

Distribution of European and African species of genus *Diaptomus* (Copepoda: Calanoida: Diaptomidae): a track analysis

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ABSTRACT

The distributional patterns of 13 species of *Diaptomus* Westwood, 1836 were analyzed using the panbiogeographical method of track analysis. Locality records were compiled from the literature and mapped for the construction of individual tracks for each species. These tracks were superimposed to find the generalized tracks. Four generalized tracks were found: (1) Siberia, Central Europe, and Iceland; (2) Northern Italy, southern France, central Spain, northern Algeria, and northern Morocco; (3) Southern France, central Spain, and northern Morocco; (4) Southern Italy, Sicily, and Albania. Five biogeographic nodes were found: (A) Southwestern Iberia, (B) Southeastern Iberia, (C) Central Iberia, (D) Cantabria, at the intersections of generalized tracks 2 and 3; and (E) Italian Peninsula Islands, at the intersection of generalized tracks 2 and 4. The main massing of the species of *Diaptomus* studied is located in the Iberian peninsula, where six of the species do occur. A model based on the fragmentation and differentiation of already widespread ancestors during the late Mesozoic and early Cenozoic, related to the opening the North Atlantic Ocean and the formation of the Mediterranean Sea, is proposed as a most parsimonious explanation for the observed patterns of geographic vicariance.

KEY WORDS

Freshwater, copepods, distributional pattern, panbiogeography.

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INTRODUCTION

The genus *Diaptomus* Westwood, 1836 (Calanoida) comprises about 80 species of copepods characterized by the presence of a single eye spot and very elongated first antennae, exceeding body length. They occur in rivers and large freshwater lakes throughout the northern hemisphere.

The fossil record of Copepoda dates back to the late Carboniferous (Selden *et al.*, 2010), but although there are already order-level phylogenies that corroborate the monophyletic status of Calanoida (Blanco-Bercial *et al.*, 2011; Eyun, 2017; Khodami *et al.*, 2017), no complete phylogeny of the Diaptomidae has been published to date. Thum (2004) provided a molecular phylogeny based on 18S rDNA for selected North American genera of Diaptomidae. Mookkaiah and Ravichandran (2016) and Sivakumar *et al.* (2016) presented molecular phylogenies of several diaptomid species, including some of those mentioned in the present study. Albeit still limited, these phylogenetic hypotheses offer a useful framework for the analysis of the evolution of calanoid copepods in relation to their distribution over geographic space.

Because of their small size, mode of reproduction, and dormant stages resistant to desiccation, copepod species have been believed to possess cosmopolitan distributions as a consequence of high rates of passive dispersal by winds and animal vectors, especially waterfowl and migratory birds (Maguire, 1963). This has led to speculation about ‘colonization waves’ (Boxshall and Jaume, 2000), ‘glacial refugia’ (Marrone *et al.*, 2017), and other dispersalist narratives to explain the biogeography of copepods. However, empirical evidence has not supported the cosmopolitanism of copepods, suggesting instead that these crustaceans have in fact limited dispersal rates and display geographical distribution patterns with considerable degrees of endemism (Jenkins and Underwood, 1998; Bohonak and Jenkins, 2003; Boxshall and Defaye, 2008; Marrone *et al.*, 2013). In the light of these findings, most recent studies of the geographical distribution of copepods have adopted a vicariant approach, under the paradigm of panbiogeography.

As first developed by Croizat (1958; 1964), and later expanded and quantified by New Zealand

researchers (Page, 1987; Craw, 1989; Henderson, 1989; Craw *et al.*, 1999; Heads, 2012). Panbiogeography has been recognized as one of the main research programs in historical biogeography (Morrone and Crisci, 1995; Crisci, 2001; Crisci *et al.*, 2003), including the biogeography of freshwater organisms (Bănărescu, 1990). The panbiogeographic method of track analysis consists of connecting the mapped locality records of different each taxa by means of lines of minimum distance, which defines the individual tracks, corresponding to the sector of geographical space where each taxon has evolved. When the individual tracks overlap for several groups, a generalized track is defined, suggesting a common history for the entire biota (Craw *et al.*, 1999).

Track analysis of distributional patterns have been performed for selected groups of copepods: Jamieson (1998) analyzed the distribution of four species of *Boeckella* Guerne and Richard, 1889 in New Zealand, Menu-Marque *et al.* (2000) studied the distribution of this same genus in South America, and Mercado-Salas *et al.* (2012) studied the distribution of the American species of *Eucyclops* Claus, 1893, using panbiogeographic methods. However, so far the panbiogeographic method has not been applied to analyze the distribution patterns of the widespread genus *Diaptomus*. Marrone *et al.* (2017) studied the distribution of Western Palearctic Diaptomidae using a macroecological approach which took into account current and historical (paleoclimatic) factors.

In this paper, the geographic distributions of 13 species of *Diaptomus* occurring in Europe and northern Africa were mapped and analyzed using the panbiogeographic method of track analysis, with the aim of finding common distribution patterns and attempting to correlate these patterns with vicariant events related to the tectonic history of the region.

MATERIALS AND METHODS

Geographic distribution data for the species included in this study were compiled from the relevant literature and stored in an electronic spreadsheet in angular degrees format. A total of 395 occurrence records were obtained for all 13 European and African species of *Diaptomus* (Tab. 1).

Table 1. Species of *Diaptomus* included in this study and number of occurrence records and respective references for each one.

Species	Number of records	References
<i>D. barabinensis</i> Stepanova, 2008	1	Stepanova (2008)
<i>D. castor</i> (Jurine, 1820)	133	Jurine (1820); Poppe (1889); Scott (1892); Barras (1900); Hartwig (1901); Scott (1902); Graeter (1903); Wolf (1903); Wolf (1905); Norman and Scott (1906); Scott (1906); Gjorgjevic (1908); Van Breemen (1908); Loppens (1908); Klausener (1908); Norman and Brady (1909); Schauf (1911); Cepèdè (1911); Hartmann (1915); Farwick (1915a); Farwick (1915b); Stephensen (1917); Haberbosch (1920); Roy (1922); Roy (1927); Roy (1931); Kiefer (1938); Gurney (1940); Herbst (1951); Smyly (1958); Kiefer and Einsle (1963); Wawrik (1966); Grainger (1966); Røben (1970); Amoros and Juget (1970); Amoros (1973a); Amoros (1973b) Amoros and Fanget (1973); Milad (1974); Hebert and Hann (1986); Preston <i>et al.</i> (1989); Garcia-Gil <i>et al.</i> (1992); Blackstock <i>et al.</i> (1993); Alonso (1998); Reynolds and Marnell (1999); Scher <i>et al.</i> (2000); Flößner <i>et al.</i> (2002); Illyova and Kubicek (2002); Rundle <i>et al.</i> (2002); Moreira (2005); Marques <i>et al.</i> (2008); Sukop (2008); Demeter and Marrone (2009); Maillet (2010); Traykov <i>et al.</i> (2011); Marrone <i>et al.</i> (2013); Brüsin <i>et al.</i> (2016); Novichkova (2016)
<i>D. castaneti</i> Burckhardt, 1920	24	Burckhard (1920); Roy (1931); Miracle (1978), Armengol (1978); Ramdani (1986); Vega <i>et al.</i> (1992); Alonso (1998); Winder <i>et al.</i> (2001); Bouzidi <i>et al.</i> (2010); Miliani <i>et al.</i> (2014)
<i>D. charini</i> Siewerth, 1928	1	Siewerth (1928)
<i>D. cyaneus</i> Gurney, 1909	136	Gurney (1909); Roy (1927); Pesta (1938); Pirocchi (1947); Kiefer (1955); Kiefer (1956); Aguesse (1957); Marazanof (1963); Stella <i>et al.</i> (1972); Miracle (1978); Cruz-Pizarro (1983); Cruz-Pizarro (1984); Ramdani (1986); Alonso (1987); Ramdani <i>et al.</i> (1989); Francisco and Rey (1994); Medina-Sanchez <i>et al.</i> (1999); Rabet (1999); Brancelj and Gorjanc (1999); Barea-Arco <i>et al.</i> (2001); Inypsa (2001); Ramdani <i>et al.</i> (2001); Samraoui (2002); Bouhbouh (2002); Guisande <i>et al.</i> (2003); Mura and Brecciaroli (2003); Ventura (2004); Marrone and Naselli-Flores (2004); Pipan (2005); Rabet <i>et al.</i> (2005); Serrano and Fahd (2005); Catalan <i>et al.</i> (2006); Alonso and Garcia-de-Lomas (2009); Bouzidi <i>et al.</i> (2010); Hamaidi <i>et al.</i> (2010); Sahuquillo and Miracle (2010); Garcia-Jurado <i>et al.</i> (2011); Alfonso and Belmonte (2011); Parco Nazionale del Gargano (2012); Garcia-Jurado <i>et al.</i> (2012); Alfonso and Belmonte (2013); Marrone <i>et al.</i> (2013); Alfonso <i>et al.</i> (2014); Miliani <i>et al.</i> (2014); Riserva Naturale Capo Gallo (2015)
<i>D. falsomirus</i> Kiefer, 1972	5	Mann (1940); Kiefer (1938); Kiefer (1972); Naidenow (1964); (Kiefer, 1972), Kiefer (1972); Samchshyna (2005)
<i>D. glacialis</i> Lilljeborg, 1889	38	Lilljeborg (1889) in Guerne and Richard (1889b); Guerne and Richard (1892); Zykoff (1905); Reed (1962); Tash and Armitage (1967); Tash (1971); Halbach and Fletchner (1976); Landvirkjun (1976); Adalsteinsson (1979); Stross <i>et al.</i> (1980); Flechtner <i>et al.</i> (1982); Hebert and Hann (1986); Malmquist <i>et al.</i> (2001); Jónasson (2002); Malmquist <i>et al.</i> (2003); Abramova (2003); Malmquist (2005); Abramova and Tuschling (2005); Stepanova (2008); Anastasia <i>et al.</i> (2009); Bogdanova (2009); Adalsteinsson (2011); Gruzdev (2014); Novichkova and Chertoprud (2015); Vinarski <i>et al.</i> (2015)
<i>D. kenitraensis</i> Kiefer, 1926	10	Kiefer (1926); Kiefer (1928); Armengol (1976); Alonso (1998); Caramujo and Boavida (2010); Marrone <i>et al.</i> (2013)
<i>D. kostromanus</i> Kiefer, 1972	2	Smirnov (1929); Kiefer (1972)
<i>D. mirus</i> Lilljeborg in Guerne and Richard, 1889	10	Lilljeborg (1889) in Guerne and Richard (1889a); Kiefer (1972); Nevsky (2006); Stepanova (2008); Yevdokimov and Yermokhin (2009); Semyonova and Aleksyuk (2010); Vizer <i>et al.</i> (2013); Nefedov (2013)
<i>D. rostripes</i> Herbst, 1955	11	Herbst (1955); Scher <i>et al.</i> (2000); Novichkova <i>et al.</i> (2014)
<i>D. serbicus</i> Gjorgjevic, 1907	23	Chichkoff (1908); Gjorgjevic (1908); Charin (1927); Kiefer (1938); Stella (1964); Damian-Georgescu (1966); Stella and Margaritora (1968); Kiefer (1972); Marrone <i>et al.</i> (2010); Alfonso and Belmonte (2011); Marrone <i>et al.</i> (2013)
<i>D. zografi</i> Kortchagin, 1887	1	Kortchagin (1887)

Distribution maps for each species were created by means of the DIVA-GIS Geographic Information System (Hijmans *et al.*, 2001; www.diva-gis.org). A Natural Earth (www.natureearthdata.com) image at 1:50 million-scale was used as background layer for all maps. Individual tracks were constructed for each

species by connecting their localities of occurrence with minimum spanning trees using the Croizat software (Cavalcanti, 2009). Generalized tracks were determined from the areas of overlap of individual tracks using the MartiTracks program (Echeverría-Londoño and Miranda-Esquivel, 2011). Biogeographic nodes

(Heads, 2004) were determined at the intersection of two or more generalized tracks. The main massings (geographic concentrations of diversity) were assessed by counting the numbers of species in each cell of a 1 x 1 degree grid using DIVA-GIS.

RESULTS AND DISCUSSION

The species studied and the number of occurrence records obtained for each are listed in [Table 1](#). Distribution maps and individual tracks for each species are presented in [Figures 1-10](#).



Figure 1. Distribution map of *Diaptomus barabinensis* (●), *D. charini* (■), *D. kostromanus* (▲), and *D. zogرافي* (◆).

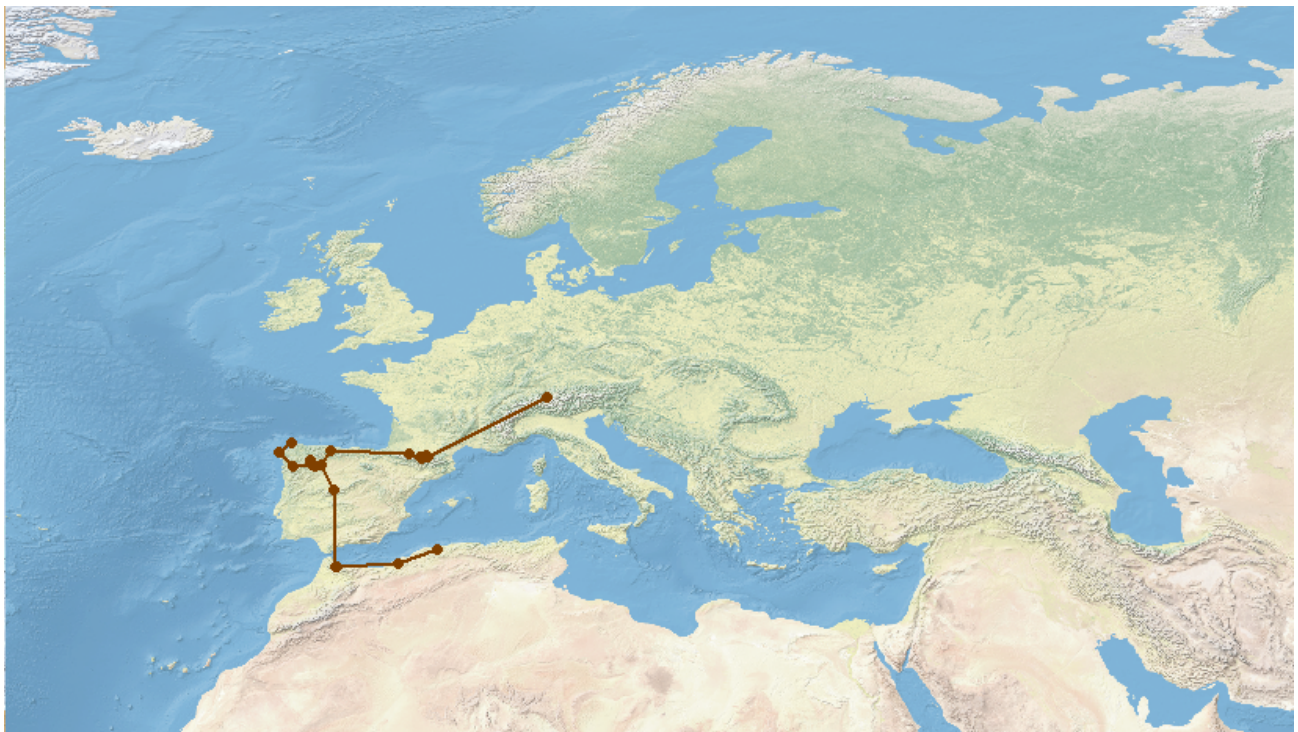


Figure 2. Individual track of *Diaptomus castaneti*.

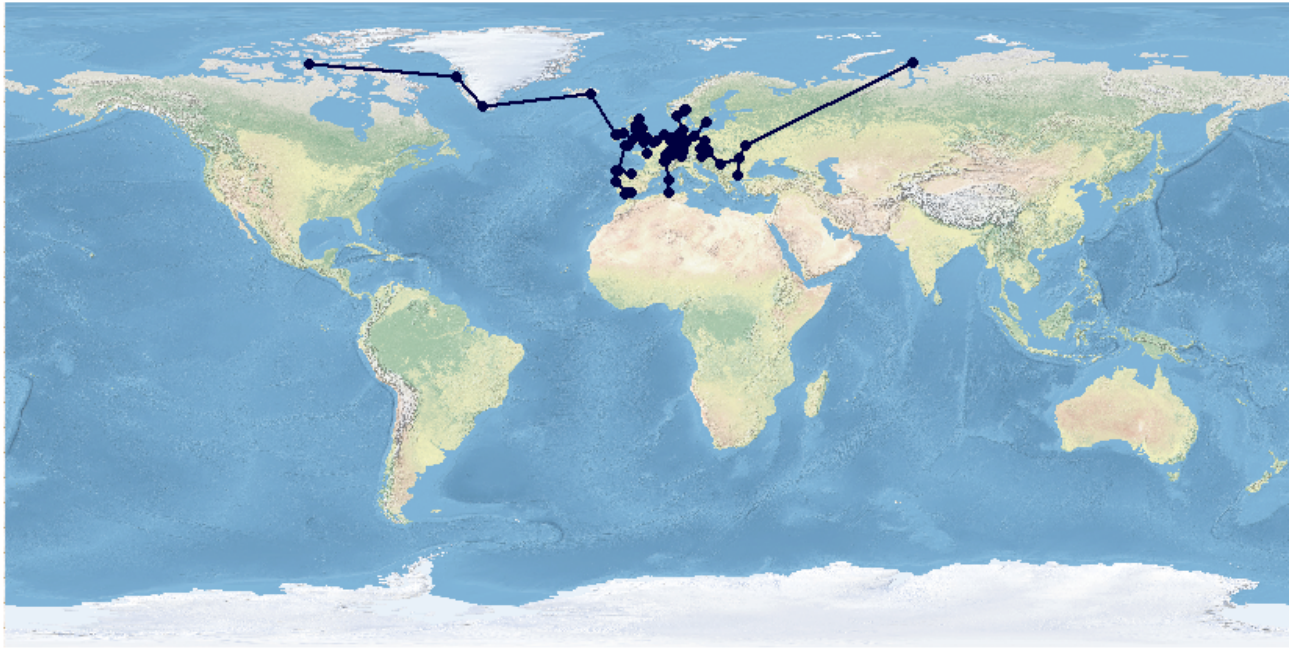


Figure 3. Individual track of *Diaptomus castor*

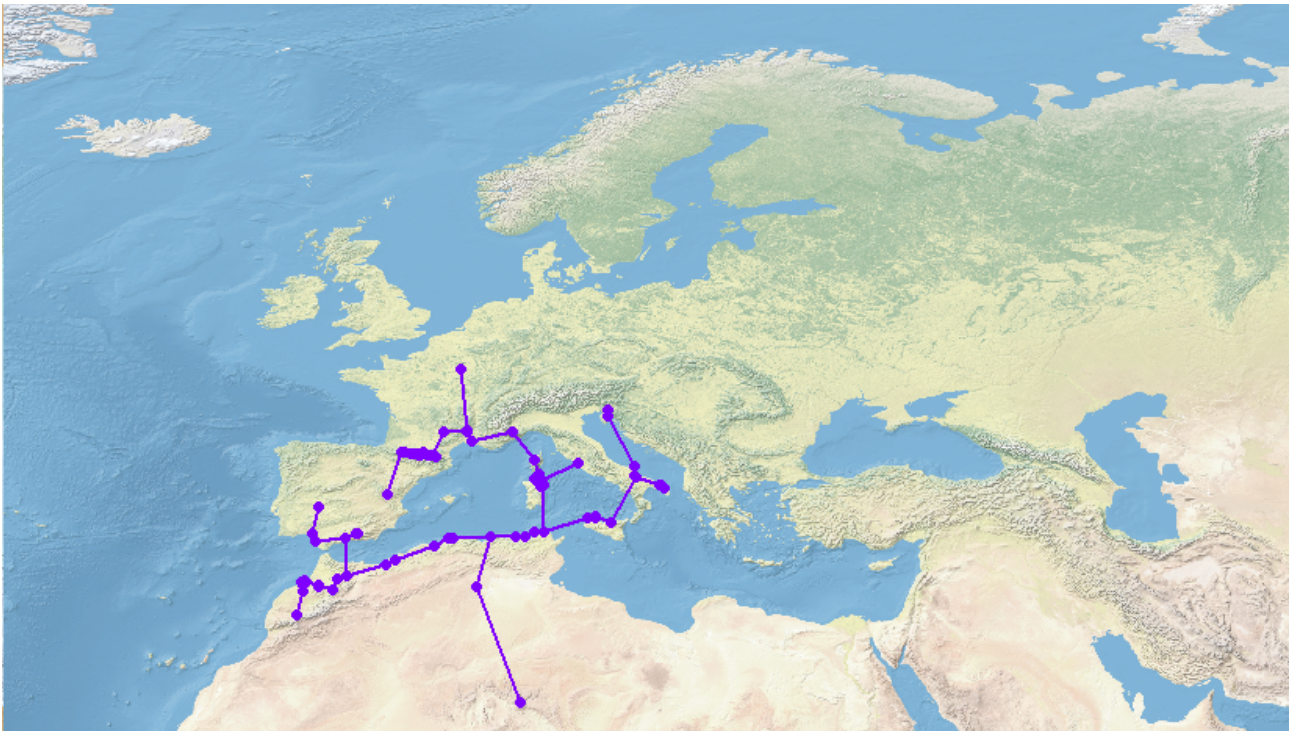


Figure 4. Individual track of *Diaptomus cyaneus*.



Figure 5. Individual track of *Diaptomus falsomirus*.

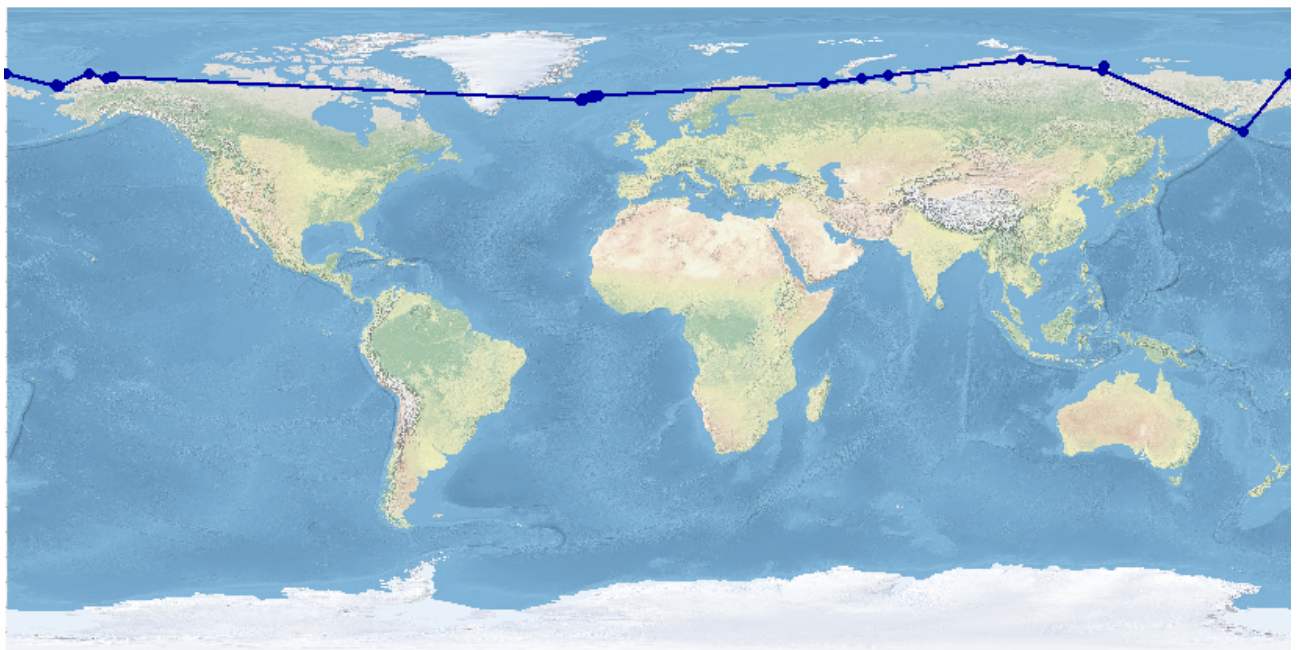


Figure 6. Individual track of *Diaptomus glacialis*.

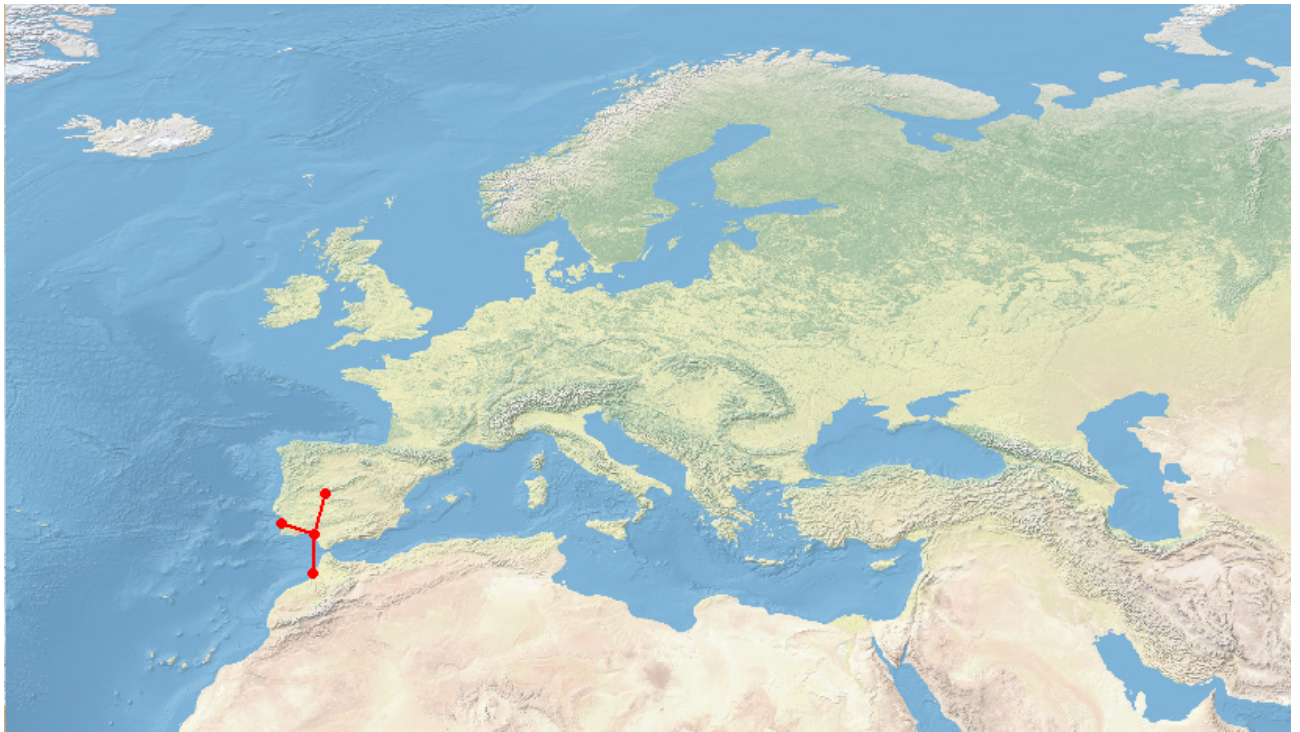


Figure 7. Individual track of *Diaptomus kenitraensis*.

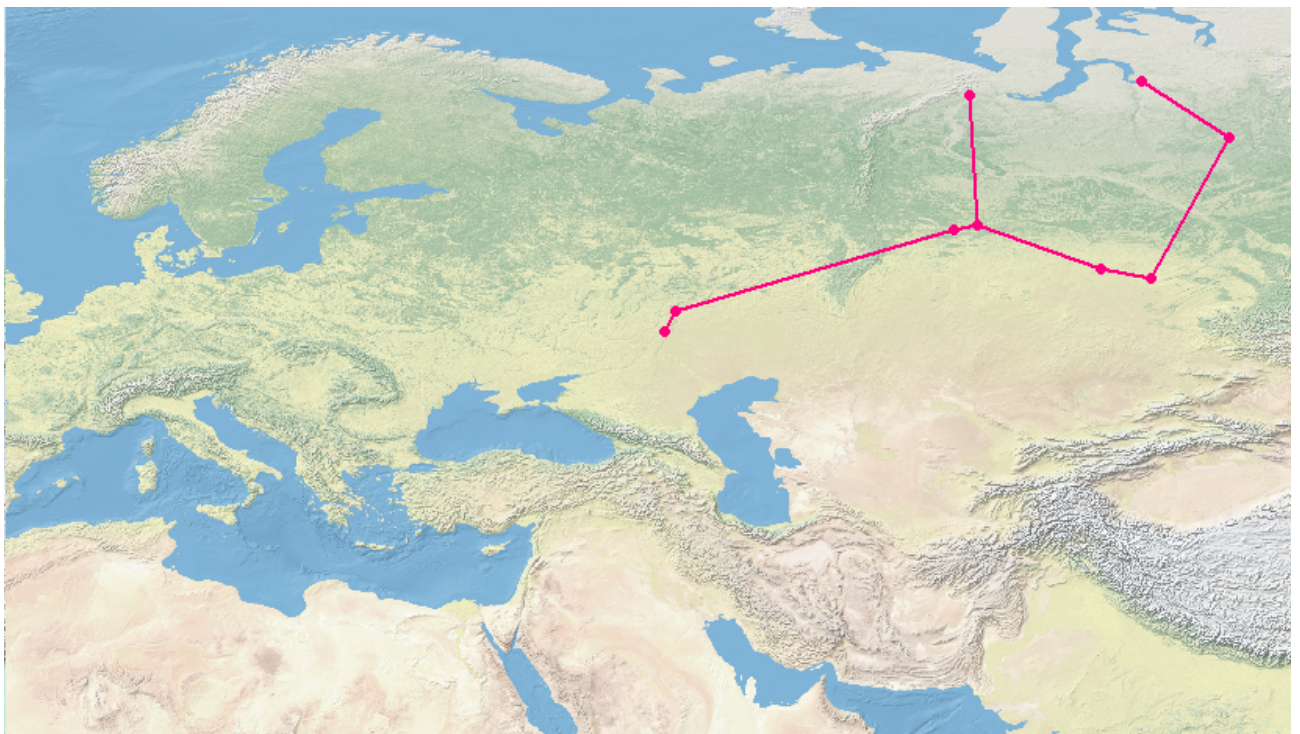


Figure 8. Individual track of *Diaptomus mirus*.

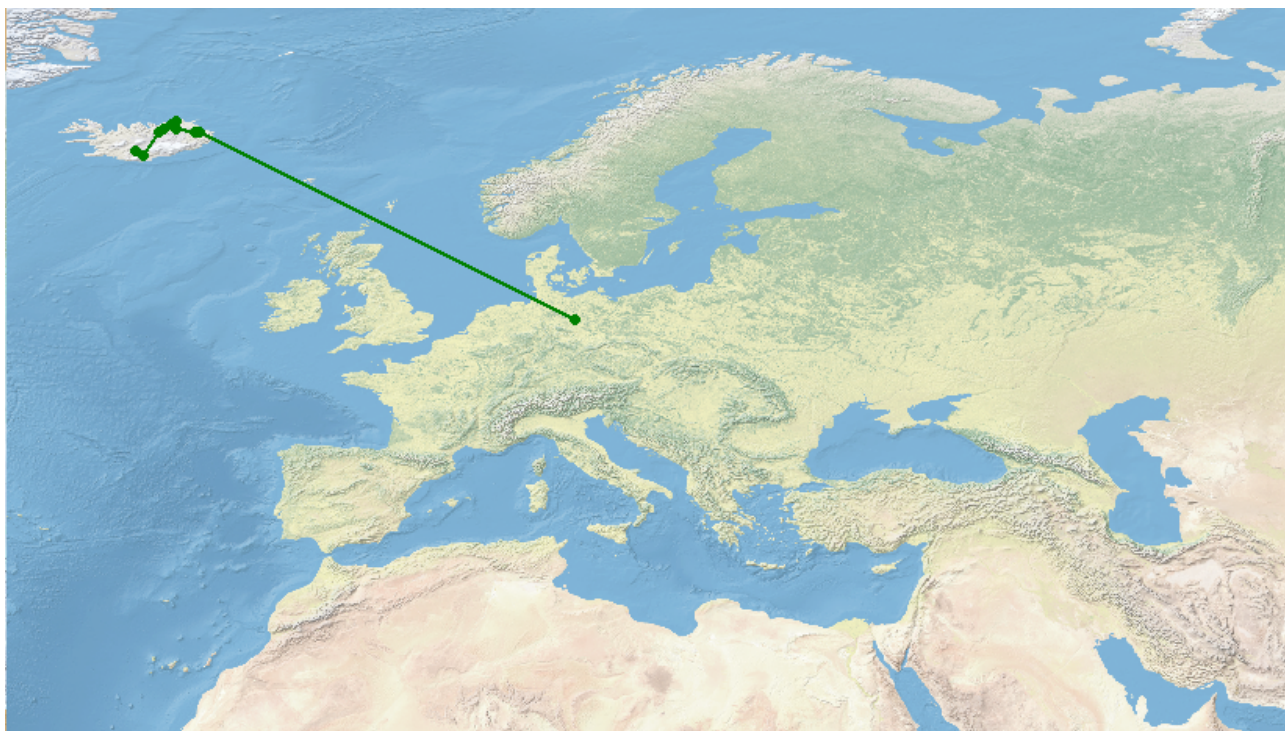


Figure 9. Individual track of *Diaptomus rostripes*.

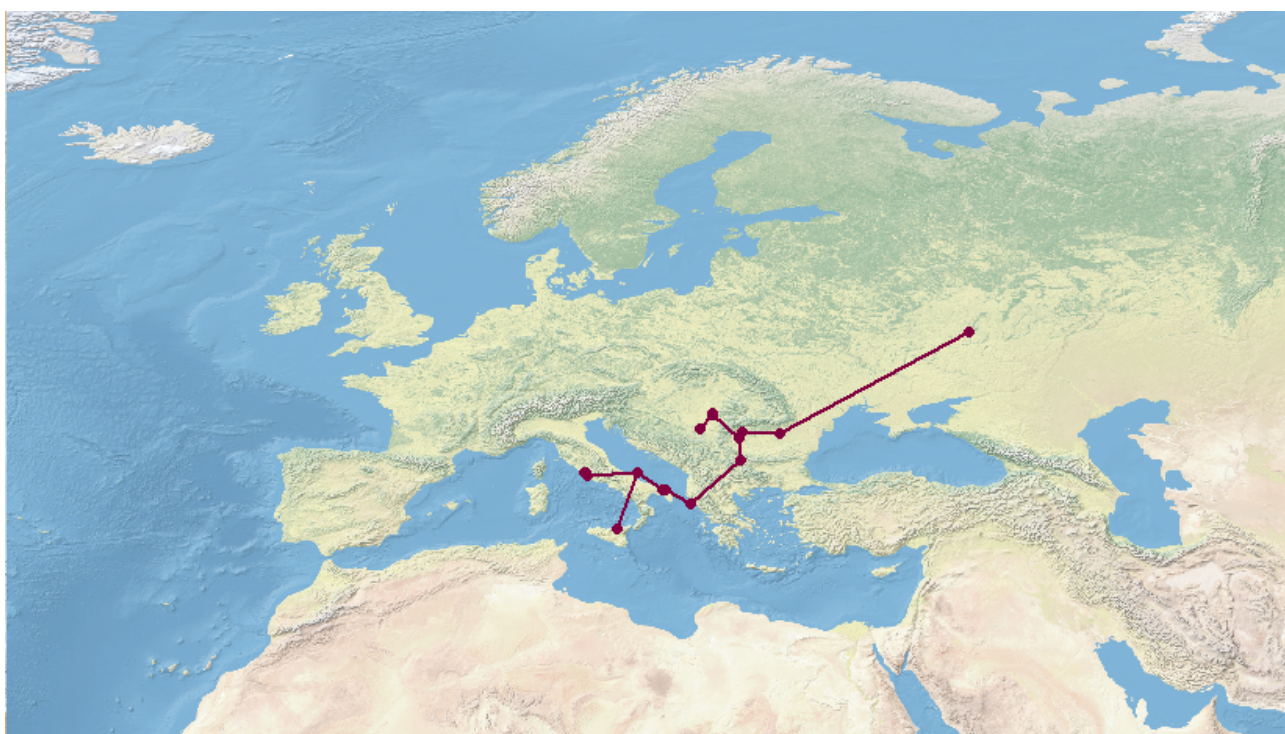


Figure 10. Individual track of *Diaptomus serbicus*.

Of the 13 species of *Diaptomus* included in this study, five (*D. barabinensis* Stepanova, 2008, *D. charini* Siewerth 1928, *D. falsomirus* Kiefer, 1972, *D. kostromanus* Kiefer, 1972, *D. zografi* Korchagin, 1887) had fewer than ten occurrence records.

Four generalized tracks were identified, based on the coincidence of the individual tracks for each species (Fig. 11). These tracks are defined as follows: (1) Siberia, Central Europe, and Iceland (including *Diaptomus glacialis* Lilljeborg, 1889, *D. rostripes* Herbst, 1955 and *D. castor* (Jurine, 1820)); (2) Northern Italy, southern France, central Spain, northern Algeria, and northern Morocco (including *D. cyaneus* Gurney, 1909, *D. castor*, and *D. castaneti* Burckhardt, 1920); (3) Southern France, central Spain, and northern Morocco (including *D. kenitraensis* Kiefer, 1926, and *D. castor*); (4) Southern Italy, Sicily, and Albania (including *D. serbicus* Gjorgjweic, 1907, and *D. castor*).

Five biogeographic nodes were determined: (A) Southwestern Iberia, (B) Southeastern Iberia, (C) Central Iberia, (D) Cantabria, at the intersections of generalized tracks 2 and 3; and (E) Italian Peninsula Islands, at the intersection of generalized tracks 2 and 4 (Fig. 11).

Diaptomus castor is the most widespread species, occurring from Iceland to northwestern Africa, followed by *D. cyaneus* which occurs from Cantabria to northwest Africa. The main massing of the species of *Diaptomus* included in the present study (Fig. 12) is located in Iberia, where six of the species occur.

The scattered highly localized endemics of northern Eurasia (*D. barabinensis*, *D. charini*, *D. kostromanus*, *D. zografi*) stands in contrast to the wider range of other species. The distribution of *D. falsomirus* (Fig. 5) appears to be centered on the Black Sea basin and is also allopatric to all other species (which are all centered west or north). Likewise, the distribution of *D. mirus* Lilljeborg in Guerne and Richard, 1889 is disjunct in north and central Eurasia (Fig. 8).

The distribution patterns of the species of *Diaptomus* included in the present study, as revealed by track analysis, suggest that two major geotectonic events had a role in shaping the evolution of these species, namely the formation of the Mediterranean Sea and the formation of Iceland.

The Mediterranean Sea has a very complex geological history, comprising not only the formation of the basin by the convergence of the African and

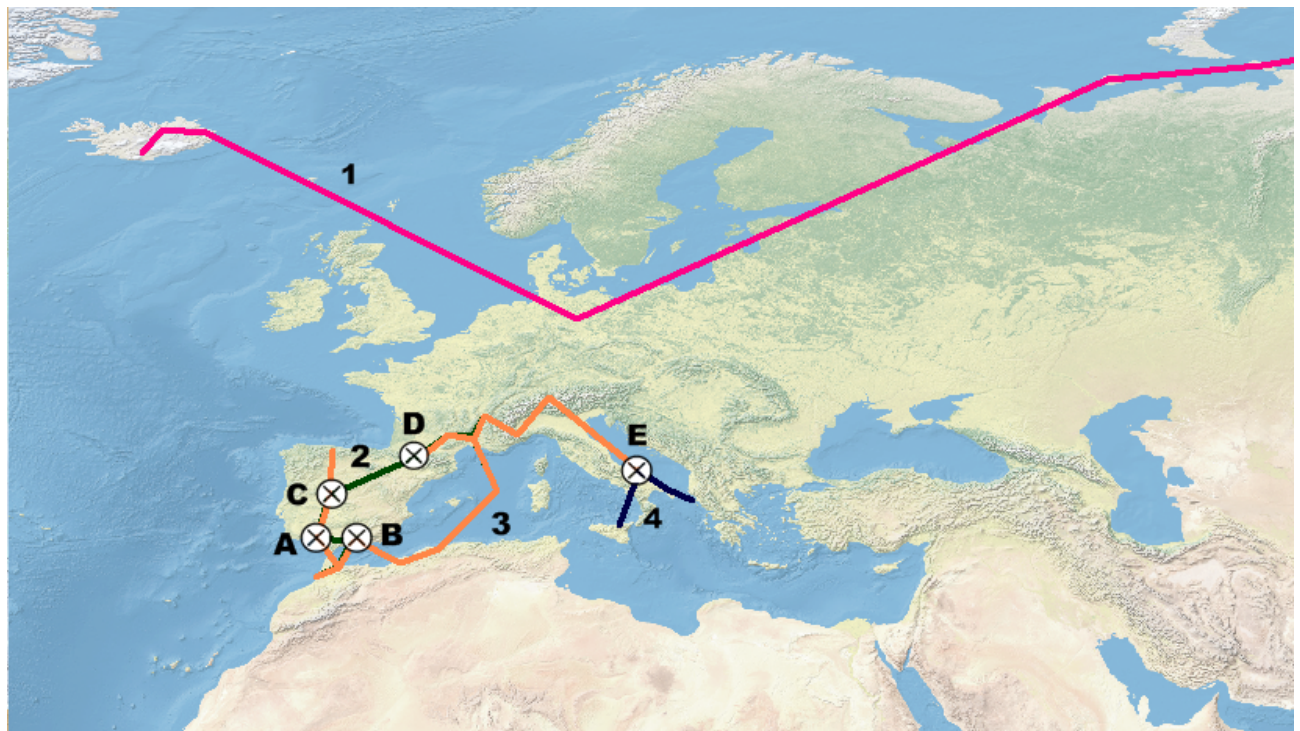


Figure 11. Generalized tracks and nodes of the species of *Diaptomus* included in this study. (1) Siberia-Central Europe-Iceland track; (2) Northern Italy-southern France-central Spain-northern Africa track; (3) Southern France-central Spain-northern Africa track; (4) Southern Italy-Sicily- Albania track. (A) Southwestern Iberia node, (B) Southeastern Iberia node, (C) Central Iberia node, (D) Cantabria node; (E) Italian Peninsula Islands node.

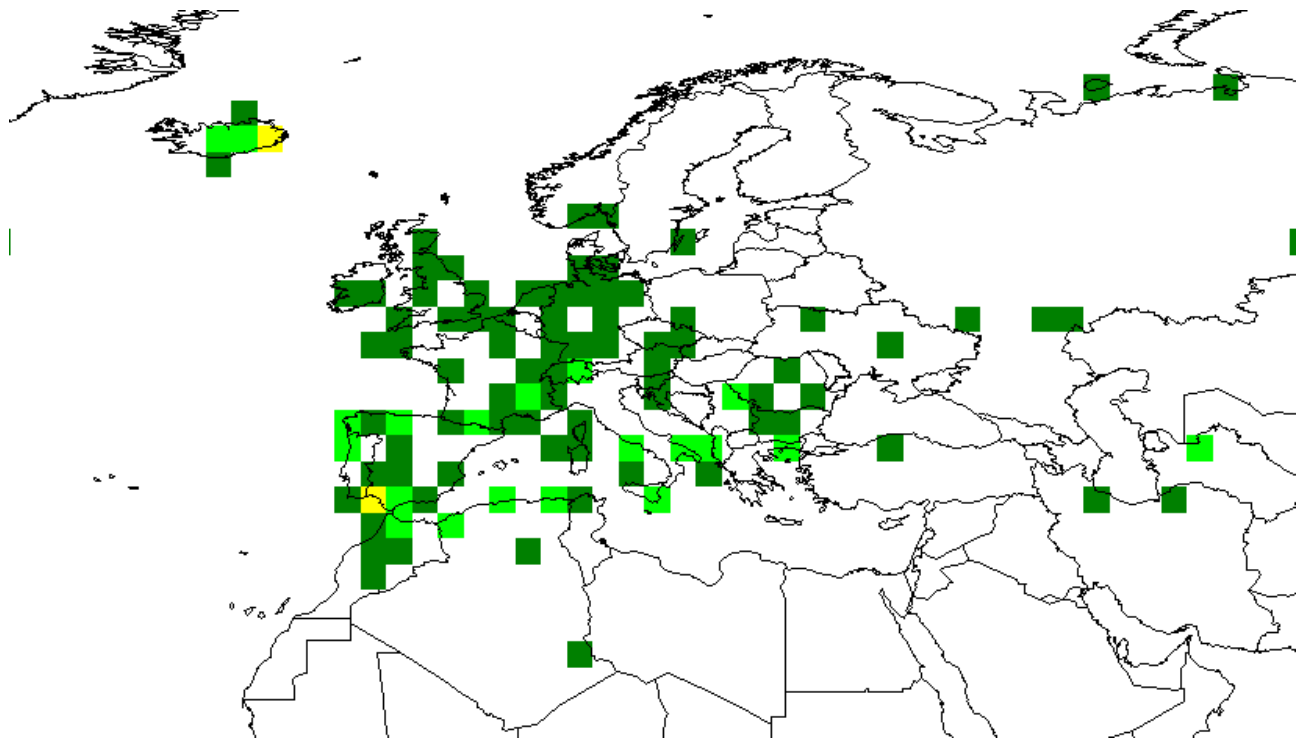


Figure 12. Centers of diversity (main massings) of the species of *Diaptomus* included in this study. Yellow: three species, light green: two species, dark green: one species.

Eurasian plates during the Late Triassic and Early Jurassic, but also several cycles of partial or complete desiccation during the Messinian age of the Late Miocene (García-Castellanos and Villaseñor, 2011). This may explain the biogeographic nodes centered in the southern Iberian peninsula and around the Strait of Gibraltar, a region that marks the sector of geographic space where biotas have fragmented and coalesced during such cycles. These patterns are also corroborated by the molecular phylogenetic tree of Mookkaiah and Ravichandran (2016), where *D. mirus*, *D. cyaneus* and *D. kenitraensis*, *D. castor* form separate clades which are consistent with the observed patterns of geographic vicariance. These branching sequences are interpreted here not as separate dispersal events but as the ‘sequence of differentiation in an already widespread ancestor’ (Heads, 2009).

Generalized track 1, formed by the distributions of *D. castor*, *D. glacialis*, and *D. rostripes* is component of a standard track first identified by Croizat (1958) which includes many more elements of the boreal biota. These three species are recorded from Iceland (with just one record for *D. castor* in the southwestern part of the island).

Iceland lies on the divergent boundary between the North American and Eurasian tectonic plates, as well as above a hotspot, the so-called Iceland plume, which is believed to have formed the island itself (Mjelde *et al.*, 2008; Torsvik *et al.*, 2015). Iceland is a relatively young island, first appearing over the ocean surface about 16 Myr ago (Foulger, 2006), and this might suggest long-distance dispersal as an explanation for the presence of these three species of *Diaptomus*. However, an alternative explanation which does not rule out vicariance is possible. First, the plume model is debatable (Heads, 2009): it may be that Iceland is not even underlain by a lower mantle plume, and volcanic activity in the island could result from processes restricted to the upper mantle and related to plate tectonics (Foulger and Anderson, 2005; Foulger and Natland, 2003; Foulger 2010; Heads, 2009). Second, island age cannot be taken as an absolute criterion for dating the age of taxa (Heads, 2009), as old taxa can survive as metapopulations on ephemeral islands of younger age formed at plate margins and fissures and now submerged (for example, on the Faroe-Rockall Plateau).

The biogeographic nodes cluster to the central and western Mediterranean. Nodes A and B lie on the edge of the western Mediterranean and may be related to the reestablishment of the connection between this basin and the Atlantic Ocean through the Strait of Gibraltar by the Zanclean flood around 5.3 Myr ago (García-Castellanos *et al.*, 2009). One node (D) is at the Pyrenees so that might suggest that the tectonic compression of the Pyrenees and its age might be a factor in differentiation at this node. The Pyrenean chain achieved its present configuration due to the collision between the microcontinent Iberia and the southwestern part of the European Plate (*i.e.*, Southern France), that approached in the onset of the Upper Cretaceous (Albian/Cenomanian), about 100 Myr ago, and collided during the Paleogene (Eocene/Oligocene), around 55 to 25 Myr ago (Choukroune, 1992). The region is bounded by major faults, and such orogenic zones are known to be associated with major biological disjunctions (Croizat, 1958; 1964; Heads, 1989). The node in Italy (E) seems to represent a boundary for distributions further west and likewise the tectonic activity in the region is pertinent to explain biological disjunction patterns in this region. This node is associated with the Apulian/Adriatic Plate, a tectonic microplate that separated from the African Plate during the Mesozoic, and generalized track 4 coincides with the Calabrian arc which marks the microplate boundary (Devoti *et al.*, 2002).

Recently, Marrone *et al.* (2017) presented an analysis of the distribution patterns of diaptomid copepods in the Palearctic, which these authors explained on the basis of effects of recent (*i.e.*, of Holocene age) climatic changes and post-glacial 'recolonizations' from putative 'refugia' in Western Europe. But this interpretation is not supported here, and instead the observed distribution patterns are explained in the light of much older geotectonic events and involved no long-distance dispersal over putative 'barriers'.

Vicariance promoted by geotectonic events extending back to the Mesozoic has played a most important role in shaping the distribution of the species of *Diaptomus* included in this study. This process give rise to analyzable patterns affecting whole biotas (the generalized tracks) and best explains the biogeographic connections observed between the copepod fauna

of continental Europe and Iceland, as well as of the Iberian and Italian peninsulas. A model based on the fragmentation and differentiation of already widespread ancestors during the late Mesozoic and early Cenozoic, related to the opening the North Atlantic Ocean and the formation of the Mediterranean Sea offers a most parsimonious explanation for these patterns.

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