

# Biogeographic hypothesis explaining the diversity of the genus *Amphimallon* Berthold, 1827, in the Mediterranean Basin (Coleoptera, Scarabaeidae, Melolonthinae, Rhizotrogini)

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## Abstract

In this paper, the analysis of the current distribution of species, or species-groups, of the Western–Palaeartic genus *Amphimallon* Berthold, 1827, based on a phylogenetic hypothesis recently provided and relevant paleogeographical events that occurred in the Mediterranean Basin from Late Paleogene (35 Myr BP) to the present, supports a biogeographical scenario to explain species diversity within this genus. The center of origin of this genus is hypothesized to be in the Iberian Peninsula. Microplate fragments drifting from the Iberian Peninsula, successive landmass suture events between the Eastern and Western Mediterranean Basins, separation of Tethys and Paratethys Oceans, re-establishment of marine connections, uplift of the Alps, and drying out of the Mediterranean are hypothesized as the principal events allowing dispersal of populations throughout Mediterranean Basin and biogeographical vicariances within the genus *Amphimallon*.

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**Keywords:** Biogeography; Coleoptera; Melolonthinae; Rhizotrogini; Mediterranean Basin; Neogene

## 1. Introduction

With some 10,000 described species, and many more still undescribed species, the Melolonthinae are an example of an extremely species rich phytophagous beetle lineage. They constitute an ecologically and taxonomically diverse group within the Scarabaeoidea (Scarabs, Chafers, June Beetles etc...). The Melolonthinae are characterized, among others, by white grub larvae that feed on the roots of grasses, palms and various groups of trees. Many species occur in grass-

lands and are crop pests (Hurpin, 1962; Britton, 1978). The most severely affected plants occur in the tropical regions, but severe damage to agriculture also has been reported in many regions. In Western Europe, damage is mainly caused by species of the genera *Melolontha* Fabricius, 1775 (Régnier, 1950; Hurpin, 1962) and *Amphimallon* Berthold, 1827 (Régnier, 1939, 1940, 1950; Gambrell, 1946; Hurpin, 1962).

*Amphimallon* belongs to a large tribe, the Rhizotrogini, which groups together about 1400 species from Palaeartic, Nearctic, Neotropical and Oriental regions (Sabatinelli and Pontuale, 1998). Based on a revision in progress, this genus is composed of approximately 60 species inhabiting the Western–Palaeartic region. It is

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Table 1  
Geological timetable

0.01 Myr BP	Holocene	Neogene
1.8 Myr BP	Pleistocene	
5.5 Myr BP	Pliocene	
23.5 Myr BP	L	Miocene
	M	
	E	
34 Myr BP	Oligocene	Paleogene

distributed across Europe (except in the northern regions), in the Middle East, from Central Asia to Siberia, and in Northern Africa (Morocco, Northern Algeria). Despite recent phylogenetic and taxonomic work focusing on the Rhizotrogini (Medvedev, 1951; Baraud, 1977, 1985, 1992; Coca Abia, 1995; Montreuil, 2000), our understanding of the diversity and evolution of this group is very limited. In this study, a biogeographic scenario is developed based upon a phylogenetic analysis. In the context of this analysis of *Amphimallon*, there are certain assumptions regarding the geological evolution of the Mediterranean Basin, which are related to the origin, the evolution and the mode of diversification of this taxon.

## 2. Materials and methods

### 2.1. Methods

In order to explain the current distribution of the species of the genus *Amphimallon* in the Mediterranean Basin, I implemented a phylogenetic hypothesis, as recommended in Humphries and Parenti (1999), and followed the methodology provided by Soulier-Perkins (1997, 2000). The phylogenetic pattern of taxon distribution areas is inferred from the phylogenetic hypothesis. This phylogenetic pattern is compared to the palaeogeographic pattern of area evolution (continental breakup, sea level variation, orogeny, etc.,...). When there is an agreement between both patterns, the explanation of the phylogenetic pattern is thought to result from the palaeogeographic evolution.

Species distributions were treated as an attribute, and were supplied for each taxon for the phylogeny, previously provided for the studied group by Montreuil (2000), and optimized (Matile, 1990; Soulier-Perkins, 1997; Montreuil, 1998; Soulier-Perkins, 2000) with MacCLADE (Maddison and Maddison, 1993). The most parsimonious hypothesis was retained. The circum-Mediterranean distribution of the genus *Amphimallon* then was analyzed, together with the results of the performed optimization and consideration of the

geological events which occurred in the Mediterranean Basin. I follow the summaries of Mediterranean Basin palaeogeography given by Rögl and Steininger (1983) and Robertson and Grasso (1995). Additionally, the works of Palmer and Cambefort (2000) provided an important paleogeographical context from Late Paleogene (35 MYBP) to the present (see Table 1 for geological timetable).

### 2.2. Phylogeny of the genus *Amphimallon*

A phylogenetic hypothesis based on morphology recently has been proposed for the genus *Amphimallon* (Montreuil, 2000, Fig. 1). Nine *Amphimallon* species-groups have been recognized within this genus and placed in three principal supergroups. The first supergroup, the *A. solstitialis* lineage, consists of the *A. pini*-group (seven species), the *A. vernale*-group (five species), the *A. solstitialis*-group (seven species), the *A. arianae*-group (two species), and the *A. peropacum*-group (one species). The second supergroup, the *A. fuscum* lineage, is comprised of the *A. fuscum*-group (eleven species) and the *A. naceyroi*-group (seven species). The third supergroup, the *A. ruficornis* lineage, contains the *A. majale* group (five species) and the *A. lusitanicum*-group (six species). A phylogenetic hypothesis, performed on these groups, shows sister-group relationships between the *A. ruficornis* lineage and *A. fuscum*+*A. solstitialis* lineages. Seven species, namely *A. amphibolum* Peyerimhoff, 1949 and six species forming the *A. scutellaris*-group, previously placed in *Amphimallon* have been excluded from this genus and are considered species *incertae sedis*. The above lineages and associated hypothesis of phylogeny will be used in this paper to support a hypothesis for historical biogeography of the genus *Amphimallon*.

### 2.3. General distribution of the genus *Amphimallon*

A general distribution map of *Amphimallon* has been drawn based on a compilation of all species distributions (Fig. 2). *Amphimallon* is widely distributed around the Mediterranean Basin, but species have not been discovered in the southeastern portion of the region, including Tunisia, Libya, and Egypt. Only one species, *A. solstitialis* (Linné), has been reported from Lebanon and Israel (Chikatunov and Pavlicek, 1997). In addition, the presence of *Amphimallon sensu stricto* among the islands of the Western Mediterranean Basin is questionable. Indeed, *Amphimallon* seems to be absent from Balearic Islands; the sole species cited from this region, as *Amphimallon*, in fact belongs to the genus

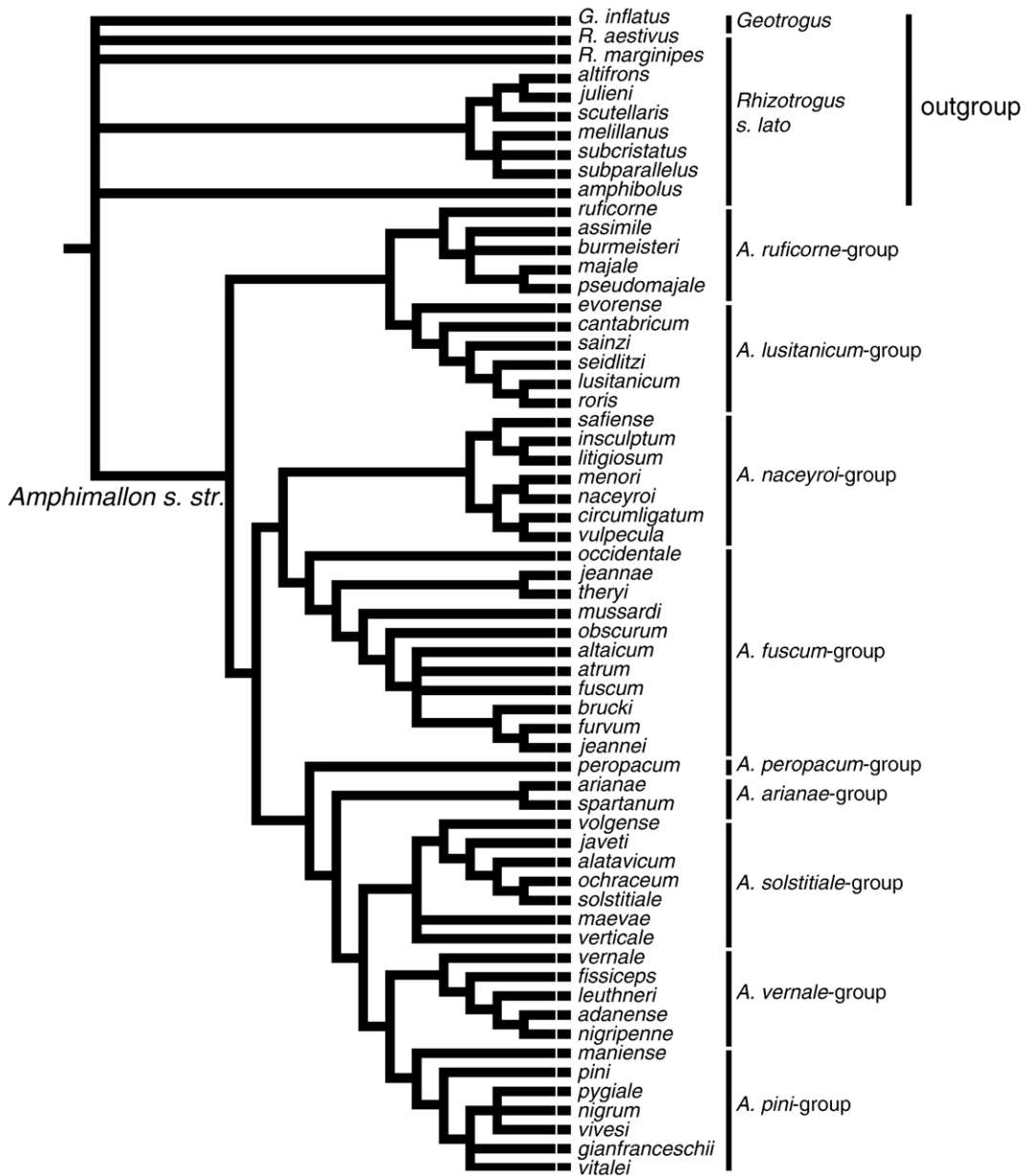


Fig. 1. Phylogenetic hypothesis of the genus *Amphimallon* based on Montreuil (2000).

*Rhizotrogus* Berthold, 1827, as established by Montreuil (1997). Concerning the Corsican–Sardinian massif, we are unaware of any citation of *Amphimallon* from Sardinia and none of the species that have been cited from Corsica in classical works dealing with this fauna are attributable to this genus (Sainte-Claire Deville, 1914, 1920, 1921, 1926; Schaefer, 1964; Paulian, 1977). Three specimens preserved in old collections and belonging to three other species have been studied from Corsica, without precise locality data. Four

recently collected Corsican specimens of *A. majale* can be added (Michard and Michard leg.), and a sole species, *A. atrum*, has been cited by Baraud (1992) from Piana, apparently from a single male, preserved in the collection of Baraud (MNHN). Consequently, there are too few specimens known from this region to confirm that these species truly belong to the Corsican fauna. Another hypothesis is that the presence of these specimens in Corsica could simply be the result of casual introductions from the continent. Nevertheless,



Fig. 2. Global distribution of the genus *Amphimallon* according to Medvedev (1951) and Baraud (1985, 1992).

examined specimens that belong to *Amphimallon* species-groups are well-represented in Iberian Peninsula, France, and Italy, and therefore could have been present in the Corsican-Sardinian Massif (see below). Collection of new material will be necessary to resolve this biogeographical issue.

#### 2.4. Distribution of *Amphimallon* species

The geographic distribution of each species was given by Medvedev (1951) and Baraud (1977, 1985, 1992) among others. However, our knowledge of the distributional limits of many species still lack precision. These accounts relied on field data, which are often incomplete, in particular for the eastern part of the genus range, such as the Middle East and Central Asia.

An analysis of the distribution of all *Amphimallon* species supports taxonomically-based delimitation of particular geographic areas. For example, many species inhabit exclusively the Iberian Peninsula. Thus, the geographic area “Iberian Peninsula” can be defined explicitly. Accordingly, nine main geographic areas

were defined (Table 2, Fig. 3). These geographic areas approximate, for the most part, those designated by Oosterbroek and Arntzen (1992) and de Jong (1998).

None of the examined species in the genus *Amphimallon* is distributed in an area corresponding exactly to one of these geographic areas. Each species is more or

Table 2  
Definition of geographic areas

	Definition of geographic areas	Abbreviations
Area 1	Northern Africa (Morocco and Northern Algeria)	NAf
Area 2	Iberian Peninsula	Ib
Area 3	Sicily and Southern Italy	SIIt
Area 4	Northern Italy	NIIt
Area 5	Southern France	SF
Area 6	Northern and Central Europe	NEu
Area 7	Balkan Peninsula (Yugoslavia, Albania, Greece, Bulgaria, Romania)	Blk
Area 8	Middle East (Turkey, Syria, Iran, Lebanon and Israel)	ME
Area 9	Southern Russia and Central Asia	CAs

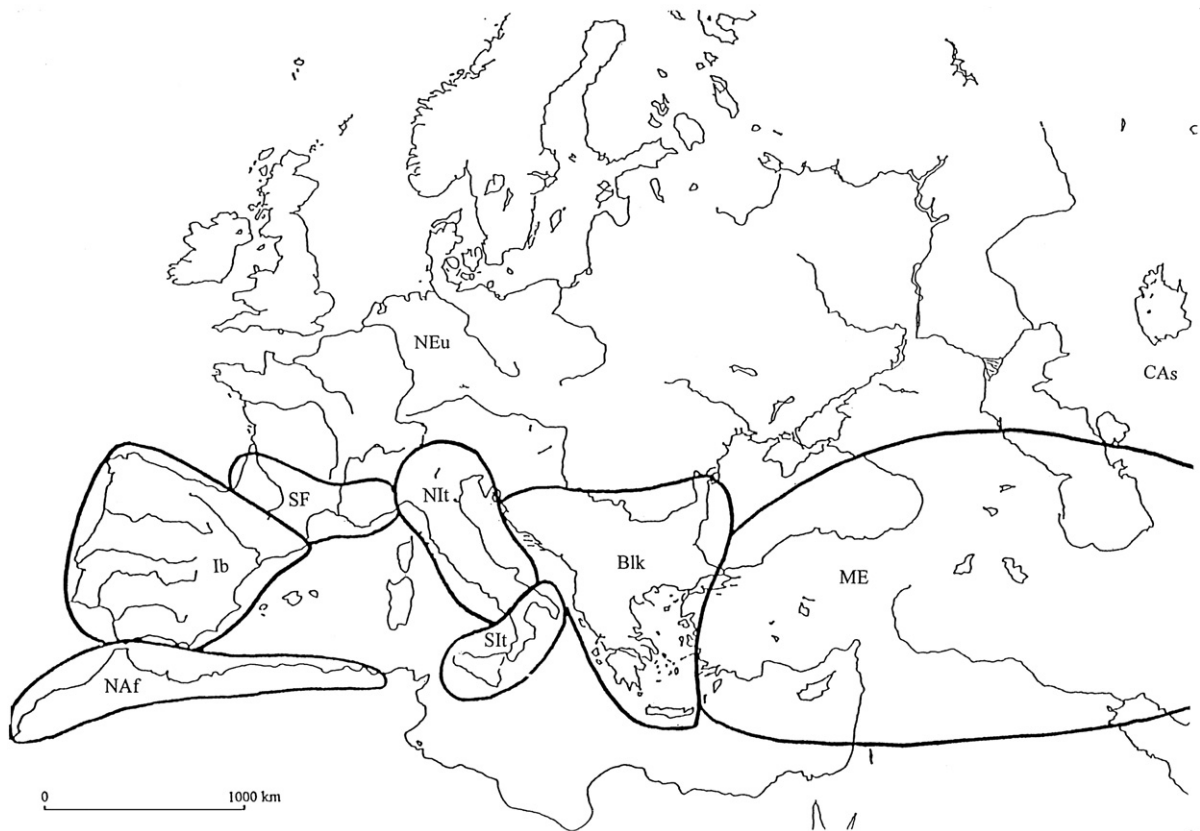


Fig. 3. Geographic areas defined for the Mediterranean Basin.

less distributed in one or more of the defined areas. As a result, species were pooled together in three categories according to the size of their biogeographic distribution.

First, there are species with restricted distributions, inhabiting confined geographic areas. Examples include a portion of Morocco, the Iberian Peninsula, or Greece. Several species such as *A. peropacum*, *A. evorensis*, *A. safiense*, *A. maniense*, *A. mussardi*, and *A. vulpecula*, appear to be highly endemic to geographically confined regions and some are known, at least presently, only from their type-locality. Second, there are species with an extensive distribution, inhabiting for example the eastern part of the Mediterranean Basin (*A. vernale*) or a large part of western or central Europe (*A. atrum*, *A. ruficorne*, and *A. majale*).

Third, there is one species, *A. solstitiale*, having an expansive area of distribution almost congruent with the entire distribution of the genus *Amphimallon*. Indeed, this species occurs as many sub-species and varieties that extends across Europe, westward to the Northern Iberian Peninsula, and eastward to Siberia and Mongolia. Table 3 summarizes presence and absence of each *Amphimallon* species in the areas defined in the Table 2.

### 3. Results and discussion

Optimization of the distribution of *Amphimallon*-species onto the hypothesis of phylogenetic relationships is presented on Fig. 4.

The hypothesis proposed here in is congruent with the evolutionary scenario hypothesis provided by Oosterbroek and Arntzen (1992), which also was used by Palmer and Cambefort (1997, 2000) and by de Jong (1998), among others.

#### 3.1. Origin of the genus *Amphimallon*

The Iberian Peninsula is hypothesized as the center of origin of *Amphimallon*. An analysis of the distribution of genera closely related to *Amphimallon* seems to support this hypothesis (Fig. 5). Relevant to this hypothesis is the work of Coca Abia (1995), who hypothesized the center of origin for the genus *Rhizotrogus* Berthold as North Africa. This genus diversified principally in North Africa and the Iberian Peninsula. Only three species have reached the western part of Mediterranean Basin (Baraud, 1992;

Table 3

Presence/absence of *Amphimallon*-species in the defined geographical areas and coding for optimisation

Taxa	Geographic areas									Coding
	1	2	3	4	5	6	7	8	9	
	NAf	Ib	SIt	NIt	SF	NEu	Blk	ME	CAs	
<i>(G. inflatus)</i>	+	–	–	–	–	–	–	–	–	1
<i>(R. aestivus)</i>	–	+	–	+	+	+	+	+	–	2 and 4 and 5 and 6 and 7 and 8
<i>(R. marginipes)</i>	–	+	–	+	+	+	–	–	–	2 and 4 and 5 and 6
<i>adanense</i>	–	–	–	–	–	–	–	+	–	8
<i>alatavicum</i>	–	–	–	–	–	–	–	–	+	9
<i>altaicum</i>	–	–	–	–	–	–	+	–	+	7 and 9
<i>(altifrons)</i>	+	–	–	–	–	–	–	–	–	1
<i>(amphibolum)</i>	+	–	–	–	–	–	–	–	–	1
<i>ariana</i>	–	–	–	–	–	–	+	–	–	7
<i>assimile</i>	–	–	–	+	+	+	–	–	–	4 and 5 and 6
<i>atrum</i>	–	+	–	+	+	+	–	–	–	2 and 4 and 5 and 6
<i>brucki</i>	–	–	–	–	–	–	+	–	–	7
<i>burmeisteri</i>	–	–	–	+	–	–	–	–	–	4 and 5 and 6
<i>cantabricum</i>	–	+	–	–	–	–	–	–	–	2
<i>circumligatum</i>	+	–	–	–	–	–	–	–	–	1
<i>evorense</i>	–	+	–	–	–	–	–	–	–	2
<i>fissiceps</i>	+	–	–	–	–	–	–	–	–	1
<i>furvum</i>	–	–	–	–	–	–	+	–	–	7
<i>fuscum</i>	–	–	+	+	–	–	–	–	–	3 and 4
<i>gianfranceschii</i>	–	–	+	–	–	–	–	–	–	3
<i>insculptum</i>	+	–	–	–	–	–	–	–	–	1
<i>javeti</i>	–	–	+	–	–	–	–	–	–	3
<i>jeannae</i>	+	–	–	–	–	–	–	–	–	1
<i>jeannei</i>	–	–	–	–	–	–	+	–	–	7
<i>(julieni)</i>	+	–	–	–	–	–	–	–	–	1
<i>leuthneri</i>	–	–	–	–	–	–	–	+	–	8
<i>litigiosum</i>	+	–	–	–	–	–	–	–	–	1
<i>lusitanicum</i>	–	+	–	–	–	–	–	–	–	2
<i>maevae</i>	–	–	–	–	–	–	+	–	–	7
<i>majale</i>	–	+	–	+	+	+	–	–	–	2 and 4 and 5 and 6
<i>maniense</i>	–	–	–	–	–	–	+	–	–	7
<i>(melillanum)</i>	+	–	–	–	–	–	–	–	–	1
<i>menori</i>	–	+	–	–	–	–	–	–	–	2
<i>mussardi</i>	+	–	–	–	–	–	–	–	–	1
<i>naceyroi</i>	–	+	–	–	–	–	–	–	–	2
<i>nigripenne</i>	–	–	–	–	–	–	–	+	–	8
<i>nigrum</i>	–	+	–	–	–	–	–	–	–	2
<i>obscurum</i>	+	–	–	–	–	–	–	–	–	1
<i>occidentale</i>	–	+	–	–	–	–	–	–	–	2
<i>ochraceum</i>	–	+	–	+	+	+	–	–	–	2 and 4 and 5 and 6
<i>peropacum</i>	–	+	–	–	–	–	–	–	–	2
<i>pini</i>	–	+	–	+	+	–	–	–	–	2 and 4 and 5
<i>pseudomajale</i>	–	–	+	–	–	–	–	–	–	3
<i>pygiale</i>	–	+	–	–	+	–	–	–	–	2 and 5
<i>roris</i>	–	+	–	–	–	–	–	–	–	2
<i>ruficorne</i>	–	–	–	–	+	+	–	–	–	5 and 6
<i>safiense</i>	+	–	–	–	–	–	–	–	–	1
<i>sainzii</i>	–	+	–	–	–	–	–	–	–	2
<i>(scutellare)</i>	+	–	–	–	–	–	–	–	–	1
<i>seidlitzii</i>	–	+	–	–	–	–	–	–	–	2
<i>solstitiale</i>	–	+	+	+	+	+	+	+	+	2 and 4 and 5 and 6 and 7 and 8 and 9
<i>spartanum</i>	–	–	–	–	–	–	+	–	–	7
<i>(subcristatum)</i>	+	–	–	–	–	–	–	–	–	1
<i>(subparallellum)</i>	+	–	–	–	–	–	–	–	–	1

(continued on next page)

Table 3 (continued)

Taxa	Geographic areas									Coding
	1	2	3	4	5	6	7	8	9	
	NAf	Ib	SIIt	NIIt	SF	NEu	Blk	ME	CAs	
<i>theryi</i>	+	–	–	–	–	–	–	–	–	1
<i>vernale</i>	–	–	–	–	–	–	+	+	–	7 and 8
<i>verticale</i>	–	–	–	–	–	–	+	–	–	7
<i>vitalei</i>	–	–	+	–	–	–	–	–	–	3
<i>vivesi</i>	–	+	–	–	–	–	–	–	–	2
<i>volgense</i>	–	–	–	–	–	–	–	–	+	9
<i>vulpecula</i>	+	–	–	–	–	–	–	–	–	1

NAf, North Africa; Ib, Iberian Peninsula; SIIt, Southern Italy; NIIt, Northern Italy; SF, Southern France; NEu, Northern and Central Europe; Blk, Balkan Peninsula; ME, Middle East; CAs, Central Asia.

Montreuil, 1999). By contrast, the genus *Geotrogus* Guérin [including *Pseudoapterogyna* Escalera according to Coca Abia, 1995] is almost exclusively distributed in North Africa. A few species have reached southernmost Europe, inhabiting the southern Iberian Peninsula and Sicily (Baraud, 1977, 1985, 1992). This group is characterized by a reduction of membranous wings for some females (*Pseudoapterogyna*), probably explaining the limited extension of this group out of North Africa. Species of the *scutellaris*-group similarly are strictly North African. A different distribution occurs for the genus *Monotropus* Erichson, which is distributed throughout the Iberian Peninsula and in southern Russia (Medvedev, 1951; Baraud, 1992). Its presumed sister-group, the genus *Tosevskiana* Pavicevic, is composed of two species inhabiting the Balkan Peninsula.

These groups collectively comprise a monophyletic group, the Rhizotrogina, suggested by Nonveiller (1960, 1965) and more recently supported by Coca Abia and Martín Piera (1991) and by Baraud (1992) [see also Coca Abia, 1995]. They constitute the occidental Rhizotrogini-lineage, differentiated in the Western Mediterranean Basin, by comparison to the other western-Palaeartic Rhizotrogini genera inhabiting Eastern Mediterranean Basin (Medvedev, 1951; Baraud, 1992). Based on this hypothesis, proposed by Oosterbroek and Arntzen (1992), the separation between these lineages could have occurred during the Oligocene (33–23 MYBP), probably within the Iberian Peninsula, when the proto-Iberian Peninsula became isolated from Europe by the orogenic uplift of the Pyrenees (Muñoz et al., 1983). In addition, separation among the main lineages of Rhizotrogina could be associated with the orogeny resulting in uplift of the Cordillera Ibérica mountain range ( $\approx 30$  Myr BP), isolating the western and the northeastern portions of the Iberian Peninsula (Guimerà, 1988).

### 3.2. Differentiation of the *Amphimallon* lineages

The separation among the three main lineages of *Amphimallon* probably occurred on the proto-Iberian Peninsula as result of vicariance events produced by the emplacement of the Cordillera Ibérica mountain range. However, it is not possible to provide here additional details about the geographical events that could have induced this separation.

#### 3.2.1. *A. ruficorne* lineage (Fig. 6)

In the Western Mediterranean Basin (Late Paleogene, 25 Myr BP), microplate fragments formerly connected with the eastern region of the proto-Iberian Peninsula, which subsequently formed the southern part of the Italian Peninsula (Calabro–Pelotitian Massif), drifted toward the east, causing the opening of the Basin during Neogene times. The separation between the *A. lusitanicum*-group and the *A. ruficorne*-group could have occurred through vicariance during this process (Fig. 6a, b).

Species of the *A. lusitanicum*-group constitute the western branch of this lineage; they were differentiated in the Iberian Peninsula, especially in its western and central portions. The isolation of species of this group, occurring on this part of the Iberian Peninsula, most distant from the Mediterranean Basin, can explain why these species were preserved from the events hereafter determined as important for the biogeographical scenario of other *Amphimallon* groups.

The *A. ruficorne*-group constitutes the eastern branch of this lineage; it differentiated within the Italian Peninsula, at that time still fragmentary and geographically isolated from southern Europe (Fig. 6b). It then dispersed towards the north when the connection between the precursor fragments of the Italian Peninsula and southern Europe was established, during the Middle Miocene, approximately 15 Myr BP (Fig. 6c). Alpine orogeny could have induced the separation and

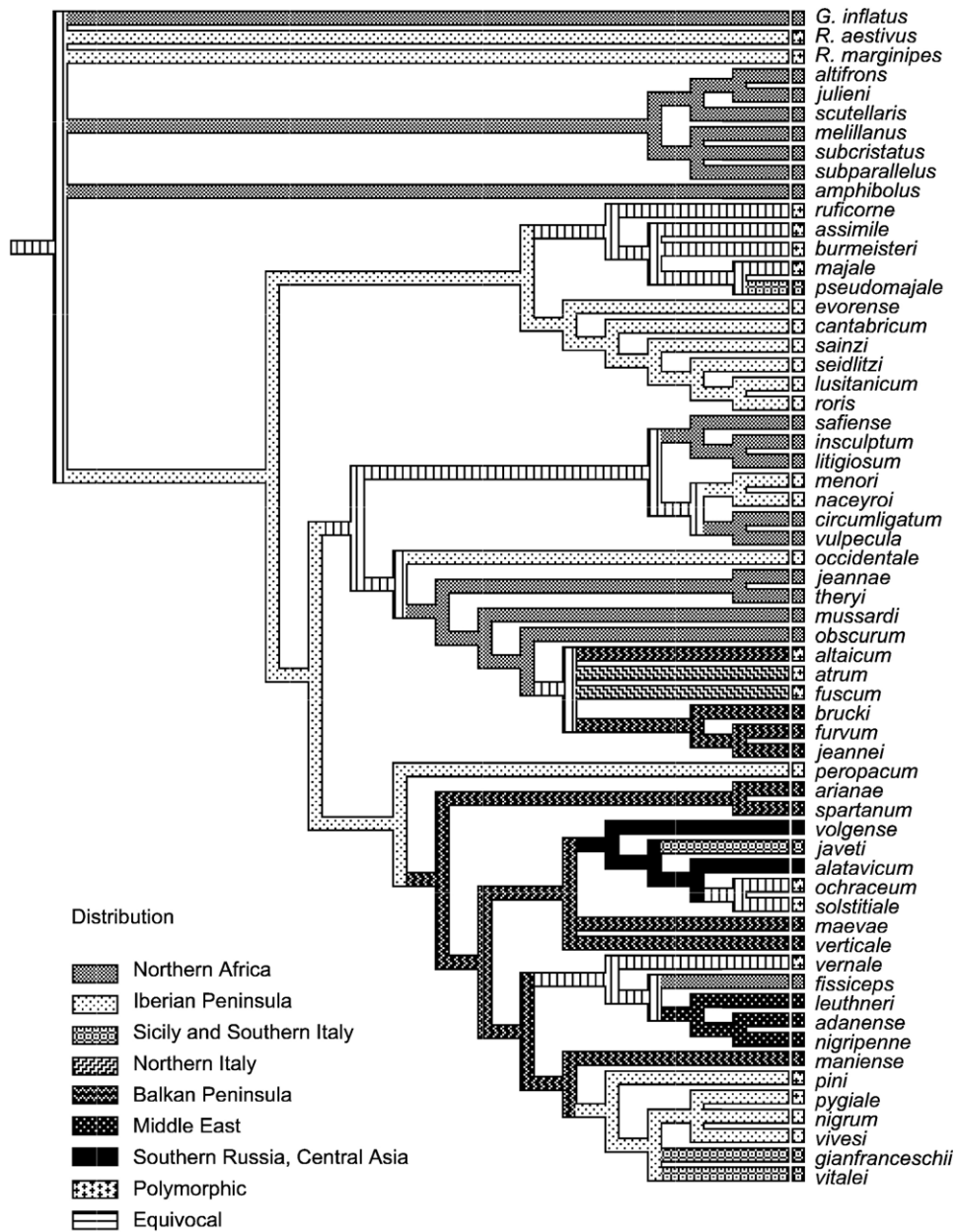


Fig. 4. Optimisation of the distribution of *Amphimallon*-species onto the phylogenetic hypothesis (options of optimisation: unordered states, soft polytomies).

differentiation of populations located on both sides of this newly-forming barrier: *A. ruficorne*, isolated in the northwest of the Alps, probably has been separated from the group inhabiting the southern area of the Alps. During the glacial and interglacial cycles during the Pleistocene (1.8–0.1 MYBP), *A. ruficorne* was pushed back towards the southernmost areas, namely southern France. However this species did not cross the Pyrenean

and Alpine barriers. Subsequently, as the end of the last Ice Age neared, this species dispersed towards the north and east, colonizing Central Europe, migrating around the Alpine mountain range towards the north.

Differentiation between *A. majale*, *A. pseudomajale*, *A. assimile* and *A. burmeisteri* is probably related to the end of the Alpine orogenesis. Two of these species, *A. assimile* and *A. burmeisteri*, are particularly related to



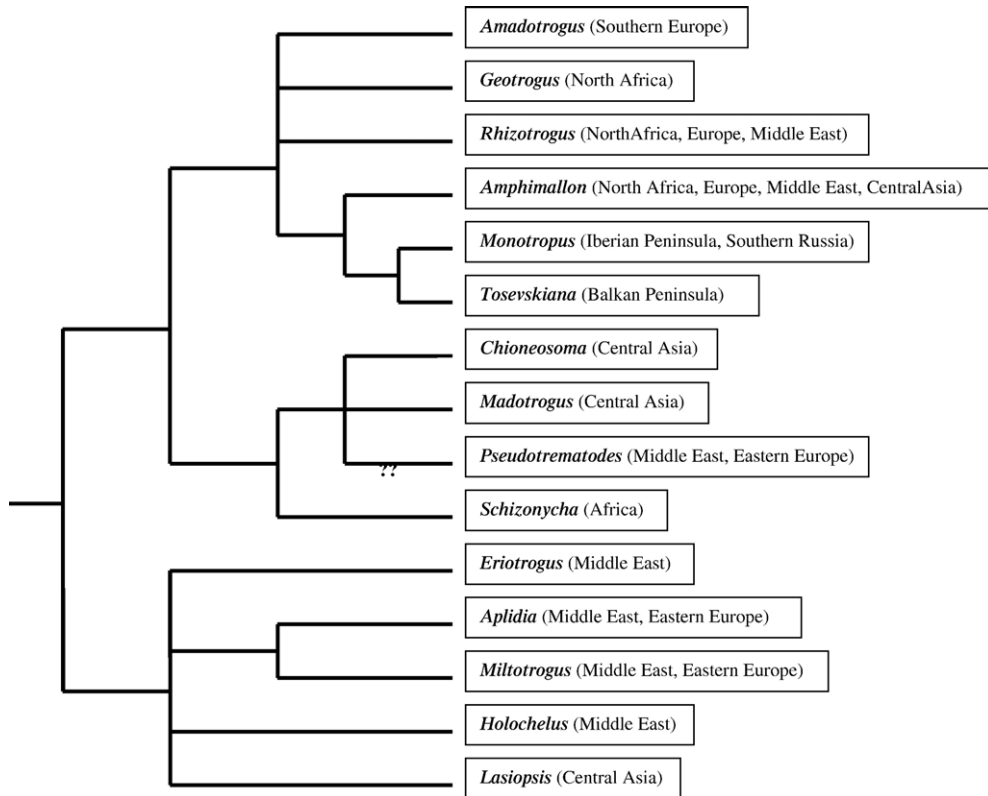


Fig. 5. Phylogeny of western Palearctic Rhizotrogini based on Coca Abia (1995) and Montreuil (2000, 2003) and their distribution according to Medvedev (1951) and Baraud (1985, 1992).

the Alpine Region and Central Europe. These two species taxonomically are very close each to other (Rößner and Krell, 2001), and their differentiation probably has occurred recently. The two other species have differentiated southward and westward of the Alps. *A. pseudomajale* currently inhabits a relictual area toward the south, on the Italian Peninsula. *A. majale* colonized lowland and intermediate elevations areas in Central and Western Europe, and reached the eastern Iberian Peninsula by passing around the Pyrenean barrier towards the east.

### 3.2.2. *A. fuscum* lineage (Figs. 7 and 8)

The center of origin of the *A. fuscum* lineage cannot be indicated precisely. One possibility is North Africa, but a more likely alternative is the Iberian Peninsula. For each of these two hypotheses, the distribution of species of the *A. naceyroi*-group and for species differentiated at the base of the *A. fuscum*-group implies the existence of a land connection between these two areas.

The separation of this lineage is probably related to the eastward drift of microplates formerly connected with the

southeastern margin of the proto-Iberian Peninsula, namely the Kabylia blocks (Fig. 7a). Separation between the blocks of larger (West) and smaller (East) Kabylia probably implied disjunction between *A. naceyroi*-group and *A. fuscum*-group by vicariance. The collision of these blocks with North Africa, inducing the suturing of Telean and Atlas mountain ranges (Early Miocene, 24–18 Myr BP; Oosterbroek and Arntzen, 1992), allowed for the dispersal and the differentiation of the basal elements of this lineage in North Africa (Fig. 7b): the first elements of the *A. naceyroi*-group deployed to the west, the first elements of the *A. fuscum*-group occurring in the east.

The basal species of the *A. fuscum*-group, *A. occidentale*, differentiated in the Iberian Peninsula and can be considered a relictual element whose isolation and differentiation would be a secondary consequence of the detachment of the Kabylia blocks. This species currently is distributed along the Atlantic coast of the Iberian Peninsula. Other species in a basal position within this group inhabit North Africa. These species likely differentiated by vicariance during the structuring of the Rif Mountains ( $\approx 9$  Myr BP; de Jong, 1998): *A. theryi*

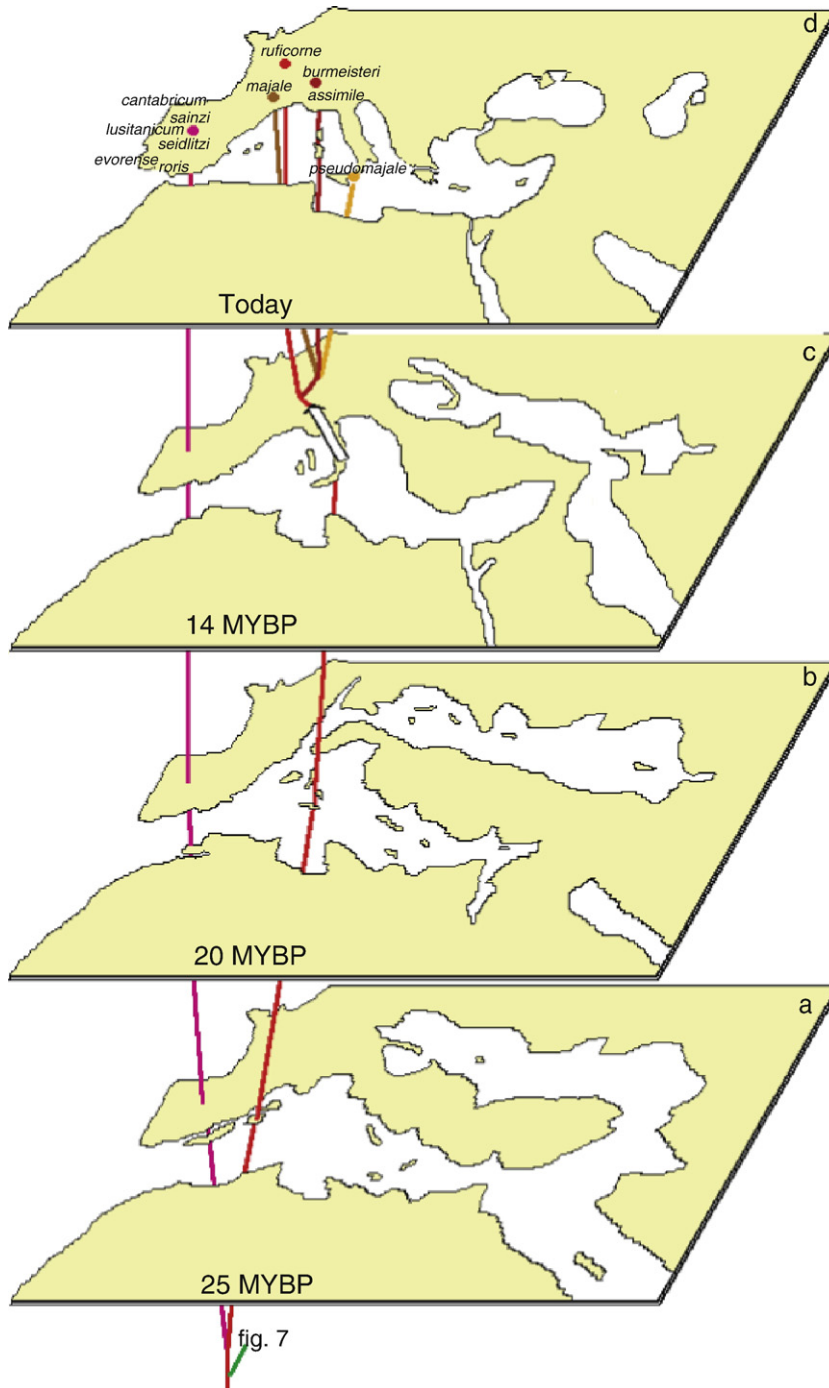


Fig. 6. Phylogenetic relationships of the *A. lusitanicum*-group and *A. ruficorne*-group mapped onto a paleogeographical representation of the evolution of the Mediterranean Basin from the Oligocene to the present.

and *A. jeannae* in the northwest of the Atlas Mountains; *A. mussardi* toward the north, inhabiting the Rif Mountains; and a monophyletic group whose origin seems to be located in northern Algeria. Drying out of the

Mediterranean attributable to the Messinian crisis of Late Miocene to Early Pliocene age, 5.5 MYBP resulted in a land connection between North Africa and the southern Italian Peninsula (de Jong, 1998). During this time,

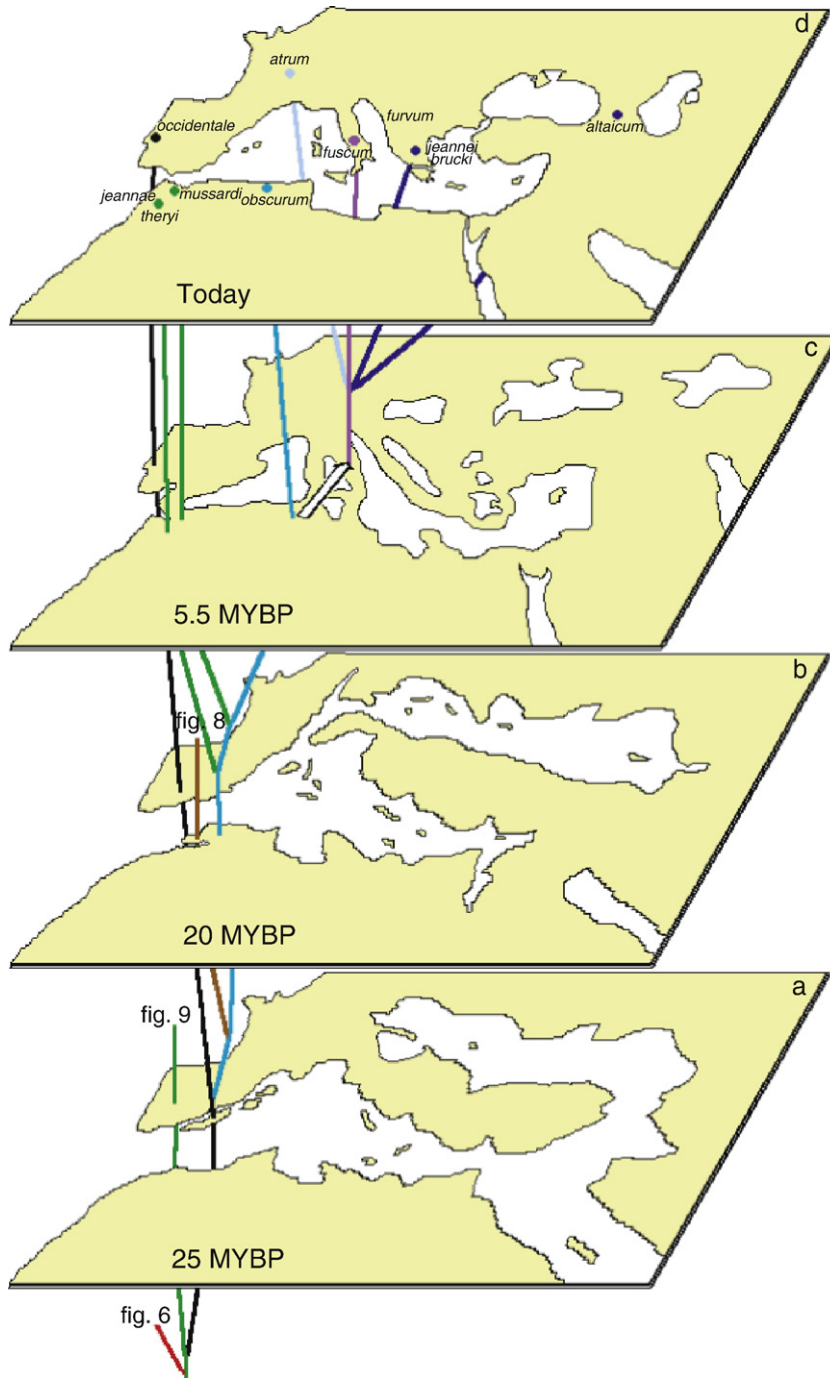


Fig. 7. Phylogenetic relationships of the *A. fuscum*-group mapped onto a paleogeographical representation of the evolution of the Mediterranean Basin from the Oligocene to the present.

dispersal was possible for species of this group from North Africa (Algeria) to southern Central Europe (Fig. 7c). At the end of this land connection at about 5 MYBP, *A. obscurum* differentiated in Algeria by vicar-

iance. The other species dispersed throughout Europe. Some of these species dispersed westward arriving at the northern Iberian Peninsula. Alternatively, other species dispersed eastward, and currently occupy the Balkan

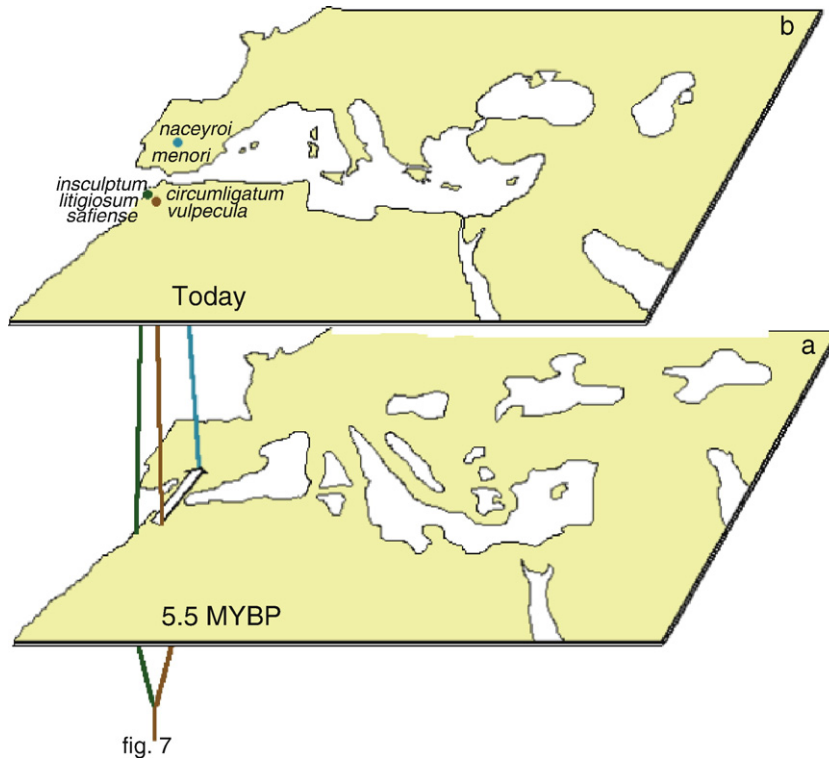


Fig. 8. Phylogenetic relationships of the *A. naceyroi*-group mapped onto a paleogeographical representation of the evolution of the Mediterranean Basin from the Pliocene to the present.

Peninsula, the Eastern Mediterranean Basin, southern Russia, the northern Caucasus region and Central Asia to the Altai Mountains. This has resulted in populations that have colonized areas other than northern Europe and became isolated in southern regions of Europe during the glacial and interglacial cycles of the Pleistocene (1.8–0.1 Myr BP). This allowed for the occurrence of speciation south of the Balkan Peninsula among taxa such as *A. furvum*, *A. brucki*, and *A. jeannei*, which currently inhabit the highest mountains. Additionally, separation was present in southern France for *A. atrum* and in the Italian Peninsula in the case of *A. fuscum* (Fig. 7d).

Most of the species belonging to the *A. naceyroi* group inhabit Morocco. Three of these species – *A. insculptum*, *A. litigiosum*, and *A. safiense* – collectively form a natural group and are differentiated along the Atlantic Moroccan coast. In addition, *A. litigiosum* was discovered in Tarifa in southern of Andalusia, a Spanish locality adjacent the Moroccan coast. The presence of this species in this locality is probably attributable to a secondary dispersal from Morocco, or possibly to recent anthropogenic introduction.

The drying out and establishment of a land connection, previously mentioned, resulted in colonisation

of the Iberian Peninsula by representatives of the *A. naceyroi*-group from North Africa (Fig. 8a). At that time a permanent marine connection between the Atlantic and Mediterranean Basin (Early Pliocene, 5 Myr BP) was restored, forming the ancestral Strait of Gibraltar. African and Iberian populations of the *A. naceyroi*-group later became isolated. *A. naceyroi* and *A. menori* subsequently have differentiated in the center of the Iberian Peninsula while species of their sister-group, *A. vulpecula* and *A. circumligatum*, have differentiated in Morocco (Fig. 8b).

The implications of a land connection among Corsica–Sardinia, North Africa and the Italian Peninsula could suggest of the presence of species belonging to the *A. fuscum*-group (*A. atrum*) and the *A. ruficorne*-group (*A. ruficorne*, *A. majale*) in Sardinia and Corsica. The sparse data collected during the recent past have not been confirmed by recent collections; nevertheless, the absence of representatives of *Amphimallon* in this area would be surprising.

### 3.2.3. *A. solstitiale* lineage (Figs. 9 and 10)

Dispersal throughout the Mediterranean became possible after the formation of a continuous landmass separating the Tethys from Paratethys Oceans during the

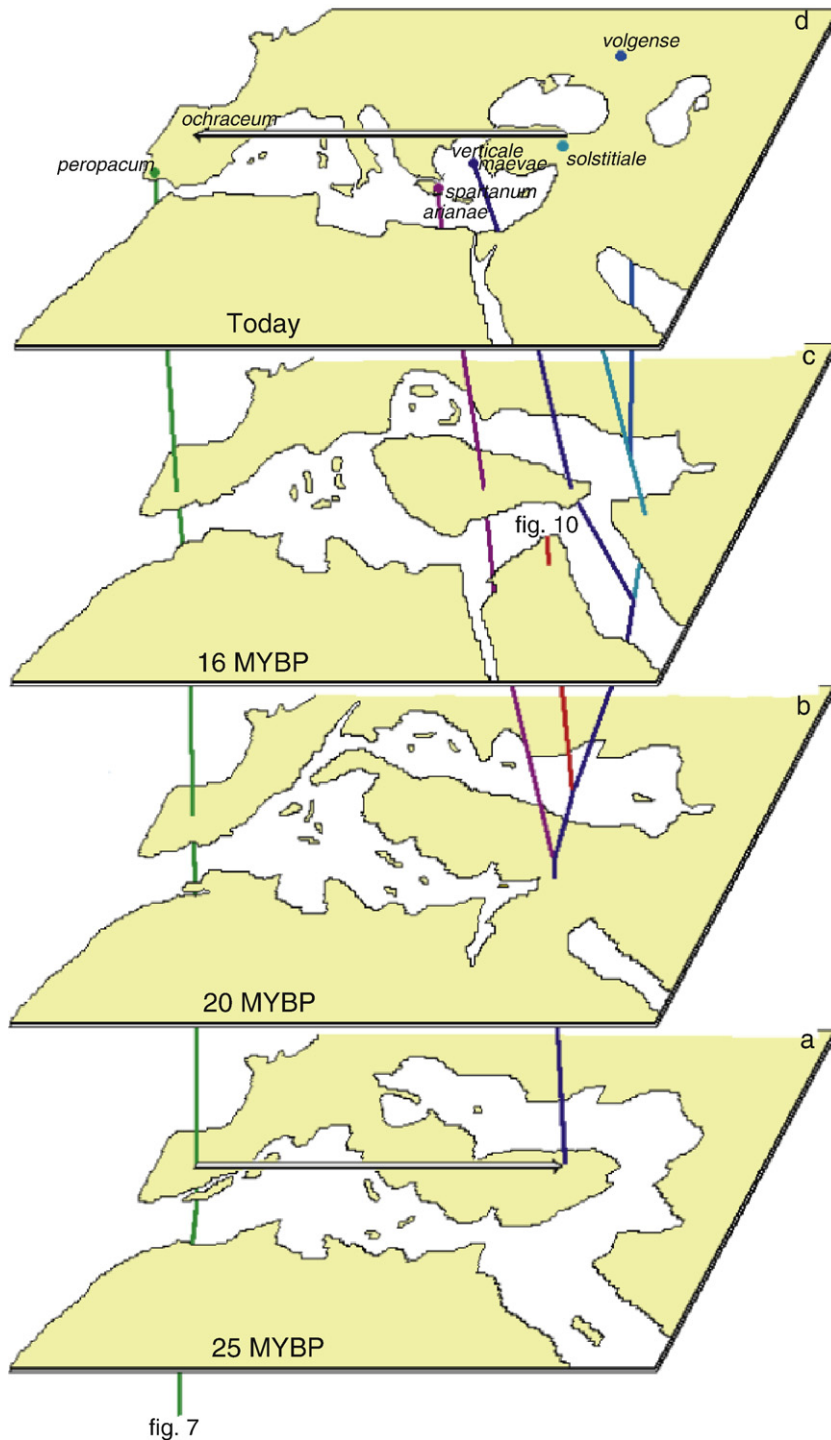


Fig. 9. Phylogenetic relationships of the *A. peropacum*-group and *A. solstitiale*-group mapped onto a paleogeographical representation of the evolution of the Mediterranean Basin from the Oligocene to the present.

late Oligocene to early Miocene at 25–20 Myr BP. This event allowed for the colonisation of the eastern Mediterranean Basin by representatives of the western Medi-

terranean *A. solstitiale* lineage (Fig. 9a). Subsequently, during the early Miocene at 20–17 Myr BP, a marine connection between the Tethys and Paratethys Oceans

was restored westward of the Alps (Fig. 9b). Vicariance between western (*A. peropacum*-group) and central + eastern (*A. arianae*-group + *A. solstitiale*-group + *A. vernale*-group + *A. pini*-group) Mediterranean lineages could have occurred during this time. The *peropacum*-group currently is composed of a sole species, narrowly localized in the southwestern region of the Iberian Peninsula.

As the oriental marine connection between Tethys and Paratethys Oceans (Middle Miocene, 17–13 Myr BP) was restored, there was separation of the Balkan Peninsula, the Middle East region, Arabian Peninsula, and Africa (Fig. 9c). Successive differentiation of the *A. arianae*-group, *A. solstitiale*-group and *A. vernale*-group + *A. pini*-group, composing the other parts of the

*A. solstitiale* lineage, could have occurred during this event. The *A. arianae*-group probably corresponds to those elements that differentiated within the Balkan Peninsula. The *A. vernale*-group + *A. pini*-group corresponds probably to the group isolated at the northern extremity of the Arabian Peninsula.

The *A. solstitiale*-group probably corresponds to the elements that differentiated in Central Asia and the Middle East. The species branching off at a basal position within this group, *A. maevae* and *A. verticale*, differentiated in the southern Balkan Peninsula. *A. volgense* inhabits Southern Russia. The representatives of the “*A. solstitiale* complex”, taking advantage of their large ecological plasticity, dispersed throughout Europe and Central Asia, westward to Iberian Peninsula,

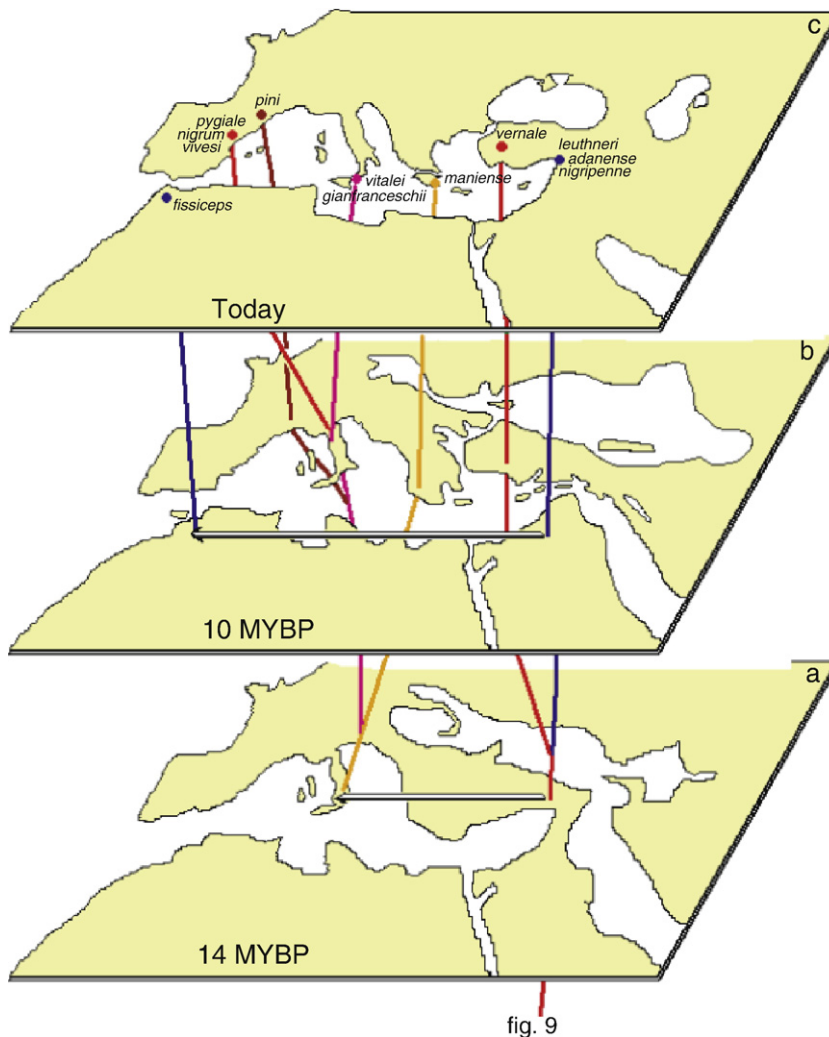


Fig. 10. Phylogenetic relationships of the *A. pini*-group and *A. vernale*-group mapped onto a paleogeographical representation of the evolution of the Mediterranean Basin from the Miocene to the present.

and eastward to Mongolia. During the Pleistocene cycle of glacial and interglacial periods (1.8–0.1 MYBP), many populations occurring in favorable habitats were isolated and have structurally diverged from each other in the southern Europe. Contacts between these different populations became possible at the end of the Pleistocene. Some speciation occurred (*A. ochraceum*, *A. alatavicum*, and *A. javeti*) while other secondary contacts failed, explaining the extreme variability of the polymorphic species *A. solstitiale* across its distribution area. Within this biogeographical context, also it should be noted that many species belonging to other groups such as *A. assimile*, *A. burmeisteri*, *A. majale*, *A. ruficorne*, and *A. atrum* currently inhabit northern and Central Europe. Presumably, these species dispersed to the north from southern Europe when conditions were favorable in these regions at the end of Pleistocene.

The continuous landmass separating Tethys from Paratethys was restored during the middle Miocene, at 15–13 Myr BP, and connected western Europe with the Levant (Fig. 10a). Dispersal of elements of the *A. vernale*-group + *A. pini*-group from Minor Asia into southern Europe became possible during this interval. When the marine connection separating the western and eastern portion of the Mediterranean Basin was restored at about 10 Myr BP (Fig. 10b), the *A. pini*-group in southwestern Europe and the *A. vernale*-group in southeastern Europe and Minor Asia were separated by vicariance. The most basal species of the *A. pini*-group became strictly localized in a relictual area south of Greece, a condition which apparently supports the vicariance hypothesis regarding populations of the eastern and eastern parts of the Mediterranean Basin.

One species of the *A. vernale*-group is currently isolated in western of North Africa. One hypothesis for this occurrence is that elements of this group dispersed throughout North Africa, from Asia Minor to Morocco. The formation of the Saharan–Arabian–Syrian desert belt during the late Miocene to early Pliocene (Fig. 10b), including especially Tunisia, Libya, and Egypt in North Africa, has probably induced the separation and differentiation of *A. fissiceps* in Morocco. This hypothesis was proposed by Sanmartin (1998) to explain the differentiation of the Melolonthine genus *Pachydemia* (*Pachydeminae*) in North Africa.

The other species belonging to *Amphimallon* – *A. adanense*, *A. leuthneri* and *A. nigripenne* – are localized southern Turkey (Adana) and northwestern of Syria (Fig. 10c). In his study of the Melolonthine genus *Aplidia* Hope, Baraud (1988) noticed that a natural group composed of many species also was confined to a restricted area of southern Turkey. From these observa-

tions, it seems that Melolonthinae have found favorable conditions for speciation in this area.

#### 4. Conclusions

Based on a cladistic analysis of morphological characters, it is possible to elucidate the principal historical–biogeographical hypothesis, in order to explain the current distribution of *Amphimallon* species groups.

1. The Iberian Peninsula is hypothesized as the center of origin for the genus *Amphimallon*. This genus belongs to a group of genera inhabiting the Western Mediterranean Basin and probably differentiated by vicariance from the other western–Palaeartic Rhizotrogini lineages in the Iberian Peninsula as consequence of the uplift of the Pyrenees at 35 MYBP.
2. As consequence of microplate fragments that drifted eastward from the proto-Iberian Peninsula (25–20 Myr BP), there was separation by vicariance of the *A. lusitanicum*-group, presently confined to the Iberian Peninsula, and the *A. ruficorne*-group, occurring in the proto-Italian Peninsula. In addition, microplate fragments drifting southwards during 25–20 Myr BP set the stage for the colonization of North Africa by elements of the *A. fuscum*-lineage.
3. During landmass interchange throughout the Mediterranean Basin as a result of the Messinian Event, elements of the *A. solstitiale* lineage colonized the eastern Mediterranean Basin at around 25 Myr BP. A marine connection between the Tethys and Paratethys Oceans west of the Alps (20 Myr BP) induced the separation between the *A. peropacum*-group of the Iberian Peninsula and a portion of the *A. solstitiale* lineage existing in the Eastern Mediterranean Basin. Subsequently, restoration of marine connection between the Tethys and Paratethys Oceans east of the Mediterranean Basin at 16 Myr BP induced the vicariant separation of the *A. arianae*-group within the Balkan Peninsula, the *A. solstitiale*-group occurring in the Middle East and the *A. vernale* + *A. pini*-group of the Arabian Peninsula. Restoration of landmass connection throughout the Mediterranean Basin at 14 Myr BP, and a subsequent marine connection at 10 Myr BP segregating the western and eastern parts of the Mediterranean Basin, caused vicariant separation between the *A. pini*-group of the Western Mediterranean Basin and the *A. vernale*-group of the Eastern Mediterranean Basin.
4. During the Messinian Crisis, commencing at 5.5 Myr BP, elements arriving from North Africa colonized

the Iberian Peninsula (*A. naceyroi*-group) and southern Central Europe (*A. fuscum*-group), where they later differentiated.

5. Many populations have been isolated and have diverged from each other in the southern regions of Europe during the glacial and interglacial cycles of the Pleistocene from 1.8 to 0.1 Myr BP. At the end of this period, northern Europe has been colonized by relatively few species of the genus *Amphimallon*.

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## References

- Baraud, J., 1977. Coleoptères Scarabaeoidea. Faune de l'Europe occidentale: Belgique, France, Grande-Bretagne, Italie, Péninsule ibérique. Suppl. nouv. Rev. Entomol., vol. 7.
- Baraud, J., 1985. Coleoptères Scarabaeoidea. Faune du Nord de l'Afrique, du Maroc et du Sinaï. Paris, Lechevalier.
- Baraud, J., 1988. Contribution à l'étude du Genre *Haplidia* Hope. Rev. Suisse Zool. 95, 539–579.
- Baraud, J., 1992. Coleoptères Scarabaeoidea d'Europe. Fédération française des Sociétés de Science Naturelles, Paris, Société Linnéenne de Lyon, Lyon. (Faune de France 78).
- Britton, E.B., 1978. A revision of the Australian chafers (Coleoptera: Scarabaeidae: Melolonthinae). Aust. J. Zool. Suppl. 60, 1–150.
- Chikatunov, V., Pavlicek, T., 1997. Catalogue of the beetles (Coleoptera) in Israel and adjacent areas: 1. Scarabaeoidea. Klapalekiana 33, 37–65.
- Coca Abia, M., 1995. Taxonomía, Filogenía y Biogeografía del Genero *Rhizotrogus* en el Mediterraneo Occidental. Ph.D. Thesis, Universidad Complutense de Madrid. Madrid, Spain.
- Coca Abia, M., Martín Piera, F., 1991. Anatomy and morphology of the genitalia in the subtribe Rhizotrogina: taxonomic implication. In: Zunino, M., Bellés, X., Blas (Eds.), Advances in Coleopterology. AEC, Barcelona, pp. 61–78.
- de Jong, H., 1998. In search of historical biogeographic patterns in the western Mediterranean terrestrial fauna. Biol. J. Linn. Soc. 65, 99–164.
- Gambrell, F.L., 1946. The European Chafer *Amphimallon majalis* and its control in lawns. J. Econ. Entomol. 39, 168–173.
- Guimerà, J., 1988. Estudi estructural de l'enllaç entre la Serralada Ibèrica i la Serralada Costera Catalana. Ph.D. Thesis, Universitat de Barcelona. Barcelona, Spain.
- Humphries, C.J., Parenti, L.R., 1999. Cladistic Biogeography. Second edition. Interpreting patterns of plant and animal distributions. Clarendon Press, Oxford.
- Hurpin, B., 1962. Super-famille des Scarabaeoidea. In: Balachowsky, A.S. (Ed.), Entomologie appliquée à l'agriculture. Traité. Tome I. Coléoptères, vol. 1. Masson, Paris.
- Maddison, W.P., Maddison, D.R., 1993. MacClade: Analysis of phylogeny and character evolution. Version 3.04. Sinauer, Sunderland, Massachusetts.
- Matile, L., 1990. Recherches sur la systématique et l'évolution des Keroplatidae. Mémoires du Muséum National d'Histoire Naturelle, Série A. Zoologie, vol. 148.
- Medvedev, S.I., 1951. Fauna SSSR, Coleoptera, X, 1. Academia Nauk SSSR, Moscow. (in Russian).
- Montreuil, O., 1997. *Amphimallon menorcanum* Reitter, 1902, nouveau synonyme de *Rhizotrogus pallidipennis* Blanchard, 1850. Boll. Soc. Hist. Nat. Balears 40, 147–149.
- Montreuil, O., 1998. Analyse phylogénétique et paraphylie des Coprini et Dichotomiini. Scénario biogéographique. Ann. Soc. Entomol. Fr. 34, 135–148 (N.S.).
- Montreuil, O., 1999. Révision de deux espèces de Grèce du genre *Amphimallon* Berthold, 1827, et description d'une nouvelle espèce. Bull. Soc. Entomol. Fr. 104, 105–108.
- Montreuil, O., 2000. Cladistic systematics of the genus *Amphimallon*. Eur. J. Entomol. 97, 253–270.
- Montreuil, O., 2003. *Tosevskiana* Pavicevic, 1985, an enigmatic genus of European Rhizotrogini. Ann. Soc. Entomol. Fr. 39, 207–210 (N.S.).
- Muñoz, J.A., Puigdefabregas, C., Fontboté, J.M., 1983. El Pireneo. In: I.G.M.E. (Ed.), Geología de España II, pp. 161–168.
- Nonveiller, G., 1960. Der Aedäagus-Bau der Rhizotrogini. XI Congrès International d'Entomologie, I, pp. 92–95.
- Nonveiller, G., 1965. Monographie der Gattung *Miltotrogus*. Entomol. Arb. Mus. G. Frey 5–105.
- Oosterbroek, P., Arntzen, J.W., 1992. Area-cladograms of Circum-Mediterranean taxa in relation to Mediterranean palaeogeography. J. Biogeogr. 19, 3–20.
- Palmer, M., Cambefort, Y., 1997. Aptérisme et diversité dans le genre *Thorectes* Mulsant, 1842: une étude phylogénétique et biogéographique des espèces méditerranéennes. Ann. Soc. Entomol. Fr. 33, 3–18 (N.S.).
- Palmer, M., Cambefort, Y., 2000. Evidence for reticulate palaeogeography: beetle diversity linked to connection–disjunction cycles of the Gibraltar Strait. J. Biogeogr. 27, 403–416.
- Paulian, A., 1977. Contribution à la connaissance de la faune entomologique de la Corse, 1ère note: Scarabaeoidea. Entomologiste 33, 6–15.
- Régner, R., 1939. Contribution à l'étude des hannetons. Un grand ennemi des gazons: *Amphimallon majalis* Razoumowsky. Ann. Epiphyt. Phytogenet. 5, 257–265.
- Régner, R., 1940. Contribution à l'étude de la biologie d'*Amphimallon majalis* Razoumowsky (= *A. rufescens* Latr.), ravageur des gazons. VI Congreso Internacional de Entomología, Madrid, 1935, pp. 729–736.
- Régner, R., 1950. Les recherches françaises sur le Hanneton Commun *Melolontha melolontha* L. Procès-verbaux du VIIe Congrès International d'Entomologie, Stockholm, 1950, pp. 672–678.
- Robertson, A.H.F., Grasso, M., 1995. Overview of the late Tertiary–Recent tectonic and palaeo-environmental development of the Mediterranean region. Terra Nova 7, 114–127.
- Rögl, F., Steininger, F.F., 1983. Vom Zerfall der Tethys zu Mediterran und Paratethys. Ann. Nat. Hist. Mus. Wien 85A, 135–163.
- Rößner, E., Krell, F.-T., 2001. *Amphimallon burmeisteri* Brenske, 1886: Designation des Lectotypus und Abgrenzung von *A. assimile* (Herbst, 1790) — die Schärmzeit als entscheidendes Bestimmungsmerkmal. Entomol. Bl. 96, 171–189.
- Sabatinelli, G., Pontuale, G., 1998. Melolonthinae and Pachydemiae of Arabia. Fauna of Saudi Arabia, vol. 17, pp. 107–146.
- Sainte-Claire Deville, J., 1914. Catalogue critique des Coléoptères de la Corse, 1er supplément, pp. 495–573.
- Sainte-Claire Deville, J., 1920. Catalogue critique des Coléoptères de la Corse, 2e supplément. Ann. Soc. entomol. Fr. 89, 377–404.



- Sainte-Claire Deville, J., 1921. Catalogue critique des Coléoptères de la Corse. 400 p. *Extract Rev. Entomol.*, pp. 1906–1914.
- Sainte-Claire Deville, J., 1926. Catalogue critique des Coléoptères de la Corse, 3e supplément. *Ann. Soc. entomol. Fr.* 95, 113–130.
- Sanmartin, I., 1998. Evolución de los Pachydeminae paleárticos. Ph.D. Thesis, Universidad Complutense de Madrid, Madrid, Spain.
- Schaefer, L., 1964. Dix voyages entomologiques en Corse. *Ann. Soc. Hortic. Hist. Nat. Hérault* 104, 119–134.
- Soulier-Perkins, A., 1997. Systématique phylogénétique et test d'hypothèses biogéographiques chez les Lophopidae. Ph.D. Thesis, Muséum National d'Histoire Naturelle, Paris, France.
- Soulier-Perkins, A., 2000. A phylogenetic and geotectonic scenario to explain the biogeography of the Lophopidae. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 160, 239–254.