidi* (Kaszab, 1978) **comb. nov**., *E. scutellatus* (Reitter, 1895) **comb. nov**., *E. servulus* (Bates, 1879) **comb. nov**., *E. subsetosus* (Reitter, 1895) **comb. nov**., *E. transversicollis* (Fairmaire, 1891) **comb. nov**., *Eurymeloe tuccia* (Rossi, 1790) [subspecies: *E. t. tuccia* (Rossi, 1790), *E. t. corrosus* (Brandt & Erichson, 1832) **comb. nov**.], *E. vignai* (Bologna, 1990) **comb. nov**., *E. zolotarevi* (Pliginskij, 1914) **comb. nov**.

(Continues)

TABLE 1 (Continued)

Genera	Type species	General Distribution	Species composition
= *Coeloemeloe* Reitter, 1911	*Meloe tuccia* Rossi, 1792 by monotypy		
Lampromeloe Reitter, 1911	*Meloe variegatus* Donovan, 1793 by subsequent designation (Aksentjev, 1988)	Palaearctic	*L. cavensis* (Petagna, 1819), *L. variegatus* (Donovan, 1793) **comb. nov**. [subspecies: *L. variegatus variegatus* (Donovan, 1793), *L. v. mandzhuricus* (Pliginskij, 1930) **comb. nov**.]
Lasiomeloe Reitter, 1911 **stat. nov**.	*Meloe olivieri* Chevrolat, 1833 by monotypy	W Asia to SE Europe	*L. olivieri* (Chevrolat, 1833)
Listromeloe Reitter, 1911 **stat. nov**.	*Meloe hungarus* Schrank von Paula, 1776 by monotypy	Central-S Europe to W Asia	*L. hungarus* (Schrank von Paula, 1776) **comb. nov**.
Meloe Linnaeus, 1758 **sensu. nov**.	*Meloe proscarabaeus* Linnaeus, 1758 by subsequent designation (Latreille, 1810)	Mainly Holartic	
Subgenus ***Meloe*** Linnaeus, 1758 **sensu. nov**.	*Meloe proscarabaeus* Linnaeus, 1758 by subsequent designation (Latreille, 1810)	Mainly Holartic	*M.* (*M.*) *abyssinicus* (Pliginskij, 1930), *M.* (*M.*) *aegyptius* Brandt & Erichson, 1832 [subspecies: *M.* (*M.*) *aegyptius aegyptius* Brandt & Erichson, 1832, *M.* (*M.*) *aegyptius subcyaneus* Wollaston, 1864], *M.* (*M.*) *americanus* Leach, 1815, *M.* (*M.*) *angusticollis* Say, 1824, *M.* (*M.*) *aruanachalae* Saha, 1979, *M.* (*M.*) *auriculatus* Marseul, 1877, *M.* (*M.*) *bellus* Jakovlev, 1897 [synonym of *M. lobatus*], *M.* (*M.*) *bitoricollis* Pinto & Selander, 1970, *M.* (*M.*) *bodemeyeri* Ganglbauer, 1900, *M.* (*M.*) *californicus* Van Dyke, 1928, *M.* (*M.*) *campanicollis* Pinto & Selander, 1970, *M.* (*M.*) *carbonaceus* LeConte, 1866, *M.* (*M.*) *coarctatus* Motschulsky, 1858, *M.* (*M.*) *dianella* Pinto & Selander, 1970, *M.* (*M.*) *dugesi* Champion, 1891, *M.* (*M.*) *exiguus* Pinto & Selander, 1970, *M.* (*M.*) *formosensis* Miwa, 1930, *M.* (*M.*) *franciscanus* Van Dyke, 1928, *M.* (*M.*) *gracilior* Fairmaire, 1891, *M.* (*M.*) *hottentotus* Péringuey 1886, *M.* (*M.*) *impressus* Kirby, 1837, *M.* (*M.*) *kulabensis* Shapovalov, 2014, *M.* (*M.*) *lobatus* Gebler, 1832, *M.* (*M.*) *medogensis* Tan, 1988, *M.* (*M.*) *menoko* Kóno, 1936, *M.* (*M.*) *modestus* Fairmaire, 1887 [incertae sedis sensu Bologna, 2020], *M.* (*M.*) *monticola* Kolbe, 1897, *M.* (*M.*) *nebulosus* Pinto & Selander, 1970, *M.* (*M.*) *niger* Kirby, 1837, *M.* (*M.*) *occultus* Pinto & Selander, 1970, *M.* (*M.*) *ovalicollis* Reitter, 1908, *M.* (*M.*) *patellicornis* Fairmaire, 1887 [synonym of *M. lobatus*], *M.* (*M.*) *poteli* Fairmaire, 1897, *M.* (*M.*) *proscarabaeus* Linnaeus, 1758 [subspecies: *M.* (*M.*) *proscarabaeus proscarabaeus* Linnaeus, 1758, *M.* (*M.*) *proscarabaeus afghanistanicus* Kaszab, 1953, *M.* (*M.*) *proscarabaeus sapporensis* Kôno, 1936, *M.* (*M.*) *proscarabaeus sericeorugosus* Aksentjev, 1987], *M.* (*M.*) *quadricollis* Van Dyke, 1928, *M.* (*M.*) *rathjensi* Borchmann, 1938, *M.* (*M.*) *rhodesianus* Péringuey, 1904, *M.* (*M.*) *scabrus* Pan & Ren, 2018, *M.* (*M.*) *semenowi* Jakovlev, 1897, *M.* (*M.*) *semicoriaceus* Fairmaire, 1891, *M.* (*M.*) *simplicicornis* Escherich, 1889, *M.* (*M.*) *strigulosus* Mannerheim, 1852, *M.* (*M.*) *subcordicollis* Fairmaire, 1887, *M.* (*M.*) *tarsalis* Jakovlev, 1897, *M.* (*M.*) *tenuipes* Jakovlev, 1897, *M.* (*M.*) *tropicus* Motschulsky, 1856, *M.* (*M.*) *vandykei* Pinto & Selander, 1970, *M.* (*M.*) *violaceus* Marsham, 1802
= *Proscarabaeus* Schrank, 1781	*Meloe proscarabaeus* Linnaeus, 1758 by absolute tautonymy		
= *Melittophagus* Kirby, 1816	*Pediculus melittae* Kirby, 1802 (=*Meloe violaceus* Marsham, 1802) by original designation		

(Continues)

TABLE 1 (Continued)

Genera	Type species	General Distribution	Species composition
= *Triungulinus* Dufour, 1828	*Triungulinus andrenatarum* Dufour, 1828 by monotypy		
= *Cnestocera* Thomson, 1859	*Meloe proscarabaeus* Linnaeus, 1758 by original designation		
Subgenus ***Anchomeloe*** Iablokoff-Khnzorian, 1983 **stat. nov**.	*Meloe autumnalis* Olivier, 1797 by monotypy	W Palaearctic	*M*. (*A*.) *autumnalis* Olivier, 1797 [subspecies: *M*. *(A.) a*. *autumnalis* Olivier, 1797 and *M*. *(A.) a*. heydeni Escherich, 1889].
Meloegonius Reitter, 1911 **stat. nov**.	*Meloe cicatricosus* Leach, 1815 by subsequent designation (Aksentjev, 1988)	W-central Palaearctic	*M. cicatricosus* (Leach, 1815), *M. rufiventris* (Germar, 1817) [subspecies: *M. r. rufiventris* (Germar, 1817), *M. r. himalaycus* (Kaszab, 1978) **comb. nov.**].
Mesomeloe Reitter, 1911 **stat. nov**.	*Meloe sulcicollis* Kraatz, 1882 (= *Meloe xanthomelas* Solsky, 1881) by subsequent designation (Aksentjev, 1988)	W-central Palaearctic	*M. bytinskii* (Kaszab, 1969) **comb. nov.**, *M. cinereovariegatus* (Heyden, 1885) **comb. nov.**, *M. coelatus* (Reiche, 1857) **comb. nov.**, *M. xanthomelas* (Solsky, 1881) **comb. nov**.
Meloenellus Reitter, 1911 **stat. nov**.	*Meloe griseopuberulus* Reitter, 1,890 by subsequent designation (Aksentjev, 1988)	W-central Asia	*M. griseopuberulus* (Reitter, 1,890) **comb. nov.**, *M. sulcipes* (Reitter, 1911) **comb. nov.** , *M. turkestanicus* (Escherich, 1,890) **comb. nov.** , *M. vlasovi* (Semenov & Arnoldi, 1937) **comb. nov**.
Micromeloe Reitter, 1911 **stat. nov**.	*Meloe uralensis* Pallas, 1773 by subsequent designation (Aksentjev, 1988)	Central-s Europe to W Asia	*M. cavicornis* (Reitter, 1898) **comb. nov.**, *M. conradti* (Heyden, 1888) **comb. nov.**, *M. decorus* (Brand & Erichson, 1832) **comb. nov.**, *M. intermedius* (Escherich, 1904) **comb. nov.**, *M. kabuliensis* (Kaszab, 1981) **comb. nov.**, *M. lopatini* (Pripisnova, 1987) **comb. nov.**, *M. pintoi* (Bologna, 2018) **comb. nov.**, *M. reitteri* (Escherich, 1889) **comb. nov.**, *M. simulans* (Reitter, 1895) **comb. nov.**, *M. terentjevi* (Kaszab, 1978) **comb. nov.**, *M. uralensis* (Pallas, 1773) **comb. nov**.
Physomeloe Reitter, 1911	*Meloe corallifer* Germar, 1818 by monotypy	Iberian Peninsula	*Physomeloe corallifer* (Germar, 1818)
Taphromeloe Reitter, 1911 **stat. nov**.	*Meloe erythrocnemus* Pallas, 1781 by monotypy	W Palaearctic	*T. erythrocnemus* (Pallas, 1782), *T. foveolatus* (Guérin de Méneville, 1842) **comb. nov**.
Treiodous Dugès, 1869 **stat. nov**.	*Treiodous barranci* Dugès, 1869 (= *Meloe laevis* Leach, 1815) by monotypy	North America to *N* South America	*T. laevis* (Leach, 1815) **comb. nov.** , *T. gracilicornis* (Champion, 1891) **comb. nov.**, *T. afer* (Bland, 1864) **comb. nov.**, *T. barbarus* (LeConte, 1861) **comb. nov.**, *T. ajax* (Pinto, 1998) **comb. nov**.

Africa) indicate a common origin 840,000 years ago (95% HPD: 370,000–1,620,000 years ago). The TMRCA of the *M. proscarabaeus* populations from the Italian Peninsula, Balearic Islands, North Africa and Central Europe is 1.03 Mya (95% HPD: 510,000–1,660,000 years ago), and that of *E. mediterraneus* populations from the Iberian Peninsula and North Africa is 160,000 years ago (95% HPD: 30,000–380,000 years ago).

3.2 | Mitochondrial phylogeography and demography

For the studied populations of *M. proscarabaeus*, represented by 35 specimens (including one Moroccan specimen of the poorly differentiated *M. aegyptius* Brandt & Erichson, 1832; see Bologna, 1991), we observed 22 haplotypes. Most haplotypes are present at low frequencies; at least five highly divergent phylogroups without a clear internal geographic structure can be discerned from the analysis (Figure 3a). Populations from the Iberian Peninsula and North Africa are grouped in different, distant phylogroups. The studied population from the island of Menorca (Balearic Islands) presents two divergent haplotypes (Figure 3a), one that is shared with Central European populations and another that is closely related to the Iberian and African haplotypes. These results indicate that at least two independent colonization events occurred on Menorca.

A total of 9 haplotypes were observed among the 12 sequenced specimens of *M. autumnalis*. This species shows a high level of intra-population haplotype diversity (Figure 3b). The studied population from Africa is closely related to the most common Iberian haplotype (two mutations).

Among the 44 sequenced specimens of *E. mediterraneus*, we found 23 haplotypes. According to the haplotype network (Figure 3c), many of the specimens from Europe and North Africa (n = 19) share a single common haplotype. Poorly differentiated haplotypes are also present at much lower frequencies in both North Africa (3 haplotypes, n = 3) and the Iberian Peninsula (19 haplotypes, n = 22).

We found 12 haplotypes among the 29 sequenced specimens of *E. tuccia*. This species shows a high level of intra-population haplotype diversity, except within La Palma (Canary Islands) population, which is represented by a unique haplotype that is closely related to the African haplotypes (Figure 3d). According to this data, a single colonization of La Palma Island took place, probably from north-western Africa. Haplotype diversity is not geographically structured in the other populations of *E. tuccia*.

Assuming that islands have been colonized from continental masses, our haplotype networks (Figure 3) show that colonization of the Canary and the Balearic Islands from continental Africa and/or Europe, or transcontinental dispersal between Africa and Europe across the Strait of Gibraltar, have occurred multiple times along the evolutionary history of each of these phoretic blister beetles. Although our sample sizes are limited, our results (one shared haplotype in *E. tuccia*, and two haplotypes separated by only one or two mutations in *M. proscarabaeus*) indicate that colonization of the Balearic Islands from the Iberian Peninsula occurred very recently. A second *E. tuccia* Balearic haplotype appears to have originated from northern Africa, from either a population that has not yet been sampled or an older colonization event with a certain degree of genetic differentiation (5–7 mutations). Transoceanic movements between the Iberian Peninsula and north-western Africa across the Strait of Gibraltar seem to have occurred multiple times for each species, as evidenced by the variation in the number of mutations among sister haplotypes: from 5 to 14 for *M. proscarabaeus*, 2 for *M. autumnalis*, 4 to 6 for *E. tuccia* and 0 to 2 for *E. mediterraneus*.

A similar demographic history was obtained from the BSP analyses for *M. autumnalis*, *E. mediterraneus*, *M. proscarabaeus*, *E. tuccia* and *P. corallifer*, suggesting a shared trend of recent demographic expansion that started around 50,000 years ago (Figure 4).

4 | DISCUSSION

4.1 | Systematics and character evolution

Our phylogenetic hypothesis challenges some previously considered relationships within *Meloe s. l.*, including the lack of monophyly of *Meloe s. l.*, *Eurymeloe* and *Treiodous*. It also changes the phylogenetic placement of some taxa. Consequently, some previous hypotheses on character evolution and homoplasy in the group need to be reinterpreted, particularly those regarding the morphological traits of first-instar larvae, which have been widely used to support or reject evolutionary groups within Meloini (Bologna, 1988, 1991; Bologna et al., 1989, 1990; Bologna & Pinto, 2001; Di Giulio et al., 2002, 2013, 2014; Pinto & Bologna, 1993; Selander, 1989).

Although our results agree with those of Bologna et al. (2008) that consider *Physomeloe* as part of Meloini, they do not support a monophyletic *Meloe*. The resolution of *Physomeloe* as the sister group of *Meloegonius* (Figure 1) renders *Meloe s. l.* paraphyletic. *Physomeloe* has long been treated as an independent genus: unlike all other Meloini, the only species of this genus has non-phoretic larvae, and both the adult and the larval morphology consistently differ from all other *Meloe s. l.* (Bologna & Aloisi, 1994). Differences with *Meloe* are so marked that *Physomeloe* was previously included in the tribe Lyttini (Bologna &

Aloisi, 1994). The distinctiveness of *Physomeloe* does not allow it to be treated as a particularly derived species of *Meloe* without breaking the taxonomic concept and diagnosis of *Meloe*. On the other hand, dividing the genus *Meloe* would be in agreement with a series of detailed anatomical studies on larval and adult specimens that suggest

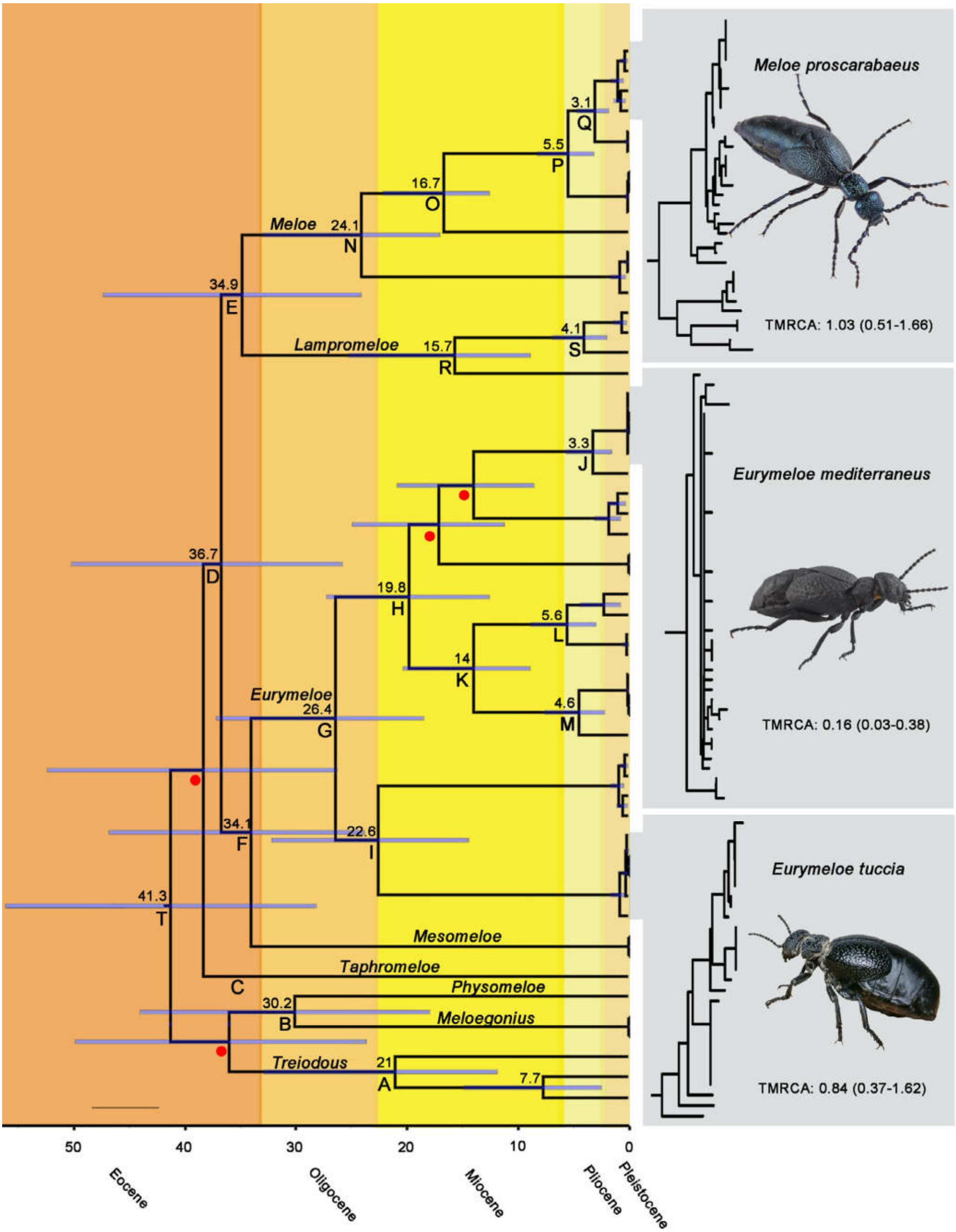

FIGURE 2 Chronogram of *Meloe s. l.* and *Physomeloe* obtained from the combined dataset using coalescence methods with BEAST. All nodal values present posterior probabilities (PP)>0.90 except for those marked with a red dot, which indicates a PP < 0.90. Horizontal bars at nodes indicate 95% HPD values. Grey boxes on the right show the results of Neighbour-Joining analysis used to depict the haplotype diversity of the widely distributed species *Meloe proscarabaeus*, *Eurymeloe mediterraneus* and *Eurymeloe tuccia*, and their respective TMRCA. Species and clade names correspond to the new classification adopted in this work

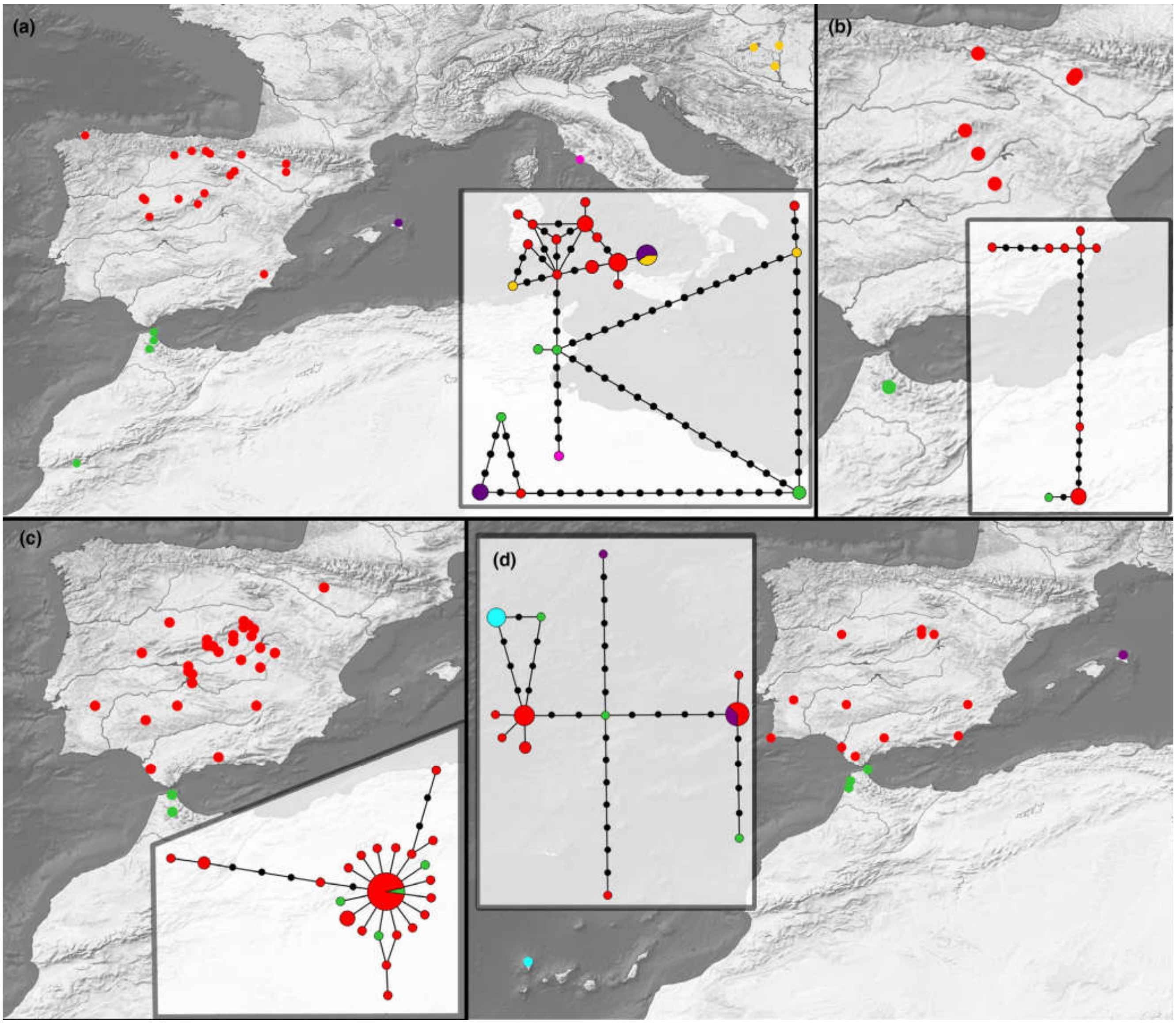

FIGURE 3 Haplotype networks based on 22, 9, 23 and 12 unique *cox1* haplotypes for, respectively, *Meloe proscarabaeus* (a), *Meloe autumnalis* (b), *Eurymeloe mediterraneus* (c) and *Eurymeloe tuccia* (d). Inferred intermediate haplotypes are represented by small black circles. Colours correspond to the geographic origin of the specimens. Species names correspond to the new classification adopted in this work

Eurymeloe (including *Coelomeloe*) and *Lampromeloe* represent independent genera (Selander, 1985, 1991). Our phylogenetic hypothesis supports the uniqueness of *Physomeloe* (Bologna et al., 2008), *Eurymeloe* and *Lampromeloe*, as previously considered by Selander (1985, 1991).

Di Giulio et al. (2002) revised the larval morphology of the subgenus *Mesomeloe* and suggested that *Eurymeloe* and *Mesomeloe* larvae have clear similarities. By contrast, adult traits of *Mesomeloe* were more similar to those of *Meloe s. str.* Our molecular phylogenetic hypothesis, in which *Mesomeloe* is a sister taxon to *Eurymeloe*, is congruent with the inferences made from larval morphology (Di Giulio et al., 2002). First-instar larvae of *Coelomeloe* (*E. tuccia*) and of the *M. brevicollis* group of *Eurymeloe* (sensu Bologna, 1988) share a clearly protruding mesothoracic

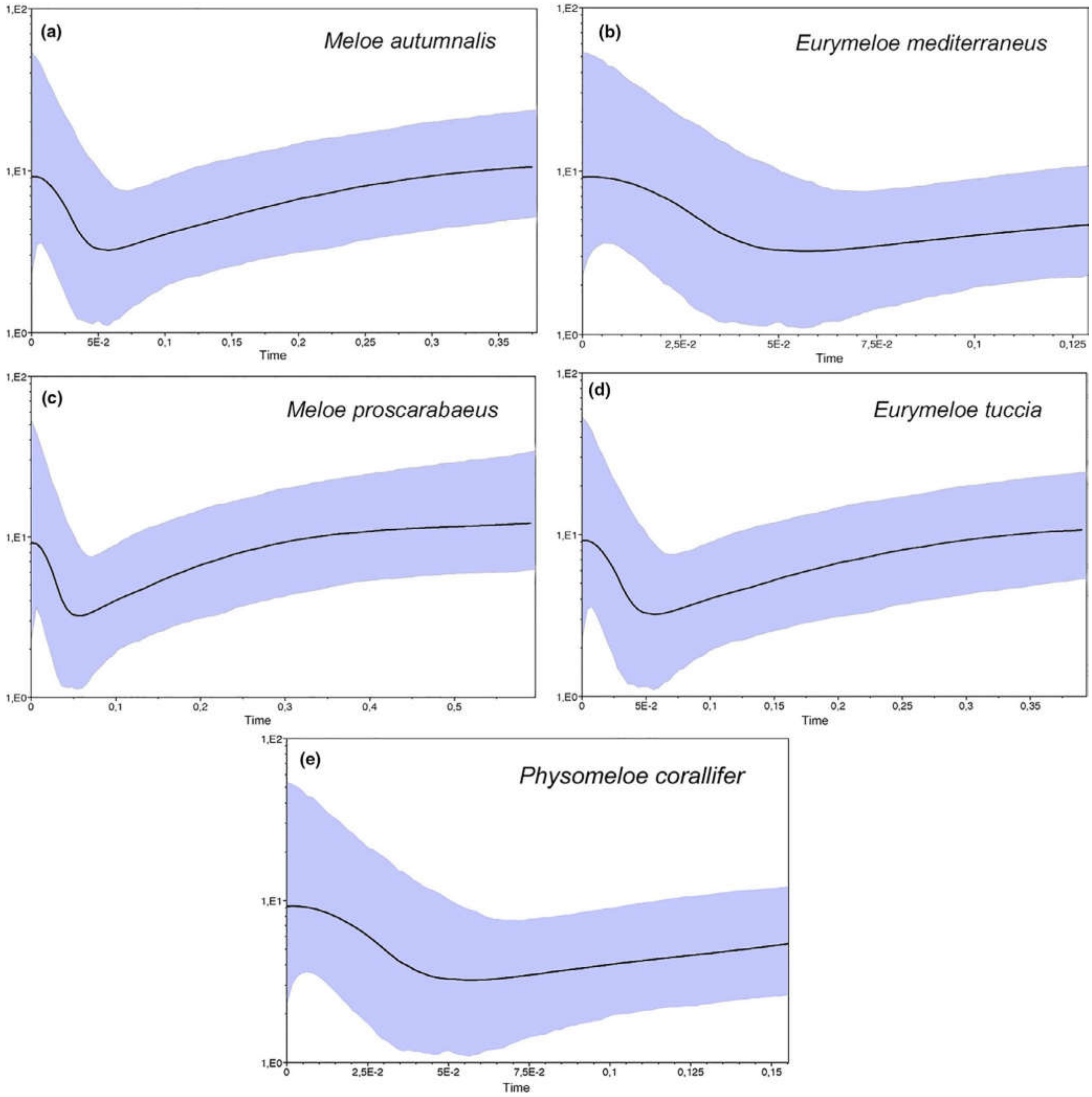

FIGURE 4 Bayesian skyline plots (BSP) showing the change in effective population size over time in (a) *Meloe autumnalis*, (b) *Eurymeloe mediterraneus*, (c) *Meloe proscarabaeus*, (d) *Eurymeloe tuccia* and (e) *Physomeloe corallifer*. Analyses were based on partial mitochondrial *cox1* and 16S sequences. y-axis: estimated population size change by generation time (Ne generation time); x-axis: time (thousands of years before present). The mean estimate is shown as a thick black line, and the 95% HDP limits are shown as a blue area. Species names correspond to the new classification adopted in this work

spiracle and a large transverse abdominal spiracle I (Di Giulio et al., 2013). As these taxa were not treated as reciprocally monophyletic, this similarity was thought to be due to parallel evolution (homoplasy) (Di Giulio et al., 2013). However, our phylogeny supports the monophyly of *Coelomeloe* and the *M. brevicollis* group (see Figure 1), making this feature a synapomorphy and a useful character for the diagnosis of this clade.

Several behavioural traits have been used to support the monophyly of some groups in Meloidae, such as those used to delimit taxa in the tribe Eupomphini (Pinto, 1984). Some of these traits have been supported as synapomorphies by recent molecular phylogenies (López-Estrada et al., 2019). However, in other cases, characters previously used to identify clades, such as those derived from the sexual behaviour of North American *Treiodous* and

Meloe s. str. (Pinto & Selander, 1970), were no longer used due to their homoplastic nature (Foster et al., 1996; Henry et al., 1999). Our molecular phylogenetic hypothesis suggests that the European *M. autumnalis*, which was previously included in *Treiodous*, is the sister taxon to *Meloe s. str*. Shared traits related to courtship behaviour (see Pinto & Selander, 1970) and larval morphology, as described by Cros (1914), support this relationship and likely represent synapomorphies for *M. autumnalis* and *Meloe s. str*. Similarly, the close relationship between *Lampromeloe* and *Meloe s. str.* is partially supported by shared traits related to larval morphology (Di Giulio et al., 2002) but not by courtship behaviour.

To accommodate these findings into a taxonomic framework that better reflects the evolutionary relationships of *Meloe s. l.*, we support the concept of *Physomeloe* as an independent genus and a formal division of *Meloe s. l.* into several genera. We propose raising all previously accepted subgenera (Bologna, 2020a; Bologna & Pinto, 2002) to a generic status (see Table 1). Therefore, besides the already recognized *Meloe s. str.* and *Physomeloe*, we formally recognize the following taxa as independent genera: *Afromeloe* Schmidt, 1913, *Alveomeloe* Pripisnova, 1987, *Chiromeloe* Reitter, 1911, *Desertimeloe* Kaszab, 1964, *Eurymeloe* Reitter, 1911, *Lampromeloe* Reitter, 1911, *Lasiomeloe* Reitter, 1911, *Listromeloe* Reitter, 1911, *Meloegonius* Reitter, 1911, *Mesomeloe* Reitter, 1911, *Meloenellus* Reitter, 1911, *Micromeloe* Reitter, 1911, *Taphromeloe* Reitter, 1911 and *Treiodous* Dugès, 1869; while *Anchomeloe* Iablokoff-Khnzorian, 1983, is recovered as subgenus of *Meloe*. The tribe Meloini is consequently composed of 16 genera (Table 1).

The recognition of *Treiodous*, *Meloe* and *Eurymeloe* as genera requires three major structural modifications. First, the inclusion of *M. autumnalis* in *Treiodous*, as previously considered, must be rejected: according to our phylogenetic analyses, *M. autumnalis* is the sister lineage to *Meloe s. str.* (see Figure 1). Consequently, *M. autumnalis* is here transferred to the genus *Meloe*, rendering *Treiodous* endemic to the American continent (*Treiodous* type species: *Treiodous barranci* Dugès, 1869 [= *Meloe laevis* Leach, 1815], by monotypy). Second, *Meloe s. str.* (type species: *Meloe proscarabaeus* Linnaeus, 1758, by subsequent designation of Latreille, 1810) is redefined and limited to the species formerly included in the subgenera *Meloe* and *Anchomeloe* Iablokoff-Khnzorian, 1983, which is here revalidated from the synonymy of *Treiodous* to include the Palaearctic species *M. autumnalis* (type-species of *Anchomeloe* by monotypy). In this sense, we follow a conservative taxonomic approach and opted to maintain the status of *Anchomeloe* as a subgenus of *Meloe*, because (1) *Anchomeloe* and *Meloe* form a monophyletic group, and (2) lack of additional and detailed morphological studies revealing deep differences between *Meloe* (*Anchomeloe*) and *Meloe* (*Meloe*). Third, *Eurymeloe* (type species: *Meloe brevicollis* Panzer, 1793, by subsequent designation of Pinto & Selander, 1970) now includes all species formerly placed in the subgenera *Eurymeloe* and *Coleomeloe* (type species: *Meloe tuccia* Rossi, 1790, by monotypy). The high support recovered in our phylogenetic hypothesis for the inclusion of *E. tuccia* within *Eurymeloe* (see Figure 1) agrees with morphological hypotheses depicting a close relationship between these two taxa (Bologna, 2020b; Di Giulio et al., 2013; Selander, 1985).

Most of the other previous classified subgenera of *Meloe*, for which we lack molecular data (i.e. *Lasiomeloe* Reitter, 1911; *Chiromeloe* Reitter, 1911; *Listromeloe* Reitter, 1911; *Micromeloe* Reitter, 1911; *Meloenellus* Reitter, 1911; *Afromeloe* Schmidt, 1913; *Trapezimeloe* Pliginskij, 1935; *Desertimeloe* Kaszab, 1964 and *Alveomeloe* Pripisnova, 1987), are morphologically well characterized (Bologna, 1991; Bologna & Pinto, 1998, 2002; Kaszab, 1964) and do not appear to have any clear close relationship to one another nor to any of the genera included in our molecular phylogenetic hypothesis. In our opinion, they likely represent independent genera and should be treated as such pending the results of future phylogenetic analyses (Table 1).

4.2 | Patterns of transmarine dispersal and island colonization in the Western Palaearctic

Processes generating disjunct distributions of sister taxa (or intraspecific lineages) have long been the subject of discussions in the field of historical biogeography, with vicariance as the formerly preferred hypothesis to explain the origin of disjunct distribution patterns (De Queiroz, 2005). However, growing evidence gathered over the last decades supports dispersal (overseas and long-distance dispersal over land) followed by isolation as a more common process than previously thought (Bell et al., 2015; De Queiroz, 2005; McGlone, 2005; Measey et al., 2006; Waters & Roy, 2004). With respect to the transmarine dispersal and island colonization events within the Western Palaearctic region, our results based on a broad sampling of *Eurymeloe tuccia, E. mediterraneus* and *Meloe proscarabaeus*, do not show any geographic structuring of the multiple haplogroups detected, suggesting the existence of recurrent transmarine dispersal and extensive intraspecific gene flow across continents and islands, precluding the differentiation of endemic lineages. This scenario of geographically widespread species distributed on both the continent and islands without a clear phylogeographic structure has been observed for recently isolated islands located close to the mainland (Barej et al., 2014; Riccieri et al., 2017); however, it is uncommon for oceanic and long-isolated continental islands (Juan et al., 1995; Macías-Hernández et al., 2016; Mas-Peinado et al., 2018).

The geographic patterns of genetic diversity found in *Meloe s. str.* and *Eurymeloe* seem to be independent of common predictable drivers of long-distance colonization, such as dispersal by wind or ocean currents (Gillespie et al., 2012), and rather appear to be random. Phoretic behaviour on Apoidea could play a dominant role in the strong migratory ability and long-distance dispersal of this set of phoretic Meloini, which would explain the lack of evident lineage isolation and genetic divergence between geographically distant populations. Several bees and other flying insects (wasps and flies) are thought to have high dispersal abilities, including transmarine dispersal events (Kratochwil et al., 2018; Mikkola, 1984; Widmer et al., 1998). Well-studied taxa of Apoidea, such as the Western Palaearctic *Bombus* Latreille, 1802, have complex phylogeographic histories that include both ancient colonization, isolation and differentiation in the Canary Islands and recent colonization in Mediterranean continental islands (including the Balearic Islands) and the Atlantic oceanic island of Madeira, where local populations are genetically closely related to those from the continent (Kratochwil et al., 2018; Widmer et al., 1998). These patterns are also supported by direct observations of the long-distance migration of *Bombus* queens across open sea (Mikkola, 1984).

The observed phylogeographic pattern of intraspecific multiple dispersals across different time frames (from almost 1 Ma, in *M. proscarabaeus* to the Holocene, 0.16 Ma, in *E. mediterraneus*) is uncommon for most known groups inhabiting oceanic archipelagos, including some non-phoretic coleopteran and arachnid species, which have diversified following the isolation from their mainland sister lineages (Contreras-Díaz et al., 2003; Macías-Hernández et al., 2016; Mas-Peinado et al., 2018; Oromí, 1979). In fact, this pattern does not appear to be widespread even among phoretic Meloidae. Despite their potential to colonize oceanic islands, some species, including *E. fernandezi* and *E. flavicomus*, are restricted to the Macaronesian islands (Bologna, 1988, 1994; García, 2008; Pardo Alcaide, 1951; Ruiz & García-París, 2009). *Eurymeloe fernandezi* split from its sister lineage during the Middle Miocene (mean = 17.1, 95 HDP = 11.20–24.96 Mya), coinciding with the emergence of the oldest island of the Canary Archipelago at about 20 Ma (Juan et al., 2000). Many Atlantic species of *Eurymeloe*, including both Macaronesian and continental ones, such as *E. gomari*, *E. baamarani* (Ruiz & García-París, 2015), *E. pallidicolor* (Martínez de la Escalera, 1909) and *E. apivorus*, have a narrow geographic distribution (Bologna, 1988, 1991, 2020a; Ruiz & García-París, 2009, 2015; Di Giulio et al., 2013). The narrow geographic ranges of these phoretic species contrast with those of the widely distributed species *E. tuccia, E. mediterraneus* and *M. proscarabaeus*. Some studies have suggested that inter- and intraspecific trait variation can result in different phylogeographic structures among co-distributed species (Massatti & Knowles, 2014; Papadopoulou & Knowles, 2015). The heterogeneous distribution ranges and diverse phylogeographic patterns observed among species within Meloini might be related to traits such as host specificity (Bologna, 1991), fecundity (which can be as high as 9,500 eggs/clutch in the widespread *M. proscarabaeus*; Lückmann, 2001; Lückmann & Assmann, 2005) or even local adaptations of first-instar larvae to produce deceptive signals and behaviour towards Apoidea host species (Saul-Gershenz et al., 2018).

Meloini dispersal and colonization may also be associated with the population density of the bee host, occurring only when densities are very high. Within this framework, the hypothesis is that the larger the source population, the greater the colonization success (Herzig, 1995). Although our BSP analyses indicate a recent demographic expansion of phoretic Meloidae, starting around 50,000 years ago (Figure 4), many species of Meloini are present now at low abundances (Bologna, 1991; García-París & Ruiz, 2011; Pinto & Selander, 1970; Ruiz & García-París, 2008). Under this scenario, small population sizes could affect a species' long-distance dispersal ability via phoresy, making it a random process that hinders successful colonization of new areas.

Likewise, phoretic species with a relatively high population density or those in the midst of a demographic expansion may be more likely to disperse over long-distance and have greater colonization success. Consequently, they should present a wider distribution, as *E. mediterraneus*, *E. tuccia* and *M. proscarabaeus* do (García, 2008; García-París et al., 2006; Lückmann & Niehuis, 2009). Altogether, the positive relationship between phoretic behaviour and population density may increase the likelihood of success of a wide range of colonization events. Future work should focus on comparative phylogeographic and demographic analyses between parasites (Meloini) and host bees (Apoidea) including mainland and island populations to test for the existence of shared biogeographic histories.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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