

Disjunct distribution of the Miocene limpet-like freshwater gastropod genus *Delminiella*

Mathias Harzhauser¹, Oleg Mandic¹, Thomas A. Neubauer¹, Elisavet Georgopoulou¹ and Andreas Hassler²

¹Geological-Palaeontological Department, Natural History Museum Vienna, Burggring 7, Vienna 1010, Austria; and

²Burgstall-St. Andrä 99, St. Andrä 9433, Austria

Correspondence: M. Harzhauser; e-mail: mathias.harzhauser@nhm-wien.ac.at

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ABSTRACT

A highly derived, limpet-like freshwater gastropod of the genus *Delminiella* was found in Miocene deposits of the palaeo-lake Lavant in the intramontane Alpine Lavant Valley in Austria. This Early Miocene genus was known so far only from several lakes of the Dinaride Lake System in southeastern Europe, where it evolved probably from lymnaeid ancestors. These two areas were separated during the late Early and early Middle Miocene by a seaway of the Paratethys Sea and no hydrological connection existed to allow migration of freshwater organisms. Although sweepstakes routes are a likely explanation for the dispersal across the marine barrier, the vector of dispersal remains unknown. The unexpected disjunct distribution of the supposedly endemic genus is a salutary example of the uncertainty in calculating endemism rates in palaeo-lakes. Small lakes are geologically underrepresented and our biogeographic knowledge might be biased by the rich fossil record of long-lived palaeo-lakes. Based on protoconch data, the placement of *Delminiella* in the planorboid family Clivunellidae is rejected and an affiliation with the Lymnaeoida is suggested. *Delminiella norica* is introduced as a new species.

INTRODUCTION

The Miocene and Pliocene lake systems of central and southern Europe are characterized by high levels of endemism—at the species level of up to 98%—and high γ -diversities, attaining several hundred species in some of the lakes (Harzhauser & Mandic, 2008). Diversity and endemism seem to be highest in large and geologically long-lived lakes and result from spectacular autochthonous radiations delimited by clear biogeographic boundaries (Neubauer *et al.*, 2015a). Two outstanding examples are the Early to Middle Miocene Dinaride Lake System (DLS) and the Late Miocene to Early Pliocene Lake Pannon (Magyar, Geary & Müller, 1999; Harzhauser & Mandic, 2008). In both, numerous phylogenetic lineages of melanopsid and lymnaeid gastropods and of dreissenid bivalves are well documented; some of these show unique morphologies, such as huge limpet-shaped lymnaeids (Gorjanović-Kramberger, 1923), decoiled, rod-shaped planorbids (Neubauer, Mandic & Harzhauser, 2011) and infaunal, burrowing dreissenids (Harzhauser & Mandic, 2010).

Despite the high level of endemism, some faunistic exchange between the various lakes is evident. Neubauer, Mandic & Harzhauser (2013a, 2015b) and Neubauer *et al.* (2013b) documented species-level relations between various lakes of the DLS. This is not so surprising in view of their geographic proximity and the probability of hydrological connections between them.

Although many genera remained restricted to the DLS, some others, such as *Prososthenia* Neumayr, 1869 and *Emmericia* Brusina, 1870, invaded other lakes and became typical elements of many Neogene freshwater assemblages (Esu & Girotti, 2001; Esu, Girotti & Truc, 2001). Similarly, many genera that evolved in Lake Pannon invaded Lake Dacia and other lakes in Pliocene times (e.g. *Valenciennius* Rousseau, 1842). Again, geographic proximity and likely hydrological connections may explain these migrations.

Despite such exceptions, most genera that evolved in one of these lakes did not manage to gain a foothold in the others (e.g. *Goniochilus* Sandberger, 1875; *Microbeliscus* Sandberger, 1875; *Papyrotheca* Brusina, 1893; *Lisinskia* Brusina, 1897 and numerous others listed in the FreshGEN database; Neubauer *et al.*, 2014, 2015a).

This pattern may be explained by the evolutionary adaptation of these taxa to peculiar ecological conditions. Many of the Neogene European lakes had aberrant water chemistry, often with increased salinity and/or high alkalinity (Mátyás *et al.*, 1996; Harzhauser, Latal & Piller, 2007). This hypothesis, however, does not explain the limited dispersal of taxa that evolved in the DLS under ‘normal’ freshwater conditions as suggested by stable isotope data (Harzhauser *et al.*, 2011). Another hypothesis was proposed by Seilacher, Reif & Wenk (2007), who considered parasite coevolution a major factor explaining limited dispersal capacities of endemic lake faunas. Whatever

mechanism might have been responsible, such dispersal barriers obviously also exist in modern ecosystems, as none of the endemic species of Lake Ohrid or Lake Baikal has managed to colonise other freshwater systems.

Nevertheless, the occurrence documented herein of a typical DLS genus in an intramontane Alpine Lake shows that dispersal might have been much more common than deduced from the patchy fossil record.

GEOLOGICAL SETTING AND DEPOSITIONAL ENVIRONMENT

The Neogene Lavant Valley is a NNW-SSE oriented basin 28 km in length and 7 km in width, within metamorphic units of the Eastern Alps (Fig. 1) (Beck-Mannagetta, 1952). Along with many other intramontane Alpine basins, its formation commenced during the Early Miocene (Sachsenhofer et al., 2003; Reischenbacher & Sachsenhofer, 2013). The basin fill, up to

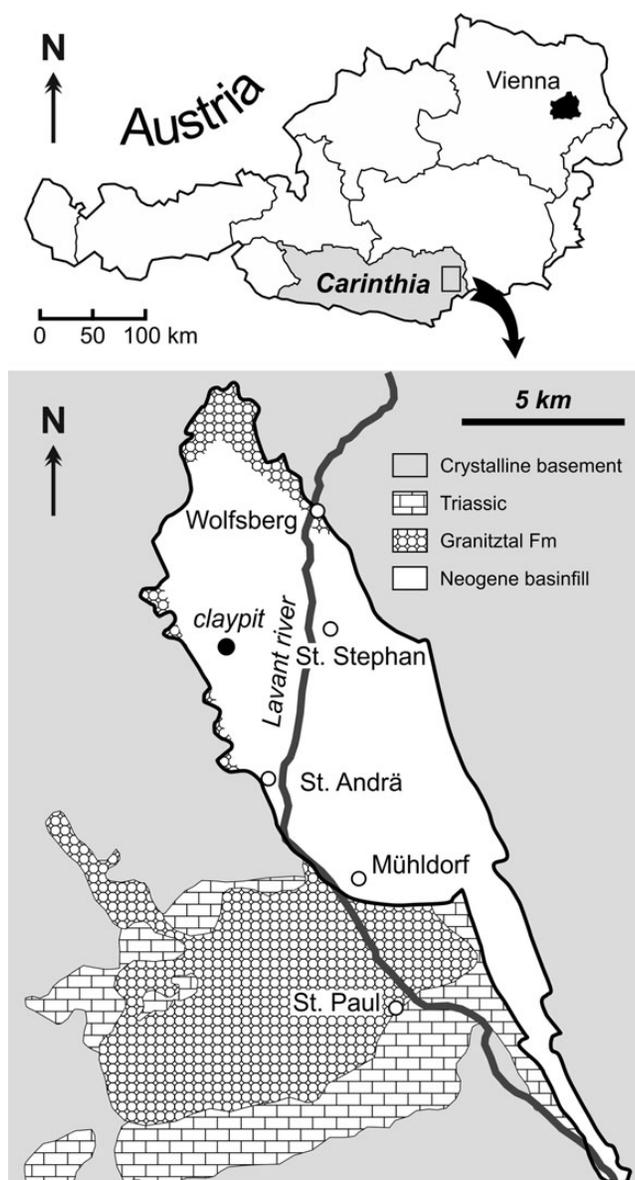


Figure 1. Geographic position of the Schaßbach claypit in the Lavant Basin. Geology modified from Reischenbacher et al. (2007).

1,000 m thick, starts in the Miocene with fluvial gravel of the Granitztal Formation. No age control is available, but from the regional context most authors consider these gravels as Lower Miocene (Burdigalian; Ottungian-Karpatian regional stages). This formation is overlain by limnic sand, silt and clay of the lower Mühldorf Formation, which includes the section studied herein. Again, no clear chronostratigraphy is available for this unit, but a late Early Miocene or early Middle Miocene age is assumed by most authors (Beck-Mannagetta, 1952; Reischenbacher et al., 2007; Reischenbacher & Sachsenhofer, 2013 and references therein). The upper boundary is clearly indicated by the age of the upper Mühldorf Formation, which represents a marine incursion that reached the area during the Langhian (late early Badenian, 14.91 Ma according to Reischenbacher et al., 2007).

Eight gastropod specimens were collected in 2014 by A.H. from dark brown, laminated and mica-rich sand silt in the clay pit Schaßbach (46°47'50.1"N, 14°48'23.6"E) at St. Andrä im Lavanttal (= Lavant Valley) in Carinthia (Austria). There, a few metres of laminated clayey-sandy silt are exploited for brick production. The deposits are rich in freshwater ostracods, fish remains and plant fossils along with rare remains of birds (Nolf & Brzobohatý, 2009; Meller et al., 2014). Based on the lithology, fossil content and depositional environment, we correlate the beds outcropping at Schaßbach with the lower Mühldorf Formation as defined by Reischenbacher et al. (2007). The lower Mühldorf Formation comprises lacustrine deposits of a Miocene lake, for which we propose the name 'Lake Lavant'. This was a small intramontane lake on the southern flanks of the eastern Alps. Based on the size of the Lavant Basin, the lake might have reached about 100 km² or less during its maximum extent. Reischenbacher et al. (2007) interpreted it as a shallow, quiet lake with prevailing anoxic condition. The ubiquitous fish skeletons, scales, otoliths and bone fragments document nutrient-rich surface-water conditions. Molluscs are unknown so far from the lower Mühldorf Formation, except for the herein described *Delminiella*.

SYSTEMATIC DESCRIPTION

Clade Panpulmonata Jörger et al., 2010

Order Hygrophila Férussac, 1822

Superfamily Lymnaeoidea Rafinesque, 1815

? Family LYMNAEIDAE Rafinesque, 1815

Genus *Delminiella* Kochansky-Devidé & Sliškoivić, 1972

Type species: Delminiella soklici Kochansky-Devidé & Sliškoivić, 1972; original designation; Early Miocene, Bosnia and Herzegovina.

***Delminiella norica* Harzhauser, Mandić & Neubauer
new species**

(Fig. 2A–F)

Types: Holotype: Natural History Museum Vienna NHMW 2015/0012/0001 (Fig. 2A–C; width $W = 16.3$ mm, height $H = 14.8$ mm); paratype 1: NHMW 2015/0012/0002 (Fig. 2D; $W = 16.1$ mm, $H = 15.2$ mm); paratype 2: NHMW 2015/0012/0003 (Fig. 2E; $W = 15.5$ mm, $H = 15.5$ mm); paratype 3: State Museum Carinthia, Department of Palaeontology, LMK-Pal 2015/01/5508 (Fig. 2F; $W = 15.15$ mm, $H = 16.6$ mm). The type-specimens are internal and external natural casts in silty sediment. For better documentation, these cavities were filled with silicone to produce positive moulds, representing the original shell surface.

ZooBank registration: urn:lsid:zoobank.org:act:7FDEB2B6-541F-4E09-985D-8F746063B5D0

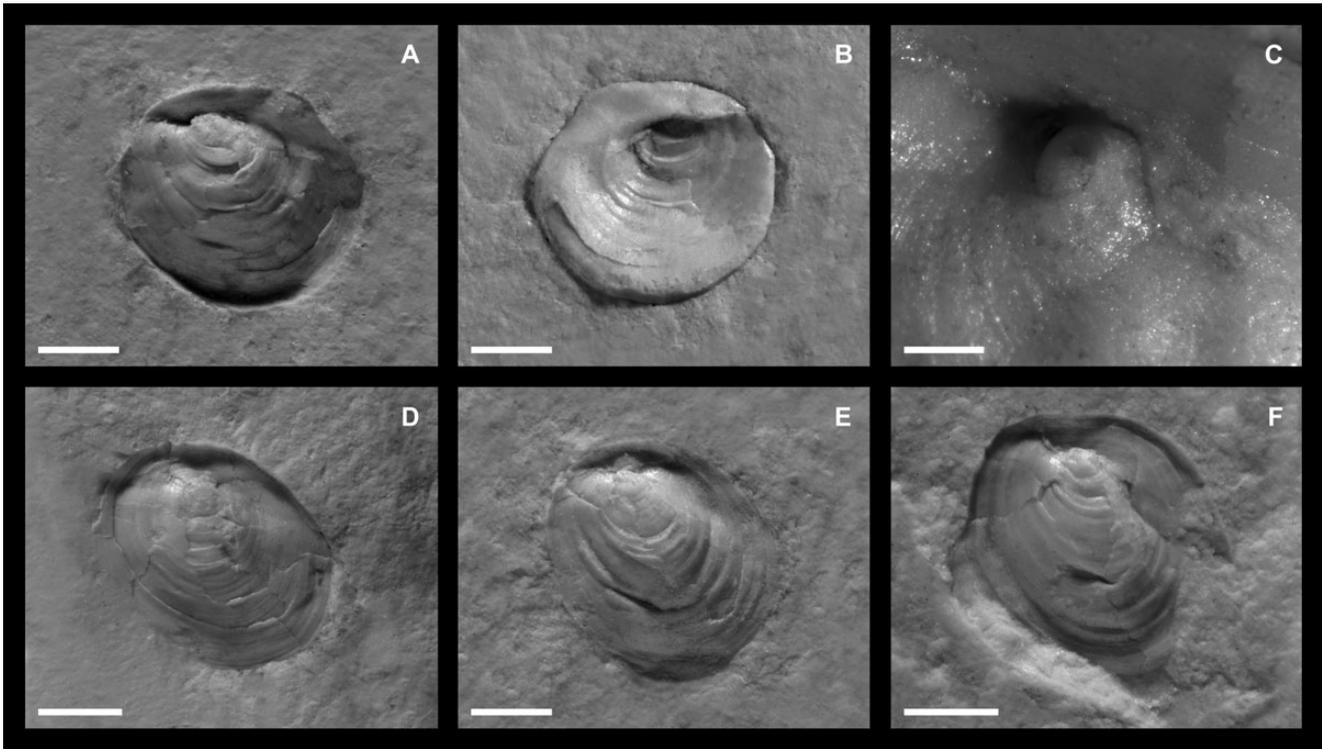


Figure 2. *Delminiella norica* Harzhauser, Mandić & Neubauer n. sp. **A–C.** Silicone moulds of holotype (NHMW2015/0012/0001). **A.** External view. **B.** Internal view. **C.** Detail of protoconch. **D.** Silicone mould of paratype 1 (NHMW2015/0012/0002). **E.** Silicone mould of paratype 2 (NHMW2015/0012/0003). **F.** Silicone mould of paratype 3 (LMK-Pal 2015/01/5508). Scale bars: **A–B, D–F** = 5 mm; **C** = 0.5 mm.

Etymology: Referring to the Roman province Noricum.

Material examined: 4 specimens in addition to types (private collection A. Hassler).

Type locality: Claypit Schaßbach (46°47'50.1"N, 14°48'23.6"E), St. Andrä im Lavanttal, Carinthia, Austria. Stratum typicum: laminated, mica-rich silt/fine-sand of the lower Mühldorf Formation (lacustrine 'fish-shale'). Age late Early Miocene.

Diagnosis: Small, low-conical, limpet-like, robust shells of subcircular to somewhat hexagonal outline, with strongly undulating surface. Apex sinistrally and posteriorly displaced, of one whorl. Two weak siphonal folds along left and right posterior margins, of which left one is always more prominent.

Description: Limpet-like shells of subcircular to slightly elliptical form with somewhat hexagonal outline. Posterior margin weakly convex to nearly straight, passing via prominent convexities into weakly concave sides on left and right. Concavities indicate very shallow siphonal folds, of which left one is always distinct, whereas right one is less prominent. Posterior margin (including adjacent right portion of margin) completely smooth on internal shell surface, wing-like. Anterior margin of three parts, well rounded on left side but slightly angulated on right side. First whorl protruding, strongly convex, regularly coiled, 0.7 mm diameter; surface probably smooth (preservation does not allow clear observation); apex orientated to left, displaced towards posterior margin; last part of first whorl extremely expanded, passing into limpet-shaped second whorl. Blunt, concentric, somewhat irregular folds form dominant sculpture on surface in addition to densely spaced, delicate growth lines, resulting in markedly undulating surface. Folds also expressed on otherwise smooth, glossy interior. In cross section, shells are

low-conical with concave flanks except for distinct concavity between apex and posterior shield. Shell margin moderately thick, slightly swollen, smooth. Most shells are dissolved, but remaining cavities suggest rather robust shells; in two specimens remnants of original shells are preserved, documenting aragonitic shell chemistry.

Remarks: All types of the *Delminiella* and *Clivunella* species and several additional specimens are stored in the Zemaljski Muzej Bosne i Hercegovine in Sarajevo. This material was studied for comparison and is partly reillustrated in Figure 3A–D. Only two *Delminiella* species are known so far: the type species *D. soklici* Kochansky-Devidé & Slišković, 1972 (Fig. 3A) and *D. excentrica* Kochansky-Devidé & Slišković, 1972 (Fig. 3B), both from the Lower Miocene of Bosnia-Herzegovina. *Delminiella soklici* attains about 15 mm in width, is characterized by distinct coiling of the first whorl, a moderately expanded last whorl and an apex that protrudes above the posterior margin (see Kochansky-Devidé & Slišković, 1972). This shape is clearly different from *D. norica*; moreover, *D. soklici* lacks a siphonal fold. *Delminiella excentrica* is much closer to *D. norica* and attains a comparable width of 14.2 mm. It differs clearly from *D. norica* in its broadly ovoid outline, the broad posterior margin and in the apex being only weakly displaced to the left side. In addition, its siphonal fold is much weaker. *Clivunella katzeri* (Gorjanović-Kramberger, 1906) (Fig. 3C) and *C. elliptica* Kochansky-Devidé & Slišković, 1972 (Fig. 3D) are much larger, attaining a height of up to 20–30 mm; they differ in their regular circular to ovoid outline, the central position of the apex and the absence of a coiled protoconch.

The genus *Delminiella* was introduced by Kochansky-Devidé & Slišković (1972) in their paper on the new family Clivunellidae. These authors included *Clivunella* Katzer, 1918 and *Delminiella* Kochansky-Devidé & Slišković, 1972 in the Clivunellidae and discussed a phylogenetic relation with the

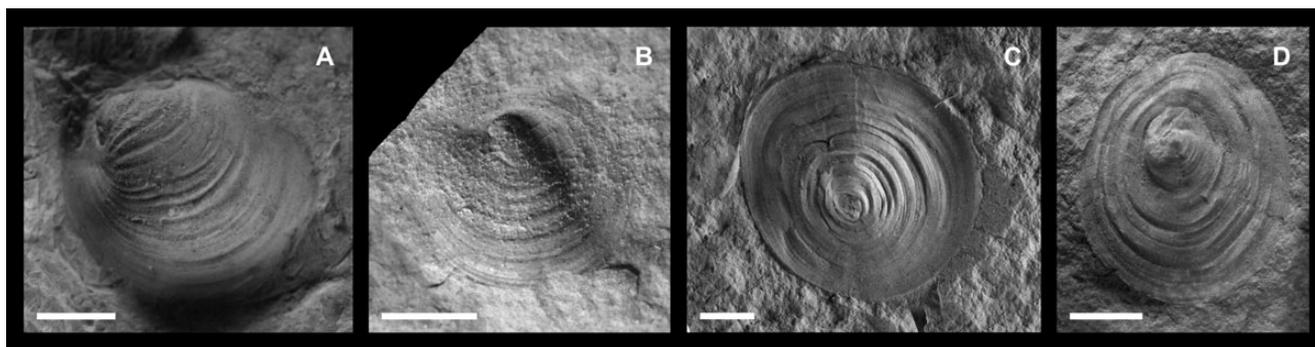


Figure 3. *Clivunella* and *Delminiella* from the Burdigalian of Livno and Tomislavgrad basins in southern Bosnia and Herzegovina (coll. Zemaljski Muzej Bosne i Hercegovine, Sarajevo). **A.** *Delminiella soklici* Kochansky-Devidé & Slišković, 1972, Vučipolje near Tomislavgrad, holotype (MG3631); illustrated in Kochansky-Devidé & Slišković (1972: pl. 3, fig. 3a, b, pl. 4, fig. 9). **B.** *Delminiella excentrica* Kochansky-Devidé & Slišković, 1972, Eminovo selo near Tomislavgrad, holotype (MG3623); illustrated in Kochansky-Devidé & Slišković (1972: pl. 4, figs 1a, b, 10). **C.** *Clivunella katzeri* (Gorjanović-Kramberger, 1906), Potkraj near Livno, MG3602; illustrated in Kochansky-Devidé & Slišković (1972: pl. 1, fig. 4). **D.** *Clivunella elliptica* Kochansky-Devidé & Slišković, 1972, Crvenice near Tomislavgrad, paratype (MG3641; not previously illustrated). Scale bars = 5 mm.

Ancylini. In our opinion, the morphological differences between *Clivunella* and *Delminiella* are too great to unite both in a single family. An ancylid relationship for *Clivunella* is difficult to verify due to the very poor preservation of the embryonic shell. This relationship, however, is clearly unlikely for *Delminiella* given the coiled initial whorl, which is present in *D. excentrica*, *D. soklici* and *D. norica*. In contrast, such a protoconch type is not present in *Ancylus* or *Acroloxus* (see Shirokaya, Roepstorff & Sitnikova, 2003; Harzhauser et al., 2011; Shirokaya et al., 2011). Therefore, we tentatively prefer to place *Delminiella* in the Lymnaeidae, although no ancestor-descendant relationship (such as in the Late Miocene *Radix*-derived Valencienniinae) can be demonstrated (Gorjanović-Kramberger, 1901, 1923).

Kochansky-Devidé & Pikija (1976) listed two additional genera within the family Clivunellidae: *Neoclivunella* Kochansky-Devidé & Pikija, 1976 and *Neodelminiella* Kochansky-Devidé & Pikija, 1976. These are based on small and moderately preserved shells from the Pannonian (Late Miocene) of Croatia, being part of the Lake Pannon fauna. Based on the palaeobiogeographic and stratigraphic context, both taxa might be more closely related to the Valencienniinae Gorjanović-Kramberger, 1923, which are endemic to Lake Pannon and represent a convergent but unrelated lineage—as already pointed out by Kochansky-Devidé & Pikija (1976). In addition, ‘*C.*’ *conica* Gorjanović-Kramberger, 1923 and ‘*C.*’ *ovata* Gorjanović-Kramberger, 1923 were described from the Upper Miocene of Lake Pannon. We strongly doubt that these species are members of the Clivunellidae. Based on its morphology, ‘*C.*’ *ovata* should be placed in the genus *Neoclivunella*. ‘*Clivunella*’ *conica* is a very high-conical species and has little in common with Clivunellidae. A fifth species was described from the Pliocene of Greece by Schütt (1976) as *C. zilchi* Schütt, 1976. This species clearly does not belong to *Clivunella* based on its coiled protoconch, which is huge compared with the small adult shell, and based on the shallow-water assemblage from which it was collected. Therefore, Clivunellidae are now considered to be a monogeneric family of uncertain taxonomic position, restricted to the Early Miocene of the DLS.

Morphologically, *Delminiella* is reminiscent of some species of the Late Miocene to Pliocene Valencienniinae Gorjanović-Kramberger, 1923 and of the lymnaeid genus *Velutinopsis* Sandberger, 1875 from Lake Pannon. Both evolved from *Radix* during the Late Miocene and their evolutionary lineages and radiations are well documented by a rich fossil record (Gorjanović-Kramberger, 1901, 1923; Moos, 1944). If these ancestor-descendant relationships are correct—and the documented succession of morphospecies in Lake Pannon deposits is

quite convincing—a direct relationship of the Valencienniinae and *Velutinopsis* with *Clivunella* and *Delminiella* seems highly unlikely.

DISCUSSION

The first occurrence of *Delminiella* was dated by Jiménez-Moreno et al. (2009) in the Pag Basin at about 17.2 Ma (Fig. 4). *Clivunella* is unknown from that basin (Bulić & Jurišić-Polšak, 2009), but very common in the Livno and Tomislavgrad basins, occurring there in the same stratigraphic interval as *Delminiella* (Kochansky-Devidé & Slišković, 1972). According to De Leeuw et al. (2011), they are restricted there to the stratigraphic unit M2 from 16.9 to 16.1 Ma and vanish from the fossil record thereafter. Thus, *Clivunella* and *Delminiella* became extinct in the DLS close to the Early/Middle Miocene boundary. Unfortunately, the species from the Lavanttal Basin is not conspecific with the DLS species and no direct biostratigraphic correlation is possible. Therefore, the occurrence of the genus in the Eastern Alpine Basin can be interpreted in two possible ways: (1) The lacustrine lower Mühldorf Formation is coeval with the *Delminiella*-bearing deposits of the DLS-basins, suggesting a late Early Miocene age. This interpretation is in agreement with stratigraphic interpretations by Reischenbacher et al. (2007), who assumed an Otnangian to Karpatian age based on the ostracod and otolith assemblages. (2) *Delminiella norica* represents a younger offshoot, which survived extirpation in the DLS at the Early/Middle Miocene boundary. In our opinion, this option is less likely as *Delminiella* existed in hydrologically independent lakes of the DLS, such as Pag, Livno-Tomislavgrad and Sarajevo, and probably vanished from all these lakes more or less simultaneously (Kochansky-Devidé & Slišković, 1972, 1978). This suggests that an external factor, such as climate change, was responsible for the abrupt disappearance of this group. This extrinsic factor would most probably also have influenced the fauna of the lakes in the Alpine area.

Limpet-like shapes evolved nearly simultaneously in two unrelated gastropod clades within the DLS. As discussed above, *Delminiella* is most probably a lymnaeid and the Clivunellidae are probably planorboids. About 4–5 Myr later, the Valencienniinae represent the second lymnaeid offshoot with large limpet-like shells. *Clivunella* and *Delminiella* are concurrent species in the lacustrine deposits of the Livno and Tomislavgrad basins (Kochansky-Devidé & Slišković, 1972), suggesting similar ecological requirements. Our field observations indicate that they were ecological generalists adapted to a broad spectrum of habitats. Based on their sedimentological contexts, *Clivunella* and

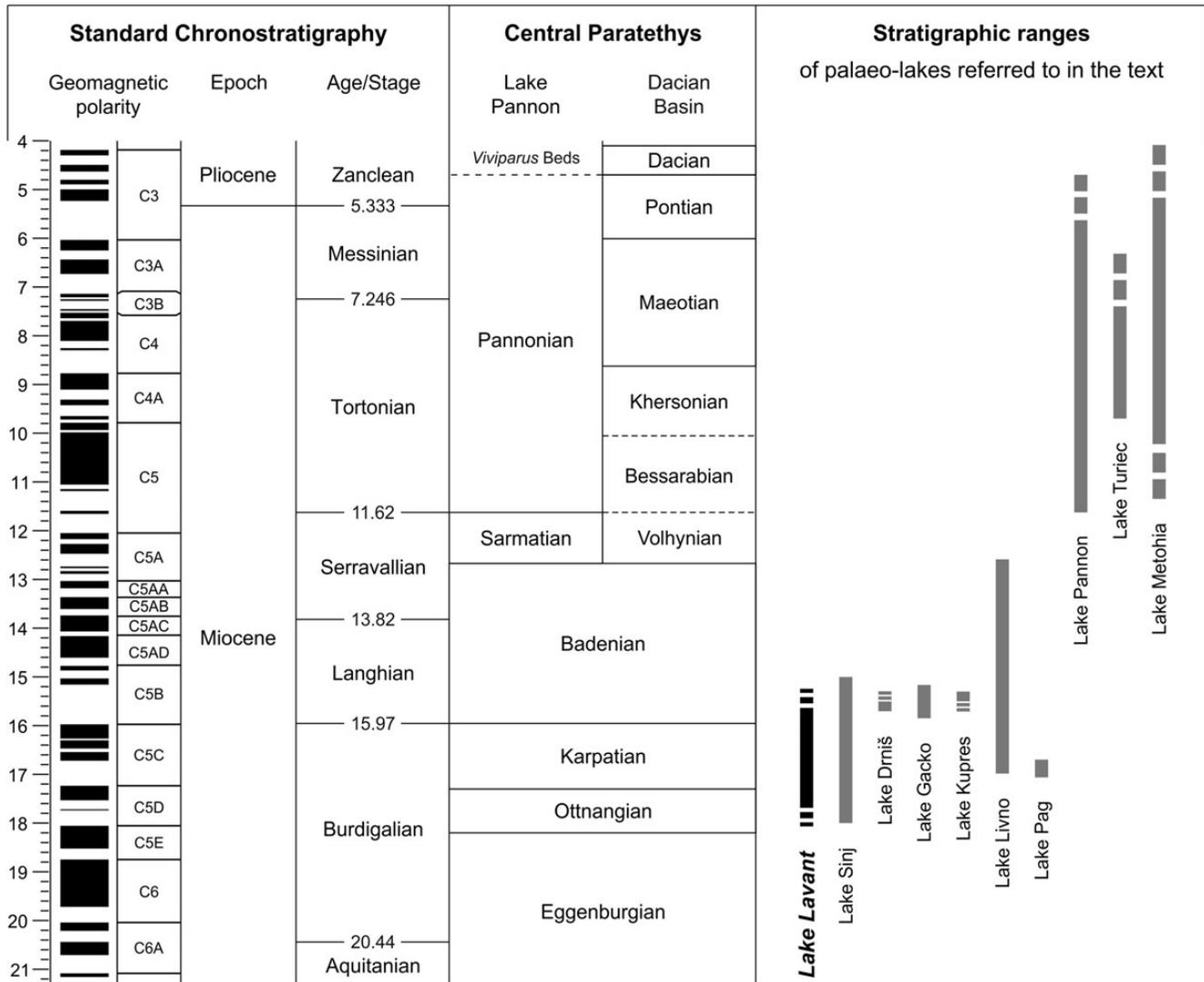


Figure 4. Stratigraphic position of lacustrine deposits of Lake Lavant and other lake systems mentioned in the text. Correlations are adopted from Harzhauser & Mandić (2008), De Leeuw *et al.* (2011) and Neubauer *et al.* (2013b, 2015c,d).

Delminiella were well adapted to muddy lake bottoms in calm, deeper water with intermittent low oxygen levels (De Leeuw *et al.*, 2011). Yet, *Delminiella* has been also found in littoral settings associated with melanopsids and neritids (Bulić & Jurišić-Polšak, 2009). This ecological flexibility may have been crucial in permitting this genus to colonize lakes outside the DLS, since the stagnant and partly anoxic conditions on the bottom of Lake Lavant were hostile for other molluscs. Similarly, the Late Miocene and Pliocene Valencienniinae are found in offshore clays deposited in dysoxic environments (Müller, Geary & Magyar, 1999; Cziczor *et al.*, 2009). The extant limpet-shaped freshwater genera *Ferrissia*, *Ancylus* and *Acroloxus* were all already present in the European lakes by the Early and Middle Miocene (e.g. Čtyroký, 1972; Neubauer *et al.*, 2013a; Harzhauser *et al.*, 2014). The FreshGEN database lists 39 species of these genera from the European Neogene (Neubauer *et al.*, 2014); none of them managed to colonize muddy offshore environments and all are small in size (<11 mm in width). Hence, the ability for adaptation to low oxygen environments seems an attribute characteristic of *Clivunella*, *Delminiella* and the Valencienniinae.

The mechanism for the arrival of this 'alien' genus in the intramontane lake remains enigmatic. The *Delminiella*-bearing DLS-lakes are situated about 250 km to the south of Lake Lavant.

During the late Burdigalian and Langhian, both areas were separated by a broad seaway linking the proto-Mediterranean Sea with the Central Paratethys Sea, i.e. the Transtethyan Trench Corridor (Fig. 5) (Rögl, 1999; Kováč *et al.*, 2007; Bartol, 2009; Mandić *et al.*, 2012). No direct connection via stepping-stone lakes and wetlands was available for the migration of the genus. A vicariance event by the formation of the seaway cannot be excluded as an explanation of the disjunct distribution pattern. This hypothesis, however, is weakened by the virtual absence of any other DLS taxon north of the seaway and the very patchy occurrence of *Delminiella* in Lake Lavant. A more likely but untestable scenario is sweepstakes dispersal. For instance, air-borne dispersal via birds has been documented for various extant aquatic molluscs (Green & Figuerola, 2005; Brochet *et al.*, 2010; Raulings *et al.*, 2011; Kappes & Haase, 2012; van Leeuwen *et al.*, 2012). The large protoconch of *D. norica* suggests direct development from large eggs. Eggs and adults of extant Hygrophila have been documented to be frequently transported by waterfowl attached to feathers and legs, but also via the gut (van Leeuwen & van der Velde, 2012; van Leeuwen *et al.*, 2012, 2013). While avian dispersal is well documented for extant freshwater gastropods, this mechanism is an untestable speculation in palaeontology. Nevertheless, Wesselingh, Cadée & Renema (1999) claimed zoochory as explanation for

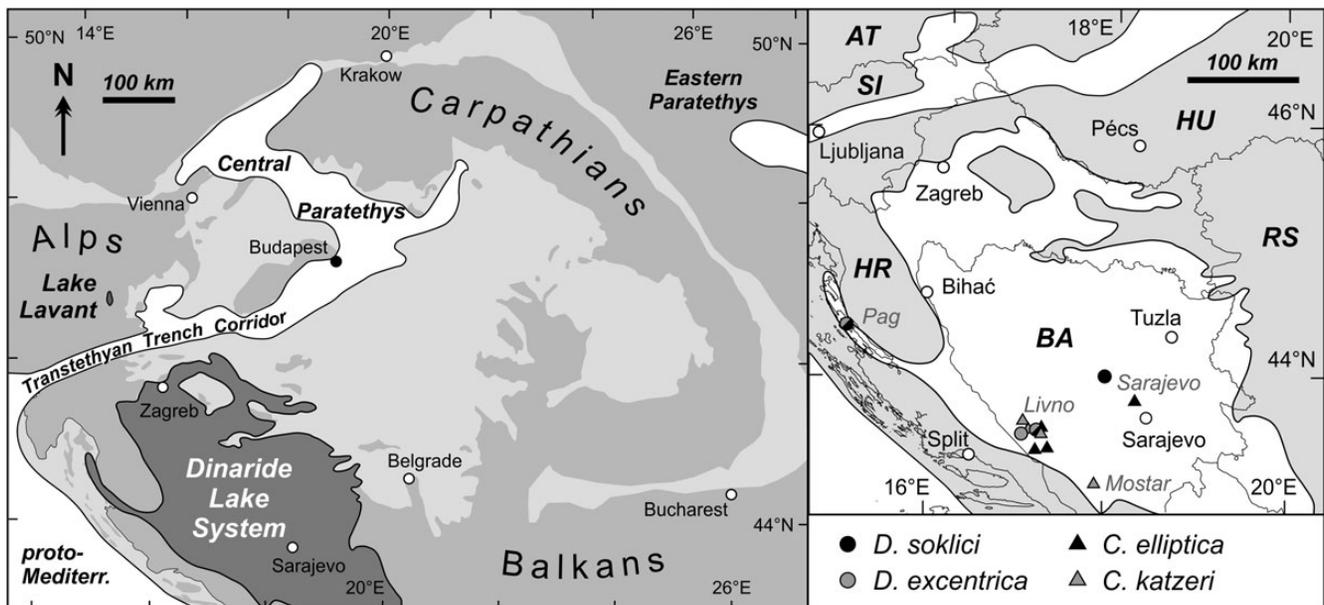


Figure 5. Palaeogeography of the latest Early Miocene (Karpatian, c. 16 Ma) modified from Rögl (1998, 1999) and Mandić *et al.* (2012) showing the position of Lake Lavant and the coeval Dinaride Lake System (DLS) separated by the marine Transtethyan Trench Corridor; occurrences of *Delminiella* and *Clivonella* in the DLS are shown in the right insert. Note the outline for the DLS indicates its maximum extent, not the actual distribution of individual palaeo-lakes.

the Miocene-Pliocene distribution of *Planorbarius* Duméril, 1806 in Europe and *Tryonia* Stimpson, 1865 in Central America. A potential second example is the erratic occurrence of the viviparid (?) genus *Popovicia* Neubauer & Harzhauser in Neubauer, Harzhauser & Pipík, 2015c (a replacement name for the preoccupied *Metohia* Popović, 1964) in the Late Miocene Lake Turiec (Slovak Republic), documented by Neubauer *et al.* (2015c). It seems most probable that this genus originated about 700 km to the south of Lake Turiec during the latest Miocene to Early Pliocene, in the Metohia Basin in Kosovo, where it radiated and displayed a large morphological disparity (Popović, 1964; Atanacković, 1990). Both lakes were surely not connected hydrologically and in the geographically intermediate Lake Pannon this genus is unknown. Thus, applying the principle of Occam's Razor and following an actualistic approach, this erratic distribution may best be interpreted as a result of avian dispersal. Of course, this hypothesis to explain the alien occurrence of the genera *Delminiella* in an intramontane Alpine basin and of *Popovicia* in an intramontane Carpathian basin (as well as the application of this idea by Wesselingh *et al.*, 1999 for *Planorbarius* and *Tryonia*) is unprovable by direct evidence.

Delminiella and *Popovicia* developed in large and long-lived lake systems and, until now, have seemed to be emblematic examples of endemic genera. Now they are recorded also from comparatively small and geologically short-lived palaeo-lakes. In contrast to the long-lived palaeo-lakes with their often enormous sedimentary record and long history of taxonomic research, the smaller and short-lived representatives are often poorly resolved. Hence, the disjunct distribution of these two genera highlights the uncertainty in estimating endemism rates in palaeo-lakes.

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