



Dispersal vs. vicariance in the Mediterranean: historical biogeography of the Palearctic Pachydeminae (Coleoptera, Scarabaeoidea)

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Abstract

Aim The geological evolution of the Mediterranean region is largely the result of the Tertiary collision of the African and Eurasian Plates, but also a mosaic of migrating island arcs, fragmenting tectonic belts, and extending back-arc basins. Such complex paleogeography has resulted in a ‘reticulate’ biogeographical history, in which Mediterranean biotas repeatedly fragmented and merged as dispersal barriers appeared and disappeared through time. In this study, dispersal-vicariance analysis (DIVA) is used to assess the relative role played by dispersal and vicariance in shaping distribution patterns in the beetle subfamily Pachydeminae Reitter, 1902 (Scarabaeoidea), an example of east-west Mediterranean disjunction.

Location The Mediterranean region, including North Africa, the western Mediterranean, Balkans–Anatolia, Middle East, Caucasus, the Iranian Plateau, and Central Asia.

Methods A phylogenetic hypothesis of the Palearctic genera of Pachydeminae in conjunction with distributional data was analysed using DIVA. This method reconstructs the ancestral distribution in a given phylogeny based on the vicariance model, while allowing dispersal and extinction to occur. Unlike other methods, DIVA does not enforce area relationships to conform to a hierarchical ‘area cladogram’, so it can be used to reconstruct ‘reticulate’ biogeographical scenarios.

Results Optimal reconstructions, requiring 23 dispersal events, suggest that the ancestor of Pachydeminae was originally present in the south-east Mediterranean region. Basal splitting within the subfamily was caused by vicariance events related to the late Tertiary collision of the African microplates Apulia and Arabia with Eurasia, and the resultant arise of successive dispersal barriers (e.g. the Red Sea, the Zagros Mountains). Subsequent diversification in Pachydeminae involved multiple speciation events within the Middle East and Iran–Afghanistan regions, which gave rise to the least speciose genera of Pachydeminae (e.g. *Otoclinus* Brenske, 1896). Finally, the presence of Pachydeminae in the western Mediterranean region seems to be the result of a recent dispersal event. The ancestor of the Iberian genera *Ceramida* Baraud, 1987 and *Elaphocera* Géné, 1836 probably dispersed from the Middle East to the Iberian Peninsula across North Africa and the Gibraltar Strait during the ‘Messinian salinity crisis’ at the end of the Miocene.

Main conclusions Although the basal diversification of Pachydeminae around the Mediterranean appears to be related to vicariance events linked to the geological formation of the Mediterranean Basin, dispersal has also played a very important role. Nearly 38% of the speciation events in the phylogeny resulted from dispersal to a new area followed by allopatric speciation between lineages. Relationships between western and eastern Mediterranean disjuncts are usually explained by dispersal through Central Europe. The biogeographical history of the Pachydeminae corroborates other biogeographical studies that consider North Africa to be an alternative dispersal route by which Mediterranean taxa could have achieved circum-Mediterranean distributions.

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Keywords

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INTRODUCTION

Dispersal and vicariance are often considered competing hypothesis in historical biogeography. Disjunct distributions can be explained either by fragmentation of widespread ancestors by vicariant (isolating) events or by dispersal across a pre-existing barrier. Most current methods of biogeographical analysis (Nelson & Platnick, 1978; Brooks, 1990; Page, 1994) are based on the vicariance model because nearly any distribution pattern can be explained by dispersal, making dispersal hypotheses very difficult to falsify (Morrone & Crisci, 1995).

In the classic vicariant scenario, geographical division of an ancestral area by consecutive dispersal barriers is followed by fragmentation (*allopatric* speciation) of its inhabiting biota (vicariance). The sequence of vicariant events can thus be directly reconstructed from the organism phylogeny, by simply replacing the name of the taxa for the areas in which they occur. The resulting pattern can be represented in the form of a hierarchical branching diagram, the 'area cladogram', which presumably reflects the biotic relationships among the areas analysed (Morrone & Crisci, 1995). The vicariance model does not incorporate dispersal except to explain the origin of the widespread ancestral distribution, i.e. all dispersal events occurred before the first split in the phylogeny. Dispersal within the cladogram is only considered *a posteriori* in interpreting incongruence between the area cladogram and a particular biogeographical scenario (Ronquist, 1997).

Recent paleogeographical reconstructions, however, indicate that many regions present a more complicated geological history than a simple sequence of vicariant landmasses. For instance, some of the Southern Hemisphere landmasses were formed through the accretion of multiple terranes and present a 'composite' biogeographical history (Sanmartín & Ronquist, in press). The Northern Hemisphere region conforms to what has been termed a 'reticulate' biogeographical scenario (Ronquist, 1997). From the Mesozoic period onwards, the Holarctic landmasses became separated and joined to each other in different combinations over time, as dispersal barriers like mid-oceanic seaways or mountain chains, appeared and disappeared through time (Smith *et al.*, 1994). This has resulted in a pattern of 'reticulate' area relationships, in which repeated episodes of vicariance and dispersal have affected the same areas at different times (Sanmartín *et al.*, 2001). These patterns are not expected to conform to the classic vicariant scenario and cannot be represented in the form of a simple branching area cladogram.

On the other hand, the advent of molecular-based phylogenies in the last decades has strengthened the role of

dispersal as a primary process in the development of concordant distribution patterns (Voelker, 1999, 2002). Estimates of divergence times based on the molecular clock can be used to roughly correlate the timing of species cladogenesis with the timing of vicariant (paleogeographical) events. In many cases, this has shown that the group studied is too young to have been affected by the presumed vicariant barrier, suggesting a recent history of dispersal, rather than vicariance, for these taxa (Voelker, 1999; Waters *et al.*, 2000; Sanmartín & Ronquist, in press, and references therein).

Recently, new methods of biogeographical reconstruction have been proposed in which both dispersal and vicariance are allowed (Page, 1995; Ronquist, 1997, 1998, 2002; Sanmartín & Ronquist, 2002). These 'event-based' methods reconstruct the pattern of ancestral distributions, by explicitly incorporating biogeographical processes into the analysis. Each of these processes (vicariance, dispersal, extinction, and sympatric speciation) is associated with a cost that should be inversely related to its likelihood: the more likely the event, the lower the cost. The optimal reconstruction is found by searching for the reconstruction that minimizes the total cost of the implied events (Ronquist, 1998, 2002). Thus, the minimum-cost reconstruction is the most likely (most parsimonious) explanation for the origin of the pattern being analysed. Because the optimality criterion being used is one of maximum parsimony, these methods are often called 'event-based parsimony methods'.

In this study, I used 'dispersal-vicariance analysis' (DIVA) (Ronquist, 1996, 1997), an event-based parsimony method, to reconstruct the biogeographical history of the subfamily Pachydeminae Reitter, 1902 (Coleoptera, Scarabaeoidea) in the Mediterranean region. Dispersal-vicariance analysis reconstructs ancestral distributions in a given phylogeny assuming a vicariance model, while at the same time allowing for dispersal and extinction to occur (Ronquist, 1997). However, unlike other biogeographical methods, DIVA does not enforce area relationships to conform to a hierarchical 'area cladogram', so it can be used to address 'reticulate' biogeographical scenarios. The latter property is essential when reconstructing the biogeographical history of the Mediterranean region. The Mediterranean Basin was formed during the Tertiary, as a result of the interaction between the African and Eurasian Plates, and several associated African microplates: Iberia, and the two main African Promontories: Apulia and Arabia (Dewey *et al.*, 1973; Dercourt *et al.*, 1986; Krijgsman, 2002). The western part of the Mediterranean region (Iberia, France, part of southern Italy) was probably formed in the early Tertiary (Eocene, 35 Myr), as a result of the collision of the Iberian and Apulian Plates with Eurasia. The eastern Mediterranean

region (Hellenic arc and Aegean basin) is of more recent date: the result of the collision of the Arabian Plate with a stable Eurasia during the mid-Miocene (16 Myr) (Krijgsman, 2002). The opposite pattern can be found between the Mediterranean basins. The eastern Mediterranean Sea (Ionian and Levantine basins) is composed of ocean seafloor flooded during the Jurassic–Cretaceous period as a result of the counterclockwise rotation of Apulia about a pole near Tunisia. The western Mediterranean Sea (Alboran, Balearic, and Tyrrhenian basins), in contrast, was flooded during the late Oligocene–early Miocene, following a second rotation of Apulia about a more distant pole, which produced convergence with both Iberia and Eurasia (Dewey *et al.*, 1973; Dercourt *et al.*, 1986).

Some paleogeographical reconstructions suggest that a landmass connection existed across the Mediterranean at various times during the Oligocene–Miocene, which separated the Tethys (proto-Mediterranean) from the Paratethys, allowing biotic dispersal over the region (Rögl & Steininger, 1983; Oosterbroek & Arntzen, 1992). Each of these 'regression-dispersal' events was followed by a new marine transgression that restored connections between the Tethys and Paratethys, and resulted in east–west vicariance of trans-Mediterranean lineages (Oosterbroek & Arntzen, 1992). Regression (dispersal) and transgression (vicariance) cycles, as well as a mosaic of migrating island arcs, extensional basins, and fragmenting tectonic belts, have resulted in a 'reticulate' biogeographical history, in which Mediterranean biotas repeatedly fragmented and merged as dispersal barriers appeared and disappeared through time (Oosterbroek & Arntzen, 1992; Martín-Piera & Sanmartín, 1999). Many Mediterranean taxa present disjunct distributions between the west and east Mediterranean, or, on a larger scale, between the western Mediterranean and Central Asia, the so-called 'Kiermack' disjunctions (Ribera & Blasco-Zumeta, 1998), with a high number of endemics in northwest Africa, Iberia, the Mediterranean Islands, Balkans–Anatolia, the Middle East, and the trans-Caucasus (Oosterbroek & Arntzen, 1992; Ribera & Blasco-Zumeta, 1998; Martín-Piera & Sanmartín, 1999, and references therein). These disjunct biogeographical patterns are probably the result of the complex (reticulate) paleogeographical history of the present Mediterranean region.

The beetle subfamily Pachydeminae Reitter, 1902 (Scarabaeoidea, Melolonthidae) is an excellent tool with which to investigate the biogeographical history of the Mediterranean region. The Pachydeminae comprise about 530 species worldwide (Lacroix, 2000), and have a cosmopolitan but very disjunct distribution. Within the Holarctic region, they are present in western North America (California and Mexico) and the southern Palearctic. In the latter region, they present a 'Turanian-Mediterranean' distribution (*sensu* Ribera & Blasco-Zumeta, 1998), with disjunctions between the West and East Mediterranean regions (e.g. genus *Elaphocera* Gené, 1836), and between the western Mediterranean and Central Asia (see discussion). Most species of Pachydeminae are characterized by their low dispersal ability (females are flightless), and reduced geographical ranges.

These characteristics (disjunct distributions and high endemism) make the Pachydeminae an especially suitable group with which to study the relative importance of history in the shaping of biogeographical patterns (Noonan, 1988).

As in the rest of Melolonthidae subfamilies (Browne & Scholtz, 1999), phylogenetic relationships within the Pachydeminae are poorly resolved. Recently, Sanmartín & Martín-Piera (2003) reviewed the systematics of the Palearctic genera, and proposed the first phylogenetic hypothesis within the subfamily. In this study, I used this phylogenetic hypothesis, in conjunction with DIVA, to reconstruct the biogeographical history of the Palearctic Pachydeminae. In particular, I wanted to assess the relative role played by dispersal and vicariance in the shaping of present biogeographical patterns in the subfamily. This is the first time DIVA is used to reconstruct the biogeographical history of a group of Mediterranean organisms.

MATERIAL AND METHODS

Areas of analysis

The Palearctic Pachydeminae comprise about 20 genera and 300 species, although there is not a definitive inventory (Lacroix, 2000). They are distributed across southern Eurasia from the Canary Islands to China, including North Africa, southern Europe (except France and Italy), Asia Minor, Middle East, Iran, Afghanistan, Caucasus, and Central Asia (Sanmartín & Martín-Piera, 2003). The majority of species occur in the southwest Palearctic (west of the Ural Mountains) around the Mediterranean region, with the eastern Palearctic only represented by a few species of *Tanyproctus* Faldermann, 1835 in China (Lacroix, 2000). Sanmartín & Martín-Piera's (2003) analysis included 49 species representing 16 Palearctic genera, among them the most widespread and largest Palearctic genera: *Tanyproctus*; *Pachydema* Castelnau, 1832; *Hemictenius* Reitter, 1897; *Ceramida* Baraud, 1987, and *Elaphocera* Gené, 1836 (89% of the total Palearctic species, see Table 1). Each genus was represented by a sample of species reflecting their morphological and geographical diversity. The Appendix shows the distribution of each of the included species. The rest of Palearctic genera not included in the analysis (see Table 1) are all monotypic or small, recently described genera (Sanmartín & Martín-Piera, 2003). Sanmartín & Martín-Piera's (2003) original study did not include any of the Chinese species of Pachydeminae. The distribution of these species is very disjunct with respect to the rest of the subfamily, and they have often been considered as part of the Oriental fauna. Also, their status within Pachydeminae is uncertain. They are currently assigned to *Tanyproctus*, a polyphyletic genus that needs to be redefined (Sanmartín & Martín-Piera, 2003). Nevertheless, a new phylogenetic analysis would be necessary to establish whether these Chinese species form an independent group or are derived from one of the Palearctic clades.

There is still an ongoing debate about the definition of areas of endemism in historical biogeography (Harold &

Table 1 Distribution of the Palearctic genera of the subfamily Pachydeminae Reitter, 1902 included in this study. The distributions follow the regions defined in Fig. 1

Genus	Distribution	N° Species
<i>Pachydema</i> Castelnau, 1832	North Africa (A), Canary Islands (B)	98
<i>Tanyproctus</i> Faldermann, 1835*	North Africa (A), eastern Mediterranean (D), Middle East (E), Caucasus region (F), Iran–Afghanistan (G), Central Asia (H)	90 (Approx.)
<i>Hemictenius</i> Reitter, 1897	Central Asia (H)	25
<i>Elaphocera</i> Gené, 1836	Northwest Africa (A), western Mediterranean (C), eastern Mediterranean (D), Middle East (E)	43
<i>Ceramida</i> Baraud, 1987	Northwest Africa (A), western Mediterranean (C)	11
<i>Leptochristina</i> Baraud & Branco, 1991	Middle East (E)	4
<i>Otoclinius</i> Brenske, 1896	Iran–Afghanistan (G)	5
<i>Atanyproctus</i> Petrovitz, 1954	Iran–Afghanistan (G)	6
<i>Alaia</i> Petrovitz, 1980	Iran–Afghanistan (G)	1
<i>Brenskiella</i> Berg, 1898	Middle East (E)	1
<i>Europteron</i> Marseul, 1867	North Africa (A)	3
<i>Kryzhanovskia</i> Nikolajev & Kabakov, 1977	Iran–Afghanistan (G)	1
<i>Pachydemocera</i> Reitter, 1902	Eastern Mediterranean (D), Middle East (E)	1
<i>Peritryssus</i> Reitter, 1918	Sicily (I)	1
<i>Pseudopachydema</i> Balthasar, 1930	Caucasus (F)	1
<i>Tanyproctoides</i> Petrovitz, 1971	Middle East (E)	1

**Tanyproctus* is also present in China (see text).

Palearctic genera not considered in this study (Lacroix, 2000): *Phalangonyx* Reitter 1889, *Jalalabadia* Balthasar, 1967, *Buettikeria* Sabatinelli & Pontuale, 1998, *Asiactenius* Nikolajev, 2000 (see text).

Mooi, 1994; Cox, 2001; Linder, 2001; Morrone, 2002). Here, an area of endemism is defined as a congruent distributional range (sympatric distribution) shared by two or more species (except for Sicily, which is only defined by the distribution of *Peritryssus excisus* Reitter, 1918; see below). Where possible, however, areas were also defined by geographical boundaries, such as the existence of geological features that could have acted as barriers to dispersal. For instance, the Middle East (area E) is separated from Iran (area G) by the Zagros Mountains, whereas the Red Sea and the Isthmus of Suez mark the geographical boundary between the Middle East and North Africa (area A).

According to these criteria, nine areas were considered in the analysis (Fig. 1; Table 1).

(A) North Africa: extending from the Atlantic Ocean (Morocco) to the Red Sea (Egypt, including the Sinai Peninsula). *Pachydema* is the most speciose genus in this region (82 species), but a few species of *Elaphocera* (e.g. *E. sulcatala* Fairmaire, 1884), *Ceramida* [e.g. *C. mauritanica* (Rambur, 1843)], and *Tanyproctus* [e.g. *Tanyproctus bicuspidatus* (Peyerimhoff, 1926)] can also be found in the coasts of North Africa. *Europteron* Marseul, 1867 (three species) is also endemic to this region. The majority of species of Pachydeminae are endemic to Northwest Africa (Morocco, Algeria, and Tunisia). This is reflected in the analysis by the predominance of northwest African species (8) against one northeast species [*P. palposa* Reitter, 1902

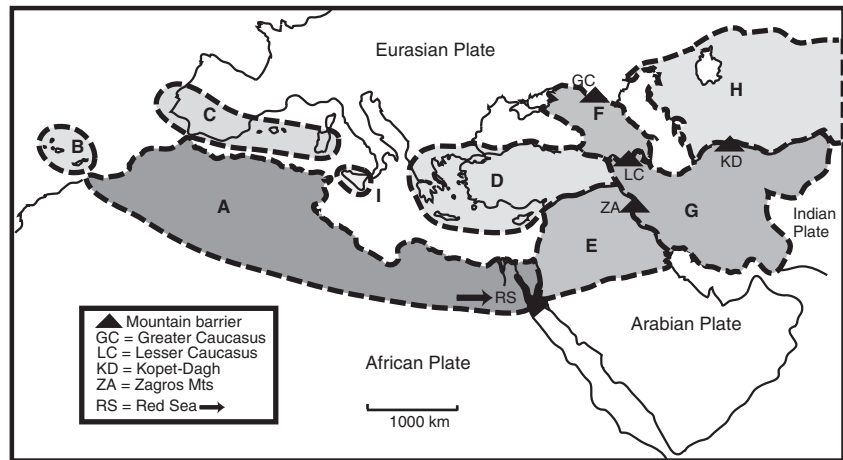
(Egypt), Appendix]. I considered North Africa, however, as a single unit in the analysis for two reasons. First, the two main African genera, *Pachydema* and *Tanyproctus*, are also present in Northeast Africa. About 10 species of *Pachydema* are endemic to Egypt, and four more are present in Lybia (e.g. *P. obscurata* Fairmaire, 1883). Two species of *Tanyproctus* occur in Egypt (e.g. *T. indscriptus* Baraud, 1979) against one in Morocco (*T. bicuspidatus*). Second, almost all species of *Pachydema* endemic to Libya are also present in Tunisia, indicating that there is no clear separation between these two regions. Probably, the paucity of species in Libya is simply the result of lack of sampling or extinction occurred during the formation of the Libyan Desert. More species of Pachydeminae are likely to be found in Lybia.

(B) The Canary Islands: sixteen species of *Pachydema* are endemic to the Canary Archipelago.

(C) Western Mediterranean region: including the Iberian Peninsula and the south-western Mediterranean Islands (the Balearic Archipelago and Sardinia). Numerous species of *Ceramida* and *Elaphocera* are endemic to this region. Curiously, no species of Pachydeminae are found in the Central Mediterranean, i.e. southern France and the Italian Peninsula.

(D) Eastern Mediterranean region (Balkans/Anatolia): including Greece, the Aegean Islands, Crete, Rhodes, and the Anatolian Peninsula (Asia Minor). *Elaphocera* with 10 species is the most speciose genus in this region, which also

Figure 1 Areas of distribution of the Palearctic genera of Pachydemiae Reitter, 1902 as defined in this study. A, North Africa, B, Canary Islands, C, western Mediterranean (Iberian Peninsula and south-western Mediterranean islands), D, eastern Mediterranean (Balkans/Anatolia and south-eastern Mediterranean Islands), E, Middle East, F, Caucasus region, G, Iran–Afghanistan, H, Central Asia, I, Sicily.



includes a few species of *Tanyproctus* [e.g. *T. reichei* (Rambur, 1843)]. The Balkans and the Anatolian Peninsula are considered here as one region because the Bosphorus Strait was not opened until the end of the Pliocene, and the fauna of both sides is usually very similar (Cheylan, 1995). Several species of Pachydemiae are widespread in Greece and Turkey [e.g. *T. reichei*; *E. gracilis* (Waltl, 1838)].

(E) Middle East: defined as the northern part of the Arabian Plate, including the Levant region (Syria, Israel, and Jordan), Iraq, and northern Saudi Arabia. There are several small genera of Pachydemiae endemic to this region (e.g. *Leptochristina* Baraud & Branco, 1991, *Pachydemocera* Reitter, 1902 (synonymy of *Elaphocera*, Sanmartín & Martín-Piera, 2003), *Brenskiella* Berg, 1898, *Tanyproctoides* Petrovitz, 1971), as well as numerous species of *Tanyproctus* (e.g. *T. rugulosus* Fairmaire, 1892), and *Elaphocera syriaca* Kraatz, 1882. A few species of *Pachydemia* are also found in this area (e.g. *P. abeillei* Fairmaire, 1881, Lacroix, 2000).

(F) The Caucasus region: including the republics of Georgia, Azerbaijan, and Armenia. The Lesser Caucasus Mountains in the south, the Greater Caucasus in the north, the Black Sea on the west, and the Caspian Sea on the east are the geographical boundaries of this region. Nearly all species of Pachydemiae present in the Caucasus region (all belonging to genus *Tanyproctus*) are also widespread in Iran (area G). The monotypic *Pseudopachydemia* Balthasar, 1930 is the only genus of Pachydemiae endemic to the Caucasus.

(G) Iran–Afghanistan: This region is delimited by the Zagros Mountains in the southwest, the Kopet-Dagh and Lesser Caucasus Mountains in the north, and the Indian Plate (Pamir Mountains) in the east. Many small genera of Pachydemiae (*Atanyproctus* Petrovitz, 1954, *Alaia* Petrovitz, 1980, *Otoclinius* Brenske, 1896, and *Kryzhanovskia* Nikolajev & Kabakov, 1977) and numerous *Tanyproctus* species [*T. persicus* (Ménétries, 1832)] are endemic to this region.

(H) Central Asia: Defined as the Turanian or trans-Caspian region, and including the republics of Turkmenistan, Uzbekistan, Tajikistan, Kirgizistan, and Kazakhstan.

Hemictenius is the only genus endemic to this region, although a few species of *Tanyproctus* occurring in Iran–Afghanistan are also widespread in Central Asia [e.g. *T. bucharicus* (Reitter, 1897)].

(I) Sicily: *Peritryssus excisus* is the only species of Pachydemiae present in Sicily. Because of its atypical morphology (Sanmartín & Martín-Piera, 2003), and the geographical isolation of Sicily, I considered this region as a separate area, instead of part of the western Mediterranean.

Phylogenetic hypothesis

Sanmartín & Martín-Piera (2003) obtained 32 most parsimonious trees (MPTs) of 284 steps (CI = 0.35, RI = 0.77), whose strict consensus is shown in Fig. 2. DIVA can only handle fully bifurcate trees. Ronquist's (1996) suggestion to work with the original trees, from which the consensus is calculated, was not followed here because of the large number of possible trees (32). Instead, the ancestral distributions were inferred from one of the 32 MPTs (Fig. 3), although biogeographical conclusions were only based on those biogeographical events supported by the consensus tree.

Although Sanmartín & Martín-Piera's strict consensus tree (Fig. 2) shows *E. syriaca* and *E. barbara* Rambur, 1843 in a tetratomy with *Ceramida* and the remaining species of *Elaphocera*, a more complete analysis involving all species of *Elaphocera* and *Ceramida* (in prep.) shows that *E. barbara* is the sister group to *Ceramida* and that *E. syriaca* is the most basal species among the remaining species of *Elaphocera*. This topology has been adopted in the biogeographical analysis presented below (Fig. 3). It should also be noted that the genus *Tanyproctus* (the most widespread in the subfamily, Table 1) is polyphyletic (Sanmartín & Martín-Piera, 2003). Some species [*T. reichei*, *T. ganglbaueri* (Brenske, 1897), *T. saulcyi* (Reiche, 1856)] are more closely related to other genera than to the remaining *Tanyproctus*, and relationships among the rest of species are not resolved (Fig. 2). Biogeographical conclusions in this part of the cladogram should therefore be taken with caution.

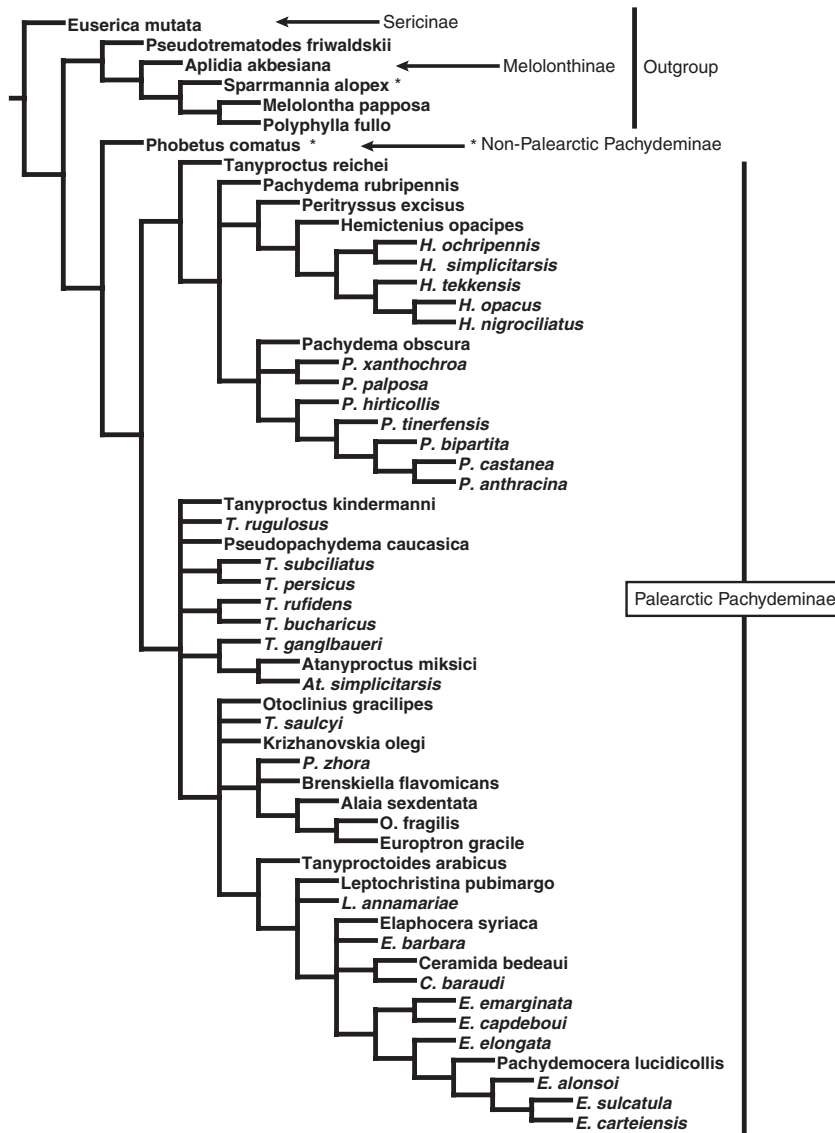


Figure 2 Phylogeny of the Palearctic Pachydeminae Reitter, 1902 (After Sanmartín & Martín-Piera, 2003). Strict consensus of 32 most parsimonious trees (MPTs) of 284 steps (CI = 0.35; RI = 0.77).

Analysis

Dispersal-vicariance analysis (Ronquist, 1997), as implemented in the computer program DIVA v. 1.1 (Ronquist, 1996), was used to reconstruct ancestral distributions on the phylogeny of Pachydeminae (Fig. 3). This method searches for the optimal reconstruction of ancestral distributions by assuming a vicariant explanation (i.e. allopatric speciation) but at the same time incorporating the potential contribution of dispersal and extinction in shaping the current distributional pattern. In DIVA, vicariance events (allopatric speciation) and duplication events (sympatric speciation, i.e. speciation within the area) carry a cost of zero, whereas dispersal and extinction events cost one per unit area added or deleted from the distribution (Ronquist, 1996). The optimal solutions are those that minimize dispersal and extinction events under a parsimony criterion. This is

because both dispersal and extinction are unpredictable events that can wipe out the traces of 'phylogenetically constrained processes' like vicariance and duplication. Thus, spurious events will be introduced in optimal reconstructions unless extinctions and dispersals carry a cost (Ronquist, 1998; Sanmartín & Ronquist, 2002). Unlike other biogeographical methods, DIVA does not rely in area cladograms, and reconstructs ancestral distributions in a given phylogeny without any prior assumptions about area relationships. Thus, it can be used to reconstruct 'reticulate' biogeographical scenarios (Ronquist, 1996,1997), such as the Mediterranean region.

One drawback of DIVA is that ancestral area optimizations become less reliable as one approaches the root node. This uncertainty is manifested in DIVA as a tendency for the root node distribution to be large and include most of the areas occupied by the terminals (Ronquist, 1996). One

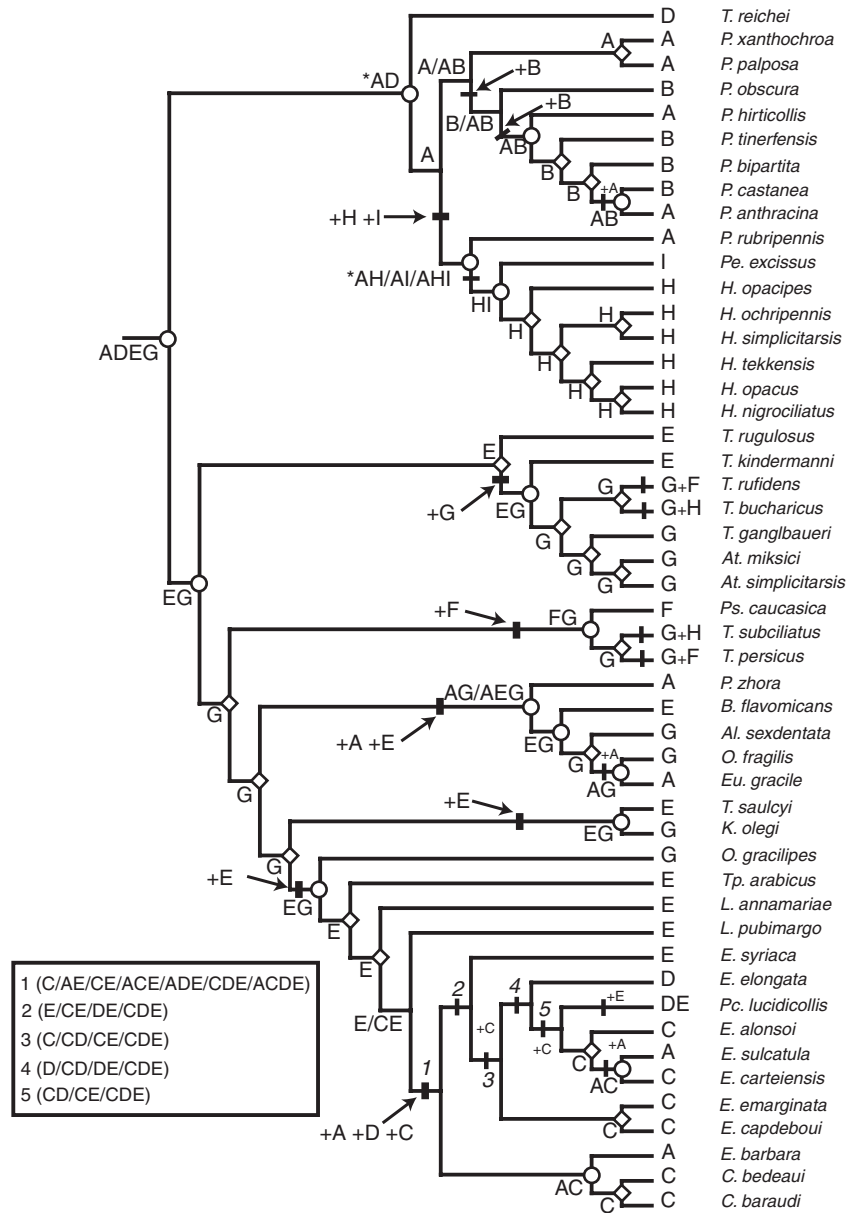


Figure 3 Summary of the optimal reconstructions of ancestral distributions of the Palearctic Pachydeminae using dispersal-vicariance analysis (DIVA). The phylogeny is one of the 32 MPTs in Sanmartín & Martín-Piera (2003). At each node, the optimal distribution is given; alternative, equally optimal distributions are separated with slash marks. Each reconstruction requires 23 dispersal events. When the sequence of dispersal events differs among the reconstructions (e.g. within *Elaphocera* Gené, 1836, see text), only one is given in the figure. Symbols: *circle*: vicariance event; *rhomb*: duplication (sympatric speciation) event; *arrow (+)*: dispersal event. Only unambiguous events are indicated in the reconstruction. (*): Nodes where extinction events were inferred because the subsequent vicariance event takes place between areas that are not geographically adjacent (Fig. 1).

way to solve this is to incorporate additional outgroups into the analysis that can help to restrict the distributions in the root node. However, the closest outgroup in Sanmartín & Martín-Piera's (2003) phylogeny (Fig. 2) is the genus *Phobetus* Le Conte, 1856, a Nearctic Pachydeminae, so it cannot be used to constrain the ingroup distribution. Another way is to impose constraints on the maximum number of unit areas allowed in ancestral distributions (using the 'maxareas' option of the 'optimize' command in DIVA). This is equivalent to asking the question: if this group has a restricted distribution in the past (a 'centre of origin'), what would be the most likely ancestral area distribution of the group? If we assume that the dispersal ability of the ancestors (i.e. their ability to achieve a

widespread distribution while maintaining species integrity) was not higher than that of the descendants, we could constrain the maximum number of areas in ancestral distributions to the number of areas in the distribution of the most widespread extant descendant. In Pachydeminae, this would imply to restrict the ancestral distributions to two unit areas, which is the distribution of the most widespread terminal species in Fig. 3.

First, I used the exact search of DIVA without restricting the number of areas in which the ancestor occurred, i.e. admitting the possibility of a widespread ancestor. Not surprisingly, the ancestral area reconstruction at the root node included all the areas analysed except the western Mediterranean (C): ABDEGHI/ABDEFGHI. It appears,

however, unlikely that the ancestor of the Palearctic Pachydeminae occurred in such a widespread distribution, covering the southern Palearctic from Morocco to the Aral-Caspian plains, while at the same time developing a long series of apomorphic features (Nordlander *et al.*, 1996). Moreover, three of the eight areas included by DIVA in the root-node distribution are unlikely to have been part of the ancestral distribution of Pachydeminae. The Canary Islands (B) is a young volcanic archipelago that has probably never been connected to the mainland (Juan *et al.*, 2000). The Caucasus region (F) is usually part of a more widespread distribution involving the Middle East or Iran (i.e. no endemics), suggesting that this area of distribution is probably the result of recent dispersal. Also, Sicily (I) is only inhabited by one species of Pachydeminae (*P. excisus*), which appears nested within one of the clades (Fig. 3), so it is unlikely to have been part of the ancestral area.

On the other hand, the disjunct distribution and reduced geographical ranges of most species of Pachydeminae suggest that they are not good dispersers and that vicariance is still the main explanation for the biogeographical relationships within the subfamily. Therefore, to assume that the group arose in a small area, a 'centre of origin', from which it dispersed to other areas (i.e. limiting the ancestral distributional range to two unit areas, the distribution of the most widespread species of Pachydeminae), is unrealistic. Therefore, I decided to carry out a constrained analysis (Fig. 3), setting the maximum number of unit areas in ancestral distributions to four, arbitrarily chosen as an intermediate value.

RESULTS AND DISCUSSION

A DIVA 'constrained' exact search limiting ancestral distributions to no more than four areas resulted in 936 alternative, equally optimal reconstructions, each requiring 23 dispersals between the areas. The optimal area reconstructions at each ancestral node are summarized in Fig. 3.

Despite the high number of alternative reconstructions, they are all very similar, only differing in the ancestral distributions at some distal nodes (e.g. *Elaphocera*, Fig. 3). All reconstructions postulate the existence of a widespread Palearctic ancestor of Pachydeminae, distributed in the southeast Mediterranean region, including North Africa (A), the eastern Mediterranean (D), the Middle East (E), and the Iran–Afghanistan region (G). Therefore, the presence of Pachydeminae in areas such as the western Mediterranean (C), the Canary Islands (B), the Caucasus (F), Central Asia (H), or Sicily (I), is considered to be the result of subsequent dispersals from the ancestral distribution.

The first three basal nodes correspond to vicariance events (Fig. 3). The most basal vicariance event (AD/EG) separated the ancestor of *Pachydema*–*Hemictenius*–*T. reichei* on North Africa and the eastern Mediterranean region (AD) from the remaining part of the Palearctic Pachydeminae on the Middle East–Iranian Plateau (EG). How old is this first split? No fossils are known of the subfamily Pachydeminae, but the main divisions of Scarabaeoidea were distinct from the beginning of the Tertiary, and the oldest fossil record

assigned to Melolonthidae (*Eophyllocerus*) is from the Eocene (Browne & Scholtz, 1999). Thus, the Pachydeminae are probably not older than the early mid-Tertiary. However, in order to date more accurately this first split (North Africa/Iran–Middle East), paleogeographical evidence is needed.

Paleogeographical reconstructions indicate that the geological evolution of the Mediterranean region was largely the result of the convergence of the African and Eurasian Plates during the Tertiary. In the mid-Jurassic (180 Myr), following the opening of the central North Atlantic between North America and Africa, the African Plate started to rotate counterclockwise towards a stable Eurasia. First, Africa moved continuously in an eastern direction but in the late Cretaceous (95 Myr), Africa's motion changed to a north-eastern directed compression (Dercourt *et al.*, 1986; De Jong, 1998). During this convergence, the old Jurassic Tethys Ocean that originally separated the African and Eurasian Plates was completely eliminated and replaced by a new ocean, the Mesogean or proto-Mediterranean. During the Eocene, continental collision between the African and Eurasian Plates increased, and was dominated by the interaction of Eurasia with three associated African microplates: Iberia, and the two main African Promontories of Apulia and Arabia (Dewey *et al.*, 1973; Dercourt *et al.*, 1986).

The Iberian microplate was part of Africa from the late Cretaceous until the Eocene (110–154 Myr), when it began to move northwards, eventually colliding with Eurasia in the late Eocene (35 Myr). The collision gave rise to the first Pyrenees. Apulia detached from Africa in the early Cretaceous (130 Myr), becoming an independent microplate until the late Cretaceous (80 Myr), after which, it behaved again as an African Promontory. Its final collision with Eurasia in the Eocene (35 Myr) initiated the deformation of the Alpine orogenic system (Dercourt *et al.*, 1986).

At the end of the Cretaceous–early Paleocene (60 Myr), the Arabian Plate began to separate from the main African Plate along the line of the Red Sea and Gulf of Aden (Thompson, 2000). When it was first formed, the Red Sea was only a chain of lakes at the deepest parts of the valley. The rifting process continued during the early Tertiary until a connection with the Mediterranean Sea was developed during the Eocene (40 Myr), which cut off the terrestrial connections between Africa and Arabia in the north (Thompson, 2000). A second phase of rifting began in the early Pliocene (5 Myr), when the uplift of the Isthmus of Suez finally cut off the Red Sea from the Mediterranean, and opened it to the Indian Ocean through the Gulf of Aden. Thus, the opening of the Red Sea and the Gulf of Aden mark the tectonic boundary between the African and Arabian Plates.

It is possible that the split between the ancestor of *T. reichei*–*Pachydema*–*Hemictenius* in North Africa (Anatolia) and the rest of Pachydeminae in the Middle East–Iran (AD/EG) corresponds to the time when the Arabian Plate and the African Plate became separated along the line of the Red Sea. Either the early Tertiary connection between the Red Sea and the Mediterranean, or the uplift of the

Isthmus of Suez in the early Pliocene, could have acted as vicariance events, responsible for the interruption of terrestrial connections between North Africa and Arabia (West Asia). This explanation agrees well with other biogeographical studies on southwest Palearctic groups that consider the opening of the Red Sea responsible for evolutionary divergences between African and Arabian (West Asian) lineages (Doadrio, 1990, Cheylan, 1995; Doadrio *et al.*, 1998; Zardoya & Doadrio, 1998). The origin of the Saharan and Arab-Syrian deserts during the late Miocene-Pliocene (6 Myr) could also have acted as additional barrier to dispersal between North Africa and West Asia; these deserts presently mark the natural boundary between the Ethiopian and temperate Palearctic biotas (Por, 1975). However, these events can only explain the vicariance between Arabia-West Asia and North Africa (A/EG), but not the vicariance with the Balkans-Anatolian region (D). According to Thompson (2000), as the Arabian Plate broke away from Africa in the early Tertiary, it began to move northeastwards, colliding with the Eurasian Plate in the mid-Miocene, 16 Myr ago (Krijgsman, 2002). One result of this collision was the westward squeezing of the Turkish Plate along the Anatolian Fault Zone, and its lateral extrusion away from the Arabia-Eurasia collision zone (Dercourt *et al.*, 1986; Krijgsman, 2002). It is possible that this event isolated the Balkans-Anatolian region (D) from the Middle East-Iranian Plateau (EG), as indicated in the first vicariance (AD/EG, Fig. 3).

It is, however, more difficult to explain the wide disjunct distribution of the clade *T. reichei*-*Pachydema*-*Hemictenius* prior to the vicariance, which includes North Africa (*Pachydema*-*Hemictenius*) and the eastern Mediterranean region (*T. reichei*): (AD, Fig. 3). Turkey, as well as Iran and Afghanistan, was derived from a Gondwanan microplate that rifted off from the margin of Gondwana during the early Triassic and collided with Eurasia during the Cretaceous. By the early Tertiary, these blocks were already part of the south-eastern margin of the Eurasian Plate (Dewey *et al.*, 1973; Dercourt *et al.*, 1986). Martín-Piera & Zunino (1983, 1985) explain the close relationship between North African and Anatolian lineages that has been found in several Scarabaeidae genera as the result of a connection between North Africa and Anatolia that was established at the beginning of the Tertiary, after the late Cretaceous collision of the Apulian Plate with Eurasia. These events, however, are probably too old to explain the wide disjunction North Africa/Anatolia observed in the clade *T. reichei*-*Pachydema*-*Hemictenius*. It is more likely that the present disjunct distribution is the result of the extinction of this clade in the intermediate areas (e.g. the Levant region, see below).

According to paleogeographical reconstructions (Rögl & Steininger, 1983 in Oosterbroek & Arntzen, 1992: Fig. 16D, p. 12), biotic exchange between Europe and North Africa across the Mediterranean became possible during the Middle Miocene (14–13 Myr) through a continuous landmass separating the Tethys from the Paratethys, and roughly corresponding to the Balkans/Anatolian (+Levant) region. This connection was interrupted in the late Miocene (10 Myr

ago), when final structuring of the Alps and a new marine transgression between the Tethys and Paratethys in the east isolated the Balkans/Anatolian block from the rest of the Mediterranean region. The biogeographical reconstruction in Fig. 3 indicates a vicariance event between *T. reichei* in the eastern Mediterranean region (Balkans-Anatolia) and the stem species of *Pachydema*-*Hemictenius* in North Africa. It is possible that *T. reichei* is the only survivor of a lineage that was originally present in the eastern Mediterranean (D) and became isolated by this late Miocene marine transgression from the ancestor of *Pachydema*-*Hemictenius* in North Africa (A). Vicariance events between the ancestor of Balkans/Asia Minor lineages and the ancestors of trans-Mediterranean lineages have been documented in several other Mediterranean groups (Oosterbroek & Arntzen, 1992, Martín-Piera & Sanmartín, 1999). Alternatively, the distribution of *T. reichei* could be the result of more recent dispersal from North Africa and the Levant. However, the first possibility, the relict character of *T. reichei*, agrees better with Sanmartín & Martín-Piera's (2003) indication that this species is atypical in its morphology, with numerous apomorphies (mouthparts, genitalia) that separate it from the rest of *Tanyproctus*.

The third vicariance event (E/G) isolated the ancestor of a clade including *Atanyproctus* and several *Tanyproctus* species, in the Middle East region (E), from the remaining part of the subfamily in the Iran-Afghanistan Plateau (G). Paleogeographical reconstructions indicate that the Miocene collision of the Arabian Plate against Eurasia resulted in the uplifting of several mountain belts surrounding the Iranian Plateau (Dercourt *et al.*, 1986). The first to be uplifted were the Zagros Mountains in southern Iran (10 Myr), which now mark the tectonic boundary between the Arabian and Eurasian Plates. As the Arabian Plate continued its indentation into Eurasia, a second phase of uplifting in the early Pliocene (5 Myr) resulted in the rise of mountain chains in northern Iran: the Kopet-Dagh and Lesser Caucasus Mountains (Dercourt *et al.*, 1986). These mountain belts now mark the geographical boundary between Iran and the Central Asia and Caucasus regions, respectively. This sequence of mountain uplifting events has often been suggested as an explanation for evolutionary divergences found in southwest Palearctic taxa between Iranian and Arabian lineages (Zagros Mountains), and between Iranian and Central Asian/Caucasian lineages (Kopet Dagh and Lesser Caucasus Mountains) (Cheylan, 1995; Macey *et al.*, 1998; Martín-Piera & Sanmartín, 1999).

The DIVA ancestral area reconstructions postulate that the ancestor of *Pachydema*-*Peritryssus*-*Hemictenius* was originally present in North Africa, where it underwent duplication (speciation within the area), and gave rise to two different lineages. One of them, the ancestor of the genus *Pachydema*, remained in North Africa, where it diversified, and afterward dispersed to the Canary Islands (+B). Sanmartín & Martín-Piera (2003) showed that the endemic Canarian species of *Pachydema* do not form a monophyletic lineage within the genus. In Fig. 2, *P. castanea* (Brullé, 1838) and *P. bipartita* (Brullé, 1838) are more closely related to the

African *P. anthracina* Fairmaire, 1860 than to the Canary *P. obscura* (Brullé, 1838) and *P. tinerfensis* Galante & Stebnicka, 1992. DIVA optimal reconstructions (Fig. 3) show that dispersal to the Canary Archipelago (+B) occurred at least two times from different African ancestors, followed by backward dispersal to North Africa (+A). This independent origin of the Canary species from different African ancestors contrasts with the traditional 'Hawaiian' model (one common ancestor radiating through the islands, Simon, 1987) found in other Canary groups (Thorpe *et al.*, 1993). Because the Canary Islands are of volcanic origin and were probably never connected to the mainland (Juan *et al.*, 2000), dispersal is the most likely explanation for the colonization of the archipelago. This is further supported by the fact that *Pachydema* is the only known genus of Palearctic Pachydeminae whose females present functional wings (Sanmartín & Martín-Piera, 2003).

The second North African lineage, i.e. the ancestor of the clade *Pachydema rubripennis* (Lucas, 1848)–*P. excisus*–*Hemictenius* probably dispersed from North Africa (*P. rubripennis*) to Sicily (+I), where *P. excisus* originated, and Central Asia (+H), where the stem species of *Hemictenius* rapidly diversified. Although there is a polytomy in the strict consensus tree (Fig. 2), *P. rubripennis* in North Africa occupies the basal position of the clade in more than 80% of the MPTs (Fig. 3), thus supporting a North African origin for the ancestor of *P. rubripennis*–*Peritryssus*–*Hemictenius*. The genus *Hemictenius* probably originated and diversified in Central Asia, as all species of *Hemictenius* are now restricted to this region (Table 1). The wide disjunction between *Hemictenius* in Central Asia and *P. rubripennis* and *P. excisus* in the western Mediterranean region (North Africa and Sicily) is probably the result of either extinction or unknown occurrences of this clade in the intermediate areas, i.e. the Middle East and Iran. Examples of vicariant distributions between the western Mediterranean and the Turanian region (Central Asia) are known in many groups of insects (Ribera & Blasco-Zumeta, 1998; Martín-Piera & Sanmartín, 1999). In any case, the split that gave rise to *Hemictenius* is probably as old as the isolation of the northern Iranian Plateau from Central Asia, which followed the uplift of the Kopet–Dagh Mountains in the early Pliocene, 5 Myr ago (see above).

How to explain the isolation of the remarkable *P. excisus* in Sicily? Sicily is a composite area that was formed during the late Oligocene–Miocene from terranes derived from the Apulian Plate, one of African microplates. Northeast Sicily is composed of early Tertiary terranes (there was a second uplift during the Pleistocene), whereas southwest Sicily is probably of late Tertiary (Oligocene–Miocene) origin (De Jong, 1998). During the late Eocene, the final collision of the Apulian plate with Eurasia initiated the deformation of the western and Corsican Alps. The southeast convergence of Apulia with respect to a more or less stable Europe led to the arise of the 'late Oligocene Alpine system', formed by the western Alps, the Betic-Rif chain, the Balearic massif, the Corsica-Sardinia block, southern Sicily, the Peloritan-Calabrian massif of southern Italy, and the Kabyliens. This system

was progressively fragmented during the late Tertiary by the formation of extensional marine basins in the western Mediterranean (De Jong, 1998). During the early Miocene (20 Myr), the Kabyliens–Calabria block (including Sicily) became separated from the Rif–Betic–Balearic belt, and started moving southeastward, opening the South Balearic basin. The Kabyliens became finally separated from the Peloritan–Calabrian (Sicily) block during the mid-late Miocene (15–7 Myr), eventually colliding with northwest Africa to form the Atlas and Tell Mountains. It is possible that the vicariance event (AI) that separated *P. excisus* in Sicily from the ancestor of the clade in North Africa (A, *P. rubripennis*) corresponds to the late Miocene separation of the Kabyliens (the future northwest Africa) from the Peloritan–Calabrian (Sicily) block. According to Voelker (1999), a land-bridge connection between Sicily and Tunisia existed before the Pleistocene, which could have facilitated faunal exchange between European and African birds. Alternatively, these events could be explained as more recent dispersal during the Pleistocene glaciations, but the atypical morphology of *Peritryssus*, with numerous apomorphies (Sanmartín & Martín-Piera, 2003), suggests that the split must be at least pre-Pleistocene.

As for the rest of the strict consensus tree (Fig. 2), the large number of polytomies makes it difficult to draw new inferences. However, several conclusions can be reached. Both the Middle East (E) and the Iran–Afghanistan region (G) have acted as important centres of diversification within Pachydeminae. DIVA optimal reconstructions (Fig. 3) postulate that these regions were the ancestral areas in the basal duplication events that gave rise to many of the least speciose genera of Pachydeminae (e.g. *Atanyproctus*, *Otoclinus*, *Leptochristina*).

There have been several dispersal events from Iran (area G) into the Caucasus region (F) and Central Asia (H), but most of these dispersals occurred at terminal tips (i.e. they are not inferred as ancestral areas at terminal nodes, Fig. 3), indicating that these events correspond to recent range expansions. In fact, except for *Pseudopachydema caucasica* Balthasar, 1930, all distributions involving the Caucasus region (F) seem to be the result of recent dispersal from Iran (G+F). There has also been frequent dispersal from Iran to the Middle East (+E, Fig. 3) but most of these dispersal events occurred at internal branches that were later split by vicariance (allopatric speciation) events (EG, Fig. 3). One of these speciation events within the Iran–Afghanistan region (G) is probably responsible for the origin of the clade *P. zhora* Normand, 1951; *Otoclinus fragilis* Petrovitz, 1980; *Europteron gracile* Marseul, 1867, and the monotypic genera *Brenskiella* and *Alaia*. Diversification within this heterogeneous clade (Sanmartín & Martín-Piera, 2003) presumably involved dispersal to North Africa and the Middle East region (+A+E), followed by vicariance (Fig. 3).

The ancestor of the clade *Tanyproctoides*, *Leptochristina*, *Elaphocera*, and *Ceramida* originated in the Middle East region (E) by sympatric speciation, probably after dispersal from Iran, the original distribution of *O. gracilipes* Brenske, 1896 (but the position of this species is not resolved in the

strict consensus, Fig. 2). Successive duplication events within the Middle East gave rise to several genera: the monotypic genus *Tanyproctoides*, the (probably) paraphyletic genus *Leptochristina* (Sanmartín & Martín-Piera, 2003), and the ancestor of *Elaphocera* and *Ceramida*.

The DIVA ancestral area reconstructions suggest that the ancestor of *Elaphocera*–*Ceramida* dispersed at some point from the Middle East (E) to North Africa (+A), the Balkans/Anatolian region (+D), and the western Mediterranean (+C), although the sequence of dispersal events is not clear because there are several possible reconstructions (Fig. 3). These dispersals were followed by a basal vicariance event that isolated the ancestor of *E. barbara*–*Ceramida* in the North Africa–western Mediterranean region (AC) from the stem species of *Elaphocera* in the Middle East (E), or alternatively in the Middle East and the eastern/western Mediterranean region (EC/ED/ECD). The basal position occupied by *E. syriaca* in the phylogeny (Fig. 3) supports the assumption that the Middle East region was probably the ancestral distribution of *Elaphocera*. Subsequent diversification within *Elaphocera* involved several dispersal events followed by vicariance between the east and west Mediterranean (E/D/C), and between the western Mediterranean and North Africa (A/C). However, this sequence of dispersal events is not clear because there are several alternative solutions for each node in the optimal reconstruction (see Fig. 3).

As pointed out above, evolution within the clade *Elaphocera*–*Ceramida*–*E. barbara* involved multiple dispersal–vicariance events between the eastern Mediterranean (Middle East/Balkans–Anatolia, DE) and the western Mediterranean regions (AC), including southern Iberia, the Balearic Islands, Sardinia, and northwest Africa (Morocco–Algeria). This east–west exchange occurred at the basal split between *Ceramida*–*E. barbara* and *Elaphocera*, but also within the phylogeny of *Elaphocera*. Dispersal from the east to the west Mediterranean could have taken place via two different routes. The ancestor of *Elaphocera* and *Ceramida* could have dispersed from the east to the west Mediterranean across Europe, entering the Iberian Peninsula from the north, and later dispersing to North Africa. Paleogeographical reconstructions show that terrestrial dispersal across Europe between the East and West Mediterranean was possible at different times during the late Oligocene–Miocene, following the establishment of a continuous landmass connection after Tethys–Paratethys marine regressions (Rögl & Steininger, 1983). According to Oosterbroek & Arntzen (1992), these connections allowed biotic dispersal throughout the Mediterranean, and gave rise to the ancestors of trans-Mediterranean lineages. Alternatively, the ancestor of *Elaphocera*–*Ceramida* could have dispersed to the western Mediterranean across North Africa, entering the Iberian Peninsula from the south. The first possibility, European dispersal and colonization from the north, appears to be less likely for two reasons. First, the distributions of *Elaphocera* and *Ceramida* in the northern part of the Mediterranean region are restricted to the southern half of the Iberian and Balkan Peninsulas, indicating that both the

Iberian Central Plateau and the Balkans probably acted as barriers to dispersal for Pachydeminae. Second, during the late Tertiary, several geological barriers could have limited dispersal across Europe. For example, the Pyrenees isolated the Iberian Peninsula from the rest of Europe during most of the Tertiary. These mountains were formed at the end of the Cretaceous as a result of the collision of the Iberian Plate with Eurasia, partially eroded during the Oligocene–Miocene, and uplifted again in the early Pliocene, 5 Myr ago (Oosterbroek & Arntzen, 1992; De Jong, 1998). On the other hand, final restructuring of the Alps/Central Italy in the late Miocene–Pliocene probably acted as another barrier to dispersal across Europe (Dercourt *et al.*, 1986; De Jong, 1998). No Pachydeminae is presently found in the Central Mediterranean region, including the Italian Peninsula and southern France.

In contrast, dispersal from the south across Africa could have been possible at the end of the Miocene during the so-called ‘Messinian salinity crisis’ (Krijgsman, 2002). In the late Miocene, the differential collapse of the Betic–Rif Belt resulted in the origin of the Gibraltar arc, and the almost complete closing of the Mediterranean Sea from the Atlantic Ocean. As a result, during the Messinian age (7–5.3 Myr), the Mediterranean experienced a massive evaporation and shrank, turning into a shallow hypersaline basin (De Jong, 1998). The Red Sea became also partially dried during this period (6.5–5 Myr), allowing biotic connections in the north between the African and Arabian Plates (Thompson, 2000). These connections, which lasted until 3.5–3 Myr, could have allowed dispersal of West Asian groups to North Africa during the late Miocene (Cheylan, 1995). North African dispersal was also probably favored by the climatic alternance of relatively humid phases with hyper-arid phases in the Saharan and Arab–Syrian deserts during the mid-Pliocene–Pleistocene (3 Myr) (Quezel & Barbero, 1993; Thompson, 2000). Therefore, the ancestors of *Elaphocera* and *Ceramida* could have dispersed from the Middle East to North Africa across the Red Sea during the late Miocene, and later dispersed to the Iberian Peninsula across the Gibraltar Strait during the partial desiccation of the Mediterranean in the Messinian. According to Krijgsman (2002), before the late Miocene, dispersal between North Africa and the Iberian Peninsula was prevented by the existence of two water corridors connecting the Atlantic to the Mediterranean: the ‘Betic Corridor’ through southern Spain and the ‘Rifian Corridor’ through northern Morocco. Although the first corridor was closed around the Tortonian (11–7 Myr), the ‘Rifian’ corridor remained opened until the Messinian salinity crisis, 6.0 Myr ago. The Messinian salinity crisis ended when the present-day Gibraltar Strait opened at the start of the Pliocene (5 Myr), restoring the connections between the Mediterranean and the Atlantic. This event can probably account for the vicariance between North African/Iberian lineages observed in the split *E. barbara*/*Ceramida* (Fig. 3), as well as in many other Mediterranean lineages (Martín-Piera & Zunino, 1983, 1985; Doadrio, 1990; Doadrio *et al.*, 1998; Zardoya & Doadrio, 1998; Martín-Piera & Sanmartín, 1999).

CONCLUSIONS

The DIVA optimal reconstructions suggest that the ancestor of the Palearctic Pachydeminae was originally present in the south-east Mediterranean region, including North Africa, the Middle East, the Iranian Plateau, and the Balkans/Anatolian region. Basal splitting within the subfamily was caused by vicariance events related to the late Tertiary collision of the African microplates Apulia and Arabia with Eurasia, and the resultant arise of successive dispersal barriers (e.g. the Red Sea, the Zagros Mountains). Genera like *Pachydema* or *Hemictenius* probably originated in this way. Subsequent diversification within Pachydeminae involved multiple speciation events within the Middle East and Iran–Afghanistan regions, which seem to have acted as centres of diversification in the subfamily. Many of the least speciose Palearctic genera (e.g. *Otoclinius*, *Leptochristina*) originated within these two regions by duplication (within-area speciation) events. In contrast, the presence of Pachydeminae in the western Mediterranean region (Iberian Peninsula and south-western Mediterranean Islands) is probably the result of a recent dispersal event. The ancestor of the Iberian genera *Elaphocera* and *Ceramida* probably dispersed from the Middle East to the Iberian Peninsula across North Africa and the Gibraltar Strait. This dispersal could have taken place during the ‘Messinian salinity crisis’ at the end of the Miocene, when the Red Sea and the Mediterranean partially dried up, allowing a short period of biotic dispersal between West Asia, North Africa, and the Iberian Peninsula.

The North African dispersal route

Comparison of the biogeographical reconstruction in Fig. 3 with previous studies on Mediterranean biogeography (Oosterbroek & Arntzen, 1992; De Jong, 1998) shows that the main difference lies in the position occupied by the Iberian Peninsula in the cladogram. According to Oosterbroek & Arntzen (1992), basal lineages in Circum-Mediterranean taxa are mainly restricted to the West Mediterranean (the Iberian Peninsula), whereas more recent lineages are present in the East Mediterranean. This agrees with paleogeographical reconstructions, which show that the western Mediterranean region (including the Iberian Plate) was already part of Eurasia at the beginning of the Tertiary, whereas the eastern Mediterranean is of more recent origin (Dercourt *et al.*, 1986; Krijgsman, 2002).

In contrast, in Pachydeminae (Fig. 3) and De Jong’s (1998) study, the Iberian Peninsula occupies a more derived position in the cladogram, suggesting that this area of distribution is the result of a more recent dispersal event from the ancestral area. Also, in both reconstructions, North Africa is placed basally, as part of the ancestral distribution of the group. According to Oosterbroek & Arntzen (1992), groups with Asia Minor-trans-Mediterranean lineages (e.g. the clade *Elaphocera*–*Ceramida*, Fig. 3) are probably younger than those with basal lineages in the Iberian Peninsula, and might be of African origin. It is, therefore,

possible that two patterns, both showing circum-Mediterranean area relationships but of different age, are present in the Mediterranean region (a characteristic of ‘reticulate’ scenarios). The oldest pattern is probably of early Tertiary age (Oosterbroek & Arntzen, 1992) and corresponds to groups with basal lineages in the Iberian Peninsula and the western Mediterranean. Trans-Mediterranean (east–west) distributions in these groups were presumably achieved by dispersal across Europe, via the landmass connection across the Mediterranean that was established at various times during the late Oligocene–Miocene (Rögl & Steininger, 1983; Oosterbroek & Arntzen, 1992). The second pattern (late Tertiary age?) corresponds to groups with more derived lineages in the Iberian Peninsula, and basal lineages in North Africa–West Asia. In these groups, trans-Mediterranean distributions were presumably achieved via dispersal across North Africa, probably during the Messinian salinity crisis at the end of the Miocene. This is probably the case of Pachydeminae. Relationships between western and eastern Mediterranean disjuncts are traditionally explained by dispersal through Central Europe, but this work corroborates recent biogeographical studies that point out North Africa as an alternative dispersal route by which Mediterranean taxa could have achieved circum-Mediterranean (east–west) distributions (Martín-Piera & Zunino, 1983, 1985; Doadrio, 1990; Doadrio *et al.*, 1998; Zardoya & Doadrio, 1998; Martín-Piera & Sanmartín, 1999).

Dispersal vs. vicariance

Basal diversification of the subfamily Pachydeminae around the Mediterranean appears to have been caused by vicariance events linked to the geological formation of the present Mediterranean geography. Vicariant division of a widespread ancestral area by successive geographical barriers (e.g. Red Sea, Zagros Mountains) is the most parsimonious explanation for ancestral distributions at basal nodes in the phylogeny. However, dispersal has also played an essential role in shaping present distribution patterns in the subfamily. DIVA optimal reconstructions required 23 dispersal events, five of which occurred within terminal branches. Because there are 48 internal nodes in the phylogeny, this means that nearly 38% of the speciation events in Pachydeminae resulted from dispersal to a new area followed by allopatric speciation between lineages (and often by sympatric speciation within each lineage). Given that the Pachydeminae are poor dispersers (females are flightless), it is surprising that dispersal has been so important in shaping their present distribution patterns. It further emphasizes the importance of explicitly considering dispersal in biogeographical reconstructions (especially in ‘reticulate’ biogeographical scenarios).

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BIOSKETCH

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Appendix Species included in the biogeographical analysis and their main geographical distribution. Adapted from Sanmartín & Martín-Piera (2003)

Genus	Species	Geographical distribution
<i>Otoclinius</i> Brenske, 1896	<i>O. fragilis</i> Petrovitz, 1980	Iran
	<i>O. gracilipes</i> Brenske, 1896	Iran
<i>Pachydemocera</i> Reitter, 1902	<i>P. lucidicollis</i> (Kraatz, 1882)	Rhodes, Syria
<i>Leptochristina</i> Baraud & Branco, 1991	<i>L. pubimargo</i> (Reitter, 1902)	Syria
	<i>L. annamariae</i> Baraud & Branco, 1991	Iraq
<i>Tanyproctus</i> Faldermann, 1835	<i>T. (B.) reichei</i> (Rambur, 1843)	Greece; Asia Minor
	<i>T. (T.) rufidens</i> (Marseul, 1879)	Iran, Caucasus
	<i>T. (B.) kindermanni</i> (Reiche, 1861)	Syria, Israel
	<i>T. (T.) bucharicus</i> (Reitter, 1897)	Afghanistan, Tajikistan
	<i>T. (T.) subciliatus</i> Reitter, 1902	Afghanistan, Turkmenistan
	<i>T. (Tca.) saulcyi</i> (Reiche, 1856)	Israel; Syria
	<i>T. (B.) rugulosus</i> Fairmaire, 1892	Syria
	<i>T. (T.) ganglbaueri</i> (Brenske, 1897)	Iran
	<i>T. (T.) persicus</i> (Ménétries, 1832)	Iran, Caucasus
<i>Pachydemia</i> Castelnau, 1832	<i>P. castanea</i> (Brullé, 1838)	Canary Islands
	<i>P. obscura</i> (Brullé, 1838)	Canary Islands
	<i>P. bipartita</i> (Brullé, 1838)	Canary Islands
	<i>P. tinerfensis</i> Galante & Stebnicka, 1992	Canary Islands
	<i>P. (A.) anthracina</i> Fairmaire, 1860	Morocco
	<i>P. (P.) hirticollis</i> (Fabricius, 1787)	Algeria; Tunis; Libya
	<i>P. (P.) xanthochroa</i> Fairmaire, 1879	Tunis
	<i>P. (S.) palposa</i> Reitter, 1902	Egypt
	<i>P. (A.) rubripennis</i> (Lucas, 1848)	Morocco; Algeria
	<i>P. (A.) zohra</i> Normand, 1951	Tunis; Libya
<i>Hemictenius</i> Reitter, 1897	<i>H. tekkensis</i> (Reitter, 1889)	Trans-Caspian; Turkmenistan
	<i>H. ochripennis</i> Reitter, 1902	Tajikistan
	<i>H. opacus</i> (Ballion, 1870)	Turkmenistan, Tajikistan
	<i>H. simplicatarsis</i> Reitter, 1897	Tajikistan
	<i>H. opacipes</i> Reitter, 1902	Buchara, Uzbekistan
	<i>H. nigrociliatus</i> Reitter, 1897	Buchara, Uzbekistan
<i>Elaphocera</i> Gené, 1836	<i>E. elongata</i> Schaufuss, 1874	Greece; Turkey
	<i>E. syriaca</i> Kraatz, 1882	Syria
	<i>E. emarginata</i> (Gyllenhal, 1817)	Sardinia
	<i>E. capdebouvi</i> Schaufuss, 1882	Balearic Islands
	<i>E. barbara</i> Rambur, 1843	Morocco; Algeria
	<i>E. sulcatula</i> Fairmaire, 1884	Morocco
	<i>E. carteiensis</i> Rambur, 1843	SE Iberian Peninsula
	<i>E. alonsoi</i> López-Colón, 1992	SE Iberian Peninsula
<i>Ceramida</i> Baraud, 1987	<i>C. bedeauvi</i> (Erichson, 1840)	S. Iberian Peninsula
	<i>C. baraudi</i> (Branco, 1981)	Portugal
<i>Europroton</i> Marseul, 1867	<i>E. gracile</i> Marseul, 1867	Algeria
<i>Peritryssus</i> Reitter, 1918	<i>P. excisus</i> Reitter, 1918	Sicilia
<i>Brenskiella</i> Berg, 1898	<i>B. flavomicans</i> (Brenske, 1896)	Israel
<i>Alaia</i> Petrovitz, 1980	<i>A. sexdentata</i> Petrovitz, 1980	Iran; Afghanistan
<i>Tanyproctoides</i> Petrovitz, 1971	<i>T. arabicus</i> (Arrow, 1932)	Saudi Arabia
<i>Atanyproctus</i> Petrovitz, 1954	<i>A. miksici</i> Petrovitz, 1965	Afghanistan
	<i>A. simplicatarsis</i> Petrovitz, 1954	Iran
<i>Pseudopachydemia</i> Balthasar, 1930	<i>P. caucasica</i> Balthasar, 1930	Caucasus
<i>Kryzhanovskia</i> Nikolajev & Kabakov, 1977	<i>K. olegi</i> Nikolajev & Kabakov, 1977	Afghanistan