Palaeobiogeography of lacustrine cockles as a tool to reconstruct palaeogeography in the Late Neogene Paratethys

Imre Magyar

MTA-MTM-ELTE Research Group for Paleontology, H–1431 Budapest, POB 137. (immagyar@mol.hu)

Abstract

Palaeobiogeography of lacustrine cardiids (subfamily Lymnocardiinae) is an effective tool in the palaeogeographic reconstruction of the Paratethyan area throughout the Neogene. Increasing endemism reflects decreasing connectivity towards the sea (as in the case of the Sarmatian Sea). Extensive formation of endemic species flocks indicates long-lived lacustrine environment (e.g. Lake Pannon). Further taxonomic study is required to improve our palaeogeographic models for the one-way migration events, such as the early Pontian and end-Messinian dispersal of lacustrine cockles into the Eastern Paratethys and into the Mediterranean, respectively.

Keywords: palaeobiogeography, palaeogeography, Paratethys, Pannonian basin, Neogene, molluscs, Cardiidae

Introduction

The term "Paratethys" was coined by Laskarev (1924) to designate the restricted marine to lacustrine biogeographic province stretching from the North Alpine Foreland Basin to Central Asia in the Early Oligocene to Recent. The Paratethys consisted of a series of basins that have been separated from the Tethys (or later from the Mediterranean Sea) by the uplift of the Alpine-Caucasian mountain chain. Connections of individual basins with each other and with the ocean were repeatedly confined or closed, triggering the evolution of specific, endemic taxa in molluscs, ostracods, fish, and other groups of the biota. Borders between parts of the Paratethys and towards the Mediterranean were dynamic: Mediterranean waters occasionally flooded the Paratethys, or vice versa, Paratethyan waters drained into the Mediterranean basins. Thus the history of the Paratethyan basins was an intricate story of opening and closing connections, catastrophic floods, and episodes of desiccation.

A brief characterization of the Paratethys, similar to the above paragraph, can be found in dozens if not hundreds of papers dealing with the geology of the region. What is the basis of these statements though? How do we perceive these isolation and connectivity events in the geological record? The question is relevant because in most cases there is no direct geological evidence for the presence of gateways connecting individual basins; most of these supposed gateways are located in subsequently elevated areas where erosion destroyed the coeval sedimentary record.

Palaeobiogeography as a tool to reconstruct isolation and connectivity events

Although some recent studies experiment with the application of chemical and isotope signals to detect inflow of marine waters into isolated or semi-isolated Paratethyan basins (Vasiliev et al. 2010, 2013), the most traditional and — so far — most effective principle to reconstruct the history of aquatic gateways in the Paratethys is palaeo-biogeography (Harzhauser & Piller 2007). Large-scale appearance of endemic forms within a given basin indicates that oceanic connections were confined and a restricted marine environment formed. Extinction of stenohaline marine organisms in a basin is usually interpreted as a sign of a change in water chemistry, a phenomenon caused by restriction of oceanic connection. Appearance of aquatic species flocks (a monophyletic assemblage of species resulting from extraordinary endemic radiations; Greenwood (1984) indicates the formation of effective barriers to biotic dispersal and gene flow, i.e. isolation from the sea and formation of a lacustrine environment. Dispersal of originally endemic species into another basin or appearance of marine species in a formerly lacustrine basin is usually

interpreted to have taken place through a newly formed gateway between the respective basins.

The palaeogeographical interpretation of a palaeobiogeographic pattern, however, is not always straightforward. Dispersal across a (former) barrier may also happen by means of wind or migrating animals, such as fish or waterfowl (e.g. WESSELINGH et al. 1999). Even when a barrier is destroyed due to geological processes, such as erosion, water level rise, or tectonic subsidence (commonly adressed as "geodispersal"), the newly established connection between aquatic basins may be either a strait providing the opportunity for two-way migrations, or a river flowing from one basin into the other and functioning as an effective filter or even barrier for upstream migration.

In addition, chronology is a key issue in understanding palaeobiogeographic changes. Non-marine basins often have uncertain chronostratigraphy, and this may make the recognition of palaeobiogeographic events difficult or impossible, leading to unfounded theories and hypotheses.

The bivalve subfamily Lymnocardiinae

One of the groups whose palaeobiogeography is very useful in palaeogeographic reconstructions comprises the non-marine cardiids (subfamily Lymnocardiinae). Cardiidae includes mostly stenohaline, normal marine bivalves that enter the fossil record in the Late Triassic and has an extant diversity of about 200 species (SCHNEIDER 1995). Lacustrine cardiids (Lymnocardiinae) include only a few extant species that live in the Caspian and Black seas and in the Aral Sea. The highly euryhaline marine genus *Cerastoderma*, which is also known to occur in Saharan lakes hundreds of kilometres away from the sea (ROSE 1972), is also assigned into this subfamily. *Cerastoderma* first appeared in the Early Oligocene and is believed to be the source of all later lymnocardiid radiations in the Paratethys. There were four radiatons, resulting in the appearance of about 70 genera and ca. 700 species, all endemic to the Paratethys or any of its subbasins (NEVESSKAJA et al. 2001; MAGYAR 2006).

Examples from the Late Neogene

Sarmatian

The most spectacular series of lymnocardiid radiations started in the Sarmatian (12.8 to 11.6 Ma) from two Badenian species, *Obsoletiformes lithopodolicus* and *Plicatiformes praeplicatus* (STUDENCKA et al. 1998). The Sarmatian cardiid fauna, evolving from these two species, includes 4 additional endemic genera and more than 40 endemic species (PARAMONOVA 1977), indicating that the Sarmatian Sea, stretching from the Vienna

basin to Aral Sea, formed an independent biogeographic unit. It is the Proto-Caspian Subprovince of HARZHAUSER & PILLER (2007). Based on the high degree of endemism, only very restricted geographical connectivity can be supposed between the Sarmatian Sea and the Mediterranean.

Pannonian

The lymnocardiid fauna of the Paratethys went extinct in the early late Miocene; only a subset of the species took refuge in the Pannonian basin. This event indicates the splitting of the once uniform Sarmatian Sea province into two palaeogeographical units: the Eastern Paratethys without cardiids (probably due to strongly reduced salinity), and the Pannonian basin, where lymnocardiids started to radiate again, thus indicating a brackish environment (HARZHAUSER & PILLER 2007). In the Pannonian basin, at least 15 genus-level taxa evolved, with more than 200 species (MÜLLER et al. 1999). This intense speciation and formation of species flocks is a characteristic feature of long-lived ("ancient") lakes, both fossil and recent (BROOKS 1950), and thus indicates that the Pannonian basin functioned as a lake at that time (Lake Pannon, Balatonian biogeographic province, HARZHAUSER & PILLER, 2007).

Within the Pannonian basin system, the lymnocardiid-bearing Upper Miocene – Lower Pliocene sedimentary layers are fairly continuous today, but there are patches, physically not connected to the main rock body (Figure 1). Were these disjunct patches deposited in Lake Pannon as well, and it is due to subsequent erosion that they are not continuous any more, or they represent the deposits of other, smaller lakes? The palaeobiogeography of cardiids can answer this question. The Upper Miocene patch of the southern Transylvanian basin lies 20-100 km east from the main sedimentary rock body of Lake Pannon. Its cockle
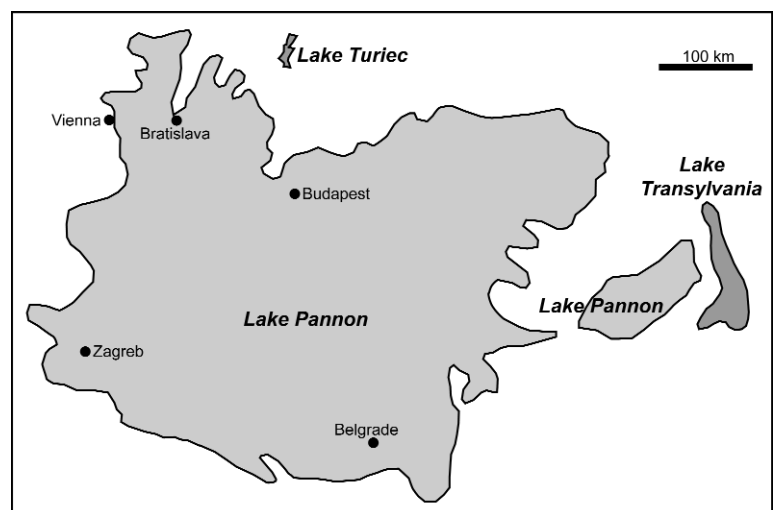

Figure 1. Late Neogene lymnocardiid-bearing lacustrine sediments in the intra-Carpathian area. Based on their mollusc fauna, the lighter gray patches in the Pannonian basin proper and in the southern part of the Transylvanian basin were deposited in Lake Pannon (Late Miocene to Early Pliocene), and their disjunct distribution is due to subsequent erosion. The darker gray patches, however, represent the deposits of Lake Turiec (Late Miocene) and Lake Transylvania (Pliocene)

fauna consists of the same taxa as as those living in the Pannonian basin proper, indicating that the Upper Miocene of the Transylvanian basin was deposited in Lake Pannon. In contrast, the cardiids of the Turiec basin, lying some 50 km distance from the continuous Lake Pannon deposits, are different from the Lake Pannon forms, and, together with the entire mollusc fauna, suggest independent origin in a separate lake (NEUBAUER et al. 2015). Similarly, cardiids from the Pliocene Brasov-Baraolt basins (JEKELIUS 1932) are different from those of Lake Pannon, indicating independent origin in a separate lake ("Lake Transylvania": HARZHAUSER & MANDIC 2008; Figure 1).

Pontian

At the beginning of the Pontian age (6.1 Ma; VASILIEV et al. 2011), a uniform lymnocardiid fauna characterized the entire Paratethys. This palaeobiogeographic pattern led to the interpretation of a large Pontian Paratethys, similar in extent to the Sarmatian Sea (NEVESSKAJA et al. 1987). A more careful chronological analysis, however, revealed that genera and even species of this uniform Pontian lymnocardiid fauna appeared in the Pannonian basin well before the beginning of the Pontian (Figure 2). The first representatives of *Euxinicardium*, *Pseudocatillus*, and *Paradacna* appeared in Lake Pannon before 9.5 Ma; *Prosodacnomya* and *Pontalmyra* are also at least 8 Ma old in the Pannonian basin (MAGYAR & SZTANÓ 2007; Figure 2). All these forms suddenly appeared in the Eastern Paratethys at the beginning of the Pontian, and quickly dispersed from the Dacian basin to the Caspian region (NEVESSKAJA 1990). Migration between Lake Pannon and the Eastern Paratethys at the beginning of the Pontian seems to have been unidirectional (west to east). The connection between Lake Pannon and the Eastern Paratethys functioned as a biogeographic filter, facilitating migration in one direction and hindering it in the other. It could have been either a marine (or lacustrine) gateway (corridor) with unidirectional stream (POPOV et al. 2006), or, more probably, a river flowing from the Pannonian basin to the Eastern Paratethys (MÜLLER et al. 1999).

Messinian

In the late Messinian, at 5.5 Ma, lymnocardiids suddenly appeared all across the Mediterranean. In spite of their wide geographic range, the fossils of these animals are poorly known. Some of them appear to be identical with the Paratethyan species even at species level (e.g. *Paradacna abichi*, *Euxinicardium subodessae*), whereas others could have been the result of Mediterranean radiations (ESU 2007). In the history of the Mediterranean this 0.2 million year long phase is called "lagomare" (ROVERI et al. 2014). At this time lymnocardiids reached their largest distribution: they thrived from the Iberian coast to Central Asia. The nature of connection between the Paratethys and the Mediterranean remains debated (KRIJGSMAN et al. 2010). The base levels of the two large basins were apparently independent from the global sea level, thus a lacustrine gateway with Paratethyan outflow into the Mediterranean or a river connection are both conceivable.

Acknowledgement

Age (Ma)	First appearance of some "Pontian" cockle genera in Lake Pannon	Mammal zone	Biozones of Lake Pannon deposits			
			microplankton	molluscs		
				profundal	sublittoral	littoral
6	P o n t i a n					
7	*Prosodacnomya* *Pontalmyra*	MN13	Galeacysta etrusca	"Dreissenomya" digitifera	Congeria rhomboidea	Prosodacnomya vutskitsi
		MN12				Prosodacnomya dainellii
8		MN11	Spiniferites validus		Congeria praerhomboidea	Prosodacnomya carbonifera
						"Lymnocardium" decorum
9	*Pseudocatillus* *Euxinicardium*	MN10	Spiniferites paradoxus	Congeria banatica	Lymnocardium soproniense	"Lymnocardium" ponticum
10	*Paradacna*	MN9			Lymnocardium conjungens
11			Pontiadinium pecsvaradensis Spiniferites bentorii oblongus		Lymnocardium schedelianum	
		MN7-8	Spiniferites bentorii pannonicus Mecsekia ultima	"Lymnocardium" praeponticum	Congeria hoernesi Congeria ornithopsis

Figure 2. The first appearance of some of the "Pontian" cockles in the stratigraphic column of Lake Pannon. These endemic genera originated in Lake Pannon, and dispersed into the Eastern Paratethys during the early Pontian migration event at 6.1 Ma

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