

The molecular phylogeny of Omalidae (Coleoptera) defines the family limits and demonstrates low dispersal propensity and ancient vicariance patterns

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Abstract. The genus-level molecular phylogeny of Omalidae Lacordaire is presented for six of seven currently recognised genera. The monophyly and internal relationships are well-supported including the taxa which were placed in other elateroid families. We conducted molecular analyses using maximum-likelihood optimality criterion and Bayesian inference and 18S, 28S rRNA, *rrnL* and *cox1* mtDNA markers (4038 homologous positions). *Euanoma* Reitter is a sister lineage to other Omalidae. *Thilmanus* Gemminger is related to *Paradrilus* Kiesenwetter and *Phaeopterus* Costa. Thilmaniinae Kazantsev (erected in Lycidae), Euanomini Kazantsev (erected in Drilidae), and Paradrilinae Kundrata *et al.* are removed from within omalid classification due to widely overlapping concepts of generic and subfamilial taxa. *Pseudeuanoma* Pic, **syn.n.** was recovered as a paraphylum and is a younger synonym of *Euanoma*. *Euanoma caligo* (Kazantsev), **comb.n.**, *E. ionica* (Pic), **comb.n.**, *E. obscura* (Pic), **comb.n.** and *E. reitteri* (Pic), **comb.n.** are newly combined with *Euanoma*. The earlier classification of incompletely metamorphosed taxa was affected by the parallel evolution of morphological traits. We report on the discovery of the incompletely metamorphosed female of *Thilmanus obscurus* Baudi and compare it with the female of *O. fontibellaquei* Geoffroy. The female is weakly sclerotised, has physogastric abdomen, vestigial elytra, no wings and simplified thoracic morphology. Furthermore, we describe allopatric ranges of ancient omalid lineages and vicariance events resulting from geological transformations in the Mediterranean. *Euanoma* was split from other Omalidae in the late Jurassic and remains restricted to the Eastern Mediterranean. *Omalisus* Geoffroy split from the Iberian genera in the Cretaceous and most species occur on southern slopes of the Alps and in the western Balkan. The separation of *Paradrilus* and *Thilmanus* + *Phaeopterus* corresponds with the isolation of the Ebro and Hesperian massifs in the Cretaceous; the fauna of Sardinia and Corsica is of Iberian origin and *Phaeopterus* dispersed from these islands to the Elba and Apennine Peninsula. The diversity of Omalidae has an ancient origin, but survived till present only in the Mediterranean, mostly in Pleistocene refugia close to the sea.

Introduction

The processes responsible for the evolution of biological diversity are at the core of evolutionary research (e.g. Toussaint *et al.*, 2014). There are lineages with thousands of described species

and a cosmopolitan distribution, yet conversely, some lineages of a similar age consist only of a few extant species and are limited to restricted ranges. Densely sampled dated phylogenies are needed to reconstruct the evolution of each group and to provide insights into their evolutionary history. Here, we study the beetle family Omalidae Lacordaire (Coleoptera: Elateroidea); an ancient and species-poor group with incompletely metamorphosed females (Bocak *et al.*, 2008). The incomplete

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metamorphosis is hypothesised for all omalids (Crowson, 1972) although the females have been described only for two species of *Omalisus* Geoffroy (Bertkau, 1891; Ochs, 1949).

In traditional classifications not based on phylogenetic analyses, Omalidae had been placed in the ‘cantharoid lineage’, an artificial assembly of soft-bodied elateroid beetles, specifically as a sister or a part of the net-winged beetles (Kleine, 1933; Crowson, 1972). However, recent molecular phylogenetic studies have shown that Omalidae is closely related to Elateridae (Bocakova *et al.*, 2007; Kundera *et al.*, 2014; McKenna *et al.*, 2015). The limits of Omalidae have changed frequently and except for *Omalisus* all currently valid omalid genera were either described in a different elateroid family or subsequently excluded from Omalidae (Kleine, 1933; Wittmer, 1944; Crowson, 1972; Bocak & Brlik, 2008; Kazantsev, 2010). Omalidae include seven genera and 23 species (Table S1; Kundera *et al.*, 2015). The genera are placed into three subfamilies (Table S2; Kazantsev, 2010; Kundera *et al.*, 2015). Omalinae include *Omalisus* and the monotypic genus *Cimbrion* Kazantsev (earlier in *Phaeopterus* Costa and *Euanoma* Reitter; see Kleine, 1933; Kundera & Bocak, 2007). Thilmaninae were originally described as a monogeneric subfamily of Lycidae (Kazantsev, 2005), where *Thilmanus* Gemminger had already been transferred by Crowson (1972). Later, they were returned to Omalidae (Bocak & Brlik, 2008) and subsequently transferred to Drilidae (Kazantsev, 2010). Additionally, Kazantsev (2010) merged genera *Thilmanus*, *Pseudeuanoma* Pic and *Euanoma* in redefined Thilmaninae, and the subfamily is currently split into Euanomini Kazantsev (originally described in Drilidae) and Thilmanini Kazantsev. A further subfamily, Paradrilinae Kundera, Baena & Bocak was recently created for *Paradrilus* Kiesenwetter, the genus, which was – until recently – placed in Drilidae (Kiesenwetter, 1866; Wittmer, 1944; Bocak, 2007).

Recently, the alpha-taxonomy and morphology of Omalidae were intensively studied, and all historical type specimens dissected, redescribed and the results reported in two morphology-based alpha-taxonomic revisions (Kundera & Bocak, 2007; Bocak & Brlik, 2008). The highest numbers of species are placed in *Euanoma*, *Pseudeuanoma* (altogether 13 spp., two of them unnamed) and *Omalisus* (5 spp.), whereas the genera *Thilmanus*, *Phaeopterus*, *Paradrilus* and *Cimbrion* each contain only one or two species (Table S1). Almost all Omalidae, with the exception of the relatively common and widespread *Omalisus fontisbellaquei* Geoffroy are rare and mostly known only from the type or a few specimens. They occur in the Mediterranean region, which maintains a diverse fauna with a high number of endemic species, and is considered to be one of the world’s major biodiversity hotspots (Myers *et al.*, 2000). The northern Mediterranean was fragmented into several separate landmasses during the Cretaceous period (Dercourt *et al.*, 2000). The configuration of landmasses was later substantially affected by the collision between the African and Eurasian tectonic plates (Jolivet & Facenna, 2000). The currently contiguous Iberian Peninsula and southern France were split into the Ebro and Hesperian blocks during the Cretaceous (Callapez *et al.*, 2015). Furthermore, the Sardinia–Corsica block separated from Iberia due to the

opening of the Liguro-Provençal basin ~30 Ma (Mya; Jolivet & Facenna, 2000; Rosenbaum *et al.*, 2002; Speranza *et al.*, 2002; van Hinsbergen *et al.*, 2014). Tectonic processes define the current distribution of insects with low dispersal power, such as cave beetles (Ribera *et al.*, 2010; Cieslak *et al.*, 2014). Similarly, the incompletely metamorphosed taxa of Elateroidea are unable to cross even shallow sea straits and their distribution depends strongly on the connectivity of landmasses (Malohlava & Bocak, 2010; Masek *et al.*, 2015). The Pleistocene aridisation and cooling destroyed wet European subtropical forest habitats which are crucial for the survival of Omalidae. Broadleaved forests were reduced to refugia in the southernmost Europe and Asia Minor during the Pleistocene, such as in western Greece, and in western and southern Turkey and the eastern coast of the Black Sea (Provan & Bennet, 2008; Médail & Diadema, 2009).

The type genera of Thilmaninae and Euanomini were not sampled in recent molecular analyses (Kundera *et al.*, 2014, 2015). The aim of the present study is to provide a robustly supported hypothesis on the limits of Omalidae and the relationships between genera with expanded, almost complete sampling of all genera. Furthermore, we reconstruct the evolutionary history of the family using the dated phylogeny. We specifically ask how the distribution and diversification of Omalidae was affected by the tectonic and climatic history of the Mediterranean. These data enable us to identify the centres of diversity in the currently semiarid region. Furthermore, we report on the discovery of the incompletely metamorphosed, wingless female of *Thilmanus*. Most incompletely metamorphosed and larviform elateroid females are only hypothesised based on the phylogenetic relationships with taxa for which incompletely metamorphosed females are known, on the similar morphological modifications of conspecific males, such as a small-bodiedness, tiny mouthparts and weak sclerotisation compared to relatives, and because of the absence of females in all collections. The discovery of the *Thilmanus obscurus* female is important in understanding the gradual character of ontogenetic modifications in elateroid lineages.

Material and methods

Laboratory procedures and sequence handling

Euanoma sp. and *Thilmanus obscurus* Baudi were sequenced for 18S rRNA (~1900 bp), the D2 loop of 28S rRNA (~700 bp), *rnl* mtDNA (~550 bp) and the *cox1-3'* end of mtDNA (723 bp), and the sequences were combined with homologous fragments in a supermatrix (Table S1). The outgroup consisted of seven elateroid families and the scirtoid family Decliniidae (Fig. 1). Wizard SV96 kit (Promega, Madison, WI, U.S.A.) was used for DNA isolation. The PCR settings and sequencing procedures follow those reported by Bocakova *et al.* (2007). The chromatograms were edited using the SEQUENCHER 4.9 software package (Gene Codes Corp., Ann Arbor, MI, U.S.A.). The sequences were submitted to GenBank under Accession Numbers KY963523–30 (Table S3).

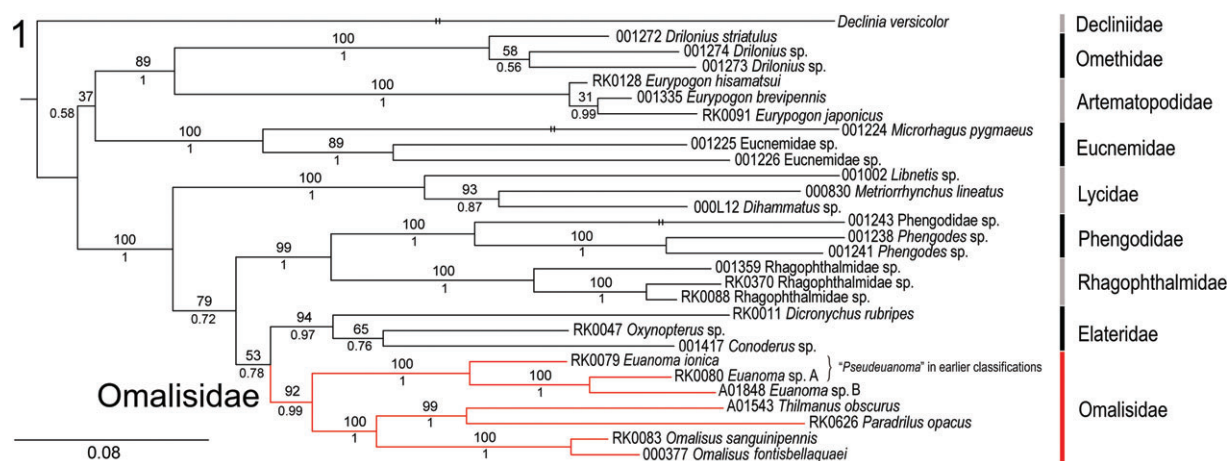


Fig. 1. The molecular phylogeny of Omalidae with bootstrap support values (BS, above branches) and posterior probabilities values (PP, below branches). [Colour figure can be viewed at wileyonlinelibrary.com].

Phylogenetic analyses

All analyses were repeated with/without *Phaeopterus unicolor* Costa for which only the *cox1* mtDNA fragment is available. The presence of this taxon negatively affected bootstrap support values (BS). Both datasets were aligned using MAFFT 7.017 (Kato & Standley, 2013) in GENEIOUS R7.1.9 (Biomatters Inc., Auckland, New Zealand) under the G-Ins-i algorithm. The concatenated supermatrices were partitioned for all fragments and codon positions when appropriate. We used the maximum-likelihood (ML) criterion and Bayesian inference for phylogenetic analyses. The ML searches were conducted in RAXML 8.2.3 (Stamatakis, 2014) on the CIPRES cluster (Miller *et al.*, 2010) with the GTRCAT model identified using jMODELTEST 2.1.7 (Darriba *et al.*, 2012) and BS were calculated from 500 pseudoreplicates using the GTRGAMMA model. The Bayesian inference was run in MrBAYES 3.2.6 (Ronquist *et al.*, 2012) under the GTR + I + G model identified as above for 6×10^7 generations, sampling a single tree every 1000 generations. The first 1000 trees were discarded as burn-in after the identification of the stationary phase and the effective sample size (ESS) in TRACER 1.5 (Drummond *et al.*, 2012). Posterior probabilities (PP) were calculated from the post-burn-in trees. All trees were visualised in FIGTREE 1.4.2 (<http://tree.bio.ed.ac.uk/software/figtree>).

Divergence dating

A single omalid fossil record was reported from the late Eocene Baltic Amber, but the genus is extinct and has an unclear position (Kirejtshuk & Kovalev, 2015). Therefore, we are not able to set its age as a prior for any extant lineage and we used the calibration prior dating the origin of Elateridae to the early Jurassic 201.0–190.8 Ma (Hettangian/Sinemurian deposit; Whalley, 1985). Alternatively, we applied a shallower calibration prior for the origin of Elateroidea (stem) at 152.0 Ma following McKenna *et al.* (2015). This prior represents the shallowest

estimation in the recent dating analyses of beetles (Toussaint *et al.*, 2017). We estimated the most recent common ancestor for Omalidae in BEAST 1.8.2 (Drummond *et al.*, 2012) with the HKY + I + G substitution model, uncorrelated relaxed clock model and birth–death process tree prior as recommended in the manual. The jMODELTEST 2.1.7 analysis recommended the GTR + I + G substitution model. Nevertheless, the second-best model HKY + I + G was applied as the best model did not reach the convergence if the stationary phase was checked in TRACER 1.5 (<http://beast.bio.ed.ac.uk/Tracer>). The ML tree was used as a strict topology for dating analyses. Both analyses ran for 6×10^7 generations sampling a single tree every 12 000 generations. The consensus tree was computed with TREEANNOTATOR 1.8.2 (<http://beast.bio.ed.ac.uk/treeannotator>) after eliminating a part of trees as a burn-in after evaluating ESS in TRACER 1.5. The final trees were visualised in FIGTREE 1.4.2.

Distribution

The literature on type localities and the collections of the Naturhistorisches Museum (Basel), Naturkundemuseum (Berlin), Zoologisches Forschungsmuseum Alexander Koenig (Bonn), Natural History Museum (London), Deutsches Entomologisches Institut (Münchenberg), Museum national d'histoire naturelle Paris (Paris), Přírodovědecké muzeum, Národní muzeum (Prague), Staatliches Museum für Naturkunde (Stuttgart), Zoologische Staatssammlung (Münich), Moravské zemské muzeum (Brno) and Muzeum i Instytut Zoologii, Polska Akademia Nauk (Warsaw) were searched for distribution data. Sometimes information was incomplete and only a country was given. These data were omitted from further analyses.

Results

The dataset contained 18S rRNA (29 specimens including outgroups), the D2 loop of 28S rRNA (28 spec.), *rnl* mtDNA (26 spec.) and the *cox1*-3' end of mtDNA (27 spec.). The

concatenated dataset consisted of 4038 homologous positions: the alignments of the *18S*, *28S*, *rrnL* and *cox1* fragments contained 2009, 760, 546 and 723 homologous positions, respectively. The phylogenetic trees inferred using the ML criterion and Bayesian inference were well-resolved (Fig. 1, Figures S1–S3). *Phaeopterus* was a sister to *Thilmanus* when *Phaeopterus unicolor* was included (BS 67%; Figure S1). All recovered topologies (i.e. with/without *Phaeopterus*) contained the *Euanoma* s.l. clade, *Thilmanus* + *Paradrilus* (+*Phaeopterus*) clade and *Omalisus* clade (Fig. 1, Figure S1). The monophyly of Omalidae was better supported in the analyses without *Phaeopterus unicolor* (BS 92% for the monophyly of Omalidae in contrast with BS 84% if *Phaeopterus* included). All shallower relationships obtained BS $\geq 99\%$ and PP 1.0 in the analyses of the dataset without *Phaeopterus* and slightly lower support in the analyses in which *Phaeopterus* was included (compare Fig. 1, Figure S1).

The dataset without *Phaeopterus* (i.e. taxon sampling as in Fig. 1) was used for dating analyses. If the calibration prior was set to the presumed time of the origin of Elateridae (201.0–190.8 Ma; Whalley, 1985), the analysis dated the deepest split in Omalidae to the middle Jurassic (174.9 Ma, 95% confidence interval CI 207.3–142.4 Ma). Furthermore, the western lineages diversified in the Early Cretaceous; the split between the clades *Thilmanus* + *Paradrilus* and *Omalisus* was inferred at 139 Ma (95% CI 172.0–101.1 Ma). The deepest split in the *Euanoma* clade was recovered at 65.1 Ma, close to the Cretaceous/Palaeogene boundary. The alternative dating analysis using the shallower calibration prior (McKenna *et al.*, 2015) dated the origin of Omalidae in the Turonian stage of the Upper Cretaceous at 85.9 Ma (95% CI 107.9–65.5 Ma). All of the subsequent splits within Omalidae were similarly shallower (Fig. 2, Figure S4).

Geographical distribution and diversity

A total of 105 geographical records were compiled from major European collections and literature for all Omalidae species except the widely distributed *O. fontisbellaquei*. The distribution data are summarised in Fig. 3 and Table S4. The ranges of the *Euanoma* clade, *Omalisus* clade and *Thilmanus* (+*Phaeopterus*) clade are allopatric. The eastern clade is represented by *Euanoma* s.l., which includes *Pseudeuanoma*. These species occur on the islands of Corfu and Cephalonia, in the western part of the Peloponnese Peninsula, in the western and southern coastal regions of Turkey, and in the wet subtropical forests in the southern and southeastern slopes of the Caucasus in Russia, Georgia and the eastern part of the Black Sea coast of Turkey. The genera *Omalisus* and *Cimbrion* occur in the central part of the Mediterranean basin and adjacent regions, in the southern slopes of the Alps, the Balkan Peninsula, the Northern Apennines, in Central and Western Europe, and northwestern Turkey. *Paradrilus* and *Thilmanus* occur exclusively in the landmasses of the Mesozoic Iberian massif (i.e. including adjacent southernmost France, Sardinia and Corsica). The range of *Phaeopterus unicolor* overlaps

with the range of the *Paradrilus* + *Thilmanus* clade (Fig. 3) and additionally reaches the western coast of the Apennine Peninsula. Most Mediterranean species occur in the coastal regions; only *Omalisus sanguinipennis* Laporte was recorded ~180 km from the sea on the southern slopes of the Alps, and two species *E. elongata* Pic and *E. kolchica* Kazantsev were recorded on the southern slopes of the Caucasus 130–270 km from the Black Sea coast (Table S4, Figure S4).

Female morphology of *Thilmanus obscurus* (Figs 4–6, 13, 15)

Adult

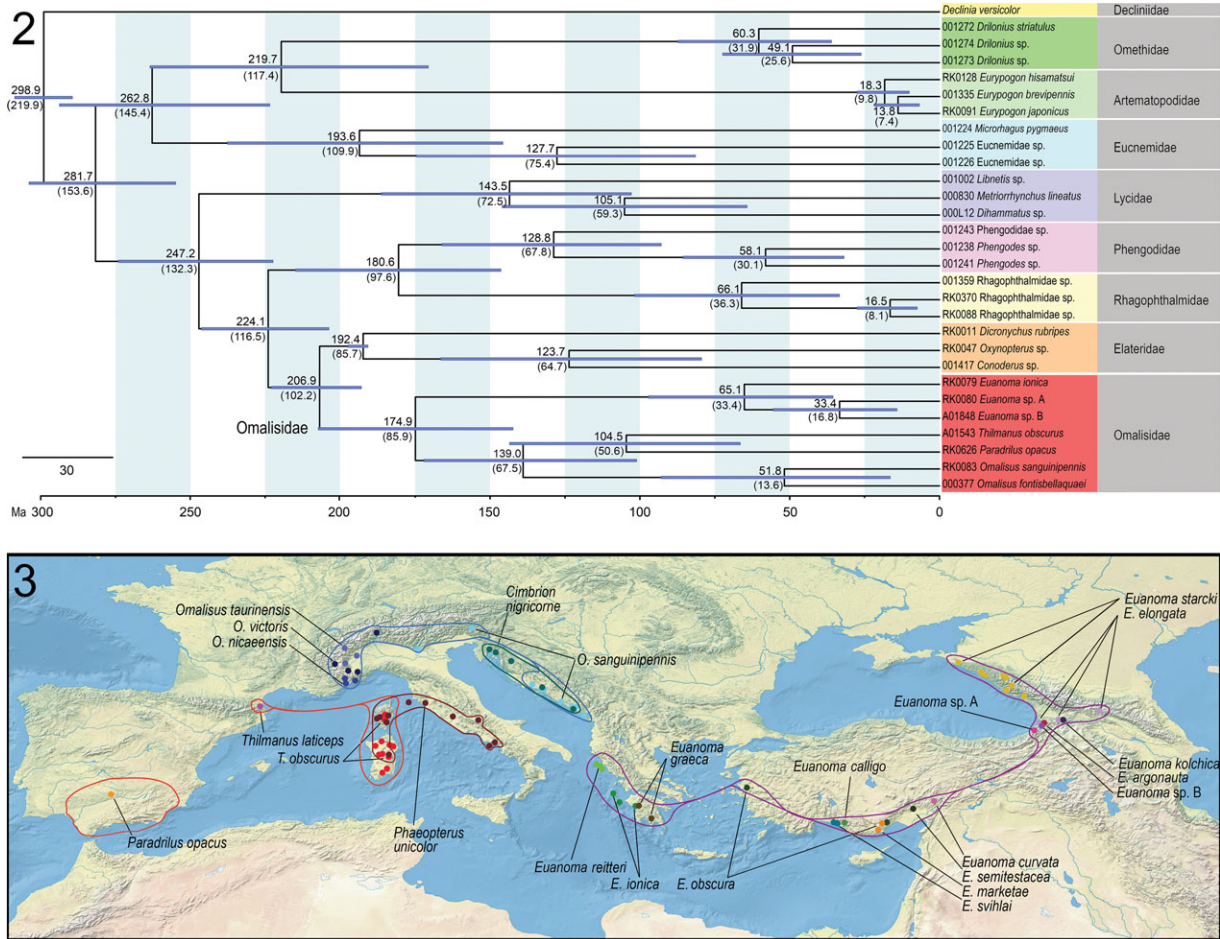
Body minute, slender, 3.4 mm long, weakly sclerotised, abdomen physogastric (Figs 4–6). Head small, cranium longer than wide, with deep median longitudinal groove, eyes widely separated, small, 0.07 mm in diameter, each with 10–11 ommatidia; mouthparts minute, mandibles slender, slightly curved, maxillary palpi 4-segmented, basal palpomere short, palpomere 2 longest, about 2× longer than wide, palpomere 3 transverse, apical palpomere triangular, pointed; labial palpi 3-segmented, apical palpomere triangular, pointed; antennae filiform, robust, 0.58 mm long, with 11 antennomeres, scapus and pedicel dark brown to black, sclerotised, antennomeres 3–11 less pigmented, possibly weakly sclerotised, antennomeres 4–10 wider than long, bearing long sparse setae. Prothorax 1.46× wider than long at midline, slightly wider than mesothorax, pronotum flat, without any keels, disc with sparse long setae, shape of pronotum as in Fig. 4. Prosternum transverse, without median prosternal process, with Y-shaped internal furca. Mesothorax transverse, frontal margin emarginate, without clearly visible sutures, metathoracic sclerites weakly sclerotised and pigmented, without sutures and keels, metathorax about 2.5× longer than mesothorax, apparently longer than prothorax, metasternum without midline; metendosternite absent. Elytra as long as mesothorax, widely rounded apically, with sparse, long setae, hindwings absent. Abdomen with free segments, widest at abdominal segments 2–4, about 1.5× wider than thorax in widest part, slender apically, sparsely pubescent. Ovipositor with weakly sclerotised, apically slender coxites, paraproctal baculi rod-like, relatively short, styli minute. Legs adult-like, fully segmented, coxae and trochanters long, trochanters obliquely attached to femora, femora and tibiae slender, flat, tarsi pentamerous.

Measurements

Body length 3.4 mm, length of head 0.28 mm, eye diameter 0.07 mm, antennae length 0.58 mm, prothorax length 0.28 mm, prothorax width 0.41 mm, width at humeri 0.63 mm, mesothorax length 0.24 mm, metathorax length 0.29 mm, abdomen length 2.09 mm.

Sexual dimorphism in *Thilmanus obscurus*

The detailed description of the male was given by Bocak & Brlik (2008). The female (Figs 4–6, 13, 15) differs from



Figs. 2–3. (2) The dated tree showing two different node ages according to divergent calibration priors. Alternative divergence time estimations based on the prior applied by McKenna *et al.* (2015) are displayed in the brackets. (3) The distribution of Omalissidae. [Colour figure can be viewed at wileyonlinelibrary.com].

the male (Figs 11, 14, 16) in the slender cranium (the cranial length/width behind eyes ratio 1.25 and 1.45 in male and female, respectively; cf. Figs 13, 14); in the reduced number of ommatidia (Figs 13, 14); the shorter, triangular antennomeres 3–10 (compare the shape of the male and female antennomere 6 in Figs 15, 16); the surface of the pronotal disc smooth, the obtuse lateral pronotal margins and the widely rounded posterior pronotal angles; in the short elytra and absent wings; in the absent metasternal midline and metendosternite; in the shorter legs and in much longer abdomen. The female is so weakly sclerotised, that the cranium of the available dry mounted specimen partly collapsed and the thorax and abdomen are flat (Figs 4–6, 11).

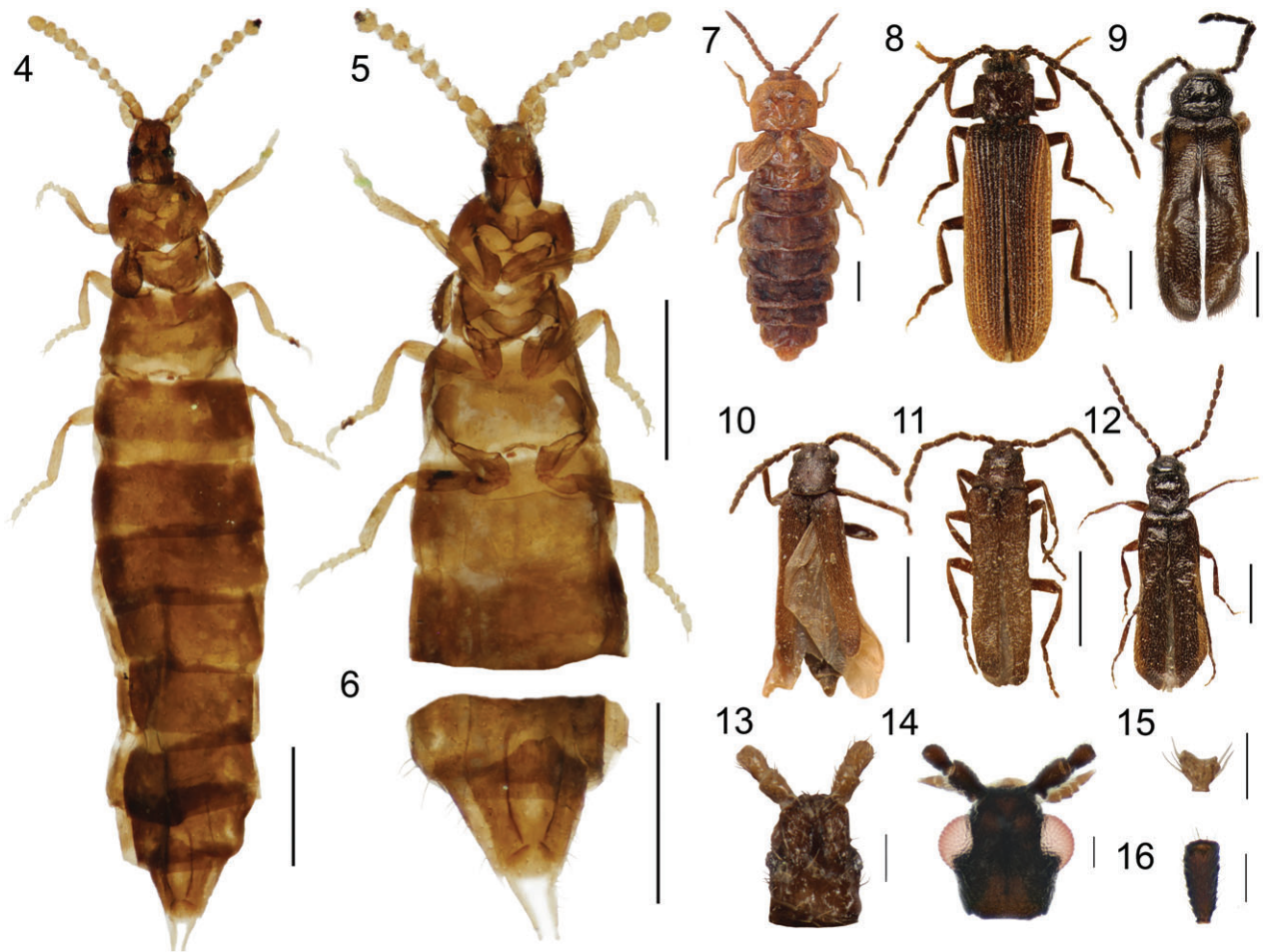
Biology and collecting circumstances

The female specimen of *Thilmanus obscurus* was collected by soil-washing and Berlese extraction, in association with other beetles characterised by adaptations to endogean life

[*Typhloreicheia* Holdhaus (Carabidae), *Scotonomus* Fauvel (Staphylinidae) and *Langelandia* Aube (Zopheridae)] and with small subendogean pulmonate gastropods (*Hypnophila* Bourguignat). The soil sample was extracted up to the depth of about 50 cm at the base of *Ceratonia siliqua* tree, in a site situated on Palaeozoic granites (Sardinia: San Vito, San Priamo, 60 m, 1 March 2010, leg. L. Fancelli) and characterised as the Mediterranean maquis with the dominance of *Pistacia lentiscus* and the *Olea europaea* trees.

Discussion

The phylogenetic position of Omalissidae in close relationship with Elateridae has been recovered by current analyses although it obtained low support. The currently recovered relationships are congruent with the results of earlier studies which used rRNA and mtDNA markers but the substantially different number of taxa (Bocakova *et al.*, 2007; Kundera *et al.*, 2014), mitogenomes (Timmermans *et al.*, 2016) and eight nuclear



Figs. 4–16. General appearance of Omalidae. (4–6) *Thilmanus obscurus* Baudi, 1872, female: (4) dorsal view, (5) ventral view, (6) abdomen, ventral view. (7,8) *Omalidis fontisbellaquei* Geoffroy, 1785: (7) female, dorsal view, (8) male, dorsal view. (9) *Euanoma* sp. B. (10) *Phaeopterus unicolor* Costa, 1857. (11) *Thilmanus obscurus*. (12) *Euanoma ionica* (Pic). (13–16) *Thilmanus obscurus*: (13) head, female, (14) head, male, (15) antennomere 6, female, (16) antennomere 6, male. Scale bars 0.5 mm (4–6), 1 mm (7–12), 0.1 mm (13–16). [Colour figure can be viewed at wileyonlinelibrary.com].

markers (McKenna *et al.*, 2015; in this case Omalidae were in the clade with two elaterid taxa Agrypninae: Drilini and Cardiophorinae, McKenna's study did not recover Elateridae as a monophylum). However, all molecular relationships are in conflict with the morphology-based analyses, which recovered Omalidae related to soft-bodied Lycidae, Lampyridae and other cantharoid lineages (Crowson, 1972; Lawrence, 1988; Lawrence *et al.*, 2011). Molecular phylogenetic analyses do not support the paraphylum consisting of Omalidae and Lycidae (Lawrence *et al.*, 2011) nor the sister relationship Lycidae + Omalidae (Crowson, 1972). We suppose that these conflicting results can be attributed to the morphology of the unrelated elateroid lineages affected by an incomplete metamorphosis (Bocakova *et al.*, 2007; Kundrata *et al.*, 2014). Similarly, Lawrence *et al.* (2011) recovered extremely modified Podabrocephalidae in the 'cantharoid clade' (now Podabrocephalinae in Byrrhoidea: Ptilodactylidae, McKenna *et al.*, 2015). Therefore, we prefer the relationships Omalidae + Elateridae as recovered

by all molecular analyses (Fig. 1; e.g. Bocakova *et al.*, 2007; Kundrata *et al.*, 2014; McKenna *et al.*, 2015). We suggest that the homology of the character states which might be affected by the incomplete sclerotisation and retention of larval characters (designated as partial neoteny *sensu* Gould, 1977 or as incomplete metamorphosis in this study) should be tested by an independent phylogenetic signal such as those provided by molecular data.

The sampling of all omalids genera, with the exception of *Cimbrion*, provides strong evidence for the monophyly of the family (Fig. 1, Figures S1, S2; Tables S1, S2). The earlier placement of *Euanoma* in Drilidae proposed by Crowson (1972) and *Thilmanus* in Lycidae or Drilidae proposed by Crowson (1972) and Kazantsev (2005, 2010), are rejected. Our analyses suggest Omalidae as a monophylum with the sister position of the *Euanoma* and the (*Omalidis*(*Thilmanus*, *Paradrilus*)) clades.

We recovered *Pseudeuanoma* as a paraphylum in the *Euanoma* clade. Three species were represented in the dataset: *P. ionica*

(the type species of *Pseudeuonoma*), an undescribed species which differs from *P. ionica* only in the shape of male genitalia and an undescribed species of *Euanoma* which was recovered in a terminal position. Kundera & Bocak (2007) published detailed redescrptions of all species and found that these two genera are morphologically similar; the only well-defined morphological differences between the type species of *Pseudeuonoma* and *Euanoma* are the relative width of the pronotum and the slender, minute body of *Pseudeuonoma*. Given that the current phylogeny is robust (Fig. 1, Figures S1, S2) and that there are no known morphological synapomorphies which support an independent position for *Pseudeuonoma*, we propose *Pseudeuonoma* Pic as a junior synonym of *Euanoma* Reitter. As a result, we propose *Euanoma caligo* (Kazantsev) **comb.n.**, *E. ionica* (Pic) **comb.n.**, *E. obscura* (Pic) **comb. n.** and *E. reitteri* (Pic) **comb.n.** as new combinations.

Paradrilus, *Thilmanus* and *Phaeopterus* formed a monophylum and were recovered as a sister clade to *Omalisus* (BS 80%, PP 1.0; Figures S1, S2) and *Phaeopterus* + *Thilmanus* were sister taxa (BS 67%). The position of *Phaeopterus* was studied previously by Kundera *et al.* (2015) and the genus was recovered as a sister taxon to *Omalisus*, albeit without any bootstrap support. Kundera's results are congruent with the traditional placement (Kleine, 1933), but in contrast with similar male genitalia of *Thilmanus* and *Phaeopterus* (Bocak & Brlik, 2008). Currently, the relationship of these two genera is supported by three lines of evidence. (i) The topology recovered using the sequence of *cox1* mtDNA (Figure S1); the rapidly evolving mitogenomic markers, such as *cox1* mtDNA, were not designed for phylogenetics, but they can provide the phylogenetic signal if terminals represented by a single mtDNA fragment are included in a multi-marker dataset (Zhou *et al.*, 2016). (ii) Their relationship is supported by similar male genitalia: *Phaeopterus* differs from *Thilmanus* in the presence of pronotal keels and elytral costae; these morphological structures are frequently lost when the adult is miniaturised (Bocak *et al.*, 2016). (iii) The partly overlapping ranges of *Phaeopterus* and its sister-taxon *Thilmanus* (Fig. 3) can be explained by a common origin; the alternative hypothesis must place the origin of *Phaeopterus* in a different landmass, and assume the rapid dispersal to the western coast of the recently formed central part of the Apennine Peninsula, extinction in the ancestral range and along the dispersal route, and dispersal to Sardinia and Corsica.

With the revised limits of the family and the synonymisation of *Pseudeuonoma*, four omalid lineages are recovered which could be classified as subfamilies: Omalisiinae (*Omalisus* and possibly *Cimbrion*), Thilmaniinae (*Thilmanus* and newly *Phaeopterus*), Paradrilinae (*Paradrilus*) and Euanomiinae (*Euanoma* only, a potential new status for the former tribe Euanomini proposed in the subfamily Thilmaniinae in Drilidae *sensu* Kazantsev, 2010). However, Thilmaniinae and Euanomiinae were proposed in other families and the generic and subfamilial classifications widely overlap (Tables S2, S5). Therefore we propose to remove subfamilial and tribal classification from within Omalidae (Table S1).

Incomplete metamorphosis in Omalidae

Most incompletely metamorphosed beetle females (i.e. neotenic forms *sensu* Gould (1977)) are recorded from Elateroidea and only a few forms are known from other beetle superfamilies (Crowson, 1972; Gould, 1977; Bocakova *et al.*, 2007; Bocak *et al.*, 2008, 2016; McMahon & Hayward, 2016). Many elateroid taxa with incompletely metamorphosed close relatives are known only in males and their fully larviform or incompletely metamorphosed females are hypothesised. Only recently, molecular studies have gradually begun to identify additional conspecific males and females (Masek *et al.*, 2015). Incompletely metamorphosed females have been confirmed in two *Omalisus*: *O. fontisbellaquei* (Figs 7, 8) and *O. nicaeensis* Lesne (Bertkau, 1891; Ochs, 1949; Burakowski, 1988) and, in the absence of females, incomplete metamorphosis was predicted for all Omalidae (Crowson, 1972). Here, the discovery of the *T. obscurus* female confirms the hypothesised incomplete metamorphosis in another genus of Omalidae.

The level of morphological modifications of incompletely metamorphosed males and females is variable and in some cases correlated between sexes (Bocak *et al.*, 2008, 2016). Males and females of *O. fontisbellaquei* are less modified than the respective sexes of *T. obscurus* (Figs 4–7). The male of *T. obscurus* is less sclerotised (Fig. 8); its tentorium consists only of vestigial ventral arms and the tentorial bridge is absent; the apical palpomeres are pointed at the apex; the lateral pronotal carinae are vestigial; the prosternum is shorter and does not have the posterior median process; the elytra are soft and flat, have no longitudinal costae and their lateral margins are not coadapted with the abdomen; the elytral pleuron is much shorter and present only at the elytral humeri. The females of both genera have a physogastric abdomen, vestigial elytra, absent wings, shortened appendages and a simply shaped pronotum. Compared with *Omalisus fontisbellaquei*, the female of *Thilmanus obscurus* is also much less sclerotised, has a slender, freely movable head, a low number of ommatidia, a simpler pronotum, shorter elytra without any costa-like structures, a more simplified structure of meso- and metathoracic sclerites, no metasternal midline and a much longer, larviform abdomen (Figs 4–6). The *Thilmanus* male is so modified that its morphology has several traits similar to Lycidae (Crowson, 1972; Kazantsev, 2005) and Drilidae (Kazantsev, 2010). The known incompletely metamorphosed females of Drilini and larviform Lycidae keep more larval traits than *Omalisus* and *Thilmanus*. The female of *Drilus* has only the head and legs metamorphosed and the neotenic females of Lycidae keep larval morphology except the presence of female genitalia and a different structure of cuticle (Bocak *et al.*, 2008; Masek *et al.*, 2015).

Modified metamorphosis and morphology-based phylogeny

The metamorphosis of holometabolous insects is affected by gradual changes in concentration of 20-hydroxyecdysone and juvenoid hormones (Naisse, 1970; Zhou & Riddiford, 2001; Suzuki *et al.*, 2008; McMahon & Hayward, 2016). In contrast

with the gradual character of modifications of metamorphosis and gradually increasing degrees of imaginalisation of adult females and males, some authors discriminate neoteny as a case when sexually mature individual is completely larviform and incomplete metamorphosis in all other cases when females differ from fully sclerotised and winged relatives (e.g. Cicero, 2008; Jeng, 2008; but see Gould, 1977, who designates as neoteny all cases when an animal, in becoming adult, retains some infantile characters). The conspecific males of neotenic or incompletely metamorphosed females are regularly soft-bodied unlike beetles which lost wings in both sexes as an ecological adaptation (e.g. some cave-dwelling beetles). If neoteny and incomplete metamorphosis are the result of a modified hormonal control system of the transition process from larva to adult, and if this similar modification evolve independently in unrelated lineages, this fact must be considered when relationships are inferred from morphology.

The long list of proposed phylogenetic relationships for Omalidae genera in various elateroid families indicates a high level of uncertainty in the recent morphological analyses. We suggest that unrelated organisms can develop similar morphological traits if their metamorphosis is incomplete; for example, similarly modified females are known in females of *Drilus concolor* and *Thylodrilus contractus* Motschulsky (Bocak *et al.*, 2010; Bousquet, 1990) and in the males of *Dexoris chome* Bocak, Grebennikov & Masek and females of *Omalisus fontisbellaquei* (Fig. 7, Bocak *et al.*, 2013). Numerous phenotypic traits present in neotenic and incompletely sclerotised elateroids were considered homologous because they are similar, and no evidence has indicated their multiple origins (Crowson, 1972; Kazantsev, 2005, 2010). As a consequence, the morphology-based phylogenetic analyses recovered cantharoid families as the monophylum which consists of soft-bodied and incompletely sclerotised forms (Lawrence *et al.*, 2011). In contrast with them, the molecular phylogenies (e.g. Kundrata *et al.*, 2014; McKenna *et al.*, 2015) indicate that phenotypically similar neotenic forms (e.g. *Platerodrilus* Pic, *Lyropaeus* Waterhouse, *Phengodes* Illiger) and incompletely metamorphosed forms (e.g. *Lampyrus* L., *Drilus*, *Omalisus* + *Thilmanus*, *Phosphaenus* etc.) evolved multiple times. The incorrect homologation of similar morphological traits in Lycidae, Omalidae and Drilini led to unstable classification of the omalid genera (Crowson, 1972; Kazantsev, 2005, 2010).

Origin and phylogeography of Omalidae

We tested two different calibration points and the earliest split in Omalidae was dated either to the Toarcian–Aalenian period of the Jurassic (175 Ma, 95% CI 207–142) or to the Santonian age of the Late Cretaceous (86 Ma, 95% CI 108–66) depending on the calibration prior. The deeper calibration is deemed more reliable in accordance with Toussaint *et al.* (2017) because the shallower calibration (McKenna *et al.*, 2015) proposes some unrealistic dates for two specific splits. (i) The deepest split in Elateridae is dated at 86 Ma in conflict with the presence of highly diversified Elateridae in the Kimmeridgian and

Oxfordian stage of Karatau (163.5–152.1 Ma; Doludenko *et al.*, 1990; Figure S3). These fossils were used for the calibration of the stem of Elateroidea by McKenna *et al.* (2015). We used representatives of Cardiophorinae and Agrypninae in our analyses which represent early split lineages of Elateridae (see Kundrata *et al.*, 2014) and the recovered deepest split within Elateridae differs only by ~15 Ma from the stem age of Elateridae (Fig. 2). (ii) The split between Neotropical Phengodidae and Oriental Rhagophthalmidae (Bocakova *et al.*, 2007, Kundrata *et al.*, 2014, McKenna *et al.*, 2015), both neotenic lineages with very limited dispersal ability, is inferred at 98 Ma (95% CI 118–76), yet at that time continents were already separated (Fig. 17).

The detailed comparison of various results is complicated by the polyphyly of Elateridae in the topologies dated by McKenna *et al.* (2015) that included five elaterid taxa (*Lissomus* Dalman, *Selonodon* Latreille, *Cardiophorus* Eschscholtz, *Ampedus* Dejean and *Drilus* Olivier, the last designated as Drilidae; this latter is not to be mistaken for Drilidae: *Ototretadrilus* Pic in McKenna's fig. 9, which is Lampyridae as stated by the authors elsewhere in their study). In McKenna's dating analysis, Elateridae were recovered as three distant lineages and an Elateridae calibration point was applied to the stem of whole Elateroidea, which is a considerably deeper node (McKenna *et al.*, 2015, current analysis, see Fig. 2). As a result, McKenna *et al.* (2015) recovered the split of Omalidae and Elateridae part (Cardiophorinae + Agrypninae: Drilini) at 108.65 Ma, significantly later than the earliest Elateridae fossils from the Karatau deposits (163.5–152.1 Ma). Toussaint *et al.* (2017) reanalysed the McKenna *et al.* dataset and dated the origin of Elateroidea at 246.02 Ma. These authors excluded all Elateroid fossils from their calibration set and therefore this age is inferred only from the non-Elateroid calibrations. Due to the uncertainty of such analyses, we consider both the shallower and deeper dates in further discussion (Fig. 2, Figure S4).

Using the deeper calibration point, we recovered the origin of Omalidae overlapping with the period of higher connectivity between hypothesised ranges of principal omalid lineages (Golonka, 2004). All recovered deep divergences are ancient enough to set the diversification of Omalidae to periods when south-west Eurasia was formed by several separate landmasses (Fig. 17). The eastern Mediterranean clade contains only *Euanoma* and is limited to the eastern Mediterranean and the eastern coast of the Black Sea (Figs 1, 4). *Euanoma* has been recorded only from the interconnected landmasses of the Eastern Mediterranean which contains the Cretaceous Eoalpin orogen, now a part of the southern Balkans, Asia Minor and southern Caucasus region (see the Eoalpin orogen, Anatolia plateau and Cimmeria plate in Fig. 17, Robertson & Dixon, 1984). The hypothesised distribution of *Euanoma* in the Cretaceous is shown in Fig. 17.

The central Mediterranean clade contains *Omalisus* and *Cimbrion*. These genera are represented by five species with ranges from the southeastern France to the southwestern part of the Balkan peninsula (Croatia, Bosnia and Montenegro) and one widespread species, *O. fontisbellaquei*. All Mediterranean species occur in a belt passing from the southern slope of the

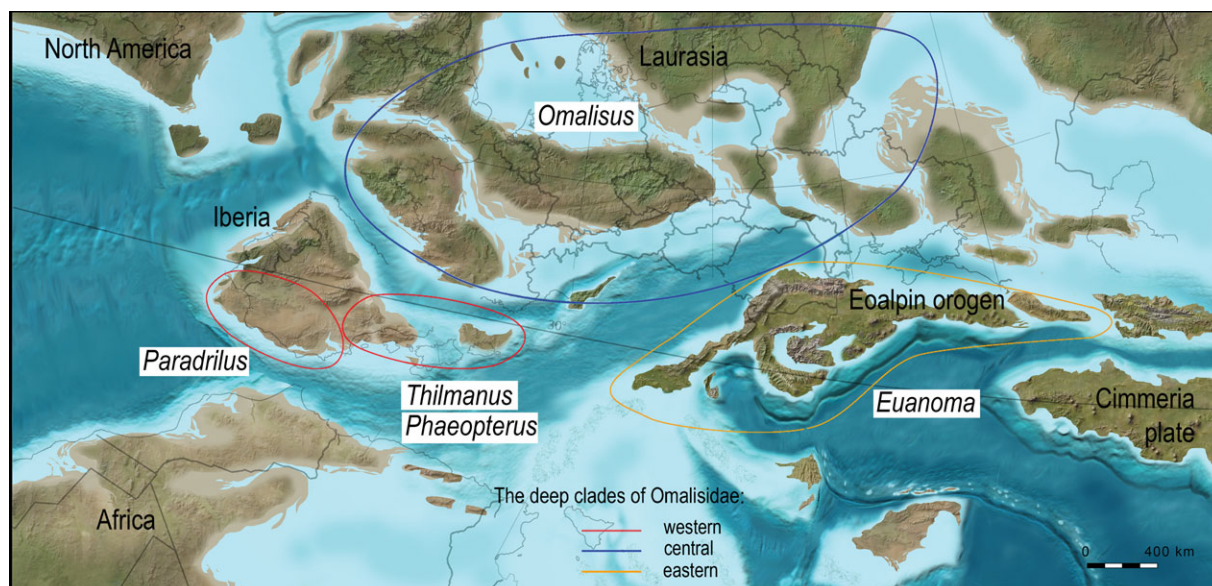


Fig. 17. The hypothesised distribution of Omalisidae in the Cretaceous, about 100 Ma (The map was provided by *Paleogeography of Europe* ©2011 Colorado Plateau Geosystems Inc.). [Colour figure can be viewed at wileyonlinelibrary.com].

western Alps, through the ancient sea coast of the Po valley to the coastal region of the Adriatic Sea (Croatia and Montenegro; Figs 3, 8; Table S1; Bocak & Brlik 2008). *Omalisus fontisbellaquei* are known from France, Central Europe, the Balkans and the Apennines.

The western Mediterranean clade (i.e. *Paradrilus*, *Thilmanus* and possibly *Phaeopterus*) is distributed in the landmasses with an Iberian origin, which includes the present-day Iberian peninsula including northeastern slopes of the Pyrenees, Sardinia and Corsica (Fancello & Rattu, 2015; Fanti & Vitali, 2014; Kundrata *et al.*, 2015). *Paradrilus* has been recorded only in the former Hesperian massif of the present-day Iberian peninsula (Table S2). *Thilmanus* occur in the landmasses derived from the Ebro massif including the Corsica–Sardinia block (Callapez *et al.*, 2015). When deep calibration is considered (104.5 Ma; 95% CI 66.5–143.5), the split between *Paradrilus* and *Thilmanus* (+*Phaeopterus*) clades is congruent with the fragmentation of Iberia into the Hesperian and Ebro massifs in the Coniacian period of the Late Cretaceous (89.9–86.3 Ma; Dercourt *et al.*, 2000). In a similar manner to numerous cases in other poorly dispersing lineages, the current allopatric distribution of two *Thilmanus* in Southern France and in Sardinia and Corsica corresponds with the separation of these islands from continental Europe (e.g. Ribera *et al.*, 2010; Cieslak *et al.*, 2014).

The relationship of *Phaeopterus* + *Thilmanus* is currently supported only by morphology and *cox1* mtDNA (see above), so alternative explanations of their distribution must be considered. *Phaeopterus* occurs sympatrically with its putative sister lineage *Thilmanus* in Sardinia and Corsica, and additionally in the Elba and the western coast of Italy. The distribution of *Phaeopterus* in continental Italy can be explained by recent dispersal from Corsica across the belt of landmasses, including

the current Tuscan Archipelago, which were available as a transitional bridge between the Corsica–Sardinia microplate and the Apennine Peninsula at the Pliocene–Quaternary boundary (Fig. 3; Hsü *et al.*, 1977; Ulzega, 1988; Casale *et al.*, 2009). Alternatively, *Phaeopterus* might be a sister taxon to *Omalisus* as was assumed by Kleine (1933). Then its present distribution (see Fanti & Vitali, 2014) can be explained only by the recent colonisation of the central part of the newly formed Apennine peninsula, Sardinia and Corsica, and subsequent extinctions in the Alps region as described earlier.

The current range of most Omalisidae is limited to the Mediterranean, despite the long evolutionary history and the tectonic history of the region. Myers *et al.* (2000) consider the Mediterranean basin as a biodiversity hotspot and they included the shores of the Eurasian and African tectonic plates in this region. Despite the African–Eurasian connectivity during the mid- or Late Cretaceous (Zarcone *et al.*, 2010; Dal Sasso *et al.*, 2016), Omalisidae are currently known only from the Eurasian plate. The incompletely metamorphosed, nonflying omalisids kept allopatric ranges in the region without any considerable dispersal barriers at least since the Upper Eocene when the contiguous European coast was uplifted by the northward drifting African tectonic plate (Golonka, 2004). The conservative allopatric distribution is common in such lineages, as was shown by Bray & Bocak (2016) who reconstructed the colonisation of a mountain plateau by *Scarelus* Waterhouse. We propose that the life history is responsible for the observed distribution. The females are wingless soil dwellers and the males are small-bodied, short-living and threatened by desiccation, and they probably have a little incentive to fly long distances. As a result, the incompletely sclerotised Omalisidae, like other

nonflying elateroids (Malohlava & Bocak, 2010; Masek *et al.*, 2015), were unable to cross sea straits before the uplift of the continuous European coast. The closely related omalid species are allopatrically distributed and the allopatric mode of speciation has been recently described in the neotenic net-winged beetles at the scale of only a few kilometers (Bray & Bocak, 2016).

We analysed the distributional records of individual omalid species in the Mediterranean from 105 localities (i.e. all species of the family except the widely distributed *O. fontibellaquei*). The current distribution of all Mediterranean species is limited to the coastal regions which were identified as refugia for the broadleaved temperate forests during the Pleistocene glacial maxima (Hewitt, 1999; Petit *et al.*, 2003). We identified a few records of species occurring over 100 km from a sea, namely *O. sanguinipennis* from the southern slopes of the Alps, and two species of *Euanoma* on the southern slopes of the Caucasus (Figs 3, 13). These ranges are located in regions which were closer to the sea up to a few million years ago and additionally located on the southern slopes of high mountain ranges (Adamia *et al.*, 2011; Garzanti *et al.*, 2011). The current ranges of Omalidae probably represent only small remnants of much more extensive ranges which followed the distribution of the humid forests covering most of Europe from the Palaeocene until the beginning of the Pleistocene (Utescher *et al.*, 2011). We propose that the lineages with modified ontogeny have a lower chance of survival in dynamically changing environments.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12271

Table S1. The list of species.

Table S2. The current subfamilial and tribal classification of Omalidae.

Table S3. The geographical distribution of Omalidae.

Table S4. The list of sequenced specimens with GenBank accession numbers.

Table S5. The revised classification of Omalidae.

Figure S1. The phylogenetic tree obtained from the maximum likelihood analysis using MAFFT alignment and including *Phaeopterus unicolor*.

Figure S2. The phylogenetic tree obtained from the Bayesian inference using MAFFT alignment without *Phaeopterus unicolor*.

Figure S3. The dated tree of Omalidae produced with a calibration prior for Elateroidea proposed by McKenna *et al.* (2015).

Figure S4. The distance of the Mediterranean localities of Omalidae from the sea (*n*, number of records).

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