



# Gastropod palaeohabitats of Miocene Lake Randeck Maar and its hinterland defined by an actualistic genus-level approach


MICHAEL W. RASSER, OLAF HÖLTKE AND RODRIGO B. SALVADOR 

## LETHAIA



Rasser, M. W., Hölte, O., Salvador, R. B. 2019: Gastropod palaeohabitats of Miocene Lake Randeck Maar and its hinterland defined by an actualistic genus-level approach. *Lethaia*, Vol. 53, pp. 229–241.

The Randeck Maar lake sediments from SW Germany were deposited during a climatic phase known as the Mid-Miocene Climatic Optimum, providing a unique window into this last favourable period for a more thermophilous fauna in Central Europe. Previous palaeoecological reconstructions of Randeck Maar's environment focused on the flora and vertebrate fauna. Here, we present a palaeoecological analysis using gastropods as proxies by means of an actualistic genus-level approach. This approach is grounded in comparisons of habitat preferences between extant and fossil congeners and thus obviously requires a sound taxonomic framework. Despite being commonly applied in the literature, this approach has hardly been defined so far. Therefore, we thoroughly delineate it, exploring its applicability, potential and shortcomings. The molluscan fauna of Randeck Maar counts with 32 species of continental snails, mostly terrestrial pulmonates, related to the following palaeohabitats: littoral, supralittoral, rocky walls, shrubland, forests and open habitats. The gastropods indicate a warm-temperate climate with a dry season, in line with previous works on Randeck Maar's flora and vertebrates. □ *MN 5 European Mammal Neogene Zone, palaeoecology, palaeoenvironmental reconstruction, pulmonate snails, volcanic maar lake.*

Michael W. Rasser [[michael.rasser@smns-bw.de](mailto:michael.rasser@smns-bw.de)], and Olaf Hölte [[ol\\_hoel@yahoo.de](mailto:ol_hoel@yahoo.de)], Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1 70191 Stuttgart, Germany; Rodrigo B. Salvador  [[salvador.rodrico.b@gmail.com](mailto:salvador.rodrico.b@gmail.com)], Museum of New Zealand Te Papa Tongarewa, 55 Cable Street 6011 Wellington, New Zealand; manuscript received on 6/03/2019; manuscript accepted on 24/05/2019.

The Randeck Maar lake sediments in SW Germany were deposited during the Mid-Miocene Climatic Optimum, which was the last time interval favourable for a more thermophilous fauna and flora in Europe (Zachos *et al.* 2001). A palaeoenvironmental reconstruction of Randeck Maar, based largely on the flora and vertebrate fauna, provided a picture of its palaeohabitats (Rasser *et al.* 2013): (1) deep- and open-water lake habitats with local and short-term mass occurrences of insect larvae, amphibians and gastropods. Fish are extremely scarce and restricted to few beds; (2) shallow parts of the lake comprising a narrow reed belt with insects and gastropods, as well as aquatic turtles, living on the exposed plant stems; and (3) crater slopes and surrounding plateaus mainly covered by subhumid, sclerophyllous to mixed-mesophytic forests. Horses and other forest dwellers preferably lived in forested habitats, whereas proboscideans and rhinocerotids occupied more open habitats.

The snail fauna of Randeck Maar comprises 32 species of continental gastropods, almost exclusively pulmonate snails, which occur in various beds

(Salvador *et al.* 2015). This paper uses the gastropods as palaeoecological proxies in an actualistic genus-level approach, which is based in habitat preferences of extant congeners of the fossils. This approach is widely applied in the palaeomalacological literature (Ložek 1964; Clarke 1979; Fordinál 1996; Albesa *et al.* 1997; Esu & Ciangherotti 2004; Moser *et al.* 2009; Salvador *et al.* 2016), but is mostly used in an informal manner, being only roughly delineated and explained so far. Therefore, we thoroughly delineate it, exploring its applicability, potential and shortcomings. We then use the Randeck Maar molluscan fauna to exemplify this approach, presenting a detailed environmental reconstruction of the setting and comparing this approach with previous work on the site's flora and vertebrates (Rasser *et al.* 2013).

## Geological setting

Randeck Maar is located on the northern margin of the Swabian Alb in SW Germany and belongs to a

large volcanic area that was active during the Early/Middle Miocene, formed by a phreatomagmatic explosion (Lorenz 1979). No radiometric data exist so far (Krochert *et al.* 2009), but small mammals indicate a MN 5 (Neogene European mammal zone) age, that is latest Early Miocene to earliest Middle Miocene (Fig. 1; Heizmann 1983; Rasser *et al.* 2013). As a result of the volcanogenic activity, a crater with a diameter of ca. 1.8 km was formed, with steep slopes and a crater rim, which in turn resulted in a lake. The lake lacked tributaries and therefore represented a protected setting with a topographic relief of 220 m and water depths of up to ca. 130 m (Rasser *et al.* 2013, 2014). Today, ca. 60 m of lake sediments is preserved.

Jankowski (1981) identified three consecutive lake stages (Fig. 2). The first one appeared immediately after the maar formation, consisting of an alluvial stage with reworked volcanites (stage 1 in Fig. 2). It was followed by a brackish and eutrophic lake stage, comprising bituminous laminites (the so-called ‘dysodil’) in the deepest parts (stage 2c), calcareous and marly laminites in the more marginal parts (stage 2b), and littoral limestones and dolomites (stage 2a). The third lake stage is characterized by massive, fossiliferous freshwater limestones (stage 3).

Most of the terrestrial gastropods come from the reworked volcanites (stages 1 and 2T), generally referred in the literature as ‘light’ (i.e. yellowish to brownish) and ‘dark’ (i.e. greyish to black) tuffites (Salvador *et al.* 2015). Ehrat & Jooss (1921) assumed that these two tuffite types were formed during two different eruptive events. Later studies starting with Seemann (1926) suggested, however, that they are distinct but synchronous facies: the dark tuffite would have been formed in the deepest part of the earliest maar stage under permanent water cover, while the light tuffite would have been formed sub-aerially in a more marginal position. The findings of Salvador *et al.* (2015) agreed well with this scenario: very few terrestrial gastropod species occur in the dark tuffite, while all freshwater ones can be found on this facies; meanwhile, most terrestrial species can be found in the light tuffite, while only a single freshwater snail was found there.

The marginal limestones and marls, as well as the calcareous laminites, are aquatic sediments (Rasser *et al.* 2013). Despite being numerically dominated by freshwater species, a large portion of the terrestrial species can be found in these facies as well, especially in the former (Table 1; Salvador *et al.* 2015). In fact, there are terrestrial species found only in this facies, such as the slugs *Deroceras* sp. and *Milax* sp., and the

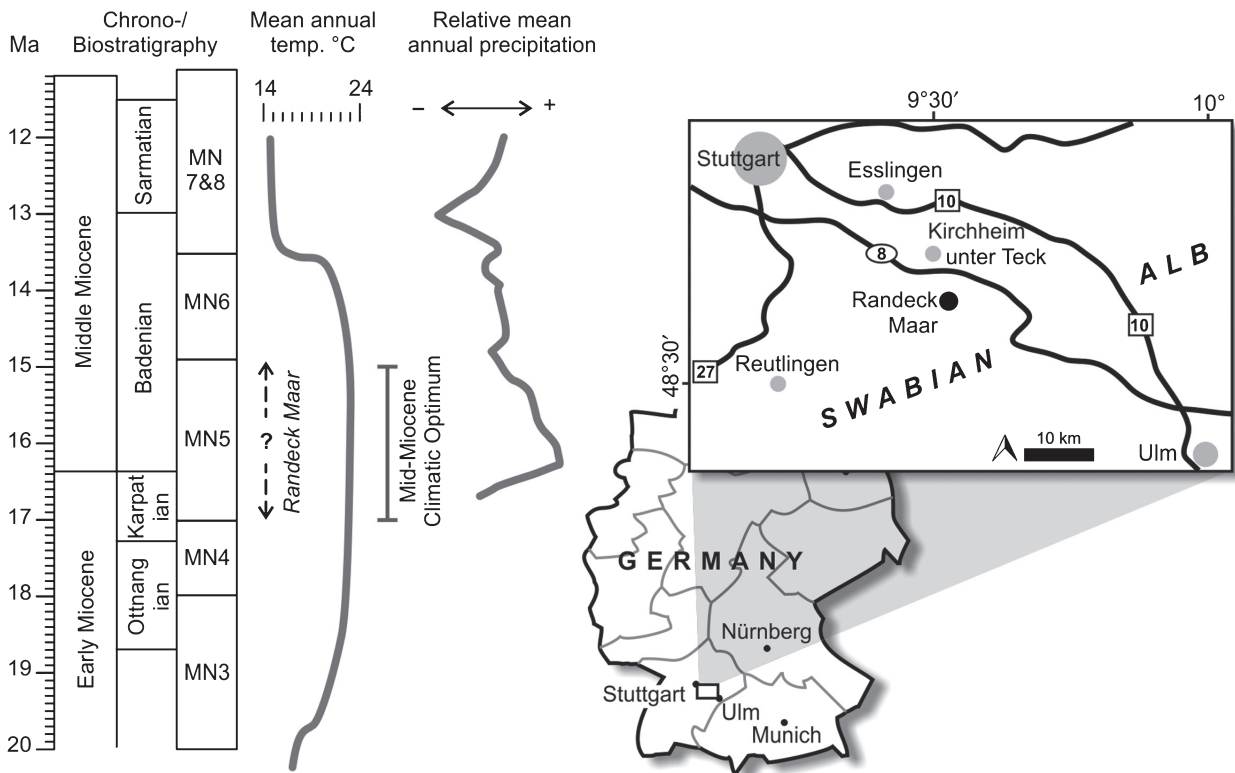


Fig. 1. Geographical location and stratigraphy of Randeck Maar Lake. Redrawn from Rasser *et al.* (2013).

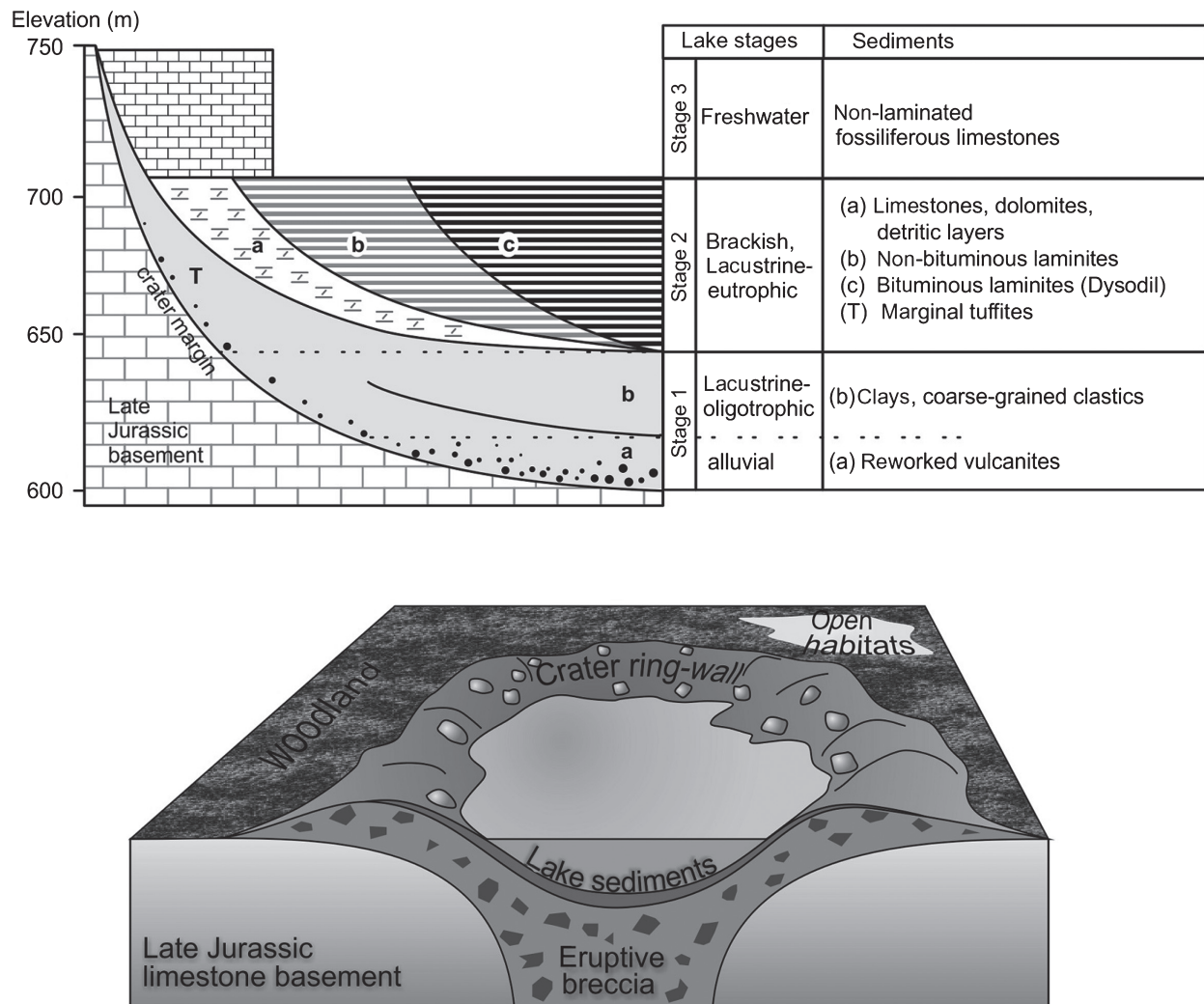


Fig. 2. Top: schematic cross-section through the Randeck Maar sediments after Jankowski (1981). See Table 1 for the distribution of snails in the different facies types. Bottom: reconstruction of the lake habitats after Rasser *et al.* (2013).

semi-slug *Testacella zellii* Klein 1853 (Table 1; Salvador *et al.* 2015).

## Material and methods

The gastropod fauna from Randeck Maar was described by Salvador *et al.* (2015); please refer to that article for the complete morphological description of the species and taxonomical discussions, as well as data on collection and material analysed. The material is housed in the collections of the Staatliches Museum für Naturkunde Stuttgart (SMNS; Stuttgart, Germany) and the Urweltmuseum Hauff (UHH; Holzmaden, Germany). For the palaeoecological reconstruction, an actualistic methodology is applied, comparing the fossil species with their closest extant congeners, as described below.

### *The actualistic genus-level approach*

There are continental gastropods adapted to virtually all kinds of ecological conditions, but snails usually tend to be restricted to (or to strongly prefer) a specific type of habitat, especially at genus level (Barker 2001; Cook 2001; Miller & Tevesz 2001; Pearce & Örstan 2006; Cameron 2016). This makes land snails excellent palaeoecological indicators. That is, ecological data (habitat preferences) from extant species are often used as a guide for palaeoecological inferences of fossil congeners.

Despite this methodology seeming rather tenuous at first sight, it is very informative and its potential for palaeoecological analysis is well established (Miller & Tevesz 2001). This actualistic approach is widely used in the literature, albeit in an informal manner and lacking a thorough explanation and

Table 1. Distribution of the gastropod species of Randeck Maar in the different facies types

Species	Stage 1	Stage 2				Stage 3
	DT	LT	ML	CL	Dys	FL
<i>Apula coarctata</i>		65	7			
<i>Archaeozonites costatus</i>		1	11			
Clausiliinae indet.			33			
<i>Deroceras</i> sp.			3			
<i>Discus pleuradrus</i>		7	4			
<i>Ferrissia deperdita</i>	4		38	33	1	
<i>Gastrocopta</i> cf. <i>acuminata</i>		1				
<i>Gastrocopta sandbergeri</i>		1				
<i>Granaria</i> sp.		218	48	3		
<i>Gyraulus kleini</i>	2		11	50	3	
<i>Hypnophila loxostoma</i>	1	254	5			
<i>Leucochroopsis kleinii</i>	7	91	22	2		
<i>Lymnaea</i> cf. <i>dilatata</i>	13	1	9	45		
<i>Milax</i> sp.			1			
<i>Negulopsis lineolata</i>		1				
<i>Opeas</i> cf. <i>minutum</i>		8				
<i>Palaeoglandina gracilis</i>	1	3				
<i>Palaeomastus filocinctus</i>		1				
<i>Palaeotachea renevieri</i>		25				
<i>Palaeotachea silvana</i>		23	6			
<i>Planorbarius mantelli</i>	8		47	40	1	2
<i>Pomatias conicus</i>	2	167	76			15
<i>Praeostophorella phacodes</i>		219	1		1	
<i>Protodrepanostoma involuta</i>		18	1			
<i>Pseudochloritis incrassata</i>		24				
<i>Pseudoleacina eburnea</i>		68				
<i>Testacella zellii</i>			10			
<i>Triptychia kleini</i>			1			
<i>Triptychia randeckiana</i>		4	31			
? <i>Truncatellina</i> sp.		6				
<i>Vallonia</i> cf. <i>lepida</i>		2				
<i>Vitrina suevica</i>		29				

The occurrence of the species in each facies is documented by the number of specimens found for each species. Specimens without precisely recorded facies of origin were not included. Abbreviations: DT, dark tuffites (stage 1); LT, light tuffites (marginal, stage 2T); ML, marginal limestones and marls (stage 2a); CL, calcareous laminites (stage 2b); Dys, dysodil (stage 2c); FL, freshwater limestones (stage 3).

formalization (Ložek 1964), so we will thoroughly discuss it here.

### Choice of genus-level taxa

Since the generic assignment of both fossil and Recent species is central to the methodology, it is necessary to explain it. In palaeontology, the working concepts of genera are the 'phylogenetic' (or 'cladistic') one and the 'phenetic' (or 'gap') one (*sensu* Allmon 1992), although the former is much rarer due to the lack of actual phylogenies. Regardless, both are used more or less simultaneously in palaeontological studies.

Genera in palaeontology might be seen as less rigid in their taxonomical framework, but they are more

often than not as soundly defined as Recent ones and can be recognized by definitive morphological characters (Forey *et al.* 2004). Genera have been used in numerous kinds of palaeontological studies, both large- and small-scale, of biodiversity, biogeography, evolutionary trends, ecology etc. (Jablonsky & Finarelli 2009 and references therein). Despite some recent criticisms (Hendricks *et al.* 2014), this taxonomic level has proven to be an invaluable tool, especially for macroinvertebrates (Williams & Gaston 1994; Sepkosky 1998; Heino & Soininen 2007; Mandelik *et al.* 2007).

Fossil gastropod taxonomy might be problematic on the species-level, given the paucity of revisionary works, but the majority of genera are deemed stable in the literature. Nevertheless, historically there have been authors that preferred not to place fossils in extant genera, leading to a large number of exclusively fossil genera (taxonomic inflation) disconnected from their Recent relatives (Nordsieck 2014). As argued by Forey *et al.* (2004), the ludicrous conclusion of this practice would be that extant genera do not have a fossil record. This could be problematic for the actualistic approach, which bases the palaeoecological reconstruction on living congeners of fossil forms. In this case, an extant genus related to the fossil one should then be found, hopefully its sister taxon. Luckily, this can be done for many (if not most) cases.

### Similar methodologies

The use of extant relatives of fossil taxa as proxies for palaeobiological questions is not a new methodology, since we can only try to understand past life based on what we can observe today. However, this approach has always suffered from two problems: (1) finding direct relatives, since some lineages are completely extinct (e.g. ammonoids, trilobites, conodonts); and (2) if a living relative is found, it does not necessarily present the same properties (physiology, ecology, behaviour) as the fossil forms.

As an attempt to solve these problems, Witmer (1995) introduced the Extant Phylogenetic Bracket concept (henceforth, EPB). The EPB uses the position of a taxon within a phylogenetic tree to infer the probability of the existence of an unpreserved trait. Simplified, this means that features present in either or both crown groups 'bracketing' the fossil group (e.g. Eusuchia and Aves are the crown groups of non-avian dinosaurs) can be used to make inferences about traits present in an extinct group (Bryant & Russell 1992; Witmer 1995). The EPB is used for soft-tissue reconstruction, as well as physiological and behavioural traits (Benton 2010). However, this

method requires a sound phylogenetic framework, which is not often available for most gastropod lineages.

Another similar approach is called the 'Nearest Living Relative' method (henceforth, NLR), applied to fossil plants in palaeoclimatological studies (for a review, see Utescher *et al.* 2014). NLR focuses on the Coexistence Approach, defining a temperature range in which all fossil plants of a given site can coexist. Their temperature requirements, of course, are based on those of extant relatives, usually congeners.

### *Applying the actualistic genus-level approach*

The actualistic approach draws on the core ideas of both the EPB and the NLR. It uses extant close relatives (optimally congeners) of fossil gastropods to define a range of habitats for the fossil taxa. The idea behind it is as follows: if all extant species of a given genus share a certain basic ecological requirement, then there is a large probability of a fossil congener sharing this requirement. This probability has varying degrees of likelihood, if one or few extant species in the genus have disparate requirements from the rest. Furthermore, the probability is very low if the extant species in the genus have a broad range of requirements, or if a genus is polyphyletic or otherwise poorly defined (e.g. wastebasket taxa). It is important to stress out that we can only talk about probabilities of the fossil species sharing the requirements of its living congeners, since this can never be actually observed.

Clearly, the actualistic approach must start with the proper identification of the fossil species. This is a critical step, since poor identifications (i.e. erroneous generic assignment) will likely lead to false assumptions and, thus, to a faulty palaeoecological reconstruction. Following this step, data on the ecological/habitat requirements of extant congeners must be gathered from the literature. This might seem a trivial step, since these data are reasonably easily available for European and North American molluscan faunas; however, such data are much scarcer for other regions. Moreover, published data on molluscan ecology might often be too generalized to be of any use (Yang *et al.* 2001).

The fossil species are then sorted into ecological/habitat/ niche groupings. The handful of resulting groups will define the palaeoenvironmental reconstruction. Quantitative data on species abundance, if available, should also be taken into account. Changes in these groups along the sedimentary profile allow reconstructing the evolution of the palaeoenvironment through time. While it is usually better to have as many species as possible for this kind of analysis,

it is not unusual for a single species to have such a narrow range of ecological requirements that it will guide the reconstruction (this is commonly observed in the NLR method).

The actualistic genus-level approach works best when the fossil species are evolutionary closer to their extant congeners. For instance, many Quaternary fossil species are still extant today, which makes the approach much more reliable for this time interval. The methodology can be safely used for many Neogene fossils, since most genera still exist. However, it becomes more tentative the further it goes back in time, since not many extant genera can be found in older periods.

Finally, beyond the taxonomic aspect of this actualistic genus-level approach, there are other sources of data to inform palaeoecological reconstructions. Some clues of habitat preferences might be gained from functional morphology (e.g. shell features). Likewise, glimpses of trophic interactions might be gained from trace fossils (e.g. predation marks).

## Palaeoecological proxies

In order to extract information out of Randeck Maar gastropods and use them as palaeoecological proxies, we investigated their closest living relatives (optimally congeners). This information is summarized below. It should be noted that not all the species present in Randeck Maar are appropriate for this type of analysis, as explained further below.

For each species, Table 1 gives the number of shells that is stored in the SMNS and UHH collections. This gives a rough idea about the abundance of each species, but it is important to note that historical collections were frequently affected by sampling biases: usually, only large and attractive shells were collected. Thus, any quantitative discussion must remain tentative.

### *Aquatic snails*

Freshwater pulmonates usually have broad geographic ranges at genus level (Zilch 1959–1960). In lakes, they are essentially benthos of the euphotic zones and thus are most common in marginal positions, while extensive populations below a water depth of 4 m are rarer (Dillon 2010). They live on various substrates, such as fleshy macrophytes or rocks, where they feed on aufwuchs or periphyton, the distribution of which is a main factor influencing their occurrence (Russel-Hunter 1978; Dillon 2010).

The pond snails (Lymnaeidae) are represented in Randeck Maar by *Lymnaea cf. dilatata* (Noulet

1854), a common species in Miocene formations, whose shells reach up to 40 mm in height. Most Lymnaeidae need to emerge from the water in order to fill their mantle cavity with oxygen, although some may remain submerged (depending on the snail's surface/volume relationship; Russel-Hunter 1978). Extant *Lymnaea* prefer richly vegetated, shallow standing or slow-flowing waters and are commonly found in ephemeral water bodies, being able to survive desiccation and freezing (Glöer 2002; Welter-Schultes 2012).

The other family of aquatic pulmonates in Randeck Maar is the Planorbidae, represented by three species. *Ferrissia deperdita* (Desmarest 1814) is a limpet that can form mass occurrences together with *Lymnaea* cf. *dilatata*. Extant congeners inhabit standing or slowly moving waters, living underneath leaves on partly exposed stems of reeds, and are not very sensitive to water quality (Glöer 2002).

*Gyraulus kleini* (Gottschick & Wenz 1916) is the most abundant aquatic snail, but it is usually poorly preserved in Randeck Maar: the fragile shells are flattened by sediment compaction. Therefore, it might be underrepresented in the material. Recent *Gyraulus* species can be found in an ample array of habitats, so their use in palaeoecological analysis is somewhat limited. Nevertheless, they usually inhabit richly vegetated, shallow standing or slow-flowing waters, sometimes even ephemeral water bodies (Welter-Schultes 2012), and are typical pioneers in colonizing new lake habitats (Gittenberger *et al.* 2004). *Gyraulus* snails can take up dissolved oxygen from the water, which allows them to live in greater depths. Species penetrating such depths remain small as adults and feed on detritus from the fine 'rain' from the waters above (Russel-Hunter 1978).

*Planorbarius mantelli* (Dunker 1848) (as *P. cornu* (Brongniart 1810) in Salvador *et al.* 2015) is also abundant and usually poorly preserved. Recent species of *Planorbarius* are found in standing or slow-moving waters, typically richly vegetated (Welter-Schultes 2012). Some species can survive desiccation and thus live in ephemeral waters as well (Glöer 2002). Representatives of this genus take up mainly pulmonary oxygen, but their haemoglobin also allows them to store large amounts of oxygen for longer dives (Russel-Hunter 1978).

### Terrestrial snails

*Pomatias conicus* (Klein 1853). The only non-pulmonate snail in Randeck Maar is the most abundant land snail species (Table 1). Recent *Pomatias* are found in Mediterranean climates in Europe, in forests or shrublands with humid and loose (usually

calcareous) soil where they can burrow (Kerney & Cameron 1979; Welter-Schultes 2012).

*Opeas* cf. *minutum* (Klein 1853): recent congeners are found in warm climates, in tropical and subtropical regions worldwide, living in leaf litter (Zilch 1959–1960; Willig *et al.* 2013).

Clausiliinae indet. Nordsieck (2007) suggested that clausiliids, up to the Middle Miocene, were mostly forest-dwelling animals, preferring humid and warm climates.

*Triptychia kleini* Schnabel 2006 and *T. randeckiana* (Kranz 1908). As Filholiidae is an extinct family, not much can be said about the habitats they occupied. Nevertheless, it is usually suggested in the literature that they were mostly forest-dwelling animals, preferring humid and warm forests (Schnabel 2007, and references therein), similar to their sister-taxon Clausiliidae (Schnabel 2006; Nordsieck 2007).

*Hypnophila loxostoma* (Reuss 1852) (described as *Cochlicopa loxostoma* (Klein, 1853) in Salvador *et al.* 2015). This species is the second most abundant land snail in Randeck Maar (Table 1). Recent European *Cochlicopa* Férussac 1821, closely related to fossil *Hypnophila*, show broad ecological amplitude, from grasslands to woods and from dry to wet environments (Häßlein 1966; Welter-Schultes 2012). It is thus of limited use in palaeoecology.

*Palaeomastus filocinctus* (Reuss 1860). This fossil genus is related to Recent *Napaeus* Albers 1850, which are endemic to the Azores and Canary Islands (Castillo *et al.* 2006). There, they have gone through extensive radiation and occur in many kinds of habitats (*e.g.* Yanes *et al.* 2009a,b, 2011a,b), rendering them largely unsuitable for palaeoecology. Nevertheless, Binder (2004) considered *P. complanatus* (Reuss 1852), known from the Early Miocene of Bulgaria, Czech Republic and supposedly Austria (Klika 1891; Wenz 1923; Binder 2004), as a subtropical forest dweller.

*Archaeozonites costatus* Sandberger 1872. As a fossil genus, any palaeoecological inference must remain tentative. Nevertheless, Lueger (1981) considered that *A. laticostatus* (Sandberger 1885), from the Miocene of Central Europe, lived under leaves or between rocks in humid forests.

*Apula coarctata* (Klein 1853). Another fossil genus, with inconclusive ecological preferences (Lueger 1981), and thus unsuitable for palaeoecology.

*Pseudochloritis incrassata* (Klein 1853). Also a fossil genus, but Binder (2008) considered their shell an adaptation for ground-dwelling, reducing water loss in drier environments. Moser *et al.* (2009) likewise suggested that the genus inhabited open and dry habitats.

*Palaeotachea renevieri* (Maillard 1892) and *P. silvana* (Klein 1853). This fossil genus is likely related to present *Cepaea* spp., which have too broad a range of habitats (Welter-Schultes 2012) to be used.

*Protodrepanostoma involuta* (Thomä 1845) (described as *Helicodonta involuta* in Salvador *et al.* 2015). This fossil genus is closely related to present *Helicodonta* Férussac 1821, which are typical forest dwellers (mainly in deciduous forests) found in humid leaf litter and rock rubble, usually on calcareous substrate (Cameron 1972; Maltz 2003, 2007; Welter-Schultes 2012). See *Leucochroopsis kleinii* (Klein 1847) below regarding the presence of pits on the shell surface.

*Leucochroopsis kleinii* (Klein 1847). This species is considered an inhabitant of relatively damp forests (Lueger 1981), but it is an entirely fossil genus. It was long considered a subgenus of *Trochulus* Chemnitz 1786. The pits on the shell surface indicate the presence of hairs, shown to increase the adherence of *Trochulus* snails (and hygromiids in general) to plant leaves during foraging, especially in high humidity settings (Pfenninger *et al.* 2005). A similar function would be expected for the hairs of helicodontids, like *Protodrepanostoma involuta* mentioned above.

*Praeostephorella phacodes* (Thomä 1845). This fossil genus is related to present *Caracollina* Beck 1837. Only a single Recent species exists in Europe, the Mediterranean *C. lenticula* (Michaud 1831), which thrives in dry areas under stones and leaf litter (Yanes *et al.* 2009b; Welter-Schultes 2012).

*Deroceras* sp. This slug genus is known from a broad range of habitats, from open grasslands (where they are more commonly found) to forests, including wetlands and anthropically disturbed areas (Welter-Schultes 2012; Rowson *et al.* 2014).

*Vitrina suevica* Sandberger 1872. Recent vitrinids are usually found in wet and shaded habitats, mainly woods (Kerney *et al.* 1983; Welter-Schultes 2012).

*Milax* sp. Recent *Milax* species are usually found on warmer calcareous rocky environments (Häblein 1966; Mildner 1981; Moorkens & Killeen 2009; Welter-Schultes 2012).

*Discus pleuradrus* (Bourguignat 1881). The three Recent European species live in leaf litter or under rocks or logs in a variety of humid and shaded places (Häblein 1966; Mildner 1981; Kerney *et al.* 1983; Tappert 2002; Welter-Schultes 2012).

*Granaria* sp. Recent *Granaria* spp. prefer dry and open (usually calcareous) habitats (Welter-Schultes 2012; Hölzke & Rasser 2013).

*Gastrocopta* cf. *acuminata* (Klein 1846) and *G. sandbergeri* Stworzewicz & Prisyazhnyuk 2006. There are no native *Gastrocopta* spp. in Europe

today. They can be found worldwide, inhabiting a very broad range of habitats and being especially diverse in North America (Zilch 1959–1960).

*Vallonia* cf. *lepida* (Reuss 1849). Extant European congeners usually live in dry open habitats – such as meadows, grasslands and eventually rocks – commonly on calcareous grounds (Häblein 1966; Kerney *et al.* 1983; Gerber 1996; Welter-Schultes 2012). Some species may also be found in wetter environments and a few, like *V. costata* (Müller 1774), even show a wide ecological range from light forest to sand dunes (Häblein 1966; Gerber 1996; Welter-Schultes 2012).

?*Truncatellina* sp. As the genus of these few poorly preserved specimens could not be precisely determined (Salvador *et al.* 2015), they are not used in the palaeoenvironmental analysis.

*Negulopsis lineolata* (Sandberger 1872) (described as *Negulus suturalis* (Sandberger 1858) in Salvador *et al.* 2015). This fossil genus is related to present *Negulus* Boettger 1889, of which very little is known. They live on leaf litter in tropical African forests (Bruggen 1994).

*Pseudoleacina eburnea* (Klein 1853). Despite being a fossil genus, it was likely a malacophagous predator, as the rest of the family (Barker & Efford 2004). Most authors considered *Pseudoleacina* spp. to be hygrophilic woodland inhabitants (e.g. Lueger 1981; Harzhauser & Binder 2004; Harzhauser & Tempfer 2004); Gall (1980), however, considered it a calciphilic and xerophilic species. The abundance of *P. eburnea* compared to that of the other terrestrial gastropods in this fauna (Table 1) suggests this species was common around the lake.

*Palaeoglandina gracilis* (Zieten 1830). *Palaeoglandina* spp. were likely malacophagous predators, as the present-day species in the family (Barker & Efford 2004). Recent European species have varied lifestyles (Cossignani & Cossignani 1995; Welter-Schultes 2012), but Moser *et al.* (2009) suggested that *Palaeoglandina* would have displayed the same lifestyle and habitat preference as North American *Euglandina rosea* (Férussac 1821). The rosy wolfsnail, as it is commonly called, is a voracious predator, and it is even found hunting partially immersed in water, where it preys on freshwater snails such as lymnaeids (Kinzie 1992).

*Testacella zellii* Klein 1853. Recent *Testacella* spp. are predatory, feeding mainly on earthworms (but also on gastropods and centipedes) and living underground, requiring a moist soil cover (Barker & Efford 2004; Liberto *et al.* 2011). This burrowing habit should make preservation in the lacustrine fossil record more difficult.

## Results and discussion

### *Reconstruction of gastropod palaeohabitats in Randeck Maar*

As seen above, extant congeners of the Randeck Maar snails exist for most species. Using the actualistic genus-level approach, we present below a detailed palaeoenvironmental reconstruction of the Randeck Maar Lake and its surroundings.

Randeck Maar terrestrial snails are surprisingly diverse, but the same does not seem to be the case for the freshwater species: only 4 out of 32. Moreover, other taxa commonly found in the German Miocene (like the abundant hydrobiids, for instance) are absent. Both these facts could be a reflection of the water chemistry in Lake Randeck Maar and the anoxic conditions at the lake bottom, as attested by the lack of fishes and the restricted benthic life (Rasser et al. 2013).

Overall, the terrestrial snails present in Randeck Maar are very diverse and seem to indicate a variety of habitats surrounding the lake, going from humid and warm forests and shrublands to more exposed rocky limestone habitats. The land snail fauna is dominated by *Pomatias conicus* (the only non-pulmonate in the fauna), *Hypnophila loxostoma*, *Granaria* sp. and *Praeostophorella phacodes* (Table 1).

As argued above, the palaeohabitat model presented by Rasser et al. (2013), focusing mainly on the flora and the vertebrate fauna (Fig. 2), is much too broad for continental snails. Therefore, we better define the gastropod palaeohabitats below, based on a schematic cross-section through the maar lake, its ring-wall, and its hinterland (Fig. 3).

The profundal realm of Lake Randeck Maar is supposed to have been subjected to (at least temporary) oxygen-depleted bottom waters, as inferred by the presence of bituminous laminated sediments (dysodil, stage 2c in Fig. 2) and the lack of bottom-dwelling animals (Rasser et al. 2013). A few planorbids (especially *Gyraulus kleini* and *Planorbarius mantelli*) can be found in these sediments but given their poor preservation, they have most likely been transported into this environment from shallower parts of the littoral rather than naturally inhabiting this zone.

Littoral sediments consist of laminated carbonates, mainly composed of micrite and diatom-rich layers (stage 2b in Fig. 2) as well as detrital carbonates rich in fossils in the most marginal portions (stage 2a in Fig. 2). Freshwater snails *Lymnaea*, *Gyraulus* and *Planorbarius* are most abundant here. There are mass occurrences of *Gyraulus* on bedding planes, which

could either represent simple accumulation of dead shells or point to mass-mortality events.

Supralittoral (marsh and reed belt): the general lake topography and plant record suggest a narrow but well-vegetated shoreline, with reeds, grasses and ferns (Rasser et al. 2013). The freshwater limpet *Ferrissia deperdita* would likely be exclusively found in this area, but the other recorded freshwater snails from the littoral area could also have inhabited the well-vegetated shallow waters. For example, mass occurrences of *Ferrissia* together with *Lymnaea* suggest that these two taxa may have lived in similar habitats. Furthermore, *Palaeoglandina gracilis* may have hunted for other snails in this environment. Surprisingly, other common hygrophilous snails usually found in these habitats in other Miocene outcrops, such as *Oxyloma* spp. (Salvador & Rasser 2017; Salvador et al. 2017), are notably absent.

Crater ring-wall boulder zone: the calciphilic species *Granaria* sp. and *Milax* sp. would be found in this open rocky environment with exposed Late Jurassic carbonate rocks. Depending on sun exposure (i.e. north versus south slopes), various microhabitats may have existed here.

There is no single species in Randeck Maar that would be restricted to the shrubland area; all of them likely would also have inhabited forested areas (Fig. 3).

Rasser et al. (2013) suggested subhumid sclerophyllous to mixed-mesophytic forests as the most likely vegetation type in Randeck Maar; this is found in seasonally dry climates, such as present-day Mediterranean. There seems to be many gastropod species that would have been restricted to the forested area, as well as many that would also have inhabited the shrublands (Fig. 3). Due to the underground formed by Late Jurassic carbonate rocks, the substrate might have been calcareous (although the influence of volcanic ash is unknown), which is supported by the abundance of gastropods. *Archaeozonites*, *Protodrepanostoma* and *Praeostophorella* lived under leaves or between rocks. *Pomatias* was burrowing here in the humid litter and so did *Testacella*, preying on earthworms and gastropods.

Most of the species from the ring-wall area would also have been found in these more open grassland areas (Figs 2, 3). Moreover, other species such as *Opeas* cf. *minutum* and *Deroceras* sp. might also have inhabited this area.

### *Limitations of the actualistic approach*

Approximately one third of the Randeck Maar gastropods could not be used for palaeoecological considerations. Several species (compare those present in



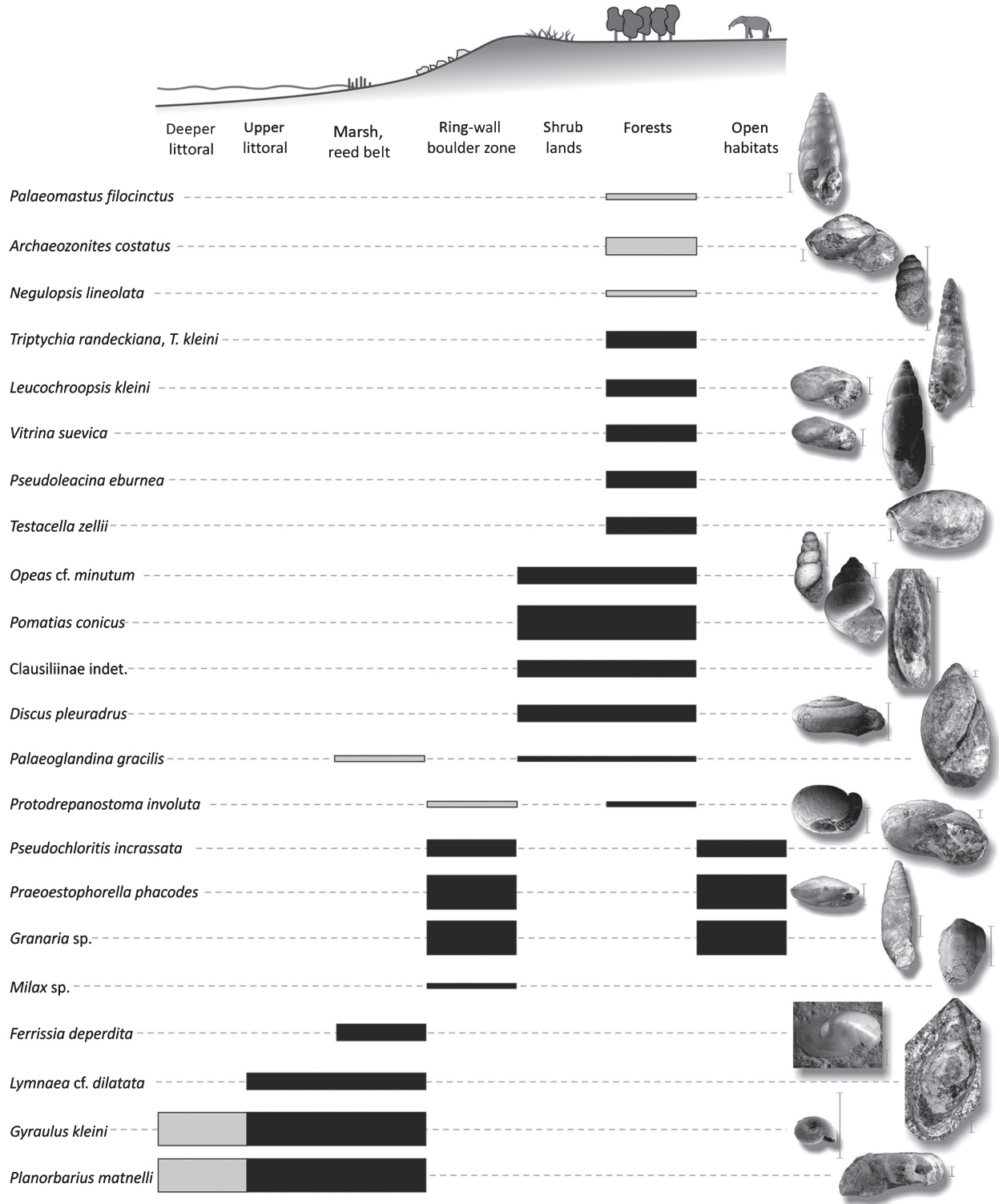


Fig. 3. Palaeohabitats of the gastropods from Lake Randeck Maar and its hinterland, based on the actualistic genus-level approach. Scale bars = 2 mm. Thickness of bar reflects the general abundance of the respective species in the studied material (see also Table 1); thin bar: <10 individuals; medium thickness: >10; thick bar: >200. Grey bars indicate more tentative reconstructions.

Table 1 and Fig. 3) were excluded from the palaeoecological analysis for the following reasons: (1) the extant species of the genera show a too broad range

of ecological requirements (e.g. *Gastrocopta*); (2) some species do not have a clear extant congener and/or their supposed sister taxa have too broad a

range of ecological requirements (e.g. *Apula* and *Palaeotachea*, respectively); and (3) the taxonomic identification is uncertain (e.g. ?*Truncatellina* sp.).

Although the following genera do not have extant representatives, they were used herein for the following reasons: (1) *Archaeozonites*, *Palaeoglandina*, *Pseudochloritis*, *Pseudoleacina* and *Triptychia*, because their palaeoecological preferences are well established in the literature; (2) *Leucochroopsis*, *Negulopsis*, *Praeostophorella* and *Protodrepanostoma*, because there is a general consensus about their relationship with extant genera; and (3) furthermore, there is additional morphological information for *Leucochroopsis* and *Protodrepanostoma* (hair pits) and *Pseudochloritis* (shell shape).

### Sampling biases

Table 1 presents the number of specimens of each gastropod species found in Randeck Maar sediments. However, the historical collections were not conducted systematically; for many specimens not include here, even proper documentation of facies or section of the outcrop was lacking. Besides, in historical collections (from museums and private collectors alike) usually only the larger and more attractive and well-preserved shells are well represented. This practice can lead to researchers 'missing' taxa with smaller shells, including some that might be more crucial for a palaeoenvironmental reconstruction.

While these sources of bias are present in the Randeck Maar material, the numbers presented here (Table 1) give a reasonable rough estimate, since we documented as much background data as possible. Nevertheless, clear signals of abundance and diversity can only be gathered from a collection done with a quantitative study in mind; likewise, taphonomical biases should be taken into account. This kind of data, if available, could add a wealth of information to the palaeoenvironmental reconstruction.

### Trophic interactions

No signs of predation were found on the studied shells. Furthermore, the gut content of vertebrates did not provide further information (Rasser, unpublished data). A comparison with the feeding behaviour of related extant taxa allows, however, certain assumptions.

With such diversity and abundance of snails in Randeck Maar, it is no surprise to attest the presence of three malacophagous species: *Pseudoleacina eburnea*, *Palaeoglandina gracilis* and *Testacella zellii*. While *Pseudoleacina eburnea* is rather small,

*Palaeoglandina gracilis* is the largest species found in Randeck Maar (together with *Pseudochloritis incrasata*), and *Testacella zellii*, judging by the proportion of (vestigial) shell to soft body in Recent congeners, should also have grown quite large. It is also worthwhile to notice that *Pseudoleacina eburnea* is among the most abundant terrestrial snails in Randeck Maar, a remarkable fact given its predatory trophic level. While *Pseudoleacina eburnea* and *Testacella zellii* would be more restricted to the humid forests and shrublands around the lake, *Palaeoglandina gracilis* (when considering its living relatives, as explained above) would have also hunted in the reed belt and perhaps also ventured in the shallower littoral area.

Other typical freshwater malacophagous predators, such as crabs and crayfish, are unknown in Randeck Maar, but water beetles of the family Hydrophilidae do occur (Rasser et al. 2013). Species of this family prey on aquatic gastropods, even specializing in this kind of prey (Archangelsky & Durand 1992; Inoda et al. 2015). Vertebrates from Randeck Maar that may have preyed on aquatic gastropods are tooth carps, newts, and amphibious and aquatic turtles.

In the terrestrial environment, insects are common in the studied sediments (Rasser et al. 2013), but whether they belong to known malacophagous groups (Barker 2004) requires further studies. Among the vertebrates, terrestrial turtles may have preyed on land snails.

### Gastropods as climate proxies

Until now, different methods have been used to reconstruct climatic conditions for the Early/Middle Miocene of Central Europe in general and Randeck Maar in particular, with mean annual temperatures ranging from 15 to 22°C (Rüffle 1963; Gregor 1986; Böhme 2003). Three gastropod species found in Randeck Maar are very intriguing in this regard, as they belong to extant tropical or island-endemic lineages (*Opeas* cf. *minutum*, *Negulopsis lineolata* and *Palaeomastus filocinctus*), which would indicate a warmer climate. Likewise, the Oleacinidae, represented in Randeck Maar by *Palaeoglandina gracilis* and *Pseudoleacina eburnea*, are presently restricted to warmer climates (Zilch 1959–1960; Welter-Schultes 2012). Similar findings in insect taxa (Rasser et al. 2013) also point to a warm-temperate to subtropical palaeoclimate for Randeck Maar. Moreover, the Randeck Maar sclerophyllous flora is indicative of a dry season, such as the present-day Mediterranean biome (Rasser et al. 2013).

## Conclusions

The Miocene fossil Lagerstätte Randeck Maar comprises 28 species of terrestrial and four species of aquatic snails. Based on an actualistic genus-level approach, they can be attributed to seven distinct freshwater and land habitats. This approach could be applied to circa two thirds of the Randeck Maar snail fauna, resulting in a reasonable reconstruction of the gastropod palaeohabitats (Fig. 3), in line with previous works (Rasser *et al.* 2013). This validates the point that continental gastropods are very useful tools for palaeoenvironmental studies.

Despite our focus on these animals, however, it is worthwhile to note that the actualistic approach could (and should) be used for mollusks in general, continental or marine. Furthermore, the potential uses of this approach for other invertebrate taxa should also be further investigated.

*Acknowledgements.* – We are deeply grateful to Karin Wolf-Schwenninger (SMNS) for the SEM images and to the anonymous reviewers for their helpful comments and suggestions. This work was partly supported by the Gesellschaft zur Förderung des Naturkundemuseums Stuttgart; RBS received a doctoral grant from CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brazil; process #245575/2012-0). The authors have no conflict of interest to declare.

## References

- Albesa, J., Calvo, J.P., Alcalá, L. & Alonso Zarza, A.M. 1997: Interpretación palaeoambiental del yacimiento de La Gloria 4 (Plioceno, Fosa de Teruel) a partir del análisis de facies y de asociaciones de gasterópodos y de mamíferos. *Cuadernos de Geología Ibérica* 22, 239–264.
- Allmon, W.D. 1992: Genera in palaeontology: definition and significance. *Historical Biology* 6, 149–158.
- Archangelsky, M. & Durand, M.E. 1992: Description of the preimaginal stages of *Dibolocelus ovatus* (Gemminger and Harold, 1868) (Coleoptera, Hydrophilidae: Hydrophilinae). *Aquatic Insects* 14, 107–116.
- Barker, G.M. 2001: Gastropods on land: phylogeny, diversity and adaptive morphology. In Barker, G.M. (ed.): *The Biology of Terrestrial Mollusks*, 1–146. CABI Publishing, Wallingford.
- Barker, G.M. 2004: *Natural Enemies of Terrestrial Molluscs*, 320 pp. CABI Publishing, Wallingford.
- Barker, G.M. & Efford, M.G. 2004: Predatory gastropods as natural enemies of terrestrial gastropods and other invertebrates. In Barker, G.M. (ed.): *Natural Enemies of Terrestrial Molluscs*, 279–404. CABI, Wallingford.
- Benton, M.J. 2010: Studying function and behavior in the fossil record. *PLoS Biology* 8, 1–5.
- Binder, H. 2004: Terrestrial, freshwater and brachyhaline Gastropoda from the Lower Miocene deposits of Oberdorf (Styria, Austria). *Annalen des Naturhistorischen Museums in Wien* 105A, 189–229.
- Binder, H. 2008: The systematic positions of the genera *Pseudochloritis* C. Boettger 1909 and *Joossia* Pfeffer 1929. *Archiv für Molluskenkunde* 137, 1–27.
- Böhme, M. 2003: The Miocene Climatic Optimum: evidence from ectothermic vertebrates of Central Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology* 195, 389–401.
- Bruggen, A.C. 1994: Revisionary notes on *Negulus* O. Boettger, 1889, a genus of minute African land snails (Gastropoda Pulmonata: Vertiginidae). *Zoologische Mededelingen* 68, 5–20.
- Bryant, H.N. & Russell, A.P. 1992: The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa. *Philosophical Transactions of the Royal Society of London B* 337, 405–418.
- Cameron, R.A.D. 1972: The distribution of *Helicodonta obvoluta* (Müll.) in Britain. *Journal of Conchology* 27, 363–369.
- Cameron, R.A.D. 2016: *Slugs and Snails*, 528 pp. William Collins, London.
- Castillo, C., Yanes, Y., Alonso, M.R. & Ibáñez, M. 2006: *Napaeus lajaensis* sp. nov. (Gastropoda: Pulmonata: Enidae) from a Quaternary Aeolian deposit of Northeast Tenerife, Canary Islands. *Zootaxa* 1307, 41–54.
- Clarke, A.H. 1979: Gastropods as indicators of trophic lake stages. *The Nautilus* 94, 138–142.
- Cook, A. 2001: Behavioural ecology: on doing the right thing, in the right place at the right time. In Barker, G.M. (ed.): *The Biology of Terrestrial Mollusks*, 447–487. CABI Publishing, Wallingford.
- Cossignani, T. & Cossignani, V. 1995: *Atlante delle Conchiglie Terrestri e Dulciacquicole Italiane*, 208 pp. L'Informatore Picens, Ancona.
- Dillon, R.T. 2010: *The Ecology of Freshwater Molluscs*, 524 pp. Cambridge University Press, Cambridge.
- Ehrat, H. & Jooss, C.H. 1921: Das Alter der vulkanischen Tuffe im Kirchheim-Uracher Gebiet und im Hegau. *Geologisch-Paläontologische Mitteilungen* 1, 1–8.
- Esu, D. & Ciangherotti, A. 2004: Palaeoecologic and palaeobiogeographic character of Middle Pliocene non-marine mollusc faunas from north-western Italy. *Rivista Italiana di Paleontologia e Stratigrafia* 110, 517–530.
- Fordinál, K. 1996: Terrestrial gastropods of the Upper Pannonian in the northern part of the Danube Basin. *Slovak Geological Magazine* 1, 5–16.
- Forey, P.L., Fortey, R.A., Kenrick, P. & Smith, A.B. 2004: Taxonomy and fossils: a critical appraisal. *Philosophical Transactions of the Royal Society of London B* 359, 639–653.
- Gall, H. 1980: Eine Gastropodenfauna aus dem Landshuter Schotter der Oberen Süßwassermolasse (Westliche Paratethys, Badenien) von Gündlkofen/Niederbayern. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie* 20, 51–77.
- Gerber, J. 1996: Revision der Gattung *Vallonia* Risso, 1826 (Mollusca: Gastropoda: Valloniidae). *Schriften zur Malakozoologie* 8, 1–227.
- Gittenberger, E., Janssen, A.W., Kuijper, W.J., Kuiper, J.G.J., Meijer, T., van der Velde, G. & de Vries, J.N. 2004: *De Nederlandse zoetwatermollusken. Recente en fossiele weekdieren uit zoet en brak water*, 288 pp. Nationaal Natuurhistorisch Museum Naturalis, KNNV Uitgeverij & EIS-Nederland, Leiden.
- Glöer, P. 2002: *Die Süßwassergastropoden Nord- und Mitteleuropas. Bestimmungsschlüssel, Lebensweise, Verbreitung*, 327 p. Conchbooks, Hackenheim.
- Gregor, H.-J. 1986: Zur Flora des Randecker Maars (Miozän, Baden-Württemberg). *Stuttgarter Beiträge zur Naturkunde B* 122, 1–29.
- Harzhauser, M. & Binder, H. 2004: Synopsis of the Late Miocene mollusc fauna of the classical sections Richardhof and Eichkogel in the Vienna Basin (Austria, Pannonian, MN 9-MN11). *Archiv für Molluskenkunde* 133, 1–57.
- Harzhauser, M. & Tempfer, P.M. 2004: Late Pannonian Wetland Ecology of the Vienna Basin based on Molluscs and Lower Vertebrate Assemblages (Late Miocene, MN 9, Austria). *Courier Forschungsinstitut Senckenberg* 246, 55–68.
- Häblein, L. 1966: Die Molluskengesellschaften des Bayerischen Waldes und des anliegenden Donautales. *Bericht der Naturforschenden Gesellschaft Augsburg* 20, 1–176.
- Heino, J. & Soininen, J. 2007: Are higher taxa adequate surrogates for species-level assemblage patterns and species richness in stream organisms? *Biological Conservation* 137, 18–89.

- Heizmann, E.P.J. 1983: Die Gattung *Cainotherium* (Cainotheriidae) im Orleanium und im Astaracium Süddeutschlands. *Ecologe Geologica Helveticae* 76, 781–825.
- Hendricks, J.R., Saupe, E.E., Myers, C.E., Hermesen, E.J. & Allmon, W.D. 2014: The generification of the fossil record. *Palaeobiology* 40, 511–528.
- Höltke, O. & Rasser, M.W. 2013: The chondrinid land snail *Granaria* (Stylommatophora: Chondrinidae) in the Miocene of the Alpine Foreland: state of the art and taxonomic reassessment. *Neues Jahrbuch für Geologie und Paläontologie* 270, 181–194.
- Inoda, T., Inoda, Y. & Rullan, J.K. 2015: Larvae of the water scavenger beetle, *Hydrophilus acuminatus* (Coleoptera: Hydrophilidae) are specialist predators of snails. *European Journal of Entomology* 112, 145–150.
- Jablonsky, D. & Finarelli, J.A. 2009: Congruence of morphologically-defined genera with molecular phylogenies. *Proceedings of the National Academy of Sciences* 106, 8262–8266.
- Jankowski, B. 1981: Die Geschichte der Sedimentation im Nördlinger Ries und Randecker Maar. *Bochumer geologische und geotechnische Arbeiten* 6, 1–315.
- Kerney, M.P. & Cameron, R.A.D. 1979: *A Field Guide to the Land Snails of Britain and North-West Europe*, 288 pp. Collins, London.
- Kerney, M.P., Cameron, R.A.D. & Jungbluth, J.H. 1983: *Die Landschnecken Nord- und Mitteleuropas*, 384 pp. Paul Parey, Hamburg.
- Kinzie, R.A.I.I.I. 1992: Predation by the introduced carnivorous snail *Euglandina rosea* on endemic aquatic lymnaeid snails in Hawaii. *Biological Conservation* 60, 149–155.
- Klika, B. 1891: Die tertiären Land- und Süßwasserconchylien des nordwestlichen Böhmen. *Archiv für die naturwissenschaftliche Landesdurchforschung von Böhmen* 7, 1–121.
- Krochert, J., Schmieder, M., Theye, T. & Buchner, E. 2009: Considerations on the age of the Urach volcanic field (Southwest Germany). *Zeitschrift der Deutschen Gesellschaft für Geowissenschaften* 160, 325–331.
- Liberto, F., Renda, W., Colomba, M.S., Giglio, S. & Sparacio, I. 2011: New records of *Testacella scutulum* Sowerby, 1821 (Gastropoda, Pulmonata, Testacellidae) from Southern Italy and Sicily. *Biodiversity Journal* 2, 27–34.
- Lorenz, V. 1979: Phreatomagmatic origin of the olivine melilitite diatremes of the Swabian Alb, Germany. In Boyd, F.R., Meyer, H.A.A. (eds): *Kimberlites, Dia-tremes, and Diamonds: Their Geology, Petrology, and Geochemistry*, pp. 354–363. American Geo-physical Union, Washington.
- Ložek, V. 1964: Quartärmollusken der Tschechoslowakei. *Rozprawy Ústředního Ústavu Geologického* 31, 1–374.
- Lueger, J.P. 1981: Die Landschnecken im Pannon und Pont des Wiener Beckens, I. Systematik. II. Fundorte, Stratigraphie, Faunenprovinzen. *Denkschriften der Kaiserlichen Akademie der Mathematisch-Naturwissenschaftlichen Klasse* 120, 1–124.
- Maltz, T.K. 2003: Life cycle and population dynamics of *Helicodonta obvoluta* (O. F. Müller, 1774) (Gastropoda: Pulmonata: Helicidae). *Folia Malacologica* 11, 63–68.
- Maltz, T.K. 2007: Shell variation in *Helicodonta obvoluta* (O.F. Müller, 1774) (Gastropoda: Pulmonata: Helicidae s. lato). *Folia Malacologica* 15, 1–23.
- Mandelik, Y., Dayan, T., Chikantunov, V. & Kravchenko, V. 2007: Reliability of a higher-taxon approach to richness, rarity, and composition assessments at the local scale. *Conservation Biology* 21, 1506–1515.
- Mildner, P. 1981: Zur Ökologie Kärntner Landgastropoden. *Carinthia II* 38, 1–93.
- Miller, B.B. & Tevesz, M.J.S. 2001: Freshwater molluscs. In Smol, J.P., Birks, H.J.B. & Last, W.M. (eds): *Tracking Environmental Change Using Lake Sediments. Volume 4: Zoological Indicators*, 153–171. Kluwer Academic Publishers, Dordrecht.
- Moorkens, E.A. & Killeen, I.J. 2009: *Database of Association with Habitat and Environmental Variables for Non-shelled Slugs and Bivalves of Britain and Ireland*, 190 pp. National Parks and Wildlife Service, Dublin.
- Moser, M., Niederhöfer, H.-J. & Falkner, G. 2009: Continental molluscs of the fossil site Sandelzhausen (Miocene; Upper Freshwater Molasse from Bavaria) and their value for palaeoecological assessment. *Paläontologische Zeitschrift* 83, 25–54.
- Nordsieck, H. 2007: *Worldwide Door Snails (Clausiliidae), Recent and Fossil*, 214 pp. ConchBooks, Hackenheim.
- Nordsieck, H. 2014: Annotated check-list of the genera of fossil land snails (Gastropoda: Stylommatophora) of western and central Europe (Cretaceous – Pliocene), with description of new taxa. *Archiv für Molluskenkunde* 143, 153–185.
- Pearce, T.A. & Örstan, A. 2006: Terrestrial Gastropoda. In Sturm, C.F., Pearce, T.A. & Valdés, A. (eds): *The Mollusks: A Guide to Their Study, Collection, and Preservation*, 261–285. American Malacological Society, Pittsburgh.
- Pfenninger, M., Hrabáková, M., Steinke, D. & Dèpraz, A. 2005: Why do snails have hairs? A Bayesian inference of character evolution. *BMC Evolutionary Biology* 5, 59.
- Rasser, M.W., Bechly, G., Böttcher, R., Ebner, M., Heizmann, E.P.J., Höltke, O., Joachim, C., Kern, A.K., Kovar-Eder, J., Nebelsick, J.H., Roth-Nebelsick, A., Schoch, R.R., Schweigert, G. & Ziegler, R. 2013: The Randeck Maar: palaeoenvironment and habitat differentiation of a Miocene lacustrine system. *Palaeogeography, Palaeoclimatology, Palaeoecology* 392, 426–453.
- Rasser, M.W., Schweigert, G., Beckenbach, E. & Müller, T. 2014: The Miocene Randeck Maar (SW Germany): Geological compilation and census of scientific excavations. *Neues Jahrbuch für Geologie und Paläontologie* 274, 209–218.
- Rowson, B., Turner, J., Anderson, R. & Symondson, B. 2014: *Slugs of Britain and Ireland: Identification, Understanding and Control*, 140 pp. FSC, Telford.
- Rüffle, L. 1963: Die obermiozäne (sarmatische) Flora vom Randecker Maar. *Paläontologische Abhandlungen* 1, 139–298.
- Russel-Hunter, W.D. 1978: Ecology of freshwater pulmonates. In Fretter, V. & Peake, J. (eds): *Pulmonates*, 335–383. Academic Press, London.
- Salvador, R.B. & Rasser, M.W. 2017: Fossil terrestrial and freshwater Gastropoda from the Early/Middle Miocene of Heuchlingen, Germany. *Archiv für Molluskenkunde* 146, 233–241.
- Salvador, R.B., Rasser, M.W. & Höltke, O. 2015: Fossil gastropods from Miocene Lake Randeck Maar and its hinterland (SW Germany). *Neues Jahrbuch für Geologie und Paläontologie* 277, 251–273.
- Salvador, R.B., Prieto, J., Mayr, C. & Rasser, M.W. 2016: New gastropod assemblages from the Early/Middle Miocene of Riedensheim and Adelschlag-Fasanerie, southern Germany. *Neues Jahrbuch für Geologie und Paläontologie* 279, 127–154.
- Salvador, R.B., Höltke, O. & Rasser, M.W. 2017: Fossil land and freshwater gastropods from the Miocene of Hohenmemmingen, Germany. *Palaeodiversity* 10, 41–48.
- Schnabel, T. 2006: Die känozoischen Filholiidae Wenz 1923. Teil 2: Die pliozänen Triptychien, nebst Bemerkungen zum Typusmaterial und zur systematischen Stellung der Filholiidae (Gastropoda: Pulmonata: Clausilioidea). *Archiv für Molluskenkunde* 135, 23–47.
- Schnabel, T. 2007: Die känozoischen Filholiidae Wenz 1923. Teil 4: Die eo- und oligozänen Vertreter der Gattung Triptychia, nebst Bemerkungen zur Ökologie und geo- bzw. stratigraphischen Verbreitung der Filholiidae sowie zur Evolution der Gattung *Triptychia* (Gastropoda, Pulmonata, Clausilioidea). *Archiv für Molluskenkunde* 136, 25–57.
- Seemann, R. 1926: Geologische Untersuchungen in einigen Maaren der Albhochfläche. *Jahreshefte des Vereins für vaterländische Naturkunde im Württemberg* 1926, 81–110.
- Sepkosky Jr, J.J. 1998: Rates of speciation in the fossil record. *Philosophical Transactions of the Royal Society of London B* 353, 315–326.
- Tappert, A. 2002: Molluskenzönosen von Waldstandorten des Pfälzerwaldes und der angrenzenden Rheinebene (unter Bildung von Zönosengruppen). *Schriften zur Malakozoologie* 19, 1–159.
- Utescher, T., Bruch, A.A., Erdei, B., François, L., Ivanov, D., Jacques, F.M.B., Kern, A.K., Liu, Y.-S., Mosbrugger, V. & Spicer, R.A. 2014: The Coexistence Approach – theoretical background and practical considerations of using plant fossils for

- climate quantification. *Palaeogeography, Palaeoclimatology, Palaeoecology* 410, 58–73.
- Welter-Schultes, F. 2012: *European Non-marine Molluscs, a Guide for Species Identification*, 760 pp. Planet Poster Editions, Göttingen.
- Wenz, W. 1923: Gastropoda Extramarina Tertiaria I–VI. In Diener, C. (ed.): *Fossilium Catalogus I: Animalia*, 1–1862. W. Junk, Berlin.
- Williams, P.H. & Gaston, K.J. 1994: Measuring more of biodiversity: can higher-taxon richness predict wholesale species richness? *Biological Conservation* 67, 211–217.
- Willig, M.R., Presley, S.J., Bloch, C.P. & Alvarez, J. 2013: Population, community, and metacommunity dynamics of terrestrial gastropods in the Luquillo Mountains: a gradient perspective. *Ecological Bulletins* 54, 117–140.
- Witmer, L.M. 1995: The extant phylogenetic bracket and the importance of reconstructing the soft parts of fossils. In Thomason, J. (ed.): *Functional Morphology in Vertebrate Palaeontology*, 19–33. Cambridge University Press, Cambridge.
- Yanes, Y., Martín, J., Santana, J., Holyoak, G.A., Holyoak, D.T., Artiles, M., Deniz, F., Alonso, M.R. & Ibáñez, M. 2009a: On the relationships of the genus *Napaeus* (Gastropoda: Pulmonata: Enidae), with the descriptions of four new species from the Canary Islands. *Journal of Natural History* 43, 2179–2207.
- Yanes, Y., Romanek, C.S., Delgado, A., Brant, H.A., Noakes, J.E., Alonso, M.R. & Ibáñez, M. 2009b: Oxygen and carbon stable isotopes of modern land snail shells as environmental indicators from a low-latitude oceanic island. *Geochimica et Cosmochimica Acta* 73, 4077–4099.
- Yanes, Y., Santana, J., Artiles, M., Deniz, F., Martín, J., Alonso, M.R. & Ibáñez, M. 2011a: Five new *Napaeus* species from Gran Canaria and El Hierro. *Zootaxa* 2901, 35–51.
- Yanes, Y., Martín, J., Santana, J., Holyoak, G.A., Holyoak, D.T., Artiles, M., Deniz, F., Alonso, M.R. & Ibáñez, M. 2011b: Four new *Napaeus* species (Gastropoda: Pulmonata: Enidae) from La Gomera (Canary Islands). *Journal of Conchology* 40, 393–407.
- Yang, J., Karrow, P.F. & Mackie, G.L. 2001: Paleocological analysis of molluscan assemblages in two marl deposits in the Waterloo region, southwestern Ontario, Canada. *Journal of Paleolimnology* 25, 313–328.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. 2001: Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292, 686–693.
- Zilch, A. 1959–1960: Euthyneura. In Wenz, W. (ed.): *Handbuch der Paläozoologie. Band 6, Teil*, volume 2, 1–834. Gebrüder Borntraeger, Berlin.