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RESEARCH PAPER

Paleoecological and isotopic analysis of fossil continental mollusks of Sandelzhausen (Miocene, Germany)

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Abstract

The fossil molluscan fauna of Sandelzhausen (Early/Middle Miocene, SE Germany) comprises a total of 44 species, mostly terrestrial pulmonate snails. Herein we present a paleoecological analysis of this fauna based on an actualistic approach and on data on stable isotopes of carbon and oxygen (assessed from specimens of the freshwater lymnaeid snail *Galba dupuyiana* and the terrestrial clausiliid snail *Pseudidyla moersingensis*). The paleoecological reconstruction achieved here is in line with previous works, with some novelties and minor modifications. The basal sediment layers point to a swampy area with ponds and/or oxbow lakes (closed system, as indicated by the covariation between oxygen and carbon isotopic signals of *G. dupuyiana*), prone to seasonal flooding events. This environment would then gradually transition into a perennial lake, as indicated by: the proportion of planorbids, the appearance of aquatic species intolerant to desiccation, and the decoupling of the covariation between oxygen and carbon isotopic signals of *G. dupuyiana*. The terrestrial habitat would have developed from a more open environment (semi-arid/sub-humid scrubland) to a sub-humid/humid denser forest afterwards. Still, species from drier and more open environments are present throughout all the layers, suggesting that these habitats persisted in the lake's hinterland. The mean annual temperature, calculated from the oxygen isotopic composition of *P. moersingensis*, ranges from 18.5 to 20.5 °C, but with no significant trend of change throughout the layers.

Keywords Gastropoda · MN 5 European Mammal Neogene zone · Paleoenvironment · Pulmonata · Stable isotope analysis

Kurzfassung

Die Molluskenfauna von Sandelzhausen (Unter-/Mittelmiozän, SE Deutschland) beinhaltet 44 Arten von vorwiegend pulmonaten Landschnecken. Wir präsentieren eine paläoökologische Analyse dieser Fauna, basierend auf einem aktualistischen Ansatz sowie auf stabilen Sauerstoff- und Kohlenstoffisotopen. Die Isotopen wurden an Schalen der lymnaeiden Süßwasserschnecke *Galba dupuyiana* und der terrestrischen clausiliiden Schnecke *Pseudidyla moersingensis* gemessen. Die paläoökologische Rekonstruktion bestätigt frühere Studien, zeigt aber auch neue Ergebnisse. Die basalen Sedimentablagerungen stellen sumpfige Bereiche mit Tümpeln und/oder Altwasserarmen mit gelegentlichen Überschwemmungen dar. Hinweise auf derartige geschlossene Systeme werden durch die parallelen Änderungen der Sauerstoff- und Kohlenstoffisotopen in Schalen von *G. dupuyiana* angezeigt. Die darüber folgende Fauna mit Planorbiden, das Erscheinen von aquatischen Arten die kein Trockenfallen vertragen, sowie die entkoppelten Änderungen der Sauerstoff- und Kohlenstoffisotopen-Signale von *G. dupuyiana*, zeigen einen Wechsel des Systems in einen mehrjährigen See an. Die terrestrischen Habitate wechselten von einem relativ offenen Lebensraum (semi-arides bis sub-humides Buschland) in einen sub-humiden bis humiden, dichteren Wald. Arten aus trockeneren und eher offenen Lebensräumen kommen in allen Schichten vor, was darauf hinweist, dass diese Habitate im Hinterland Bestand hatten. Die aus den Sauerstoffisotopen der Schalen von *P. moersingensis* errechnete

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durchschnittliche Jahrestemperatur liegt zwischen 18,5 und 20,5 °C. Im Verlaufe der Sedimentation gab es keine eindeutigen Temperaturschwankungen.

Schlüsselwörter Gastropoda · MN 5 European Mammal Neogene Zone · Paläoenvironment-Rekonstruktion · Pulmonata · Stabile Isotopen

Introduction

Lacustrine sediments and their biogenic carbonates are considered important sources of paleoenvironmental information (Filippi et al. 1997; Anadón et al. 2007; Deocampo 2010). Among the continental carbonate-producing animals, mollusks can be reliable paleoecological and paleoenvironmental indicators (Goodfriend 1992; Miller and Tevesz 2001; Yang et al. 2001; Mienis and Ashkenazi 2011).

There are two main approaches that have been used to reconstruct past climatic and environmental settings based on continental mollusks: analyses of faunal composition and of the isotope content of shell carbonate (Goodfriend 1992). The first one is usually a qualitative method regarding the species composition of the fossil assemblage, based on comparisons with the ecology of recent animals; this procedure may be accompanied by quantitative analyses, such as relative abundance of species and/or ecological groups. This is possible because continental mollusks, especially land snails, tend to be restricted to certain habitats at a genus level, thus making them good paleoecological proxies (Barker 2001; Cook 2001; Moine et al. 2002; Pearce and Örstan 2006). Therefore, ecological data of habitats known from recent genera can be extrapolated to congeneric fossil species. This actualistic approach is very informative, being well-established and successfully explored in the literature (e.g., Sparks 1961; Nuttall 1990; Fordinál 1996; Albesa et al. 1997; Esu and Ciangherotti 2004).

The analysis of stable isotopes (oxygen and carbon) of shell carbonate can provide key information for paleoenvironmental and paleoclimatological reconstruction, being extensively explored for both freshwater (e.g., Vonhof et al. 1998; Leng et al. 1999; Tütken et al. 2006) and terrestrial gastropods (e.g., Lécolle 1985; Goodfriend 1992; Goodfriend and Ellis 2002). The usefulness and reliability of both $\delta^{18}O$ and $\delta^{13}C$ analysis is well-established, although values of the latter are deemed more difficult to interpret, especially for land snails (Stuiver 1970; Fritz and Poplawski 1974; Miller and Tevesz 2001; Balakrishnan and Yapp 2004; McConnaughey and Gillikin 2008).

Using more than one proxy usually allows a better paleoenvironmental interpretation (Grimes et al. 2003; Latal et al. 2006; De Francesco et al. 2007) and thus both of the above methods can be used together to retrieve more information from the fossil record. The environment of the Middle Miocene fluvio-lacustrine setting of Sandelzhausen, southeast Germany, has been amply explored, albeit dealing with vertebrates and ostracods (e.g., Fahlbusch et al. 1972; Witt 1998; Böhme 2010; Tütken and Vennemann 2009). The mollusks from Sandelzhausen have already been studied before (Moser et al. 2009b), but only from an actualistic perspective. Therefore, in the present work we explore both methodologies (actualistic and isotope analyses) for the continental fossil molluscan fauna of Sandelzhausen. We use comparisons with the Recent molluscan fauna and data from shell isotopes (oxygen and carbon) to reconstruct the paleoenvironmental conditions of this setting. Finally, we compare our results with data from the literature, thus placing one more piece in the Sandelzhausen puzzle.

Geological setting

The Sandelzhausen fossil site is one of the most important Miocene sites in Europe, with a fauna of more than 200 metazoan species, including mollusks, ostracods and representatives of all vertebrate classes (Moser et al. 2009a, and references therein). It is located near the city of Mainburg, Lower Bavaria, 60 km north of Munich in SE Germany (Fig. 1), being part of the unit known as Upper Freshwater Molasse (“*Obere Süßwassermolasse*”, abbreviated OSM). Its fossils belong to a subunit of the OSM called “*Nördlicher Vollschotter*”, composed primarily of marl and gravel (Moser et al. 2009a). The age of the fossiliferous deposits of Sandelzhausen was established by stratigraphic, biostratigraphic and magnetostratigraphic correlations, being slightly older than 16 Ma and deposited during the Early/Middle Miocene (Burdigalian/Langhian) transition (MN 5 European Mammal Neogene zone; Moser et al. 2009a).

The classification of the facies from the Sandelzhausen deposits was first established by Fahlbusch and Gall (1970), receiving only some later refinement (Moser et al. 2009a). In summary, from bottom to top: layer A: marly gravels, sometimes cemented by carbonates; fossil content rare and limited to robust skeletal parts; layer B: gravel-rich marl, in which size and number of carbonate pebbles diminish upwards, with intercalated sand horizons; origin of most macrovertebrate fossils; layer C: fossil-rich marl; divided into three smaller layers (C1, C2 and C3) by a black, organic rich layer (C2); layer D: marl (mainly silt) with few pebbles and diffuse carbonates and calcareous nodules; rich in fossils, many in excellent preservation state due to a less intense

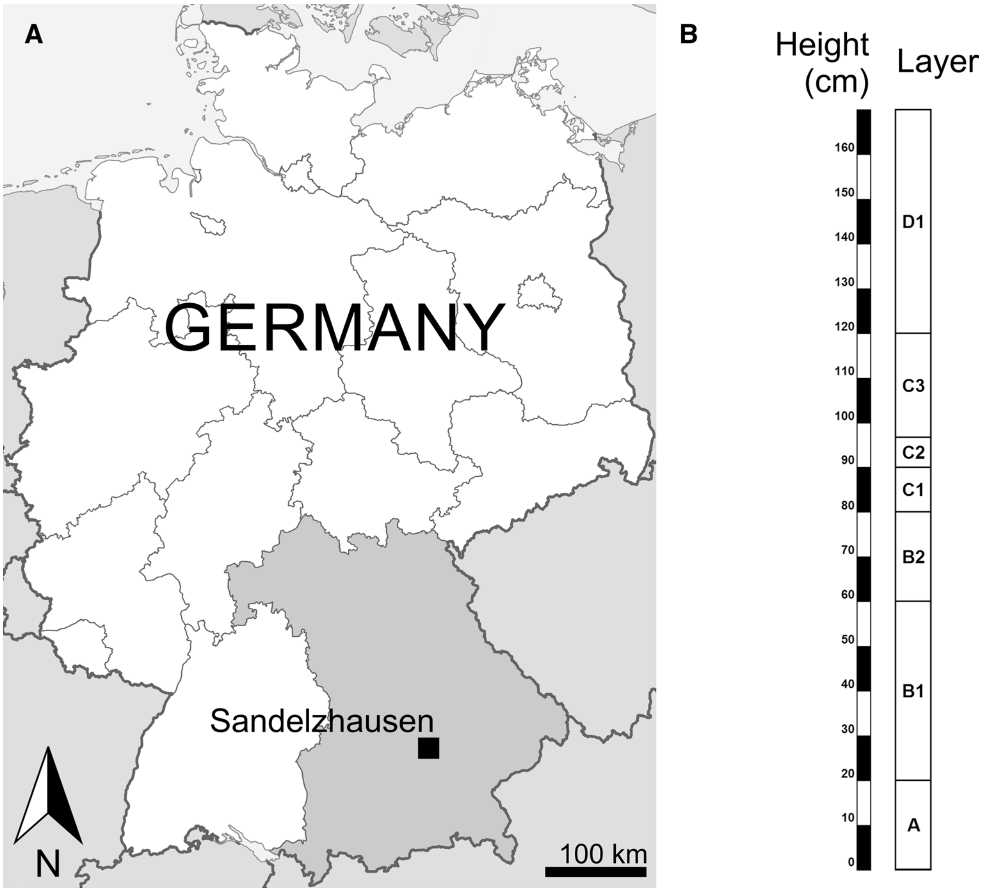


Fig. 1 **A** Map showing the location of Sandelzhausen. **B** Division in layers of the sedimentary profile of Sandelzhausen, with height of sediment measured in centimeters (upwards from the base; see Moser et al. 2009a); figure modified from Moser et al. (2009b)

compaction; layer E: silty clays with microvertebrate fossils; layer F: laminite with alternating light and dark bands, carbonate concretions and desiccation cracks; no fossils.

The sediment and fossils are deemed to have been deposited quickly and no time averaging was detected (Tütken and Vennemann 2009). For a more thorough description of the site's lithology, see Moser et al. (2009a). Fossil mollusks were found from layer A to D.

Materials and methods

Fossil gastropod specimens

Two species of pulmonate snails were chosen for isotope analysis, the freshwater lymnaeid *Galba dupuyiana* (Noulet, 1854) and the terrestrial clausiliid *Pseudidyla moersingensis* (O. Boettger, 1877). Further information on these species can be found, respectively, in Salvador and Rasser (2014) and Salvador (2015). They were chosen for the present study for the following reasons: (1) they are extremely abundant and, more importantly, the specimens are well-preserved; as such, enough specimens for the analysis could be gathered. (2) They are present throughout most of the mollusk-bearing sediment layers (unfortunately, the material from layers B1 and C1 were dubiously labeled, fragmentary or recrystallized).

It was argued by Shanahan et al. (2005) that non-pulmonate snails represent better the isotope composition of the water. Unfortunately, these taxa are very poorly represented in Sandelzhausen, with very few specimens with dubious stratigraphic provenance and poor preservation (Salvador 2013a). As such, the abundant and well-preserved pulmonates, with precise stratigraphical data, were used in the present work. Regardless, the shells of freshwater mollusks, pulmonates included, are deposited in isotopic equilibrium (both oxygen and carbon) with the water and so their isotope contents are still very useful paleoenvironmental indicators (see Sect. 3.3).

All specimens used here stem from the digging site PQ 10-G of Moser et al. (2009a, b), where the snails were collected in intervals of 5–15 cm. Nine of these intervals were chosen (the same for both species), spanning layers B2, C3 and D1 (Table 1; Fig. 1), which contain the better-preserved specimens. Up to four specimens of each species from each interval were analyzed, depending on availability and preservation state; all suitable specimens were used while retaining at least one specimen from each layer as vouchers. The lots

Table 1 Oxygen and carbon isotope values for all specimens of the two gastropod species, with a standard deviation (SD) when applicable

Species	BSPG lot	Layer	Height in sediment	$\delta^{18}O$ (‰)				SD	$\delta^{13}C$ (‰)				SD
Pseudidyla moersingensis (O. Boettger, 1877)	BSPG 1959 II 17282	B2	~ 67.5 cm	−3.50	−3.95	−4.66	–	0.59	−5.04	−6.90	−6.32	–	0.95
	BSPG 1959 II 17283	C3	~ 100 cm	−4.12	−3.81	–	–	0.22	−4.99	−5.72	–	–	0.52
	BSPG 1959 II 17284	C3	~ 107.5 cm	−3.14	−3.07	−3.29	–	0.11	−4.11	−6.81	−7.54	–	1.81
	BSPG 1959 II 17285	C3	~ 117.5 cm	−3.26	−3.19	−2.26	−2.74	0.46	−7.10	−5.88	−6.63	−7.61	0.73
	BSPG 1959 II 17286	D1	~ 137.5 cm	−2.88	−3.93	–	–	0.75	−4.78	−5.31	–	–	0.38
	BSPG 1959 II 17287	D1	~ 142.5 cm	−2.37	–	–	–	–	−4.89	–	–	–	–
	BSPG 1959 II 17288	D1	~ 152.5 cm	−3.40	−3.45	−1.83	–	0.92	−5.18	−6.58	−4.23	–	1.18
	BSPG 1959 II 17289	D1	~ 157.5 cm	−1.80	−3.55	−3.34	−4.54	1.13	−3.51	−3.83	−4.33	−6.87	1.53
Galba dupuyiana (Noulet, 1854)	BSPG 1959 II 17477	B2	~ 67.5 cm	−2.50	−2.64	−2.06	−1.46	0.53	−7.21	−5.73	−3.05	−6.91	1.90
	BSPG 1959 II 17476	C3	~ 100 cm	−2.19	−2.36	−5.21	–	1.70	−5.59	−5.21	−9.79	–	2.54
	BSPG 1959 II 17478	C3	~ 107.5 cm	−5.54	−3.30	−2.84	–	1.44	−6.52	−2.95	−0.18	–	3.18
	BSPG 1959 II 17479	C3	~ 117.5 cm	−1.53	−4.66	−4.92	−3.98	1.55	−8.03	−6.42	−8.27	−4.30	1.83
	BSPG 1959 II 17482	D1	~ 137.5 cm	−0.56	−2.13	−3.10	−2.21	1.06	−9.11	−9.35	−8.39	−9.17	0.42
	BSPG 1959 II 17483	D1	~ 142.5 cm	−2.25	−2.93	–	–	0.48	−8.80	−8.13	–	–	0.47
	BSPG 1959 II 17484	D1	~ 152.5 cm	−2.81	−1.85	−3.52	−1.95	0.79	−10.05	−2.89	−7.90	−7.47	3.01
	BSPG 1959 II 17485	D1	~ 157.5 cm	−2.86	−2.14	−0.52	−5.91	2.26	−8.25	−7.69	−3.00	−7.24	2.40
	BSPG 1959 II 17486	D1	~ 165 cm	−2.58	−2.72	−0.98	−3.40	1.02	−7.25	−7.31	−10.54	−7.26	1.63

Note that, for some layers, poor preservation or lack of material precluded achieving the desired number ($n = 4$) of measurements. The SNSB-BSPG collection number of each lot is also given, as well as the height (and layer) in the sediment profile (for more info on the latter, see Moser et al. 2009a, b) are listed in Table 1 and are housed in the collection of the Bayerische Staatssammlung für Paläontologie und Geologie (SNSB-BSPG; Munich, Germany).

Shell preparation and mineralogical characterization

The selected specimens were cleaned with distilled water and ultrasonic bath to remove adhering sediments. Afterwards, any remaining sediment was mechanically removed under a stereomicroscope and the specimens were cleaned in distilled water once again. After being air-dried, the entire specimen (i.e., the shell) was crushed and ground, and the whole homogenized powder was used for the isotope analysis. According to Shanahan et al. (2005), this is a safer procedure because it avoids any variation in isotope composition along the shell growth (which might be seasonally restricted) and results in an averaged value.

To characterize the phase content of the shells from all sediment layers, separated single shells (a total of eight randomly chosen specimens) were analyzed by X-ray diffraction (XRD) without prior grinding. Due to the small size of the objects, a BRUKER D8 discover microdiffractometer at the Department of Geoscience of the Eberhard Karls Universität Tübingen was used for local phase analysis, equipped with a monocapillary optic with a 300-µm beam diameter and a large 2-dimensional detector (µ-XRD^2; Berthold et al. 2009). In all chosen shells, aragonite was identified as the only carbonate phase and none showed hints of recrystallization, such as crystallite coarsening. It is generally assumed that if no recrystallization of shell carbonate occurred, the original isotopic composition has been preserved (Grossman and Ku 1986; Latal et al. 2004, 2006) and thus the shells can be used for paleoenvironmental analyses.

Isotope analysis

The isotope ratios ($^{18}O/^{16}O$ and $^{13}C/^{12}C$) from the snail shells are reported in the conventional δ-notation in per mil (‰) relative to the Vienna Pee Dee Belemnite (VPDB) reference scale (Coplen 1994). Carbonate samples were digested 90 min at 70 °C in 100% phosphoric acid using a ThermoFisher Gasbench II and the resulting CO_2 was measured in a Finnigan Mat 252 gas source mass spectrometer with a reproducibility of ca. 0.1‰ (for both oxygen and carbon). Samples were normalized to a Lasa marble standard that was calibrated against NBS 18 and NBS 19. The isotope analyses were all conducted at the Department of Geosciences of the Eberhard-Karls Universität Tübingen.

Shell carbonate in freshwater snails is produced in oxygen isotope equilibrium with lake water and in carbon isotopic equilibrium with total dissolved inorganic carbon (DIC) in the water (Leng et al. 1999; Miller and Tevesz 2001; McConnaughey and Gillikin 2008). The effect of diet in carbon isotope composition is negligible (Fritz and Poplawski 1974). Fractionation of oxygen and carbon isotopes is reported to occur between the snails' shells and the host water, but rarely exceeding 2.5‰ (Fritz and Poplawski 1974; Vonhof et al. 1998). It is thus assumed that stable isotope ratios found in fossil shells closely reflect the isotopic composition of the water during the growing season (Fritz and Poplawski 1974; Vonhof et al. 1998; Anadón et al. 2007).

In land snails, shell carbonate forms in oxygen and carbon isotope equilibrium with body fluid water (Balakrishnan and Yapp 2004). The oxygen isotope composition of the body fluid water closely reflects that of its main source (i.e., rain water), being only ca. 2‰ enriched relative to it and usually not showing further effects of evaporative enrichment (Lécolle 1985; Goodfriend and Ellis 2002; Balakrishnan and Yapp 2004; Zanchetta et al. 2005). Land snail shells are thus sensitive indicators of changes in the oxygen isotope composition of rainwater through time (Goodfriend and Ellis 2002). The carbon isotope composition of the shell is mainly related to diet (DIC plays only a minor role), but often with a considerable enrichment of ^{13}C (Francey 1983; Balakrishnan and Yapp 2004; McConnaughey and Gillikin 2008).

Finally, an exploratory analysis of radiogenic strontium isotopes was conducted with the remaining scant material available. This analysis is described in the Supplementary Material.

Actualistic ecological analysis

The continental molluscan fauna of Sandelzhausen is almost exclusively composed of pulmonate snails, being fully described elsewhere (Salvador 2013a, b, 2015; Salvador and Rasser 2014). These works served as the basis for the stratigraphical distribution of the species presented here and the paleoecological analysis.

The actualistic ecological analysis focuses on the genus level: based on the known ecological preferences of extant congeners gathered from the literature, potential paleohabitats of the fossil snails are inferred. Thus, if all (or the vast majority of) extant species of a given genus show the same habitat preferences, there is a high likelihood that the fossil species shared these preferences (especially if this does not contradict other proxies, such as sedimentary and taphonomical signals). On the other hand, if the extant species inhabit a wide range of habitats, they are of very limited use (or no use at all) for paleoecological inferences. Additionally, some clues might be gained from functional morphology, since some shell features might hint at further paleoecological information.

The work of Moser et al. (2009b) has already dealt with the paleoecology of Sandelzhausen's fossil mollusks, determining by this actualistic approach which kinds of habitats were present in each facies. These authors deemed that the variation of the molluscan fauna throughout the sediment layers in Sandelzhausen are a true ecological signal related to environmental changes not biased by taphonomic processes. Nevertheless, since this kind of study relies heavily on taxonomy, the paleoecological analysis of Moser et al. (2009b) is repeated here, using the revised taxonomy of Sandelzhausen's mollusks (Salvador 2013a, b, 2015; Salvador and Rasser 2014), which brings about important changes regarding the identity of several species and thus has a large impact in the paleoecological interpretations.

Statistical analyses

Analyses were performed in R version 3.2.1 (18-06-2015; R Core Team 2015). We used mixed effect models (lmer package) to test if the isotope values of the shells were explained by the height of the specimen on the sediment profile (and, by extension, the prevailing paleoenvironmental conditions during that time slice), the type of isotope (oxygen or carbon) or the interaction between type and height (i.e., whether the slopes of the resulting curves differed). The samples from which each pair of isotopes were extracted were included as a random effect to correct for the non-independence of these values. A simple regression analysis was used to correlate average ambient temperature and height in the sediment, considering each of the mathematical calculations separately (see Sect. 4.1).

Results

The isotopic values of each sample can be found in Table 1. Overall, the values obtained fall within a reasonable interval of variation for each layer (Table 1), with a possible exception being the carbon isotope values from the shells of *G. dupuyiana* in some layers (heights ~ 107.5 and ~ 152.5 cm; Table 1), which display large standard deviations when compared to the rest (including oxygen isotopes and *P. moersingensis*). With the present material, it is not possible to know whether this is a natural variation or an artifact (e.g., one specimen might have shown a very small degree of recrystallization), but these two cases do not seem to have an impact in the overall trend (see Sect. 4.2).

Table 2 lists all mollusk species occurring in Sandelzhausen, with data on presence/absence for each layer and abundance. There is a clear variation in both the isotopic values (Table 1) and the faunal composition (Table 2) throughout the layers. This will be explored in further detail in the discussion.

Oxygen isotope analysis

The δ^{18}O values of land snail shells can be used to calculate the mean annual temperature (MAT) of the paleoenvironment. To achieve this, there are two equations proposed in the literature. Firstly, Lécolle (1985) proposed an equation calibrated for the Recent land snail fauna (as a whole) of the Mediterranean region of France:

$$\mathrm{T}(^\circ\mathrm{C}) = 1.72 \times \delta^{18}\mathrm{O}_{\text{shell aragonite (VPDB)}} + 15.46 \left(R^2 = 0.8\right)$$

Secondly, Zanchetta et al. (2005) did a similar study for the Recent Italian snails, providing the following equation:

$$\mathrm{T}(^\circ\mathrm{C}) = 1.15 \times \delta^{18}\mathrm{O}_{\text{shell aragonite (VPDB)}} + 15.79 \left(R^2 = 0.36\right)$$

The MAT results of entering the δ^{18}O values of the land snail *P. moersingensis* into these equations are given in Fig. 2. The MATs recovered display similar patterns, but there is no significant trend of temperature variation throughout the studied sediment profile ($p = 0.07$ for both equations).

Carbon isotope analysis

Here, the main interest in the carbon isotope values lies in knowing whether they co-vary with the oxygen isotopes. This seems to be the case in Sandelzhausen from layer B2 to the beginning of layer C3 (heights 60–100 cm; Fig. 3), despite the scarce and scattered data points. Taking only these lower parts of the section into account, the interaction of height and type of isotopes did not significantly correlate with the isotope value (Table 3). This means that the slopes of the curves do not differ for these layers (Fig. 3). However, from the bottom of layer C3 onwards (> 100 cm) the interaction between the two isotope types was significant (Table 3). This means that the slopes of the isotopes are significantly different (i.e., the values do not co-vary; Fig. 3).

When the whole dataset was considered and when only the lower heights were taken into account, the interaction of height (and, by extension, the prevailing paleoenvironmental conditions during that time slice) and type of isotopes did not significantly correlate with the isotope value (Table 3). However, when considering heights greater than 100 cm, the interaction was significant, meaning that the slopes for each isotope type were significantly different (Table 3).

Mollusk assemblage: paleoecology

A list of all the mollusk species found in Sandelzhausen, as well as their presence/absence in each sedimentary layer, are given in Table 2. For the actualistic paleoecological

Table 2 Occurrence of mollusk species in the sedimentary layers of Sandelzhausen, from B1 (bottom) to D1 (top)

Species	Layers					Species	Layers				
	B1	B2	C1	C3	D1		B1	B2	C1	C3	D1
Bivalvia						*Deroceras* sp.			?	?	
Sphaerium sp.	?	?	?	?		*Discus pleuradrus* (Bourguignat, 1881)					x
Unionidae indet.					x	Endodontidae indet.				x	
Caenogastropoda						*Gastrocopta nouletiana* (Dupuy, 1850)		x			xx
Bithynia sp.				?	?	*Gastrocopta acuminata* (von Klein, 1846)					x
Pomatias sp.	?	?	?			*Granaria* cf. *grossecostata* (Gottschick and Wenz, 1919)		x		x	
Neritimorpha						*Granaria* sp.		x		x	
Theodoxus sp.					x	*?Helicodonta* sp.	?	?	?	?	?
Lower Heterobranchia						*Janulus supracostatus* (von Sandberger, 1873–1875)	?	?	?	?	?
Valvata sp.				x		*Leucochroopsis kleini* (von Klein, 1846)			?	?	x
Hygrophila						*Lucilla subteres* (Clessin, 1877)	?	?	?		
Ferrissia deperdita (Desmarest, 1814)	?	?	?			*Oxyloma minima* (von Klein, 1853)				x	
Galba dupuyiana (Noulet, 1854)	?	xxx	xx	xxx	xxx	*Palaeoglandina* sp.	x				x
Gyraulus albertanus (Clessin, 1877)		xx		xx	xxx	*Palaeotachea* cf. *eversa* (Deshayes, 1851)	x	x	x	x	xx
Gyraulus applanatus (Thomä, 1845)				xx	xxx	*Palaeotachea* cf. *sylvestrina* (von Schlotheim, 1820)	x	x	x	x	x
Hippeutis sp.					x	*Pseudidyla moersingensis* (Boettger, 1877)	?	xx	x	xxx	xx
Lymnaea dilatata (Noulet, 1854)	?	?	xx	xx	xx	*Pseudochloritis* cf. *incrassata* (von Klein, 1853)	x	x	x	x	x
Planorbarius mantelli (Dunker, 1848)	xx	xx	xx	xx	xxx	?*Pyramidula* sp.	?	?	?	?	?
Radix socialis (von Zieten, 1830–1833)					xx	*Strobilops* sp.	?	?	?	?	
Segmentina larteti (Noulet, 1854)			?	?	x	*Testacella zellii* (von Klein, 1853)	?	?	?		
Eupulmonata						*Triptychia* sp.		x		x	
Apula cf. *coarctata* (von Klein, 1853)				x	x	*Urticicola perchtae* (Salvador, 2013b)				x	x
Archaeozonites sp.		x	x	x		*Vallonia lepida* (Reuss, 1849)					x
Carychium eumicrum (Bourguignat, 1857)	?	?	?	?	?	*Vertigo callosa* (Reuss, 1849)		x		x	xx
Carychium galli Salvador, 2015				x		*Vitrina* sp.				x	

The thin coal layer (C2) was suppressed, since fossils are rarely found there (this layer is interpreted as a wildfire event by Moser et al. 2009a, b). Symbols: x rare species (1–10 specimens); xx common species (11–100 specimens); xxx abundant species (> 100 specimens); ? precise layer undefined

Fig. 2 Evolution of MAT throughout the sediment section of Sandelzhausen calculated from shell δ^{18}O values of *P. moersingensis* using the MAT-δ^{18}O equations for land snails of Lécolle (1985; open circles) and Zanchetta et al. (2005; black circles)

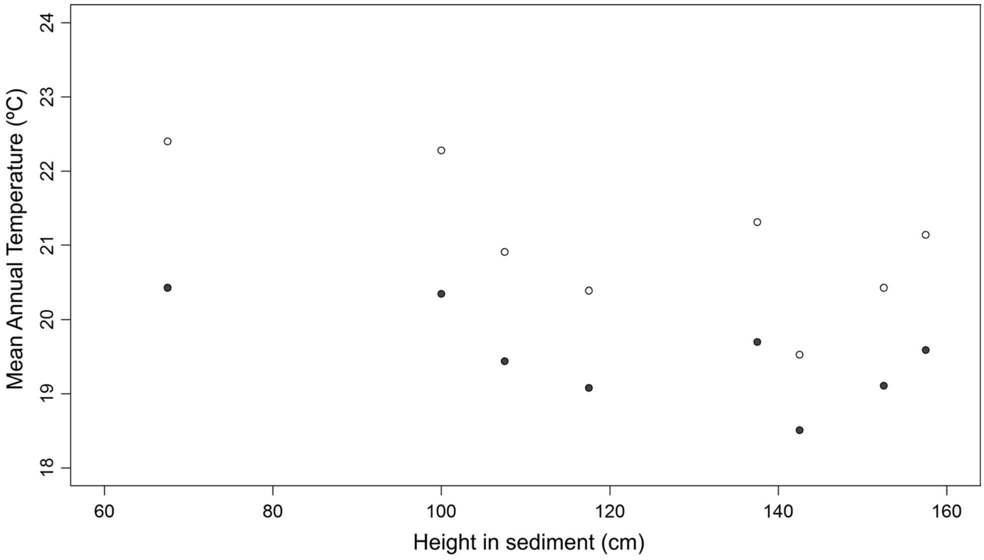
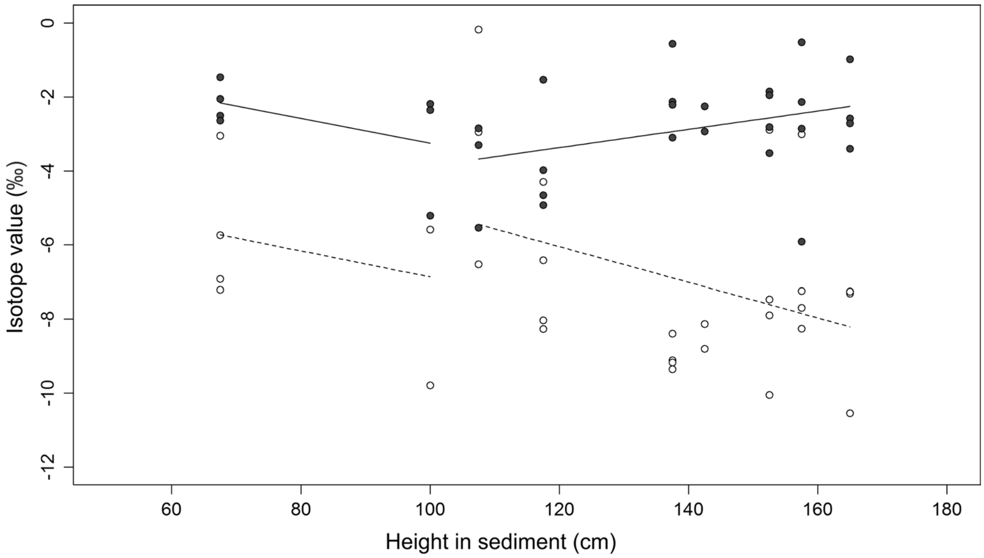


Fig. 3 Oxygen (black circles) and carbon (open circles) isotope values for each interval of the sediment profile. The curves represent the intervals from layer B2 to the beginning of layer C3 (60–100 cm) and from the bottom of layer C3 onwards (> 100 cm). The slopes of the curves for the bottom interval do not differ, while those of the upper interval clearly do



analysis we used 32 different species (some identified only to genus level). The remaining 12 species were excluded for the following reasons: (1) *Deroceras*, *Urticicola*, *Vertigo*, *Lucilla*, *Gastrocopta* and *Strobilops*: their Recent congeners have too broad a range of habitats to be useful for such an analysis (Kerney et al. 1983; Welter-Schultes 2012; Rowson et al. 2014); (2) *Palaeotachea*: entirely fossil genus whose nearest living relatives (*Cepaea* and allied genera) also have a much too broad habitat range (e.g., Welter-Schultes 2012); (3) Specimens with uncertain identification: ?*Pyramidula* sp. (Salvador 2015), Endodontidae indet. (Salvador and Rasser 2014) and Unionidae indet. (Moser et al. 2009b; Salvador 2013a).

Discussion

Oxygen isotope analysis

The interpretation of shell δ^{18}O data from fossil snails depends to a large extent on studies of modern analogues (Yanes et al. 2008, 2009; Colonese et al. 2014). Zanchetta et al. (2005) stated that equations relating shell δ^{18}O and MAT reflect the countries' Recent fauna and climate. As the climate during the Middle Miocene was warmer than today (e.g., Böhme 2003; Böhme et al. 2007; Bruch et al. 2007), the equations from the Mediterranean faunas used

Table 3 Linear mixed effect model results, explaining the isotope value in the shell in relation to the height of the sediment (and, by extension, the prevailing paleoenvironmental conditions during that time slice), type of isotope and interaction between sediment and isotope

	Estimate	s.e.	*F* test	Ndf	Ddf	*P* value
(a) Whole dataset						
Height:isotope			3.91	1.00	30.00	0.06
Isotope			72.04	1.00	31.00	**< 0.01***
Height			2.03	1.00	30.00	0.16
Height:isotope (oxygen)	0.03	0.01				
Isotope (carbon)	−6.87	0.35				
Isotope (oxygen)	−2.80	0.35				
Height	−0.01	0.01				
(b) Height 60–100 cm						
Height:isotope			0.00	1.00	5.00	0.97
Isotope			40.64	1.00	6.00	**< 0.01***
Height			0.89	1.00	5.00	0.39
Height:isotope (oxygen)	0.00	0.04				
Isotope (carbon)	−6.21	0.64				
Isotope (oxygen)	−2.63	0.64				
Height	−0.03	0.04				
(b) Height > 100 cm						
Height:isotope			7.13	1.00	23.00	**0.01***
Height:isotope (oxygen)	0.07	0.03				
Isotope (carbon)	−0.29	2.81				
Isotope (oxygen)	−6.33	2.81				
Height	−0.05	0.02				

Statistics are given at the point of exclusion of the term from the model. In case of significant interactions, estimates are given for the terms in the presence of the interaction

s.e. standard error, *ndf* numerator degrees of freedom, *ddf* denominator degrees of freedom

herein (Lécolle 1985; Zanchetta et al. 2005) are probably well-suited for Sandelzhausen. Moreover, the molluscan faunal composition of Sandelzhausen (and of the OSM, in general; see below) also more closely resembles the Recent Mediterranean one.

The MAT values obtained from the equations (Fig. 2; approximately 19.5–22.5 °C from the equation of Lécolle 1985; approximately 18.5–20.5 °C from the equation of Zanchetta et al. 2005) seem to indicate a warm climate (likely sub-tropical) and compare well to those obtained by Böhme (2010) in her study of the ectothermic fossil vertebrates of Sandelzhausen: 18.0–20.8 °C. Böhme (2010) proposed more semi-arid/sub-humid climate conditions for the basal layers and more sub-humid/humid conditions for the upper layers. However, as stated above, no statistically significant overall decrease or increase in MAT could be detected based on snail $\delta^{18}O_{shell}$ values (Fig. 2) throughout the sediment profile.

As a cautionary note, the calculated MAT might be a little biased because usually no shell growth takes place during drier months or those with temperature extremes (either too warm or too cold). As such, the MAT only reflects the temperatures that prevail during the snails' growing season (Balakrishnan and Yapp 2004). At least regarding temperature, low seasonal variability in MAT was suggested by Tütken and Vennemann (2009) based on a single intra-tooth δ^{18}O profile of a *Gomphotherium* tusk.

Finally, methods for deducing (water) temperature from freshwater snails are still not fully developed (Tevesz et al. 1997; Miller and Tevesz 2001) and only some tentative species-specific equations for Recent species have been proposed so far (e.g., Grossman and Ku 1986; White et al. 1999). These equations have been used for fossil snails, even for species belonging to very distinct taxonomical groups (Grimes et al. 2003; Tütken et al. 2006), but these results should be treated with much caution (Filippi et al. 1997; De Francesco et al. 2007). As such, we refrain here from using data on freshwater species for temperature reconstruction.

Carbon isotope analysis

Land snail shell δ^{13}C values reflect mainly the carbon isotope composition of the snail's diet (Goodfriend and Ellis 2002; Stott 2002; Metref et al. 2003; McConnaughey and Gillikin 2008; Zhang et al. 2014). It is often used to infer dietary preference for a particular kind of plant material (C_3, C_4 or CAM plants; Goodfriend and Ellis 2002; Baldini et al. 2007). As such, carbon isotope changes in a time series of fossil snails can reflect changes in vegetation that, in turn, are caused by climatic changes (Goodfriend and Ellis 2002; McConnaughey and Gillikin 2008; Colonese et al. 2014). Nevertheless, the scarcity of shell carbon isotope data of Recent snails hampers further analysis. Another proxy for the type of vegetation cover are $\delta^{13}C$ values of mammal teeth; fossil teeth from Sandelzhausen indicate that only C_3 plants were present in the surrounding (Tütken and Vennemann 2009), which is to be expected since C_3 plants formed the Neogene flora of Central Europe (Blondel et al. 1997; Cerling et al. 1997). Finally, snails seem to incorporate carbon from ingested limestone in carbonate-rich regions (such as Sandelzhausen), which would be reflected in the shells' isotopic composition and thus complicate inferences regarding the paleoflora and vegetation cover (Goodfriend and Hood 1983; Yanes 2015).

However, the combined analysis of $\delta^{13}C$ and $\delta^{18}O$ values of freshwater snail shells might be instructive to reconstruct the paleohydrology of lake basins. In closed-lake systems, the two values usually co-vary in lacustrine carbonates (Talbot 1990; Li and Ku 1997; Deocampo 2010). This seems to happen in Sandelzhausen from layer B2 to the beginning of layer C3 (60–100 cm; Fig. 3). In this lower part of the sediment profile, the slopes of the $\delta^{13}C$ and $\delta^{18}O$ curves are the same (i.e., the values co-vary), which could indicate that the lake was a closed system at this time. However, since there are only few measurements available from these layers (and only from two time slices), this signal could be biased.

On the other hand, when the values of the two isotope ratios do not co-vary, it is an indication of an open lake system (Talbot 1990; Alonzo-Zarza 2003; Tanner 2010). This seems to happen in Sandelzhausen from the bottom of layer C3 onwards (> 100 cm; Fig. 3): the slopes of the curves do not co-vary, indicating an open lake. At this stage, the $\delta^{13}C$ and $\delta^{18}O$ values seem to be inversely related (Fig. 3); this has been related with changes in lake level in other localities (e.g., Tevesz et al. 1997).

This is in line with the environmental reconstructions of Sandelzhausen by previous authors (Fahlbusch et al. 1972; Witt 1998; Böhme 2010; Moser et al. 2009b) and sedimentological data (Schmid 2002). For the lower layers (up to basal layer C3), a swampy area is proposed, composed of several ponds and/or oxbow lakes, and prone to seasonal flooding events. The environment would then gradually transition, along uppermost layer C3 and basal layer D1, to a perennial lake. Böhme (2010) argues that a full lake condition was achieved only by the end of layer D1, but the present results seem to indicate that this might have been achieved a little earlier (middle layer D1), especially when regarding the taxonomic composition of the molluscan fauna (see Sect. 5.3; see also Moser et al. 2009b).

Finally, the low $\delta^{13}C$ values, especially in the later stages of the Sandelzhausen lake (Fig. 3) indicate a great amount of photosynthetic activity and thus abundant organic matter (hence DIC with lower $\delta^{13}C$ values; Tevesz et al. 1997; Zanchetta et al. 1999; Miller and Tevesz 2001). This would also be in line with the proposed increase in riparian vegetation in the upper layers and possibly slightly eutrophic conditions (Böhme 2010).

Mollusk assemblage: paleoecology

Using the actualistic ecological approach based on habitat preferences of Recent congeners, we could reconstruct the scenario below.

Freshwater species

Most of the Recent congeners of the freshwater species can be found in a variety of environments, but the fauna in Sandelzhausen seem to share one characteristic: preference for richly vegetated, slow-moving or standing waters (Welter-Schultes 2012). Many of the genera (*Galba, Lymnaea*, *Gyraulus* and to some degree *Ferrissia*) count with Recent representatives capable of surviving varying degrees of desiccation and, thus, can be commonly found inhabiting temporary water bodies (Chapuis et al. 2007; Glöer 2002; Welter-Schultes 2012).

These species occur in almost all the sedimentary layers in Sandelzhausen (Table 2), but layers C3 and D1 also have species more typical of large consolidated water bodies and/or that do not tolerate desiccation (Bandel 2001; Zettler et al. 2004; Bunje 2005; Welter-Schultes 2012): *Gyraulus*, *Theodoxus*, *Bithynia*, *Valvata*, *Radix* and *Hippeutis*. As such, the trend proposed by Moser et al. (2009b) from temporary waters in Sandelzhausen's bottom layers to a perennial lake seems to hold. *Segmentina larteti*, judging by the Recent *Segmentina nitida* commonly found in marshy environments (Clark 2011; Welter-Schultes 2012), would have inhabited the littoral well-vegetated area of the lake.

Moser et al. (2009b) also proposed that alongside this change in the environment, there would be a change in abundance between the lymnaeids and planorbids, with the former being more abundant in the basal layers (i.e., in the temporary waters setting) and being substituted by the latter in the top layers (i.e., the lake). Nevertheless, Salvador and Rasser (2014) pointed out that, despite the massive appearance of *Gyraulus* spp. from layer C3 onwards, the lymnaeid *Galba dupuyiana* remained a very abundant species in the lake, making room for *Gyraulus* spp. but not being substituted.

Terrestrial species

The majority of land snail species found in Sandelzhausen are usual inhabitants of humid forests, such as *Carychium*, *Oxyloma*, *Discus*, *Pomatias*, *Testacella* and *Vitrina* (Häßlein 1966; Mildner 1981; Kerney et al. 1983; Tappert 2002; Barker and Efford 2004; Liberto et al. 2011; Welter-Schultes 2012). Furthermore, *Carychium* and *Oxyloma* species are hygrophilous, usually living on very richly vegetated areas surrounding water bodies (Welter-Schultes 2012). The following fossil genera are also supposed to inhabit damp woods and tend towards warmer environments: *Pseudidyla*, *Triptychia* and *Leucochroopsis* (Lueger 1981; Harzhauser and Binder 2004; Harzhauser and Tempfer 2004; Nordsieck 2007; Schnabel 2007); moreover, the pits on the shell surface of *Leucochroopsis* indicate the presence of hairs, a feature related to high humidity habitats (Pfenninger et al. 2005). The fossil genera *Archaeozonites* and *Palaeoglandina* are often considered to have inhabited moist forests (e.g., Lueger 1981), but there are propositions in favor of drier and more open environments (Moser et al. 2009b). Even if not considering the last two problematic genera, the damp wood snails seem to be more concentrated in layers C3 and D1 (Tables 2, 4). *Pomatias* and *Testacella*, in particular, occur in the basal layers (either B or C1; Tables 2, 4) and Recent species are known to thrive in both forests and shrublands, provided it is a humid environment (Kerney and Cameron 1979; Barker and Efford 2004; Welter-Schultes 2012; Rowson et al. 2014).

Table 4 Occurrence of land snail species in the sedimentary layers of Sandelzhausen, separated by habitat type. Only the most significant species for the paleoecological analysis were included

Habitat type/species	Layers	
	B1–C1	C3–D1
Open/dry		
Apula cf. *coarctata*		x
Granaria cf. *grossecostata*	x	x
Granaria sp.	x	x
Pseudochloritis cf. *incrassata*	x	x
Vallonia lepida		x
Shrubland/forest		
Pomatias sp.	x	
Testacella zellii	x	
Warm humid forest		
Carychium eumicrum	?	?
Carychium galli		x
Discus pleuradrus		x
Janulus supracostatus		x
Leucochroopsis kleini		x
Oxyloma minima		x
Pseudidyla moersingensis	x	x
Triptychia sp.	x	x
Vitrina sp.		x

The genus *Janulus* is a curious case. *Janulus supracostatus* is well-known from the German Silvana beds ("Silvanaschichten", in German) and the single specimen found in Sandelzhausen does not have proper stratigraphical data (but Moser et al. 2009b lists it as probably stemming from layers C2 or C3). *Janulus* was a widespread genus in Europe since the Oligocene, but today is a relict genus, surviving only on the Madeiran Archipelago and the Canary Islands (Waldén 1983; Cameron et al. 2007; Seddon 2008; Castro et al. 2014). These archipelagos have other relict species, such as the laurel forest, and its biome composition and subtropical climate is deemed reminiscent of the warm climate predominant in Tertiary continental Europe (Waldén 1983; Press and Short 1994; Capelo 2004). Moreover, and more importantly, laurel forests are known from southern Germany during the Early/Middle Miocene (e.g., Böhme et al. 2007), so a close relationship between this snail genus and this type of vegetation could exist (see also Castro et al. 2014).

Some of the species in Sandelzhausen should have preferred drier and more open habitats. *Granaria* is a good indicator of these environments, being often found on calcareous rocks (Welter-Schultes 2012; Höltke and Rasser 2013). The fossil genus *Apula*, and more specifically *A. coarctata*, is thought to have preferred drier environments (Lueger 1981). The bulky shells of the fossil genus *Pseudochloritis*, with their bent apertural region, are considered an adaptation for ground-dwelling gastropods to reduce water loss (Binder 2008); thus Moser et al. (2009b) proposed that these animals would have inhabited drier habitats, similar to Recent Balkanese Ariantinae. Finally, extant European *Vallonia* species usually inhabit dry open areas (often calcareous), such as meadows, grasslands and even rocks, but some may also be found in more humid environments (Häßlein 1966; Kerney et al. 1983; Gerber 1996; Welter-Schultes 2012). These species are scattered throughout all the layers in Sandelzhausen (Tables 2, 4), so it is plausible to imagine that in the lake's hinterland more open areas were always present. Such areas would have been perhaps more distant from the lake, as already argued by Moser et al. (2009b), since these species are somewhat rare.

Finally, with such a diverse and abundant fauna in Sandelzhausen, it is hardly surprising to find malacophagous species, namely *Palaeoglandina* sp. and *Testacella zellii*. Recent *Testacella* species feed mainly on earthworms, but also prey upon gastropods and centipedes, living underground and requiring a moist soil cover (Barker and Efford 2004; Liberto et al. 2011). The fossil genus *Palaeoglandina* was very likely composed of malacophagous predators, as the Recent member of the family (Barker and Efford 2004). Recent European species display varied lifestyles (e.g., Cossignani and Cossignani 1995; Welter-Schultes 2012), but Moser et al. (2009b) suggested (based on shell morphology) that *Palaeoglandina* would be akin to the Recent North American *Euglandina rosea* in both lifestyle and habitat. This species is a remarkable predator, even hunting partially immersed in water, preying upon freshwater snails (Kinzie 1992). *Palaeoglandina* curiously occurs only in the bottommost and uppermost layers of Sandelzhausen (Table 2). The temporary waters of layer B and the littoral areas of layer D1 would perhaps represent a good hunting ground for this snail. On the other hand, this could simply be a sample bias, since many of the recovered *Paleogalandina* stem from samples lacking stratigraphical data (Salvador 2013b).

Conclusions

The data on the fossil mollusks presented here is in line with previous environmental reconstructions of Sandelzhausen. From layer B1 to basal layer C3, the environment of the Sandelzhausen site would be a swampy area with ponds and/or oxbow lakes, prone to seasonal flooding events. From the middle of layer C3 onwards, Sandelzhausen gradually became a perennial lake (this status would have been achieved by middle to end of layer D1), as indicated by: (1) an increase in the proportion of planorbids (but with no meaningful significant decrease in the raw number of lymnaeids); (2) the appearance of species that do not tolerate desiccation; and (3) the decoupling of the covariation between shell δ^{18}O and δ^{13}C values of the freshwater snail *G. dupuyiana*. A possible increasing trend in shell ^{87}Sr/^{86}Sr (see Supplementary Material) might indicate a change in the hydrology of Sandelzhausen, which could have been caused by changes in the catchment area of the newly formed lake (starting in uppermost layer C3) and/or increased weathering triggered by an increase in precipitation.

The terrestrial habitat would have gone from a more relatively open environment (semi-arid/sub-humid scrubland, but more densely vegetated areas could have existed as a minor component of the environment) in layers B1 to basal C3, to a sub-humid/humid denser forest in layer D1 (Table 4). This largely agrees with previous findings, but the material analyzed here shows that the species from drier and more open environments are present throughout all the layers (Table 4), suggesting that these habitats persisted in the lake's hinterland instead of disappearing.

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