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A gastropod-based biogeographic scheme for the European Neogene freshwater systems

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A B S T R A C T

For the first time a palaeobiogeographic framework is proposed for European Neogene freshwater systems. The distribution of 2226 species-group taxa of freshwater gastropods from over 2700 Miocene and Pliocene localities was evaluated. The localities were grouped into palaeo-freshwater systems based on latest palaeogeographic reconstructions. Cluster analyses were computed for four time slices, i.e., Early Miocene, Middle Miocene, Late Miocene, and Pliocene. The analyses demonstrate a generally high degree of provincialism for the Neogene freshwater systems and allow the definition of biogeographic units. The delimitations are based on the cluster analyses, the degree of endemicity, and geographical coherence. The Early Miocene is characterised by a relatively low degree of provincialism suggesting the distinction of three regions. Coinciding with the development of many endemic systems on the Dinarian–Anatolian Island and in central Europe, the Middle Miocene demonstrates a higher degree of provincialism, allowing the definition of six biogeographic regions. With the onset of the Late Miocene the retreat of the Central Paratethys and development of the huge Lake Pannon massively shaped faunal evolution and palaeobiogeography in general. The formation of the 'Lago-mare' environment fringing the Mediterranean Basin as well as the development of several restricted freshwater systems in western Europe additionally promoted biogeographic division. The increasing provincialism allowed the delimitation of six biogeographic regions, three of which could be subdivided into seven dominions. With the disappearance of Lake Pannon and the decline of western European and Mediterranean faunas at the Miocene–Pliocene boundary, biodiversity hotspots shifted towards eastern and southeastern Europe. For the Pliocene, four biogeographic regions, five dominions, and four provinces were defined.

Most of the here proposed biogeographic units and faunal differences are governed by the varied existence of large, long-lived systems. Because of their prolonged duration they immensely influenced the community composition on the family level, differences of the relative species richnesses per biogeographic region, and the rising rate of endemicity. The underlying mechanism for this pattern is the ongoing continentalization of Europe triggered by the Alpidic orogenesis and the simultaneous retreat of the Paratethys Sea. The continuing restriction of this huge intracontinental sea from the Mediterranean promoted the evolution of endemic freshwater faunas. The arising long-lived systems like Lake Pannon, Lake Dacia or Lake Slavonia persisted over several millions of years and stimulated the evolution of highly diverse and endemic faunas.

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1. Introduction

Freshwater systems are centres of global biodiversity. Despite covering an area of only 0.8% of Earth's surface, freshwater ecosystems are estimated to harbour at least 100,000 animal and plant species, or nearly 6% of all described species (Dudgeon et al., 2006). Abell et al. (2008) established a biogeographic framework for the extant freshwater ecoregions of the world based on the distribution of freshwater fish. A similar approach was presented by Reyjol et al. (2007) on the European scale. Beyond that, several studies exist discussing general global patterns and their evolutionary background, partly also incorporating data from the fossil record (Starobogatov, 1970; Gray, 1988; Taylor, 1988; Strong et al., 2008). However, studies explicitly examining biogeographic relationships of fossil freshwater faunas are scarce and usually lack a statistic approach. The fossil freshwater record is regularly biassed towards lowland and lake deposits, while many other habitats, like springs or groundwater, which accommodate high gastropod diversities, are underrepresented (Strong et al., 2008). Moreover, when going further back in time, preservational issues additionally hamper sound estimations and reconstructions of freshwater biodiversity.

The first to ever investigate biogeographical relationships between fossil European continental freshwater bodies based on statistical analyses were Harzhauser and Mandic (2008). They demonstrated a high degree of provincialism of freshwater gastropods for 12 selected lake systems of the Neogene period. Unlike most other stratigraphic intervals, the Neogene is marked by an excellent fossil record of freshwater ecosystems in Europe. Particularly the mollusc faunas of the Miocene and Pliocene periods are well-documented by many hundred taxonomic studies published over the last 200 years and provide a comprehensive data basis. A recent effort to list all valid species-group taxa of freshwater gastropods of the European Neogene yielded over two thousand names (Neubauer et al., 2014a, b). The high species numbers are especially influenced by long-lived lake systems, like the Late Miocene Lake Pannon or the Early–Middle Miocene Dinaride Lake System, which harboured rich and highly endemic mollusc faunas and were centres of isolated evolution (e.g., Magyar et al., 1999; Geary et al., 2000; Wesselingh, 2007; Harzhauser and Mandic, 2008; Neubauer et al., 2011, 2013a–c).

For the present study we incorporated all available data for freshwater gastropod faunas from the literature to establish a pan-European biogeographic framework for the Neogene (Fig. 1). Statistical analyses on the gastropod species compositions of 146 fossil freshwater bodies are performed to test for biogeographic clustering, general family-level composition, degree and variation of endemicity, and spatial relationships. To our knowledge such a study has never been conducted before for fossil freshwater faunas at the European scale.

2. Methods

The present study is based on extensive literature research: 410 publications on European Neogene freshwater gastropod faunas were acquired and evaluated. In total 2226 species-group taxa (species and subspecies) from over 2700 localities were included for the entire Neogene period (23.03–2.588 Ma; Gradstein et al., 2012; Fig. 2). Although the general geographic frame is Europe we also integrated Turkey and marginal territories of Azerbaijan, Georgia, and Kazakhstan, because these regions accommodate closely related gastropod faunas and the palaeogeographic units studied do not end at the political boundaries of modern Europe. The data were not simply uncritically adopted but were checked by taxonomic specialists (T.A.N., M.H., O.M., and several colleagues mentioned in the acknowledgments). Uncertain records and obvious misidentifications were excluded as far as possible. Taxonomic history was also considered: changes to faunal lists by revisions of earlier works were implemented accordingly. Moreover, the systematics of all taxa was updated according to latest published concepts (Neubauer et al., 2014a, b). Thereby the comparability of the taxonomic units is guaranteed. To obtain a sound temporal framework, all the stratigraphic ages of the localities were checked and updated where necessary, following latest published concepts. Localities were grouped into freshwater palaeoenvironments, i.e., lakes (majority), wetlands, rivers, and brackish embayments. Data from marginal settings of marine environments, i.e., in-washed from tributary rivers, were included as well, since they characterise the fauna of the adjacent hinterland. For some systems no predefined names were found in the literature and they are named herein (usually after the largest village/city in the respective basin or the prevailing usage of the basin name in the geological literature). The apparent data insufficiency in certain regions is largely not due to research bias but is a result of geological history and lack of deposits. Especially north of c. 52° latitude no surface outcrops exist as they have been eroded by the advancing ice shield during the Pleistocene (e.g., Molnar, 2004; Sternai et al., 2012).

2.1. Distinction of palaeobiogeographical units

Prior to the cluster analysis we tested the relevance of the dataset, i.e., that species are not independently distributed across palaeoenvironments. We divided the presence–absence matrix into equal halves, randomly distributing the taxa. For each of the two new matrices a principal components analysis (PCA) was computed. For each analysis a Euclidean distance matrix was calculated from the scores of the first two components. The correlation of both matrices was tested by applying a Mantel test (Mantel, 1967). If the data are biogeographically structured, a strong relationship between both matrices can be expected (Reyjol et al., 2007).

For the cluster analyses, systems with one species only as well as species occurring in only one system (single-system endemics; compare Triantis et al., 2008) were excluded as any clustering would be arbitrary; this concerns 48 systems. Long-lived palaeoenvironments that underwent radical environmental and therefore faunistic changes (like the Dacian or Aquitaine basins) were subdivided into faunistically more sensible units that reflect the different environmental stages of the respective systems more accurately. This