# Taxonomy and paleoecology of Early/Middle Miocene continental mollusks of the North Alpine Foreland Basin in southern Germany

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“The beginning of wisdom is to call things by their proper name.”

(Confucius)

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# i. Abbreviations and Symbols

**Institutions: BSPG** = Bayerische Staatssammlung für Paläontologie und Geologie (Munich, Germany); **LfU** = Bayerisches Landesamt für Umwelt (Hof, Germany); **PIMUZ** = Paläontologisches Institut und Museum der Universität Zürich (Zurich, Switzerland); **SMNS** = Staatliches Museum für Naturkunde Stuttgart (Stuttgart, Germany); **UHH** = Urweltmuseum Hauff (Holzmaden, Germany).

**Measurements: D** = shell width (greatest diameter); **H** = shell height.

**Others: MAT** = Mean Annual Temperature; **MN** = European Mammal Neogene zone; **NAFB** = North Alpine Foreland Basin; **OBM** = Upper Brackish Molasse ("Obere Brackwassermolasse"); **OSM** = Upper Freshwater Molasse ("Obere Süßwassermolasse"); **USM** = Lower Freshwater Molasse ("Untere Süßwassermolasse"); **VPDB** = Vienna Pee Dee Belemnite isotope standard; **XRD** = X-Ray Diffraction.

**Symbols:** $\boldsymbol{\delta^{13}C}$ = ratio of the stable isotopes of carbon, $^{13}C/^{12}C$ (in ‰); $\boldsymbol{\delta^{18}O}$ = ratio of the stable isotopes of oxygen, $^{18}O/^{16}O$ (in ‰); $\boldsymbol{\delta^{87}Sr}$ = ratio of the radiogenic per stable isotopes of strontium, $^{87}Sr/^{86}Sr$ (in ‰).

## ii. Kurzfassung

Land- und Süßwassermollusken sind häufige Faunenelemente in den meisten rezenten und fossilen kontinentalen Lebensräumen. Trotzdem wird diese Organismengruppe in paläontologischen Studien häufig übersehen und wissenschaftliche Bearbeitungen beschränkten sich meist auf Alpha-Taxonomie. In den Museen finden sich Mollusken von vielen Lokalitäten, die im 19. und 20. Jahrhundert gesammelt, aber nie tiefergehend bearbeitet wurden, wodurch ihr wissenschaftliches Potential nie richtig erschlossen wurde. In meiner Doktorarbeit konzentrierte ich mich auf die Taxonomie und Palökologie kontinentaler Mollusken von verschiedenen Unter- bis Mittelmiozänen (vorwiegend Obere Süßwassermolasse, OSM) Lokalitäten Süddeutschlands (Bayern und Baden-Württemberg). Eine detaillierte taxonomische Bearbeitung dieser Fossilien lieferte eine solide Basis für weiterführende palökologische Studien mit aktualistischen Ansätzen und der Analyse stabiler Isotope. Die ausgewählten Fossilienfunstellen sind: (1) Sandelzhausen (44 Arten); (2) Randeck Maar (32 Arten); (3) Riedensheim (34 Arten) und Adelschlag-Fasanerie (17 Arten); (4) verschiedene Aufschlüsse in den Regionen Biberach, Ravensburg und Neu-Ulm (insgesamt 20 Arten); (5) Gündlkofen (20 Arten); (6) Oggenhausen (17 Arten); (7) Bechingen (19 Arten) und Daugendorf (13 Arten) sowie (8) verschiedene Bohrkerne in Ostbayern, welche auch Sedimente der Unteren Süßwassermolasse (USM) und Oberen Brackwassermolasse (OBM) (insgesamt 24 Arten) beinhalten. Diese Fossillagerstätten stellen Seen, Flusssysteme und ephemerale Wasserkörper dar, wie Altarme und ausgetrocknete Flußmäander. Eine Ausnahme sind die brackischen OBM-Sedimente von Ostbayern. In Sandelzhausen und vor allem in Riedensheim konnte gezeigt werden, wie ein Wechsel der Wasserkörper einen Wechsel der Schneckenfauna mit sich zieht. Für die Umgebung dieser Wasserkörper konnte eine Vielzahl von Habitaten nachgewiesen werden: Von litoralen Schilfgürteln über Buschland bis zu eher geschlossenen und humiden Wäldern. Offene, felsige Bereiche waren ebenfalls häufig. Zur Zeit der OSM zeigte Süddeutschland ein warm-temperiertes bis subtropisches (mediterranes) Klima. Dieses Klima und die eher kalkigen Untergründe dürften ein sehr vorteilhaftes Milieu für kontinentale Schnecken dargestellt haben. In manchen dieser Habitaten ist die Diversität überraschend hoch, oft übersteigt sie 30 Arten. In Anbetracht der Tatsache, dass es sich meist um kleinräumige Lokalitäten handelt, und dass viele Arten höchstwahrscheinlich gar nicht fossil überliefert sind, ist diese Diversität bemerkenswert.

# iii. Abstract

Land and freshwater mollusks are abundant animals in most Recent continental settings. Likewise, this applies for several fossiliferous deposits. Yet, these animals are often overlooked in paleontological studies, which until relatively recently rarely went beyond alpha taxonomy. Molluscan material from several localities collected during the 19th and 20th centuries is stored in museum collections and never thoroughly studied. As such, their potential remain largely locked away. For my doctoral research, I focused on the taxonomy and paleoecology of the continental molluscan faunas from several Early to Middle Miocene localities (mainly belonging to the Upper Freshwater Molasse, or OSM) from the North Alpine Foreland Basin in southern Germany (Bavaria and Baden-Württemberg states). A thorough taxonomic treatment of the fossils creates a solid basis for a follow-up paleoecological study (with both actualistic and stable isotope analyses). The localities selected for study were: (1) Sandelzhausen (44 species); (2) Randeck Maar (32 species); (3) Riedensheim (34 species) and Adelschlag-Fasanerie (17 species); (4) several outcrops in the districts of Biberach, Ravensburg and Neu-Ulm (total 20 species); (5) Gündlkofen (20 species); (6) Oggenhausen (17 species); (7) Bechingen (19 species) and Daugendorf (13 species); and (8) several boreholes in Eastern Bavaria, also including sediments from the Lower Freshwater Molasse (USM) and Upper Brackish Molasse (OBM) layers (total of 24 species). These localities represent lakes, river systems and more ephemeral water bodies, such as oxbow lakes and abandoned river meanders (the exception being the brackish OBM layers from Eastern Bavaria). In Sandelzhausen and Riedensheim in particular, changes in the water bodies and their respective fauna can be seen through time. In the vicinities of these water bodies, several types of habitats could be found: from littoral reed-belts, through shrublands, to more closed and humid woods; open rocky areas were also very common. During the deposition of OSM layers, southern Germany would have shown a warm temperate to subtropical (Mediterranean-like) climate. This favorable climate and the often calcareous grounds should have composed a welcoming scenario for continental snails. In some of these localities, the diversity of gastropods is astounding, often exceeding 30 species. This is a remarkable richness, especially considering the small size of most localities and the fact that many species likely have not been preserved in the fossil record.

# 1. General Introduction

Land and freshwater mollusks are abundant animals in most continental settings. Likewise, this applies for most fossiliferous deposits. Yet, the potential of these animals is often overlooked in paleontological studies, which until relatively recently rarely went beyond alpha taxonomy. New methodologies and tools for data analysis have led to an increase in the popularity of paleoecological and paleoenvironmental studies, while taxonomy became “unfashionable”, despite being the most critical aspect of any (paleo)biological research. Yet, both are inextricably intertwined.

For my doctoral research, I focused on the taxonomy and paleoecology of the molluscan faunas from several localities from the North Alpine Foreland Basin (NAFB) in southern Germany, all belonging to the Miocene epoch. A brief description of the localities, their geology and fossil content, as well as data on the material studied, can be found in Section 1.1. The methodological aspects of both the taxonomy and paleoecology studies can be found in Section 1.2.

Continental mollusks, and in special land snails, can be used for a broad range of studies, including paleobiogeography, biostratigraphy and, more important for the present discussion, paleoecology and paleoenvironmental reconstructions. In the latter case, the reconstruction can be achieved by two kinds of analysis, complementary to one another: (1) an actualistic ecological approach (see Section 1.2.2.1), heavily dependent on previous solid taxonomical work; and (2) stable isotope analysis (oxygen and carbon) of the shell’s calcium carbonate, whose composition reflects the mollusks’ environment (see Section 1.2.2.2).

## 1.1. Fossil sites

The localities studied here were chosen due to the following reasons: (1) belonging to the Early/Middle Miocene OSM levels of the NAFB; (2) virtual absence of former works with the molluscan fauna or clear need of revisionary work; (3) availability, quantity and easiness of access of the material.

The NAFB stretches over 1000 km, from France to Austria, along the axis of the Alps, being formed during the Oligocene and Miocene. In the German segment of the NAFB, the succession is divided into two megacycles (*e.g.*, Bachmann & Müller, 1992; Doppler et al. 2005): (1) the first, spanning the early Oligocene (Rupelian) to earliest Miocene (Aquitanian), is comprised (from bottom to top) by the Lower Marine Molasse, the Lower Brackish Molasse, and the Lower Freshwater Molasse (USM); (2) the other includes the Upper Marine Molasse, the Upper Brackish Molasse (OBM) and Upper Freshwater Molasse (OSM) deposits, spanning the late Early Miocene (latest Aquitanian) to early Late Miocene (Tortonian).

### 1.1.1. Sandelzhausen

Sandelzhausen 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). Its rich mollusk record was studied by Gall (1972), who identified 49 gastropods and two bivalves in the material recovered, but based his work heavily on younger faunas, and Moser et al. (2009b), who dealt mainly with paleoecological questions.

Sandelzhausen was located near the city of Mainburg (Bavaria); its fossils belong to a member of the OSM called Nördlicher Vollschotter (Moser et al., 2009a). The age of the deposits was established by stratigraphic, biostratigraphic and magnetostratigraphic correlations: ca. 16.47–16.27 Ma, belonging to the MN 5 zone (Moser et al., 2009a). The classification of the facies of the Sandelzhausen deposits was first established by Fahlbusch & Gall (1970), later refinement by Moser et al. (2009a). They go (bottom to top) from Layer A to F; gastropods occur in the marly Layers B, C and D.

The material from Sandelzhausen is housed at the BSPG (record number BSPG 1959 II); for a complete list, see Salvador (2013a, 2013b, 2015) and Salvador & Rasser (2014). Unfortunately, the specimens identified by Moser et al. (2009b) as “?Discidae (fam., gen. et sp. indet.)” and “?Endodontidae sp. nov. (fam. et gen. indet.)” could not be found. Moreover, the specimen (BSPG 1959 II 16148) identified as *Zonitoides silvanus* (Wenz) by Gall (1972) and as ?Endodontidae gen. nov. by Moser et al. (2009b) is now just fragments and cannot be properly identified.

### 1.1.2. Randeck Maar

The Randeck Maar lake sediments are well known as an important fossil Lagerstätte (*e.g.*, Schweigert & Bechly, 2001), but there are few works dealing specifically with the gastropods (no bivalves have ever been found). Both Ehrat & Jooss (1921) and Seemann (1926) offered simple species lists, indicating the facies in which they occur. More recently, Rasser et al. (2013) presented a preliminary identification of the material, but within the context of a broader paleoenvironmental analysis.

Randeck Maar belongs to a large volcanic area that was active during the Early/Middle Miocene and small mammals indicate a MN 5 age (Rasser et al., 2013). Due to its volcanogenic origin, a crater with a diameter of ca. 1800 m, steep slopes and a crater rim was formed. The resulting lake lacked tributaries and therefore represented a protected setting with a topographic relief of ca. 220 m and water depths of up to ca. 130 m (Rasser et al. 2013, 2014). Today, ca. 60 m of lake sediments are preserved.

Jankowski (1981) separated three consecutive lake stages. Stage 1 appeared immediately after maar formation, starting with alluvial sediments with reworked vulcanites. It is followed by Stage 2, a brackish and lacustrine-eutrophic lake stage, which comprises bituminous laminites (dysodil) in the deepest parts, calcareous and marly laminites ("Süßwasserkalk" in the older German literature) in the more marginal parts, as well as littoral limestones and dolomites. Stage 3 is characterized by massive, fossiliferous freshwater limestones. Most of the gastropods originate from the reworked vulcanites, generally referred to as "light tuffite" and "dark tuffite", which are two different, synchronous facies types. While the dark tuffite contains both terrestrial and freshwater snail, the light tuffites contain almost only terrestrial snails (Ehrat & Joss, 1921; Seemann, 1926; Salvador et al., 2015a). The dark tuffite would have been formed in the deepest part of the lake under permanent water cover, while the light tuffite formed subaerially in a more marginal position. The calcareous laminites are aquatic sediments, being thus dominated by aquatic gastropods (Rasser et al., 2013).

Various excavations have taken place in the Randeck Maar since the middle of the 19th century and continue to this day. Most of the available gastropods originate from excavations lacking sufficient documentation, which makes the attribution to certain facies/habitat types difficult (Rasser et al., 2013). All the molluscan material (ca. 2000 specimens) from the Randeck Maar is housed in the SMNS and the UHH; the full list can be found in Salvador et al. (2015a). Unfortunately, part of the historical material is lost and the presence of one species, *Joossia insignis* (von Zieten), could not be confirmed.

### 1.1.3. Riedensheim and Adelschlag-Fasanerie

Fossil samples were recently collected from two new OSM localities in Bavaria: Riedensheim (in the municipality of Rennertshofen) and Fasanerie (in the municipality of Adelschlag). These two sites are not accessible anymore, but have delivered rich fossil assemblages. All the gastropod material found in there is housed in the BSPG and SMNS; for a complete list, see Salvador et al. (2016b).

The outcrop of Riedensheim belonged to the company Hoffmann Mineral, where several meters of Miocene sand and marls were exposed. Three gastropod-rich marly layers are present, named Riedensheim 1 (bottom), 2 and 4 (top); the supposed sandy layer 3 was deemed to be a lateral differentiation of layer 2. The sand pit of Fasanerie presents three gastropod-bearing facies: (1) a thick layer of reddish to brownish clay ("Adelschlag-Fasanerie clay"), unconformably overlain by (2) sandy and vertebrate-rich strata ("Adelschlag-Fasanerie sand"); and (3) displaced blocks of gastropod-rich limestones ("Adelschlag-Fasanerie limestone"). For more information on the geological setting, see Salvador et al. (2016b).

### 1.1.4. Biberach, Ravensburg and Neu-Ulm

Sach (1999) described several Middle Miocene fossil sites in the district of Biberach, Baden-Württemberg, with his main focus being the lithology, sedimentology, biostratigraphy and the fossil mammals. This author also listed many mollusk-bearing sites, but, since they were not the objective of his study, he did not provide a formal treatment of them. These mollusks are also listed, but neither described nor figured, in a recently published catalogue of Early/Middle Miocene fossil sites from southern Germany (Sach, 2014). This catalogue also brings species lists of a few other newly discovered mollusk-bearing fossil sites in the neighboring districts of Ravensburg (Baden-Württemberg) and Neu-Ulm (Bavaria).

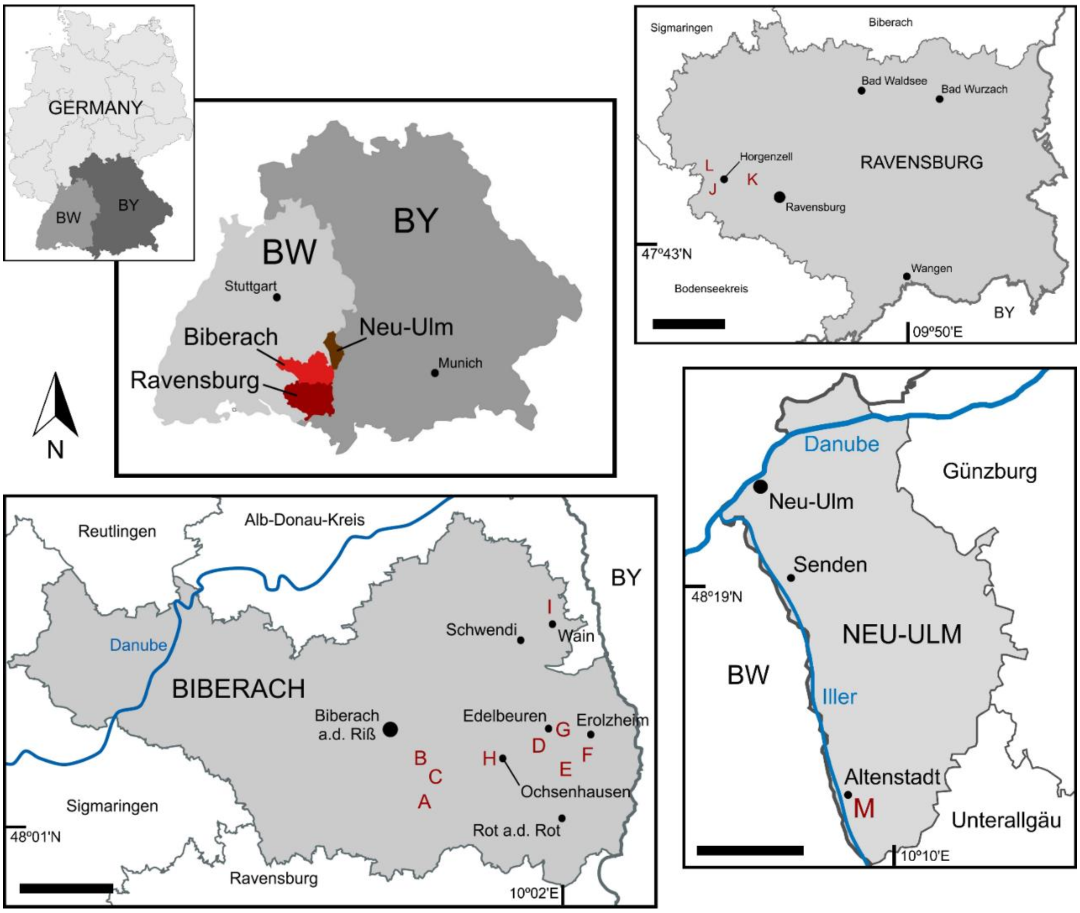

**Figure 1.** Map of the districts of Neu-Ulm (in Bavaria, BY), Biberach and Ravensburg (in Baden-Württemberg, BW), indicating the Middle Miocene fossil sites (names according to Sach 1999, 2014): **A**, Wannenwaldtobel 1+2; **B**, Tobel Oelhalde-Nord; **C**, Tobel Oelhalde-Süd; **D**, Edelbeuren-Schlachtberg; **E**, Binnrot; **F**, Bonlanden; **G**, Edelbeuren-Maurerkopf; **H**, Heselsberg; **I**, Auttagershofen; **J**, Burgerbachtobel 1; **K**, Schmalegger Tobel; **L**, Lattentobel; **M**, Altenstadt-Untereichen. Scale bars = 10 km. Image reproduced from Salvador et al. (2015b).

The molluscan material from thirteen of these sites (Fig. 1) was analyzed, all housed in the SMNS. See Salvador et al. (2015b) for a complete list of the material and description of each site. All the studied fossil sites are of MN 5 and MN 6 ages, belonging to the OSM. More specifically: four sites (Bonlanden, Burgerbachtobel 1, Lattentobel and Schmalegger Tobel) dated from the MN 6 zone; three sites (Wannenwaldtobel 1+2, Tobel Oelhalde-Süd and Tobel Oelhalde-Nord) belong to the transitional period MN 5/6; and the remaining sites date from the MN 5 zone.

### 1.1.5. Gündlkofen

The mollusks from Gündlkofen (Bruckberg municipality, Bavaria) were reported by Gall (1980), who first described the site and listed 34 land and freshwater gastropod species from there. He also offered an age estimate and a paleoecological reconstruction, but neither figured nor properly described most of the snails. Further works presented a fraction of the material from Gündlkofen, but dealt only with specific taxa (*e.g.*, Schnabel 2006, 2007, for Filholiidae). A more thorough treatment of the material was lacking.

All material from the Gündlkofen fossil site comes from a single fine sand/marl horizon, half meter thick, in a gravel pit located 750 m northwest of Gündlkofen. Based on fossil and lithological evidence, Gall (1980), following Meier (1965), related it to the lower section of the Nördlicher Vollschotter (which in turn is a member of the OSM), suggesting an age of roughly 15 Ma for the site, correlating it with the Middle Silvana-beds (“Silvanaschichten”) and the Langhian/Badenian stages (MN 5–6). The material is housed at the BSPG (record number BSPG 1952 XVIII); see Salvador (2014) for a full account. Unfortunately, part of the original material was missing (lots BSPG 1952 XVIII 9, 13, 19, 24, 52, 55) and the record of four species of Clausilioidea could not be confirmed.

### 1.1.6. Oggenhausen

The deposits of Oggenhausen (a village near Heidenheim, Baden-Württemberg, on the margin of the Swabian Alb) were first described by Schlosser (1926), who studied the vertebrate remains. Berz & Jooss (1927) studied the gastropods, with samples stemming from various outcrops around the village. Böttcher et al. (2009) described a second coeval site, named “Oggenhausen 2” (the first site then became “Oggenhausen 1”), reported some gastropod species.

The deposits belong to the OSM and more specifically to the Silvana Beds. The precise location of the several outcrops from Oggenhausen 1 is now untraceable. Oggenhausen 2 was found in 1980 during highway construction and presents two facies: a basal limestone one and a marl/clay one, both containing gastropods. Biostratigraphic correlation of Oggenhausen 2, by mammalian teeth, places it in zone MN 5. Its relation to Oggenhausen 1 remains unclear, but Böttcher et al. (2009) consider the latter to be of roughly the same age. For more details, see Böttcher et al. (2009).

All the material of Berz & Jooss (1927) and Böttcher et al. (2009) was revised, alongside additional samples from Oggenhausen 2 from the SMNS; for a complete list of the material, see Salvador & Rasser (2016b). Two of the original specimens from Berz & Jooss (1927) could not be found: *Triptychia (Triptychia) grandis* (Klein, 1846) [accepted now as *Triptychia kleini* Schnabel, 2006] and *Gastrocopta* aff. *acuminata acuminata* (Klein, 1846).

### 1.1.7. Bechingen and Daugendorf

Bechingen and Daugendorf (ca. 2 km south of the former) are two neighborhoods of the town of Riedlingen (Baden-Württemberg) bordering the Tautschbuch mountain range. The Tautschbuch is a somewhat coherent carbonate unit belonging to the OSM and located on the southern border of the Swabian Alb (southern Germany). It has several mollusk-bearing fossil outcrops that, with the exception of Zwiefaltendorf (Schlickum, 1976), have never been thoroughly studied.

The scarce information on the Tautschbuch's geology can be found in Schwarz (1913) and Haag (1960); biostratigraphic data is not available. Based on the snail fauna and literature data, the Tautschbuch is deemed part of the Silvana-beds of the OSM and thus tentatively dated as Langhian. The molluscan material likely comes from blocks of "Silvana limestone" reworked in Pleistocene moraine sediments, found on a sand pit to the south of Bechingen, in the Maueresch (Engel, 1908; Schwarz, 1913; Zöbelein, 1973). Daugendorf has never been mentioned as a fossil site. It is either the same sand pit as above or another nearby pit containing the same moraine sediments. The material is housed at the SMNS and the PIMUZ; see Salvador & Rasser (2016a) for a full account.

### 1.1.8. Eastern Bavaria

Numerous samples from the cores of 11 new boreholes (Fig. 2) located in the Molasse Basin of eastern Bavaria were studied. In this case, not only the material from the OSM layers was studied, but also the richer sample of the underlying OBM (Kirchberg and Grimmelfingen Formations; upper Burdigalian) and USM (Aquitanian) layers (Fig. 3). The mollusks of the USM have been scarcely studied, but those of the OBM are better known (*e.g.*, Krauss, 1852; Schlickum, 1963, 1966, 1970a, 1970b; Kowalke & Reichenbacher, 2005; Schneider & Prieto, 2011).

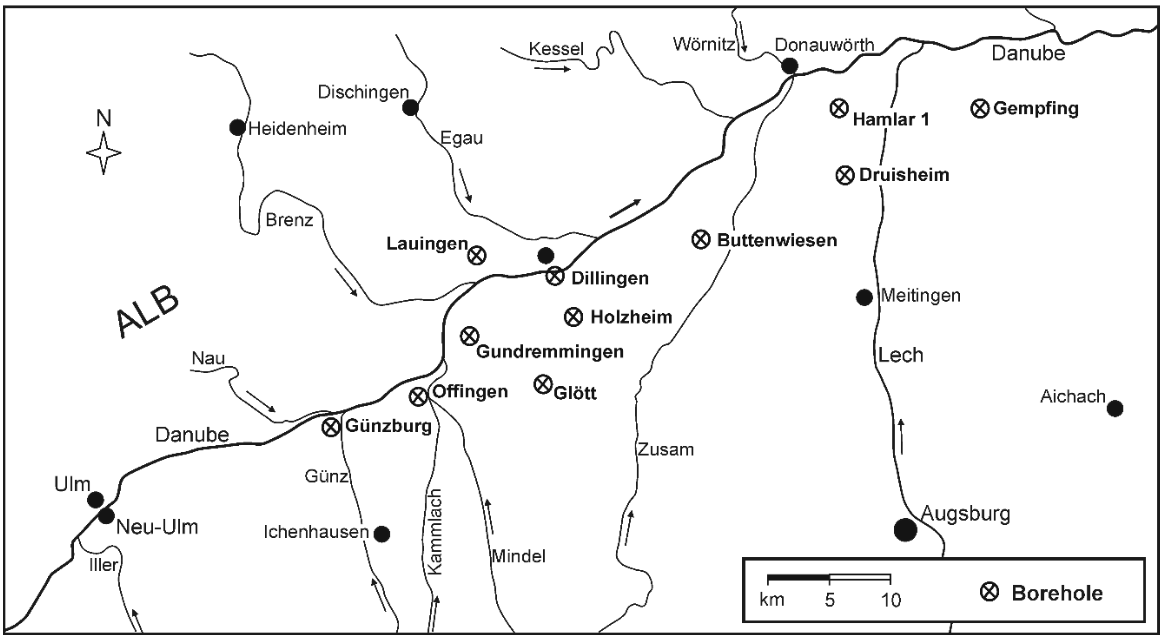

**Figure 2.** Geographic location of the 11 boreholes studied. Image reproduced from Salvador et al. (2016a).

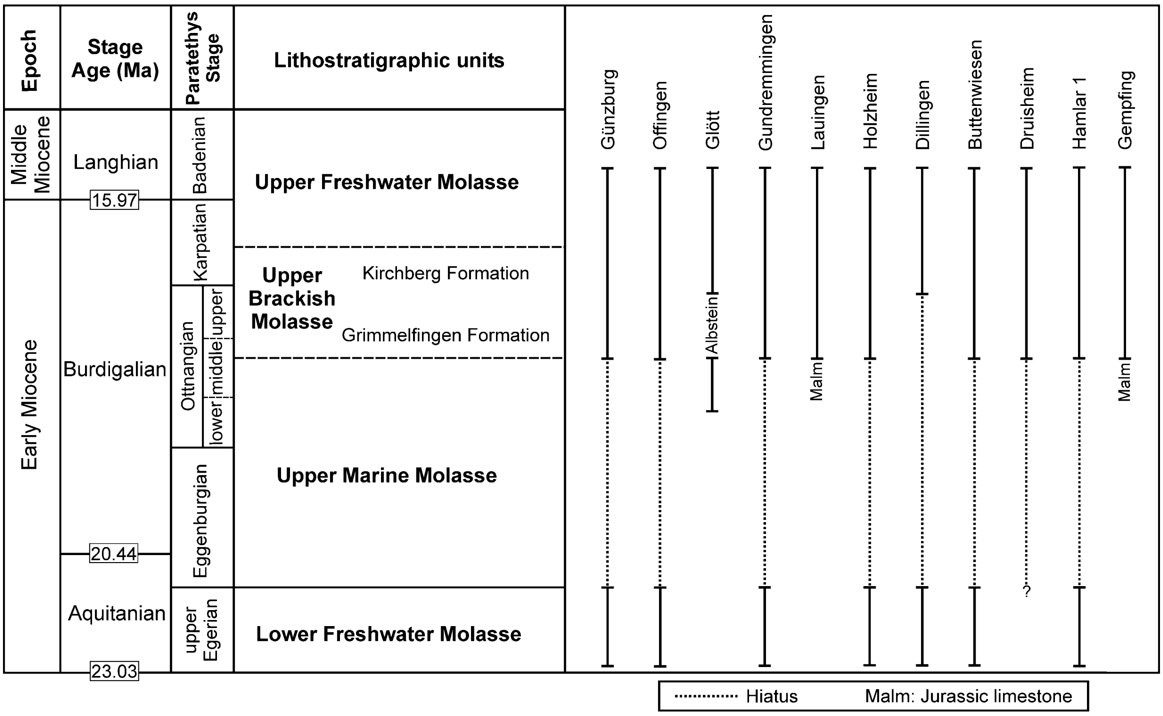

**Figure 3.** Miocene lithostratigraphic units in the south German Molasse Basin (after Doppler et al., 2005; Reichenbacher et al., 2013) and stratigraphic range of drill cores. Dotted lines indicate stratigraphic units not present in the drill cores. Image reproduced from Salvador et al. (2016a).

With the present material, a much more comprehensive taxonomical study of the mollusks was possible, allowing new paleoecological considerations. The cores are stored in the LfU (Hof) and the fossils in the LfU (Munich; under the single record number LfU-SPR2014). For more information on the geological setting and list of studied material, refer to Reichenbacher et al. (2013) and Salvador et al. (2016a).

## 1.2. Methodology

Here is explained the main aspects of the methodology used in my doctoral research, separated under my two main topics: taxonomy and paleoecology.

### 1.2.1. Taxonomy

The taxonomic portion of my work consisted mainly in species identification, with occasional instances of more typical taxonomic work, such as revisions, description of new species, solving nomenclatural issues etc. This assures a solid base for supporting research in other fields (Mayr & Ashlocke, 1969; Winston, 1999; Wiley & Lieberman, 2011). An unidentified and/or unnamed species is of no use to anyone and, thus, any work dealing with such "species" will have only very dubious validity (Isely, 1972; Winston, 1999; Wheeler, 2008).

Taxonomic work must abide by certain requirements (Winston, 1999; Valdecasas, 2011; Wiley & Lieberman, 2011): (1) Be in accordance with the ICZN (1999, presently, the 4th edition). (2) Present the analysis of type specimens or, if not possible, at least topotypes. In the case of a new species, the type(s) should be designated. (3) Present the history of the given taxon (*i.e.*, the synonymy). (4) Present diagnostic features of the taxon, even when there are morphometric data, molecular data or images; for fossils in particular, diagnosis is based on morphological characters, so it must consist of sufficient features to allow distinction (*i.e.*, a "unique combination of characters"; Forey et al., 2004; Wheeler, 2008). (5) When appropriate, clearly explain any reasons for nomenclatural acts. (6) Always present images illustrating the taxon (especially type specimens). (7) Be precise with the taxon's geographic occurrence. In Paleontology, the stratigraphic occurrence is equally important (Shaw, 1971).

Due to the intrinsic nature of fossils, there is less information to be gathered than in living animals, which also count with ecological, behavioral, molecular, physiological and anatomical data. Nevertheless, this does not necessarily make fossil species "less valid" than living ones, since a well-documented set of morphological characters is enough for a proper diagnosis (Farris, 1976; Forey et al., 2004; Wheeler, 2008). It should also be noted that the majority of Recent species (*e.g.*, mollusks' shells) is described based only on external morphology ("morphospecies concept") and often this is done with less care than in fossils (paleontologists usually try extracting the most out of their specimens; Forey et al., 2004).

In Malacology, in particular, a few authors consider conchological characters insufficient, stating that shells are inclined towards homoplasies that confound classification (*e.g.*, Wagner, 2001; Mordan & Wade, 2008). Certainly, the shell might not suffice in some cases (*e.g.*, freshwater snails; Baker, 1945), but in the majority of cases it can alone offer much information. Shell characters are good at indicating the affinities of a species at the family level and are especially useful at the generic level (Vermeij, 1993, 2002). Again, it should be noted that this is only possible when using the aforementioned “unique combination of characters” and not a single character as is usually common practice (Forey et al., 2004).

In the present work, gastropod classification follows Bouchet et al. (2005), with further modifications pointed out by Nordsieck (2014) for the European fossil land snails. Likewise, bivalve classification follows Bouchet & Rocroi (2010) and Carter et al. (2011).

### 1.2.2. Paleoecology

The potential of continental snails is often overlooked in paleontological studies, which, until very recently, rarely went beyond taxonomy. These animals can be used for a broad range of studies, especially in paleoecology and paleoenvironmental reconstructions. This can be achieved by two kinds of analyses, complementary to one another: (1) an actualistic approach (Rasser et al., submitted); (2) stable isotope analysis (oxygen and carbon) of the calcium carbonate of the shell. These methodologies are described below.

#### 1.2.2.1. Actualistic approach

There are continental gastropods adapted to all kinds of ecological conditions but, below the family level and especially within a genus, they usually are restricted to (or strongly prefer) a single kind of habitat (Barker, 2001; Cook, 2001; Miller & Tevesz, 2001; Pearce & Örstan, 2006). Therefore, ecological data (habitat preferences) from extant genera are often used as a guide for paleoecological inferences of fossil congeners.

This actualistic approach is widely used in the literature (*e.g.*, Ložek, 1964; Clarke, 1979; Fordinál, 1996; Albesa et al., 1997; Esu & Ciangherotti, 2004; Moser et al., 2009), but in an almost informal way. It has been only roughly delineated and explained. This approach joins two know paleoecological methodologies from the literature, namely, the Extant Phylogenetic Bracket (used to infer the probability of the existence of an unpreserved trait) and the Nearest Living Relative method (used in paleobotanical studies for climate reconstruction). It uses close extant relatives (congeners) of fossil gastropods to define a range of habitats for the fossil taxa. If all extant species of a given genus share a certain basic ecological requirement, then there is a good probability that a fossil congener would have shared this requirement.

The actualistic approach starts 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 paleoecological reconstruction. Following this, data on the ecological requirements of extant congeners is gathered from the literature and the fossil species are sorted into ecological/habitat/niche groupings. The handful of resulting groups will define the paleoenvironmental reconstruction. Quantitative data on species abundance, if available, should also be taken into account. Changes in these groups along the sedimentary profile allows to track environmental changes through time. Besides taxonomy, there are other sources of data to inform paleoecological reconstructions, such as functional morphology (*e.g.*, shell shape and structures) and trophic interactions (*e.g.*, trace fossils).

#### 1.2.2.2. Stable isotope analysis

The analysis of stable isotopes (oxygen and carbon) of shell carbonate can provide key information for paleoenvironmental/paleoclimatological reconstructions, being extensively explored for both freshwater (e.g., Vonhof et al., 1998; Leng et al., 1999; Tütken et al., 2006) and land snails (e.g., Lécolle, 1985; Goodfriend, 1992; Goodfriend & Ellis, 2002).

Shell carbonate in freshwater snails is produced in oxygen isotope equilibrium with lake water and in carbon isotopic equilibrium with total dissolved inorganic carbon in the water (Leng et al., 1999; Miller & Tevesz, 2001; McConnaughey & Gillikin, 2008). It is assumed that isotopic ratios found in fossil shells closely reflect the isotopic signatures of the water during the growth season (Fritz & Poplawski, 1974; Vonhof et al., 1998; Anadón et al., 2007). In land snails, shell carbonate crystallizes in oxygen and carbon isotope equilibrium with body fluid water (Balakrishnan & Yapp, 2004). The oxygen isotope composition of this body fluid water closely approaches that of its main source, rain water (Lécolle, 1985; Goodfriend & Ellis, 2002; Balakrishnan & Yapp, 2004; Zanchetta et al., 2005), while carbon isotope composition is mainly related to diet (Balakrishnan & Yapp, 2004; McConnaughey & Gillikin, 2008).

The specimens (shells) used in such analyses must be cleaned with distilled water and ultrasonic bath, being then air-dried and crushed and ground. This results in a completely homogenized powder, which will give an averaged value (Shanahan et al., 2005). The samples then go through X-Ray Diffraction (XRD) measurements to confirm if all shell material is the original aragonite, *i.e.*, that they do not show signs of recrystallization and thus retain the original isotopic composition (Grossman & Ku, 1986; Latal et al., 2004, 2006).

In my doctoral studies, XRD and stable isotope measurements were conducted at *Eberhard Karls Tübingen Universität*; strontium isotope measurements were conducted at *Rheinische Friedrich-Wilhelms-Universität Bonn*. Isotope values are in conventional per mil (δ‰) deviations of isotope ratios ($^{18}O/^{16}O$ and $^{13}C/^{12}C$) from standard VPDB (Coplen, 1994).

# 2. Objectives

Traditionally, molluscan fossils received much less attention than vertebrates in published studies. As such, material from several localities collected during the 19th and 20th centuries was stored in museum collections, in dire need of revisionary work and systematic accounts. Moreover, by remaining virtually unknown, their potential for paleoecological and paleoenvironmental studies remained largely locked away.

The original objective of my doctoral project was to study one of these cases, the rich molluscan fauna from Sandelzhausen. A thorough taxonomic revision of the material would create a solid basis for a follow-up paleoecological study (with both actualistic and stable isotope analyses). However, this was accomplished much quicker than expected and I was able to do the same kind of study for several additional localities and faunas (see Section 1.1) during my doctoral studies.

These additional localities were chosen according to the reasons given in Section 1.1 above. By doing this, I was able to refine the knowledge on the continental molluscan fauna of the Early/Middle Miocene of the NAFB in southern Germany in the fields of taxonomy, paleoecology and paleobiogeography. Moreover, the study of these selected localities also allowed the strengthening of the message that a thorough taxonomic work is indispensable for subsequent paleoecological (and also paleobiogeographical) works.

## 2.1. Expected output of the doctoral research

The original output of my doctoral project would be a couple of articles on the taxonomy and paleoecology of the molluscan fauna of Sandelzhausen. As more localities and faunas were added, the actual output greatly exceeded that (see Sections 3.1 to 3.2). As a result, a total of 11 published papers and three presently submitted manuscripts stem from my doctoral research.

When taken together, they form a reasonable contribution to the knowledge of the continental molluscan fauna of the Early/Middle Miocene of Germany. Moreover, new data helps to refine the environmental reconstructions for this period.

# 3. List of Publications

Here are listed all the articles deriving from my doctoral research, counting with published papers and submitted manuscripts (Sections 3.1 and 3.2). For co-authored papers, Section 3.3 describes the significance of my personal contribution to the articles.

Finally, Section 3.4 lists my other publications not directly linked with the doctoral research per se, but published during the time of my doctoral studies (articles in press, accepted or submitted manuscripts are not listed). The list includes both academic papers and articles in magazines/newsletters dedicated to science outreach. Electronic versions of all articles (PDF files) can be found in my website: *https://rodrigobsalvador.wordpress.com/*.

## 3.1. Published papers

Salvador, R.B. 2013a. The fossil land and freshwater mollusks of Sandelzhausen (Early/Middle Miocene, Germany): Caenogastropoda, Neritimorpha, lower Heterobranchia and Bivalvia. Strombus, 20: 19–26.

Salvador, R.B. 2013b. The fossil pulmonate snails of Sandelzhausen (Early/Middle Miocene, Germany): Succineidae, Testacelloidea and Helicoidea. Zootaxa, 3721: 157–171.

Salvador, R.B. 2014. The fossil land and freshwater snails of Gündlkofen (Middle Miocene, Germany). Zootaxa, 3785: 271–287.

Salvador, R.B. 2015. The fossil pulmonate snails of Sandelzhausen (Early/Middle Miocene, Germany): Ellobiidae, Pupilloidea, and Clausilioidea. Paläontologische Zeitschrift, 89: 37–50.

Salvador, R.B. & Rasser, M.W. 2014. The fossil pulmonate snails of Sandelzhausen (Early/Middle Miocene, Germany) (Hygrophila, Punctoidea and limacoids). Archiv fur Molluskenkunde, 143: 187–202.

Salvador, R.B. & Rasser, M.W. 2016. Fossil land and freshwater gastropods from the Middle Miocene of Bechingen and Daugendorf, southwestern Germany. Archiv für Molluskenkunde 145(1): 111–124.

Salvador, R.B. & Rasser, M.W. 2016. The fossil land and freshwater snails of Oggenhausen (Middle Miocene, Germany). Revista Brasileira de Paleontologia, 9(1): 41–52.

Salvador, R.B.; Pippèrr, M.; Reichenbacher, B.; Rasser, M.W. 2016a. Early Miocene continental gastropods from new localities of the Molasse Basin in southern Germany. Paläontologische Zeitschrift: published online [DOI 10.1007/s12542-016-0291-y].

Salvador, R.B.; Prieto, J.; Mayr, C.; Rasser, M.W. 2016b. New gastropod assemblages from the Early/Middle Miocene of Riedensheim and Adelschlag-Fasanerie, southern Germany. Neues Jahrbuch fur Geologie und Palaontologie, Abhandlungen, 279(2): 127–154.

Salvador, R.B.; Rasser, M.W.; Höltke, O. 2015a. Fossil gastropods from Miocene Lake Randeck Maar and its hinterland (SW Germany). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 277(3): 251–273.

Salvador, R.B.; Sach, V.J.; Valentas-Romera, B.L. 2015b. The fossil continental mollusks in the Upper Freshwater Molasse (Middle Miocene) of the districts of Biberach, Ravensburg and Neu-Ulm, Germany. Revista Brasileira de Paleontologia, 18(2): 201– 216.

## 3.2. Submitted manuscripts

HÖLTKE, O.; SALVADOR, R.B.; RASSER, M.W. Submitted. Paleobiogeography of Middle Miocene terrestrial gastropods in Central Europe, with special emphasis on the Upper Freshwater Molasse. Palaeogeography, Palaeoclimatology, Palaeoecology.

RASSER, M.W.; SALVADOR, R.B.; HÖLTKE, O. Submitted. The gastropod palaeohabitats of lake Randeck Maar and its hinterland (Miocene, SW Germany) using the "Extant Genus Bracket". Palaeogeography, Palaeoclimatology, Palaeoecology.

SALVADOR, R.B.; TÜTKEN, T; TOMOTANI, B.M.; BERTHOLD, C.; RASSER, M.W. Submitted. Paleoecological and isotopic analysis of fossil continental mollusks of Sandelzhausen (Early/Middle Miocene, Germany). Paläontologische Zeitschrift.

## 3.3. Personal contribution in co-authored papers

In accordance with the "Rules and Guidelines for Doctoral Studies in the Faculty of Science of the University of Tübingen" ("*Promotionsordnung der Mathematisch-Naturwissenschaftlichen Fakultät der Universität Tübingen*", Amtliche Bekanntmachungen der Universität Tübingen, 2015, Nr. 5, pp. 149–162), the required document declaring the significance of my personal contribution in co-authored papers is presented on the very end of this thesis, after the Appendix 9Section 7).

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## 3.4. Other publications

Cavallari, D.C.; Cunha, B.R.; Salvador, R.B. 2014. Dangers to malacological collections: Bynesian decay and pyrite decay. Collection Forum, 28: 35–46.

Cavallari, D.C.; Salvador, R.B.; Simone, L.R.L. 2013. New records of *Pseudotorinia architae* (Gastropoda, Architectonicidae) from southeastern Brazil. Strombus, 20: 6–11.

Cavallari, D.C.; Salvador, R.B.; Simone, L.R.L. 2013. Redescription of *Solatisonax cabrali* (Gastropoda, Architectonicidae), with two new records from southeastern Brazil. Strombus, 20: 12–18.

Cavallari, D.C.; Salvador, R.B.; Simone, L.R.L. 2014. Taxonomical study on the Architectonicidae (Gastropoda, Heterobranchia) collected by the Marion Dufresne (MD55) expedition to SE Brazil. Spixiana, 37: 35–43.

Cavallari, D.C.; Salvador, R.B.; Simone, L.R.L. 2016. *Solariella quadricincta* Quinn, 1992 and *S. staminea* Quinn, 1992 are synonyms of *S. carvalhoi* Lopes & Cardoso, 1958 from the SW Atlantic (Gastropoda: Solariellidae). Zootaxa, 4109(1): 96–100.

Cunha, C.M.; Salvador, R.B.; Simone, L.R.L. 2015. The terrestrial microgastropods of Trindade Island, Brazil (Gastropoda: Pulmonata). Spixiana, 38(1): 139–143.

Fernández, M.S; García, R.A.; Fiorelli, L.E.; Scolaro, A.; Salvador, R.B.; Cotaro, C.N.; Kaiser, G.W.; Dyke, G.J. 2013. A Large Accumulation of Avian Eggs from the Late Cretaceous of Patagonia (Argentina) Reveals a Novel Nesting Strategy in Mesozoic Birds. Plos One, 8: e61030.

Salvador, R.B. & Cavallari, D.C. 2013. A New *Oxychona* species (Gastropoda: Pulmonata: Orthalicidae) from Bahia state, Brazil. Journal of Conchology, 41: 315–318.

Salvador, R.B. & Cavallari, D.C. 2013. Taxonomic revision of *Leiostracus onager* and *Leiostracus subtuszonatus* (Gastropoda: Pulmonata: Orthalicidae). Journal of Conchology, 41: 511–518.

Salvador, R.B. & Cavallari, D.C. 2014. A new species of *Leiostracus* from Bahia, Brazil (Gastropoda, Pulmonata, Orthalicidae). Iheringia, Série Zoologia, 104: 39–42.

Salvador, R.B. & Cavallari, D.C. 2014. A new species of *Leiostracus* (Gastropoda, Pulmonata, Orthalicoidea) from Espírito Santo, Brazil. Iheringia, Série Zoologia, 104: 364–366.

Salvador, R.B. & Cunha, C.M. 2016. Taxonomic revision of the fossil genera *Bulimactaeon*, *Hemiauricula* (= *Liocarenus*) and *Nucleopsis*, with description of a new Recent genus and species (Gastropoda: Heterobranchia: Acteonidae). Journal of Molluscan Studies: published online [DOI 10.1093/mollus/eyw010].

Salvador, R.B. & Simone, L.R.L. 2013. Taxonomic reassessment of *Planorbis llanerensis* from the Neogene of Monagas state, Venezuela (Gastropoda, Planorbidae). Strombus, 20: 1–5.

Salvador, R.B. & Simone, L.R.L. 2013. Taxonomic revision of the fossil pulmonate mollusks of Itaboraí Basin (Paleocene), Brazil. Papéis Avulsos de Zoologia, 53: 4–56.

SALVADOR, R.B. & SIMONE, L.R.L. 2014. New species of *Cyclodontina* from Bahia, Brazil (Gastropoda, Pulmonata, Odontostomidae). Iheringia, Série Zoologia, 104: 484–487.

SALVADOR, R.B. & SIMONE, L.R.L. 2015. Taxonomical study on a sample of land snails from Alcobaça (Bahia, Brazil), with description of a new species. Stuttgarter Beiträge zur Naturkunde A, 8: 1–7.

SALVADOR, R.B. & SIMONE, L.R.L. 2016. A new species of *Kora* from Bahia, Brazil (Gastropoda: Pulmonata: Orthalicoidea), with an emended diagnosis of the genus. Stuttgarter Beiträge zur Naturkunde A, Neue Serie, 9: 1–7.

SALVADOR, R.B. & TOMOTANI, B.M. 2014. The Kraken: when myth encounters science. História, Ciências, Saúde – Manguinhos, 21: 971–994.

SALVADOR, R.B.; CAVALLARI, D.C.; BREURE, A.S.H. 2014. Corrigendum to “Taxonomic revision of *Leiostracus onager* and *Leiostracus subtuszonatus* (Gastropoda: Pulmonata: Orthalicidae)” by Salvador & Cavallari (2013). Journal of Conchology, 41: 627–628.

SALVADOR, R.B.; CAVALLARI, D.C.; SIMONE, L.R.L. 2014. Seguenziidae (Gastropoda: Vetigastropoda) from SE Brazil collected by the Marion Dufresne (MD55) expedition. Zootaxa, 3878: 536–550.

SALVADOR, R.B.; CAVALLARI, D.C.; SIMONE, L.R.L. 2015. Taxonomical study on a sample of land snails from southeastern Tocantins state, Brazil, with description of a new species. Journal of Conchology, 42: 67–78.

SALVADOR, R.B.; CAVALLARI, D.C.; SIMONE, L.R.L. 2016. Taxonomical study on a sample of land snails from Alto Ribeira Park (São Paulo, Brazil), with description of a new species. Archiv für Molluskenkunde, 145: 59–68.

SALVADOR, R.B.; CUNHA, C.M.; SIMONE, L.R.L. 2013. Taxonomic revision of the orthalicid land snails (Pulmonata: Stylommatophora) from Trindade Island, Brazil. Journal of Natural History, 47: 949–961.

SALVADOR, R.B.; HÖLTKE, O.; RASSER, M.W.; KADOLSKY, D. 2016. Annotated type catalogue of the continental fossil gastropods in the Staatliches Museum für Naturkunde Stuttgart, Germany. Palaeodiversity, 9: 15–70.

SALVADOR, R.B.; RIBEIRO, G.; CAVALLARI, D.C. 2015. Mollusks on Brazilian postage stamps. Strombus, 22: 19–28.

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SALVADOR, R.B.; SILVA, N.G.; ALVES, R.J.V.; MOURA, R.L.; SIMONE, L.R.L. 2014. New records of Helicina inaequistriata (Gastropoda: Helicinidae) from Rio de Janeiro and São Paulo states, Brazil. Check List, 10: 936–938.

SIMONE, L.R.L. & SALVADOR. 2016. Taxonomical study on a sample of land snails from Nanuque (Minas Gerais, Brazil), with descriptions of three new species. Stuttgarter Beiträge zur Naturkunde A, Neue Serie, 9: 9–30.

### 3.4.1. Science outreach

CAVALLARI, D.C.; SALVADOR, R.B.; SIMONE, L.R.L. 2016. A possible land snail diversity hotspot in Bahia state, Brazil. Tentacle, 24: 14–16.

SALVADOR, R.B. 2014. Geeky nature. Journal of Geek Studies, 1(1-2): 41–45.

SALVADOR, R.B. 2014. Praise Helix!. Journal of Geek Studies, 1(1-2): 9–12.

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SALVADOR, R.B. 2015. The real-life origins of the legendary Kraken. The Conversation, 30-Dec-2015. Available from: https://theconversation.com/the-real-life-origins-of-the-legendary-kraken-52058

SALVADOR, R.B. 2016. The biology of giant war centipedes. Journal of Geek Studies, 3(1): 1–11.

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SALVADOR, R.B. & SIMONE, L.R.L. 2015. The discovery and possible extinction of a *Leiostracus* land snail in southeastern Brasil. Tentacle, 22: 7–8.

SALVADOR, R.B. & TOMOTANI, B.M. 2015. The birds of James Bond. Journal of Geek Studies, 2(1): 1–9.

SALVADOR, R.B.; CUNHA, C.M.; SIMONE, L.R.L. 2013. The pulmonate snails of Trindade Island, Brasil. Tentacle, 21: 38–39.

# 4. Results and Discussion

Here are given the main results, in a very brief manner for each locality, regarding the molluscan fauna, their paleoecology, and paleoenvironment. For a thorough analysis, please refer to the full articles (Section 7). A general discussion can be found in Section 5. In view of later revisionary works, some species here appear with different (and more up-to-date) names than in some papers.

## 4.1. Sandelzhausen

The snail fauna of Sandelzhausen comprises a total of 44 continental gastropod species (Table 1), mostly terrestrial pulmonates (Salvador, 2013a, 2013b, 2015; Salvador & Rasser, 2014). Two new species were described from this material: *Urticicola perchtae* Salvador, 2013 (family Hygromiidae; Figs. 4A–C) and *Carychium galli* Salvador, 2015 (family Carychiidae; Figs. 4D–E).

**Table 1.** Occurrence of mollusk species in the sedimentary layers of Sandelzhausen, from B1 (bottom) to D1 (top). The thin coal layer (C2; interpreted as a wildfire event by Moser et al., 2009a, 2009b) was suppressed, since fossils are rarely found there. Symbols: **x**, 0–10 specimens; **xx**, 11–100 specimens; **xxx**, >100 specimens; **?**, precise layer unknown.

| | Layers | | | | | | Layers | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **B1** | **B2** | **C1** | **C3** | **D1** | **Species** | **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* (Klein, 1846) | | | | | x |
| *Pomatias* sp. | ? | ? | ? | | | *Granaria* cf. *grossecostata* (Gottschick & Wenz, 1919) | | x | | x | |
| NERITIMORPHA | | | | | | *Granaria* sp. | | x | | x | |
| *Theodoxus* sp. | | | | | x | *?Helicodonta* sp. | ? | ? | ? | ? | ? |
| Lower HETEROBRANCHIA | | | | | | *Janulus supracostatus* (Sandberger, 1873) | ? | ? | ? | ? | ? |
| *Valvata* sp. | | | | x | | *Leucochroopsis kleini* (Klein, 1847) | | | ? | ? | x |
| HYGROPHILA | | | | | | *Lucilla subteres* (Clessin, 1877) | ? | ? | ? | | |
| *Ferrissia deperdita* (Desmarest, 1814) | ? | ? | ? | | | *Oxyloma minima* (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* (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* (Klein, 1853) | x | x | x | x | x |
| *Planorbarius mantelli* (Dunker, 1848) | xx | xx | xx | xx | xxx | ?*Pyramidula* sp. | ? | ? | ? | ? | ? |
| *Radix socialis* (von Zieten, 1830) | | | | | xx | *Strobilops* sp. | ? | ? | ? | ? | |
| *Segmentina larteti* (Noulet, 1854) | | | ? | ? | x | *Testacella zellii* Klein, 1853 | ? | ? | ? | | |
| EUPULMONATA | | | | | | *Triptychia* sp. | | x | | x | |
| *Apula* cf. *coarctata* (Klein, 1853) | | | | x | x | *Urticicola perchtae* Salvador, 2013 | | | | 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 | |

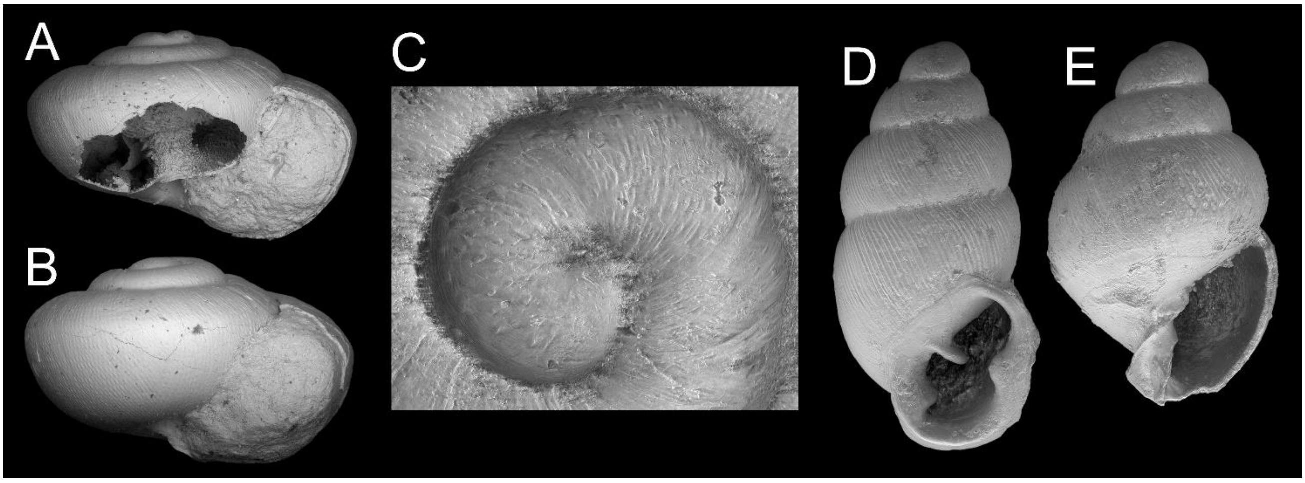

**Figure 4.** New species described from Sandelzhausen. **A.** *Urticicola perchtae*, holotype (BSPG 1959 II 17312; H = 3.5 mm, D = 2.1 mm). **B.** *U. perchtae*, paratype (BSPG 1959 II 17313; H = 2.9 mm, D = 1.9 mm). **C.** *U. perchtae*, holotype, protoconch detail. **D.** *Carychium galli*, holotype (BSPG 1959 II 17271; H = 1.6 mm, D = 0.8 mm). **E.** *C. galli*, paratype, broken specimen showing internal lamella (BSPG 1959 II 17274; H = 1.1 mm).

Two snail species were chosen for the isotope analysis, the freshwater lymnaeid *Galba dupuyiana* and the terrestrial clausiliid *Pseudidyla moersingensis*, due to: (1) they are extremely abundant, so enough well-preserved specimens could be more easily gathered; (2) they are present throughout all the mollusk-bearing sediment layers and the entire lake. The aim was four samples of each species for each sediment interval (ca. 5–10 cm in the profile), but for some layers poor preservation or lack of material precluded this (Table 2).

**Table 2.** Isotope values (VPDB standard) by height (cm) on sediment profile; standard deviation (SD) shown on a separate column, when applicable. Layers *sensu* Moser et al. (2009).

| Species | Layer | Height in sediment | δ $^{18}$O (‰) | | | | SD | δ $^{13}$C (‰) | | | | SD | δ $^{87}$Sr (‰) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pseudidyla moersingensis* (O. Boettger, 1877) | B2 | ~67.5 cm | -3.50 | -3.95 | -4.66 | - | 0.59 | -5.04 | -6.90 | -6.32 | - | 0.95 | - |
| | C3 | ~100 cm | -4.12 | -3.81 | - | - | 0.22 | -4.99 | -5.72 | - | - | 0.52 | - |
| | C3 | ~107.5 cm | -3.14 | -3.07 | -3.29 | - | 0.11 | -4.11 | -6.81 | -7.54 | - | 1.81 | - |
| | C3 | ~117.5 cm | -3.26 | -3.19 | -2.26 | -2.74 | 0.46 | -7.10 | -5.88 | -6.63 | -7.61 | 0.73 | - |
| | D1 | ~137.5 cm | -2.88 | -3.93 | - | - | 0.75 | -4.78 | -5.31 | - | - | 0.38 | - |
| | D1 | ~142.5 cm | -2.37 | - | - | - | - | -4.89 | - | - | - | - | 0.710833 |
| | D1 | ~152.5 cm | -3.40 | -3.45 | -1.83 | - | 0.92 | -5.18 | -6.58 | -4.23 | - | 1.18 | - |
| | 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) | B2 | ~67.5 cm | -2.50 | -2.64 | -2.06 | -1.46 | 0.53 | -7.21 | -5.73 | -3.05 | -6.91 | 1.90 | 0.710471 |
| | C3 | ~100 cm | -2.19 | -2.36 | -5.21 | - | 1.70 | -5.59 | -5.21 | -9.79 | - | 2.54 | 0.710645 |
| | C3 | ~107.5 cm | -5.54 | -3.30 | -2.84 | - | 1.44 | -6.52 | -2.95 | -0.18 | - | 3.18 | - |
| | C3 | ~117.5 cm | -1.53 | -4.66 | -4.92 | -3.98 | 1.55 | -8.03 | -6.42 | -8.27 | -4.30 | 1.83 | - |
| | D1 | ~137.5 cm | -0.56 | -2.13 | -3.10 | -2.21 | 1.06 | -9.11 | -9.35 | -8.39 | -9.17 | 0.42 | - |
| | D1 | ~142.5 cm | -2.25 | -2.93 | - | - | 0.48 | -8.80 | -8.13 | - | - | 0.47 | 0.710790 |
| | D1 | ~152.5 cm | -2.81 | -1.85 | -3.52 | -1.95 | 0.79 | -10.05 | -2.89 | -7.90 | -7.47 | 3.01 | - |
| | D1 | ~157.5 cm | -2.86 | -2.14 | -0.52 | -5.91 | 2.26 | -8.25 | -7.69 | -3.00 | -7.24 | 2.40 | - |
| | D1 | ~165 cm | -2.58 | -2.72 | -0.98 | -3.40 | 1.02 | -7.25 | -7.31 | -10.54 | -7.26 | 1.63 | - |

The whole paleoecological analysis can be found in Salvador et al. (submitted); only the main results are discussed below.

The $\delta^{18}O$ values of land snail shells can be used to calculate the MAT. For this, there are two equations proposed in the literature: (1) Lécolle (1985), calibrated by the Recent land snail fauna of France; and (2) Zanchetta et al. (2005), with Recent Italian snails. The results of imputing the $\delta^{18}O$ values of the land snail *P. moersingensis* in these equations can be seen in Figure 5. Mean Annual Temperature (MAT) was not significantly correlated to height in the sediment for both equations; this means that there is no clear trend of temperature variation throughout the studied sediment profile. The obtained MAT values (Fig. 5) indicate a sub-tropical climate and compare well to those obtained by Böhme (2009) for the ectothermic vertebrates of Sandelzhausen: 18.0–20.8 °C.

As a cautionary note, the calculated MAT might be a little overestimated because there usually is no shell growth during the coldest and/or drier months; as such, the MAT values would reflect the warmer and/or wetter months of the snails' growing season (Balakrishnan & Yapp, 2004). However, if there was no clear dry or cold season (a low seasonality was suggested by Tütken & Vennemann, 2009), the snails could grow throughout the whole year.

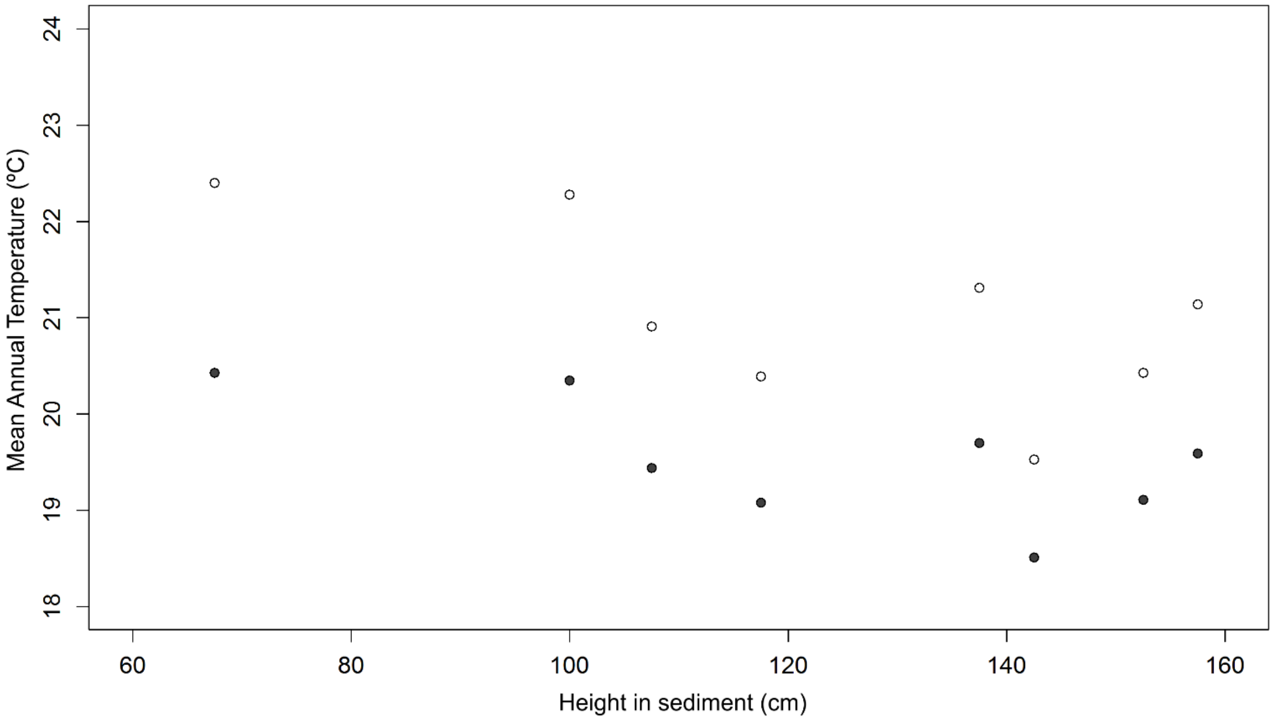

**Figure 5.** MAT, shown by height in the sediment profile (in cm), obtained by imputing the $\delta^{18}O$ values of *P. moersingensis* in the equations of Lécolle (1985) [white dots] and Zanchetta et al. (2005) [black dots].

The $\delta^{13}$C values of freshwater snail shells is better analyzed together with their respective $\delta^{18}$O values. For instance, it is known that in closed-lake systems, the two values usually co-vary in carbonates (Talbot, 1990; Li & Ku, 1997; Deocampo, 2010). This seems to happen in Sandelzhausen from layer B2 to the beginning of layer C3 (heights 60 to 100 cm; Fig. 6): the slopes of the curves do not differ, indicating that the lake was a closed system. (However, there are only two measurements from these layers, so this 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). In Sandelzhausen, this happens from the bottom of layer C3 onwards (heights greater than 100 cm; Fig. 6): the curves do not co-vary, indicating an open lake.

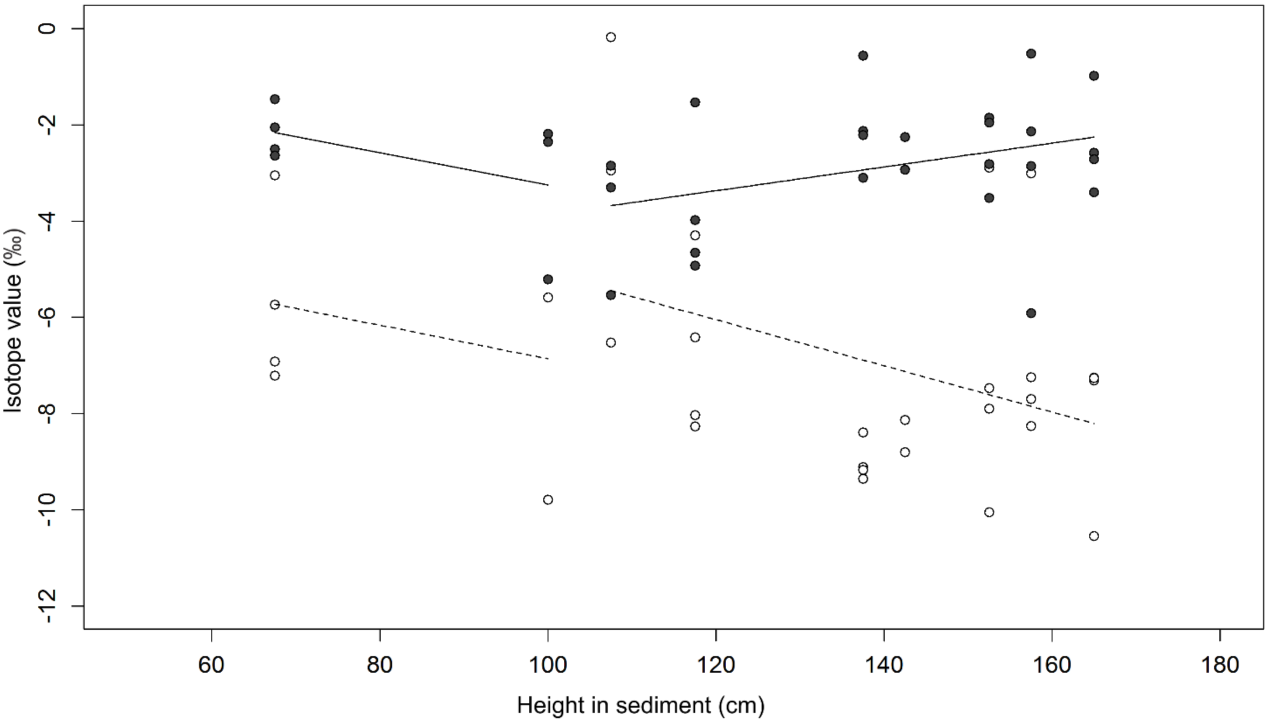

**Figure 6.** Oxygen [black dots] and carbon [white dots] isotope values for each interval of the sediment profile. The curves represent the intervals from layer B2 to the beginning of layer C3 (heights 60 to 100 cm) and from the bottom of layer C3 onwards (heights greater than 100 cm). The slopes of the curves for the bottom interval do not differ, while those of the upper interval clearly do.

This is in line with the environmental reconstructions of Sandelzhausen by previous authors (Fahlbusch et al., 1972; Witt, 1998; Böhme, 2009; Moser et al., 2009b) and sedimentological data (Schmid, 2002). The recovered values are also in accordance with general values obtained for the Miocene Climatic Optimum (*e.g.*, Böhme, 2003). For the lower layers (up to basal layer C3), it is proposed a swampy area, 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 (2009) 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 signal of the molluscan faunal composition (see below; Moser et al., 2009b). Moreover, the low $\delta^{13}C$ values, especially in the later stages of Sandelzhausen (Fig. 6) indicates a great amount of photosynthetic activity and thus abundant organic matter (Tevesz et al., 1997; Zanchetta et al., 1999; Miller & Tevesz, 2001). This is also in line with the increase in riparian vegetation in the upper layers and slightly eutrophic conditions proposed by Böhme (2009).

Finally, there is a marked increase in strontium isotope values throughout the layers in Sandelzhausen. This would likely reflect a change in the catchment area and thus water source of the forming lake starting in layer C3. The change to perennial lake was formerly attributed to an increase in precipitation values (Böhme, 2009), but it seems now more likely that new tributaries started to discharge in the Sandelzhausen lake region.

Using the actualistic ecological approach based on habitat preferences of Recent congeners, the following scenario was reconstructed. The freshwater snails show preference for richly vegetated slow moving or standing waters. Layers C3 and D1 have species more typical of large consolidate water bodies, showing a trend from more temporary waters to a perennial lake, in agreement with what was previously proposed in the literature.

For the terrestrial species, most are usual inhabitants of humid forests (*Carychium* and *Oxyloma*, in particular, are hygrophilous, living on richly vegetated areas surrounding water bodies), especially on the upper layers. Some of the land snails prefer drier and more open habitats, however. These species are scattered throughout all layers in Sandelzhausen, so it is plausible that the lake’s hinterland would have always counted with more open areas.

As such, the paleoecological reconstruction based on the fossil mollusks is in line with previous works (Fahlbusch et al., 1972; Witt, 1998; Böhme, 2009; Moser et al., 2009b; Tütken & Vennemann, 2009). From layer B1 to basal layer C3, Sandelzhausen 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 decrease in the number of lymnaeids), (2) the appearance of species that do not tolerate desiccation, and (3) the decoupling of the covariation between oxygen and carbon isotopic signals of the freshwater snail *G. dupuyiana*.

The changes in the strontium isotopic signal would thus reflect a change in the water source of this newly formed lake.

The terrestrial habitat would have gone from a more relatively open environment (semi-arid/sub-humid scrubland; 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. This largely agrees with previous findings. Despite plant remains being scarce in Sandelzhausen proper, they are well known from nearby coeval deposits showing evergreen to deciduous subtropical forests (*e.g.*, Jechorek & Kovar-Eder, 2004; Böhme et al., 2007), with a larger amount of rainfall when compare to the Recent (Böhme et al., 2011). However, the material analyzed here shows that the species from drier and more open environments are present throughout all the layers, suggesting that these habitats persisted in the lake's hinterland instead of disappearing (*contra* Moser et al., 2009b).

## 4.2. Randeck Maar

The snail fauna of the Randeck Maar now comprises a total of 32 continental gastropod species (Table 3); mostly terrestrial pulmonates (Salvador et al., 2015a). The terrestrial snails are surprisingly diverse, but the same does not seem to be the case for the freshwater species (only 4 out of 32 species). This could be a reflection of the water chemistry in the lake and the anoxic conditions at the bottom, as attested by the lack of fishes and other benthic life (Rasser et al., 2013). The freshwater species would thus inhabit the littoral and supralittoral (marsh and reed belt) zones of the lake (Figure 7).

The diverse land snail fauna is dominated by *Pomatias conicus* (curiously the only non-pulmonate in the fauna), *Cochlicopa loxostoma*, Granaria sp. and Praeoestophorella phacodes. This assembly indicates a variety of habitats surrounding the lake, going from humid and warm forests and shrublands to more exposed rocky limestone habitats (especially in the crater-ring wall). All types of environments and the species indicating them are summarized on Figure 7.

Some land snails species (mainly *Opeas minutum*, *Negulopsis lineolata* and *Palaeomastus filocinctus*, whose Recent allied taxa are either island-endemic or tropical species), the insects and the sclerophyllous flora (Rasser et al., 2013) indicate a warm-temperate climate with a dry season, similar to the present-day Mediterranean biome.

**Table 3.** Distribution of the gastropod species of Randeck Maar in the different facies types. Specimens without precisely recorded facies of origin were not included. Lake stages according to Jankowski (1981). Layers: **DT**, dark tuffites; **LT**, light tuffites; **ML**, marginal limestones and marls; **CL**, calcareous laminites; **Dys**, dysodil; **FL**, freshwater limestones. Number of specimens found (collection not controlled for quantitative analysis): **x**, 1-10 specimens; **xx**, 11-60 specimens; **xxx**, >60 specimens.

| | **Stage 1** | **Stage 2** | | | | **Stage 3** |
|---|---|---|---|---|---|---|
| **Species** | **DT** | **LT** | **ML** | **CL** | **Dys** | **FL** |
| *Apula coarctata* (Klein, 1853) | | xxx | x | | | |
| *Archaeozonites costatus* Sandberger, 1875 | | xxx | xx | | | |
| Clausiliinae indet. | | | xx | | | |
| *Cochlicopa loxostoma* (Klein, 1853) | x | xxx | x | | | |
| *Deroceras* sp. | | | x | | | |
| *Discus pleuradrus* (Bourguignat, 1881) | | xxx | x | | | |
| *Ferrissia deperdita* (Desmarest, 1814) | x | | xx | xx | x | |
| *Gastrocopta* cf. *acuminata* (Klein, 1846) | | x | | | | |
| *Gastrocopta sandbergeri* Stworzewicz & Prisyazhnyuk, 2006 | | x | | | | |
| *Granaria* sp. | | xxx | xx | xx | | |
| *Gyraulus kleini* (Gottschick & Wenz, 1916) | x | | xx | xx | x | |
| *Helicodonta involuta* (Thomä, 1845) | | xx | x | | | |
| *Leucochroopsis kleini* (Klein, 1846) | x | xxx | xx | xx | | |
| *Lymnaea* cf. *dilatata* (Noulet, 1854) | xx | x | x | xx | | |
| *Milax* sp. | | | x | | | |
| *Negulopsis lineolata* (Sandberger, 1872) | | x | | | | |
| *Opeas* cf. *minutum* (Klein, 1853) | | x | | | | |
| *Palaeoglandina gracilis* (von Zieten, 1830) | x | x | | | | |
| *Palaeomastus filocinctus* (Reuss, 1861) | | x | | | | |
| *Palaeotachea renevieri* (Maillard, 1892) | | xx | | | | |
| *Palaeotachea silvana* (Klein, 1853) | ? | xx | x | | | |
| *Planorbarius mantelli* (Dunker, 1848) | x | | xx | xx | x | x |
| *Pomatias conicus* (Klein, 1853) | x | xxx | xxx | | | xx |
| *Praeoestophorella phacodes* (Thomä, 1845) | | xxx | x | | x | |
| *Pseudochloritis incrassata* (Klein, 1853) | | xx | | | | |
| *Pseudoleacina eburnea* (Klein, 1853) | | xxx | | | | |
| *Testacella zellii* Klein, 1853 | | | x | | | |
| *Triptychia kleini* Schnabel, 2006 | | | x | | | |
| *Triptychia randeckiana* (Kranz, 1908) | | x | xx | | | |
| ?*Truncatellina sp.* | | x | | | | |
| *Vallonia* cf. *lepida* (Reuss, 1849) | | x | | | | |
| *Vitrina suevica* Sandberger, 1875 | | xx | | | | |

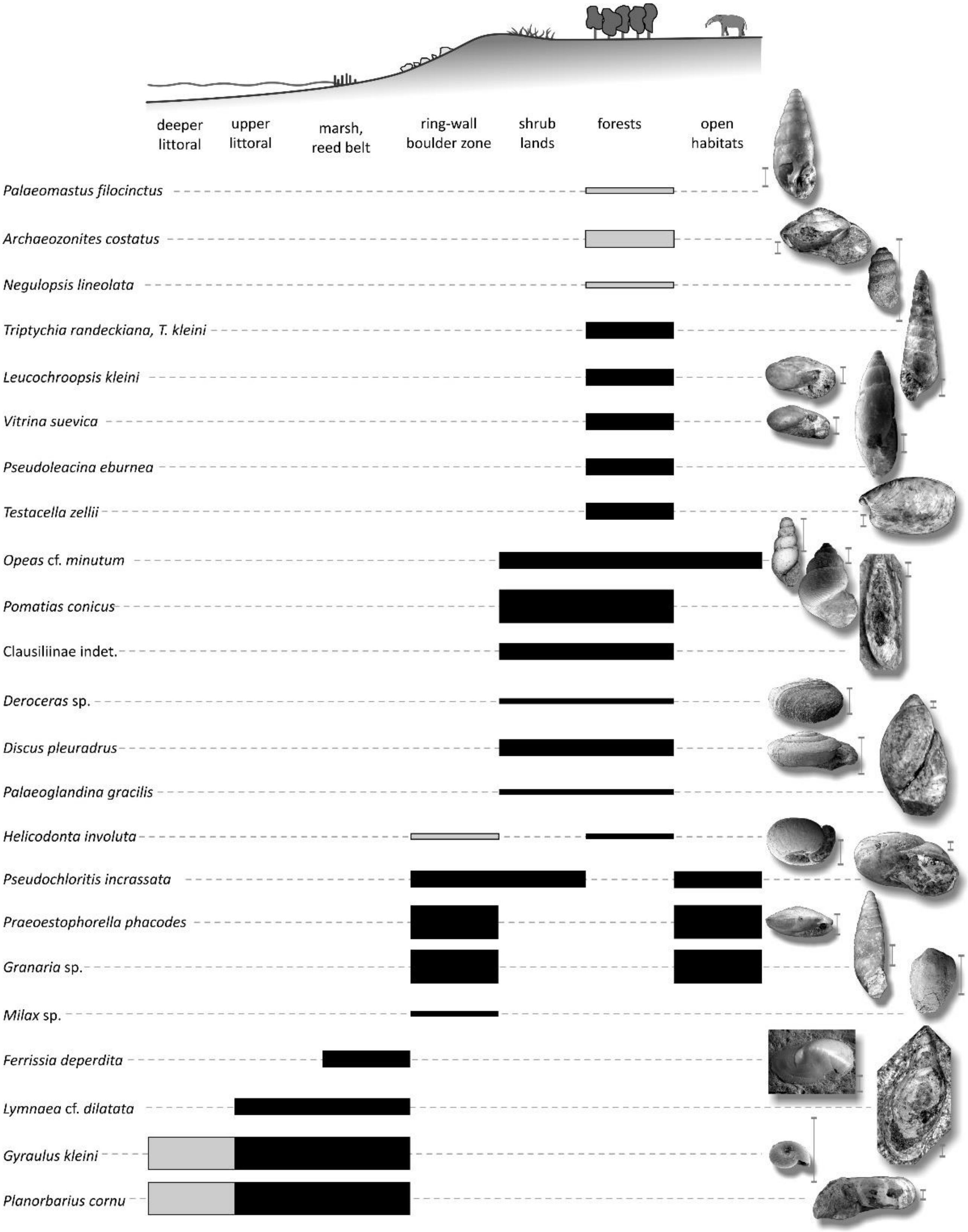

**Figure 7.** Paleohabitats of the gastropods from Lake Randeck Maar and its hinterland. Scale bars = 2mm. Thickness of bar reflects the general abundance of the species: thin bar, <10 individuals; medium bar, >10; thick bar, >200. The light grey bars indicate more uncertainty in the paleoecological interpretations. Image reproduced from Rasser et al. (submitted).

## 4.3. Riedensheim and Adelschlag-Fasanerie

Seventeen and 35 gastropod species (almost exclusively pulmonates) were foundin Adelschlag-Fasanerie and Riedensheim, respectively (Salvador et al., 2016b); thirteen species are shared by both assemblages (Table 4). Of these, the following species have their distribution reasonably expanded: *Azeca peneckei*, *Carychium (Carychium) galli*, *Vitrea ammoni* and *Urticicola perchtae*; and possibly *Stagnicola* cf. *praebouiletti* and *Truncatellina* cf. *pantherae*. The nomenclature of the species *Negulopsis suturalis* (Sandberger, 1858) was corrected; the accepted name is *Negulopsis lineolata* (Sandberger, 1872).

**Table 4.** Occurrence of fossil gastropod species (and total number of specimens recovered) on each site and layer (an "*" indicates that the number refers to opercula). The horizontal lines delimitates the groups Caenogastropoda, Basommatophora and Eupulmonata, in this order.

| | **Adelschlag-Fasanerie** | | | **Riedensheim** | | |
|---|---|---|---|---|---|---|
| **Species** | **limestone** | **clay** | **sand** | **1** | **2** | **4** |
| *Bithynia* sp. | | | 6* | 6* | 1* + 1 | |
| *Pseudamnicola suevicus* (Gottschick, 1928) | | 16 | | | | >30 |
| *Pomatias* sp. | | | | | 1* | |
| *Ferrissia deperdita* (Desmarest, 1814) | | | | 2 | 1 | |
| *Galba dupuyiana* (Noulet, 1854) | | >30 | | >30 | >40 | >50 |
| *Gyraulus albertanus* (Clessin, 1877) | | >20 | | 15 | >30 | >20 |
| *Gyraulus applanatus* (Thomä, 1845) | | >80 | 8 | >20 | >50 | >120 |
| *Hippeutis subfontanus* (Clessin, 1877) | | | | | | 5 |
| *Lymnaea* cf. *dilatata* Noulet, 1854 | 8 | | | 14 | 1 | 19 |
| *Planorbarius cornu* (Brongniart, 1810) | >30 | >40 | 5 | >20 | >30 | >50 |
| *Stagnicola* cf. *praebouiletti* (Schlickum, 1970) | | | | | 1 | |
| *Archaeozonites* sp. | | | | | 2 | 6 |
| *Azeca peneckei* Andreae, 1892 | | | | | | >30 |
| *Carychium eumicrum* Bourguignat, 1857 | | | | | | 5 |
| *Carychium galli* Salvador, 2015 | | 12 | | 2 | 7 | >100 |
| *Carychium nouleti* Bourguignat, 1857 | | 6 | | | | |
| *Deroceras* sp. | | | 4 | | 1 | 4 |
| *Discus pleuradrus* (Bourguignat, 1881) | | 12 | | | 4 | >80 |
| *Gastrocopta acuminata* (Klein, 1846) | | 4 | | | 2 | >40 |
| *Gastrocopta nouletiana* (Dupuy, 1850) | | | | | | >100 |
| *Granaria* sp. | | 2 | | | 1 | 10 |
| *Leucochroopsis* sp. | | | | | 5 | 5 |
| *Megalotachea silvana* (Klein, 1853) | | | 1 | | | |
| *Negulopsis lineolata* (Sandberger, 1872) | | | | | | 1 |
| *Oxyloma minima* (Klein, 1853) | | 2 | | | | 8 |
| *Palaeotachea renevieri* (Maillard, 1892) | | | 1 | | | |
| *Pseudidyla moersingensis* (Boettger, 1877) | | | | 9 | >20 | >100 |
| *Pseudochloritis* sp. | | | | 9 | 5 | 11 |
| *Pseudoleacina* sp. | | | | | | 1 |
| *Strobilops costata* (Clessin, 1877) | | | | | | 8 |
| *Strobilops uniplicata* (Braun *in* Walchner, 1851) | | | | | 1 | |
| *Testacella* sp. | | | | | | 3 |
| *Truncatellina* cf. *pantherae* Harzhauser & Neubauer *in* Harzhauser et al. 2014 | | | | | | 3 |
| *Vertigo angulifera* Boettger, 1884 | | | | | | 13 |
| *Vertigo callosa* (Reuss, 1849) | | 2 | | | | |
| *Urticicola perchtae* Salvador, 2013 | | | | | | 2 |
| *Vitrea ammoni* (Clessin, 1894) | | | | 1 | 3 | >80 |
| *Vitrina suevica* Sandberger, 1872 | | | | | | 2 |

The fauna from Adelschlag-Fasanerie, much impoverished in comparison to Riedensheim. The basal layers points to a carbonate-rich freshwater lake, which went through gradual shallowing. The depositional system thus indicates the transition from a flood plain environment that was rapidly covered by fluvial channel deposits. As in Riedensheim, the presence of the hygrophilous genera *Carychium* and *Oxyloma* seem to indicate a well-vegetated area surrounding the water body and the terrestrial *Discus* is a reasonable indicator of humid forests.

The fossil-bearing strata of Riedensheim probably represent oxbow lakes or floodplain ditches in which the aquatic gastropods lived and the land snails were deposited at river highstands or during flash floods. The basal layers exhibit a rich freshwater gastropod community living in stagnant or slow moving waters. The appearance of *Hippeutis* in the topmost layer of the fossil-bearing strata, as well as the upward increase in land snail diversity, could point to a shallowing of the water body.

The abundance of the diminutive and fragile *Carychium galli* and *Oxyloma minima* seems to point to a very richly vegetated and humid area. The vast majority of land snail species are inhabitants of humid (and usually warm) forests: *Discus*, *Vitrina*, *Pseudoleacina*, *Pseudidyla*, *Leucochroopsis* and *Archaeozonites*. Eventual patches of more open rocky or grassland areas should have existed beyond that, as indicated by *Granaria*, *Truncatellina* and supposedly *Pseudochloritis*.

A study of the stable carbon and oxygen isotopes of the shells from these localities is currently underway, using the same species as for Sandelzhausen (see Section 4.1 above).

## 4.4. Biberach, Ravensburg and Neu-Ulm

In total, 20 species of gastropods and bivalves were found in the material (Salvador et al., 2015b); their occurrence for each of the sites can be seen in Table 5. Sach (1999) presented a paleoenvironmental interpretation of the fossiliferous horizons of the Biberach district, proposing a large meandering river system surrounded by alluvial and gallery forests. This interpretation was based upon the cross-stratification lithology of the finely grained sandy sediments and on the evaluation of the fossil remains found, especially mammals, fishes, turtles and mollusks.

Shells of freshwater mollusks would have been concentrated by the streams' waters, while periodical floods would have transported the shells of terrestrial snails from the neighboring area into the river system. The calcareous sediments (marls and freshwater limestones present on some sites), however, were calmly deposited in the stagnant waters of ponds and small lakes. A very similar fluvial environment of meandering rivers, still water habitats and neighboring alluvial forests can also be assumed for the fossiliferous horizons in the districts of Ravensburg and Neu-Ulm. The molluscan freshwater fauna is consistent with these interpretations.

In the immediate vicinity of the water bodies, there were humid alluvial and gallery forests that went through periodical floods (Sach, 1999). These forests would have provided favorable conditions for the land snails. There is also indication, mainly based on plant and mammal remains, of drier forests and open areas (Sach, 1999), but, despite snails of such habitats being rather common in coeval sites, there is no such fauna in the present material.

**Table 5.** Molluscan species occurring in the middle Miocene fossil sites of the districts of Biberach, Ravensburg and Neu-Ulm. Fossil sites (names according to Sach, 1999, 2014): **A**, Wannenwaldtobel 1 and 2; **B**, Tobel Oelhalde-Nord; **C**, Tobel Oelhalde-Süd; **D**, Edelbeuren-Schlachtberg; **E**, Binnrot; **F**, Bonlanden; **G**, Edelbeuren-Maurerkopf; **H**, Heselsberg; **I**, Auttagershofen; **J**, Burgerbachtobel 1; **K**, Schmalegger Tobel; **L**, Lattentobel; **M**, Altenstadt-Untereichen. Number of specimens found (collection not controlled for quantitative analysis): **x**, 1-10 specimens; **xx**, 11-60 specimens; **xxx**, >60 specimens. An "**S**" indicates a species listed by Sach (1999, 2014) that could not be found in the material (fossils were too fragmentary and were not collected or kept).

| | **Biberach** | | | | | | | | | **Ravensburg** | | | **Neu-Ulm** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **A** | **B** | **C** | **D** | **E** | **F** | **G** | **H** | **I** | **J** | **K** | **L** | **M** |
| CAENOGASTROPODA | | | | | | | | | | | | | |
| *Bithynia* sp. | | | | | | | xxx | | S | | | | |
| *Pomatias* sp. | | | | | | | | | | x | | | |
| *Tinnyea laureae* (Mathéron, 1843) | | | | | | | | | | | | | x |
| NERITIMORPHA | | | | | | | | | | | | | |
| *Theodoxus* sp. | | | | | | | | | | | | | x |
| HYGROPHILA | | | | | | | | | | | | | |
| *Galba* cf. *dupuyiana* (Noulet, 1854) | xxx | | | | | | x | | x | | | | |
| *Gyraulus applanatus* (Thomä, 1845) | xxx | | | | | | x | | | | | | |
| *Lymnaea dilatata* (Noulet, 1854) | x | | x | | | x | xxx | x | | x | | | x |
| *Planorbarius mantelli* (Dunker, 1848) | x | x | x | x | | x | xxx | | | | | | x |
| STYLOMMATOPHORA | | | | | | | | | | | | | |
| *Archaeozonites costatus* Sandberger, 1875 | | | | x | x | | x | | | | | | x |
| Clausiliidae indet. | | | | | | | x | | | | | | |
| *Deroceras* sp. | x | | | S | | xx | xxx | | | xx | | | |
| *Klikia* sp. | | | | | | S | xxx | x | | S | | | x |
| *Opeas minutum* (Klein, 1853) | | | | | | | x | | | | | | |
| *Palaeotachea renevieri* (Maillard, 1892) | | xx | xx | | | xx | xx | x | x | x | | | |
| *Palaeotachea silvana* (Klein, 1853) | xx | xx | xx | xx | x | xx | xxx | x | x | x | | | xx |
| *Pseudochloritis incrassata* (Klein, 1853) | x | x | x | xx | x | | xxx | x | | S | x | | x |
| *Triptychia* sp. | | | | | | | x | | | | | | |
| BIVALVIA | | | | | | | | | | | | | |
| *Margaritifera flabellata* (Goldfuss, 1837) | x | x | x | x | x | x | x | x | | x | x | x | x |
| *Sphaerium* aff. *rivicola* (Lamarck, 1818) | | | | | x | | | | | | | | |
| *Unio kirchbergensis* Krauss, 1852 | | | | | | | | | | | | | x |

## 4.5. Gündlkofen

Following the revision (Salvador, 2014), 20 species are listed for Gündlkofen. Operculate snails: *Bithynia* sp. and *Pomatias consobrina* (Sandberger, 1875). Pulmonata: *Apula* cf. *coarctata* (Klein, 1853), *Archaeozonites* sp., *Azeca* cf. *lubricella* Boettger, 1870, Clausiliidae indet. (possibly *Pseudidyla* sp.), *Deroceras* sp., *Discus* sp., *Granaria* sp., *Gyraulus* sp., *Lucilla subteres* (Clessin, 1877), *Palaeoglandina gracilis* (von Zieten, 1830), *Palaeotachea* cf. *eversa* (Deshayes, 1851), *Palaeotachea* cf. *sylvestrina* (Schlotheim, 1820), *Pseudochloritis* cf. *incrassata* (Klein, 1853), *Pseudoleacina* sp., *Testacella schuetti* Schlickum, 1967, *Triptychia* sp., Gastrodontoidea indet.

The molluscan fauna from Gündlkofen is remarkable for the near absence of freshwater species: only a single *Gyraulus* sp. and three opercula of *Bithynia* sp. were recovered. These genera are usually related to still waters, which, together with lithological features, led Gall (1980) to propose that Gündlkofen represents an environment like an oxbow lake.

The terrestrial snails of Gündlkofen were defined as a relatively hygrophilic assemblage by Gall (1980). The present work agrees with this statement, since most of the genera prefer conditions that are more humid. The area seems to have been covered with a damp and warm forest and scrubland (Gall, 1980). Nevertheless, a few species more oriented towards drier or rockier environments (*Pseudochloritis* cf. *incrassata*, *Granaria* sp., and perhaps *Paleotachea* cf. *eversa* and *Palaeoglandina gracilis*) occur in a considerable number, possibly indicating a variety of habitats near the site.

## 4.6. Oggenhausen

After the revision, six gastropod species are known from Oggenhausen 1, and 13 from Oggenhausen 2 (Table 6; Salvador & Rasser, 2016b). For the latter, there are new records: *Gyraulus applanatus*, *Megalotachea silvana*, *Palaeotachea renevieri*, *Granaria* sp., *Gastrocopta acuminata* and ?*Truncatellina* sp. There could be some degree of preservation bias in Oggenhausen 2, since the more extensive and careful collection undertook there did not recovered microgastropods.

As remarked by Berz & Jooss (1927), the snail fauna from Oggenhausen 1 is unusual for its lack of freshwater species (with the exception of *Tinnyea lauraea*). This fact, allied to the lack of microgastropods and the poor and often fragmentary preservation of the larger specimens, led Berz & Jooss (1927) to propose rough transport conditions. Oggenhausen 2 shows better preservation and the usual freshwater taxa found in other German OSM sites.

Böttcher et al. (2009) proposed that the deposits of Oggenhausen 2 could be interpreted as a shallow lake (or possibly an oxbow lake formed by the river that deposited Oggenhausen 1), surrounded by lush vegetation. The scarce snail fauna does not add much information, since the genera recorded from the sites are not very useful for a paleoecological analysis. Regardless, the freshwater genera are consistent with slow-flowing or stagnant waters, while the terrestrial *Discus* and *Urticicola* are consistent with lusher and more humid vegetation.

**Table 6.** Species recorded for each site. The "?" indicates unconfirmed records of Berz & Jooss (1927).

| **Species** | **Oggenhausen 1** | **Oggenhausen 2** |
|---|---|---|
| CAENOGASTROPODA | | |
| *Pomatias conicus* (Klein, 1853) | x | |
| *Tinnyea lauraea* (Mathéron, 1843) | x | |
| HYGROPHILA | | |
| *Galba dupuyiana* (Noulet, 1854) | | x |
| *Gyraulus applanatus* (Thomä, 1845) | | x |
| *Lymnaea* cf. *dilatata* (Noulet, 1854) | | x |
| *Planorbarius mantelli* (Dunker, 1848) | | x |
| STYLOMMATOPHORA | | |
| *Archaeozonites* sp. | x | |
| *Discus pleuradrus* (Bourguignat, 1881) | | x |
| *Gastrocopta acuminata* (Klein, 1846) | ? | x |
| *Gastrocopta nouletiana* (Dupuy, 1850) | | x |
| *Granaria* sp. | | x |
| *Megalotachea silvana* (Klein, 1853) | x | x |
| *Palaeotachea renevieri* (Maillard, 1892) | x | x |
| *Pseudochloritis incrassata* (Klein, 1853) | x | x |
| *Triptychia kleini* Schnabel, 2006 | ? | |
| ?*Truncatellina* sp. | | x |
| *Urticicola perchtae* Salvador, 2013 | | x |

## 4.7. Bechingen and Daugendorf

In total, 19 gastropod species were found in Bechingen and 11 Daugendorf (Table 7; Salvador & Rasser, 2016a). Moreover, external molds from Daugendorf could belong to *Granaria* and *Archaeozonites*. A few authors had already referred to single species from Bechingen (Jooss, 1910, 1918; Gottschick, 1911; Fischer & Wenz, 1914; Wenz, 1923; Schlickum, 1976), but the vast majority of species reported here are new. Daugendorf was never reported in the literature, so all its records are new. *Pseudoleacina eburnea* (Klein, 1853) and *Janulus supracostatus* (Sandberger, 1872) were not found in Bechingen, contrary to former authors.

**Table 7.** List of species recorded from Bechingen and Daugendorf. An "?" indicates a doubtful identification based on external molds.

| **Species** | **Bechingen** | **Daugendorf** |
|---|---|---|
| CAENOGASTROPODA | | |
| *Bithynia glabra* (von Zieten, 1832) | x | |
| *Pomatias* cf. *conicus* (Klein, 1853) | x | |
| *Tinnyea* cf. *lauraea* (Mathéron, 1843) | x | |
| HYGROPHILA | | |
| *Ferrissia deperdita* (Desmarest, 1814) | x | |
| *Gyraulus applanatus* (Thomä, 1845) | x | x |
| *Lymnaea dilatata* (Noulet, 1854) | x | x |
| *Planorbarius mantelli* (Dunker, 1848) | x | x |
| *Radix socialis* (von Zieten, 1830) | x | |
| STYLOMMATOPHORA | | |
| *Apula coarctata* (Klein, 1853) | x | x |
| *Archaeozonites* sp. | | ? |
| *Discus pleuradrus* (Bourguignat, 1881) | x | x |
| *Gastrocopta* cf. *acuminata* (Klein, 1846) | x | x |
| *Granaria* sp. | | ? |
| *Hypnophila loxostoma* (Klein, 1853) | x | |
| *Klikia giengensis* (Klein, 1846) | x | |
| *Leucochroopsis kleinii* (Klein, 1846) | x | x |
| *Opeas minutum* (Klein, 1853) | x | x |
| *Oxyloma minima* (Klein, 1853) | x | |
| *Palaeoglandina gracilis* (von Zieten, 1830) | x | |
| *Palaeotachea silvana* (Klein, 1853) | x | x |
| *Praeoestophorella phacodes* (Thomä, 1845) | | x |
| *Pseudochloritis incrassata* (Klein, 1853) | x | x |

Werner (2014) proposed for the Tautschbuch region a paleoenvironment consisting of shallow temporary lakes or ponds surrounded by reeds. Despite the snail fauna being scarce, it agrees with this scenario. The freshwater snails indicate richly vegetated, stagnant or slow moving water. *Ferrissia* is a typical inhabitant of reed-belts. *Oxyloma* species are hygrophilous, living in humid forests and meadows, but often found in reed belts. Among the terrestrial snails, *Opeas*, *Leucochroopsis*, *Archaeozonites* and *Discus* are indicative of humid warm woods. *Pomatias* would have thrived in humid forests and shrublands, while *Psedochloritis* and *Granaria* indicate drier and more open habitats.

## 4.8. Eastern Bavaria

In total, 24 species of terrestrial and freshwater gastropods were found (Salvador et al., 2016a); their stratigraphical distribution can be seen on Table 8. We provided remarks on the taxonomy of some species, including a revision of *Theodoxus cyrtocelis* (Krauss, 1852), *T.*

*obstusangula* (Krauss, 1852) and *T. sparsus* (Krauss, 1852); the latter can be considered a synonym of *T. cyrtocelis*. Moreover, the stratigraphic range of *Ctyrokya conoidea* was increased to also include the upper Kirchberg Formation.

**Table 8.** List of species found and their general stratigraphical occurrence (considering all boreholes together). The presence of *Nematurella bavarica* and *Ctyrokya conoidea* in the OSM is interpreted as reworked material from older OBM layers (see Salvador et al., 2016a). Abbreviations: GF, Grimmelfingen Formation; lKF, lower Kirchberg Formation; uKF, upper Kirchberg Formation.

| | | **OBM** | | | |
|---|---|---|---|---|---|
| **Species** | **OSM** | **uKF** | **lKF** | **GF** | **USM** |
| CAENOGASTROPODA | | | | | |
| *Bithynia glabra* (von Zieten, 1830) | x | x | x | x | x |
| *Ctyrokya conoidea* (Krauss, 1852) | ? | x | x | | |
| *Hydrobia semiconvexa* Sandberger, 1875 | | x | x | | |
| *Melanopsis impressa* Krauss, 1852 | | x | x | | |
| *Nematurella bavarica* Sandberger, 1875 | ? | x | x | x | |
| *Tinnyea lauraea* (Mathéron, 1843) | | x | x | | |
| ?*Truncatella* sp. | | | x | | |
| *Viviparus* cf. *suevicus* Wenz, 1919 | | | x | | |
| NERITIMORPHA | | | | | |
| *Theodoxus cyrtocelis* (Krauss, 1852) | x | x | x | x | x |
| *Theodoxus obtusangula* (Krauss, 1852) | | | x | | |
| HETEROBRANCHIA | | | | | |
| ?*Valvata* sp. | | x | x | | |
| HYGROPHILA | | | | | |
| *Ferrissia* cf. *wittmanni* (Schlickum, 1964) | | x | | x | |
| *Gyraulus albertanus* (Clessin, 1877) | x | x | | x | |
| *Gyraulus applanatus* (Thomä, 1845) | x | x | x | x | x |
| *Lymnaea dilatata* (Noulet, 1854) | x | x | | x | x |
| *Planorbarius mantelli* (Dunker, 1848) | x | x | x | x | x |
| *Stagnicola armaniacensis* (Noulet, 1857) | x | x | x | x | x |
| *Stagnicola praebouilleti* Schlickum, 1970 | | x | | x | |
| EUPULMONATA | | | | | |
| *Archaeozonites* sp. | | x | | | |
| *Carychium* cf. *galli* Salvador, 2015 | | | | x | |
| ?*Discus* sp. | | | | x | x |
| *Leucochroopsis* sp. | | x | | | |
| *Megalotachea* cf. *silvana* (Klein, 1853) | x | x | | x | |
| *Palaeotachea* sp. | | | | | x |

Finally, some specimens of *Nematurella bavarica* and *Stagnicola armaniacensis* showed a circular hole on their body whorls (Fig. 8). These holes are consistent with those reported by Rasser & Covich (2014) for the freshwater snails of Steinheim am Albuch (Middle Miocene, SW Germany), related to predation by cyprinid fishes. These ichnofossils are studied in more detail by Rasser et al. (in press), who describe them as a new ichnospecies of the ichnogenus *Nihilichnus* Mikuláš et al. 2006.

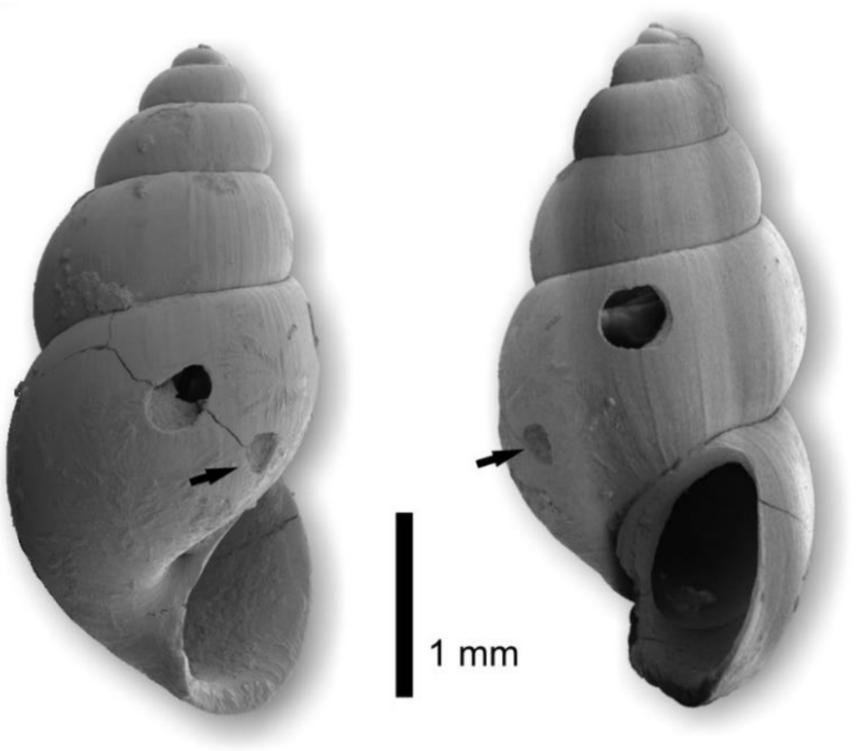

**Figure 8.** The trace fossil *Nihilichnus* sp. nov. in shells of *Nematurella bavarica* (LfU-SPR2014-041); the arrows show the initial stage of an unfinished hole. Image reproduced, with modifications, from Rasser et al. (in press).

Some paleoecological interpretations for each unit (USM, OBM and OSM) are presented below, based on the recovered gastropod fauna.

**USM:** The molluscan fauna is composed mainly of freshwater snails, related to richly-vegetated standing or slow-flowing waters. The scarce land snails material indicate a hot humid temperate to sub-tropical climate and a reasonably well-vegetated area. This scenario fits the few previous studies that have dealt with the paleoecology of the USM (*e.g.*, Reichenbacher & Weidmann, 1992; Reichenbacher, 1996; Schäfer, 2005, 2011; Weidmann et al., 2014).

**OBM (Grimmelfingen Fm.):** These beds have a fauna more typical of freshwater environments, as indicated by the richness and abundance of freshwater species: *Bithynia*, *Theodoxus* and the basommatophoran pulmonates. Almost all previous reports on the paleoenvironment of this formation refer to marine or brackish faunal elements (Reichenbacher et al., 1998, 2013; Sach & Heizmann, 2001). The gastropods indicate that the environment may have been much less brackish and estuarine than previously thought: either freshwater or of very low salinity levels. On land, the gastropods *Carychium*, *Archaeozonites* and *Leucochroopsis* are indicatives of humid forests.

**OBM (lower Kirchberg Fm.):** The molluscan fauna of these layers is very different to that of the Grimmelfingen Fm., likely indicating changes in the environmental conditions.

These beds “lose” much of its pulmonate aquatic fauna and shows the richest operculate snail fauna of all layers studied (Table 8). The typical brackish fauna includes the hydrobiids, possibly ?*Truncatella* sp. and several brackish water bivalves (not studied here, but known from previous reports, *e.g.*, Schlickum, 1963; Reichenbacher, 1989). The environment is thus interpreted as low brackish to brackish, since the salinity levels still would have to allow the scarce pulmonate snails, alongside *Bithynia*, *Theodoxus* and *Viviparus*. This is consistent with suggestions based on the fish fauna (Reichenbacher, 1993).

**OBM (upper Kirchberg Fm.):** In general, these layers have a fauna of operculate snails similar to the lower levels, but, at the same time, have a more diverse basommatophoran fauna. This should indicate a fully or nearly freshwater environment. A similar assumption has previously been presented based on the microfossil-assemblages and especially the fish otoliths (Reichenbacher, 1989, 1993). There are some differences regarding the distinct boreholes, however. The freshwater snails of the northeasternmost boreholes (Druisheim, Gempfing and Hamlar 1; Fig. 2) are more commonly related to brackish environments (similar to the lower Kirchberg Fm.), while the remaining southwestern localities possessed fully or nearly freshwater environments.

**OSM:** Here, most operculate snails disappear, causing the diversity of aquatic species to greatly decrease. This is consistent with other faunas from the German OSM (*e.g.*, Salvador & Rasser, 2014; Salvador et al., 2015, 2016b). Most of the species present prefer richly-vegetated standing or slow-moving waters.

## 4.8. Paleobiogeography

Continental gastropods, especially the pulmonates, are a crucial faunal element in Miocene continental deposits. Despite their abundance in the European fossil record, however, only few attempts have been made to study them from a paleobiogeographical point of view. As such, our investigation focused on well-known (and gastropod-rich) deposits of the Middle Miocene (MN 4–5 to 7–8) of Central Europe, with special emphasis on the OSM localities. We compared the land snail faunas of 28 distinct localities (Table 9; Fig. 9).

The chosen localities all counted with at least eight different terrestrial gastropod species and had a published species list (see Höltke et al., submitted, for a full account of the literature used and the full list of species, totaling 109). Likewise, data on the age of the sediments of each locality comes from the most up-to-date publications. The gathered dataset was subject to two types of analyses: (1) cluster analysis, and (2) non-metric multidimensional scaling (NMDS; not shown here). For both types, two distinct similarity matrices, Kulczynski (1927) and Ochiai (1957), were used for the presence-absence data of the species in order to test for stability of the groupings. The analyses were carried out in PAST 2.17c (Hammer et al., 2001).

**Table 9.** List of all localities used for the paleobiogeographical analysis, alongside their MN age.

| Locality | Country | Age | Locality | Country | Age |
|---|---|---|---|---|---|
| Adelschlag-Fasanierie | Germany | MN 5 | Lake Rein | Austria | MN 5 |
| Altheim (near Ehingen) | Germany | MN 5 | Mátraszőlős | Hungary | MN 7 |
| Amstetten-Stubersheim | Germany | MN 4-5 | Mörsingen | Germany | MN 5 |
| Bakony Mts C | Hungary | MN 5 | Oggenhausen | Germany | MN 5 |
| Bakony Mts D | Hungary | MN 5-6 | Opole | Poland | MN 7 |
| Bakony Mts E | Hungary | MN 6 | Pfänder | Austria | MN 5 |
| Bakony Mts F | Hungary | MN 7-8 | Randeck Maar | Germany | MN 5 |
| Bechingen | Germany | MN 5 | Riedensheim | Germany | MN 5 |
| Bełchatów | Poland | MN 5-6 | Sandelzhausen | Germany | MN 5 |
| Gratkorn Basin | Austria | MN 7-8 | Sansan | France | MN 6 |
| Gündlkofen | Germany | MN 5-6 | Steinheim | Germany | MN 7 |
| Harthausen auf der Scheer | Germany | MN 4-5 | Stoffelberg (near Ehingen) | Germany | MN 5 |
| Hohenmemmingen | Germany | MN 5 | Undorf | Germany | MN 5 |
| Korneuburg Basin | Austria | MN 5 | Zwierzyniec | Poland | MN 7-8 |

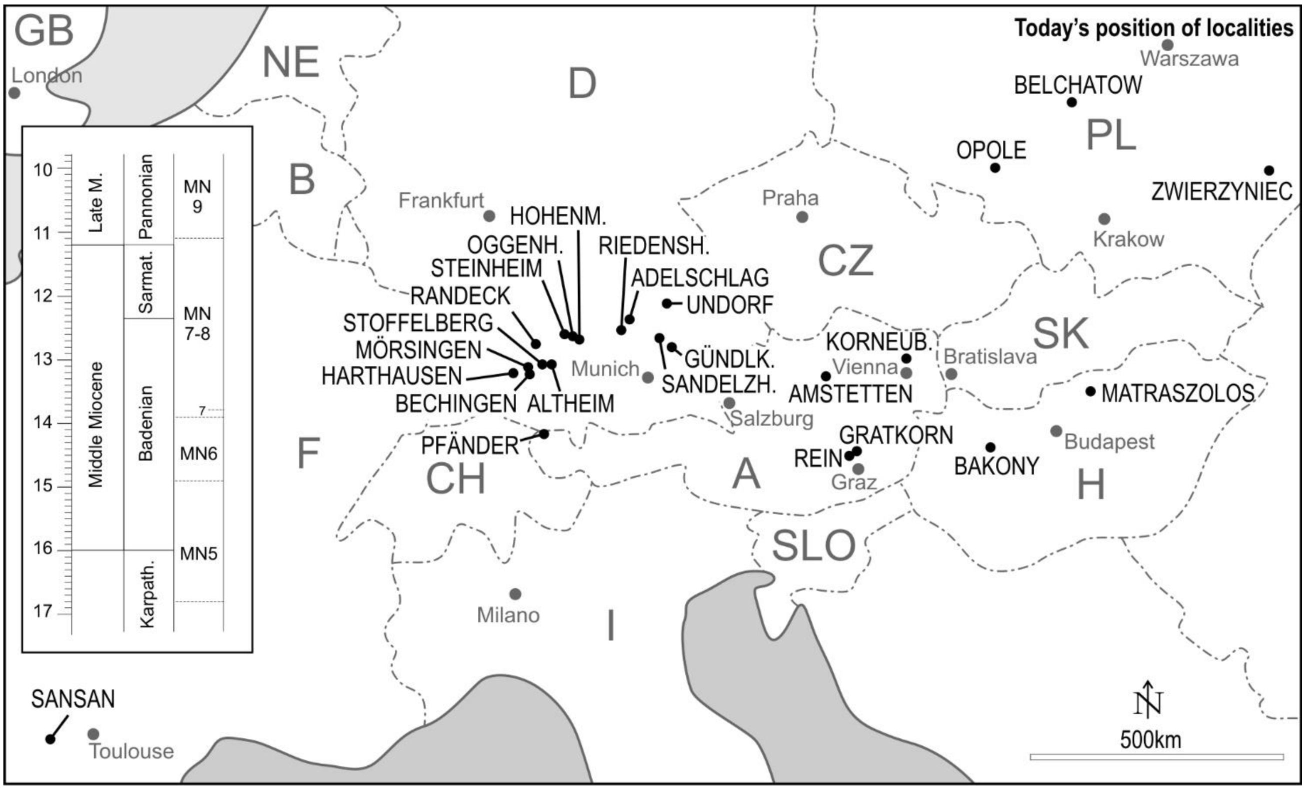

**Figure 9.** Localities used in the paleobiogeographical analysis. MN zones after Kälin & Kempf (2009).

For both cluster and NMDS analyses (and independent of the index used), the same grouping patterns were recovered. The single exception is that Korneuburger Basin is isolated on its own "cluster" by the Kulczynski index, while it is grouped with two others by the Ochiai index (Fig. 10). The focus here will be the OSM localities of southern Germany; a discussion encompassing all localities can be found in Höltke et al. (submitted).

As expected, the OSM localities form one all-embracing cluster, containing three well-defined groups within it (Clusters #4, 5 and 6 on Figure 10). Cluster #4 is an unexpected group composed of Steinheim am Albuch and two non-OSM localities, Zwierzyniec and Sansan. Since it is not related to the localities studied in this thesis, this cluster will not be further discussed here.

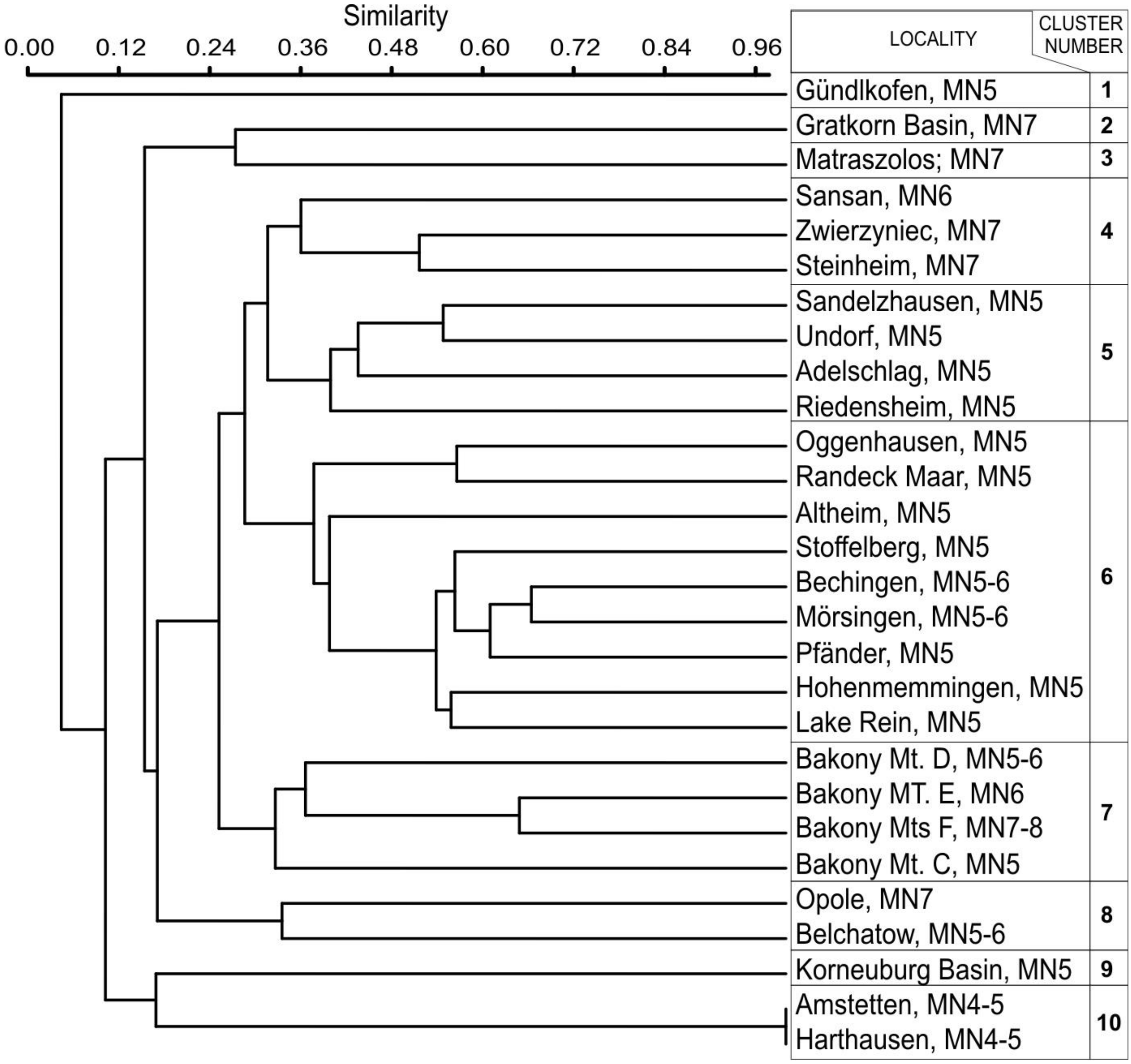

**Figure 10.** Result of the cluster analysis using the Ochiai index.

Clusters #5 and 6 are interesting because they clearly separate the localities of the two southern Germany states, Bavaria and Baden-Württemberg. Cluster #5 is a group composed of the Bavarian localities Riedensheim, Adelschlag-Fasanerie, Sandelzhausen and Undorf. This close relationship was already alluded to by Salvador et al. (2016b), on a more qualitative assessment of the faunas. However, the absence of the Bavarian OSM locality Gündlkofen is remarkable; it forms an outlying cluster (#1) of its own, well separated from the rest. This may be due to the following reasons: (1) only 9 different species are identified from there, which might bias the analysis; (2) Gündlkofen is the single OSM locality where some species occur (*e.g.*, *Testacella schuetti*); (3) as suggested by Gall (1980), the deposits of Gündlkofen could be reasonably younger (maybe MN 6) than the other Bavarian localities.

Cluster #6 is a group composed of all the OSM localities of Baden-Württemberg state and curiously, including Lake Rein (a non-OSM locality in Austria). The presence of Lake Rein is curious at first sight, but not completely unexpected, as it shares 18 species (from 33) with coeval OSM deposits.

# 5. Conclusion

During the deposition of OSM layers, southern Germany would have shown a warm temperate to subtropical (Mediterranean-like) climate. Some of the fossil gastropod genera (*e.g.*, *Azeca*, *Palaeomastus*, *Negulopsis*, *Janulus* and *Opeas*), as well as other components of the fossil fauna and flora (such as laurel forests) of these localities, also point to a similarity with the present day Mediterranean and subtropical climates such as seen on the Azores, the Madeiran Archipelago and Canary Islands (*e.g.*, Waldén, 1983; Press & Short, 1994; Capelo, 2004; Cameron et al., 2007; Seddon, 2008).

The favorable climate of Miocene Germany, culminating in the Mid-Miocene Climatic Optimum, alongside the often calcareous grounds, should have composed a welcoming scenario for continental snails. Neubauer et al. (2015) show that, for freshwater snails, species richness peaks at the Optimum, but no similar study has been done for land snails. In some of the fossil localities studied herein, the diversity of gastropods is astounding, often reaching 30–40 species. This is a large number, especially considering the small size of most localities and that many species likely have not been preserved in the fossil record. This number should be comparable to some Recent subtropical and tropical Old-World localities (*e.g.*, Cameron & Pokryszko, 2005, and references therein).

Although the several localities studied here share many species (especially the freshwater ones), some seem to be more closely related among themselves. Sandelzhausen, Riedensheim and Adelschlag-Fasanerie share more than half of their species with each other (and are also very similar to the nearby and possibly coeval Undorf locality). Gündlkofen, also geographically close, although sharing ca. 40% of its fauna with Sandelzhausen, is different enough to have been considered slightly younger by Gall (1980).

Randeck Maar, more geographically distant, while sharing several species, bears a more distinct assemblage. The material from the remaining localities (Oggenhausen, Bechingen, Daugendorf, Biberach, Ravensburg and Neu-Ulm) is too scarce to offer any meaningful comparison, but seem to be more closely related to Randeck Maar.

The terrestrial fauna of the OSM layers of the Eastern Bavaria boreholes is also too scarce for comparisons. Meanwhile, the freshwater OBM fauna of these same boreholes is less diverse than usually found in the literature, likely due to an inflation of species description leading to several synonymous names.

Finally, the series of studies that presented here argues for the greater strength of paleoecological analyses when based on a thorough taxonomic framework and integrated with complementary data, such as isotope analyses. As the paleoecological actualistic approach depends on data from Recent molluscan species, the isotope analysis of fossils would likewise greatly benefit from more systematical studies on extant species, investigating, for instance, differences in intraspecific shell isotope signal across distinct habitats and differences in composition among species of a higher taxa (*e.g.*, family-level) inhabiting similar habitats.

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# 7. Appendix

Here are presented all the articles deriving from my doctoral research, counting mostly with published papers, but also with three manuscripts. The first two manuscripts are presently submitted to the journal “*Palaeogeography, Palaeoclimatology, Palaeoecology*”, while the last one is submitted to the journal “*Paläontologische Zeitschrift*”. The published articles appear here exactly as they are in print, while the remaining three appear in manuscript form.

The supplementary material of Salvador et al. (2016a, 2016b) are originally available online only and thus are not presented here. They can be downloaded from the journals’ websites or from the following address: *https://rodrigobsalvador.wordpress.com/*

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# The fossil land and freshwater mollusks of Sandelzhausen (Early/Middle Miocene, Germany): Caenogastropoda, Neritimorpha, lower Heterobranchia and Bivalvia

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**Salvador R.B.** (2013)The fossil land and freshwater mollusks of Sandelzhausen (Early/Middle Miocene, Germany): Caenogastropoda, Neritimorpha, lower Heterobranchia and Bivalvia. *Strombus* 20(1-2): 19–26.

## ABSTRACT

Sandelzhausen is a rich Early/Middle Miocene (Mammal Neogene zone MN5) fossil site near Mainburg, Southern Germany. Hundreds of fossil continental mollusks, almost exclusively pulmonates snails, were recovered during the excavations, but never received due attention by researchers. Here, a taxonomical treatment of the non-pulmonate fossil mollusks from Sandelzhausen is presented, dealing with the Caenogastropoda, Neritimorpha, lower Heterobranchia and Bivalvia. The following species were found in the material: *Bithynia* sp. (Bithyniidae); *Pomatias* sp. (Pomatiidae); *Theodoxus* sp. (Neritidae); *Valvata* sp. (Valvatidae); *Sphaerium* sp. (Sphaeriidae). Unfortunately, the poor preservation of the material precludes a more precise identification.

**Keywords:** Burdigalian-Langhian, MN5 European Mammal Neogene zone, Mollusca, non-pulmonate snails, Upper Freshwater Molasse.

## INTRODUCTION

The Sandelzhausen fossil site is an important continental site in Europe that has yielded thousands of specimens (Moser *et al.* 2009a), among which there are numerous land and freshwater mollusks. Still, only two works dealt specifically with the mollusks: Gall (1972), who identified 49 gastropods and two bivalves in the material recovered, but based his work heavily on younger faunas and did not figure the specimens; and Moser *et al.* (2009b), who dealt with paleoecological questions, also presenting a very preliminary list of the species. Here is presented the taxonomic treatment of the non-pulmonate mollusks from Sandelzhausen, dealing with land and freshwater snails and bivalves. The pulmonate snails are treated elsewhere (Salvador 2013a, 2013b; Salvador & Rasser in preparation)

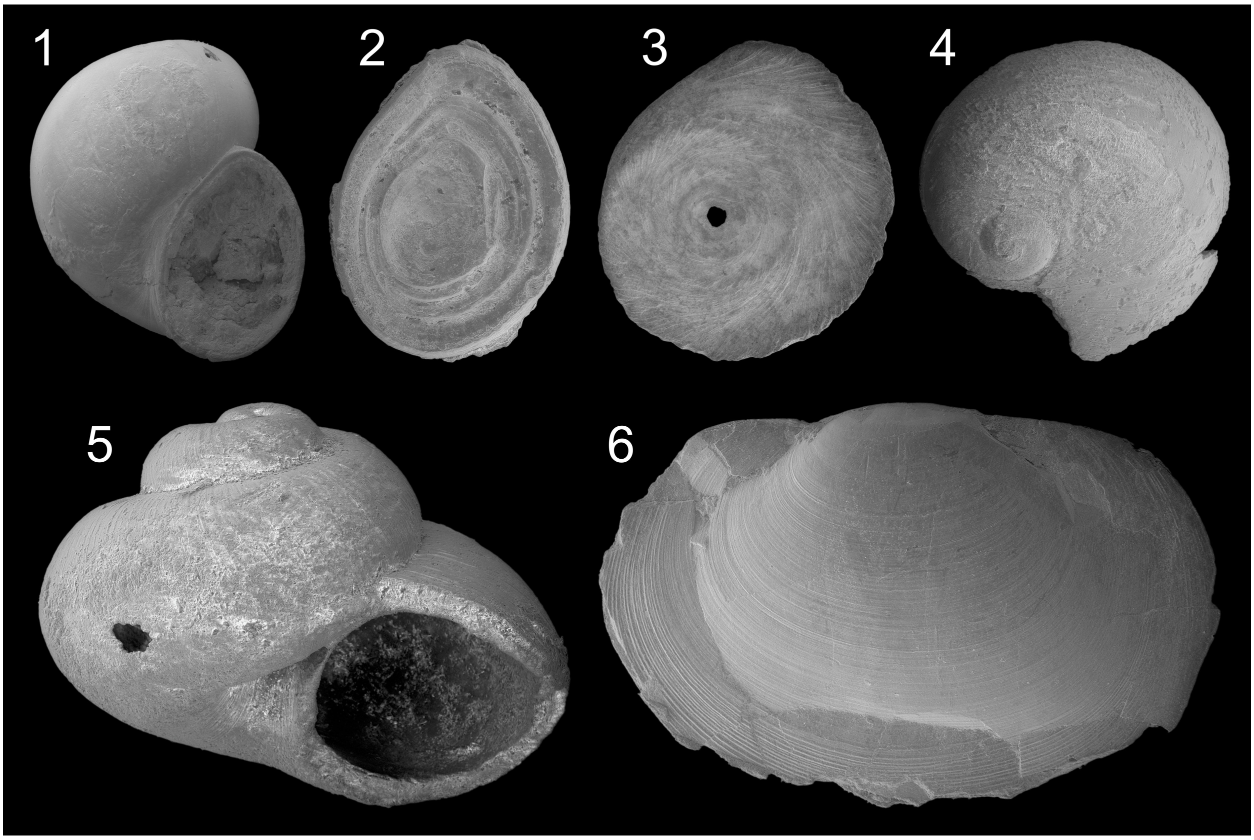

**Figure 1.** *Bithynia* sp., fragmentary specimen (BSPG 1959 II 17714; D = 3.7 mm). **Figure 2.** *Bithynia* sp., operculum (BSPG 1959 II 17715; h = 2.1 mm). **Figure 3.** *Pomatias* sp., operculum(BSPG 1959 II 17713; h = 8.7 mm). **Figure 4.** *Theodoxus* sp., fragmentary specimen (BSPG 1959 II 17716; D = 3.6 mm). **Figure 5.** *Valvata* sp., juvenile (BSPG 1959 II 17717; H = 1.6 mm). **Figure 6.** *Sphaerium* sp. (BSPG 1959 II 17720; L = 4.5 mm).

## GEOLOGICAL SETTING

Sandelzhausen fossil site was located in the vicinities of the city of Mainburg, 60 km north of Munich, in the Molasse Basin (Molassebecken) of southern Germany, which harbors the "formation" known as Upper Freshwater Molasse (Ober Süßwassermolasse, OSM; Moser *et al.* 2009a). The fossils from Sandelzhausen fossils belong to a member of the OSM called Nördlicher Vollschotter, composed primarily of marl and gravel (Moser *et al.* 2009a). The age of these deposits was established by stratigraphic, biostratigraphic and magnetostratigraphic correlations: the Early/ Middle Miocene Burdigalian/Langhian boundary (~16.47–16.27 Ma; Moser *et al.* 2009a), within the early middle MN5 European Mammal Neogene zone (corresponding to the Karpatian/Badenian boundary in terms of regional Paratethys stratigraphy; Harzhauser & Piller 2007).

The division into facies was established by Fahlbusch & Gall (1970) and Moser *et al.* (2009a): **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 pebbles diminish upwards, with intercalated sand horizons; origin of most macrovertebrate fossils; **Layer C:** fossil rich marl; divided in 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 carbonatic nodules; rich in fossils, many in excellent preservation state due to a less intense compaction; **Layer E:** silty clays with microvertebrate fossils; **Layer F:** laminite with alternating light and dark bands, carbonate concretions and desiccation cracks; no fossils. Fossil mollusks can be found from layer A to D.

For a more throughout description of the lithology of the site, see Moser *et al*. (2009a).

## MATERIAL AND METHODS

All the material from Sandelzhausen is housed in the collection of the Bayerische Staatssammlung für Paläontologie und Geologie (BSPG; Munich, Germany) under the record number BSPG 1959 II. All available material was examined in the present work; a list of the analyzed material can be found onthe species descriptions below. A portion of the material has data on the layer of origin, but the remaining either cannot be safely attributed to the layers or completely lack stratigraphical data (including the sample labeled as "Grube Bergmaier", or "pit Bergmaier" in English); for more information on this, refer to Salvador (2013a). As such, only the samples that can correctly be attributed to layers are used here to determine the stratigraphical range of the species. Moreover, here is also presented the previous identification of the material given by Gall (1972) and Moser *et al*. (2009b) in order to facilitate the correlation of the material for future workers.

Specimens in a good state of preservation were measured either with a digital caliper or with the aid of computer software. Selected specimens were examined by scanning electron microscopy (SEM) in the Staatliches Museum für Naturkunde Stuttgart (SMNS; Stuttgart, Germany). Shell measurements abbreviations: H = shell height; D = shell greatest width; h = aperture/operculum height; d = aperture/operculum width; L = shell length.

Unfortunately, part of the material described by Gall (1972) and Moser *et al*. (2009b) could not be found at the BSPG collection: *Pisidium* sp. (Gall 1972: Nr. 2; Moser *et al*. 2009b: Nr. 69) and Unionidae gen. indet. sp. nov. (Moser *et al*. 2009b: Nr. 67). Moser *et al*. (2009b) argued correctly that the specimen they analyzed and described (their fig. 9a) would be a new species, although the genus assignment remained doubtful. However, the only material present at the BSPG collection was the fragments of the left valve (BSPG 1959 II 12303; Moser *et al*. 2009b: fig. 9b).

## SYSTEMATICS

### Gastropoda

### Caenogastropoda

Family Bithyniidae

Genus *Bithynia* Leach, 1818

*Bithynia* sp.

(Figures 1–2)

**Material examined:** BSPG 1959 II 17714 (1 shell), 17715 (13 opercula).

**Stratigraphic occurrence:** The shell fragment comes from the Grube Bergmaier site, while the opercula lack stratigraphical data; nevertheless, Moser *et al*. (2009b) indicate Layers C2, C3 or D.

**Description:** Shell small. Teleoconch smooth. Whorl profile convex. Aperture oval, elongated, pointed at the upper portion. Peristome simple. Umbilicus imperforate. Operculum with concentric growth pattern.

**Measures (in mm):** BSPG 1959 II 17714 (incomplete specimen): D = 3.7; h = 2.9; d = 1.9.

**Previous identification of the material:** Gall (1972: Nr. 48 and 49): respectively, *Bithynia glabra glabra* (von Zieten) and *Bithynia* sp. Moser *et al.* (2009b: Nr. 5): *Bithynia* sp.

**Discussion:** Only a single shell fragment (and many opercula) is present in the material from Sandelzhausen. The whorl and aperture profile indicates the genus *Bithynia*. However, it is not possible to proceed further than genus level in the identification, since: (1) there seems to be some degree of morphological variation in each species; and (2) diagnostic features include not only aperture and body whorl but also suture, apex and shell profile, features not preserved in the present specimen. Recent *Bithynia* species live in richly vegetated slow moving or standing waters, some are also found in temporary water bodies (Welter-Schultes 2012).

### Family Pomatiidae

### Genus *Pomatias* Studer, 1789

### *Pomatias* sp.

(Figure 3)

**Material examined:** BSPG 1959 II 17713 (1operculum).

**Stratigraphic occurrence:**The material lacks stratigraphical data, but Moser *et al.* (2009b) indicate either Layer B or C1.

**Measures (in mm):** operculum, h = 8.7,d = 7.7.

**Previous identification of the material:** Gall (1972: Nr. 47): *Pomatias* sp. Moser *et al.* (2009b: Nr. 4): *Pomatias* sp.

**Discussion:** Only a single operculum was found in the material from Sandelzhausen. It belongs to the genus *Pomatias*, but further identification is not possible. Nevertheless, by its large size and number of whorls, this operculum likely belongs to *P. consorbina* (Sandberger, 1874), the largest species known from the German Middle Miocene, as already remarked by Gall (1972). Recent species live in forests or shrublands, with humid soil where they can burrow (Welter-Schultes 2012).

## **Neritimorpha**

### Family Neritidae

### Genus *Theodoxus* Montfort, 1810

### *Theodoxus* sp.

(Figure 4)

**Material examined:** BSPG 1959 II 17716 (1 shell).

**Stratigraphic occurrence:** The material lacks stratigraphical data, but Moser *et al*. (2009b) indicate Layer D.

**Description:** Shell small, with quickly growing whorls. Protoconch (~1 whorl) smooth, dome-shaped; transition to teleoconch clear. Teleoconch sculptured by well-marked axial ripples. Suture shallow, but well-marked. Whorls profile convex.

**Measures (in mm):** incomplete specimen, H = 3.7, D = 3.6.

**Previous identification of the material:** Gall (1972: Nr. 51): *Theodoxus* sp. Moser *et al*. (2009b: Nr. 2): *Theodoxus* sp.

**Discussion:** The fragmentary nature of the single specimen found in Sandelzhausen precludes identification beyond genus level. The habitat range of recent *Theodoxus* species is very variable, so its use for paleoecological inferences is very limited; nevertheless, all species seem to prefer rocky substrates on water depths of circa 5 m and are intolerable to drought (Welter-Schultes 2012).

### Heterobranchia

Family Valvatidae

Genus *Valvata* O.F. Müller, 1773

*Valvata* sp.

(Figure 5)

**Material examined:** BSPG 1959 II 17717 (1 shell).

**Stratigraphic occurrence:** The material lacks stratigraphical data, but Moser *et al*. (2009b) indicate either Layer C2 or C3.

**Description:** Shell small. Protoconch (~1 whorl) rounded, sculptured by numerous fine spiral striae for ca. ¾ whorl and then interdigitating with the teleoconch sculpture for another ¼ whorl; transition to teleoconch clear. Teleoconch sculptured by numerous prosocline parallel fine axial striae. Suture deep, well-marked. Whorls profile convex. Aperture rounded.

**Measures (in mm):** BSPG 1959 II 17717 (juvenile specimen): H = 1.6, D = 1.9.

**Previous identification of the material:** Gall (1972: Nr. 50): *Valvata (Cincinna)* cf. *radiatula radiatula* Sandberger. Moser *et al*. (2009b: Nr. 7): *Valvata (Cincinna)* sp.

**Discussion:** Since only the early whorls are preserved, a more precise identification of this material is not possible. The overall shell shape and protoconch size and sculpture pattern are consistent with the genus *Valvata* (Binder 1967; Riedel 1993). Regarding the previous identification, however, it should be noted that the name *Cincinna* Hübner, 1810 was considered invalid by Welter-Schultes (2012), since it was never published and does not comply with the ICZN. The habitats of recent *Valvata* species are highly variable and thus its use for paleoecological inferences is limited; nevertheless, they usually inhabit lakes, from shallow to very deep waters, and some can live in temporary water bodies, enduring periods of drought (WELTER-SCHULTES 2012).

### Bivalvia

### Heterodonta

Family Sphaeriidae

Genus *Sphaerium* Scopoli, 1777

*Sphaerium* sp.

(Figure 6)

**Material examined:** BSPG 1959 II 17720 (2 complete shells), 17721 (4 complete shells and 1 valve fragment).

**Stratigraphic occurrence:** BSPG 1959 II 17721 specimens come from the Grube Bergmaier site, while the others lack stratigraphical data; nevertheless, Moser *et al.* (2009b) indicate Layers B or C.

**Description:** Shell small, elliptical, with fine well-marked concentric ribs; moderately bulbous; shell height ~2/3 shell length. Umbo central; anterior and posterior regions of shell roughly the same size. Prodissoconch apparently smooth.

**Measures (in mm):** BSPG 1959 II 17720 (deformed specimen): H = 2.9, L = 4.5.

**Previous identification of the material:** Gall (1972: Nr. 1): *Sphaerium* sp. Moser *et al.* (2009b: Nr. 68): *Sphaerium* sp.

**Discussion:** Most specimens are juveniles and the preservation of the single adult specimen is very poor, with the valves flattened together and the umbonal region much deformed. The hinge also cannot be examined and thus identification beyond genus level is not possible. The overall shell shape and size conforms well to European recent and fossil *Sphaerium* species. *Sphaerium* is well known from the Miocene of Central Europe and material similar to the specimens from Sandelzhausen have often been identified as recent species such as *S. rivicola* (Lamarck, 1818) (*e.g.*, LUEGER 1979; SCHNEIDER & PRIETO 2011; from the Late and Middle/Late Miocene, respectively). Recent *Sphaerium* inhabits a broad range of habitats and thus offer very limited paleoecological information (WELTER-SCHULTES 2012).

## DISCUSSION

Among freshwater snails, the non-pulmonates tend to be less diverse than the pulmonates in geologically short-lived water bodies, tending to be more diverse and abundant in deeper and/or faster moving perennial waters (Dillon 2000; Welter-Schultes 2012). This last case is especially true in many Neogene fossil lakes of Central Europe (*e.g.*, Harzhauser & Mandic 2008; Neubauer *et al*. 2013). In Sandelzhausen, the non-pulmonates snails (and bivalves) are represented by a very fragmentary material, being strikingly few in number, especially when compared to the richness of freshwater pulmonate taxa (Moser *et al*. 2009b; Salvador & Rasser in preparation). Sandelzhausen, for most of the duration where mollusks occur, was a temporary water body, turning into a perennial but shallow lake only towards the end of Layer D1 (Böhme 2009; Tütken & Vennemann 2009). However, most (if not all) of the species here seem to occur in layers other than D1. As such, they could represent unsuccessful colonization of the lake or incidental transport into the lake sediment from neighboring regions. The exception would perhaps be *Bythinia*, since recent species live in slow moving or standing waters, sometimes temporary (Welter-Schultes 2012). A more elaborated paleoecological and paleoenvironmental treatment of the entire molluscan fauna from Sandelzhausenis currently being conducted and will be presented in a future work.

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**Salvador R.B.** (2013b). The fossil pulmonate snails of Sandelzhausen (Early/Middle Miocene, Germany): Succineidae, Testacelloidea and Helicoidea. *Zootaxa* 3721(2): 157–171.

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# The fossil pulmonate snails of Sandelzhausen (Early/Middle Miocene, Germany): Succineidae, Testacelloidea and Helicoidea

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## Abstract

Sandelzhausen is an Early/Middle Miocene (Mammal Neogene zone MN5) fossil site near Mainburg, S Germany, and despite its small size it harbors a rich fossil record. Hundreds of fossil continental mollusks, almost exclusively pulmonates snails, were recovered during the excavations, but never received due attention by researchers. Here, the second part of a formal taxonomical treatment of the fossil pulmonates from Sandelzhausen is presented, dealing with the superfamilies Succineoidea, Testacelloidea and Helicoidea, and including the description of a new hygromiid species. The following species were found in the material: *Succinea minima* (Succineidae); *Palaeoglandina* sp. (Spiraxidae); *Testacella zellii* (Testacellidae); *Klikia* cf. *coarctata* (Elonidae); *Cepaea* cf. *eversa*, *Cepaea* cf. *sylvestrina* and *Tropidomphalus* cf. *incrassatus* (Helicidae); *?Helicodonta* sp. and Helicodontidae indet. (Helicodontidae); *Leucochroopsis kleinii* and *Urticicola perchtae* **sp. nov.** (Hygromiidae).

**Key words:** Gastropoda, MN5 European Mammal Neogene zone, Pulmonata, Stylommatophora, *Urticicola perchtae* new species

## Introduction

The Sandelzhausen fossil site is one of the most important continental sites in Europe (Moser *et al*. 2009a) and its bounty include hundreds of specimens of gastropods. Still, only two works dealt specifically with the mollusks: Gall (1972), who identified 49 gastropods and two bivalves in the material recovered, but based his work heavily on younger faunas; and Moser *et al*. (2009b), who dealt with paleoecological questions. Here is presented the second part of a formal taxonomic treatment of the continental mollusks from Sandelzhausen (for the first part, see Salvador, in press), dealing with the superfamilies Succineoidea, Testacelloidea and Helicoidea, and including the description of a new hygromiid species. Works describing the remaining fauna will soon follow.

## Geological setting

Sandelzhausen fossil site was located in the vicinities of the city of Mainburg, 60 km north of Munich, in the Molasse Basin (Molassebecken) of southern Germany, which harbors the "formation" known as Upper Freshwater Molasse (Ober Sü?wassermolasse, OSM; Moser *et al*. 2009a).The fossils belong to a member of the OSM called Nördlicher Vollschotter, composed primarily of marl and gravel (Moser *et al*. 2009a). The age of the deposits was established by stratigraphic, biostratigraphic and magnetostratigraphic correlations: the Early/Middle Miocene Burdigalian/Langhian boundary (~16.47–16.27 Ma; Moser *et al*. 2009a), within the early-middle MN5 European Mammal Neogene zone.

The division of Sandelzhausen deposits into facies was established by Fahlbusch and Gall (1970), receiving only some posterior refinement (Moser *et al*. 2009a): **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

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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 carbonatic nodules; rich in fossils, many in excellent preservation state due to a less intense compaction; **Layer E:** silty clays with microvertebrate fossils; **Layer F:** laminite with alternating light and dark bands, carbonate concretions and desiccation cracks; no fossils. Fossil mollusks can be found from layer A to D. For a more throughout description of the site's lithology, please refer to Moser *et al*. (2009a).

## Material and methods

All the material from Sandelzhausen is housed at the collection of the Bayerische Staatssammlung für Paläontologie und Geologie (BSPG; Munich, Germany) under the record number BSPG 1959 II; everything was examined for the present work. A list of examined material follows each species description. A portion of the material either cannot be unmistakably attributed to the sediment layers (including the sample labeled as "Grube Bergmaier"; for more information on this refer to Salvador, in press). As such, only the samples that can correctly be attributed to layers are used here to determine the stratigraphical range of the species. All specimens in a good state of preservation were measured either with a digital caliper or with the aid of computer software. Selected specimens were examined by scanning electronic microscopy (SEM) in the Staatliches Museum für Naturkunde Stuttgart (SMNS; Stuttgart, Germany). Shell measurements abbreviations: H = shell height; D = shell greatest width; h = aperture height; d = aperture width.

As explained above, the mollusks from Sandelzhausen received little attention and only two works attempted to identify the specimens: Gall (1972) and Moser *et al*. (2009b). The identification offered in these works is given here in order to facilitate the correlation of the material for future workers. A single remark should be made here: specimens of the supposed species Hygromiidae gen. indet. sp. 1 referred to by Moser *et al*. (2009b: Nr. 61) could not be confidently identified among the material, for lack of information on the labels. Likely, the specimens of this supposed species were here allocated in one or more of the described hygromiid and helicodontid species.

Finally, a quick remark regarding the taxonomy of *Cepaea* Held is in order. The traditional division in subspecies of the two *Cepaea* species treated herein is avoided. The fossils from Sandelzhausen have historically been identified as some of these subspecies (Gall, 1972), but a more cautious approach is preferred until these taxa have received proper revisionary work.

## Systematics

### Order Pulmonata

### Suborder Stylommatophora

### Superfamily Succineoidea

### Family Succineidae

### Genus *Succinea* Draparnaud

### *Succinea minima* Klein, 1853

(Figs. 1–2)

*Succinea minima* Klein, 1853: 205; Kókay, 2006: 74 (pl. 27, fig. 13).
*Succinea (Amphibina) minima minima*: Wenz, 1923b: 893.
*Succinea (Hydrotropa?) minima*: Schlickum, 1976: 11 (pl. 2, fig. 34).
Succineidae (gen. et sp. indet.): Moser *et al*., 2009b: 47.

**Material examined.** BSPG 1959 II 17471 (1 spcm.); 17680 (1 spcm.).

**Stratigraphic occurrence.** Layer C3 (1 spcm.). The other specimen comes from the Grube Bergmeier site.

**Description.** Shell diminutive, succineiform. Protoconch smooth; transition to teleoconch unclear. Teleoconch smooth, except for growth lines. Suture deep, well-marked. Whorls rapidly growing. Aperture very large, oval. Umbilicus imperforate.

**Measurements (in mm).** BSPG 1959 II 17471 (incomplete specimen; Figs. 1–2): 1¼ whorls; H = 2.6; D = 1.5.

**Previous identification of the material.** Moser *et al*. (2009b: Nr. 28): Succineidae (gen. et sp. indet.).

**Discussion.** *Succinea minima* is easily recognizable by its succineiform shell (protoconch and shell growth pattern) and remarkably small size. It is known from many fossil sites throughout the Miocene of Central Europe (Kókay 2006). Recent species inhabits very humid areas, preferably close to a water body (Welter-Schultes 2012).

### Superfamily Testacelloidea

### Family Spiraxidae

### Genus *Palaeoglandina* Wenz

### *Palaeoglandina* sp.

(Figs. 3–4)

**Material examined.** BSPG 1959 II 16145 (1 spcm.), 16146 (1 spcm.), 17302 (1 spcm.), 17303 (1 spcm.), 17304 (1 spcm.), 17305 (1 spcm.), 17306 (2 spcm.), 17307 (1 spcm.), 17308 (11 spcm.), 17319 (1 spcm.), 17727 (1 spcm.), 17728 (2 spcm.), 17729 (1 spcm.).

**Stratigraphic occurrence.** Layers B1 (3 spcm.) and D1 (1 spcm.). Moreover, 19 specimens are from excavation sites for which no profile is available, but, based on their height in the sediment and their preservation, they are likely from layer B (18 spcm.) and either C3 or D1 (1 spcm.). Finally, a single specimen stems from a sample without stratigraphical data.

**Description.** Shell large, fusiform; greatest width on last whorl. Whorls' profile slightly convex. Suture well-marked, deep and apparently slightly incised. Teleoconch sculptured by regularly distributed, well-marked ribs. Whorls rapidly increasing in size. Aperture with no apparent callus. Poor preservation prevents a better description of other conchological features.

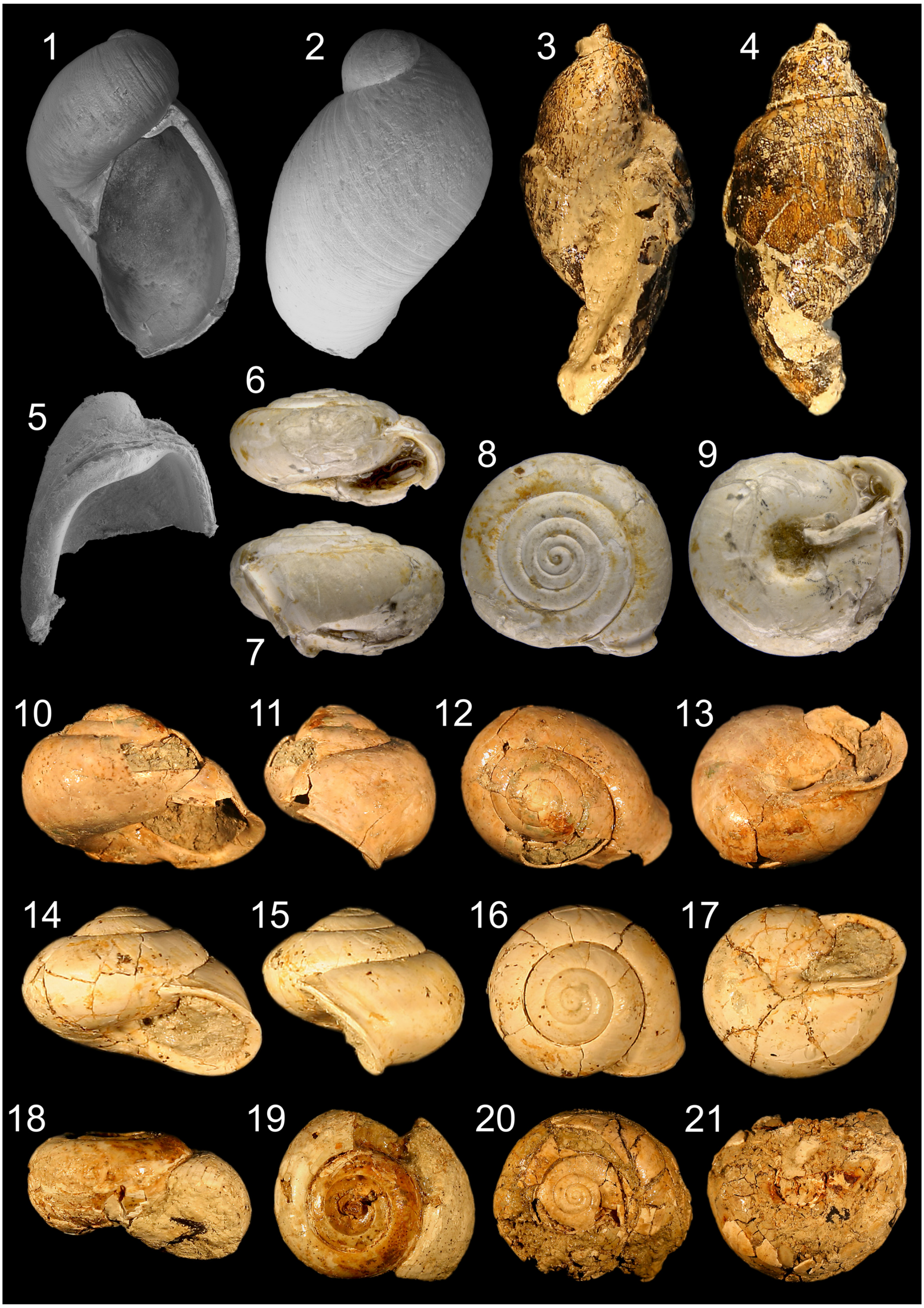
**Measurements (in mm).** BSPG 1959 II 16145 (incomplete specimen; Figs. 3–4): H = 49.7; D = 21.7.

**Previous identification of the material.** Gall (1972: Nr. 23): *Palaeoglandina gracilis porrecta* (Gobanz). Moser *et al*. (2009b: Nr. 43): *Palaeoglandina* sp.

**Discussion.** The Euglandininae, in which *Palaeoglandina* belongs, were commonly classified within Oleacinidae, but were moved to Spiraxidae by Thompson (2010). *Palaeoglandina* is widespread throughout Europe since the Paleocene, but became extinct in the Early Pleistocene (Zilch 1959–1960; Esu *et al*. 1993). The poor preservation of the specimens from Sandelzhausen precludes a proper identification; however, the known coeval (or nearly so) species in Central Europe are: *P. gracilis* (von Zieten), from the Upper Oligocene to Miocene MN7 (including the MN5 fossil site Randeck Maar, in southern Germany; Rasser *et al*. submitted), and *P. dactylina* Binder, from the MN4 site Oberdorf, Austria (Binder 2004).

The habitat and behavior of this fossil genus is unknown, of course. However, it is well known that, for land snails, both habitat and behavior tend not to vary much in genus level and sometimes even in family level (Barker 2001; Cook 2001; Pearce & Örstan 2006). As such, it seems natural to expect that, like the rest of the family, *Palaeoglandina* must have been a predator and very likely a malacophagous one (Barker & Efford 2004). Moreover, Moser *et al*. (2009b) suggested that the fossil *Palaeoglandina* from Sandelzhausen had the same lifestyle and habitat as the Recent *Euglandina rosea* (Férussac) based on its *Lebensformtyp* (meaning, in this case, the overall shell shape).

Finally, some specimens (*e.g.*, BSPG 1959 II 17302) show a glossy shell surface of a light brown color, very similar to living relatives, which could be a remnant of the original coloration. Both Gall (1972) and Moser *et al*. (2009b) mention that a few of the fossils from Sandelzhausen preserved their original colors, but do not indicate which.



**FIGURES 1–21. 1–2.** *Succinea minima* (BSPG 1959 II 17471; H = 2.6 mm). **3–4.** *Palaeoglandina* sp. (BSPG 1959 II 16145; H = 49.7 mm). **5.** *Testacella zelli* (BSPG 1959 II 17689; H = 2.3 mm). **6–9.** *Klikia* cf. *coarctata* (BSPG 1959 II 16144; D = 9.3 mm). **10–13.** *Cepaea* cf. *eversa* (BSPG 1959 II 16162; D = 26.0 mm). **14–17.** *Cepaea* cf. *sylvestrina* (BSPG 1959 II 16156; D = 19.9 mm). **18–19.** *Tropidomphalus* cf. *incrassatus* (BSPG 1959 II 456; D = 28.8 mm). **20–21.** *Tropidomphalus* cf. *incrassatus* (BSPG 1959 II 457; D = 35.1 mm).

## Family Testacellidae

### Genus *Testacella* Draparnaud

### *Testacella zellii* Klein, 1853
(Fig. 5)

*Testacella zellii* Klein, 1853: 204 (pl. 5, fig. 1).
*Testacella larteti larteti* [sic]: Gall, 1972: 7.
*Testacella zelli* [sic]: Schlickum, 1976: 15 (pl. 3, fig. 51).
*Testacella* sp.: Moser *et al*., 2009b: 48.

**Material examined.** BSPG 1959 II 17689 (1 spcm.).

**Stratigraphic occurrence.** The single specimen has no stratigraphical data, but Moser *et al*. (2009b) indicate either layer B or C1.

**Description.** Shell small, ear-shaped, vestigial. Apex starkly pointed. Shell smooth, except for growth lines. Aperture large and elongated, with a near right angle on the encounter between parietal and palatal regions; parietal and columellar region greatly thickened.

**Measurements (in mm).** ¾ whorl; H = 1.7; D = 2.3.

**Previous identification of the material.** Gall (1972: Nr. 3): *Testacella larteti larteti* [sic] Dupuy. Moser *et al*. (2009b: Nr. 42): *Testacella* sp.

**Discussion.** The shell is vestigial in this monotypic family and, therefore, is of very limited taxonomical value. The single specimen found in Sandelzhausen is fragmentary; nevertheless it presents some distinctive features. As already stated by Moser *et al*. (2009b), the present specimen differs from *T. lartetii* Dupuy by being much deeper and by having an almost right angle on its aperture and thus cannot be classified as this species. These features, alongside the starkly pointed apex, compare fittingly to *T. zellii*, a species known only from a few fossil sites of the German Early/Middle Miocene Silvana-beds (*Silvanaschichten*; Schlickum, 1976).

Recent *Testacella* species are voracious predators, preying on slugs, snails, centipedes and, especially, earthworms; living mainly underground and requiring, at least, a moderately moist soil cover (Barker & Efford, 2004). This burrowing habit should make it difficult for the shells to be carried away post-mortem and preserved in the lake sediments, hence its rarity in Sandelzhausen.

## Superfamily Helicoidea

## Family Elonidae

### Genus *Klikia* Pilsbry

### *Klikia* cf. *coarctata* (Klein, 1853)
(Figs. 6–9)

*Helix coarctata* Klein, 1853: 206 (pl. 5, fig. 6).
*Klikia (Apula) coarctata coarctata*: Wenz, 1923a: 534.
*Klikia (Klikia) giengensis giengensis*: Gall, 1972: 10.
*Klikia (Apula) coarctata*: Schlickum, 1976: 17 (pl. 4, fig. 60); Kókay, 2006: 92.
*Soosia (Prosoosia)* cf. *godarti*: Moser *et al*., 2009b: 49 (fig. 6B).

**Material examined.** BSPG 1959 II 16144 (1 spcm.), 17301 (1 spcm.).

**Stratigraphic occurrence.** Layers C3 (probably) and D1. Specimen BSPG 1959 II – 16144 comes from a sand lens in the western part of the fossil site, which is probably layer C3 according to Moser *et al*. (2009b).

**Description.** Shell small, depressed; shell height ~1/2 its width. Protoconch (~1 whorl) blunt, wide, apparently smooth; transition to teleoconch unclear. Teleoconch sculptured by regularly distributed fine papillae, giving the impression of axial striae; papillae apparently stronger closer to suture and to umbilicus. Whorls' profile slightly convex. Suture well-marked, deep. Whorls regularly increasing in size, but with a decrease in size in the last quarter of body whorl. Body whorl with conspicuous constriction right before the aperture ("extralabial depression" *sensu* Binder, 2008). Aperture crescent-shaped; aperture height ~4/5 its width; aperture width ~2/5 shell width. Peristome greatly reflected.

**Measurements (in mm).** BSPG 1959 II 16144 (Figs.6–9): 4¾ whorls; H = 5.0; D = 9.3; h = 3.3; d = 4.0.

**Previous identification of the material.** Gall (1972: Nr. 18): *Klikia (Klikia) giengensis giengensis* (Klein). Moser *et al*. (2009b: Nr. 54, fig. 6B): *Soosia (Prosoosia)* cf. *godarti* Michaud *sensu* Sandberger.

**Discussion.** The specimens from Sandelzhausen compares fittingly with *K. coarctata*, a species from the Silvanaschichten of southwestern Germany (MN5–6; Klein 1853; Schlickum 1976). However, one of the main features of this species, a covered umbilicus (Klein 1853; Harzhauser & Binder 2004), cannot be seen in the material from Sandelzhausen, since the single complete shell preserved shows a collapsed umbilical region. In any case, the degree in which the umbilicus is covered seems to be variable in some *Klikia* species (Harzhauser & Binder 2004) and as such, it might not be such a useful diagnostic character.

## Family Helicidae

### Genus *Cepaea* Held

### *Cepaea* cf. *eversa* Deshayes, 1851

(Figs. 10–13)

*Helix eversa* Deshayes, 1851: 395 (pl. 1, figs. 5–7).
*Cepaea eversa eversa*: Wenz, 1923a: 617.
*Hemicycla asperula* cf. *leymerieana*: Gall, 1972: 10.
*Cepaea eversa larteti* (in part): Gall, 1972: 10; Gall, 1973: 10 (pl.1, figs. 4–6).
*Cepaea silvana silvana* (in part): Gall, 1972: 11.
*Cepaea eversa*: Hír & Kókay, 2004: 89.
*"Cepaea"* sp. 1. (in part): Moser *et al*., 2009b: 50.
*"Cepaea"* sp. 2.: Moser *et al*., 2009b: 50.

**Material examined.** BSPG 1959 II 460 (1 spcm.), 461 (1 spcm.), 16157 (1 spcm.), 16158 (1 spcm.), 16160 (1 spcm.), 16162 (1 spcm.), 16165 (1 spcm.), 16166 (1 spcm.), 16167 (1 spcm.), 16168 (1 spcm.), 17336 (1 spcm.), 17337 (1 spcm.), 17338 (1 spcm.), 17339 (2 spcm.), 17340 (1 spcm.), 17341 (1 spcm.), 17342 (1 spcm.), 17343 (1 spcm.), 17344 (1 spcm.), 17345 (1 spcm.), 17346 (1 spcm.), 17347 (1 spcm.), 17376 (1 spcm.), 17377 (1 spcm.), 17378 (1 spcm.), 17379 (1 spcm.), 17380 (1 spcm.), 17381 (1 spcm.), 17382 (1 spcm.), 17383 (1 spcm.), 17384 (1 spcm.), 17385 (1 spcm.), 17386 (1 spcm.), 17387 (1 spcm.), 17388 (1 spcm.), 17389 (1 spcm.), 17782 (1 spcm.), 17783 (1 spcm.), 17784 (1 spcm.), 17785 (1 spcm.), 17786 (1 spcm.), 17787 (2 spcm.), 17788 (1 spcm.), 17789 (1 spcm.), 17790 (1 spcm.), 17791 (1 spcm.), 17792 (1 spcm.), 17793 (1 spcm.), 17794 (1 spcm.), 17795 (1 spcm.), 17796 (1 spcm.), 17797 (1 spcm.), 17798 (1 spcm.), 17799 (1 spcm.), 17800 (1 spcm.), 17801 (1 spcm.), 17802 (1 spcm.), 17803 (1 spcm.), 17804 (2 spcm.), 17805 (1 spcm.).

**Stratigraphic occurrence.** Layers B1 (5 spcm.), B2 (5 spcm.), C1 (3 spcm.), C2 (1 spcm.), D1 (7 spcm.). Moreover, 37 specimens are from excavation sites for which no profile is available, but, based on their height in the sediment and their preservation, it is possible to infer the layer of origin for some: 1 is likely from layer C1, 1 from C3, 12 from D, 3 from either B2 or C1, and 7 are from either C3 or D.

**Description.** Shell large, 4½ to 4¾ whorls, with depressed spire; shell length ~2/3 its width. Protoconch flattened, smooth; transition to teleoconch unclear. Teleoconch smooth, except for growth lines. Suture well-marked. Body whorl slightly bent downwards near aperture; apertural region enlarged. Aperture prosocline, crescent-shaped, with strong callus; aperture length ~1/2 its width and ~1/2 shell length; aperture width ~1/2 shell width. Peristome markedly reflexed; thickened on basal and columellar regions. Umbilicus imperforate, with a marked callus formed by the peristome. On two specimens (BSPG 1959 II 16160 and 17339) it is possible to observe, under UV light, vestiges of three colored broad parallel spiral bands, the topmost one right below the carina, the other two regularly spaced on basal portion of whorl.

**Measurements (in mm).** BSPG 1959 II 16162 (deformed specimen; Figs. 10–13): H = 18.4; D = 26.0; h = 8.1; d = 14.3.

**Previous identification of the material.** Gall (1972: Nr. 19 and, in part, 20–21): respectively, *Hemicycla asperula* cf. *leymerieana* (Noulet), *Cepaea silvana silvana* (Klein) and *Cepaea eversa larteti* (Boissy). Moser *et al.* (2009b: Nr. 64, in part, and 65): respectively, *"Cepaea"* sp. 1. and *"Cepaea"* sp. 2.

**Discussion.** The specimens from Sandelzhausen compare well with *C. eversa*, but are always larger, with half whorl more than typical *C. eversa* specimens. Moreover, the peristome of the present specimens is more reflected and only thickened on the basal and columellar regions, while typical *C. eversa* has the entire peristome thickened and not much reflected. Nevertheless, *C. eversa* seems to be a very variable species regarding shell morphology (Hír & Kókay 2004). It is also a very frequent species in Middle Miocene (MN 5–7) deposits of Central and Western Europe (Hír & Kókay 2004).

### *Cepaea* cf. *sylvestrina* Schlotheim, 1820
(Figs. 14–17)

*Helix sylvestrina* Schlotheim, 1820: 99.
*Cepaea sylvestrina sylvestrina*: Wenz, 1923a: 690.
*Cepaea sylvestrina*: Truc, 1971: 282.
*Cepaea eversa larteti* (in part): Gall, 1972: 10; Gall, 1973: 10 (pl.1, figs. 4–6).
*Cepaea silvana silvana* (in part): Gall, 1972: 11.
*"Cepaea"* sp. 1. (in part): Moser *et al*., 2009b: 50.

**Material examined.** BSPG 1959 II 459 (1 spcm.), 16156 (1 spcm.), 17447 (2 spcm.), 17448 (2 spcm.), 17447 (1 spcm.), 17449 (1 spcm.), 17450 (1 spcm.), 17451 (1 spcm.), 17452 (1 spcm.), 17453 (1 spcm.), 17454 (1 spcm.), 17455 (1 spcm.), 17456 (2 spcm.), 17457 (1 spcm.), 17458 (1 spcm.), 17459 (1 spcm.), 17460 (1 spcm.), 17461 (1 spcm.), 17462 (1 spcm.), 17463 (1 spcm.), 17464 (1 spcm.), 17465 (1 spcm.), 17466 (1 spcm.), 17467 (1 spcm.), 17468 (1 spcm.), 17766 (1 spcm.), 17767 (1 spcm.), 17768 (1 spcm.), 17769 (1 spcm.), 17770 (1 spcm.), 17771 (1 spcm.), 17772 (1 spcm.), 17773 (1 spcm.), 17774 (1 spcm.), 17775 (1 spcm.), 17776 (2 spcm.), 17777 (1 spcm.), 17778 (1 spcm.), 17779 (3 spcm.), 17780 (2 spcm.), 17781 (2 spcm.).

**Stratigraphic occurrence.** Layers B1 (1 spcm.), B2 (2 spcm.), C (undetermined; 1 spcm.), C1 (3 spcm.), C3 (1 spcm.), D1 (4 spcm.). Moreover, 25 specimens are from excavation sites for which no profile is available, but, based on their height in the sediment and their preservation, it is possible to infer the layer of origin for some: 3 are likely from layer D, 4 from either B2 or C1, 9 from either C3 or D.

**Description.** Shell medium-sized, ~4 whorls, helicoid; whorls quickly but regularly growing; shell length ~2/3 its width. Protoconch flattened, smooth; transition to teleoconch unclear. Teleoconch smooth, except for growth lines. Suture well-marked. Body whorl slightly bent downwards; faint carina apparently present. Aperture prosocline, crescent-shaped; callus faint. Peristome markedly thickened and reflexed. Umbilicus imperforate. On a single specimen (BSPG 1959 II 16156) it is possible to observe, under UV light, vestiges of three colored fine parallel spiral bands, the topmost one right below the carina, the other two regularly spaced on basal portion of whorl.

**Measurements (in mm).** BSPG 1959 II 16156 (Figs. 14–17): 4 whorls; H = 13.7; D = 19.9; h = 6.9; d = 10.0.

**Previous identification of the material.** Gall (1972: Nr. 20 and 21, in part): respectively, *Cepaea silvana silvana* (Klein) and *Cepaea eversa larteti* (Boissy). Moser *et al*. (2009b: Nr. 64, in part): *"Cepaea"* sp. 1.

**Discussion.** The specimens from Sandelzhausen compare well with *C. sylvestrina*, but the typical specimens of the latter are taller and have a rounder profile, especially the body whorl. Moreover, typical *C. sylvestrina* have the apertural region bent more markedly downwards. Finally, the present specimens have a more distinct carina and less convex whorls. However, it cannot be completely excluded that these are artifacts due to preservational biases (for more, see the Discussion chapter below). The vestiges of colored bands can be seen in a single specimen of *C.* cf. *sylvestrina* and two of *C.* cf. *eversa* (see above). The pattern is trifasciate in both species, but the bands are much broader in *C.* cf. *eversa*. This trifasciate pattern occurs in recent *Cepaea* species and was found to be the most common one in fossils of *C. sylvestrina gottschicki* Wenz from Poland (Górka 2008). *Cepaea sylvestrina* is known throughout the Middle and Late Miocene of Central Europe.

**Remarks.** Truc (1971) alludes to the possibility that *C. sylvestrina* belongs in the genus *Megalotachea*. Zilch (1959–1960), however, considers *Megalotachea* a synonym of *Cepaea* s. str.

### Genus *Tropidomphalus* Pilsbry

### *Tropidomphalus* cf. *incrassatus* (Klein, 1853)

(Figs. 18–21)

*Helix inflexa* Klein, 1847: 71 (pl. 1, fig. 12).
*Helix incrassata* Klein, 1853: 208 (pl. 5, fig. 6).
*Tropidomphalus (Pseudochloritis) extinctus*: Gall, 1972: 9; Gall, 1973: 10 (pl.1, fig. 1).
*Tropidomphalus (Pseudochloritis) incrasstus incrassatus*: Wenz, 1923a: 510; Gall, 1972: 9; Schlickum, 1976: 16 (pl. 4, fig. 56).
*Tropidomphalus (Pseudochloritis) zelli*: Gall, 1972: 9.
*Tropidomphalus* ? sp.: Gall, 1972: 10; Gall, 1973: 10 (pl.1, figs. 2–3).
*Tropidomphalus (Pseudochloritis) incrassatus*: Kókay, 2006: 90 (pl. 34, figs. 12–14).
*Pseudochloritis incrassata*: Binder, 2008: 172 (pl. 3, figs. 2–4, pl. 6, fig. 2).
*Tropidomphalus (Pseudochlorites)* [sic] sp.: Moser *et al*., 2009b: 49.

**Material examined.** BSPG 1959 II 456 (1 spcm.), 457 (1 spcm.), 458 (1 spcm.), 16153 (1 spcm.), 16154 (1 spcm.), 16155 (4 spcm.), 16163 (1 spcm.), 17318 (1 spcm.), 17322 (1 spcm.), 17323 (1 spcm.), 17324 (1 spcm.), 17325 (1 spcm.), 17326 (1 spcm.), 17327 (2 spcm.), 17328 (1 spcm.), 17329 (1 spcm.), 17330 (1 spcm.), 17331 (1 spcm.), 17332 (1 spcm.), 17333 (1 spcm.), 17334 (1 spcm.), 17335 (1 spcm.), 17348 (1 spcm.), 17349 (1 spcm.), 17350 (1 spcm.), 17351 (1 spcm.), 17353 (1 spcm.), 17354 (1 spcm.), 17355 (1 spcm.), 17356 (1 spcm.), 17357 (1 spcm.), 17358 (2 spcm.), 17359 (4 spcm.), 17360 (1 spcm.), 17361 (2 spcm.), 17362 (1 spcm.), 17363 (1 spcm.), 17364 (4 spcm.), 17365 (1 spcm.), 17366 (2 spcm.), 17367 (1 spcm.), 17368 (1 spcm.), 17369 (1 spcm.), 17370 (1 spcm.), 17473 (1 spcm.), 17730 (1 spcm.), 17731 (1 spcm.), 17732 (1 spcm.), 17733 (2 spcm.), 17734 (2 spcm.), 17735 (1 spcm.), 17736 (1 spcm.), 17737 (1 spcm.), 17738 (4 spcm.), 17739 (1 spcm.), 17740 (1 spcm.), 17741 (2 spcm.), 17742 (1 spcm.), 17743 (1 spcm.), 17744 (1 spcm.), 17745 (1 spcm.), 17746 (2 spcm.), 17747 (1 spcm.), 17748 (1 spcm.), 17749 (1 spcm.), 17750 (1 spcm.), 17751 (3 spcm.), 17752 (1 spcm.), 17753 (1 spcm.), 17754 (1 spcm.), 17755 (1 spcm.), 17756 (2 spcm.), 17757 (4 spcm.), 17758 (1 spcm.), 17759 (1 spcm.), 17760 (1 spcm.), 17761 (1 spcm.), 17762 (1 spcm.), 17763 (4 spcm.), 17764 (3 spcm.), 17765 (1 spcm.).

**Stratigraphic occurrence.** Layers B (undetermined; 10 spcm.), B1 (3 spcm.), B2 (2 spcm.), C (undetermined; 5 spcm.), C1 (7 spcm.), C2 (2 spcm.), C3 (2 spcm.) and D1 (4 spcm.). Moreover, 68 specimens are from excavation sites for which no profile is available, but, based on their height in the sediment and their preservation, it is possible to infer the layer of origin for some: 1 is likely from layer B (undetermined), 1 from C (undetermined), 3 from C1, 2 from C3, 8 from D1, 13 from either B or C, 9 from either B2 or C1, and 10 from either C3 or D1. Finally, 4 specimens stem from the Grube Bergmaier site and 2 specimens completely lack locality and stratigraphical data.

**Description.** Shell large, 4½ whorls, helicoid to disc-shaped, with flattened spire; shell length ~1/2 its width. Protoconch (1¼ whorl) flattened, large in relation to following whorl; sculptured by fine striae dotted with weak papillae; transition to teleoconch unclear. Teleoconch sculptured by thickened growth lines and irregular weak furrows, with regularly arranged papillae. Suture deep, well-marked. Body whorl enlarged, slightly bent downwards, with conspicuous constriction right before the aperture ("extralabial depression" *sensu* Binder 2008). Aperture prosocline; no callus apparent. Peristome markedly thickened and reflexed, slightly covering umbilicus. Umbilicus wide.

**Measurements (in mm).** BSPG 1959 II 456 (incomplete specimen; Figs. 18–19): H = 15.9; D = 28.8.

**Previous identification of the material.** Gall (1972: Nr. 13–16): respectively, *Tropidomphalus (Pseudochloritis) extinctus* (Rambur), *Tropidomphalus (Pseudochloritis) incrasstus incrassatus* (Klein), *Tropidomphalus (Pseudochloritis) zelli* (Kurr), *Tropidomphalus* ? sp. Moser *et al*. (2009b: Nr. 56): *Tropidomphalus (Pseudochlorites)* [sic] sp.

**Discussion.** The specimens from Sandelzhausen, despite their poor preservation, seem to conform well to the great morphological variation shown by *Tropidomphalus incrassatus* (Binder 2008). This species is known from the Middle Miocene of Poland (Górka 2008), Austria, many localities in Germany (Binder 2008) and perhaps also

Hungary (Kókay 2006). Some of the specimens are poorly preserved, with varying degrees of deformation, which alters the overall shell shape and its size and may influence classification as different species (for more, see the Discussion chapter below).

Binder (2008) considers the shell of *Tropidomphalus*, based especially on the angulation of the body whorl and aperture, an adaptation for ground-dwelling to reduce water loss in drier environments. Moser *et al*. (2009) suggest that the genus inhabited drier and more open habitats, having a "way of life like strong-shelled Balkanese representatives of Ariantinae".

**Remarks.** *T. incrassatus* is considered to belong to the subgenus *Pseudochloritis* Boettger, 1909. Nordsieck (1986) was the first to regard *Pseudochloritis* as a distinct genus, but did not offer any explanation for his decision. Binder (2008) revised the genus and separated it from *Tropidomphalus* basically based on the width of the umbilicus (narrow in *Pseudochloritis*, wide in *Tropidomphalus*) and protoconch sculpture. However, protoconch sculpture does not seem to be constant in each subgenera and the width of the umbilicus greatly varies even intraspecifically for specimens of different localities. As such, here we maintain the species only as *T. incrassatus* and question the usefulness of the subgenus *Pseudochloritis*.

Finally, there is some uncertainty as to the position of the genus *Tropidomphalus* Pilsbry inside Helicoidea, belonging either to the Elonidae or Helicidae (Zilch 1959–1960; Binder 2008; Moser *et al*. 2009b). Here the latter was preferred, in accordance with Binder (2008).

### Helicidae indet.

**Material examined.** *Cepaea* sp.: BSPG 1959 II 16195 (1 spcm.), 16164 (1 spcm.), 17390 (1 spcm.), 17391 (2 spcm.), 17392 (2 spcm.), 17393 (1 spcm.), 17394 (1 spcm.), 17395 (1 spcm.), 17396 (10 spcm.), 17397 (1 spcm.), 17398 (8 spcm.), 17399 (1 spcm.), 17400 (1 spcm.), 17401 (1 spcm.), 17402 (1 spcm.), 17403 (4 spcm.), 17404 (1 spcm.), 17405 (2 spcm.), 17406 (1 spcm.), 17407 (1 spcm.), 17408 (1 spcm.), 17409 (1 spcm.), 17410 (1 spcm.), 17411 (1 spcm.), 17412 (1 spcm.), 17413 (1 spcm.), 17414 (1 spcm.), 17415 (1 spcm.), 17416 (1 spcm.), 17417 (1 spcm.), 17418 (1 spcm.), 17419 (1 spcm.), 17420 (1 spcm.), 17421 (2 spcm.), 17422 (1 spcm.), 17423 (1 spcm.), 17424 (1 spcm.), 17425 (1 spcm.), 17426 (1 spcm.), 17427 (1 spcm.), 17428 (1 spcm.), 17429 (2 spcm.), 17430 (1 spcm.), 17431 (1 spcm.), 17432 (1 spcm.), 17433 (1 spcm.), 17434 (1 spcm.), 17435 (1 spcm.), 17436 (1 spcm.), 17437 (1 spcm.), 17438 (1 spcm.), 17439 (1 spcm.), 17440 (1 spcm.), 17441 (1 spcm.), 17442 (1 spcm.), 17443 (1 spcm.), 17444 (2 spcm.), 17445 (1 spcm.), 17446 (1 spcm.), 17672 (1 spcm.), 17673 (1 spcm.), 17674 (2 spcm.), 17806 (1 spcm.), 17807 (1 spcm.), 17808 (2 spcm.), 17809 (1 spcm.), 17810 (1 spcm.), 17811 (1 spcm.), 17812 (1 spcm.), 17813 (1 spcm.), 17814 (4 spcm.), 17815 (1 spcm.), 17816 (1 spcm.), 17817 (3 spcm.), 17818 (1 spcm.), 17819 (1 spcm.), 17820 (1 spcm.), 17821 (1 spcm.), 17822 (1 spcm.), 17823 (1 spcm.), 17824 (1 spcm.), 17825 (1 spcm.), 17826 (1 spcm.), 17827 (2 spcm.), 17828 (1 spcm.), 17829 (1 spcm.), 17830 (1 spcm.), 17831 (2 spcm.), 17832 (1 spcm.), 17833 (1 spcm.), 17834 (1 spcm.), 17835 (1 spcm.), 17836 (1 spcm.), 17837 (1 spcm.).
Helicidae indet.: BSPG 1959 II 17320 (1 spcm.), 17321 (numerous fragments), 17469 (1 spcm.).

**Stratigraphic occurrence.** *Cepaea* sp.: Layers B (undetermined; 6 spcm.), B1 (2 spcm.), B2 (2 spcm.), C (undetermined; 5 spcm.), C1 (2 spcm.), C2 (1 spcm.), C3 (4 spcm.), D1 (18 spcm.) and D2 (1 spcm.). Moreover, 67 specimens are from excavation sites for which no profile is available, but, based on their height in the sediment and their preservation, it is possible to infer the layer of origin for some: 1 is likely from layer C3, 2 from D, 7 from either B or C, 2 from either B2 or C1, 3 from either C or D, and 15 from either C3 or D1. Finally, 8 specimens are from the Grube Bergmaier site and 9 specimens have no stratigraphical data at all.

Helicidae indet.: Layer D1 (1 spcm.) and either B2 or C1 (1 spcm.). Many fragments from the Grube Bergmaier site.

**Previous identification of the material.** Moser *et al.* (2009b: Nr. 66): "*Cepaea*" sp. Otherwise, same as genera *Cepaea* and *Tropidomphalus* above. Moreover, two supposed helicodontids indicated by Moser *et al.* (2009b: Nr. 58 and 59; respectively, ?Helicodontidae fam., gen. et sp. indet. 1 and 2) are actually helicid spire tops.

**Discussion.** Unfortunately, a good portion of the material from Sandelzhausen is composed of unidentifiable helicid fragments or more complete but deformed shells that cannot be confidently identified (see Discussion below for more on preservational biases). Some fragments can be assigned to *Cepaea* while, for others, any determination below family level is not possible.

## Family Helicodontidae

### Genus *Helicodonta* Férussac

*?Helicodonta* sp.
(Figs. 22–23)

**Material examined.** BSPG 1959 II 17678 (1 spcm.).

**Stratigraphic occurrence.** Likely layer C3.

**Description.** Shell diminutive, discoid, with depressed spire; shell height ~3/5 shell length. Protoconch sculptured by axial ribs; transition to teleoconch unclear. Teleoconch sculptured on its upper portion by strong, slightly prosocline ribs (distance between ribs equal to width of rib); lateral and basal regions sculptured by numerous scale-like elongated papillae. Suture well-marked. Whorl profile convex; whorls closely packed together, growing regularly. Umbilicus broad, deep.

**Measurements (in mm).** 3¾ whorl; H = 2.6; D = 4.3.

**Previous identification of the material.** None.

**Discussion.** The present specimen is somewhat deformed and lacks the aperture; nevertheless, the discoid shape, depressed spired, whorl profile and the closely packed whorls seem to indicate the genus *Helicodonta*. This genus is known in Europe since the Upper Oligocene (Zilch 1959–1960).

### Helicodontidae indet.

(Figs. 24–25)

**Material examined.** BSPG 1959 II 17300 (1 spcm.).

**Stratigraphic occurrence.** Layer D1.

**Description.** Shell diminutive, seemingly planispiral; whorls regularly increasing in width and height. Protoconch (1¼ whorl) blunt, smooth; transition to teleoconch unclear. Teleoconch sculptured by regularly distributed fine vertically elongated scales. Spire flat. Suture well-marked. Umbilicus apparently narrow.

**Measurements (in mm).** Incomplete specimen; 2¼ whorls; H = 2.0; D = 3.7.

**Previous identification of the material.** Gall (1972: Nr. 12): *Helicodonta (Helicodonta) involuta scabiosa* (Sandberger). Moser *et al*. (2009b: Nr. 57): ?*Protodrepanostoma* sp.

**Discussion.** As only the first whorls are preserved it is very hard to offer a more precise classification. The overall profile of the shell, with a completely flat spire and a strong carina, as well as the sculpture pattern with papillae, is consistent with the helicodontids. However, the specimen from Sandelzhausen is somewhat unusual: its whorls are not as closely packed as is the rule for the family and it seems to have a much narrower umbilicus. Hence, the classification of previous authors in either *Protodrepanostoma* Germain or *Helicodonta* Férussac does not seem appropriate.

**Remarks.** As indicated in Helicidae indet. above, the two other helicodontids indicated by Moser *et al.* (2009b: Nr. 58 and 59; respectively, ?Helicodontidae fam., gen. et sp. indet. 1 and 2) actually are helicid spire tops, which can be seen by the shape and size of the protoconch and the shape of the later whorls.

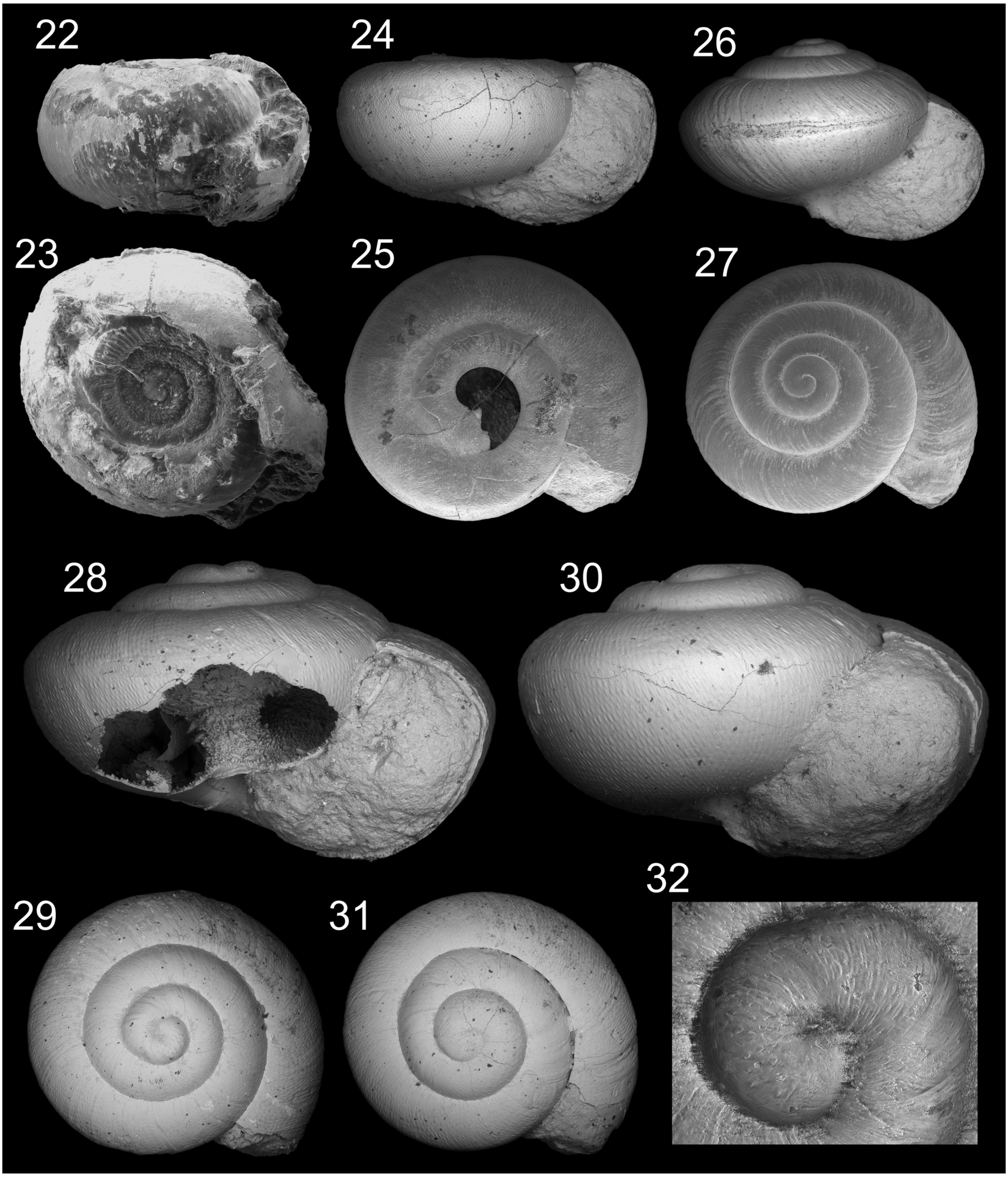
## Family Hygromiidae

### Genus *Leucochroopsis* O. Boettger

***Leucochroopsis kleinii* (Klein, 1847)**
(Figs. 26–27)

*Helix kleinii* Klein, 1847: 69 (pl. 1, fig. 8).
*Trichia (Leucochroopsis) kleini kleini* [sic]: 429.
*Leucochroopsis kleini kleini* [sic]: Gall, 1972: 9.
*Klikia (Apula)* sp.: Gall, 1972: 10.

*Leucochroopsis kleini* [sic]: Schlickum, 1976: 15 (pl. 3, fig. 52); Harzhauser & Binder: 2004: 25 (pl. 11, figs. 8–10).
*Soosia* sp.: Moser *et al*., 2009b: 49.
*Trichiopsis* sp.: Moser *et al*., 2009b: 50 (fig. 6E).
Hygromiidae gen. indet. sp. 3: Moser *et al*., 2009b: 50.



**FIGURES 22–32. 22–23.** *?Helicodonta* sp. (BSPG 1959 II 17678; D = 4.3 mm). **24–25.** Helicodontidae indet. (BSPG 1959 II 17300; D = 3.7 mm). **26–27.** *Leucochroopsis kleinii* (BSPG 1959 II 16147; D = 5.0 mm). **28–29.** *Urticicola perchtae* **sp. nov.** (holotype; BSPG 1959 II 17312; H = 3.5 mm). **30–31.** *Urticicola perchtae* **sp. nov.** (paratype; BSPG 1959 II 17313; H = 2.9 mm). **32.** *Urticicola perchtae* **sp. nov.**, protoconch detail (holotype; BSPG 1959 II 17312).

**Material examined.** BSPG 1959 II 16147 (1 spcm.), 17314 (3 spcm.), 17315 (3 spcm.), 17316 (14 spcm.), 17317 (2 spcm.), 17470 (1 spcm), 17472 (1 spcm.), 17475 (1 spcm.), 17722 (1 spcm.), 17723 (1 spcm.), 17724 (1 spcm.), 17725 (1 spcm.), 17726 (1 spcm.),.

**Stratigraphic occurrence.** Layers C (2 spcm.) and D1 (22 spcm.). The other specimens stem from samples for which no profile is available, but based on their height in the sediment and their preservation, 3 likely come from layer C3, 2 from D1, 1 from either B or C, and 1 from C or D1.

**Description.** Shell small, with a depressed conical spire and a rounded inferior portion. Protoconch (~1¼ whorl) large, blunt, smooth; transition to teleoconch unclear. Teleoconch sculptured by fine regularly distributed well-marked papillae; growth lines sometimes more marked. Whorls' profile convex. Suture well-marked, but not too deep. Whorls regularly increasing in size. Whorls with a smooth keel-like angulation. Aperture apparently crescent-shaped and slightly prosocline. Umbilicus apparently rimate.

**Measurements (in mm).** 4 whorls (all specimens are juvenile); H = ~4.0; D = ~6.3.

**Previous identification of the material.** Gall (1972: Nr. 11 and 17): respectively, *Leucochroopsis kleini kleini* [sic] (Klein) and *Klikia (Apula)* sp. Moser *et al*. (2009b: Nr. 55, 60 and 63): respectively, *Soosia* sp., *Trichiopsis* sp. and Hygromiidae gen. indet. sp. 3.

**Discussion.** *Leucochroopsis kleinii* is known from the Middle Miocene of the Silvanaschichten, Germany, to the Late Miocene of Vienna Basin (Klein 1847; Schlickum 1976; Harzhauser & Binder 2004). Although the status of the genus and of its species has been recently called into question (Moser *et al*. 2009b), the specimens from Sandelzhausen compare fittingly with Klein's original material from the Silvanaschichten (housed at the SMNS), which are approximately of the same age. The more poorly preserved specimens were identified as distinct species by previous authors (Gall 1972; Moser *et al*. 2009b), but their size, protoconch shape and teleoconch sculpture are all indicative of *L. kleinii*.

### Genus *Urticicola* Lindholm

### *Urticicola perchtae* sp. nov.

(Figs. 28–32)

Hygromiidae gen. indet. sp. 2: Moser *et al*., 2009b: 50.
*Leucochroopsis* sp.: Böttcher *et al*., 2009: 241 (figs. 13–14).

**Type material.** Holotype: BSPG 1959 II 17312 (Figs. 28–29, 32). Paratype: BSPG 1959 II 17313 (1 spcm.; Figs. 30–31).

**Etymology.** Perchta (or Berchta) is a Germanic goddess from the Alpine region (including Bavaria), probably derived from the ancient Celtic Lady of the Beasts and being a southern counterpart of the northern German Holda (Grimm, 1882; Motz, 1984). Although her image was much deteriorated under Christian influence (to the point of becoming a simple evil spirit or witch), she was originally a goddess of winter, spinning and beasts and was said to wear a beautiful white garb, her name meaning "the bright one" (Grimm, 1882; Motz, 1984). It seems an appropriate name for this Bavarian fossil, which is bright white with a delicate sculpture as its "garb".

**Type locality.** Sandelzhausen, Mainburg, Germany; 48°37'36.9" N, 11°48'11.6"E; 493 m height.

**Stratigraphic occurrence.** Layer D1.

**Age:** Middle Miocene, Burdigalian/Langhian boundary (early middle MN5 European Mammal Neogene zone; 16.47 or 16.27 Ma; Moser *et al*. 2009a).

**Diagnosis.** Shell small, umbilicated; suture deep; whorls convex, with keel-like angulation.

**Description.** Shell small, depressed; whorls regularly increasing in size. Protoconch (~1¼ whorl) blunt, sculptured by very fine axial striae and scattered knobs near the suture; transition to teleoconch unclear. Teleoconch sculptured by regularly distributed and vertically-elongated fine scales; portion near suture sculptured by fine axial striae. Whorls' profile convex. Suture well-marked, deep. Whorls with a smooth but prominent keel-like angulation. Umbilicated.

**Measurements (in mm). Holotype:** 3 whorls; H = 3.5; D = 2.1. **Paratype:** 2½ whorls; H = 2.9; D = 1.9.

**Previous identification of the material.** Moser *et al*. (2009b: Nr. 62): Hygromiidae gen. indet. sp. 2.

**Discussion.** *Urticicola* was previously considered a subgenus of *Zenobiella* Gude & Woodward, but is now regarded as a separate entity based on its shell sculpture (with scale-like structures), a broader umbilicus and a more pronounced keel (Welter-Schultes 2012). The name *Urticicola* was originally described as a subgenus and its grammatical gender was not stated. Manganelli *et al*. (1995) claimed that this name and most names ending in "-cola" have been traditionally regarded as feminine. However, Welter-Schultes (2012) argues that it should be considered masculine under the Art. 30.1.4.2 of the ICZN.

*Urticicola perchtae* is the first fossil record of the genus (fossil *Zenobiella* are known from the Pleistocene; Zilch 1959–1960). It is very similar to the Recent *U. glabellus* (Draparnaud) from Eastern France, differing by its smaller size, a deeper suture and more convex whorls, giving its spire a profile similar to a step pyramid. Moreover, it differs from the Recent central European species *U. umbrosus* (Pfeiffer) by its more rounded profile, a higher body whorl and a narrower umbilicus. Unfortunately, only two juvenile specimens were found in Sandelzhausen and thus a description of the apertural region is presently not possible.

**Remarks.** A careful examination of the original material studied by Böttcher *et al*. (2009: figs. 13–14) revealed that their so-called *Leucochroopsis* sp. (SMNS 68657) is actually a specimen of *U. perchtae*. Their material stems from the locality of Oggenhausen 2, in southern Germany, and is coeval with Sandelzhausen (MN5).

## Discussion

As stated by Gall (1973) and Moser *et al*. (2009b), the preservation of some of the specimens from Sandelzhausen may present some problems for taxonomy. The fossils can be compressed or expanded, producing a more flattened or rounded overall appearance and thus hampering a precise taxonomic determination at species level. This preservational bias affects almost exclusively the larger fossils, namely *Paleoglandina*, the helicids and the larger forms of planorbids and lymnaeids. As remarked by Gall (1973) for the helicids, a blown-up specimen of species "A" might appear as a member of the more spherical species "B". Nevertheless, despite his own warnings, Gall (1972) identified many *Cepaea* and *Tropidomphalus* species in Sandelzhausen.

Bearing this preservational bias in mind, here a great care was taken when identifying the specimens from Sandelzhausen. For a more reliable identification, other characters besides overall shell shape were used (such as presence and size of the umbilicus, protoconch shape and sculpture) and material from the original descriptions (and later revisions) of German *Cepaea* and *Tropidomphalus* species, housed at the SMNS, were analyzed. Even so, as already noted by Moser *et al*. (2009b), identification beyond the genus level must unfortunately remain tentative. Moreover, as in Salvador (in press), comparisons were preferably conducted with species of roughly the same age and close geographic occurrence.

The number of species present in Sandelzhausen appears to have been slightly overestimated by Gall (1972) and Moser *et al*. (2009b), as some of their supposed species collapsed into a single entity (as was already the case in Salvador in press). Nevertheless, previously unknown species have now been found in the abundant material from Sandelzhausen, such as *?Helicodonta* sp., and thus its land snail fauna still is proving itself very diverse.

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# The fossil land and freshwater snails of Gündlkofen (Middle Miocene, Germany)

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## Abstract

The molluscan fauna from the Middle Miocene (MN 5–6) fossil site of Gündlkofen in southern Germany was first reported by Gall (1980: *Mitt. Bayer. Staatssaml. Paläont. hist. Geol.*, 20, 51–77). He listed 34 continental gastropod species, which were neither figured nor properly described in many cases. Here a revision of his identifications is presented, with a full description of the material and illustration of the best preserved specimens. Following this revision, 20 species are listed for Gündlkofen. Unfortunately, part of the original material was missing and the record of a few species could not be confirmed. The depositional environment seems to have been a temporary water body, like an oxbow lake, surrounded by a humid and warm forest and scrubland.

**Key words:** Caenogastropoda, Gastropoda, MN 5–6 European Mammal Neogene zones, Pulmonata

## Introduction

The molluscan fauna from the Middle Miocene fossil site of Gündlkofen in southern Germany was reported by Gall (1980), who first described the site and listed 34 land and freshwater gastropod species from there. He also offered an age estimate for the site and conducted a paleoecological reconstruction based on the mollusks. Nevertheless, he neither figured nor properly described most of the snails in his work. Moreover, his identification of the larger snails was biased due to the bad preservation of the material, resulting in deformation of the shells. Further works present a fraction of the material from Gündlkofen, but, since they dealt only with very specific taxa (*e.g.*, Schnabel 2006, 2007, for the family Filholiidae), a complete treatment of the material is still lacking. As such, a revision of Gall's classification is presented here, with a full description of the material and illustration of the best preserved specimens.

## Geological setting

As described by Gall (1980), all material from the Gündlkofen fossil site comes from a single fine sand/marl horizon, half meter thick, in a gravel pit located 750 m northwest of Gündlkofen (a small region part of the Bruckberg municipality in Bavaria, SW Germany). The site is located in the Molasse Basin of southern Germany. Based on fossil and lithological evidence, Gall (1980), following Meier (1965), related it to the lower section of the Nördlicher Vollschotter, which in turn is a member of the Upper Freshwater Molasse ("Obere Süßwassermolasse", OSM; Abdul Aziz *et al*. 2008). As such, Gall (1980) suggested an age of roughly 15 Ma for the site, correlating it with the Middle Silvana-beds ("Silvanaschichten") and the Langhian/Badenian stages (Middle Miocene; MN 5–6 European Mammal Neogene zones). For a more thorough description of the site's lithology and age correlation see Gall (1980).

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## Material and methods

All the material from Gündlkofen is housed at the collection of the Bayerische Staatssammlung für Paläontologie und Geologie (BSPG; Munich, Germany) under the record number BSPG 1952 XVIII. All available specimens were analyzed; a list of the examined material follows each species description. Preservation of most of the material is very poor. In order to facilitate future comparative work, here is offered the identification of the material according to Gall (1980) and a brief description of the available specimens for each species. Selected specimens were examined by scanning electronic microscopy (SEM) in the Staatliches Museum für Naturkunde Stuttgart (SMNS; Stuttgart, Germany). Shell measurements abbreviations: H = shell length; D = greatest shell width; h = aperture/operculum height; d = aperture/operculum width.

Unfortunately, part of the original material was missing and the record of some species could not be confirmed. The following lots, as listed by Gall (1980), could not be found: BSPG 1952 XVIII 9 and 55, *Triptychia* cf. *obliqueplicata* (Sandberger); BSPG 1952 XVIII 13, *Serrulina ptycholarynx* (Boettger); BSPG 1952 XVIII 19, *Orcula* sp.; BSPG 1952 XVIII 24, *Triptychia* cf. *bacillifera* (Sandberger); BSPG 1952 XVIII 52, *Triptychia (Milne-Edwardsia?)* sp. Part of this missing material was analyzed by Nordsieck (1981b) and Schnabel (2006). Nordsieck (1981b) studied the *Serrulina ptycholarynx* from Gündlkofen and classified it as a new subspecies: *Serrulastra (Serruplica) ptycholarynx galli* Nordsieck. Schnabel (2006) analyzed the rest of the material: **(1)** he described a new subspecies, *T. solida schaireri* Schnabel, for Gall's *T.* cf. *obliqueplicata*; **(2)** he described a new species, *T. teutonica* Schnabel, for Gündlkofen, but it is impossible to tell to which (if any) of Gall's species he is referring to; **(3)** finally, he indicates a *Triptychia* (?) n. sp. 5, referring specifically to Gall's *Triptychia (Milne-Edwardsia?)* sp.

Finally, some taxonomic remarks should be made: **(1)** The classification of Bouchet *et al.* (2005) is followed here, treating the genus *Archaeozonites* Sandberger (and the Archaeozonitinae) as Gastrodontoidea *incertae sedis* (rather than its traditional allocation within Zonitidae). **(2)** The traditional subspecific division of the *Cepaea* Held species treated herein is avoided. A more cautious approach is preferred until these taxa have received proper revisionary work. Moreover, the poor preservation of the specimens hampers a precise taxonomic determination at species level, thus making classification at subspecies level even more tentative (see Discussion chapter below). **(3)** There is uncertainty about the position of the genus *Tropidomphalus* Pilsbry, normally assigned either to Elonidae or Helicidae (Zilch 1959–1960; Binder 2008; Moser *et al.* 2009). Here the latter was preferred, in accordance with Binder (2008). **(4)** The Euglandininae, in which *Palaeoglandina* Wenz belongs, were commonly classified within Oleacinidae, but were moved to Spiraxidae by Thompson (2010). This decision is followed here.

## Systematics

### Caenogastropoda

### Superfamily Littorinoidea

### Family Pomatiidae

### Genus *Pomatias* Studer

### *Pomatias consobrina* (Sandberger, 1874)

(Figs. 1–2)

*Cyclostoma consobrinum*: Sandberger, 1874: 606 (pl. 29, fig. 33a [non 33b–c]).
*Pomatias consobrinum*: Wenz, 1923: 1805; Schütt, 1967: 201; Schlickum, 1976: 2 (pl. 1, fig. 1); Gall, 1980: 67; Stworzewicz, 1995: 26.
*Pomatias* sp.: Gall, 1980: 67.
*Pomatias consorbinum* [sic]: Kókay, 2006: 34 (pl. 4, fig. 3).

**Material examined.** BSPG 1952 XVIII 17 (14 spcm., 29 opercula), 44 (1 spcm.).

**Description.** Shell medium-sized, trochiform. Protoconch (~1½ whorl) smooth; transition to teleoconch clear.

Teleoconch sculpture reticulated, with stronger spiral ribs and weaker axial ribs; distance between spiral ribs equal to twice their width; distance between axial ribs roughly equal to their width. Whorl profile greatly convex; spire stepped. Suture deep. Aperture rounded. Umbilicus narrow. Operculum with spiral growth.

**Previous identification of the material.** Gall (1980: Nr. 32 and 33): respectively, *Pomatias consobrinum* (Sandberger) and *Pomatias* sp.

**Discussion.** The present specimens compare well with *P. consobrina*, being easily identified by its size and strong reticulate sculpture (Stworzewicz 1995; Kókay 2006). The species is known from the Middle Miocene (MN 5–8) of Germany, Hungary and Austria (Schlickum 1976; Kókay 2006).

**Paleoecological remarks.** Recent species live in forests or shrublands, with more humid soil where they can burrow (Welter-Schultes 2012).

### Superfamily Rissooidea

### Family Bithyniidae

### Genus *Bithynia* Leach

### *Bithynia* sp.

(Fig. 3)

**Material examined.** BSPG 1952 XVIII 18 (3 opercula).

**Previous identification of the material.** Gall (1980: Nr. 34): *Bithynia (Bithynia)* cf. *glabra* (Zieten).

**Discussion.** The only fossils of this genus in the material from Gündlkofen are opercula; their overall shape and concentric growth pattern indicate the genus *Bithynia*, but identification at species level is impossible.

**Paleoecological remarks.** Recent *Bithynia* species live in richly vegetated slow moving or standing waters, some are also found in temporary water bodies (Welter-Schultes 2012).

### Pulmonata

### Hygrophila

### Superfamily Planorboidea

### Family Planorbidae

### Genus *Gyraulus* Charpentier

### *Gyraulus* sp.

(Figs. 4–5)

**Material examined.** BSPG 1952 XVIII 16 (1 spcm.).

**Description.** Shell diminutive, pseudodextral, planispiral. Protoconch flattened; transition to teleoconch unclear. Teleoconch smooth, except for well-marked growth lines. Spire depressed. Suture very deep. Whorls rapidly growing. Whorl profile asymmetrical, with faint keel on lower portion of whorl. Aperture large, rounded.

**Previous identification of the material.** Gall (1980: Nr. 30): *Gyraulus (Gyraulus) trochiformis* cf. *kleini* (Gottschick & Wenz).

**Discussion.** The single specimen from Gündlkofen is a juvenile and, due to its poor preservation (lacking protoconch sculpture) and the known conchological variation in the genus (Meier-Brook 1983; Rasser 2013), classification beyond genus level is presently not possible.

**Paleoecological remarks.** Recent *Gyraulus* are found in various habitats, so their use in paleoecological analysis is limited; still, they usually thrive in richly vegetated, shallow standing or slow-flowing waters, sometimes even temporary water bodies (Welter-Schultes 2012).

### Stylommatophora

### Superfamily Clausilioidea

### Family Clausiliidae

### Clausiliidae indet.

(Figs. 6–8)

**Material examined.** BSPG 1952 XVIII 36 (1 spcm.), 37 (6 spcm.).

**Previous identification of the material.** Gall (1980: Nr. 19 and 20): respectively, *Pseudidyla moersingensis* (Boettger) and Clausiliidae gen. et sp. indet.

**Discussion.** Due to the very fragmentary nature of the present specimens, a more precise identification is not feasible. Nevertheless, it should be noted that there are two distinct morphs of spire tops: one larger, with higher whorls (Fig. 6), and one smaller, with the whorls more closely packed together and growing more quickly in width (Fig. 7). There is also a single apertural fragment (Fig. 8) that was identified by Gall (1980) as *Pseudidyla moersingensis* (Boettger), a species known from the Middle to Late Miocene of Germany (Nordsieck 1981a, 1982). Its overall shape and dentition seem to indicate the genus *Pseudidyla* (Boettger 1877), but due to the fragmentary nature of the present specimens, it is impossible to safely assign them to *P. moersingensis*.

Moreover, Gall (1980: Nr. 18) also lists another clausiliid, *Serrulina ptycholarynx* (Boettger), for Gündlkofen; however, as explained above, the lot unfortunately could not be found at the BSPG collection. It should be noted, however, that Nordsieck (1981b) classified Gall's *S. ptycholarynx* as a new subspecies, *Serrulastra (Serruplica) ptycholarynx galli* Nordsieck, and figures the holotype (pl. 8, fig. 18), which consists in a fragmentary body whorl with an intact aperture. The shell sculpture, aperture shape and dentition is congruent with the group of genera *Serrulastra* Nordsieck, *Serrulina* Mousson and *Serrulella* Nordsieck *in* Zilch. The distinction between these genera, (and their myriad of subgenera, species and subspecies) is very tenuous and classification of fragmentary fossil material is thus further complicated. As such, the validity of this subspecies should be taken carefully.

Finally, the only thing that can be safely said about the clausiliids from Gündlkofen is that they represent two species, one probably belonging to the genus *Pseudidyla* and the other to *Serrulastra* or *Serrulina* and likely the species *S. ptycholarynx*.

**Paleoecological remarks.** Nordsieck (2007) suggests that clausiliids up to the Middle Miocene were mostly wood-dwelling animals, preferring humid and warm environments.

### Family Filholiidae

### Genus *Triptychia* Sandberger

### *Triptychia* sp.

(Fig. 9)

**Material examined.** BSPG 1952 XVIII 53 (16 spcm.).

**Description.** Shell medium-sized, multispiral, sinistral; spire conical, with early spire slightly concave. Protoconch (~2 whorls) smooth, bulbous; transition to teleoconch clear. Teleoconch sculptured by orthocline axial ribs; distance between ribs roughly equal to rib width. Suture shallow, but well-marked. Whorl profile flat.

**Previous identification of the material.** Gall (1980: Nr. 24): *Triptychia* sp.

**Discussion.** The few sinistral spire fragments clearly belong to *Triptychia* due to their overall conical profile, flattened whorls and a shallow but well-marked suture. Unfortunately, it is impossible to proceed further in the identification, since the aperture region (with the most important diagnostic features) is not preserved. As explained above, Gall (1980) and Schnabel (2006) list three *Triptychia* species each for Gündlkofen, but their identification differs in all cases. Unfortunately, the lots that would contain these specimens could not be found at the BSPG collection. Nevertheless, the present specimens compare well with the *Triptychia* (?) n. sp. 5 of Schnabel (2006), which is the *Triptychia (Milne-Edwardsia?)* sp. of Gall (1980).

**Paleoecological remarks.** Filholiidae is a completely fossil family. It is usually suggested that filholiids were mostly wood-dwelling animals preferring humid and warm forests (Schnabel 2007).

## Superfamily Cochlicopoidea

## Family Cochlicopidae

## Genus *Azeca* Fleming

### *Azeca* cf. *lubricella* Boettger, 1870

(Fig. 10)

*Azeca lubricella* Boettger, 1870: 292.
*Azeca (Azeca) lubricella lubricella*: Wenz, 1923: 1092.
*Azeca lubricella lubricella*: Schlickum, 1976: 8 (pl. 1, fig. 21).
*Azeca* cf. *lubricella lubricella*: Gall, 1980: 66.

**Material examined.** BSPG 1952 XVIII 45 (2 spcm.).

**Previous identification of the material.** Gall (1980: Nr. 29): *Azeca* cf. *lubricella lubricella* Boettger.

**Discussion.** The present specimens are simply apertural fragments, where two teeth (one columellar and one palatal) can be seen. While the aperture shape and dentition seem to clearly indicate the genus *Azeca*, identification beyond that remains rather tentative. Still, the dentition of the present specimens agree very well with *Azeca lubricella*, a species typical from the Silvana-beds in the Middle Miocene of Southern Germany (Schlickum 1976).

**Paleoecological remarks.** The single recent species in the genus, *Azeca goodalli* (Férussac), lives in leaf litter in woodlands or shrublands, often with calcareous soil (Welter-Schultes 2012). Schlickum (1976) states that *A. lubricella* specifically may have lived on the immediate vicinity of a water body.

## Superfamily Gastrodontoidea

### Gastrodontoidea indet.

(Fig. 11)

**Material examined.** BSPG 1952 XVIII 38 (4 spcm).

**Description.** Shell small, discoid; spire depressed. Teleoconch sculptured by axial ribs; distance between ribs equal to width of rib. Suture well-marked. Aperture apparently circular. Umbilicus wide, deep.

**Previous identification of the material.** Gall (1980: Nr. 5): *Aegopinella subnitens* (Klein).

**Discussion.** The present specimens are extremely poorly preserved and any attempt on identification beyond this level would be very tentative. Gall (1980) justified his identification by means of the teleoconch sculpture, made of axial and spiral ribs. Nevertheless, this sculpture cannot be observed; only axial ribs are visible.

## Gastrodontoidea *incertae sedis*

## Subfamily Archaeozonitinae

## Genus *Archaeozonites* Sandberger

### *Archaeozonites* sp.

(Figs. 12–13)

**Material examined.** BSPG 1952 XVIII 2 (1 spcm.), 42 (1 spcm.), 43 (1 spcm.), 50b (1 spcm.).

**Description.** Protoconch (~1 whorl) flattened, sculptured by fine riblets that grow coarser towards teleoconch. Teleoconch sculptured by numerous strong parallel prosocline ribs; distance between ribs equal to width of rib. Suture weakly marked. Spire trochiform; whorls profile flattened to slightly convex. Umbilicus wide, deep.

**Previous identification of the material.** Gall (1980: Nr. 2, 3, 4 and, in part, 13): respectively, *Archaeozonites* cf. *costatus costatus* Sandberger, *Archaeozonites costatus subcostatus* Sandberger, *Archaeozonites* sp. and *Tropidomphalus* sp.

**Discussion.** The present specimens, despite very deformed or fragmentary, show the main diagnostic features of the genus *Archaeozonites*: the strong ribs, the flattened whorl profile, weakly marked suture, the broad conical profile of the spire and a wide umbilicus. Nevertheless, the poor preservation precludes going further than genus level in the classification and the differentiation in two subspecies as Gall (1980) proposed is not possible. Nevertheless, the specimens from Gündlkofen resemble the Central European Miocene species *A. costatus* (Sandberger) and *A. laticostatus* (Sandberger), mainly due to their sculpture pattern. The genus is known in Europe from the Middle Eocene to the Late Pliocene (Zilch 1959–1960).

**Paleoecological remarks.** As a fossil genus, any paleoecological inference must remain tentative. Nevertheless, Lueger (1981) considers that *A. laticostatus* lived under leaves or between rocks in moist forests.

## Superfamily Helicoidea

## Family Elonidae

### Genus *Klikia* Pilsbry

### *Klikia* cf. *coarctata* (Klein, 1853)

(Fig. 14)

*Helix coarctata* Klein, 1853: 206 (pl. 5, fig. 6).
*Klikia (Apula) coarctata coarctata*: Wenz, 1923: 534.
*Klikia (Apula) coarctata*: Schlickum, 1976: 17 (pl. 4, fig. 60); Kókay, 2006: 92.
*Klikia (Apula)* cf. *coarctata coarctata*: Gall, 1980: 60.
*Klikia* cf. *coarctata*: Salvador, 2013b: 161 (figs. 6–9).

**Material examined.** BSPG 1952 XVIII 7 (1 spcm.).

**Description.** Shell small, depressed. Protoconch blunt, wide, smooth. Teleoconch sculptured by regularly distributed fine papillae, giving the impression of axial striae. Whorls' profile slightly convex. Suture well-marked, deep. Whorls regularly increasing in size. Aperture crescent-shaped.

**Previous identification of the material.** Gall (1980: Nr. 14): *Klikia (Apula)* cf. *coarctata coarctata* (Klein).

**Discussion.** The single specimen from Gündlkofen, despite being slightly deformed, compares fittingly with *K. coarctata*, a species from the Middle Miocene of southern Germany (MN 5–6; Klein 1853; Schlickum 1976; Salvador 2013b). However, a more certain identification is not possible, since one of the main features of this species, a covered umbilicus (Klein 1853; Harzhauser & Binder 2004), cannot be observed.

**Paleoecological remarks.** As a fossil genus, comparison with living relatives is somewhat tentative. Nevertheless, Lueger (1981) suggested that species in this genus preferred drier environments.

## Family Helicidae

### Genus Cepaea Held

### *Cepaea* cf. *eversa* Deshayes, 1851

(Figs. 15–16)

*Helix eversa* Deshayes, 1851: 395 (pl. 1, figs. 5–7).
*Cepaea eversa eversa*: Wenz, 1923: 617.
*Cepaea eversa larteti*: Gall, 1980: 60.
*Cepaea eversa*: Hír & Kókay, 2004: 89.
*Cepaea* cf. *eversa*: Salvador, 2013b: 162 (figs. 10–13).

**Material examined.** BSPG 1952 XVIII 8 (19 spcm.)

**Description.** Shell large, 4½ to 4¾ whorls. Protoconch flattened, smooth; transition to teleoconch unclear. Teleoconch smooth, except for growth lines. Suture well-marked. Whorl profile flat on first whorls. Body whorl rounded, slightly bent downwards near aperture. Aperture prosocline, rounded. Peristome reflexed; slightly thickened on basal and columellar regions. Umbilicus imperforate.

**Previous identification of the material.** Gall (1980: Nr. 15): *Cepaea eversa larteti* (Boissy).

**Discussion.** The present specimens from Sandelzhausen compare reasonably well with *C. eversa* and can be differentiated from the specimens of *C.* cf. *sylvestrina* Schlotheim (see below) by a larger size, a higher spire, a rounder aperture and one quarter to one half additional whorl. Nevertheless, the specimens of *C. eversa* from Gündlkofen are always larger, also with half whorl more, than typical specimens. Nevertheless, as common in the genus, *C. eversa* seems to be a very variable species regarding shell morphology (Hír & Kókay 2004). It is a frequent species in Middle Miocene (MN 5–7) deposits of Central and Western Europe (Hír & Kókay 2004).

**Paleoecological remarks.** Recent *Cepaea* have too broad a range of habitats (Welter-Schultes 2012) to be useful for a paleoenvironmental analysis.

### *Cepaea* cf. *sylvestrina* Schlotheim, 1820

(Figs. 17–18)

*Helix sylvestrina* Schlotheim, 1820: 99.
*Cepaea sylvestrina sylvestrina*: Wenz, 1923: 690.
*Cepaea sylvestrina*: Truc, 1971: 282.
*Cepaea silvana silvana*: Gall, 1980: 61.
*Cepaea* cf. *sylvestrina*: Salvador, 2013b: 163 (figs. 14–17).

**Material examined.** BSPG 1952 XVIII 49 (10 spcm.).

**Description.** Shell large, 4¼–4½ whorls, helicoid; whorls regularly growing. Protoconch flattened, smooth; transition to teleoconch unclear. Teleoconch smooth, except for growth lines. Whorl profile flat on first whorls. Suture well-marked. Body whorl slightly bent downwards. Aperture prosocline, crescent-shaped; callus faint. Peristome markedly thickened and reflexed. Umbilicus imperforate.

**Previous identification of the material.** Gall (1980: Nr. 16): *Cepaea silvana silvana* (Klein).

**Discussion.** The specimens from Gündlkofen compare reasonably well with *C. sylvestrina*, but are slightly larger, with one quarter to one half additional whorl when compared to typical *C. sylvestrina*; nevertheless, this species seem to be quite variable morphologically. *Cepaea silvana* Klein, another common species in the German Middle Miocene, is even smaller, with fewer whorls and a more rounded overall profile, and might be simply a morphological extreme of *C. sylvestrina*.

**Paleoecological remarks.** As *C.* cf. *eversa* above.

### *Cepaea* sp.

**Material examined.** BSPG 1952XVIII 19 (4 spcm.).

**Previous identification of the material.** Gall (1980: Nr. 17): *Cepaea* sp.

**Discussion.** These few protoconch and spire top fragments cannot be confidently assigned to any particular species of *Cepaea*.

### Genus *Tropidomphalus* Pilsbry

#### *Tropidomphalus* cf. *incrassatus* (Klein, 1853)
(Figs. 19–20)

*Helix inflexa* Klein, 1847: 71 (pl. 1, fig. 12).
*Helix incrassata* Klein, 1853: 208 (pl. 5, fig. 6).
*Tropidomphalus (Pseudochloritis) incrasstus incrassatus*: Wenz, 1923: 510; Schlickum, 1976: 16 (pl. 4, fig. 56).
*Tropidomphalus (Pseudochloritis) incrasstus incrassatus*: Gall, 1980: 59.
*Tropidomphalus (Pseudochloritis) zelli*: Gall, 1980: 60.
*Tropidomphalus* sp.: Gall, 1980: 60.
*Tropidomphalus (Pseudochloritis) incrassatus*: Kókay, 2006: 90 (pl. 34, figs. 12–14).
*Pseudochloritis incrassata*: Binder, 2008: 172 (pl. 3, figs. 2–4, pl. 6, fig. 2).
*Tropidomphalus* cf. *incrassatus*: Salvador, 2013b: 164 (figs. 18–21).

**Material examined.** BSPG 1952 XVIII 5 (7 spcm.), 6 (1 spcm.), 50 (3 spcm.), 51 (2 spcm.).

**Description.** Shell large, 4½ whorls, helicoid to disc-shaped, with flattened spire. Protoconch (1¼ whorl) flattened, large in relation to following whorl; sculptured by fine striae dotted with weak papillae; transition to teleoconch unclear. Teleoconch sculptured by thickened growth lines and irregular weak furrows, with regularly arranged papillae. Suture deep, well-marked. Body whorl enlarged, slightly bent downwards, with conspicuous constriction right before the aperture ("extralabial depression" *sensu* Binder 2008). Aperture prosocline; no callus apparent. Peristome markedly thickened and reflexed, slightly covering umbilicus. Umbilicus wide.

**Previous identification of the material.** Gall (1980: Nr. 11, 12 and 13): respectively, *Tropidomphalus (Pseudochloritis) incrasstus incrassatus* (Klein), *Tropidomphalus (Pseudochloritis) zelli* (Kurr) and *Tropidomphalus* sp.

**Discussion.** *T. incrassatus* is considered to belong to the subgenus *Pseudochloritis* Boettger, recently elevated to genus status by Binder (2008). Nevertheless, as Salvador (2013b) questioned the delimitation and the usefulness of the subgenus *Pseudochloritis*, here the allocation in *Tropidomphalus* is maintained.

The present specimens, despite their poor preservation, seem to conform well to the great morphological variation shown by *Tropidomphalus incrassatus* (Binder 2008), a species known from the Middle Miocene of Central Europe (Kókay 2006; Binder 2008). All specimens show varying degrees of deformation that alter the overall shell shape, size and proportions; this may have led Gall (1980) to identify a large deformed specimen as *T. zelli* (Kurr). For more details on preservation and their impact on taxonomy see the Discussion chapter below.

**Paleoecological remarks.** Binder (2008) considers the shell of *Tropidomphalus*, based mainly on the angulation of the body whorl and prosocline aperture, an adaptation for ground-dwelling by reducing water loss in drier environments. Moser *et al.* (2009) suggest that the genus inhabited drier and more open habitats, having a "way of life like strong-shelled Balkanese representatives of Ariantinae".

## Superfamily Limacoidea

### Family Limacidae

### Genus *Limax* Linnaeus

#### *Limax* sp.
(Fig. 21)

**Material examined.** BSPG 1952 XVIII 3 (15 spcm.), 39 (19 spcm), 40 (7 spcm.).

**Description.** Shell small, vestigial, oval; shell width ~2/3 length. Nucleus slightly bent laterally; nucleus region higher than remainder of shell. Shell with marked concentric growth lines.

**Previous identification of the material.** Gall (1980: Nr. 6, 7 and 8): respectively, *Limax* sp., *Milax* sp. and *Parmacella* sp.

**Discussion.** The shells of limacids are vestigial and internal and thus of very limited taxonomical value. As such, the identification of the present material cannot proceed further than genus level. The genus *Limax* is known in Europe from the Late Oligocene onwards (Zilch 1959–1960).

Gall (1980) identified some specimens as belonging to the genera *Parmacella* Cuvier and *Milax* Grey. The shell of *Parmacella* slugs are also vestigial, but exhibit a very characteristic inflated and prominent protoconch. This diagnostic feature is not present in the specimens from Gündlkofen. The shells of *Milax* are inflated and markedly convex, with a central elevated nucleus, features that cannot be seen in the present specimens.

**Paleoecological remarks.** Recent *Limax* species occupy a variety of habitats, but usually live in damp leaf litter (Welter-Schultes 2012).

### Superfamily Punctoidea

### Family Discidae

### Genus *Discus* Fitzinger

### *Discus* sp.

(Fig. 22)

**Material examined.** BSPG 1952 XVIII 41 (3 spcm.).

**Description.** Shell diminutive, discoid. Protoconch (~1¼ whorl) flat, smooth; transition to teleoconch clear. Teleoconch sculptured by fine but well-marked parallel prosocline ribs; distance among ribs equal to width of rib. Whorl profile convex. Suture well-marked. Whorls regularly growing.

**Previous identification of the material.** Gall (1980: Nr. 9): *Discus* sp.

**Discussion.** The material is very fragmentary, but a generic assignment is possible by the distinct shell shape and sculpture pattern. Moreover, the well-marked sculpture compare well with *D. pleuradrus* (Bourguignat), a species widespread during the Middle and Upper Miocene of Central Europe (Böttcher *et al*. 2009).

**Paleoecological remarks.** Recent European species live in damp woodlands or grasslands (Welter-Schultes 2012).

### Superfamily Pupilloidea

### Family Chondrinidae

### Genus *Granaria* Held

### *Granaria* sp.

(Fig. 23)

**Material examined.** BSPG 1952 VIII 46 (1 spcm.), 47 (2 spcm.).

**Description.** Shell small, with acuminated spire top. Protoconch (1½ whorl) narrow, rounded, smooth; transition to teleoconch unclear. Whorl profile convex. Suture deep. Teleoconch sculptured by regularly distributed, very fine prosocline ribs; distance between ribs approximately twice rib width.

**Previous identification of the material.** Gall (1980: Nr. 31): *Cochlostoma* sp.

**Discussion.** Only spire fragments remain and thus a more precise identification is not possible. The regular whorl growth and the fine, straight and regular ribs indicate the genus *Granaria* (Höltke & Rasser 2013). Moreover, the present specimens are indistinguishable from the *Granaria* sp. described from the Middle Miocene (MN 5) of Sandelzhausen, southeastern Germany (Salvador 2014).

**Paleoecological remarks.** Recent *Granaria* species prefer dry and open habitats, usually calcareous (Welter-Schultes 2012).

### Family Helicodiscidae

### Genus *Lucilla* Lowe

### *Lucilla subteres* (Clessin, 1877)

(Fig. 24)

*Helix (Patula) subteres* Clessin, 1877: 35.
*Patula subteres*: Clessin, 1885: 76 (pl. 7, fig. 6).
*Pyramidula subteres*: Wenz, 1923: 1062.
*Helicodiscus (Hebetodiscus) subteres*: Schlickum, 1976: 11 (pl. 2, fig. 35); Schlickum, 1979: 68 (fig. 2); Gall, 1980: 65; Kókay, 2006: 74 (pl. 27, figs. 14–16).

**Material examined.** BSPG 1952 XVIII 4 (1 spcm.).

**Description.** Shell diminutive, discoid, with flattened spire. Protoconch (~1¼ whorl) flat, apparently smooth; transition to teleoconch unclear. Teleoconch smooth, but with well-marked growth lines. Whorl profile convex. Suture well-marked, deep. Whorls regularly growing. Aperture round. Umbilicus wide.

**Previous identification of the material.** Gall (1980: Nr. 28): *Helicodiscus (Hebetodiscus) subteres* (Clessin).

**Discussion.** The present specimen compares well to *L. subteres*, a species known from Miocene (MN 5–6) sites of Southern Germany and Hungary (Schlickum 1976, 1979; Kókay 2006). The species of *Lucilla* were usually classified in the genus *Helicodiscus* Morse and, more specifically, in the subgenus *Hebetodiscus* H.B. Baker. *Hebetodiscus*, however, was later considered a distinct genus by Bequaert & Miller (1973), which, in turn, was then regarded as a synonym of *Lucilla* by Falkner *et al*. (2002). As such, some authors (*e.g.*, Hubricht 1985; Hotopp *et al*. 2010) state that this whole *Helicodiscus* complex should be revised. Until then, the current approach of treating *Lucilla* as a distinct genus (*e.g.*, Moser *et al*. 2009; Gargominy *et al*. 2011; Welter-Schultes 2012) is followed here.

**Paleoecological remarks.** The two recent European *Lucilla* species are subterranean (*L. scintilla* Lowe is even blind), living deeper in the soil than other land snails (Welter-Schultes 2012). If the extinct species shared this habit, the increased difficulty for their preservation would explain the scarce fossil record of the genus.

## Superfamily Testacelloidea

### Family Oleacinidae

### Genus *Pseudoleacina* Wenz

### *Pseudoleacina* sp.

(Fig. 25)

**Material examined.** BSPG 1952 XVIII 15 (1 spcm.).

**Description.** Shell small, fusiform with bulbous body whorl. Teleoconch apparently sculptured by marked axial ribs only directly below suture. Suture well-marked but not too deep, slightly incised. Body whorl very large. Aperture greatly elongated vertically. Umbilicus imperforate.

**Previous identification of the material.** Gall (1980: Nr. 26): *Pseudoleacina* sp.

**Discussion.** As remarked by Gall (1980), the present specimen does not conform well to any other Miocene species of *Pseudoleacina*, mainly by its large size and bulbous body whorl. Gall (1980) also called attention to the sculpture pattern: strong axial ribs only present right below the suture; this feature is known only in *Pseudoleacina rakosdensis* (Gaál), from the Sarmatian (MN 7–8) of Rákosd, Romania (Gaál 1911; Kókay 2006). Despite this fact, the poor preservation of the present specimen precludes a more confident determination.

**Paleoecological remarks.** *Pseudoleacina* is a fossil genus, but like the rest of the family it might have been a malacophagous predator (Barker & Efford 2004). Moreover, most authors consider *Pseudoleacina* species as hygrophilic woodland inhabitants (*e.g.*, Lueger 1981; Harzhauser & Binder 2004; Harzhauser & Tempfer 2004), but some (*e.g.*, Gall 1980) consider it a calciphilic and xerophilic species.

### Family Spiraxidae

### Genus *Palaeoglandina* Wenz

### *Palaeoglandina* cf. *gracilis* (Zieten, 1830)

(Fig. 26)

*Limnaea gracilis* Zieten, 1830: 39 (pl. 30, fig. 3).
*Poiretia (Palaeoglandina) gracilis gracilis*: Wenz, 1923: 839.
*Palaeoglandina gracilis*: Zilch, 1959–1960: 457 (fig. 1627).
*Palaeoglandina gracilis porrecta*: Gall, 1980: 64.

**Material examined.** BSPG 1952 XVIII 14 (3 spcm.).

**Description.** Shell large, fusiform; greatest width on last whorl. Teleoconch sculptured by regularly distributed, well-marked coarse ribs; distance between ribs equal to rib width. Aperture drop-shaped, vertically elongated; no apparent callus. Peristome simple, but slightly thickened on columellar region. Umbilicus imperforated.

**Previous identification of the material.** Gall (1980: Nr. 25): *Palaeoglandina gracilis porrecta* (Gobanz).

**Discussion.** The fragmentary and deformed preservation of the present material precludes a more precise identification. Nevertheless, the specimens are reminiscent of *P. gracilis* by their broad shell, strong sculpture and elongated aperture. *Palaeoglandina gracilis* is known from the Late Oligocene to the Middle Miocene (MN 7) of Central Europe (Salvador 2013b).

**Paleoecological remarks.** The genus *Palaeoglandina* is known since the Paleocene, being widespread throughout Europe and becoming extinct in the Early Pleistocene (Zilch 1959–1960; Esu *et al*. 1993). Likely, as the recent species in the family, *Palaeoglandina* was a malacophagous predator (Barker & Efford 2004); some authors (*e.g.*, Moser *et al*. 2009) even suggested that it should have displayed the same lifestyle and habitat as the recent North American *Euglandina rosea* (Férussac), living on the leaf litter or on trees, with a wide habitat tolerance (Hubricht 1985; Davis *et al*. 2004).

### Family Testacellidae

### Genus *Testacella* Draparnaud

### *Testacella schuetti* Schlickum, 1967

(Fig. 27)

*Testacella schuetti* Schlickum, 1967: 63 (fig. 1); Harzhauser *et al*., 2008: 53 (figs. 7.2–7.3); Nardi & Bodon, 2011: 159 (table 3).
*Testacella* (*Testacella*) *schuetti*: Schütt, 1967: 218 (fig. 19).
*Testacella zelli*: Gall, 1980: 56.

**Material examined.** BSPG 1952 XVIII 22 (5 spcm.).

**Description.** Shell small, ear-shaped, vestigial; shell width ~3/5 shell length. Apex pointed, curved. Shell with well-marked growth lines. Aperture elongated, oval; parietal and columellar region greatly thickened.

**Previous identification of the material.** Gall (1980: Nr. 1): *Testacella zelli* Klein [sic].

**Discussion.** The shell is vestigial in this monotypic family and, therefore, is of very limited taxonomical value. Despite being slightly larger, the present specimens compare well with *T. schuetti* by its oval aperture, low shell and a pointed but curved apex. The species is known from few Middle Miocene (Sarmatian, MN 7–8) sites of the Styrian Basin and North-Alpine Foreland Basin (type locality: Hollabrunn, Austria; Schlickum 1967; Harzhauser *et al*. 2008). As such, the present record is the oldest for the species.

**Paleoecological remarks.** Recent *Testacella* are voracious predators, feeding on earthworms, gastropods and centipedes, and live mainly underground, thus requiring a moist soil cover (Barker & Efford 2004). This burrowing habit should make preservation in the fossil record difficult.

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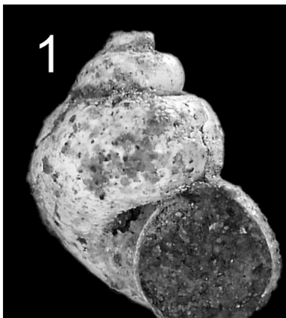

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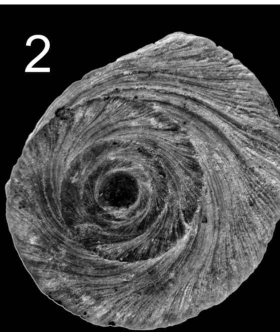

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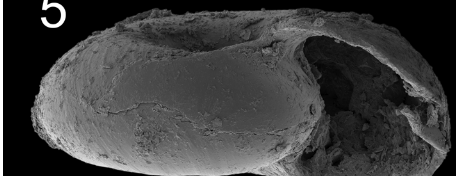

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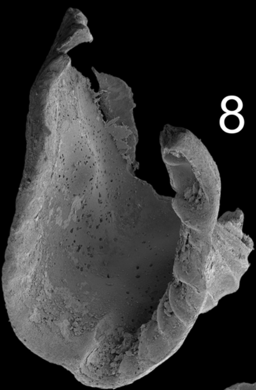

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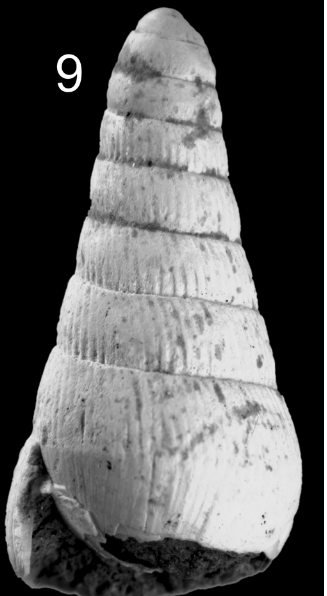

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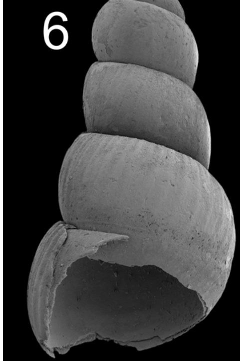

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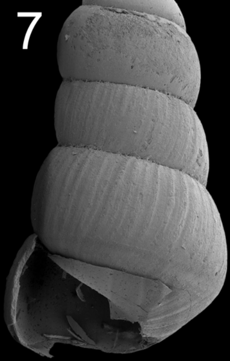

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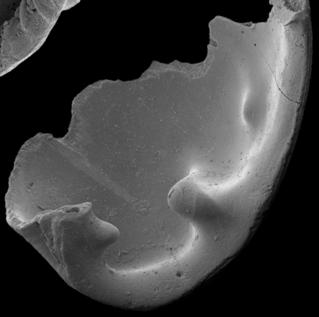

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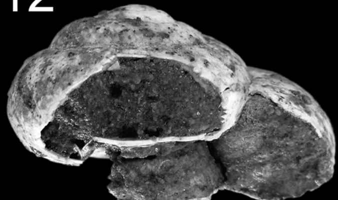

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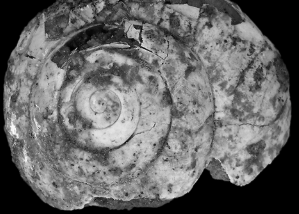

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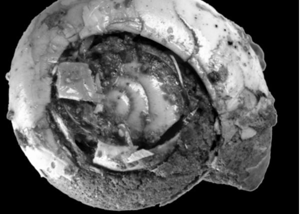

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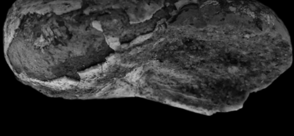

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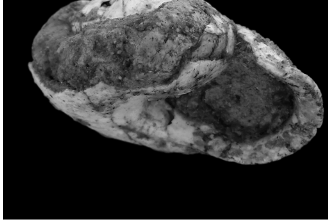

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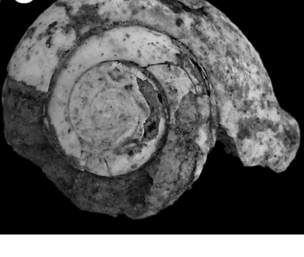

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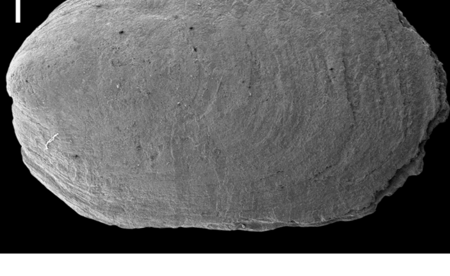

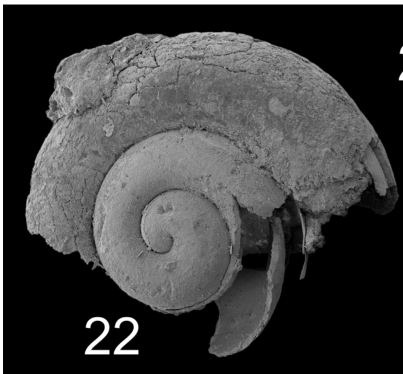

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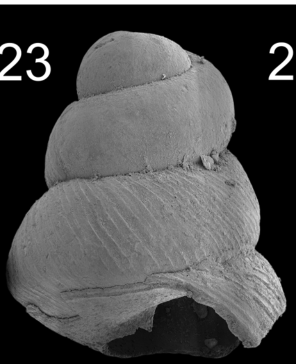

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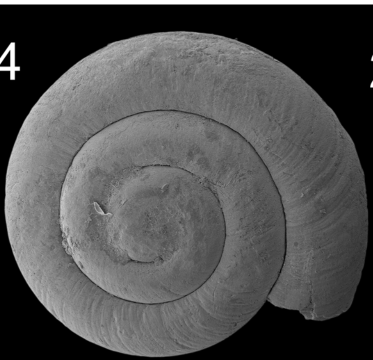

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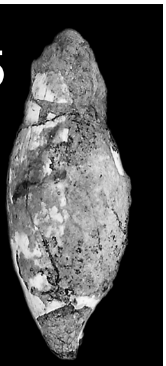

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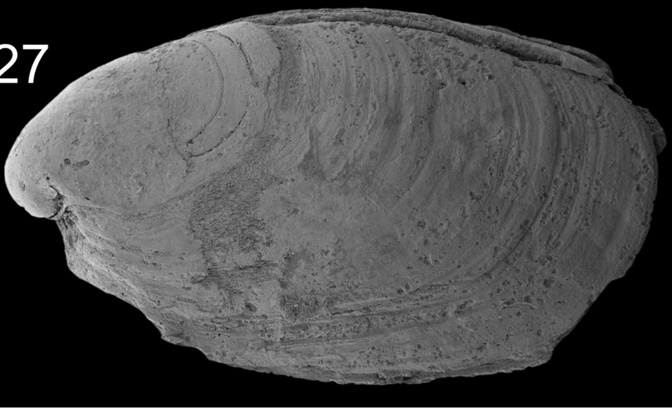

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**FIGURE 22.** *Discus* sp., juvenile (BSPG 1952 XVIII 41; D = 1.5 mm).
**FIGURE 23.** *Granaria* sp. (BSPG 1952 XVIII 47; H = 1.6 mm).
**FIGURE 24.** *Lucilla subteres* (BSPG 1952 XVIII 4; D = 1.7 mm).
**FIGURE 25.** *Pseudoleacina* sp. (BSPG 1952 XVIII 15; H = 16.3 mm, D = 6.2 mm).
**FIGURE 26.** *Palaeoglandina gracilis* (BSPG 1952 XVIII 14; H = 38.2 mm, D = 22.3 mm, h = 28.2 mm, d = 14.5 mm).
**FIGURE 27.** *Testacella schuetti* (BSPG 1952 XVIII 22; H = 4.7 mm, D = 2.7 mm).

**FIGURE 1.** *Pomatias consobrina* (BSPG 1952 XVIII 17; H = 15.8 mm, D = 14.1 mm).
**FIGURE 2.** *Pomatias consobrina*, operculum (BSPG 1952 XVIII 17; h = 7.3 mm, d = 6.3 mm).
**FIGURE 3.** *Bithynia* sp., operculum (BSPG 1952 XVIII 18; h = 3.3 mm, d = 2.4 mm).
**FIGUREs 4–5.** *Gyraulus* sp., juvenile (BSPG 1952 XVIII 16; H = 0.4 mm, D = 0.7 mm).
**FIGURE 6.** Clausiliidae indet., spire fragment (BSPG 1952 XVIII 37; H = 2.9 mm).
**FIGURE 7.** Clausiliidae indet., spire fragment (BSPG 1952 XVIII 37; H = 2.3 mm).
**FIGURE 8.** Clausiliidae indet. (possibly *Pseudidyla*), aperture fragment (BSPG 1952 XVIII 36; h = 2.3 mm, d = 1.3 mm).
**FIGURE 9.** *Triptychia* sp. (BSPG 1952 XVIII 53; H = 10.2 mm, D = 5.1 mm).
**FIGURE 10.** *Azeca* cf. *lubricella*, aperture fragment (BSPG 1952 XVIII 45; h = 2.0 mm).
**FIGURE 11.** Gastrodontoidea indet. (BSPG 1952 XVIII 38; D = 9.0 mm).
**FIGUREs 12–13.** *Archaeozonites* sp. (BSPG 1952 XVIII 42; H = 17.6 mm, D = 28.6 mm).
**FIGURE 14.** *Klikia* cf. *coarctata* (BSPG 1952 XVIII 7; D = 7.8 mm).
**FIGURES 15–16.** *Cepaea* cf. *eversa* (BSPG 1952 XVIII 8; H = 20.3 mm; D = 27.4 mm; h = 10.3 mm; d = 14.3mm).
**FIGURES 17–18.** *Cepaea* cf. *sylvestrina* (BSPG 1952 XVIII 49; H = 16.4 mm; D = 25.2 mm; h = 9.1 mm; d = 13.5 mm).
**FIGURES 19–20.** *Tropidomphalus* cf. *incrassatus* (BSPG 1952 XVIII 5; H = 14.1 mm; D = 28.8 mm; h = 11.7 mm; d = 17.7 mm).
**FIGURE 21.** *Limax* sp. (BSPG 1952 XVIII 3; H = 5.9 mm, D = 3.7 mm).

## Discussion

**Taxonomy and preservation.** The preservation of the larger specimens from many OSM fossil sites may present some problems for taxonomy (Gall 1973; Moser *et al*. 2009; Salvador 2013b). The fossils can be compressed or inflated, producing a more flattened or rounded overall appearance and thus hampering a precise taxonomic determination at species level. As remarked by Gall (1973) for the helicids of Sandelzhausen (MN 5), a locality just a few kilometers away from Gündlkofen, a "blown-up" specimen of species "A" might appear as a member of the more spherical species "B". Nevertheless, this bias is often not considered when identifying the larger fossil snails, and authors end up identifying or describing many species or subspecies more than actually present (*e.g.*, Gall 1972).

In the case of Gündlkofen this preservation bias affects the specimens of *Palaeoglandina*, *Archaeozonites*, *Cepaea* and *Tropidomphalus*. As such, here a great care was taken when identifying the specimens, using characters other than overall shell shape and using material from the original descriptions (and later revisions) of other Middle Miocene sites from Southern Germany (housed at the SMNS and BSPG). Nevertheless, the identification beyond genus level must unfortunately remain tentative.

Largely due to this preservation bias, Gall (1980) slightly overestimated the number of species in Gündlkofen, listing 34 species for the site. This number was reduced to 20 in the present work. Nevertheless, it should be noted that the lots of five of Gall's supposed species could not be found, as explained above, so the actual number of species in Gündlkofen could be a little higher.

**Remarks on the paleoenvironment.** The molluscan fauna from Gündlkofen is remarkable for the near absence of freshwater species: only a single *Gyraulus* sp. and three opercula of *Bithynia* sp. were recovered. The lack of other hygrophilous microgastropods such as the Carychiinae and Succineidae, commonly found in the German Miocene (*e.g.*, Strauch 1977), is also striking. *Gyraulus* and *Bithynia* are usually related to still (and often temporary) waters (Welter-Schultes 2012), which, together with features of the site's lithology, led Gall (1980) to propose that Gündlkofen represents an environment like an oxbow lake.

Gall (1980) defined the mollusks of Gündlkofen as a relatively hygrophilic assemblage. The present work agrees with this statement, since most of the genera prefer more humid conditions; land snail habitats tend not to vary much in genus level, facilitating comparisons with the recent fauna (Barker 2001; Cook 2001; Pearce & Örstan 2006) and thus being very useful for environmental reconstructions. As such, the area seems to have been covered with a damp and warm forest and scrubland (Gall 1980). Nevertheless, a few species more oriented towards drier (such as *Tropidomphalus* cf. *incrassatus* and perhaps also *Cepaea* cf. *eversa*) or rockier environments (likely *Palaeoglandina* and *Milax*; Gall 1980) occur in a considerable number, possibly indicating a variety of habitats near the site. Since most of these species have sturdier shells, they could have been transported from farther away.

Finally, the most obvious comparison of the fossil molluscan fauna from Gündlkofen is with Sandelzhausen, a neighboring and nearly coeval site (Salvador 2013a, 2013b, 2014; Salvador & Rasser submitted). Gall (1980) already examined this relationship and the present work largely agrees with his findings. After the present revision Gündlkofen shares nearly 80% of its land snail genera and 40% of its species with Sandelzhausen; this percentage is a little lower than that given by Gall (1980), but still meaningful. Nevertheless, Sandelzhausen has also attracted different hygrophilous species to its riparian zone, *e.g.*, *Succinea minima* Klein and members of the genus *Carychium* O.F. Müller (Salvador 2013b, 2014), due to its richer freshwater environment (Gall 1972; Moser *et al*. 2009; Salvador & Rasser submitted). As these conditions seem not to be present in Gündlkofen (Gall 1980), some differences in faunal compositions will inevitably be found; moreover, Gündlkofen appears to be slightly younger than Sandelzhausen (Gall 1980), which could also account for differences in their faunas.

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RESEARCH PAPER

# The fossil pulmonate snails of Sandelzhausen (Early/Middle Miocene, Germany): Ellobiidae, Pupilloidea, and Clausilioidea

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**Abstract** Sandelzhausen is an Early/Middle Miocene (Mammal Neogene zone MN5) fossil site near Mainburg, S Germany, that despite its small size harbors a rich fossil record. Thousands of fossil continental mollusks, almost exclusively pulmonate snails, were recovered during the excavations, but did not receive much attention from researchers. Here, the first part of a formal taxonomic treatment of Sandelzhausen's fossil pulmonates is presented, dealing with the superfamilies Ellobioidea, Pupilloidea, and Clausilioidea, and including the description of a new species. The following species were found in the material: *Carychium eumicron* and *Carychium galli* sp. nov. (Ellobiidae); *Granaria* cf. *grossecostata* and *Granaria* sp. (Chondrinidae); *Gastrocopta acuminata* and *Gastrocopta nouletiana* (Gastrocoptidae); *?Pyramidula* sp. (Pyramidulidae); *Strobilops* sp. (Strobilopsidae); *Vallonia lepida* (Valloniidae); *Vertigo callosa* (Vertiginidae); *Pseudidyla moersingensis* (Clausiliidae); *Triptychia* sp. (Filholiidae).

**Keywords** *Carychium galli* new species · Gastropoda · MN5 European Mammal Neogene zone · Pulmonata · Stylommatophora

**Kurzfassung** Sandelzhausen ist eine mittelmiozäne (Säugerzone MN5) Fossilfundstelle nahe Mainburg in Süddeutschland. Trotz Ihrer geringen geographischen Ausdehnung bietet sie eine reiche Fauna an kontinentalen Mollusken, nahezu ausschließlich pulmonate Gastropoden, die bei Ausgrabungen geborgen wurden, aber nur wenig wissenschaftliche Beachtung fanden. Vorliegende Studie stellt den ersten Teil einer formalen taxonomischen Bearbeitung der fossilen Pulmonaten von Sandelzhausen dar. Sie behandelt die Überfamilien Ellobioidea, Pupilloidea und Clausilioidea, einschließlich der Beschreibung einer neuen Art. Folgende Arten wurden gefunden: *Carychium eumicron* and *Carychium galli* sp. nov. (Ellobiidae); *Granaria* cf. *grossecostata* und *Granaria* sp. (Chondrinidae); *Gastrocopta acuminata* und *Gastrocopta nouletiana* (Gastrocoptidae); *?Pyramidula* sp. (Pyramidulidae); *Strobilops* sp. (Strobilopsidae); *Vallonia lepida* (Valloniidae); *Vertigo callosa* (Vertiginidae); *Pseudidyla moersingensis* (Clausiliidae); *Triptychia* sp. (Filholiidae).

**Schlüsselwörter** *Carychium galli* nov. spec. · Gastropoda · Mammal Neogene Zone MN5 · Pulmonata · Stylommatophora

## Introduction

The Sandelzhausen fossil site is a Fossil-Lagerstätte and one of the most important continental sites in Europe (Moser et al. 2009a). Besides some plant remains, a fauna of more than 200 metazoan species (and 50,000 specimens) was collected, including mollusks, ostracods, and representatives of all vertebrate classes, although the mammals have received the most attention (Moser et al. 2009a, and references therein). Gastropods were among the first fossils found in Sandelzhausen, and thousands of specimens were collected before the site was closed in the last decade. Only three works dealt specifically with these mollusks. Gall (1972) identified 49 gastropod and two bivalve species, but

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based his work heavily on faunas such as Sansan, in France, that are now known to be younger (Moser et al. 2009b). Gall (1973) dealt with aspects of the taphonomy and preservation of the larger shells. Moser et al. (2009b) dealt with paleoecological questions, and thus presented only a preliminary classification of the mollusks. The present study is the first part of a taxonomic treatment of the fossil mollusks from Sandelzhausen, dealing with the superfamilies Ellobioidea, Pupilloidea, and Clausilioidea (12 species in total). Further works describing the remaining fauna will soon follow (e.g., Salvador 2013).

## Geological setting

The Sandelzhausen fossil site was located in the vicinity of the city of Mainburg, 60 km north of Munich, in the Molasse Basin (Molassebecken) of southern Germany, which harbors the "formation" known as the Upper Freshwater Molasse (Ober Süßwassermolasse, OSM; Moser et al. 2009a). The fossils from Sandelzhausen derive from a member of the OSM called Nördlicher Vollschotter, composed primarily of marl and gravel (Moser et al. 2009a). The age of these fossiliferous deposits was established by stratigraphic, biostratigraphic, and magnetostratigraphic correlations: the Early/Middle Miocene Burdigalian/Langhian boundary, early middle MN5 European Mammal Neogene zone (~16.47–16.27 Ma; Moser et al. 2009a).

The facies types of the deposits from Sandelzhausen were studied by Fahlbusch and Gall (1970) and Moser et al. (2009a). 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 the size and number of 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 carbonatic nodules; rich in fossils, many in an excellent state of preservation due to a less intense compaction; *layer E:* silty clays with microvertebrate fossils; *Layer F:* laminite with alternating light and dark bands, carbonate concretions and desiccation cracks; no fossils. Fossil mollusks can be found in layers A to D; a more detailed description of the lithology was given by Moser et al. (2009a).

## Materials and methods

All of the material from Sandelzhausen is housed at the collection of the Bayerische Staatssammlung für Paläontologie und Geologie (BSPG; Munich, Germany) under the record number BSPG 1959 II. All available specimens of the three superfamilies were analyzed for this work; a list of the examined material follows each species description. All specimens in a good state of preservation were measured either with digital calipers or with the aid of computer software. Abbreviations used with shell measurements: H = shell length; D = shell greatest width; S = spire length (excluding aperture); S′ = spire length (excluding body whorl); h = aperture height; d = aperture width. The spire angle used here is the "mean spire angle" sensu Moore (1960). Selected specimens were examined by scanning electronic microscopy (SEM) in the Staatliches Museum für Naturkunde Stuttgart (SMNS; Stuttgart, Germany). Since only two works have attempted to identify the mollusks from Sandelzhausen (Gall 1972; Moser et al. 2009b), the previous identification given by these authors was included here in order to facilitate future correspondence among the works.

The excavation site in Sandelzhausen was divided into a square grid, so a good part of the material has precise data about where it was found. A portion of the material shows data on the original height within the section and can thus be attributed to the layers published by Fahlbusch and Gall (1970) and Moser et al. (2009b). However, a good portion of the material, despite having the original height in the sediment recorded, cannot be unmistakably attributed to the layers, since the given measurements are not precise enough (Markus Moser, personal communication). Moreover, many specimens completely lack locality data, while some have labels that cannot be traced back to a precise point within the excavation site, such as the samples labeled "Grube Bergmaier" (taken during the earliest test excavations by Richard Dehm; Moser et al. 2009b) and "Testprofil 1966" (a test section preceding the start of the main excavations). As such, only the samples that can be attributed to distinct layers were taken into account here to determine the stratigraphical range of each species.

## Systematics

### Superfamily Ellobioidea Pfeiffer, 1854
### Family Ellobiidae Pfeiffer, 1854
Genus *Carychium* O.F. Müller, 1773

*Carychium (Carychiella) eumicron* Bourguignat, 1857
(Fig. 1)

*Carychium eumicron* Bourguignat, 1857: 253.
*Carychium eumicron peneckei*: Wenz, 1923b: 1190; Gall, 1972: 14.
*Carychium (Carychiella) eumicron*: Strauch, 1977: 159 (pl. 14, figs. 13–15; pl. 17, fig. 53; pl. 19, fig. 76).

*Carychium eumicrum*: Stworzewicz, 1999a: 264 (figs. 5–6).
*Carychium* sp. 3: Moser et al., 2009b: 47.

**Material examined:** BSPG 1959 II 17272 (2 specimens).

**Stratigraphic occurrence:** Unknown (the sample lacks stratigraphical data).

**Description:** Shell diminutive, pupiform to fusiform; apex narrow, acuminated; greatest width on body whorl (width ~1/2 shell length). Protoconch (~1 whorl) dome-shaped, smooth, rapidly increasing in size; transition to teleoconch unclear. Whorl profile convex. Suture well-marked, deep. Teleoconch smooth, except for fine growth lines. Aperture ellipsoid; ~2/5 shell length. Peristome narrow, very weakly reflexed. Two apertural barriers: a well-marked parietal lamella and a very faint median palatal tooth. Umbilicus rimate, very shallow.

**Measurements (in mm):** 3½ to 4 whorls; $H = 1.2$; $D = 0.6$; $S = 0.8$; $S' = 0.5$; $h = 0.4$; $d = 0.4$.

**Previous identification of the material:** Gall (1972: Nr. 30): *Carychium eumicron peneckei* Flach. (Moser et al. 2009b: Nr. 27): *Carychium* sp. 3.

**Discussion:** The subgenus *Carychiella* Strauch, 1977 is easily recognized by its much smaller size than other Carychiinae. The specimens from Sandelzhausen fit well with *C. eumicron* in terms of their size, aperture shape. and weak dentition (the strength of the apertural barriers is variable in the species, but the columellar lamella is always almost invisible or completely lacking; Strauch 1977; Stworzewicz 1999a). The species is known from Central Europe from the Late Oligocene to Middle Miocene, and the division in subspecies is deemed unnecessary (Strauch 1977; Stworzewicz 1999a).

*Carychium (Carychium) galli* sp. nov.
(Figs. 2, 3 and 4)

*Carychium nouleti nouleti*: Gall, 1972: 14.
*Carychium nouleti gibbum*: Gall, 1972: 14.
*Carychium* sp. 1: Moser et al.: 2009b: 47.
*Carychium* sp. 2: Moser et al.: 2009b: 47.

**Type material:** Holotype: BSPG 1959 II 17271 (Fig. 2). Paratypes: 17273 (23 specimens; Fig. 4), 17274 (~100 specimens; Fig. 3), 17675 (1 specimen).

**Etymology:** Named in honor of Horst Gall (1938–1980), the first paleontologist to work with the mollusks from Sandelzhausen (Dehm 1980).

**Type locality:** Sandelzhausen, Mainburg, Germany; 48°37′36.9″N 11°48′11.6″E; 493 m height.

**Stratigraphical occurrence:** Layer C3 (1 specimen). Moreover, 23 specimens come from the "Grube Bergmaier" sample and ~100 others (including the holotype) from samples with no stratigraphical data.

**Age:** Early/Middle Miocene, Burdigalian/Langhian boundary (early middle MN5 European Mammal Neogene zone; 16.47 or 16.27 Ma; Moser et al. 2009a).

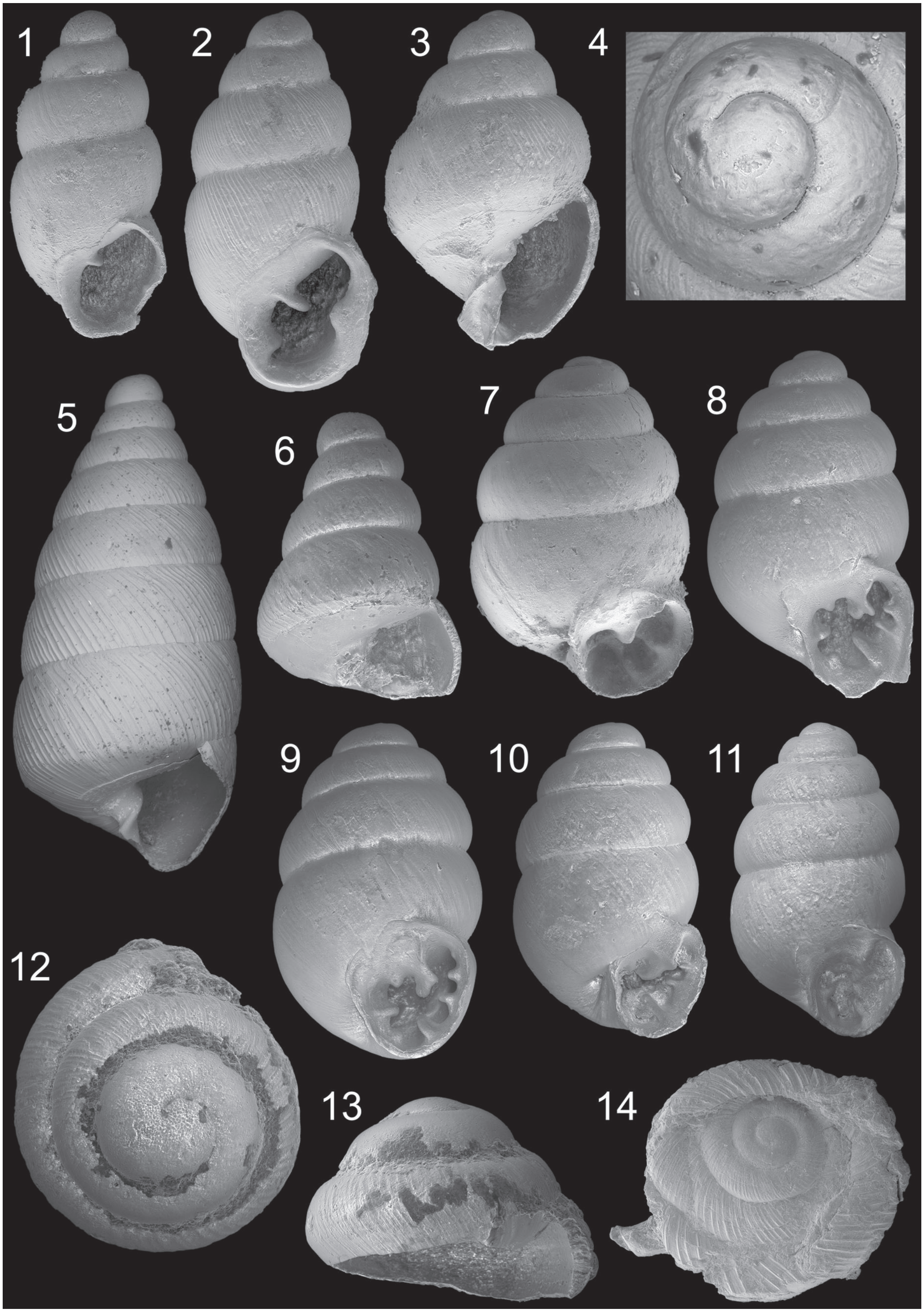
**Diagnosis:** Shell pupiform to fusiform; sculptured by slightly prosocline and very fine axial ribs; peristome thickened and strongly reflexed; encounter of regions of peristome rounded to strongly angled; parietal lamella (columellar apparatus) simple and narrow; palatal tooth strong and distinct.

**Description:** Shell diminutive, pupiform to fusiform; greatest width on body whorl (width ~1/2 shell length); apex may be very narrow in some specimens, giving them a more acuminated appearance. Spire angle ~50°. Protoconch (1½ whorl) dome-shaped and rapidly increasing in size, smooth; transition to teleoconch unclear. Whorl profile convex. Suture well-marked, deep. Teleoconch sculptured by slightly prosocline and very fine axial ribs; distance between ribs approximately equal to width of rib. Aperture trapezoid; ~2/5 shell length and ~1/2 shell width. Peristome thickened and greatly reflexed; parietal callus present, but not much developed. Separation of peristome regions (parietal, palatal, basal, and columellar) varies from rounded to very strongly angled. Three apertural barriers: columellar lamella, parietal lamella, and median palatal tooth. Columellar lamella weak, not running too deep towards shell interior (~1/4 whorl). Parietal lamella narrow, but high and strong, continuing towards interior of shell to form a narrow, small and simple (i.e., without any sinuosity) internal lamellae (or columellar apparatus). Palatal tooth strong, distinct. Umbilicus rimate, very shallow.

**Measurements (in mm):** 4 to 4½ whorls; $H = \sim 1.7$; $D = \sim 0.8$; $S = \sim 0.9$; $S' = \sim 0.7$; $h = \sim 0.7$; $d = \sim 0.6$.
**Holotype:** 4¼ whorls; $H = 1.6$; $D = 0.8$; $S = 0.9$; $S' = 0.7$; $h = 0.7$; $d = 0.6$.

**Previous identification of the material:** (Gall 1972: Nr. 31 and 32): *Carychium nouleti nouleti* Bourguignat, 1857 and *C. n. gibbum* Sandberger, 1874. (Moser et al. 2009b: Nr. 25 and 26): *Carychium* sp. 1 and *Carychium* sp. 2.

**Discussion:** Both Gall (1972) and Moser et al. (2009b) suggested that, excluding the diminutive *Carychium eumicron*, two larger species of the genus occurred in the deposits from Sandelzhausen: a broad form and a more slender and taller one. However, both fossil and Recent *Carychium* species can show a good amount of variability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◀**Fig. 1–14** **1** *Carychium eumicron* (BSPG 1959 II 17272; *H* = 1.2 mm). **2** *Carychium galli* sp. nov. (BSPG 1959 II 17271, holotype; *H* = 1.6 mm). **3** *Carychium galli* sp. nov., internal lamella detail (BSPG 1959 II 17274, paratype; *H* = 1.1 mm). **4** *Carychium galli* sp. nov., protoconch detail (BSPG 1959 II 17273, paratype). **5** *Granaria* cf. *grossecostata* (BSPG 1959 II 16151; *H* = 5.6 mm). **6** *Granaria* sp. (BSPG 1959 II 17266; *H* = 2.5 mm). **7** *Gastrocopta acuminata* (BSPG 1959 II 17254; *H* = 2.4 mm). **8** *Gastrocopta nouletiana* (BSPG 1959 II 17244; *H* = 2.1 mm). **9** *Gastrocopta nouletiana* (BSPG 1959 II 17244; *H* = 2.0 mm). **10** *Gastrocopta nouletiana* (BSPG 1959 II 17240; *H* = 2.0 mm). **11** *Gastrocopta nouletiana* (BSPG 1959 II 17241; *H* = 2.2 mm). **12**, **13** *?Pyramidula* sp. (BSPG 1959 II 17270; *H* = 1.4 mm, *D* = 1.4 mm). **14** *Strobilops* sp., deformed specimen (BSPG 1959 II 17297; *D* = 2.2 mm)

in their shells, not only in overall shell shape but especially in the whorls' height and relative proportion (Bulman 1990; Stworzewicz 1999a). In the material from Sandelzhausen, two forms—one broader and the other slender—do indeed occur, but there are also many intermediate forms and, moreover, the difference in overall shell shape is not as pronounced. Moreover, these forms cannot be distinguished using other characters, such as apertural barriers and the shape of the internal portion of the parietal lamella (important characters in the taxonomy of the group; Strauch 1977; Stworzewicz 1999a). Therefore, it appears that only a single *Carychium* species is present in this material.

One of the most important characteristics of the genus is the distinction between forms with simple or sinuous internal lamellae (the parietal lamella on the aperture is the outermost portion of a columellar apparatus). This difference led Strauch (1977) to diagnose two subgenera: *Carychium* s. str., with a simple lamella, and *Saraphia* Risso, 1826, with a sinuous one. Though this division does not always seem to be entirely applicable to recent species (Bank and Gittenberger 1985), the Tertiary fossils seem to be clearly divided in this way (Strauch 1977; Stworzewicz 1999a).

The species that most closely resembles *Carychium (Carychium) galli* sp. nov. is *Carychium nouleti* Bourguignat, 1857, a Miocene fossil known from many localities throughout Central Europe (Strauch 1977; Stworzewicz 1999a), and originally described from Sansan (MN6), France. This is reflected in Gall's (1972) previous classification of the material from Sandelzhausen as two subspecies of *C. nouleti*. Its overall shell shape is strikingly similar, although *C. galli* is somewhat broader and more fusiform, while *C. nouleti* has a more acuminated spire. However, the main feature distinguishing *C. galli* from *C. nouleti* (and from all other similar Miocene species) is its simple internal lamella (Fig. 3); all others have sinuous lamellae (Strauch 1977). This simple internal lamella of *C. galli* places it in the subgenus *Carychium* s. str. of Strauch (1977). *Carychium* is a very widespread genus in the Miocene of Central Europe, but no form with a simple internal lamella has been reported from this period; so far, species presenting this character are restricted to a time interval ranging from the Pliocene to the Recent (Strauch 1977). As such, *C. galli* is the earliest known form of the subgenus.

Other diagnostic features of *C. galli* are its thickened and greatly reflexed peristome, a well-developed and distinct palatal tooth, and the angles formed by the encounter of the regions of the peristome (Fig. 2).

**Superfamily Pupilloidea Turton, 1831**
**Family Chondrinidae Steenberg, 1925**
Genus *Granaria* Held, 1838

*Granaria* cf. *grossecostata* (Gottschick and Wenz, 1919) (Fig. 5)

*Torquilla schübleri grossecostata* Gottschick and Wenz, 1919: 4 (pl. 1, fig. 3).
*Abida antiqua grossecostata*: Wenz, 1923a: 942.
*Napaeus?* sp. (in part): Gall, 1972: 13.
*Granaria* sp. 1: Moser et al., 2009b: 48 (fig. 6I).

**Material examined:** BSPG 1959 II 16151 (1 specimen), 17262 (5 specimens), 17263 (3 specimens), 17264 (4 specimens), 17265 (1 specimen), 17681 (1 specimen).

**Stratigraphic occurrence:** Layers B2 (1 specimen) and C3 (5 specimens). Moreover, 6 specimens were found in the "Grube Bergmaier" sample, and 3 others on a sample without stratigraphical data.

**Description:** Shell small, multispiral, pupiform to conical; greatest width on last whorl. Spire angle ~35°. Protoconch (1½ whorl) blunt, wide, smooth; transition to teleoconch clear. Whorl profile slightly convex. Suture well-marked, but not deep; approximately perpendicular to columellar axis on first whorls, becoming more oblique on last whorls. Teleoconch sculptured by regularly distributed, fine, well-marked, prosocline ribs; ribs finer on first whorls of teleoconch, but becoming coarser towards the aperture; distance between ribs approximately twice the rib's size; ~80 ribs on last whorl. Whorls regularly increasing in size towards aperture. Columellar lamella ("Columellaris" sensu Gittenberger, 1973) present.

**Measurements (in mm):** BSPG 1959 II 16151 (incomplete specimen): 7½ whorls; *H* = 5.6; *D* = 2.6.

**Previous identification of the material:** (Gall 1972: Nr. 29, in part): *Napaeus?* sp. (Moser et al. 2009b: Nr. 32, fig. 6I; Fig. 5 herein): *Granaria* sp. 1.

**Discussion:** Chondrinids are well documented throughout the Miocene of Central Europe and all fossil forms are classified into the genus *Granaria* due to their apertural teeth and lamellae as well as their usually large size (Gittenberger 1973; Höltke and Rasser 2013). The apertural teeth and lamellae are the most important diagnostic features at both genus and species level (Gittenberger 1973; Höltke and Rasser 2013). Unfortunately, this feature cannot be seen in the specimens from Sandelzhausen: the most complete shell (BSPG 1959 II-16151; for all others, only the spire tops are preserved) lacks an aperture, and only the columellar lamellae (the "Columellaris" sensu Gittenberger, 1973) can be seen. However, this specimen, albeit incomplete, is strikingly similar to *G. grossecostata*, mainly in terms of its conical shell profile, deeply marked suture, slightly convex whorls, and fine, well-marked, and regular prosocline ribs. *G. grossecostata* was considered a subspecies of *G. schuebleri* (Klein, 1846), but was deemed a full species in the recent revision of fossil *Granaria* by Höltke and Rasser (2013). *G. grossecostata* occurs in Steinheim am Albuch (Middle Miocene, MN7; Gottschick and Wenz 1919; Höltke and Rasser 2013), a locality geographically close (ca. 130 km) to Sandelzhausen but somewhat younger. Therefore, as the apertural region and its dentition are unknown, the present material is only tentatively identified as *G.* cf. *grossecostata*.

*Granaria* sp.
(Fig. 6)

**Material examined:** BSPG 1959 II 17266 (1 specimen), 17267 (1 specimen), 17268 (2 specimens), 17269 (6 specimens); 17298 (3 specimens), 17299 (1 specimen), 17682 (7 specimens).

**Stratigraphic occurrence:** Layers B2 (1 specimen) and C3 (2 specimens). Moreover, 12 specimens were found in the "Grube Bergmaier" sample and 6 others on a sample without stratigraphical data.

**Description:** Shell small, multispiral, with acuminated spire top. Protoconch (1½ whorl) narrow, rounded, smooth; transition to teleoconch unclear. Whorl profile convex. Suture deep; obliquely (diagonally) positioned in relation to columellar axis. Teleoconch sculptured by regularly distributed, very fine (sometimes indistinct) prosocline ribs; distance between ribs approximately twice the size of the rib.

**Measurements (in mm):** BSPG 1959 II 17266 (incomplete specimen): 4 whorls; $H = 2.5$; $D = 1.7$.

**Previous identification of the material:** Gall (1972: Nr. 29, in part): *Napaeus?* sp. Moser et al. (2009b: Nr. 33 and 39): *Granaria* sp. 2 and ?Chondrinidae/?Enidae (fam., gen. et sp. indet.). Moreover, the specimens identified as *Cochlostoma* sp. (Caenogastropoda: Diplommatinidae) by Moser et al. (2009b: Nr. 3) are only spire top fragments and are indistinguishable from the spires of *Granaria* sp.

**Discussion:** The best-preserved specimen is composed of only 4 whorls, including the protoconch (BSPG 1959 II-17266). Even so, this second *Granaria* species from Sandelzhausen can be distinguished from the above-described *G.* cf. *grossecostata* by its more acute spire, narrower and more rounded protoconch, higher and more convex whorls, and by the ribs being very fine and sometimes almost indistinct. A more precise identification is not possible.

**Family Gastrocoptidae Pilsbry, 1918**
Genus *Gastrocopta* Wollaston, 1878

*Gastrocopta acuminata* (Klein, 1846)
(Fig. 7)

*Pupa acuminata* Klein, 1846: 75 (pl. 1, fig. 19).
*Gastrocopta (Albinula) acuminata acuminata*: Wenz, 1923a: 916; Gall, 1972: 13.
*Gastrocopta acuminata*: Stworzewicz, 1999b: 161 (figs. 56–58).
*Gastrocopta (Albinula) acuminata*: Manganelli & Giusti, 2000: 60 (pl. 1, figs. 1–6; pl. 2, figs. 1–7); Moser et al., 2009b: 48.

**Material examined:** BSPG 1959 II 17254 (1 specimen), 17255 (1 specimen), 17683 (2 specimens), 17685 (9 specimens).

**Stratigraphic occurrence:** Layer D1 (2 specimens). Moreover, 2 specimens come from the Grube Bergmaier site and 9 others from a sample without stratigraphical data.

**Description:** Shell diminutive, ovate; greatest width on body whorl (width ~2/3 shell length). Spire angle 45°–50°. Protoconch (1¼ whorl) blunt, smooth; transition to teleoconch clear. Whorl profile convex. Suture well-marked, deep. Teleoconch smooth, except for growth lines. Body whorl ~1/2 shell length. Aperture rounded triangular; aperture ~1/3 shell length and ~1/2 shell width. Peristome reflexed; parietal callus present. Four apertural barriers: upper palatal tooth, lower palatal tooth, columellar lamella, anguloparietal lamella. Anguloparietal lamella bifid. Palatal teeth roughly equal in size. Columellar lamella weak. Umbilicus narrow.

**Measurements (in mm):** BSPG 1959 II 17254: 4½ whorls; $H = 2.5$; $D = 1.6$; $S = 1.8$; $S' = 1.2$; $h = 0.7$; $d = 0.8$.

**Previous identification of the material:** Gall (1972: Nr. 25): *G. (Albinula) acuminata acuminata* (Klein, 1846). Moser et al. (2009b: Nr. 37): *G. (Albinula) acuminata* (Klein, 1846).

**Discussion:** The specimens from Sandelzhausen compare well to *G. acuminata*, as recently revised by Manganelli and Giusti (2000). This species is commonly found in the European fossil record, occurring from the Middle Miocene (MN 5) to the Late Pliocene and perhaps even the Early Pleistocene (Stworzewicz 1999b).

*Gastrocopta nouletiana* (Dupuy, 1850)
(Figs. 8, 9, 10 and 11)

*Pupa Nouletiana* Dupuy, 1850: 309 (pl. 15, fig. 6).
*Gastrocopta (Sinalbinula) nouletiana nouletiana*: Wenz, 1923a: 930; Gall, 1972: 13.
*Gastrocopta nouletiana*: Stworzewicz, 1999b: 163 (figs. 59–61).
*Gastrocopta (Sinalbinula) nouletiana*: Moser et al., 2009b: 48 (fig. 6G).

**Material examined:** BSPG 1959 II 16149 (1 specimen), 17240 (1 specimen), 17241 (7 specimens), 17242 (14 specimens), 17243 (1 specimen), 17244 (12 specimens), 17245 (17 specimens), 17246 (1 specimen), 17247 (1 specimen), 17248 (2 specimens), 17249 (5 specimens), 17250 (2 specimens), 17251 (1 specimen), 17252 (2 specimens), 17253 (1 specimen), 17687 (27 specimens).

**Stratigraphic occurrence:** Layers B2 (1 specimen) and D1 (58 specimens). Moreover, 7 specimens were found in the "Grube Bergmaier" sample, and 28 lack stratigraphical data.

**Description:** Shell diminutive, ovate; greatest width on body whorl (width ~1/2 shell length). Spire angle 45–50°. Protoconch (1½ whorl) blunt, smooth; transition to teleoconch unclear. Whorl profile convex. Suture well-marked, deep. Teleoconch smooth, except for growth lines. Body whorl ~2/5 shell length. Aperture rounded triangular to almost circular; aperture ~1/3 shell length and ~3/5 shell width. Peristome reflexed; parietal callus present. Apertural barriers totaling 7: suprapalatal tooth, upper palatal tooth, lower palatal tooth, basal tooth, columellar lamella, infraparietal lamella, anguloparietal lamella. Infraparietal lamella and/or the suprapalatal tooth lacking in some specimens. Anguloparietal lamella with overall bifid aspect: angular lamella vertically positioned, large, thick; parietal lamella narrow, folded towards the outer lip. After the anguloparietal lamella, the strongest barrier is the lower palatal tooth. Umbilicus very narrow, deep.

**Measurements (in mm):** 4½ to 5 whorls; $H = \sim 2.1$; $D = \sim 1.2$; $S = \sim 1.3$; $S' = \sim 0.9$; $h = \sim 0.7$; $d = \sim 0.7$.

**Previous identification of the material:** Gall (1972: Nr. 26): *G. (Sinalbinula) nouletiana nouletiana* (Dupuy, 1850). Moser et al. (2009b: Nr. 38, fig. 6G): *G. (Sinalbinula) nouletiana* (Dupuy, 1850).

**Discussion:** *Gastrocopta nouletiana* is a frequent species throughout the Miocene European fossil record; its type locality is Sansan (MN6), in France (Dupuy 1850). The specimens from Sandelzhausen fit well with this species when taking into account the aperture and dentition (especially the way in which the parietal and angular lamellae are united into the anguloparietal lamella), the most important features in the family's taxonomy. The specimens from Sandelzhausen show some variation in overall shell shape, from more ovate shells (e.g., Fig. 10) to more elongated and slender ones (e.g., Fig. 12); moreover, more elongated specimens usually have circa half a whorl more than the more ovate ones. The anguloparietal lamella has an overall bifid aspect, with the angular lamella being vertically positioned and larger and thicker than the parietal one, which is folded towards the outer lip. After the anguloparietal lamella, the strongest barrier is the lower palatal tooth. The total number of apertural barriers is seven, but this may sometimes vary: a few specimens lack the infraparietal lamella and/or the suprapalatal tooth; in the other specimens, these barriers are the weakest ones.

Interestingly, some of the more elongated and slender specimens mentioned above resemble *G. sandbergeri* Stworzewicz and Prisyazhnyuk, 2006, a species from Bełchatów (type locality; MN5, Poland) and Steinheim am Albuch (MN7-8, Germany), formerly known as *G. suevica* Sandberger, 1875, a nomen nudum (Stworzewicz and Prisyazhnyuk, 2006). According to Stworzewicz and Prisyazhnyuk (2006), *G. sandbergeri* can be distinguished from *G. nouletiana* by being somewhat more slender, having a weaker crest on the body whorl, and having generally weaker teeth. All of these features can sometimes be seen in *G. nouletiana* specimens from Sandelzhausen, but not necessarily all of them together in the same specimen. Therefore, it seems that this simply represents the spectrum of morphological variation of *G. nouletiana* in Sandelzhausen; moreover, this also raises the possibility that *G. sandbergeri* might be a synonym of *G. nouletiana*.

### Family Pyramidulidae Kennard and B.B. Woodward, 1914

Genus *Pyramidula* Fitzinger, 1833

*Pyramidula* sp.
(Figs. 12, 13)

**Material examined:** BSPG 1959 II 17270 (1 specimen).

**Stratigraphic occurrence:** The single specimen unfortunately comes from a sample without stratigraphical data.

**Description:** Shell diminutive, pyramidal-depressed. Protoconch (1½ whorl) smooth; transition to teleoconch clear. Whorl profile highly convex. Suture deep. Teleoconch sculptured by very fine (sometimes indistinct) prosocline ribs.

**Measurements (in mm):** BSPG 1959 II 17270 (incomplete specimen): 2½ whorls; $H = 1.4$; $D = 1.4$.

**Previous identification of the material:** Moser et al. (2009b: Nr. 34): *Truncatellina* sp.

**Discussion:** The single and fragmentary specimen recovered is undoubtedly a pupilloid and, based on the overall shell shape, the deep suture, and the positioning, height, and convexity of the whorls, seems to belong in the Pyramidulidae. Unfortunately, as the body whorl and aperture are not known, the present identification must remain tentative. Pyramidulids are otherwise unknown in the Tertiary fossil record of Central Europe, and this could be a very interesting record from not only a paleobiogeographical perspective, but also from a paleoecological one, since the Recent species inhabits dry and exposed calcareous rocks (Kerney et al. 1983; Gittenberger and Bank 1996).

**Family Strobilopsidae Wenz *in* Fischer & Wenz, 1915**
Genus *Strobilops* Pilsbry, 1893

*Strobilops* sp.
(Fig. 14)

**Material examined:** BSPG 1959 II 17297 (5 specimens); 17688 (1 specimen).

**Stratigraphic occurrence:** All specimens come from a sample lacking stratigraphical data, but Moser et al. (2009b) stated that *Strobilops* occurs in layers B and C.

**Description:** Shell diminutive. Protoconch (~1 whorl) smooth. Teleoconch sculptured by numerous fine parallel prosocline ribs, stronger on upper portion of whorl; distance between ribs roughly equal to width of rib. Aperture with at least one parietal lamella. Umbilicus wide. Peristome reflexed. Poor preservation precludes a more precise description.

**Measurements (in mm):** BSPG 1959 II 17297 (deformed specimen): 3½ whorls; $D = 2.2$.

**Previous identification of the material:** Gall (1972: Nr. 10, in part): *Discus (Discus) pleuradra pleuradra* (Bourguignat) [sic]. Moser et al. (2009b: Nr. 29 and 30): respectively, *Strobilops (Strobilops)* sp. nov. and *Strobilops (Discostrobilops)* sp.

**Discussion:** The preservation of this material is very poor: all specimens are flattened and deformed. Some features, however, point to the genus *Strobilops*, such as the size, the sculpture pattern, the reflexed peristome, and—especially—the presence of at least one parietal lamella. Moreover, the wide umbilicus and the positioning of the parietal lamella and the aperture could point to the subgenus *Discostrobilops* Pilsbry, 1927, but that is very tentative. *Strobilops* has a rich fossil record in Europe, from the Eocene to the Pliocene (Zilch 1959–1960), but Recent species are restricted to the Americas (Zilch 1959–1960; Moser et al. 2009b).

Moser et al. (2009b) suggested the occurrence of two *Strobilops* species in Sandelzhausen, belonging to different subgenera; however, they did not offer a way to diagnose between these two forms, but stated that both can be diagnosed from other Miocene forms by their fine, sharp, and closely spaced ribs. Here, it is suggested that these two supposed species cannot be distinguished with the present material, and that only one strobilopsid species occurs in Sandelzhausen.

As remarked by Moser et al. (2009b), the sculpture pattern of *Strobilops* sp. from Sandelzhausen is unknown in the European Miocene, although *S. uniplicatus* (Braun, 1851) and *S. subconoideus* Jooss, 1912 show near-similar patterns. Moser et al. (2009b) then suggested that this could be a new species. This scenario seems very likely, but describing a new species based on such poorly preserved material seems unwarranted.

**Family Valloniidae Morse, 1864**
Genus *Vallonia* Risso, 1826

*Vallonia lepida* (Reuss, 1849)
(Figs. 15, 16)

*Helix lepida* Reuss, 1849: 24 (pl. 2, fig. 4).
*Helix (Vallonia) subpulchella* Sandberger, 1874: 544 (pl. 29, figs. 3a–c).
*Vallonia lepida lepida*: Wenz, 1923a: 903.
*Vallonia subpulchella subpulchella*: Gall, 1972: 12.
*Vallonia lepida*: Moser et al., 2009b: 47.

**Material examined:** BSPG 1959 II 17296 (1 specimen).

**Stratigraphic occurrence:** The specimen lacks stratigraphical data, but probably comes from layer D1.

**Description:** Shell diminutive; spire flat, depressed; shell length ~1/2 its width. Protoconch (~1 whorl) smooth. Teleoconch sculpture by fine parallel prosocline ribs; distance between ribs equal to width of rib. Whorls regularly growing; whorl profile convex. Suture deep, well-marked. Apertural region slightly tilted towards base. Aperture circular, prosocline; ~1/2 shell width. Peristome greatly reflexed. Umbilicus wide.

**Measurements (in mm):** BSPG 1959 II 17296: 2¾ whorls; $H = 1.3$; $D = 2.4$; $h = 0.7$; $d = 1.2$.

**Previous identification of the material:** Gall (1972: Nr. 24): *Vallonia subpulchella subpulchella* (Sandberger, 1874). Moser et al. (2009b: Nr. 31): *Vallonia lepida* (Reuss, 1849).

**Discussion:** The overall shell shape and size, number and shape of whorls, and the smooth teleoconch with coarse growth lines compares well to *V. lepida*, a species from Central Europe (Gerber 1996). Other Central European Miocene species are *V. subpulchella* (Sandberger, 1874) and *V. subcyclophorella* (Gottschick, 1911). Gerber (1996) recently considered *V. subpulchella* a synonym of *V. lepida*, since there seems to be no clear morphological characters to distinguish them. However, Gerber (1996) points out that it is common practice (e.g., Harzhauser and Kowalke 2002; Harzhauser et al. 2008) to identify older forms (Middle Oligocene to Early Miocene) as *V. lepida* and younger forms (Middle to Late Miocene) as *V. subpulchella*. *Vallonia subcyclophorella* (MN5 to MN 10) is easily diagnosed by its strong ribs (Stworzewicz 1999b).

**Family Vertiginidae Fitzinger,** 1833
Genus *Vertigo* O.F. Müller, 1773

*Vertigo callosa* (Reuss, 1849)
(Figs. 17, 18)

*Pupa callosa* Reuss, 1849: 30 (pl. 3, fig. 7).
*Vertigo (Vertigo) callosa cardiostoma*: Gall, 1972: 13.
*Vertigo callosa*: Stworzewicz, 1999b: 137 (figs. 6–7).
*Vertigo (Vertigo) callosa*: Wenz, 1923a: 983; Moser et al., 2009b: 48.
*Vertigo* sp.: Moser et al., 2009b: 48.

**Material examined:** BSPG 1959 II 17256 (1 specimen), 17257 (7 specimens), 17258 (10 specimens), 17259 (5 specimens), 17260 (1 specimen), 17261 (3 specimens), 17686 (8 specimens).

**Stratigraphic occurrence:** Layers B2 (1 specimen), C3 (1 specimen) and D1 (15 specimens). Moreover, 7 specimens were found in the "Grube Bergmaier" sample and 11 others in samples without stratigraphical data.

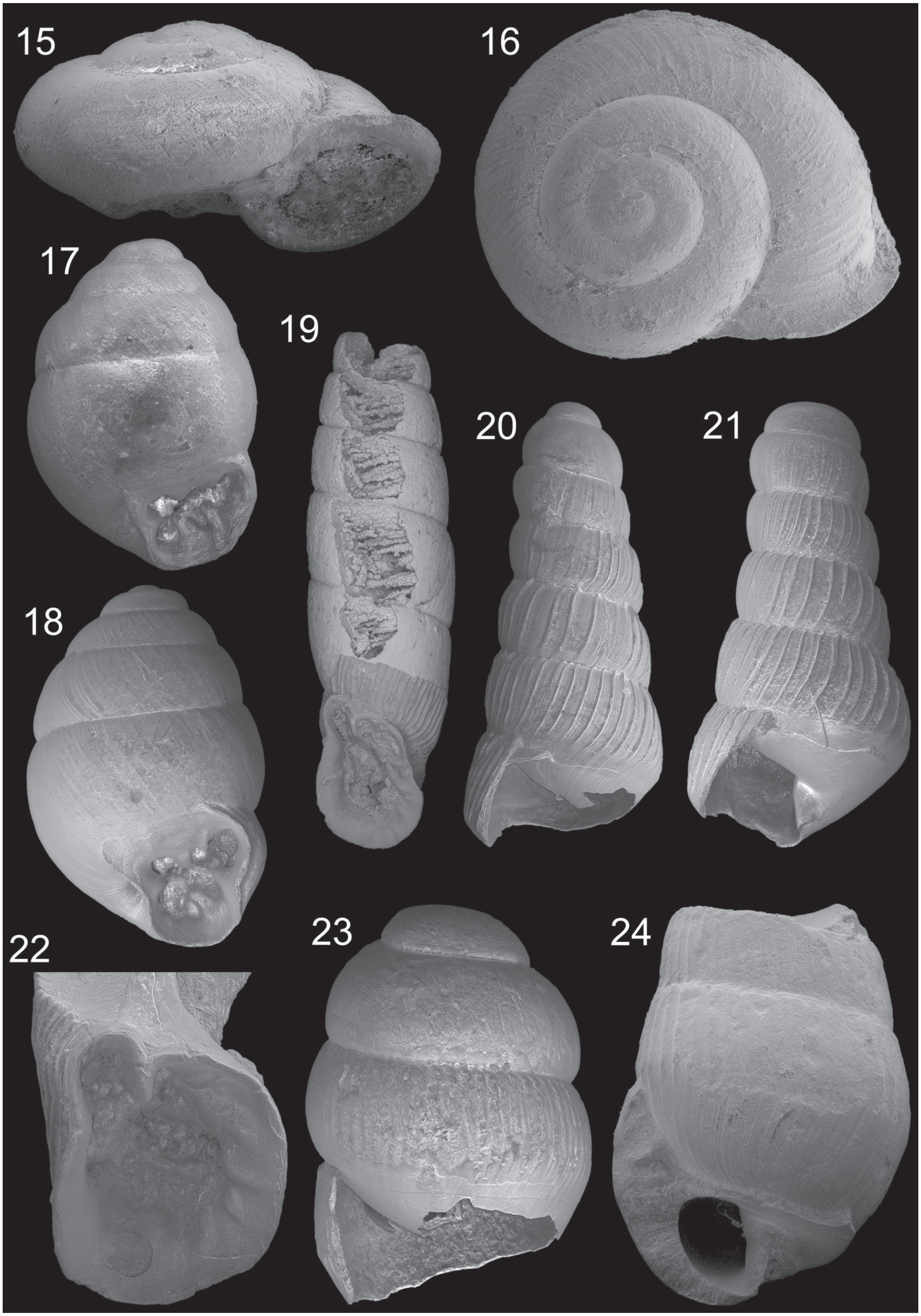
**Description:** Shell diminutive, ovate; greatest width on penultimate whorl (width ~3/4 shell length). Spire angle 55°–60°. Protoconch (1¼ whorl) blunt, smooth; transition to teleoconch clear. Whorl profile convex. Suture well-marked, but not deep. Teleoconch smooth, except for growth lines. Body whorl ~3/5 shell length. Aperture rounded triangular to more trapezoid; aperture ~1/3 shell length and ~1/2 shell width. Peristome slightly reflexed; parietal callus weak. Body whorl forming slight callosity near the peristome; body whorl with slight depression on its surface, near the peristome, corresponding to upper palatal tooth (a second depression, corresponding to the lower palatal, may also be present). Apertural barriers totaling five: upper palatal tooth, lower palatal tooth, columellar lamella, parietal lamella, angular lamella. A sixth barrier, namely the basal tooth, may also be present, but very weakly developed. The strongest barriers are the palatal teeth. Angular lamella and upper palatal tooth are in close proximity, and form an elongated (sometimes more circular) sinulus. Umbilicus narrow, deep.

**Measurements (in mm):** 4½–5 whorls; $H = \sim 2.0$; $D = \sim 1.4$; $S = \sim 1.3$; $S' = \sim 0.8$; $h = \sim 0.6$; $d = \sim 0.7$.

**Previous identification of the material:** Gall (1972: Nr. 27): *V. (Vertigo) callosa cardiostoma* (Sandberger, 1923). Moser et al. (2009b: Nr. 35 and 36): *V. (Vertigo) callosa* (Reus, 1849) and *Vertigo* sp. (the latter could refer to the forms that resemble *V. diversidens*; see below).

**Discussion:** *V. callosa* is one of the most common fossil vertiginids in the European Neogene, supposedly ranging from the Late Oligocene to the Late Miocene and occurring in many localities throughout central Europe (Stworzewicz 1999b). It was originally described from the Early Miocene freshwater limestones of northwestern Czech Republic (Reuss 1849). The species is well known for a great amount of variability in size, overall shell shape, aperture shape, and dentition, both among individuals and among populations as well (Stworzewicz 1999b). This seems to hold true for the specimens from Sandelzhausen, which can vary in: (1) overall shape (from ovate to more cylindrical); (2) size (sometimes with a difference of about half a whorl); (3) height of the aperture (some specimens with a higher aperture than more "typical" *V. callosa* specimens); (4) the number of teeth (the basal tooth is present in only a few specimens and is rather weakly developed); and (5) in the strength of the teeth (normally, the lower palatal is stronger than the upper palatal, but the opposite can be seen on some specimens).

Overall, all specimens from Sandelzhausen bear a single feature that distinguishes them from more typical *V. callosa*, namely, the more weakly developed teeth. The weaker teeth and the possible absence of the basal tooth are more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◀ **Figs. 15–24** **15**, **16** *Vallonia lepida* (BSPG 1959 II 17296; $D = 2.4$ mm). **17** *Vertigo callosa* (BSPG 1959 II 17257; $H = 1.9$ mm). **18** *Vertigo callosa* (BSPG 1959 II 17256; $H = 2.0$ mm). **19** *Pseudidyla moersingensis* (BSPG 1959 II 17279; $H = 7.4$ mm). **20** *Pseudidyla moersingensis*, spire top (BSPG 1959 II 17276; $H = 3.6$ mm). **21** *Pseudidyla moersingensis*, spire top (BSPG 1959 II 17277; $H = 3.0$ mm). **22** *Pseudidyla moersingensis*, aperture (BSPG 1959 II 17275; $h = 2.0$ mm). **23** *Triptychia* sp. (BSPG 1959 II 17293; $h = 1.9$ mm). **24** *Triptychia* sp. (BSPG 1959 II 17719; $H = 2.9$ mm)

akin to *V. protacta* (Sandberger, 1874), a rare species known from the Upper Oligocene to the Upper Miocene of central Europe (Stworzewicz 1999b). However, this species is smaller, has weaker angular and upper palatal teeth, and lacks the depression on the surface of the body whorl, near the peristome. Moreover, some authors have pointed to somewhat smaller specimens of *V. callosa*, similar to the ones from Sandelzhausen, that bear only 5 teeth (lack the basal one), from Steinheim am Albuch (MN7-8; Gottschick and Wenz 1919) and Hollabrunn, in Austria (MN7-8; Schütt 1967).

Moreover, some of the specimens from Sandelzhausen more closely resemble another Miocene species, *V. diversidens* (Sandberger, 1875) (sometimes regarded as a subspecies or synonym of *V. callosa*), by having more acuminated spires, a slightly more circular sinulus, and a more marked second depression on the surface of the body whorl, near the peristome, and located more basally, that corresponds to the lower palatal tooth (the other depression, corresponding to the upper palatal, is typical of *V. callosa*). Although *V. diversidens* is reported to have up to 7 or more teeth, and only rarely 6 (Stworzewicz 1999b), it is hard to satisfactorily separate it from *V. callosa*; so both species seem to be indistinguishable from one another.

**Superfamily Clausilioidea J.E. Gray, 1855**
**Family Clausiliidae J.E. Gray, 1855**
Genus *Pseudidyla* O. Boettger, 1877

*Pseudidyla moersingensis* (O. Boettger, 1877)
(Figs. 19, 20, 21 and 22)
*Clausilia (Pseudidyla) mörsingensis* O. Boettger, 1877: 89 (pl. 3, fig. 32–34).
*Pseudidyla moersingensis zandtensis*: Wenz, 1923a: 792; Gall, 1972: 12.
Clausiliidae gen. indet. sp. 1: Moser et al., 2009b: 48.
Clausiliidae gen. indet. sp. 2: Moser et al., 2009b: 48.

**Material examined:** BSPG 1959 II 17275 (>150 specimens), 17276 (>300 specimens), 17277 (>300 specimens), 17278 (1 specimen), 17279 (1 specimen), 17280 (1 specimen), 17281 (1 specimen), 17282 (34 specimens), 17283 (13 specimens), 17284 (>50 specimens), 17285 (41 specimens), 17286 (4 specimens), 17287 (10 specimens), 17288 (23 specimens), 17289 (13 specimens), 17290 (5 specimens), 17291 (1 specimen), 17295 (2 specimens), 17676 (1 specimen).

**Stratigraphic occurrence:** Layers B2 (35 specimens), C (undetermined; 1 specimen), C1 (1 specimen), C3 (>100 specimens), and D1 (>50 specimens). Moreover, >450 specimens were found in the "Grube Bergmaier" sample, 1 on the "Testprofil 1966" sample (label indicates only "layer C"), >300 on samples without data on place of origin, and a single specimen labeled as belonging to either layer B or C.

**Description:** Shell small, sinistral, multispiral, slender, cylindrical-fusiform, with acuminated apex. Greatest width on penultimate whorl (antepenultimate whorl). Protoconch (~2 whorls) rounded, smooth. Whorl profile slightly convex. Suture well-marked, but not deep, oblique (diagonal) to columellar axis. Teleoconch sculptured by well-marked sinuous parallel axial ribs (~80–90 on penultimate whorl) that become stronger towards the aperture; distance between ribs approximately twice the rib width, but distance is greater on early teleoconch whorls. Body whorl non-apostrophic, with two crests on its basal surface (the lower one stronger than the upper) and a light furrow between them. Aperture roughly oval, with a small rounded area between parietal lamella and palatal region. Peristome slightly thickened, greatly reflexed. Always present apertural barriers: parietal lamella (strong, vertical); columellar lamella (leading to the clausilium); basal lamella (beginning deeper on the body whorl inner surface); two folds preceding columellar lamellar and one fold preceding basal lamella; principal lamella (deeper on the body whorl's inner palatal surface). Other apertural barriers, not always present: one to two basal folds; one supracolumellar fold; one infraparietal fold. Very weak fold-like marks very rarely present on the palatal region. Umbilicus imperforated.

**Measurements (in mm):** BSPG 1959 II 17279 (incomplete specimen): 7 whorls; $H = 7.4$; $D = 2.0$; $h = 2.2$; $d = 1.6$.

**Previous identification of the material:** Gall (1972: Nr. 22): *Pseudidyla moersingensis zandtensis* (Boettger, 1877). Moser et al. (2009b: Nr. 40 and 41): Clausiliidae gen. indet. sp. 1 and Clausiliidae gen. indet. sp. 2.

**Discussion:** The material from Sandelzhausen, especially when taking into account the aperture with its lamellae and folds, compares well to *Pseudidyla moersingensis*, a species known from the Middle to the Upper Miocene of Germany (MN5-MN8; type locality and age: Mörsingen, MN5; Zilch 1959–1960; Nordsieck 1981, 1982). The two subspecies of *P. moersingensis* are now considered synonyms (Nordsieck 2007). Most of the present specimens are broken spire tops or apertures, but rare almost-complete specimens also remain. In Sandelzhausen, *P. moersingensis* seems to show some variability in the shape and size of the protoconch and shell apex, ranging from a very narrow protoconch, with the two whorls having the same width (Fig. 21), to a broader and more conical shell profile (Fig. 20). The two extreme types of shape of the apices could indicate two distinct species, but a whole range of intermediate forms can be found. The most common form is the narrow one, with the broader one and intermediates appearing in roughly the same proportions. Moreover, judging by the sizes of the many broken apertures, the shell size seems to be quite variable too, for occasional very large apertures (in comparison to the "regular" ones) can be found. The larger and broader form mentioned by Moser et al. (2009b) as a possible second clausiliid species (BSPG 1959 II-17291; incomplete specimen) is very likely just a larger *P. moersingensis*, since many intermediate forms link it to the smaller one.

Additionally, the number and strength of the apertural folds may also vary. Naturally, the parietal lamella (or superior lamella) is always present, and so are the columellar lamella (leading to the clausilium) and the basal lamella (beginning deeper on the body whorl's inner surface), as well as the small folds that precede them (two for the columellar and one for the basal). One or various smaller folds, in varying numbers, may be absent or be very weakly formed: one or two basal folds, one supracolumellar fold, and one infraparietal fold. Finally, sometimes there are numerous very weak marks resembling diminutive folds on the palatal region.

*Pseudidyla moersingensis* is the most abundant species among the terrestrial snails from Sandelzhausen, suggesting the presence of a favorable habitat for this species, woody with a humid warm-temperate climate (Nordsieck 2007). This is especially true for layer C3, from where most of the material was recovered.

**Family Filholiidae Wenz,** 1923a
Genus *Triptychia* Sandberger, 1874

*Triptychia* sp.
(Figs. 23, 24)

**Material examined:** BSPG 1959 II 17292 (1 specimen), 17293 (1 specimen), 17294 (1 specimen), 17719 (2 specimens).

**Stratigraphic occurrence:** Layers B2 (1 specimen) and C3 (1 specimen). Moreover, 1 specimen was found in the "Grube Bergmaier" sample, and 2 specimens completely lack stratigraphical data.

**Description:** Protoconch (~2 whorls) smooth; transition to teleoconch clear. Beginning of teleoconch of the same width as protoconch; sculptured by vertical and slightly curved ribs; distance between ribs roughly equal to width of rib; ribs become well-marked and orthocline on later whorls. Suture shallow, but well-marked. Whorl profile flat.

**Measurements (in mm):** BSPG 1959 II 17293 (incomplete specimen; Fig. 23): 3 whorls; $H = 1.9$; $D = 1.4$. BSPG 1959 II 17719 (incomplete specimen): $H = 2.9$; $D = 2.1$.

**Previous identification of the material:** Neither Gall (1972) nor Moser et al. (2009b) mentioned these specimens.

**Discussion:** Only 4 protoconchs and a spire fragment of this sinistral species are at hand. The protoconchs are easily recognizable by their much larger size and more cylindrical apex when compared to the clausiliids. Their allocation to *Triptychia* is due to the conical spire profile, with flattened whorls and a shallow but well-marked suture.

## Concluding remarks

Not only the fossils from Sandelzhausen but also the majority of Miocene continental snail faunas from Central Europe are in need of taxonomical revision (Strauch 1977; Esu 1999). The lack of proper taxonomical knowledge hampers comparative and integrative works (i.e., those dealing with more than one fossil site) in fields like paleobiogeography and paleoecology. In the literature, it is possible to find countless species, subspecies, and varieties that are described based on one or very few specimens. These are most likely synonyms; a common scenario is for two extreme forms of a continuum to be described as two distinct taxa. As a result, some fossil sites have unrealistic numbers of co-occurring congeneric "species" with minimal differences among them. As such, this myriad of synonyms leads to overinflated species richness and diversity numbers: some sites show tens of co-occurring species, numbers that are far greater than what is commonly found in Recent local faunas (Solem 1981, 1984; Schilthuizen 2011). Nevertheless, the molluskan fossil fauna from Sandelzhausen is very rich and diverse, and is invaluable for future paleoecological and paleogeographical studies.

Furthermore, primary targets for revisions should be the many species that supposedly occur throughout the whole Miocene (and sometimes since the Oligocene), encompassing vast stretches of time. Despite not being completely impossible, that is very unlikely, especially if we take into account: (1) the tendency of the pulmonates to have more restricted distributions and to evolve rather rapidly (Solem 1981, 1984; Barker 2001); and (2) the many climatic changes that happened in Europe during the Miocene and likely affected the molluskan fauna (Esu 1999). To illustrate this line of thought, in the Clausiliidae, a group that has been thoroughly revised, the species showed high evolutionary rates and small stratigraphical ranges, with most being restricted to one mammal zone (Nordsieck 2007). As such, for the present classification of the material from Sandelzhausen, it was found to be more useful to also take the type locality and age of each species into account, preferably comparing the specimens with species of roughly the same age.

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# The fossil pulmonate snails of Sandelzhausen (Early/Middle Miocene, Germany)

## (Hygrophila, Punctoidea and limacoids)

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## Abstract

Sandelzhausen is an Early/Middle Miocene (Mammal Neogene zone MN5) fossil site near Mainburg, southern Germany, home to a very rich fossil record. Hundreds of fossil continental mollusks, almost exclusively pulmonates snails, were recovered during the excavations, but received scarce attention by researchers. Here is presented the third and last part of a taxonomical treatment of the fossil pulmonates from Sandelzhausen, dealing with the superfamilies Lymnaeoidea, Planorboidea, Punctoidea, Gastrodontoidea and Limacoidea. The following species were found in the material: *Galba dupuyiana*, *Lymnaea dilatata* and *Radix socialis* (Lymnaeidae); *Ferrissia deperdita*, *Gyraulus albertanus*, *Gyraulus dealbatus*, *Hippeutis* sp., *Planorbarius cornu* and *Segmentina lartetii* (Planorbidae); *Discus pleuradrus* (Discidae); *Lucilla subteres* (Helicodiscidae); *Janulus supracostatus* (Gastrodontidae); *Archaeozonites* sp. (Gastrodontoidea *incertae sedis*: Archaeozonitinae); *Limax* sp. (Limacidae); *Vitrina* sp. (Vitrinidae).

**Key words**: Basommatophora, Gastropoda, MN5 European Mammal Neogene zone, Pulmonata, Stylommatophora.

## Introduction

The Sandelzhausen fossil site is one of the most important Cenozoic continental sites in Europe (Moser et al. 2009a) and its rich record includes hundreds of gastropods. Still, only two works dealt specifically with the mollusks: Gall (1972), who identified 49 gastropods and two bivalves in the material recovered, but based his work heavily on younger faunas; and Moser et al. (2009b), who dealt with paleoecological questions. Here is presented the third and last part of the taxonomic treatment of the pulmonate snails from Sandelzhausen (for the first parts see Salvador 2013b, 2014b), dealing with the superfamilies Lymnaeoidea, Planorboidea, Punctoidea, Gastrodontoidea and Limacoidea. For the non-pulmonate snails and bivalves see Salvador (2013a).

### Geological Setting

Sandelzhausen fossil site was located in the vicinities of the city of Mainburg, 60 Km north of Munich, in the Molasse Basin (Molassebecken) of southern Germany,

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which harbors the stratigraphical group known as Upper Freshwater Molasse (Ober Süßwassermolasse, OSM; Moser et al. 2009a). The fossils from Sandelzhausen belong to a member of the OSM called Nördlicher Vollschotter, composed primarily of marl and gravel (Moser et al. 2009a). The age of these deposits was established by stratigraphic, biostratigraphic and magnetostratigraphic correlations: the Middle Miocene Burdigalian/Langhian boundary (~16.47–16.27 Ma; Moser et al. 2009a), within the early middle MN5 European Mammal Neogene zone.

The division of the deposits of Sandelzhausen into facies was established by Fahlbusch & Gall (1970), receiving further refinement by Moser et al. (2009a): 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 pebbles diminish upwards, with intercalated sand horizons; origin of most macrovertebrate fossils; Layer C: fossil rich marl; divided in 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 carbonatic nodules; rich in fossils, many in excellent preservation state due to a less intense compaction; Layer E: silty clays with microvertebrate fossils; Layer F: laminite with alternating light and dark bands, carbonate concretions and desiccation cracks; no fossils. Fossil mollusks can be found from layer A to D. For a more throughout description of the lithology of the site, please refer to Moser et al. (2009a).

## Material and methods

The material from Sandelzhausen is housed at the collection of the Bayerische Staatssammlung für Paläontologie und Geologie (BSPG; Munich, Germany) under the record number BSPG 1959 II. The list of all examined material can be found in Appendix 1. A portion of the material states the layer to which it belongs, but the remaining either cannot be unmistakably attributed to the layers or completely lack stratigraphical data (including the samples labeled as “Grube Bergmaier”; for more information on these, refer to Salvador 2013b). As such, only the samples that can correctly be attributed to layers are used here to determine the species’ stratigraphical range. Specimens in a good state of preservation were measured either with a digital caliper or with the aid of computer software. Selected specimens were examined by scanning electron microscopy (SEM) in the Staatliches Museum für Naturkunde Stuttgart (SMNS; Stuttgart, Germany). The following abbreviations for shell measurements are used throughout the text: H = shell height; D = shell greatest width; h = aperture height; d = aperture width.

As explained above, the mollusks from Sandelzhausen received scarce attention and only two works attempted to identify the specimens: Gall (1972) and Moser et al. (2009b). Here the identification offered in these works is given in order to facilitate the correlation of the material for future workers. We have refrained from presenting these former identifications in the synonymy to avoid confusion; they are listed in a separate section under each species.

Unfortunately, the specimens identified by Moser et al. (2009b: Nr. 46 and 47) as, respectively, ?Discidae (fam., gen. et sp. indet.) and ?Endodontidae sp. nov. (fam. et gen. indet.), could not be found among the material. Either these specimens could be missing or, more likely, they could simply not be properly labeled and thus were identified differently here. Moreover, the single specimen (BSPG 1959 II 16148) identified as *Zonitoides silvanus* (Wenz) by Gall (1972: Nr. 6) and as ?Endodontidae gen. nov. by Moser et al. (2009b: Nr. 48, fig 6F) is now just fragments and cannot be properly identified. Moser et al. (2009b) suggested the species identification of Gall (1972) was correct, but that a new genus should be created to house it in the family Endodontidae. Regrettably, this matter cannot be presently addressed.

# Systematics

### Hygrophila

### Superfamily Lymnaeoidea

### Family Lymnaeidae

### Genus ***Galba*** Schrank 1803

### ***Galba dupuyiana*** (Noulet 1854)

Figs 1–7

1845 *Limnea Dupuyiana* Noulet: 108.
1874 *Limneus Dupuyianus* – Sandberger: 543 (pl. 28, fig. 27; wrong number and captions in original work).
1923 *Radix (Radix) dupuyana* [sic] – Wenz: 1242.
2000 *Galba* (*Galba*) *dupuyiana* – Fischer: 135 (fig. 4).
2006 *Galba dupuyana* [sic] – Kókay: 50 (pl. 16, figs. 14–16).
2009 *Galba dupuyiana* – Böttcher et al.: 239 (figs. 2/1–2).

Stratigraphic occurrence: Layers B (undetermined; 7 spcm.), B2 (>200 spcm.), C (undetermined; 6 spcm.), C1 (11 spcm.), C2 (3 spcm.), C3 (>300) and D1 (>1200 spcm.). Moreover, 82 specimens come from excavation sites for which no profile is available, but, based on their height in the sediment and their preservation, they are likely from Layers C (20 spcm.), C1 (9 spcm.), C3 (8 spcm.), D1 (4 spcm.), either B or C

(38 spcm.), and either C3 or D1 (7 spcm.). Finally, a large amount of specimens come from the Grube Bergmaier site (>350 spcm.) or completely lack locality data (>1200 spcm.).

Description: Shell small, lymnaeiform; shell width ~1/2 shell height. Protoconch (~1 whorl) rounded, smooth; transition to teleoconch unclear. Teleoconch smooth, except for well-marked growth lines. Suture deep, well-marked. Whorls profile convex. Aperture oval, narrow, elongated; ~2/3 shell height. Peristome simple, almost completely covering umbilicus. Umbilicus rimate.

Measurements (in mm): 4–4½ whorls; H = 5.0–7.0; D = 2.5–3.5; h = 3.0–4.5; d = 1.5–2.5.

Previous identification of the material: GALL (1972: in part, Nr. 33–36): respectively, *Lymnaea turrita* (KLEIN), *Lymnaea turrita* (KLEIN), *Radix* (*Radix*) *socialis socialis* (ZIETEN), *Radix* (*Radix*) *socialis dilatata* (NOULET), *Radix* (*Radix*) *socialis praelongata* (GOTTSCHICK & WENZ). MOSER et al. (2009b: Nr. 9 and, in part, 10–12): respectively, *Stagnicola* sp./*Omphiscola* sp., *Radix* sp., *Lymnaea* sp. and Lymnaeidae indet. Moreover, the specimens identified as *Galba* (*Galba*) *subtruncatula* (CLESSIN) by GALL (1972: Nr. 37) and the single specimen (Fig. 7) identified as *Galba* sp. by MOSER et al. (2009b: Nr. 8) are juvenile shells or broken apexes of *G. dupuyiana*, usually of the more slender forms (see below).

Discussion: This is by far the most abundant lymnaeid in Sandelzhausen. The present specimens compare well to *G. dupuyiana*, originally described from Sansan (MN6, France; FISCHER 2000), but known throughout the Middle Miocene of West and Central Europe (KÓKAY 2006). There are two distinct extreme morphological varieties of this species in Sandelzhausen: a broader form (Fig. 1; referred to as *Stagnicola* sp. by MOSER et al. 2009b) and a slender form (Fig. 6; likely referred to as *Omphiscola* sp. by MOSER et al. 2009b). The slender form usually has an extra half whorl, more convex whorls and a deeper suture. These two extremes are linked by numerous transitional forms (Figs. 2–5). The same variation was seen in specimens of *G. dupuyiana* from the fossil site of Oggenhausen 2 (MN5, SW Germany; BÖTTCHER et al. 2009), which are remarkably similar to the present fossils (including in their slightly larger size when compared to Sansan). Curiously, in the material from Sandelzhausen, the broader form is dominant from Layer B to the basal portion of Layer D, but there is a marked increase in the proportion of the slender form towards the upper portion of Layer D.

### Genus ***Lymnaea*** LAMARCK 1799

### ***Lymnaea dilatata*** (NOULET 1854)

Figs 8–9

1854 *Limnea dilatata* NOULET: 107.
1923 *Radix* (*Radix*) *socialis dilatata* – WENZ: 1277.
2000 *Lymnaea dilatata* – FISCHER: 136 (figs. 1–2)
2005 *Lymnaea dilatata* – KOWALKE & REICHENBACHER: 630 (figs. 9.4–95.).

Stratigraphic occurrence: Layers B (undetermined; 37 spcm.), B1 (21 spcm.), B2 (6 spcm., C (undetermined; 4 spcm.), C1 (4 spcm.), C2 (2 spcm.), and D1 (34 spcm.). Moreover, ~150 specimens come from excavation sites for which no profile is available, but, based on the height in the sediment and the preservation, it is possible to infer the origin of some: they are likely from Layers B (1 spcm.), C3 (2 spcm.), D1 (8 spcm.), either B2 or C1 (10 spcm.), either B or C (24 spcm.), and either C3 or D1 (>80 spcm.). Finally, two specimens come from the Grube Bergmaier sample and five come from sites completely lacking locality data.

Description: Shell large, lymnaeiform; spire acuminated, proportionately small; shell width ~1/2 shell height. Protoconch (~1½ whorl) rounded, smooth; transition to teleoconch unclear. Teleoconch smooth, except for growth lines. Suture well-marked. Whorls profile slightly convex. Body whorl proportionately large. Aperture oval, elongated; ~2/3 shell height, ~2/3 shell width. Peristome simple. Umbilicus imperforate.

Measurements (in mm): 4½–5½ whorls; H = 3.2–3.9; D = 1.6–1.9; h = ~2.2; d = ~1.1.

Previous identification of the material: GALL (1972: Nr. 35, in part): *Radix* (*Radix*) *socialis dilatata* (NOULET). MOSER et al. (2009b: in part, Nr. 11–12): respectively, *Lymnaea* sp. and Lymnaeidae indet.

Discussion: The specimens from Sandelzhausen compare well to *L. dilatata*, diagnosed by its acuminated and proportionately short spire and the proportionately large body whorl. The species was originally described from Sansan (MN6, France; FISCHER 2000), but it is known from the whole Miocene of West and Central Europe (BINDER 2004). Some authors (*e.g.*, WENZ 1923) have placed *L. dilatata* in the genus *Radix* MONTFORT 1810, but, as argued by FISCHER (2000), it seems more appropriately placed in *Lymnaea*.

### Genus ***Radix*** MONTFORT 1810

### ***Radix socialis*** (ZIETEN 1830)

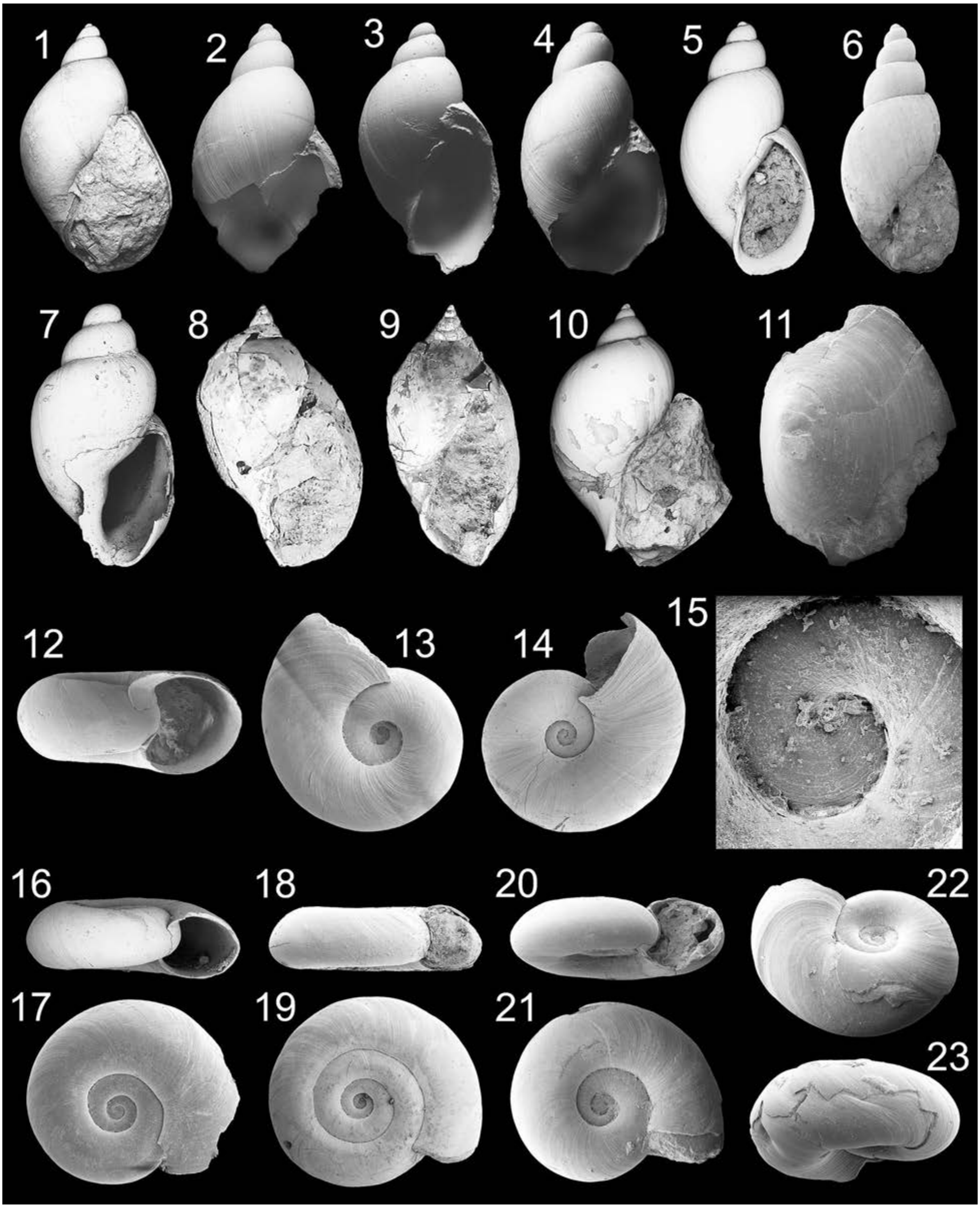
Fig. 10

1830 *Limnaea socialis* ZIETEN: 40 (pl. 30, f. 4).
1923 *Radix* (*Radix*) *socialis socialis* – WENZ: 1272.

Stratigraphic occurrence: Layer D1.

Description: Shell small, rounded lymnaeiform; shell width ~2/3 shell height. Protoconch rounded, smooth; transition to teleoconch unclear. Teleoconch smooth, except for growth lines. Suture deep, well-marked. Whorls profile markedly convex. Aperture apparently oval, elongated. Peristome apparently simple, sharp. Umbilicus apparently imperforate.

Measurements (in mm): BSPG 1959 II – 17568 (young specimen): 3¾ whorls; H = 11.2; D = 6.9.



Figs 1–7. *Galba dupuyiana*. Fig. 1, broad form (BSPG 1959 II 17485 spcm. #1; H = 7.4 mm). Fig. 2. BSPG 1959 II 17488 spcm. #1; H = 5.8 mm; Fig. 3. BSPG 1959 II 17488 spcm. #2; H = 4.8 mm; Fig. 4. BSPG 1959 II 17488 spcm. #3; H = 5.0 mm; Fig. 5. BSPG 1959 II 17485 spcm. #2; H = 5.8 mm; Fig. 6. slender form (BSPG 1959 II 17486; H = 6.8 mm); Fig. 7. spire apex (BSPG 1959 II 17476; H = 2.3 mm). — Figs. 8–9 *Lymnaea dilatata*. Fig. 8. BSPG 1959 II 17519; H = 32.3 mm; spire top collapsed into the shell gives it a rounded appearance; Fig. 9. BSPG 1959 II 17520; H = 32.7 mm; compressed specimen. — Fig. 10. *Radix socialis* (BSPG 1959 II 17568; H = 11.2). — Fig. 11. *Ferrissia deperdita* (BSPG 1959 II 17706; D = 2.9). — Figs 12–15 *Gyraulus albertanus*. Fig. 12. apertural view (BSPG 1959 II 17677; D = 2.9 mm); Fig. 13. apical view BSPG 1959 II 17677; D = 2.7 mm; Fig. 14. umbilical view (BSPG 1959 II 17677; D = 2.5 mm); Fig. 15. *Gyraulus albertanus*, protoconch detail (BSPG 1959 II

Previous identification of the material: Gall (1972: in part, Nr. 33, 34 and 36): respectively, *Lymnaea turrita* (Klein), *Radix* (*Radix*) *socialis socialis* (Zieten), *Radix* (*Radix*) *socialis praelongata* (Gottschick & Wenz). Moser et al. (2009b: in part, Nr. 10 and 12): respectively, *Radix* sp. and Lymnaeidae indet.

Discussion: Despite previous classifications, only a few specimens from Sandelzhausen display diagnostic features of the genus *Radix*, such as the proportionately diminutive spire and large body whorl. Only young or broken specimens are present in the material, but they compare extraordinarily well to the specimens of *Radix socialis s. str.* from the type locality (Steinheim Basin, MN 7–8, SW Germany), housed at the SMNS collection and possibly used on the species' original description and/or later revisionary works from the early 20th century.

Remarks: Despite Wenz (1923) having listed many subspecies of *Radix socialis*, they have been more recently treated as distinct entities, such as *Lymnaea dilatata* above (*e.g.*, Fischer 2000; Kowalke & Reichenbacher 2005). Here such decision is followed and the name *R. socialis* is used in its original meaning (*i.e.*, *R. socialis socialis*).

## Superfamily Planorboidea

## Family Planorbidae

## Genus ***Ferrissia*** Walker 1903

### ***Ferrissia deperdita*** (Desmarest 1814)

Fig. 11

| | |
|---|---|
| 1814 | *Ancylus deperditus* Desmarest: 19 (pl. 1, fig. 14). |
| 1923 | *Pseudancylus deperditus deperditus* – Wenz: 1692. |
| 1976 | *Ferrissia deperdita* – Schlickum: 7 (pl. 1; fig. 20). |
| 2006 | *Ferrissia deperdita* – Kókay: 60 (pl. 20, fig. 15, pl. 21, fig. 1). |
| 2014 | *Ferrissia deperdita* – Harzhauser et al.: 17 (pl. 5, figs. 1, 2, 5, 12). |

Stratigraphic occurrence: Unfortunately, the sample lacks stratigraphical data. Moser et al. (2009b), however, indicates either Layer B or C1.

Description: Shell diminutive, cap-shaped, elliptical. Shell apex slightly bent to the right. Protoconch cap-like, smooth; transition to teleoconch unclear. Teleoconch smooth, but with well-marked growth lines.

Measurements (in mm): H = 1.6; D = 2.9; h = 3.5.

Previous identification of the material: Gall (1972: Nr. 46): *Ancylus deperditus* cf. *deperditus* (Desmarest 1814). Moser et al. (2009b: Nr. 23): *?Ancylus* sp. nov.

Discussion: Moser et al. (2009b) suggested that the present specimens belonged to a new species, but did not provide the reasons for it. However, the specimens from Sandelzhausen compare fittingly with *F. deperdita*, from the Middle Miocene of Hungary, Austria, southern Germany, Switzerland and France (Schlickum 1976, Kókay 2006; Harzhauser et al. 2014).

## Genus ***Gyraulus*** Charpentier 1837

### ***Gyraulus albertanus*** (Clessin 1877)

Figs 12–15

| | |
|---|---|
| 1877 | *Planorbis albertanus* Clessin: 40. |
| 1914 | *Gyraulus albertanus* – Fischer & Wenz: 57. |
| 1923 | *Gyraulus* (*Gyraulus*) *albertanus* – Wenz: 1541. |
| 1972 | *Gyraulus* (*Gyraulus*) *albertanus* – Gall: 16. |
| 2009b | *Menetus* (*Dilatata*) *albertanus* – Moser et al.: 46. |

Stratigraphic occurrence: Layers B2 (16 spcm.), C3 (50 spcm.), D1 (>600 spcm.). Moreover, three specimens come from an excavation site for which no profile is available, but, based on their position in the section and their preservation, they are either from Layer C3 or D1. Finally, there are five specimens from the Grube Bergmaier site and a single specimen lacking stratigraphical data.

Description: Shell diminutive, pseudodextral, planispiral; shell height ~1/2 shell width. Protoconch (~1¼ whorl) sculptured by faint spiral striae (more easily seen on the nucleus); transition to teleoconch unclear. Teleoconch sculptured by numerous very well-marked growth lines. Spire depressed. Suture very deep. Whorls rapidly growing. Aperture rounded. Peristome simple, sharp. Umbilicus narrow, deep.

Measurements (in mm): 2¾–3 whorls; H = 1.0–1.2; D = 2.3–2.8.

Previous identification of the material: Gall (1972: Nr. 40): *Gyraulus* (*Gyraulus*) *albertanus* (Clessin). Moser et al. (2009b: Nr. 14 and 15): respectively, *Menetus* (*Dilatata*) *albertanus* (Clessin) and *Menetus* (*Dilatata*) sp.

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17676). — Figs 16–17 *Gyraulus dealbatus*. Fig. 16. typical form from basal sedimentary layers (BSPG 1959 II 18030 spcm. #1; D = 2.8 mm); Fig. 17. typical form from basal sedimentary layers (BSPG 1959 II 18030 spcm. #2; D = 2.4 mm). — Figs 18–21 *Gyraulus* cf. *dealbatus*. Fig. 18. form similar to *G. applanatus* (BSPG 1959 II 18043; D = 2.2 mm); Fig. 19. form similar to *G. applanatus* (BSPG 1959 II 18044; D = 4.2 mm); Fig. 20. form similar to *G. kleini* (BSPG 1959 II 18020 spcm. #1; D = 2.9 mm); Fig. 21. form similar to *G. kleini* (BSPG 1959 II 18020 spcm. #1; D = 2.4 mm). — Figs 22–23 *Gyraulus dealbatus*. Fig. 22. with marks of shell breakage and repair (BSPG 1959 II 17310 spcm. #1; D =1.9 mm); Fig. 23. with marks of shell breakage and repair (BSPG 1959 II 17310 spcm. #2; D = 1.9 mm).

Discussion: The specimens from Sandelzhausen compare fittingly with *Planorbis albertanus*, albeit being slightly smaller (0.5 to 1.0 mm smaller) and usually having slightly higher apertures. This species was originally described from the southeastern German fossil site Undorf (MN 5; CLESSIN 1885), just a few kilometers north of Sandelzhausen. Later, FISCHER & WENZ (1914) transferred the species to the genus *Gyraulus*. More recently, the species was allocated in the genus *Menetus* H. ADAMS & A. ADAMS 1855 by MOSER et al. (2009b).

Nevertheless, this latest classification is not appropriate. In the first place, *Menetus* is a recent North-American genus and its shell features (BAKER 1945) are strikingly different from those observed in this European fossil. Moreover, when all the conchological features of *P. albertanus* are taken together (the protoconch shape, umbilical region, aperture shape, lack of a keel, and the fast growth in whorl size, both in width and height), the species seems much more akin to the genera *Planorbis* O.F. MÜLLER 1774 or *Gyraulus*, of which both fossil and recent species are common in Europe (ZILCH 1959, WELTER-SCHULTES 2012). Furthermore, the protoconch sculpture consists of a series of spiral striae (Fig. 15), characteristic of the genus *Gyraulus* (GORTHNER 1993). As such, the species is here classified as *Gyraulus albertanus*.

MOSER et al. (2009b) identified two morphs of "*Menetus*" in Sandelzhausen, the "typical *M. albertanus*" and a thicker form, stating that they could be distinguished even in broken or juvenile specimens, with few whorls. However, such morphs are far from being clearly distinguishable, especially in juveniles. Moreover, the vast amount of specimens available shows that the thicker form is just an extreme of shell height in a single species' gradient of variation. This variation can be seen in Sandelzhausen throughout all layers in which the species occurs.

### ***Gyraulus dealbatus*** (BRAUN 1851)

Figs 16–23

1851 *Planorbis dealbatus* BRAUN: 1134.
1923 *Gyraulus* (*Gyraulus*) *trochiformis dealbatus* – WENZ: 1591.
2004 *Gyraulus dealbatus* – BINDER: 193 (pl. 2, figs. 1a–c).
2006 *Gyraulus trochiformis dealbatus* – KÓKAY: 57 (pl. 19, fig. 15).

Stratigraphic occurrence: Layers C (undetermined; 10 spcm.), C3 (>100 spcm.), D1 (>2000 spcm.). Moreover, a some specimens come from an excavation site for which no profile is available, but based on their height in the sediment and their preservation they are likely from Layer C3 (1 spcm.), either B or C (>50 spcm.), either B2 or C1 (4 spcm.), and either C3 or D1 (>50 spcm.). Finally, there are >50 specimens from the Grube Bergmaier site and >250 specimens completely lacking stratigraphical data.

Description: Shell diminutive, pseudodextral, planispiral; shell height ~1/3 shell width. Protoconch (~1 whorl) sculptured by fine spiral striae; transition to teleoconch unclear. Teleoconch smooth, except for growth lines. Spire depressed. Suture deep, well-marked. Whorls somewhat rapidly growing, especially body whorl. Body whorl rounded with a faint keel on its median portion. Aperture oval, slightly inclined diagonally. Peristome simple, sharp. Umbilicus wide, shallow.

Measurements (in mm): 3¼–3½ whorls; H = 1.0–1.3; D = 2.9–3.4.

Previous identification of the material: GALL (1972: Nr. 41–43, in part): respectively, *Gyraulus* (*Gyraulus*) cf. *goussardianus* (NOULET), *Gyraulus* (*Gyraulus*) *trochiformis ludovici* (NOULET) and *Gyraulus* (*Gyraulus*) *trochiformis kleini* (GOTTSCHIK & WENZ). MOSER et al. (2009b: Nr. 16, 18, 19, in part, and 20): respectively, *Drepanotrema* sp. 1, *Gyraulus* sp. 1, *Gyraulus* sp. 2 and *Gyraulus* sp. nov.

Discussion: The specimens from Sandelzhausen compare fittingly with *Gyraulus dealbatus*, from the Early Miocene of Austria (MN 4; BINDER 2004), by the aperture shape, rapidly growing whorls and a rounded body whorl profile with a faint keel on its median portion. These typical forms (as in the description above; Figs. 16–17) can be found in the basal layers from Sandelzhausen and already show some morphological variation: the shell may be thicker or thinner; the body whorl profile can be more rounded, with a less pronounced keel, or more angular, with a pronounced keel; and the keel may rarely be more basally positioned.

Moreover, a morphological extreme of the species can be found (Figs. 18–19, as *Gyraulus* cf. *dealbatus*): the shell is flattened (shell height ~1/4 shell width); the whorls grow regularly and slowly, more closely packed together; there is a well-marked carina on the laterobasal portion of the body whorl; and the aperture is smaller and shaped as an arrowhead, usually slightly inclined diagonally. This form is very reminiscent of another species, namely *G. applanatus* (THOMAE 1845). When this form starts to show up (basal Layer D1), it is rare and not so easily distinguished from the typical *G. dealbatus*. However, as one goes up along the layers, the specimens become more numerous and the differentiation clearer. Finally, the typical forms seem, in the upper portion of Layer D1 (Figs. 20–21, as *Gyraulus* cf. *dealbatus*), to acquire a reminiscence to yet another species, namely *G. kleini* (GOTTSCHICK & WENZ 1916).

GOTTSCHICK & WENZ (1916) had already noted that these three species showed some sort of gradation among themselves in material from Hohenmemmingen (MN 5–6, Germany). On the other hand, KOWALKE & REICHENBACHER (2005), when seeing the same variation in specimens from the Lower Miocene of Bavaria, Germany, considered *G. dealbatus* a synonym of *G. applanatus*. The protoconchs of the present specimens have been damaged by the collection method and, thus, are of little help. This matter is currently under study and will be published elsewhere.

Remarks: Some shells show markings of shell breakage and later shell repair (Figs. 22–23). The strange pattern of the breakage however, makes it difficult to assess whether it was caused by predators or not.

### Genus ***Hippeutis*** Charpentier 1837

#### ***Hippeutis*** sp.

Figs 24–25

Stratigraphic occurrence: Layer D1.

Description: Shell diminutive, involute, planispiral; shell height ~1/3 shell width. Strong keel on central portion of whorl. Upper and lower portions of shell convex (upper portion slightly more than lower). Protoconch (~¾ whorl) small, sculptured by strong axial striae; transition to teleoconch clear. Teleoconch smooth, but with well-marked growth lines. Suture well-marked, slightly incised. Whorls regularly increasing in size towards aperture. Aperture large, V-shaped, near symmetrical, with bent tip; ~2/5 shell width. Peristome simple, sharp. Umbilicus wide and shallow.

Measurements (in mm): juvenile specimen; 1¾ whorl; H = 0.4; D = 1.3; h = 0.3; d = 0.5.

Previous identification of the material: Gall (1972: Nr. 44): *Hippeutis subfontanus subfontanus* (Clessin 1877). Moser et al. (2009b: Nr. 21): *Hippeutis* sp.

Discussion: The present specimen can be assigned to the genus *Hippeutis* based on its shell profile and aperture shape. However, since it is a juvenile with few whorls, a more precise identification is not possible, although it indeed compares well with *H. subfontanus* (Clessin 1877) from Undorf (MN 5; Germany), a fossil site located very close to Sandelzhausen. The genus is known from the Paleocene of Europe (Zilch 1959). The recent *H. complanatus* (Linnaeus 1758) lives in slow shallow waters (also temporary) rich in vegetation and doesn't tolerate desiccation (Welter-Schultes 2012).

### Genus ***Planorbarius*** Duméril 1806

#### ***Planorbarius cornu*** (Brongniart 1810)

Figs 26–28

1810 *Planorbis cornu* Brongniart: 371 (pl. 22, fig. 6).
1923 *Coretus cornu cornu* – Wenz: 1426.
1970 *Planorbarius cornu* – Schlickum: 149 (pl. 10, fig. 7).
2004 *Planorbarius cornu* – Binder: 193 (pl. 2, figs. 2–3).
2006 *Planorbarius cornu cornu* – Kókay: 58 (pl. 20, fig. 6).
2009 *Planorbarius cornu cornu* – Böttcher et al.: 239 (figs. 2/4–6).

Stratigraphic occurrence: Layers B (undetermined; 74 spcm.), B1 (87 spcm.), B2 (38 spcm.), C (undetermined; 7 spcm.), C1 (1 spcm.), C2 (4 spcm.), C3 (20 spcm.) and D1 (>150 spcm.). Moreover, ~200 specimens come from excavation sites for which no profile is available, but, based on their height in the sediment and their preservation, they are likely from C3 (12 spcm.), either B or C (34 spcm.), B2 or C1 (>70 spcm.), and either C3 or D1 (17 spcm.). Finally, 32 specimens come from the Grube Bergmaier site and ~150 completely lack locality data.

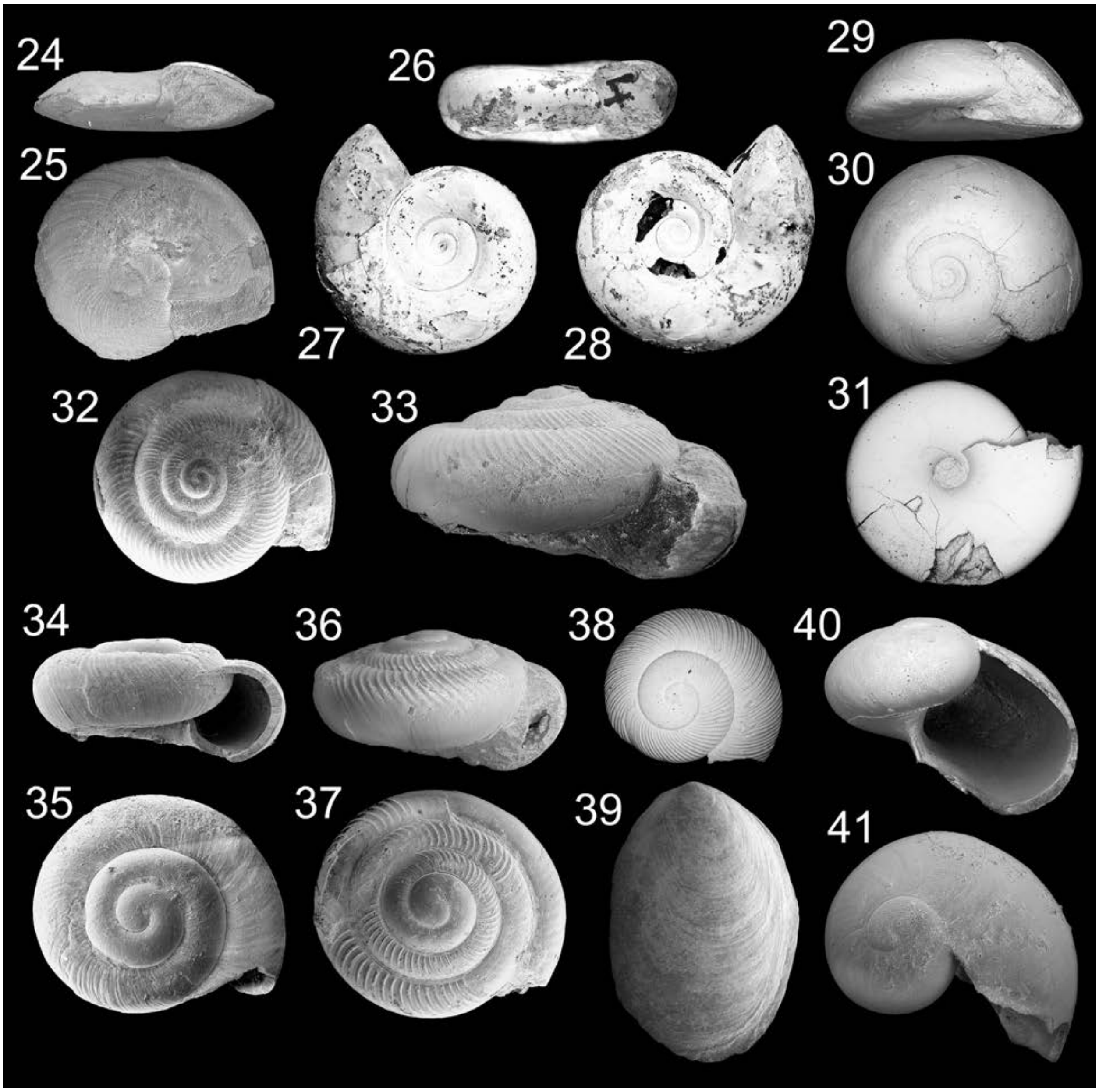
Description: Shell large, sinistral, planispiral; shell height ~1/3 shell width. Protoconch (~1 whorl) sculptured by spiral lines of regularly organized circular pits (giving the impression of a reticulated pattern under light microscopy); transition to teleoconch clear. Teleoconch sculpture by spiral striae on first ~1½ whorl; smooth on the rest, except for growth lines. Spire very depressed. Suture deep, well-marked. Whorls regularly growing. Aperture rounded to oval. Peristome apparently simple, sharp. Umbilicus very wide, deep.

Measurements (in mm): BSPG 1959 II 462: 5 whorls; H = 7.0; D = 22.7.

Previous identification of the material: Gall (1972: Nr. 38 and 39): respectively, *Planorbarius cornu mantelli* (Dunker) and *Planorbarius* cf. *sansaniensis* (Noulet). Moser et al. (2009b: Nr. 13): *Planorbarius* sp.

Discussion: The conchological features (size, overall shape and proportions, proto- and teleoconch sculpture) of the present specimens compare well with Middle Miocene material of *Planorbarius cornu* from France, Germany and Czech Republic. The species is known in Europe for a long time span, from the Middle Eocene to the Late Miocene (Kókay 2006), being especially abundant in the Freshwater Molasse (Süßwassermolasse) of southern Germany (Schlickum 1970). The long time span of this species likely indicates that it is actually an agglomerate of species. The exclusively Miocene *P. mantelli* (Dunker 1848), for instance, is often considered a synonym or a subspecies of *P. cornu*, but could be a valid taxa (Harzhauser et al. 2014). Since this species complex is in dire need of a thorough revision, we prefer for the moment the more conservative classification as *P. cornu*.

Moser et al. (2009b) identified two morphs of this species in Sandelzhausen, one thick and more involute and the other thin and more evolute, that were previously identified as two separate species by Gall (1972). Nevertheless, as already made clear by Moser et al. (2009b), the large amount of material available shows that all intermediate forms are present; moreover, it is almost impossible to identify the morphs based on juvenile shells with just a few whorls. Moser et al. (2009b) suggested that this could be a speciation process, but that does not seem to be case, since the same variability can be equally seen in samples from all of the layers in Sandelzhausen. Moreover, the same sort of variation is found in samples of *P. cornu* (housed at the SMNS) from other West and Central European Miocene fossil sites.



Figs 24–25. *Hippeutis* sp., juvenile (BSPG 1959 II 17704; D = 1.3 mm). — Figs 26–28. *Planorbarius cornu* (BSPG 1959 II 462; D = 22.7 mm). — Figs 29–31. *Segmentina lartetii*. Fig. 31 BSPG 1959 II 17309; D = 3.3 mm; Fig. 31. BSPG 1959 II 17310; D = 3.7 mm). — Figs 32–33. *Discus pleuradrus* (BSPG 1959 II 16152; D = 4.1 mm). — Figs 34–35. *Lucilla subteres* (BSPG 1959 II 18015; D = 1.6). — Figs 36–37. *Janulus supracostatus* (BSPG 1959 II 16150; D = 3.0 mm). — Fig. 38. *Archaeozonites* sp., protoconch detail (BSPG 1959 II 17374; D = 4.7 mm). — Fig. 39. *Limax* sp. (BSPG 1959 II 17692; D = 6.3 mm). — Figs 40–41. *Vitrina* sp. (BSPG 1959 II 17690; D = 1.8 mm; juvenile).

### Genus **Segmentina** Fleming 1818

### **Segmentina lartetii** (Noulet 1854)

Figs 29–31

1854 *Planorbis Lartetii* Noulet: 104.
1923 *Segmentina larteti larteti* [sic] – Wenz: 1663.
1976 *Segmentina larteti larteti* [sic] – Schlickum: 6 (pl. 1, fig. 18).
1998 *Segmentina larteti* [sic] – Finger: 15 (pl. 7, figs. A–C).
2006 *Segmentina larteti* [sic] – Kókay: 58 (pl. 20, fig. 5).
2014 *Segmentina lartetii* – Harzhauser et al.: 16 (pl. 2, figs. 12–16).

Stratigraphic occurrence: Layer C (1 spcm.) and D1 (2 spcm.). Moreover, a single specimen comes from an excavation site for which no profile is available, but, based on its height in the sediment and its preservation, it is likely from Layer B.

Description: Shell diminutive, pseudodextral, involute, lenticular to almost planispiral; shell height ~1/5 shell width. Upper surface of shell flattened, almost concave; lower surface very convex, with a flattened spire; an angular portion separates the two sides. Protoconch small, smooth; transition to teleoconch unclear. Teleoconch smooth, but with well-marked growth lines. Suture well-marked, slightly incised. Whorls regularly increasing in size towards aperture. Aperture V-shaped, but asymmetrical; ~1/3 shell width. Peristome simple, sharp. Umbilicus open on basal surface of shell, but narrow and deep on upper surface. Broken whorl sections reveal axial folds, running from the center to the keel, on the inner basal portion of whorls.

Measurements (in mm): 4–5 whorls; H = ~1.2; D = ~4.5.

Previous identification of the material: Gall (1972: Nr. 45): *Segmentina larteti larteti* [sic] (Noulet 1854). Moser et al. (2009b: Nr. 6): *Segmentina* sp.

Discussion: This is a somewhat rare species among the freshwater snails from Sandelzhausen, as it seems to be the case in other localities where it occurs. Nevertheless, it seems to have been very widespread throughout central Europe, with records from France, Germany, Switzerland, Hungary, Czech Republic, Austria and Italy, and a time span ranging from the Middle Miocene to the Early Pliocene (Esu 1984, Harzhauser et al. 2014). The single Pliocene record of the species, from Sardinia, Italy, was deemed as a surviving relict population by Esu (1984). The single recent species in the genus is *S. nitida* (Müller 1774), which occurs in almost all the European continent, living in permanent calm and shallow brackish waters (Welter-Schultes 2012). As such, the genus' occurrence in the fossil record has been deemed to point to swampy stagnant lakes (Harzhauser & Tempfer 2004, Moser et al. 2009b).

## Stylommatophora

## Superfamily Punctoidea

## Family Discidae

### Genus ***Discus*** Fitzinger 1833

### ***Discus pleuradrus*** (Bourguignat 1881)

Figs 32–33

1881 *Helix pleuradra* Bourguignat: 53 (pl. 3, figs. 67–72).
1923 *Gonyodiscus* (*Gonyodiscus*) *pleuradra pleuradra* – Wenz: 341.
1942 *Gonyodiscus* (*Gonyodiscus*) *pleuradra pleuradra* – Wenz & Edlauer: 93.
1967 *Discus* (*Discus*) *pleuradrus* – Schütt: 213 (fig. 16).
1976 *Discus* (*Discus*) *pleuradrus* – Schlickum: 12 (pl. 2, fig. 37).
2000 *Discus* (*Discus*) *pleuradra* [sic] – Fischer: 145 (fig. 21).
2009 *Discus pleuradrus* – Böttcher et al.: 239 (figs. 2/10–11).
2014 *Discus pleuradrus* – Harzhauser et al.: 29 (pl. 9, figs. 8–13).

Stratigraphic occurrence: Layer D1 (1 spcm.). Moreover, three specimens come from a sample lacking stratigraphical data.

Description: Shell diminutive, discoid; shell height ~1/2 shell width. Protoconch (~1¼ whorl) flat, smooth; transition to teleoconch clear. Teleoconch sculpture by strong parallel prosocline ribs; distance among ribs equal to width of rib. Whorl profile convex. Suture well-marked. Whorls regularly growing. Body whorl with very faint keel on median-upper portion. Aperture oval. Umbilicus wide.

Measurements (in mm): BSPG 1959 II 16152 (juvenile specimen): 4 whorls; H = 2.2; D = 4.1.

Previous identification of the material: Gall (1972: Nr. 10, in part): *Discus* (*Discus*) *pleuradra pleuradra* (Bourguignat) [sic]. Moser et al. (2009b: Nr. 45): *Discus* cf. *pleuradrus* (Bourguignat).

Discussion: The present specimens compare well with *Discus pleuradrus*, originally described from Sansan (MN6), France (Bourguignat 1881). The species is known from the entire Miocene of Central and Western Europe, being especially widespread during the Middle and Upper Miocene (Böttcher et al. 2009). Nevertheless, Early and Late Miocene records could actually be of other species (Moser et al. 2009b), what would restrict *D. pleuradrus* to France, southern Germany, and Austria (Harzhauser et al. 2014).

## Family Helicodiscidae

### Genus ***Lucilla*** Lowe 1852

### ***Lucilla subteres*** (Clessin 1877)

Figs 34–35

1877 *Helix* (*Patula*) *subteres* Clessin: 35.
1885 *Patula subteres* – Clessin: 76 (pl. 7, fig. 6).
1923 *Pyramidula subteres* – Wenz: 1062.
1976 *Helicodiscus* (*Hebetodiscus*) *subteres* – Schlickum: 11 (pl. 2, fig. 35).
1979 *Helicodiscus* (*Hebetodiscus*) *subteres* – Schlickum: 68 (fig. 2).
1980 *Helicodiscus* (*Hebetodiscus*) *subteres* – Gall: 65.
2006 *Helicodiscus* (*Hebetodiscus*) *subteres* – Kókay: 74 (pl. 27, figs. 14–16).
2014a *Lucilla subteres* – Salvador: 280 (fig. 24).

Stratigraphic occurrence: The specimen lacks stratigraphical data, but Moser et al. (2009b) indicated Layers B/C1.

Description: Shell diminutive, discoid, with flattened spire. Protoconch (~1½ whorl) flat, sculptured by numerous fine spiral striae; transition to teleoconch unclear. Teleoconch smooth, but with well-marked growth lines. Whorl profile convex. Suture well-marked, deep. Whorls regularly growing. Aperture round. Umbilicus wide.

Measurements (in mm): juvenile specimen: 2¾ whorls; H = 0.7; D = 1.6.

Previous identification of the material: Gall (1972: Nr. 10, in part): *Discus* (*Discus*) *pleuradra pleuradra* (Bourguignat). Moser et al. (2009b: Nr. 44): *Lucilla* sp. nov.

Discussion: Moser et al. (2009b) stated that this single specimen would be a new species, based on a flatter spire, more rapidly growing whorls and an overall more delicate appearance when compared to *L. subteres*. Nevertheless, the present specimen compares well to the type material of *L. subteres* (SMNS 68502), as well as with material from other localities. The diagnostic features listed by MOSER et al. (2009b) are just impressions due to the single specimen from Sandelzhausen being a juvenile, with less than three whorls. *Lucilla subteres* is known from Miocene (MN 5-6) sites of Southern Germany (type locality: Undorf) and Hungary (SCHLICKUM 1976, 1979, KÓKAY 2006, SALVADOR 2014b).

*Lucilla* species were usually classified in the genus *Helicodiscus* MORSE 1864 and, more specifically, in the subgenus *Hebetodiscus* H.B. BAKER 1929. BEQUAERT & MILLER (1973), however, later considered *Hebetodiscus* as a valid genus, which in turn was regarded as a synonym of *Lucilla* by FALKNER et al. (2002). As such, some authors (*e.g.*, HUBRICHT 1985, HOTOPP et al. 2010) state that this whole *Helicodiscus* complex should be revised. Until then, the current approach of treating *Lucilla* as a distinct genus (*e.g.*, GARGOMINY et al. 2011, WELTER-SCHULTES 2012) is followed here.

Remarks: The two recent European *Lucilla* species are subterranean, living deeper in the soils than other land snails; one of them, *Lucilla scintilla* (LOWE 1852) is even blind (WELTER-SCHULTES 2012). If the extinct *Lucilla* species were also subterranean, it would greatly difficult their preservation in the fossil record and so explain the few records and small number of specimens found until now (SCHLICKUM 1979).

### Superfamily Gastrodontoidea

### Family Gastrodontidae

### Genus **Janulus** LOWE 1852

### **Janulus supracostatus** (SANDBERGER 1873)

Figs 36–37

1873 *Patula supracostata* SANDBERGER: pl. 29, fig. 2.
1923 *Janulus supracostatus* – WENZ: 304.
1976 *Janulus supracostatus* – SCHLICKUM: 13 (pl. 3, fig. 43).

Stratigraphic occurrence: Unknown; the single specimen comes from an undetermined locality within the basin.

Description: Shell diminutive, discoid; shell height ~2/3 shell width. Protoconch (~1 whorl) flat, smooth; transition to teleoconch clear. Teleoconch sculpture by strong parallel prosocline ribs; distance among ribs equal to width of rib. Sculpture only present in upper portion of whorls; basal portion (below keel) smooth, except for growth lines. Whorl profile slightly convex. Suture well-marked, deep. Whorls regularly growing. Body whorl with marked keel on upper portion. Aperture narrow, rounded crescent-shaped. Umbilicus wide.

Measurements (in mm): BSPG 1959 II 16150 (juvenile specimen): 3¾ whorls; H = 1.8; D = 3.0.

Previous identification of the material: GALL (1972: Nr. 7): *Janulus* cf. *supracostatus* (SANDBERGER). MOSER et al. (2009b: Nr. 49): *Janulus* cf. *supracostatus* (SANDBERGER).

Discussion: The single specimen from Sandelzhausen can be easily identified as *Janulus supracostatus* by its ribs, which do not extend themselves to the basal portion of the whorls. The species was originally described from the Silvana-beds (Silvanaschichten) of south-western Germany (MN 5–6).

### Gastrodontoidea *incertae sedis*

### Subfamily Archaeozonitinae

### Genus **Archaeozonites** SANDBERGER 1873

### **Archaeozonites** sp.

Fig. 38

Stratigraphic occurrence: Layers B2 (1 spcm.), C (undetermined; 1 spcm.) and C3 (1 spcm.). Moreover, 16 specimens are from excavation sites for which no profile is available, but, based on their height in the sediment and their preservation, it is possible to infer the layer of origin as C (6 spcm.), C3 (1 spcm.) and either B or C (5 spcm.). Finally, 2 specimens are from the Grube Bergmaier site.

Description: Protoconch (~1 whorl) flattened, sculptured by fine riblets that grow coarser towards teleoconch. Teleoconch sculptured by numerous strong parallel prosocline ribs; distance between ribs equal to width of rib. Suture weakly marked. Spire conical; whorls profile flattened. Umbilicus wide, deep.

Measurements (in mm): BSPG 1959 II 16143 (deformed, incomplete specimen): 5 whorls; D = 21.1.

Previous identification of the material: GALL (1972: Nr. 5): *Archaeozonites costatus costatus* SANDBERGER. MOSER et al. (2009b: Nr. 50): *Archaeozonites* sp.

Discussion: A few specimens, almost all fragments of spire apexes, show a remarkable sculpture consisting of very strong ribs, present even in part of the protoconch (although more weakly marked). However, a single more complete specimen was preserved, although much deformed. It lacks the apertural region and it is greatly compressed, but the main diagnostic features of the genus *Archaeozonites* can be seen: the strong ribs, the flattened whorl profile, weakly marked suture, the broad conical profile of the spire and a wide umbilicus. Nevertheless, it is impossible to advance further than genus level in the classification. Still, the specimens from Sandelzhausen resemble the Central European Miocene species *A. costatus* (SANDBERGER 1876) and *A. laticostatus* (SANDBERGER 1885). The genus is known in Europe from the Middle Eocene to the Late Pliocene (ZILCH 1959).

Remarks: Here the work of BOUCHET et al. (2005) is followed, treating the genus *Archaeozonites* and the subfamily Archaeozonitinae as belonging to Gastrodontoidea *incertae sedis* rather than its traditional allocation within Zonitidae (Zonitoidea).

### Superfamily Limacoidea

### Family Limacidae

### Genus ***Limax*** Linnaeus 1758

### ***Limax*** sp.

Fig. 39

Stratigraphic occurrence: Layer C (2 spcm). Moreover, 13 specimens stem from the Grube Bergmeier site and 4 lack stratigraphical data.

Description: Shell small, vestigial, oval; shell width ~2/3 length. Nucleus slightly bent laterally; nucleus region higher than remainder of shell.

Measurements (in mm): BSPG 1959 II 17692 (Fig. 35): D = 6.3.

Previous identification of the material: Gall (1972: Nr. 8 and 9): respectively, *Limax* sp. and *Milax* sp. Moser et al. (2009b: Nr. 51 and 53): respectively, *Milax* sp. and *Limax* spp.

Discussion: The shells of limacids are vestigial and internal and thus of very limited taxonomical value; therefore, the identification of the material from Sandelzhausen cannot proceed further than genus level. *Limax* is known in Europe since the Late Oligocene (Zilch 1959).

Both Gall (1972) and Moser et al. (2009b) indicated the presence of the genus *Milax* Grey 1855 in Sandelzhausen. The shells of *Milax* are inflated and markedly convex, with a central elevated nucleus, features that cannot be seen in the present specimens. Moreover, Moser et al. (2009b) suggested that there would be more than one species of *Milax* and *Limax* in Sandelzhausen, but did not provide arguments to support this. The only visible difference among the specimens from Sandelzhausen is the size, which would more likely indicate juveniles rather than distinct species. Little taxonomic information can be extracted from *Limax* shells and diagnosis of several species seems unwarranted.

### Family Vitrinidae

### Genus ***Vitrina*** Draparnaud 1801

### ***Vitrina*** sp.

Figs 40–41

Stratigraphic occurrence: The specimens lack stratigraphical data, but Moser et al. (2009b) indicated Layers C2/C3.

Description: Shell small, discoid, with flattened spire and rapidly expanding whorls. Protoconch (~1 whorl) sculptured by spiral rows of punctae; transition to teleoconch unclear. Teleoconch smooth, except for growth lines. Suture well-marked but not too deep. Aperture oval, prosocline.

Measurements (in mm): juvenile specimen: 1½ whorl; H = 1.6; D = 1.8.

Previous identification of the material: Gall (1972: Nr. 4): *Vitrina* cf. *suevica suevica* (Sandberger). Moser et al. (2009b: Nr. 52): *Vitrina* sp. nov.

Discussion: The shells of vitrinids are simplified and thus do not present many useful taxonomical characters. Moreover, the two specimens from Sandelzhausen are just juvenile shells (with a maximum of 1½ whorl), which reduces even further the possibility of a precise classification. Nevertheless, Moser et al. (2009b) questioned the identification of Gall (1972) as *V. suevica* (Sandberger 1876), a species well known from the Middle Miocene of Germany (Schütt 1967), and suggested that these specimens could represent a new species. They based their proposition solely on the “more spherical shape” of the shell, which is a feature common to juvenile vitrinids due to the rapidly expanding whorls. As such, here a more conservative approach is preferred and identification remains at genus level only.

## Discussion

The large specimens from Sandelzhausen (namely *Palaeoglandina*, *Lymnaea*, *Planorbarius* and the helicids) are preserved in very deformed states: the shells are compressed, collapsed or expanded. This may present some problems for taxonomy (Gall 1973, Moser et al. 2009b, Salvador 2013b) and thus identification should proceed with caution. Nevertheless, contrary to the stylommatophorans (Salvador 2013b; and *Archaeozonites* sp. described here), some of the large basommatophoran specimens are well-preserved enough to allow a more confident identification as *Lymnaea dilatata* and *Planorbarius cornu*.

Some of the specimens from Sandelzhausen were here classified as species from somewhat younger faunas from the Middle Miocene (*e.g.*, *Galba dupuyiana*, *Segmentina lartetii*). Comparisons among distinctive geological time slices must always be approached cautiously. Gall (1972) identified a large portion of Sandelzhausen’ material as species from the French site of Sansan (MN 6), which led Moser et al. (2009b) to state that Gall’s identification should be revised and comparisons should be made with material of the same age (MN 5). Nevertheless, Moser et al. (2009b) identified some basommatophoran species as belonging to recent

North-American genera. Salvador (2013b, 2014b) conducted a revision and found many differences in relation to Gall's identification of the stylommatophorans, but here, for the basommatophorans, a different scenario can be seen: the species from Sandelzhausen indeed seem to be related to younger Central European faunas such as Sansan and Steinheim. This could be due to the lack of useful conchological features in basommatophoran taxonomy, which makes species hard to diagnose. However, this seems rather unlikely due to the number of species studied here that fall in this case and also to the very close morphological affinity of the fossils from Sandelzhausen to younger basommatophoran faunas.

The most abundant species in Sandelzhausen are the planorbid *Gyraulus dealbatus* and the lymnaeid *Galba dupuyiana*. Regarding the lymnaeids in particular, Moser et al. (2009b) stated that the most abundant genus of this family in Sandelzhausen was *Radix*. Here, however, the specimens were classified as *Galba dupuyiana* and only very few *Radix* specimens were identified (as *Radix socialis*), restricted to the uppermost portions of Layer D1. A freshwater fauna dominated by *Galba* is very unusual and Böttcher et al. (2009) reported a similar scenario for the coeval fossil site of Oggenhausen 2 (MN 5, SW Germany). The paleoecological significance of these curious findings (the larger *Lymnaea dilatata* is also very common) will be more thoroughly explored in a future work.

Finally, as already seen in Salvador (2013b, 2014b), the number of species present in Sandelzhausen appears to have been overestimated by Moser et al. (2009b). Most of the classification of Moser et al. (2009b) considered as species extreme forms of a continuous of morphological variation and sometimes also juvenile specimens. This is especially true for the basommatophorans. It is also curious to notice that these species show the same variation throughout the entire basin and also throughout all the layers (the deposition of these sediments is deemed to have occurred rather rapidly; Tütken & Vennemann 2009). *Galba dupuyiana* is almost an exception, for, despite the conchological variation being the same throughout the layers, there is a slight change in proportion between the slender and broader forms in the upper portion of Layer D1, as explained above. But there is no clear substitution of a morph (or species) for another in an upper layer. Moreover, another curious exception is the various forms of *Gyraulus dealbatus* along the sediment layers, a matter that will be further explored in a future work.

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## Appendix 1. List of analyzed material.

Here is listed all the material from Sandelzhausen available for each species. The order in which the species are presented below is the same as they appear in the main body of the text.

*Galba dupuyiana* (Noulet 1854): BSPG 1959 II 17476 (>150 spcm.), 17477 (>200 spcm.), 17478 (>100 spcm.), 17479 (60 spcm.), 17480 (17 spcm.), 17481 (26 spcm.), 17482 (>150 spcm.), 17483 (>200 spcm.), 17484 (>300 spcm.), 17485 (>300 spcm.), 17486 (>200 spcm.), 17487 (>1200 spcm.), 17488 (>350 spcm.), 17489 (6 spcm.), 17490 (5 spcm.), 17491 (6 spcm.), 17492 (18 spcm.), 17493 (12 spcm.), 17494 (7 spcm.), 17495 (3 spcm.), 17496 (24 spcm.), 17497 (20 spcm.), 17498 (9 spcm.), 17499 (1 spcm.), 17500 (1 spcm.), 17501 (1 spcm.), 17502 (1 spcm.), 17503 (1 spcm.), 17504 (1 spcm.), 17505 (6 spcm.), 17506 (11 spcm.), 17507 (1 spcm.), 17508 (2 spcm.), 17509 (1 spcm.), 17510 (3 spcm.), 17511 (2 spcm.), 17512 (3 spcm.), 17513 (1 spcm.), 17514 (6 spcm.), 17515 (2 spcm.), 17516 (1 spcm.), 17517 (8 spcm.), 17518 (5 spcm.), 17707 (2 spcm.), 17708 (1 spcm.), 17709 (1 spcm.), 17710 (1 spcm.), 17711 (1 spcm.), 17712 (8 spcm.).

*Lymnaea dilatata* (Noulet 1854): BSPG 1959 II 465 (1 spcm.), 466 (1 spcm.), 16133 (1 spcm.), 16134 (2 spcm.), 17519 (1 spcm.), 17520 (5 spcm.), 17521 (1 spcm.), 17522 (1 spcm.), 17523 (1 spcm.), 17524 (1 spcm.), 17525 (1 spcm.), 17526 (1 spcm.), 17527 (1 spcm.), 17528 (3 spcm.), 17529 (5 spcm.), 17530 (5 spcm.), 17531 (1 spcm.), 17532 (2 spcm.), 17533 (1 spcm.), 17534 (1 spcm.), 17535 (1 spcm.), 17536 (2 spcm.), 17537 (2 spcm.), 17538 (1 spcm.), 17539 (2 spcm.), 17540 (2 spcm.), 17541 (1 spcm.), 17542 (1 spcm.), 17543 (1 spcm.), 17544 (1 spcm.), 17545 (2 spcm.), 17546 (1 spcm.), 17547 (1 spcm.), 17548 (1 spcm.), 17549 (1 spcm.), 17550 (1 spcm.), 17551 (1 spcm.), 17552 (3 spcm.), 17553 (1 spcm.), 17554 (1 spcm.), 17555 (1 spcm.), 17556 (3 spcm.), 17557 (2 spcm.), 17558 (1 spcm.), 17559 (3 spcm.), 17560 (1 spcm.), 17561 (2 spcm.), 17562 (1 spcm.), 17563 (7 spcm.), 17564 (3 spcm.), 17565 (1 spcm.), 17566 (1 spcm.), 17567 (1 spcm.), 17573 (1 spcm.), 17575 (1 spcm.), 17576 (1 spcm.), 17577 (1 spcm.), 17578 (1 spcm.), 17579 (2 spcm.), 17580 (1 spcm.), 17581 (1 spcm.), 17582 (3 spcm.), 17583 (2 spcm.), 17584 (3 spcm.), 17585 (1 spcm.), 17586 (1 spcm.), 17587 (1 spcm.), 17588 (1 spcm.), 17589 (2 spcm.), 17590 (2 spcm.), 17718 (2 spcm.), 17931 (1 spcm.), 17932 (3 spcm.), 17933 (1 spcm.), 17934 (1 spcm.), 17935 (4 spcm.), 17936 (1 spcm.), 17937 (1 spcm.), 17938 (15 spcm.), 17939 (5 spcm.), 17940 (4 spcm.), 17941 (2 spcm.), 17942 (4 spcm.), 17943 (1 spcm.), 17944 (8 spcm.), 17945 (1 spcm.), 17946 (5 spcm.), 17947 (3 spcm.), 17948 (11 spcm.), 17949 (1 spcm.), 17950 (1 spcm.), 17951 (1 spcm.), 17952 (1 spcm.), 17953 (1 spcm.), 17954 (1 spcm.), 17955 (1 spcm.), 17956 (5 spcm.), 17957 (3 spcm.), 17958 (5 spcm.), 17959 (3 spcm.), 17960 (4 spcm.), 17961 (1 spcm.), 17962 (15 spcm.), 17963 (5 spcm.), 17964 (2 spcm.), 17965 (1 spcm.), 17966 (10 spcm.), 17967 (1 spcm.), 17968 (1 spcm.), 17969 (5 spcm.), 17970 (1 spcm.), 17971 (1 spcm.), 17972 (4 spcm.), 17973 (3 spcm.), 17974 (1 spcm.), 17975 (1 spcm.), 17976 (2 spcm.), 17977 (1 spcm.), 17978 (1 spcm.), 17979 (1 spcm.), 17980 (1 spcm.), 17981 (1 spcm.), 17982 (1 spcm.), 17983 (4 spcm.), 17984 (1 spcm.), 17985 (1 spcm.), 17986 (2 spcm.), 17987 (2 spcm.), 17988 (1 spcm.), 17989 (1 spcm.), 17990 (1 spcm.), 17991 (2 spcm.), 17992 (1 spcm.), 17993 (1 spcm.), 17994 (1 spcm.), 17995 (1 spcm.), 17996 (1 spcm.), 17997 (1 spcm.), 17998 (1 spcm.), 17999 (1 spcm.), 18000 (9 spcm.), 18001 (1 spcm.), 18002 (4 spcm.), 18003 (1 spcm.), 18004 (1 spcm.), 18005 (3 spcm.), 18006 (1 spcm.), 18007 (1 spcm.), 18008 (3 spcm.), 18009 (1 spcm.), 18010 (1 spcm.), 18011 (4 spcm.), 18012 (9 spcm.), 18013 (3 spcm.), 18014 (1 spcm.).

*Radix socialis* (Zieten 1830): BSPG 1959 II 17568 (8 spcm.), 17569 (2 spcm.), 17570 (22 spcm.), 17571 (1 spcm.), 17572 (1 spcm.), 17574 (1 spcm.).

*Ferrissia deperdita* (Desmarest 1814): BSPG 1959 II 17706 (6 spcm.).

*Gyraulus albertanus* (Clessin 1877): BSPG 1959 II 17659 (16 spcm.), 17660 (5 spcm.), 17661 (37 spcm.), 17662 (8 spcm.), 17663 (2 spcm.), 17664 (50 spcm.), 17665 (45 spcm.), 17666 (>200 spcm.), 17667 (>200 spcm.), 17668 (>150 spcm.), 17669 (5 spcm.), 17670 (1 spcm.), 17705 (3 spcm.).

*Gyraulus dealbatus* (Braun 1851): BSPG 1959 II 18017 (>800 spcm.), 18018 (>400 spcm.), 18019 (>200 spcm.), 18020 (>100 spcm.), 18021 (4 spcm.), 18022 (>100 spcm.), 18023 (>50 spcm.), 18024 (>50 spcm.), 18025 (1 spcm.), 18026 (1 spcm.), 18027 (>50 spcm.), 18028 (29 spcm.), 18029 (>50 spcm.), 18030 (15 spcm.), 18031 (9 spcm.), 18032 (>50 spcm.), 18033 (>200 spcm.), 18034 (>50 spcm.), 18035 (3 spcm.), 18036 (7 spcm.), 18037 (4 spcm.), 18038 (2 spcm.), 18039 (>50 spcm.), 18040 (1 spcm.), 18041 (>200 spcm.), 18042 (3 spcm.), 18043 (4 spcm.), 18044 (>150 spcm.), 18045 (4 spcm.), 18046 (2 spcm.), 18047 (>50 spcm.), 18048 (1 spcm.), 18049 (1 spcm.).

*Hippeutis* sp.: BSPG 1959 II 17704 (1 spcm.).

*Planorbarius cornu* (Brongniart 1810): BSPG 1959 II 462 (1 spcm.), 463 (1 spcm.), 464 (1 spcm.), 13135 (1 spcm.), 13136 (1 spcm.), 16138 (1 spcm.), 16139 (1 spcm.), 16140 (1 spcm.), 16141 (1 spcm.), 17591 (19 spcm.), 17592 (9 spcm.), 17593 (6 spcm.), 17594 (1 spcm.), 17595 (8 spcm.), 17596 (7 spcm.), 17597 (>50 spcm.), 17598 (47 spcm.), 17599 (>50 spcm.), 17600 (1 spcm.), 17600 (1 spcm.), 17601 (2 spcm.), 17602 (1 spcm.), 17603 (1 spcm.), 17604 (1 spcm.), 17605 (1 spcm.), 17606 (>50 spcm.), 17607 (3 spcm.), 17608 (32 spcm.), 17609 (1 spcm.), 17610 (1 spcm.), 17611 (1 spcm.), 17612 (1 spcm.), 17613 (1 spcm.), 17614 (1 spcm.), 17615 (1 spcm.), 17616 (2 spcm.), 17617 (1 spcm.), 17618 (2 spcm.), 17619 (1 spcm.), 17620 (>140 spcm.), 17621 (2 spcm.), 17622 (2 spcm.), 17623 (1 spcm.), 17624 (1 spcm.), 17625 (2 spcm.), 17626 (1 spcm.), 17627 (1 spcm.), 17628 (2 spcm.), 17629 (3 spcm.), 17630 (2 spcm.), 17631 (2 spcm.), 17632 (1 spcm.), 17633 (1 spcm.), 17634 (1 spcm.), 17635 (1 spcm.), 17636 (1 spcm.), 17637 (3 spcm.), 17638 (1 spcm.), 17639 (1 spcm.), 17640 (2 spcm.), 17641 (1 spcm.), 17642 (1 spcm.), 17643 (1 spcm.), 17644 (2 spcm.), 17645 (1 spcm.), 17646 (1 spcm.), 17647 (1 spcm.), 17648 (1 spcm.), 17649 (1 spcm.), 17650 (1 spcm.), 17651 (1 spcm.), 17652 (1 spcm.), 17653 (1 spcm.), 17654 (1 spcm.), 17655 (1 spcm.), 17656 (1 spcm.), 17657 (4 spcm.), 17677 (12 spcm.), 17838 (8 spcm.), 17839 (2 spcm.), 17840 (1 spcm.), 17841 (1 spcm.), 17842 (1 spcm.), 17843 (10 spcm.), 17844 (4 spcm.), 17845 (2 spcm.), 17846 (24 spcm.), 17847 (15 spcm.), 17848 (1 spcm.), 17849 (3 spcm.), 17850 (7 spcm.), 17851 (2 spcm.), 17852 (3 spcm.), 17853 (2 spcm.), 17854 (4 spcm.), 17855 (2 spcm.), 17856 (1 spcm.), 17857 (10 spcm.), 17858 (5 spcm.), 17859 (7 spcm.), 17860 (21 spcm.), 17861 (2 spcm.), 17862 (4 spcm.), 17863 (4 spcm.), 17865 (11 spcm.), 17866 (1 spcm.), 17867 (1 spcm.), 17868 (1 spcm.), 17869 (16 spcm.), 17870 (2 spcm.), 17871 (7 spcm.), 17872 (1 spcm.), 17873 (1 spcm.), 17874 (2 spcm.), 17875 (4 spcm.), 17876 (1 spcm.), 17877 (1 spcm.), 17878 (1 spcm.), 17879 (1 spcm.), 17880 (4 spcm.), 17881 (13 spcm.), 17882 (1 spcm.), 17883 (6 spcm.), 17884 (1 spcm.), 17885 (1 spcm.), 17886 (1 spcm.), 17887 (1 spcm.), 17888 (1 spcm.), 17889 (1 spcm.), 17890 (1 spcm.), 17891 (1 spcm.), 17892 (1 spcm.), 17893 (1 spcm.), 17894 (1 spcm.), 17895 (2 spcm.), 17896 (1 spcm.), 17897 (2 spcm.), 17898 (2 spcm.), 17899 (1 spcm.), 17900 (1 spcm.), 17901 (1 spcm.), 17902 (1 spcm.), 17903 (1 spcm.), 17904 (1 spcm.), 17905 (2 spcm.), 17906 (2 spcm.), 17907 (3 spcm.), 17908 (3 spcm.), 17909 (1 spcm.), 17910 (1 spcm.), 17911 (2 spcm.), 17912 (3 spcm.), 17913 (3 spcm.), 17914 (1 spcm.), 17915 (1 spcm.), 17916 (1 spcm.), 17917 (1 spcm.), 17918 (2 spcm.), 17919 (1 spcm.), 17920 (3 spcm.), 17921 (1 spcm.), 17922 (2 spcm.), 17923 (1 spcm.), 17924 (2 spcm.), 17925 (1 spcm.), 17926 (1 spcm.), 17927 (1 spcm.), 17928 (1 spcm.), 17929 (6 spcm.), 17930 (2 spcm.).

*Segmentina lartetii* (Noulet 1854): BSPG 1959 II 16141 (1 spcm.), 17309 (1 spcm.), 17310 (1 spcm.), 17311 (1 spcm.).

*Discus pleuradrus* (Bourguignat 1881): BSPG 1959 II 16152 (1 spcm.), 17658 (3 spcm.).

*Lucilla subteres* (Clessin 1877): BSPG 1959 II 18015 (1 spcm.).

*Janulus supracostatus* (Sandberger 1873): BSPG 1959 II 16150 (1 spcm.).

*Archaeozonites* sp.: BSPG 1959 II 16143 (1 spcm.), 17371 (1 spcm.), 17372 (2 spcm.), 17373 (1 spcm.), 17374 (3 spcm.), 17375 (1 spcm.), 17474 (1 spcm.), 17679 (3 spcm.), 17696 (1 spcm.), 17697 (1 spcm.), 17698 (1 spcm.), 17699 (1 spcm.), 17700 (1 spcm.), 17701 (2 spcm.), 18016 (3 spcm.).

*Limax* sp.: BSPG 1959 II 17691 (1 spcm.), 17692 (1 spcm), 17693 (12 spcm.), 17694 (4 spcm.), 17695 (1 spcm.).

*Vitrina* sp.: BSPG 1959 II 17690 (2 spcm.).

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# Fossil land and freshwater gastropods from the Middle Miocene of Bechingen and Daugendorf, southwestern Germany

RODRIGO B. SALVADOR & MICHAEL W. RASSER

## Abstract

This study presents a taxonomic treatment of the fossil land and freshwater gastropods from Bechingen and Daugendorf (Riedlingen, Baden-Württemberg state, SW Germany). The fossils stem from the Tautschbuch carbonate unit, which belongs to the so-called Silvana Beds of the Upper Freshwater Molasse. Nineteen gastropod species (mainly pulmonates) are reported here from Bechingen and eleven from Daugendorf, belonging to the families: Pachychilidae, Bithynidae, Pomatiidae, Lymnaeidae, Planorbidae, Subulinidae, Cochlicopidae, Elonidae, Helicidae, Hygromiidae, Trissexodontidae, Discidae, Gastrocoptidae, Succineidae, Oleacinidae and possibly Chondrinidae and Zonitidae. Two species previously mentioned on the literature from Bechingen were not found in the present material: *Pseudoleacina eburnea* and *Janulus supracostatus*. The gastropod fauna agrees with the previously proposed paleoenvironment consisting of shallow temporary lakes or ponds surrounded by reeds.

**Key words**: Caenogastropoda, Langhian, Pulmonata, Silvana Beds, Tautschbuch, Upper Freshwater Molasse.

## Introduction

The Upper Freshwater Molasse ("Obere Süßwassermolasse", in German; abbreviated OSM) is remarkable for its numerous fossiliferous outcrops (*e.g.*, SANDBERGER 1870–1875, WENZ 1923, ABDUL-AZIZ et al. 2008, 2010, KÄLIN & KEMPF 2009). The Tautschbuch is a somewhat coherent carbonate unit belonging to the OSM and located on the southern border of the Swabian Alb (southern Germany). The Tautschbuch and its surroundings have several mollusk-bearing fossil outcrops, such as Zwiefaltendorf, Mörsingen, Gauingen, Bechingen and Emerberg. With the exception of Zwiefaltendorf (SCHLICKUM 1976), the molluscan faunas of these localities were not studied in recent times. The present work provides a taxonomical account of the mollusks from Bechingen and the less-known neighbouring locality Daugendorf.

### Geological setting and localities

Bechingen and Daugendorf (ca. 2 km south of the former; Fig. 1) are two neighbourhoods of the town of Riedlingen (Biberach district, Baden-Württemberg state, SW Germany); both are located to the east of the Tautschbuch hills. Only scarce information on the Tautschbuch's geology can be found in SCHWARZ (1913) and HAAG (1960). It is part of a formerly huge and continuous freshwater carbonate platform situated at the southern margin of the Swabian Alb, along the Danube River (Fig. 1). The Miocene carbonates discordantly overlay Jurassic and older Miocene rocks (the interval between the latest Jurassic and the Miocene was a time of emersion and erosion in the course of Alpine orogeny). WERNER (2014) provides

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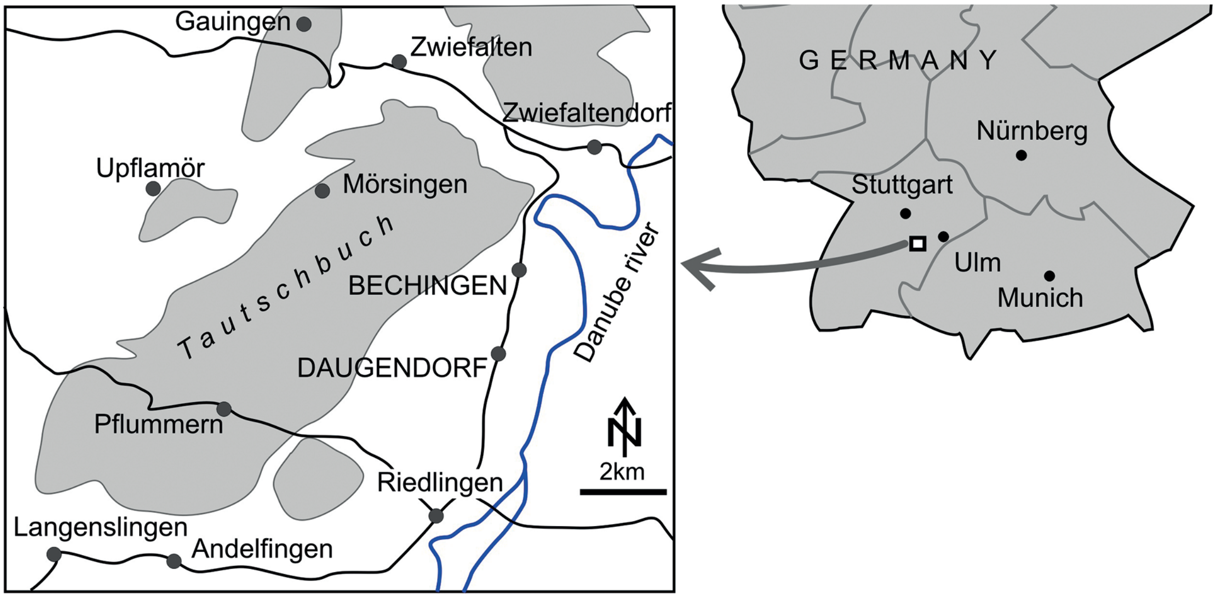

Figure 1. Map showing Bechingen and Daugendorf, located between the Tautschbuch area and the Danube River. Further localities indicated on the surrounding regions are those known from the literature to have mollusk-bearing OSM sediments. The grey areas on the inset map are the remains of an extensive Miocene freshwater carbonate platform formed by the Sylvana Beds.

some new data on the limestones from this area, proposing a paleoenvironment consisting of shallow temporary lakes or ponds surrounded by reeds. Unfortunately, actual biostratigraphic data of the Tautschbuch are not available. Based on the snail fauna and literature data, the Tautschbuch is deemed part of the Silvana Beds ("Silvanaschichten" or "Silvanakalk") and thus is tentatively dated as Langhian (early "Badenian", Middle Miocene; Höltke, pers. comm.). The Silvana Beds are part of the Obere Süßwassermolasse ("Upper Freshwater Molasse") in the North Alpine Foreland Basin, which is a freshwater sequence that was situated between the northward-migrating Alps in the South, and the Swabian Alb in the North (*e.g.*, Kuhlemann & Kempf 2002).

The collection of the Staatliches Museum für Naturkunde Stuttgart (Stuttgart, Germany) houses fossil snails labeled as Bechingen and Daugendorf, but without further information. There is no single work in the literature dealing specifically with Bechingen, but the locality was reasonably known, since several authors reported molluscan fossils from it (Jooss 1910, 1918, Gottschick 1911, Fischer & Wenz 1914, Wenz 1923, Schlickum 1976). According to Zöbelein (1973), there used to be an abandoned sand pit to the south of Bechingen, in the Maueresch area, that contained Pleistocene moraine sediments with blocks of "Silvana limestone" (containing continental gastropods) coming from the Tautschbuch hills. This gravel pit was also briefly mentioned by Engel (1908) and Schwarz (1913) to contain blocks of "Silvana limestone". The material studied in this paper certainly comes from this pit. The village Daugendorf has never been mentioned as a fossil site. It is either the same abandoned sand pit as above, or another pit that has been abandoned a long time ago and contained the same moraine sediments.

## Material and methods

All main museum collections in Germany, Switzerland and Austria were contacted in search for mollusks from these localities. Unfortunately, only the Staatliches Museum für Naturkunde Stuttgart (SMNS; Stuttgart, Germany) and the Paläontologisches Institut und Museum der Universität Zürich (PIMUZ; Zurich, Switzerland) have specimens in their collections. This material consists almost entirely of specimens gathered in the early 20th century by several collectors and included in the collections of Carlo G.H. Jooss and Konrad Miller housed in the SMNS (see also Salvador et al. in press). The few later specimens date from the 1960's and 70's, collected by Helmut Hölder and M. Katzür.

All species are figured and discussed, including data on their diagnostic features and distribution. The majority of the specimens analyzed do not have precise locality or stratigraphic data, although some lots from Bechingen indicate collection in a gravel pit ("Kiesgrube"; see above). The list of analyzed material can be found under each species entry; an asterisk (*) after the lot's number means that it is a rock sample with several inscrusted specimens.

There is no single work in the literature dealing specifically with the molluscs from Bechingen. Previous authors often refer to single species recorded from there (Jooss 1910, 1918, Gottschick 1911, Fischer & Wenz 1914, Wenz 1923, Schlickum 1976). As such, literature data can be used to slightly complement the presently available material. The vast majority of species presented here have never been reported from Bechingen before. The locality of Daugendorf, as mentioned above, has never been reported in the literature.

The classification used here follows Bouchet et al. (2005) and Nordsieck (2014). The superfamilies, however, are arranged in alphabetical order. Specimens were measured either with a digital caliper or with the aid of the computer software Leica Application Suite (LAS, v.3.8.0) and ImageJ (Rasband 2012). The following abbreviations are used throughout the article for shell measurements: H = shell height (parallel to coiling axis); D = greatest shell width (perpendicular to H).

## Systematic Paleontology

### Caenogastropoda

### Superfamily Cerithioidea

### Family Pachychilidae

### Genus ***Tinnyea*** Hantken 1887

### ***Tinnyea*** cf. ***lauraea*** (Mathéron 1843)

Fig. 2

Material examined: Bechingen: SMNS 67854 (1 spc.), 106783 (1 spc.).

Remarks: Despite the poor preservation of the present material, the specimens' turriform shell and relatively large size allow a tentative identification as *T. lauraea*. This species is known from the Oligocene to the Pliocene of Central Europe (Harzhauser et al. 2002); such a large time span is considered an indication that this is a still unresolved species complex (Kadolsky 1995).

### Superfamily Littorinoidea

### Family Pomatiidae

### Genus ***Pomatias*** Studer 1789

### ***Pomatias*** cf. ***conicus*** (Klein 1853)

Fig. 3

Material examined: Bechingen: SMNS 106784 (4 spc.), 106817 (2 spc.), 106818 (1 spcm.), 106807*.

Remarks: This species can be identified by its trochiform shell and strongly convex whorl profile. Although most specimens are internal molds, a few well preserved external molds retain the characteristic teleoconch sculpture pattern of the shell (reticulated, with stronger spiral ribs and weaker axial ribs), allowing the tentative identification at species level. *Pomatias conicus* is a common species, known from the Middle to Late Miocene of Hungary, Austria and the Silvana Beds of southwestern Germany and Switzerland (Klein 1853, Harzhauser & Binder 2004, Kókay 2006). Despite being common in the fossil record, no opercula of this species were found in the present material.

### Superfamily Rissooidea

### Family Bithyniidae

### Genus ***Bithynia*** Leach 1818

### ***Bithynia glabra*** (Zieten 1832)

Fig. 4

1830 *Cyclostoma glabrum* Zieten, p. 42, pl. 31, fig. 9.
1852 *Paludina tentaculata*, – Krauss, p. 140 [non *Helix tentaculata* Linnaeus 1758, p. 774].
1872 *Bythinia* [sic] *gracilis* Sandberger, pl. 28, figs. 16–16a.
1875 *Bythinia* [sic] *gracilis*, – Sandberger, p. 561.
1964 *Bithynia glabra*, – Schlickum, p. 9.
1966 *Bithynia dunkeri*, – Schlickum, p. 324, pl. 12, figs. 19–21.
1966 *Bithynia glabra*, – Schlickum, p. 324, pl. 12, fig. 22.
1989 *Bithynia* cf. *glabra,* – Reichenbacher, p. 144, pl. 1, fig. 4.
1989 *Bithynia dunkeri,* – Reichenbacher, p. 144, pl. 1, figs. 6–7.
2005 *Bithynia* cf. *glabra,* – Kowalke & Reichenbacher, p. 629, figs. 8.1–8.2.
2014 *Bithynia glabra*, – Neubauer et al., supplementary material 1.

Material examined: Bechingen: SMNS 68142 (3 spc.), 106810 (1 spc.).

Remarks: The conical and imperforate small shell, with a wide circular aperture and complete peristome allows the identification as *B. glabra*, a common species in the Early and Middle Miocene of Germany. Although fossil opercula of *Bithynia* are commonly recovered, none was found in the present material.

### Pulmonata

### Hygrophila

### Superfamily Lymnaeoidea

### Family Lymnaeidae

### Genus ***Lymnaea*** Lamarck 1799

### ***Lymnaea dilatata*** Noulet 1854

Fig. 5

1854 *Limnea dilatata* Noulet, p. 107.
1923 *Radix* (*Radix*) *socialis dilatata*, – Wenz, p. 1277.
2000 *Lymnaea dilatata*, – Fischer, p. 136, figs. 1–2.
2006 *Radix dilatata*, – Kókay, p. 52, pl. 17, fig. 14.
2014 *Radix dilatata*, – Neubauer et al., supplementary material 1.
2014 *Lymnaea dilatata*, – Salvador & Rasser, p. 189, figs. 8–9.

2015b *Lymnaea dilatata*, – Salvador et al., p. 204, figs. 2F–G.
2016 *Lymnaea dilatata*, – Salvador et al., p. 133, fig. 2G.

Material examined: Bechingen: SMNS 23314*, 67606 (1 spc.), 67655 (1 spc.), 106806 (3 spc.), 106809*, 106810*, 106796*, 106803 (1 spc.), 106807*. Daugendorf: SMNS 107212 (1 spc.).

Remarks: *Lymnaea dilatata* is diagnosed by its large lymnaeid shell, a proportionately small and acuminate spire, rapidly-expanding and slightly convex whorls, a roughly oval body whorl and a large ellipsoid aperture. This species is widely known from the entire Miocene of Western and Central Europe (Binder 2004, Kókay 2006).

### Genus ***Radix*** Montfort 1810

### ***Radix socialis*** (Zieten 1830)

Fig. 6

1830 *Limnaea socialis* Zieten, 40, pl. 30, fig. 4.
1846 *Limnaeus socialis* var. *elongata* Klein, p. 85, pl. 2, figs. 8a–b [non *Limneus elongatus* Draparnaud 1805, nec de Serres 1844].
1846 *Limnaeus socialis* var. *intermedia* Klein, p. 85, pl. 2, figs. 9a–b [non *Lymnaea intermedia* (Férussac) Lamarck 1822].
1846 *Limnaeus socialis* var. *striata* Klein, p. 85, pl. 2, figs. 10a–b [?non *Limnaeus striatus* Zieten, 1832].
1913 *Limnaea turrita* var. *milleri* Jooss, p. 61, figs. 5–6.
1923 *Radix* (*Radix*) *socialis socialis*, – Wenz, p. 1272.
2014 *Radix socialis*, – Neubauer et al., supplementary material 1.
2014 *Radix socialis*, – Salvador & Rasser, p. 189, fig. 10.

Material examined: Bechingen: SMNS 106794 (1 spc.), 106803 (1 spc.).

Remarks: The present material display the diagnostic features of the genus, such as the proportionately minute spire, round overall shell profile and proportionately large body whorl. It compares extraordinarily well to the specimens (housed in the SMNS) of *Radix socialis socialis* from the type locality (Steinheim Basin, southwestern Germany; MN 7–8) and the type material of its synonymized subspecies (*elongata* Klein 1846, SMNS 23911, 5 spc.; *intermedia* Klein 1846, SMNS 23905, 3 spc.; *striata* Klein 1846, SMNS 23904, 2 spc.).

### Superfamily Planorboidea

### Family Planorbidae

### Genus ***Ferrissia*** Walker 1903

### ***Ferrissia deperdita*** (Desmarest 1814)

Fig. 7

1814 *Ancylus deperditus* Desmarest, p. 19, pl. 1, fig. 14.
1923 *Pseudancylus deperditus deperditus*, – Wenz, p. 1692.
1976 *Ferrissia deperdita*, – Schlickum, p. 7, pl. 1, fig. 20.
2006 *Ferrissia deperdita*, – Kókay, p. 60, pl. 20, fig. 15, pl. 21, fig. 1.
2014b *Ferrissia deperdita,* – Harzhauser et al., p. 17, pl. 5, figs. 1, 2, 5, 12,
2014 *Ferrissia deperdita*, – Neubauer et al., supplementary material 1.
2014 *Ferrissia deperdita*, – Salvador & Rasser, p. 191, fig. 11.
2015a *Ferrissia deperdita*, – Salvador et al., p. 256, fig. 3C.
2016 *Ferrissia deperdita*, – Salvador et al., p. 134, fig. 2H.

Material examined: Bechingen: SMNS 67926 (1 spc.).

Remarks: The specimen compares well to *F. deperdita*, with a cap-like smooth protoconch, gradually transitioning to a teleoconch bearing well-marked growth lines. This species is recorded from the Middle Miocene of Hungary, Austria, southern Germany, France and Switzerland (Schlickum 1976, Kókay 2006, Harzhauser et al. 2014b).

### Genus ***Gyraulus*** Charpentier 1837

### ***Gyraulus applanatus*** (Thomä 1845)

Fig. 8

1845 *Planorbis applanatus* Thomä, p. 150.
1851 *Planorbis dealbatus* Braun, p. 1134.
1911 *Gyraulus laevis*, – Gottschick, p. 515.
1923 *Gyraulus* (*Gyraulus*) *trochiformis applanatus*, – Wenz, p. 1579.
1923 *Gyraulus* (*Gyraulus*) *trochiformis dealbatus*, – Wenz, p. 1591.
1964 *Gyraulus trochiformis dealbatus*, – Schlickum, p. 15, pl. 2, fig. 35.
1970a *Gyraulus trochiformis applanatus*, – Schlickum, p. 148, pl. 10, fig. 6.
1970b *Gyraulus trochiformis applanatus*, – Schlickum, p. 180.
1973 *Gyraulus trochiformis dealbatus*, – Steininger et al., p. 451, pl. 9, fig. 11a–b.
1989 *Gyraulus trochiformis dealbatus*, – Reichenbacher, p. 172, pl. 1, fig. 11.
1995 *Gyraulus dealbatus*, – Kadolsky, p. 40, fig. 47.
2004 *Gyraulus dealbatus*, – Binder, p. 193, pl. 2, figs. 1a–c.
2005 *Gyraulus applanatus,* – Kowalke & Reichenbacher, p. 631, figs. 9.1–9.3.
2006 *Gyraulus applanatus*, – Kókay, p. 56, pl. 19, figs. 13–14.
2006 *Gyraulus trochiformis dealbatus*, – Kókay, p. 57, pl. 19, fig. 15.
2014 *Gyraulus applanatus*, – Neubauer et al., supplementary material 1.
2014 *Gyraulus dealbatus*, – Neubauer et al., supplementary material 1.
2014 *Gyraulus dealbatus*, – Salvador & Rasser, p. 192, figs. 16–23.
2015b *Gyraulus applanatus*, – Salvador et al., p. 205, figs. 2H–I.
2016 *Gyraulus applanatus*, – Salvador et al., p. 134, fig. 2K–M.

Material examined: Bechingen: SMNS 23314*, 67784 (1 spc.), 106794 (1 spc.), 106809*, 106810*, 106796*, 106803*, 106807*. Daugendorf: SMNS 106813 (2 spc.), SMNS 107207 (14 spc.).

Remarks: The present specimens, although poorly preserved, compare well to *G. applanatus*, by their flattened shell profile and closely packed whorls. This species is known for a great deal of conchological variation, occurring in several localities from the Early/ Middle Miocene of southern Germany (Gottschick & Wenz 1916, Kowalke & Reichenbacher 2005, Salvador & Rasser 2014). *Gyraulus dealbatus* was considered an extreme of morphological variation and the species was synonymized with *G. applanatus* by Kowalke & Reichenbacher (2005).

### Genus *Planorbarius* Duméril 1806

### ***Planorbarius mantelli*** (Dunker 1848)

Figs 9–11

1848 *Planorbis Mantelli* Dunker: p. 159, pl. 21, figs. 27–29.
1923 *Coretus cornu mantelli*, – Wenz, p. 1452.
1966 *Planorbarius cornu*, – Schlickum, p. 326, pl. 13, fig. 27.
1970a *Planorbarius cornu*, – Schlickum, p. 149, pl. 10, fig. 7.
1989 *Planorbarius cornu*, – Reichenbacher, p. 172, pl. 1, fig. 10.
2004 *Planorbarius cornu*, – Binder, p. 193, pl. 2, figs. 2–3.
2006 *Planorbarius cornu cornu*, – Kókay, p. 58, pl. 20, fig. 6.
2009 *Planorbarius cornu cornu*, – Böttcher et al., p. 239, figs. 2.4–2.6.
2014b *Planorbarius mantelli*, – Harzhauser et al.: p. 15, pl. 3, figs. 5, 7–13, 15–16.
2014 *Planorbarius mantelli,* – Neubauer et al: supplementary material 1.
2014 *Planorbarius cornu*, – Salvador & Rasser: p. 193, figs. 26–28.
2015a *Planorbarius cornu*, – Salvador et al., p. 256, figs. 3G–H.
2015 *Planorbarius cornu*, – Salvador et al., p. 205, fig. 2J.
2016 *Planorbarius cornu*, – Salvador et al., p. 135, fig. 2P–Q.

Material examined: Bechingen: SMNS 23314*, 67841 (10 spc.), 67856 (7 spc.), 106790 (16 spc.), 106791 (14 spc.), 106797 (7 spc.), 106798 (36 spc.), 106799 (8 spc.), 106801 (3 spc.), 106809*, 106810*, 106817 (1 spc.), 106826 (7 spc.), 106827 (1 spc.), 106828 (1 spc.), 106795*, 106796*, 106803 (1 spc.), 106807*, 106808*. Daugendorf: SMNS 106793 (3 spc.), 106821 (10 spc.); PIMUZ 011610*.

Remarks: The shell's characteristic flattened shape, whorl growth pattern and unique sculpture (protoconch with spiral lines of regularly organized circular pits and teleoconch with spiral striae on the first ca. 1½ whorl; the remainder of the teleoconch is marked only by coarse growth lines) enables the identification as *P. mantelli*. This species is very abundant in OSM sediments, being known from the late Early to the Late Miocene of Central Europe (Harzhauser et al. 2014b). Specimens of *P. mantelli* from these localities and ages have been usually identified as *P. cornu* (Brongniart 1810), which occurs from the Late Oligocene to Early Miocene. These two species are actually hard to differentiate, being presently separated by their age alone and, thus, in dire need of revisionary work.

### Eupulmonata

### Stylommatophora

### Superfamily Achatinoidea

### Family Subulinidae

### Genus *Opeas* Albers 1850

### ***Opeas minutum*** (Klein 1853)

Fig. 12

1853 *Bulimus minutus* Klein, p. 212, pl. 5, fig. 9.
1923 *Opeas minutum*, – Wenz, p. 872.
1926 *Opeas minutum*, – Seemann, p. 92.
1976 *Opeas* (*Opeas*) *minutum*, – Schlickum, p. 14, pl. 3, fi g. 46.
2006 *Opeas minutum*, – Kókay, p. 80, pl. 30, fig. 16.
2014b *Opeas minutum*, – Harzhauser et al., 2014b, p. 28, pl. 9, figs. 3–5, 7.
2015 *Opeas minutum*, – Salvador et al., p. 206, fig. 2K.

Material examined: Bechingen: SMNS 67039 (1 spc.). Daugendorf: SMNS 107206 (1 spc.), SMNS 107209 (1 spc.).

Remarks: This species is easily diagnosed in European Miocene depositis by its small and typical subulinid shell. *Opeas minutum* is known from the Early to Middle Miocene of Hungary, Austria, Germany and Switzerland (Harzhauser et al. 2014b, Salvador et al. 2015b).

### Superfamily Cochlicopoidea

### Family Cochlicopidae

### Genus *Hypnophila* Bourguignat 1858

### ***Hypnophila loxostoma*** (Klein 1853) comb. nov.

Fig. 13

1853 *Achatina loxostoma* Klein, p. 214, pl. 5, fig. 12.
1923 *Cochlicopa subrimata loxostoma*, – Wenz, p. 1107.
1926 *Cochlicopa subrimata loxostoma*, – Seemann, p. 90.
1954 *Cochlicopa subrimata loxostoma*, – Papp & Thenius, p. 21, pl. 4, fig. 7a–c.
1981 *Cochlicopa subrimata loxostoma*, – Lueger, p. 16, pl. 1, fig. 4.
2013 *Cochlicopa subrimata loxostoma*, – Rasser et al., p. 440, pl. 4, fig. 6.
2013 *Cochlicopa subrimata*, – Rasser et al., p. 434, pl. 4, fig. 6.
2015a *Cochlicopa loxostoma*, – Salvador et al., 258, fig. 3O.

Material examined: Bechingen: SMNS 106786 (5 spc.).

Remarks: This species has traditionally been classified in the genus *Cochlicopa* Férussac 1821. Harzhauser et al. (2014a), however, transferred the coeval and morphologically similar *H. subrimata* (Reuss *in* Reuss & Meyer 1849) to the genus *Hypnophila*. This decision is followed here, resulting in the new combination *Hypnophila loxostoma*.

In fact, *H. loxostoma* has been usually considered a subspecies of *H. subrimata* in the literature, but Harzhauser et al. (2014b) has since shown that the topotypes of the latter differ from specimens stemming from other localities. Salvador et al. (2015a) thus considered *H. loxostoma*, known from the OSM layers in Germany, a distinct species, diagnosed by a much wider aperture, with a taller columellar region.

## Superfamily Helicoidea

## Family Elonidae

### Genus ***Apula*** C. Boettger 1909

### ***Apula coarctata*** (Klein 1853)

Figs 14–16

1853 *Helix coarctata* Klein, p. 206, pl. 5, fig. 6.
1923 *Klikia* (*Apula*) *coarctata coarctata*, – Wenz, p. 534.
1926 *Klikia* (*Apula*) *coarctata coarctata*, – Seemann, p. 92.
1976 *Klikia* (*Apula*) *coarctata,* – Schlickum, p. 17, pl. 4, fig. 60.
2006 *Klikia* (*Apula*) *coarctata*, – Kókay, p. 92.
2013 *Klikia coarctata,* – Rasser et al., p. 440, pl. 4, fig. 9.
2013 *Klikia coarctata*, – Salvador, p. 161, figs. 6–9.
2014b *Apula coarctata*, – Harzhauser et al., p. 34, pl. 11, figs. 5–8, 21.
2015a *Apula coarctata*, – Salvador et al., p. 259, figs. 3S–U.

Material examined: Bechingen: SMNS 66290 (1 spc.), 66315 (4 spc.), 106789 (7 spc.). Daugendorf: SMNS 106812 (2 spc.).

Remarks: The specimens compare fittingly with the original description of *A. coarctata* and topotypes housed in the SMNS collection by their raised spire profile and a high and round body whorl. *Apula coarctata* is a common species in the Miocene of Central Europe, with records from Hungary, Austria, Germany and Switzerland (Harzhauser et al. 2014b).

### Genus ***Klikia*** Pilsbry 1895

### ***Klikia giengensis*** (Klein 1846)

Figs 17–19

1846 *Helix Giengensis* Klein, p. 69, pl. 1, fig. 9.
1914 *Klikia osculum*, – Fischer & Wenz, p. 70.
1923 *Klikia* (*Klikia*) *giengensis giengensis*, – Wenz, p. 539.
1976 *Klikia* (*Klikia*) *giengensis*, – Schlickum, p. 16, pl. 4, fig. 58.
2004 *Klikia giengensis*, – Binder, p. 203, pl. 6, figs. 3a–b.
2006 *Klikia* (*Klikia*) *giengensis*, – Kókay, p. 91, pl. 35, fig. 9.
2014b *Klikia giengensis*, – Harzhauser et al., p. 33, pl. 11, figs. 9–11, 9–22

Material examined: Bechingen: SMNS 66275 (3 spc.).

Remarks: This species can be distinguished in the material from the similar *A. coarctata* by its smaller size, greatly reflected peristome, a slight indentation on the upper palatal region of the aperture, a deep and wide umbilicus, and the stronger teleoconch sculpture consisting of numeros papillae. *Klikia giengensis* is known from several Miocene localities of Ukraine, Poland, Hungary, Austria, Germany and France (Harzhauser et al. 2014b).

## Family Helicidae

### Genus ***Palaeotachea*** Jooss 1912

### ***Palaeotachea silvana*** (Klein 1853)

Figs 20–22

1853 *Helix silvana* Klein, p. 205, pl. 5, fig. 2.
1923 *Cepaea silvana silvana*, – Wenz, p. 667.
1976 *Cepaea silvana silvana*, – Schlickum, p. 17, pl. 4, figs. 62–63.
1989 *Cepaea silvana silvana*, – Reichenbacher, p. 165, pl. 2, figs. 17–19.
2006 *Cepaea silvana*, – Kókay, p. 93, pl. 36, figs. 2–3.
2013 *Cepaea silvana*, – Rasser et al., p. 440.
2015a *Megalotachea silvana*, – Salvador et al., p. 261, figs. 4C–D.
2015 *Megalotachea silvana*, – Salvador et al., p. 208, figs. 2U–W.
2016 *Megalotachea silvana*, – Salvador et al., p. 137, fig. 3A–C.

Material examined: Bechingen: SMNS 23314*, 66635 (2 spc.), 66652 (2 spc.), 66665 (1 spc.), 66842 (2 spc.), 106781 (1 spc.), 106782 (2 spc.), 106792 (7 spc.), 106802 (3 spc.), 106816 (1 spc.), 106829 (1 spc.), 106795*, 106803 (3

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Figure 2. *Tinnyea* cf. *lauraea*, internal mold (SMNS 106783; H = 21.7 mm, D = 9.1 mm). Figure 3. *Pomatias* cf. *conicus*, internal mold (SMNS 106784; H = 12.0 mm, D = 10.1 mm). Figure 4. *Bithynia glabra* (SMNS 68142; H = 4.7 mm, D = 3.2 mm). Figure 5. *Lymnaea dilatata* (SMNS 67606; H = 18.9 mm, D = 8.9 mm). Figure 6. *Radix socialis*, embedded in the matrix (SMNS 106794; H = 27.6 mm, D = 16.8 mm). A small specimen of *Gyraulus applanatus* can be seen on the top left, also embedded in the matrix. Figure 7. *Ferrissia deperdita*, embedded in the matrix (SMNS 67926; H = 2.4 mm, D = 1.9 mm). Figure 8. *Gyraulus applanatus* (SMNS 67425; D = 4.0 mm). Figures 9–11. *Planorbarius mantelli*, juvenile specimen (SMNS 67856; H = 8.3 mm, D = 20.7 mm). Figure 12. *Opeas minutum* (SMNS 67039; H = 7.2 mm, D = 2.4 mm). Figure 13. *Hypnophila loxostoma* comb. nov. (SMNS 106786; H = 5.5 mm, D = 2.3 mm). Figures 14–16. *Apula coarctata* (SMNS 66290; H = 6.8 mm, D = 11.3 mm). Figures 17–19. *Klikia giengensis* (SMNS 66275; H = 6.2 mm, D = 9.5 mm). Figures 20–22. *Palaeotachea silvana* (SMNS 66635; H = 13.6 mm, D = 20.7 mm). Figures 23–25. *Pseudochloritis incrassata* (SMNS 66208; H = 13.7 mm, D = 21.5 mm). Figure 26. *Leucochroopsis kleinii* (SMNS 106787; H = 4.3 mm, D = 6.3 mm). Figures 27–29. *Praeoestophorella phacodes* (SMNS 107208; H = 2.2 mm, D = 3.9 mm). Figure 30. *Discus pleuradrus* (SMNS 65789; H = 4.2 mm, D = 6.6 mm).


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spc.). Daugendorf: SMNS 66647 (2 spc.), 106822 (3 spc.); PIMUZ 011663 (29 spc.).

Remarks: The present material compares well to *P. silvana* (syntype: SMNS 22738) in size, spire profile, and overall shell shape and proportions. This is a very common species in the Silvana Beds, which are named after this species. On some specimens (SMNS 66635, 106795) it is possible to observe under UV light (and even with the naked eye) two kinds of patterns of colored spiral bands: bi- and trifasciate. A wide variety of banding patterns is commonly found in Recent Helicidae and is known to occur in fossil specimens of *Pseudochloritis* and *Palaeotachea* (*e.g.*, Górka 2008, Salvador 2013, Salvador et al. 2015b).

### Genus ***Pseudochloritis*** Boettger 1909

#### ***Pseudochloritis incrassata*** (Klein 1853)

Figs 23–25

1846 *Helix inflexa* Klein, p. 71, pl. 1, fig. 12 [*non* Zieten 1832].
1853 *Helix incrassata* Klein, p. 208, pl. 5, fig. 6.
1923 *Tropidomphalus* (*Pseudochloritis*) *incrasstus incrassatus,* – Wenz, p. 510.
1926 *Tropidomphalus* (*Pseudochloritis*) *incrasstus incrassatus*, – Seemann, p. 91.
1976 *Tropidomphalus* (*Pseudochloritis*) *incrasstus incrassatus*, – Schlickum, p. 16, pl. 4, fig. 56.
2006 *Tropidomphalus* (*Pseudochloritis*) *incrassatus*, – Kókay, p. 90, pl. 34, figs. 12–14.
2008 *Pseudochloritis incrassata*, – Binder, p. 172, pl. 3, figs. 2–4, pl. 6, fig. 2.
2013 *Pseudochloritis incrassata,* – Rasser et al., p. 434, pl. 4, fig. 12.
2013 *Tropidomphalus* (*Pseudochloritis*) *incrassata* [sic], – Rasser et al., p. 440.
2014b *Pseudochloritis incrassata*, – Harzhauser et al., p. 35, pl. 12, figs. 9–16, 19–24.
2015 *Pseudochloritis incrassata,* – Höltke & Rasser, p. 1, figs. 4.3, 5.1–5.2, 6.11–6.12.
2015a *Pseudochloritis incrassata*, – Salvador et al., p. 261, figs. 4E–G.
2015 *Pseudochloritis incrassata,* – Salvador et al., p. 207, figs. 3A–C.

Material examined: Bechingen: SMNS 23314*, 66208 (1 spc.), 106804 (2 spc.), 106815 (4 spc.), 106827 (1 spc.), 106808 (2 spc.). Daugendorf: 106820 (1 spc.); PIMUZ 011663 (1 spc.).

Remarks: This species can be identified by its helicoid shell, with a strongly depressed spire and characteristic sculpture (preserved only in fragmentary specimens and consisting of: protoconch with fine striae dotted with weak papillae, teleoconch with well-marked growth lines and irregular weak furrows, with regularly arranged papillae). On one specimen (SMNS 66208) it is possible to observe under UV light a single colored spiral band immediate below the shoulder. *Pseudochloritis incrassata* is known from the Middle Miocene of Poland, Austria, several localities in Germany, and possibly also Hungary (Kókay 2006, Binder 2008, Górka 2008).

## Family Hygromiidae

### Genus ***Leucochroopsis*** O. Boettger 1908

#### ***Leucochroopsis kleinii*** (Klein 1846)

Fig. 26

1846 *Helix kleinii* Klein, p. 69, pl. 1, fig. 8.
1923 *Trichia* (*Leucochroopsis*) *kleini kleini* [sic], – Wenz, p. 429.
1926 *Trichia* (*Leucochroopsis*) *kleini kleini* [sic], – Seemann, p. 91.
1972 *Leucochroopsis kleini kleini* [sic], – Gall, p. 9.
1976 *Leucochroopsis kleini* [sic], – Schlickum, p. 15, pl. 3, fig. 52.
2004 *Leucochroopsis kleini* [sic], – Harzhauser & Binder, p. 25, pl. 11, figs. 8–10.
2013 *Leucochroopsis kleini* [sic], – Rasser et al., p. 440, pl. 4, fig. 10.
2013 *Leucochroopsis kleinii*, – Salvador, p. 166, figs. 26–27.
2014b *Leucochroopsis kleinii*, – Harzhauser et al., p. 35, pl. 11, figs. 12–14.
2015a *Leucochroopsis kleinii*, – Salvador et al., p. 262, figs. 4K–M.

Material examined: Bechingen: SMNS 65952 (6 spc.), 106787 (8 spc.), 106800 (1 spc.). Daugendorf: SMNS 106814 (1 spc.), SMNS 107210 (5 spc.).

Remarks: *Leucochroopsis kleinii* is easily identified by its small shell, with a depressed conical spire and a rounded base, and by its sculpture (protoconch with fine parallel striae and teleoconch with fine regularly distributed well-marked scales, giving the impression of prosocline axial striae). The species is widely known from the Middle Miocene of the Silvana Beds to the Late Miocene of the Vienna Basin (Schlickum 1976, Harzhauser & Binder 2004).

## Family Trissexodontidae

### Genus ***Praeoestophorella*** Pfeffer 1930

#### ***Praeoestophorella phacodes*** (Thomä 1845)

Figs 27–29

1845 *Helix phacodes* Thomä, p. 142, pl. 2, fig. 8.
1921 *Oestophora phacodes subphacodes,* – Ehrat & Jooss, p. 3.
1923 *Caracollina phacodes phacodes,* – Wenz, p. 461.
1926 *Caracollina phacodes barreri*, – Seemann, p. 91.
1976 *Caracollina phacodes barreri*, – Schlickum, p. 16, pl. 4, fig. 55.
2013 *Caracollina phacodes*, – Rasser et al., p. 439, pl. 4, fig. 5.
2014a *Praeoestophorella phacodes*, – Harzhauser et al., p. 887.
2015a *Praeoestophorella phacodes*, – Salvador et al., p. 263, figs. 4N–P.

Material examined: Daugendorf: SMNS 107208 (3 spc.).

Remarks: This species is easily identified by its small lenticular shell with a marked keel. Despite the present specimens being all juvenile, they compare well to the conchological features of *Praeoestophorella phacodes*, a species known since the Late Oligocene and very common in OSM sediments (Salvador et al. 2015a). The present specimens display much weaker and more numerous axial ribs than seen in other OSM localities. This variation in teleoconch sculpture had already been noticed by Sandberger (1870–1875) for other German Miocene material and resulted in the description of several subspecies (*e.g.*, Wenz 1923), the validity of which should be the focus of future revisionary work.

### Superfamily Punctoidea

### Family Discidae

### Genus ***Discus*** Fitzinger 1833

### ***Discus pleuradrus*** (Bourguignat 1881)

Fig. 30

1881 *Helix pleuradra* Bourguignat, p. 53, pl. 3, figs. 67–72.
1923 *Gonyodiscus* (*Gonyodiscus*) *pleuradra pleuradra*, – Wenz, p. 341.
1942 *Gonyodiscus* (*Gonyodiscus*) *pleuradra pleuradra*, – Wenz & Edlauer, p. 93.
1967 *Discus* (*Discus*) *pleuradrus*, – Schütt, p. 213, fig. 16.
1976 *Discus* (*Discus*) *pleuradrus*, – Schlickum, p. 12, pl. 2, fig. 37.
1981 *Discus* (*Discus*) *pleuradrus,* – Lueger, p. 40, pl. 4, figs. 6–7.
2000 *Discus* (*Discus*) *pleuradra* [sic], – Fischer, p. 145, fig. 21.
2004 *Discus pleuradrus,* – Harzhauser & Binder, p. 22, pl. 7, figs. 9–11.
2006 *Discus pleuradrus,* – Kókay, p. 75, pl. 28, figs. 3–4.
2009 *Discus pleuradrus,* – Böttcher et al., p. 239, figs. 2/10–11.
2013 *Discus pleuradrus,* – Rasser et al., p. 439.
2014b *Discus pleuradrus,* – Harzhauser et al., p. 29, pl. 9, figs. 8–13.
2014 *Discus pleuradrus,* – Salvador & Rasser, p. 195, figs. 32–33.
2015a *Discus pleuradrus*, – Salvador et al., p. 264, figs. 4U–W.
2016 *Discus pleuradrus*, – Salvador et al., p. 140, fig. 3M–N.

Material examined: Bechingen: SMNS 65789 (1 spc.). Daugendorf: SMNS 107211 (1 spc.).

Remarks: This specimens compare well with *D. pleuradrus*, given their discoid shell, with a faint shoulder, low spire, whorls regularly increasing in size, a wide umbilicus and the teleoconch sculptured by strong prosocline ribs. This is a common species in the Miocene of Central and Western Europe (Kókay 2006, Böttcher et al. 2009). Early and Late Miocene records could represent another species, which would restrict *D. pleuradrus* to the Middle Miocene of Austria, Germany and France (Moser et al. 2009, Harzhauser et al. 2014b).

### Superfamily Pupilloidea

### Family Gastrocoptidae

### Genus ***Gastrocopta*** Wollaston 1878

### ***Gastrocopta*** cf. ***acuminata*** (Klein 1846)

Fig. 31

Material examined: Bechingen: SMNS 67425 (2 spc.), 106785 (6 spc.). Daugendorf: SMNS 106811 (7 spc.

Remarks: Despite the poor preservation, the present material compares well to *G. acuminata* (syntypes: SMNS 106361, 2 spc.) due to the overall rounded shell shape and the proportionately larger size when compared to coeval congeners. The species is recorded from the Middle Miocene to the Late Pliocene, and maybe Early Pleistocene, of Europe (Stworzewicz 1999, Manganelli & Giusti 2000).

### Superfamily Succineoidea

### Family Succineidae

### Genus ***Oxyloma*** Westerlund 1885

### ***Oxyloma minima*** (Klein 1853)

Figs 32–33

1853 *Succinea minima* Klein, p. 205.
1923 *Succinea* (*Amphibina*) *minima minima*, – Wenz, p. 893.
1976 *Succinea* (*Hydrotropa?*) *minima*, – Schlickum, p. 11, pl. 2, fig. 34.
2006 *Succinea minima*, – Kókay, p. 74, pl. 27, fig. 13.
2013 *Succinea minima*, – Salvador, p. 158, figs. 1–2.
2014b *Oxyloma minima*, – Harzhauser et al., p. 27, pl. 9, figs. 1–2, 6.
2016 *Oxyloma minima*, – Salvador et al., p. 143, fig. 4C–D.

Material examined: Bechingen: SMNS 67065 (1 spc.), 106788 (5 spc.).

Remarks: *Oxyloma minima* is easily identified in fossil samples by its small succineiform shell, the growth pattern of its whorls and the incised suture. The present material compares well to the syntypes (SMNS 106410, 2 spc.). Despite the fossils of *O. minima* being usually scarce, the species is known from several outcrops from the Early/Middle Miocene of Germany, Hungary, Austria and possibly Ukraine (Kókay 2006; Harzhauser et al. 2014b).

### Superfamily Testacelloidea

### Family Oleacinidae

### Genus ***Palaeoglandina*** Wenz 1914

### ***Palaeoglandina gracilis*** (Zieten 1830)

Fig. 34

1830 *Limnaea gracilis* Zieten, p. 39, pl. 30, fig. 3.
1923 *Poiretia* (*Palaeoglandina*) *gracilis gracilis*, – Wenz, p. 839.
1960 *Palaeoglandina gracilis*, – Zilch, p. 457, fig. 1627.
2015a *Palaeoglandina gracilis*, – Salvador et al., p. 267, fig. 5E.

Figure 31. *Gastrocopta* cf. *acuminata* (SMNS 106785; H = 2.4 mm, D = 1.6 mm). Figures 32–33. *Oxyloma minima* (SMNS 106788; H = 8.7 mm, D = 4.4 mm). Figure 34. *Palaeoglandina gracilis*, partially embedded in the matrix (SMNS 106805; H = 38.4 mm).

Material examined: Bechingen: SMNS 106805 (3 spc.).

Remarks: The present material compares well with *P. gracilis* by the large size, broad fusiform shell, elongated aperture, and strong sculpture, consisting of regularly distributed well-marked opistocline ribs. This species is known from the Late Oligocene to the Middle Miocene of Central Europe (Salvador 2013).

## Discussion

In total, twenty gastropod species were found in the Bechingen/Daugendorf material (Table 1). All species, with the exception of *Praeoestophorella phacodes*, occur in Bechingen, but only eleven occur in Daugendorf (Table 1). Moreover, in the material from Daugendorf, there are some external molds whose size, shape and sculpture pattern suggest the presence of the genera *Archaeozonites* Sandberger 1873 (Zonitidae; SMNS 106793) and *Granaria* Held 1838 (Chondrinidae; SMNS 106819); this would raise the count to thirteen species for this locality. Additionaly, some species listed by previous authors from Bechingen were not found in the present material: *Pseudoleacina eburnea* (Klein 1853) (Jooss 1910: 20, Wenz 1923: 858) and *Janulus supracostatus* (Sandberger 1872) (Jooss 1918: 290, Wenz 1923: 305, Schlickum 1976: 13). All of the presently listed species have been reported from the geographically close and likely coeval locality of Zwiefaltendorf, which is likewise composed of reworked material (Schlickum 1976). This is not surprising, if we are dealing with the same rocks reworked by Pleistocene morain sediments (Zöbelein 1973).

Werner (2014) proposed for the neighboring Tautschbuch localities a paleoenvironment consisting of shallow temporary lakes or ponds surrounded by reeds. Despite the snail fauna being scarce, it agrees with this scenario. The extant congeners of the freshwater snails can be found in several different environments, but they share a preference for richly vegetated, stagnant or slow moving water (Welter-Schultes 2012). *Ferrissia*, in particular, is a typical inhabitant of reed-belts on the upper littoral zone of water bodies (Glöer 2002). *Oxyloma* species are hygrophilous, living in very humid forests and meadows, and often found in reed belts surrounding water bodies (Welter-Schultes 2012).

In terrestrial environment, *Opeas*, *Leucochroopsis, Discus* and *Archaeozonites* (and *Janulus* and *Pseudoleacina*, recorded from the literature) are thought to inhabit humid (and generally) warm woods (Zilch 1959–1960, Lueger 1981, Kerney et al. 1983, Harzhauser & Tempfer 2004, Willig et al. 2013). Recent *Pomatias* would also prefer humid environments, living in both forests and shrublands (Kerney & Cameron 1979, Welter-Schultes 2012). The genera *Pseudochloritis*, *Praeoestophorella* (allied to the Recent *Caracollina* Beck, 1837) and *Granaria* would represent drier and more open habitats (Binder 2008, Moser et al. 2009, Welter-Schultes 2012, Höltke & Rasser 2013).

This high variablity of snail habitats is not surprising, since the snails may come from a variety of layers reworked during the Pleistocene. The Tautschbuch area contains more then 100 meters of OSM sediments and thus provide a variety of different habitats changing through time and space.

Table 1. List of molluscan species recorded from the OSM localities Bechingen and Daugendorf. An "?" indicates a doubtful identification based on external molds. — Be = Bechingen, Dau = Daugendorf

| Species | Be | Dau |
|---|---|---|
| Caenogastropoda | | |
| *Bithynia glabra* (Zieten 1832) | x | |
| *Pomatias* cf. *conicus* (Klein 1853) | x | |
| *Tinnyea* cf. *lauraea* (Mathéron 1843) | x | |
| Hygrophila | | |
| *Ferrissia deperdita* (Desmarest 1814) | x | |
| *Gyraulus applanatus* (Thomä 1845) | x | x |
| *Lymnaea dilatata* (Noulet 1854) | x | x |
| *Planorbarius mantelli* (Dunker 1848) | x | x |
| *Radix socialis* (Zieten 1830) | x | |
| Stylommatophora | | |
| *Apula coarctata* (Klein 1853) | x | x |
| *Archaeozonites* sp. | | ? |
| *Discus pleuradrus* (Bourguignat 1881) | x | x |
| *Gastrocopta* cf. *acuminata* (Klein 1846) | x | x |
| *Granaria* sp. | | ? |
| *Hypnophila loxostoma* (Klein 1853) | x | |
| *Klikia giengensis* (Klein 1846) | x | |
| *Leucochroopsis kleinii* (Klein 1846) | x | x |
| *Opeas minutum* (Klein 1853) | x | x |
| *Oxyloma minima* (Klein 1853) | x | |
| *Palaeoglandina gracilis* (Zieten 1830) | x | |
| *Palaeotachea silvana* (Klein 1853) | x | x |
| *Praeoestophorella phacodes* (Thomä 1845) | | x |
| *Pseudochloritis incrassata* (Klein 1853) | x | x |

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# THE FOSSIL LAND AND FRESHWATER SNAILS OF OGGENHAUSEN (MIDDLE MIOCENE, GERMANY)

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ABSTRACT – The Middle Miocene fossil site of Oggenhausen in southern Germany was first described in the 1920's, with reports of nine gastropod species. Much later, in the 2000's, a second and coeval site was described, named Oggenhausen 2 and counting with eight gastropod species, all of them distinct from the first site (hence named Oggenhausen 1). Here we present a revision of the historical material from Oggenhausen 1 alongside new material from Oggenhausen 2. After the revision, six species are known from Oggenhausen 1 (the records of *Triptychia kleini* and *Gastrocopta acuminata* could not be confirmed) and 13 from Oggenhausen 2. The following are new records for Oggenhausen 2: *Lymnaea* cf. *dilatata*, *Gyraulus applanatus*, *Megalotachea silvana*, *Palaeotachea renevieri*, *Granaria* sp., *Gastrocopta acuminata* and ?*Truncatellina* sp. Oggenhausen 2 is interpreted as a shallow lake or an oxbow lake, formed by the river that deposited the layers of Oggenhausen 1. The freshwater snails are consistent with slow-flowing or stagnant waters, while the terrestrial species indicate that the area surrounding the lake was covered by humid vegetation.

**Key words:** Caenogastropoda, Gastropoda, Hygrophila, OSM, Stylommatophora.

RESUMO – O afloramento fossilífero de Oggenhausen (Mioceno Médio, sul da Alemanha) foi originalmente descrito na década de 1920 e nove espécies de gastrópodes foram encontradas nos sedimentos. Posteriormente, na década de 2000, um segundo (e contemporâneo) afloramento foi descrito como Oggenhausen 2, contando com oito espécies de gastrópodes, todas distintas do primeiro afloramento (nomeado Oggenhausen 1). O presente trabalho traz uma revisão do material histórico de Oggenhausen 1, assim como material inédito de Oggenhausen 2. Após a revisão, constatou-se a presença de seis espécies em Oggenhausen 1 (os registros de *Triptychia kleini* e *Gastrocopta acuminata* não puderam ser confirmados) e treze em Oggenhausen 2. Os registros inéditos para Oggenhausen 2 são: *Lymnaea* cf. *dilatata*, *Gyraulus applanatus*, *Megalotachea silvana*, *Palaeotachea renevieri*, *Granaria* sp., *Gastrocopta acuminata* e ?*Truncatellina* sp. Oggenhausen 2 é considerado um lago raso ou um meandro abandonado do rio que depositou as camadas de Oggenhausen 1. Os gastrópodes dulciaquícolas são consistentes com águas estagnadas ou de fluxo lento, enquanto as espécies terrestres indicam que a área ao redor do lago era coberta por uma vegetação mais fechada e úmida.

**Palavras-chave:** Caenogastropoda, Gastropoda, Hygrophila, OSM, Stylommatophora.

## INTRODUCTION

The Middle Miocene fossil site of Oggenhausen, a village in southern Germany near to the town of Heidenheim in Baden-Württemberg state, was first described by Schlosser (1926), who dealt with the vertebrate remains. Berz & Jooss (1927) studied the gastropods from this locality, with samples stemming from various sites around the village. They reported the following species (names as they appear in the original publication): *Zonites (Aegopis) costatus costatus*, *Tropidomphalus (Pseudochloritis) incrassatus incrassatus*, *Cepaea renevieri coniuncta*, *C. silvana silvana*, *C. eversa larteti*, *Triptychia (Triptychia) grandis*, *Gastrocopta* aff. *G. acuminata acuminata*, *Tudorella conica conica* and *Melanatria escheri turrita*.

Böttcher *et al.* (2009) described a second coeval site in Oggenhausen, named "Oggenhausen 2". Henceforth, the first site described by Schlosser (1926) and Berz & Jooss (1927) was referred to as "Oggenhausen 1". Böttcher *et al.* (2009) reported eight gastropod species from this second site (*Galba dupuyiana*, *Radix* sp., *Planorbarius cornu*, *Anisus* sp., *Gastrocopta* cf. *G. nouletiana*, *Discus pleuradrus*, *Leucochroopsis* sp. and *Cepaea* sp.), all belonging to the Pulmonata.

Here we present a revision of the historical material of Berz & Jooss (1927), providing figures for the first time, and revising the material from Oggenhausen 2, also introducing new material that was housed in the collection of the Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany. Moreover, several of the species listed here represent new distribution records for Oggenhausen.

## GEOLOGICAL SETTING

Oggenhausen as a whole is located at the northern margin of the North Alpine Foreland Basin (Figure 1) and its

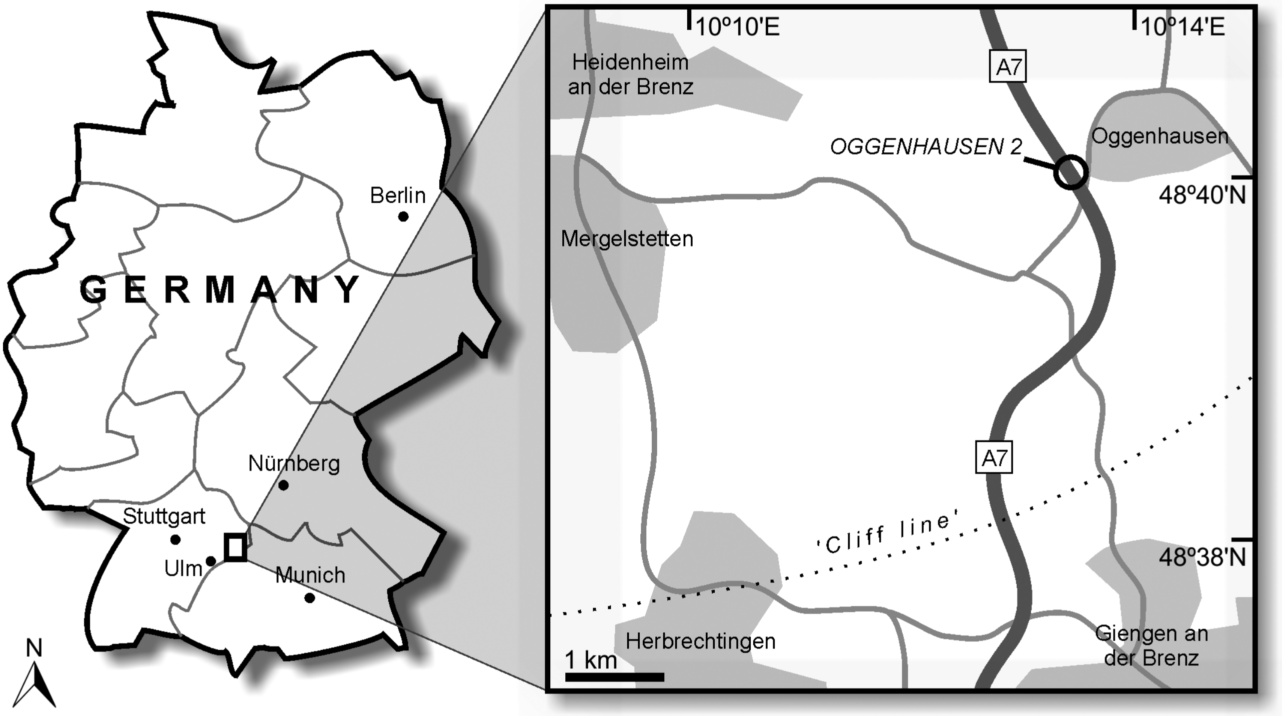

**Figure 1.** Map of Germany showing the location of the fossil outcrops of Oggenhausen 2 (modified after Böttcher *et al.*, 2009). The exact location of the outcrops of Oggenhausen 1 is unknown.

outcrops belong to the Upper Freshwater Molasse ("Obere Süßwassermolasse", OSM) stratigraphic unit (more specifically to the so-called Silvana Beds, or "Silvanaschichten"). The site Oggenhausen 1 ("Oggenhausen N' Ulm" in the original; Schlosser, 1926) contained a handful of distinct small outcrops, explored by Berz & Jooss (1927). Unfortunately, the precise location of these outcrops is now untraceable. The fossil-bearing sediments from this locality were referred to as "Oggenhausen-Sande" (Böttcher *et al.*, 2009).

Later, in 1980, another fossil site was found in the Oggenhausen area (called "Oggenhausen 2" by Böttcher *et al.*, 2009; Figure 1). This outcrop lies ~1.5 km to the south of Oggenhausen 1 (topographically deeper than that locality by *ca*. 30 m, but not confirmedly stratigraphically older) and was artificially created by highway construction (Heizmann, 1983; Böttcher *et al.*, 2009). There were two main facies outcropping in the locality, a basal limestone one and a marl/clay one, both bearing fossil gastropods (for more details, see Böttcher *et al.*, 2009).

Biostratigraphic correlation of Oggenhausen 2 is possible due to the presence of small mammalian teeth, correlating the deposits to the middle of the European Mammal Neogene zone MN 5 (Böttcher *et al.*, 2009; Reichenbacher *et al.*, 2013). However, the stratigraphic relation between the sediments of Oggenhausen 1 and 2 remains unclear, due to the different mammalian faunas found in each locality (see Böttcher *et al.*, 2009 for more details). Nevertheless, Böttcher *et al.* (2009) considers that Oggenhausen 1 also belong to the middle of the MN 5 zone (this zone goes from *ca*. 17 to 16 Ma; Reichenbacher *et al.*, 2013).

## MATERIAL AND METHODS

The original material of Berz & Jooss (1927) from Oggenhausen 1 and of Böttcher *et al.* (2009; sample of 600 kg, screenwashed with a minimum mesh size of 0.5 mm) from Oggenhausen 2 are housed in the collection of the Staatliches Museum für Naturkunde Stuttgart (**SMNS**), Stuttgart, Germany. The collection also housed additional material from Oggenhausen 2 that was not examined by Böttcher *et al.* (2009) and that is studied here for the first time.

Unfortunately two of the original specimens from Berz & Jooss (1927) could not be found, namely the single specimens known of *Triptychia* (*Triptychia*) *grandis* (Klein, 1846) and *Gastrocopta* aff. *G. acuminata acuminata* (Klein, 1846) (Berz & Jooss, 1927: species nrs. 6 and 7, respectively). *Triptychia grandis* has been recently renamed as *Triptychia kleini* Schnabel, 2006.

Preservation is poor for the largest part of the gastropod material, although reasonably well-preserved specimens could be found for nearly all species. Some taxa are known only from fragmentary specimens and their identification must remain tentative. Gastropod classification follows Bouchet & Rocroi (2005), with further modifications of Nordsieck (2014) regarding the European fossil land snail fauna. All species are figured and information on their diagnostic features is provided in the "Remarks" section of each species. Specimens were measured either with a digital caliper or with the aid of computer software (Leica Application Suite [LAS] v.3.8.0). The following abbreviations for shell measures are used throughout the text: **H**, shell height; **D**, = shell greatest width (diameter).

## SYSTEMATIC PALEONTOLOGY

Clade CAENOGASTROPODA Cox, 1960
Superfamily CERITHIOIDEA Fleming, 1822
Family PACHYCHILIDAE P. Fischer & Crosse, 1822

*Tinnyea* Hantken, 1887

**Type species.** *Tinnyea vasarhelyii* Hantken, 1887.

*Tinnyea lauraea* (Mathéron, 1842)
(Figures 2A-B)

1842 *Melania lauraea* Mathéron, p. 291, pl. 36, figs. 23-24.
1927 *Melanatria escheri turrita* Brongniart: Berz & Jooss, p. 206.
1953 *Brotia (Tinnyea) escheri* (Brongniart): Papp, p. 128, pl. 3, fig. 29.
1976 *Brotia (Tinnyea) escheri* (Brongniart): Schlickum, p. 4, pl. 1, fig. 9.
2000 *Brotia (Tinnyea) escheri* (Brongniart): Mikuz & Pavsic, p. 44, pl.1, figs. 1-8.
2014 *Tinnyea lauraea* (Mathéron): Neubauer *et al.*, supplementary material 1.
2015b *Tinnyea lauraea* (Mathéron): Salvador *et al.*, p. 203, figs. 2A-B.

**Material examined.** Oggenhausen 1: SMNS 68388 (one spc.).
**Dimensions.** SMNS 68388 (fragmentary specimen): H = 13.7 mm.
**Remarks.** The species can be identified by its turreted shell and characteristic teleoconch sculpture (very strong opisthocline and slightly curved axial ribs on first whorls and both axial ribs and spiral cords on remaining whorls). The name *Tinnyea escheri* Brongniart, 1822 was considered a *nomen nudum* (Kadolsky, 1995; Kowalke, 2004), for which the earliest valid name available is *T. lauraea.*

Berz & Jooss (1927) identified this single specimen as belonging to the subspecies *Tinnyea lauraea turrita*, which would differ from the nominate subspecies by its simple and straight ribs, instead of spiny or knobby ones (Kókay, 2006). Harzhauser *et al.* (2002), however, state that the species has a great morphological plasticity (as Recent Pachychilidae do), which led to the description of several superfluous subspecies. *T. lauraea* is known from the Oligocene–Pliocene of Central Europe (Harzhauser *et al.*, 2002), but such large time span suggests that the species is actually an unresolved species complex (Kadolsky, 1995).

*Tinnyea* has been commonly considered a subgenus of *Brotia* H. Adams, 1866 (Pacaud & Le Renard, 1995). Harzhauser *et al.* (2002), however, consider *Tinnyea* a separate genus based on protoconch development and sculpture. This classification is followed here.

Superfamily LITTORINOIDEA Children, 1843
Family POMATIIDAE Newton, 1891

*Pomatias* Studer, 1789

**Type species.** *Nerita elegans* Müller, 1774.

*Pomatias conicus* (Klein, 1853)
(Figure 2C)

1853 *Cyclostoma conicum* Klein, p. 217, pl. 5, fig. 14.
1823 *Tudorella conica conica* (Klein): Wenz, p. 1820.
1927 *Tudorella conica conica* (Klein): Berz & Jooss, p. 206.
1953 *Pomatias conicus conicus* (Klein): Papp & Thenius, p. 21, pl. 3, fig. 7.
1976 *Tudorella conica* (Klein): Schlickum, p. 3, pl. 1, fig. 2-3.
1981 *Pomatias conica* (Klein) [sic]: Lueger, p. 10, pl. 1, figs. 11-12, pl. 6, fig. 3.
2006 *Pomatias conica* (Klein) [sic]: Kókay, p. 33, pl. 4, fig. 4.
2002 *Pomatias conicus* (Klein): Harzhauser & Kowalke, p. 70, pl. 10, figs. 6-8.
2015a *Pomatias conicus* (Klein): Salvador *et al.*, p. 253, fig. 3A.
2004 *Pomatias conicum* (Klein) [sic]: Harzhauser & Binder, p. 7, pl.1, figs. 7-11.

**Material examined.** Oggenhausen 1: SMNS 68038 (one spc.), 68041 (one spc.).
**Dimensions.** SMNS 68041 (fragmentary specimen): H = 5.9 mm, D = 5.7 mm.
**Remarks.** The species can be identified by its trochiform shell, with greatly rounded whorls and the teleoconch sculpture (reticulated, with stronger spiral ribs and weaker axial ribs). *Pomatias conicus* is known from the Middle to Late Miocene of Central Europe, being commonly found in the Silvana-beds ("Silvanaschichten") of Germany and Switzerland (Klein, 1853; Harzhauser & Binder, 2004; Salvador *et al.*, 2015a).

Clade PULMONATA Cuvier, 1814
Clade HYGROPHILA Férussac, 1822
Superfamily LYMNAEOIDEA Rafinesque, 1815
Family LYMNAEIDAE Rafinesque, 1815

*Galba* Schrank, 1803

**Type species.** *Buccinum truncatulum* Müller, 1774.

*Galba dupuyiana* (Noulet, 1854)
(Figures 2D-E)

1854 *Limnea Dupuyiana* Noulet, p. 108.
1923 *Radix (Radix) dupuyana* (Noulet) [sic]: Wenz, p. 1242.
2000 *Galba* (*Galba*) *dupuyiana* (Noulet): Fischer, p. 135, fig. 4.
2006 *Galba dupuyana* (Noulet) [sic]: Kókay, p. 50, pl. 16, figs. 14-16.
2009 *Galba dupuyiana* (Noulet): Böttcher *et al.*, p. 239, figs. 2/1-2/2.
2014 *Galba dupuyiana* (Noulet): Neubauer *et al.*, supplementary material 1.

2014 *Galba dupuyiana* (Noulet): Salvador & Rasser, p. 188, figs. 1-7.
2016 *Galba dupuyiana* (Noulet): Salvador *et al.*, p. 133, fig. 2E.

**Material examined.** Oggenhausen 2: SMNS 68650 (one spc.), 68651 (one spc.). 101672 (>50 spc.).
**Dimensions.** 4 – 4½ whorls, H = 5.0 – 6.0 mm, D = 2.5 – 3.0 mm.
**Remarks.** As remarked by Böttcher *et al.* (2009: figs. 2/1-2/2), there are two extreme shell forms in Oggenhausen 2, a more slender one, with a more deeply marked suture (Figure 2D), and a broader one (Figure 2E). Transitional forms from slender to broad can also be found in the material (Böttcher *et al.*, 2009). The same variability was observed in the abundant *G. dupuyiana* specimens from Sandelzhausen (Salvador & Rasser, 2014). This species is known from the Middle Miocene of Central and West Europe (Fischer, 2000; Kókay, 2006).

### *Lymnaea* Lamarck, 1799

**Type species.** *Helix stagnalis* Linnæus, 1758.

### *Lymnaea* cf. *L. dilatata* (Noulet, 1854)
(Figure 2F)

2009 *Radix* sp.: Böttcher *et al.*, p. 239, fig. 2/3.

**Material examined.** Oggenhausen 2: SMNS 68652 (one spc.).
**Dimensions.** SMNS 68652: H = 7.2 mm.
**Remarks.** Despite being a juvenile or fragmentary specimen, it is very reminiscent of *Lymnaea dilatata*, due to its proportionately small and acuminated spire, with quickly growing whorls. This species is known from the entire Miocene of Central and West Europe (Fischer, 2000; Binder, 2004; Kókay, 2006).

### Superfamily PLANORBOIDEA Rafinesque, 1815
### Family PLANORBIDAE Rafinesque, 1815

### *Gyraulus* Charpentier, 1837

**Type species.** *Planorbis albus* Müller, 1774.

### *Gyraulus applanatus* (Thomä, 1845)
(Figures 2G-H)

1845 *Planorbis applanatus* Thomä, p. 150.
1851 *Planorbis dealbatus* Braun, p. 1134.
1923 *Gyraulus (Gyraulus) trochiformis applanatus* (Thomä): Wenz, p. 1579.
1923 *Gyraulus (Gyraulus) trochiformis dealbatus* (Braun): Wenz, p. 1591.
1964 *Gyraulus trochiformis dealbatus* (Braun): Schlickum, p. 15, pl. 2, fig. 35.
1970a *Gyraulus trochiformis applanatus* (Thomä): Schlickum, p. 148, pl. 10, fig. 6.
1970b *Gyraulus trochiformis applanatus* (Thomä): Schlickum, p. 180.
1995 *Gyraulus dealbatus* (Braun): Kadolsky, p. 40, fig. 47.
1989 *Gyraulus trochiformis dealbatus* (Braun): Reichenbacher, 172, pl. 1, fig. 11.
2004 *Gyraulus dealbatus* (Braun): Binder, p. 193, pl. 2, figs. 1a-c.
2005 *Gyraulus applanatus* (Thomä): Kowalke & Reichenbacher, p. 631, figs. 9.1-9.3.
2006 *Gyraulus applanatus* (Thomä): Kókay, p. 56, pl. 19, figs. 13-14.
2006 *Gyraulus trochiformis dealbatus* (Braun): Kókay, p. 57, pl. 19, fig. 15.
2009 *Anisus* sp.: Böttcher *et al.*, p. 239, figs. 2/7-2/9.
2014 *Gyraulus applanatus* (Thomä): Neubauer *et al.*, supplementary material 1.
2014 *Gyraulus dealbatus* (Braun): Neubauer *et al.*, supplementary material 1.
2014 *Gyraulus dealbatus* (Braun): Salvador & Rasser, p. 192, figs. 16-23.
2015b *Gyraulus applanatus* (Thomae): Salvador *et al.*, p. 205, figs. 2H-I.
2016 *Gyraulus applanatus* (Thomae): Salvador *et al.*, p. 134, figs. 2K-M.

**Material examined.** Oggenhausen 2: SMNS 68654 (three spc.), 101379 (42 spc.), 101380 (40 spc.), 101673 (>50 spc.).
**Dimensions.** 3¼ – 3½ whorls, H = 1.0 – 1.3 mm, D = 3.0 – 4.0 mm.
**Remarks.** The specimens identified as *Anisus* sp. by Böttcher *et al.* (2009) belongs to the morphologically variable species *Gyraulus applanatus*. The more flattened and stronger keeled forms indeed show a remarkable resemblance to species of *Anisus* Studer, 1820, but are recognizable as *Gyraulus* by their protoconch sculpture (with numerous fine spiral striae) and low number of rapidly growing whorls. Species of *Anisus* also present a larger number of whorls and a strongly angulated profile.

*Gyraulus applanatus* is recorded from the Early and Middle Miocene of Germany, being known for a great deal of morphological variation (Kowalke & Reichenbacher, 2005; Salvador & Rasser, 2014). This variability is also seen in Oggenhausen 2, from more rounded shells to more flattened ones, with all intermediate forms in between.

### *Planorbarius* Duméril, 1805

**Type species.** *Helix cornea* Linnaeus, 1758.

### *Planorbarius mantelli* (Dunker, 1848)
(Figures 2I-J)

1848 *Planorbis Mantelli* Dunker, p. 159, pl. 21, figs. 27-29.
1966 *Planorbarius cornu* (Brongniart): Schlickum, p. 326, pl. 13, fig. 27.
1970a *Planorbarius cornu* (Brongniart): Schlickum, p. 149, pl. 10, fig. 7.
1989 *Planorbarius cornu* (Brongniart): Reichenbacher, p. 172, pl. 1, fig. 10.
2004 *Planorbarius cornu* (Brongniart): Binder, p. 193, pl. 2, figs. 2-3.

2006 *Planorbarius cornu cornu* (Brongniart): Kókay, p. 58, pl. 20, fig. 6.
2009 *Planorbarius cornu* (Brongniart): Böttcher *et al.*, p. 239, figs. 2/4-2/6.
2014 *Planorbarius cornu* (Brongniart): Salvador & Rasser, p. 193, figs. 26-28.
2014 *Planorbarius mantelli* (Dunker): Harzhauser *et al.*, p. 15, pl. 3, figs. 5, 7-13, 15-16.
2014 *Planorbarius mantelli* (Dunker): Neubauer *et al.*, supplementary material 1.
2015a *Planorbarius cornu* (Brongniart): Salvador *et al.*, p. 256, figs. 3G-H.
2015b *Planorbarius cornu* (Brongniart): Salvador *et al.*, p. 205, fig. 2J.
2016 *Planorbarius cornu* (Brongniart): Salvador *et al.*, 135, figs. 2P-Q.

**Material examined.** Oggenhausen 2: SMNS 68653 (one spc.), 101670 (20 spc.).
**Dimensions.** SMNS 68653 (juvenile specimen): H = 3.9 mm, D = 7.7 mm.
**Remarks.** Despite only juveniles and fragmentary specimens being preserved, the shape and unique sculpture of the shell allow identification as *Planorbarius mantelli*. The protoconch sculpture (see Böttcher *et al.*, 2009: fig. 2/6) consists of spiral lines composed of regularly disposed circular pits; teleoconch is sculptured by spiral striae on first ~1½ whorl and smooth on the remaining whorls (except for well-marked growth lines).

This species is known from the late Early Miocene to the Late Miocene of Central Europe (Harzhauser *et al.*, 2014). Specimens of *Planorbarius mantelli* from these ages and regions are usually referred to as *P. cornu* (Brongniart, 1810) in the literature. *Planorbarius cornu* is a form recorded from the Late Oligocene to Early Miocene (Harzhauser *et al.*, 2014) and very hard to diagnose from *P. mantelli*. This species complex is in urgent need of a thorough revision.

### Clade STYLOMMATOPHORA A. Schmidt, 1855
### Superfamily HELICOIDEA Rafinesque, 1815
### Family HELICIDAE Rafinesque, 1815

### *Megalotachea* Pfeffer, 1929

**Type species.** *Helix turonensis* Deshayes, 1831.

### *Megalotachea silvana* (Klein, 1853)
(Figures 2K-M)

1853 *Helix silvana* Klein, p. 205, pl. 5, fig. 2.
1923 *Cepaea silvana Silvana* (Klein): Wenz, p. 667.
1927 *Cepaea eversa larteti* (Boissy): Berz & Jooss, p. 205.
1927 *Cepaea sylvana sylvana* (Klein) [sic]: Berz & Jooss, p. 204.
1976 *Cepaea silvana Silvana* (Klein): Schlickum, p. 17, pl. 4, figs. 62-63.
1989 *Cepaea silvana Silvana* (Klein): Reichenbacher, p. 165, pl. 2, figs. 17-19.
2006 *Cepaea silvana* (Klein): Kókay, p. 93, pl. 36, figs. 2-3.
2009 *Cepaea* sp.: Böttcher, *et al.*, p. 241, fig. 2/15.
2015a *Megalotachea silvana* (Klein): Salvador *et al.*, p. 261, figs. 4C-D.
2015b *Megalotachea silvana* (Klein): Salvador *et al.*, p. 208, figs. 2U-W.
2016 *Megalotachea silvana* (Klein): Salvador *et al.*, p. 137, figs. 3A-C.

**Material examined.** Oggenhausen 1: SMNS 66796 (four spc.), 66814 (two spc.), 66849 (five spc.), 66850 (two spc.), 66876 (one spc.), 101668 (one spc.). Oggenhausen 2: SMNS 68658 (one spc.), 101373 (one spc.), 101374 (six spc.), 101375 (two spc.).
**Dimensions.** 4 – 4½ whorls, H = 13.5 – 19.1 mm, D = 18.5 – 24.5 mm.
**Remarks.** *Megalotachea silvana* is distinguished from its congeners by its smaller size, more flattened shell profile and by the presence of a faint keel. On four specimens (two of each lot: SMNS 101374 and 101375) it is possible to observe under UV light a trifasciate pattern of colored spiral bands. A similar pattern, albeit with narrower bands, was seen on one of the *Palaeotachea renevieri* specimens (see below). This trifasciate pattern occurs in Recent helicids (*e.g.* Welter-Schultes, 2012) and was found to be the commonest one in fossils of *M. sylvestrina* (Schlotheim, 1820) from Poland (Górka, 2008).

Berz & Jooss (1927) identified a single and slightly larger specimen of *Megalotachea silvana* (SMNS 66876) as *M. eversa* Deshayes, 1851, which is a morphologically very similar species, diagnosed mainly by its much larger size. However, this specimen from Oggenhausen 1, as well as two more somewhat larger shells from Oggenhausen 2 (one specimen from each lot: SMNS 101374 and 101375), are still much smaller than the typical *M. eversa* and conchologically indistinguishable from *M. silvana*. In their paper, Berz & Jooss (1927) mention more than one specimen of *M. eversa* from different places in Oggenhausen 1, but only the single specimen mentioned above was found.

### *Palaeotachea* Jooss, 1912

**Type species.** *Helix crepidostoma* Sandberger, 1872

### *Palaeotachea renevieri* (Maillard, 1892)
(Figures 2N-P)

1892 *Helix (Macularia) Renevieri* Maillard, p. 43, pl. 3, fig. 18.
1923 *Cepaea renevieri* (Maillard): Wenz, p. 652.
1927 *Cepaea renevieri coniuncta* Berz & Jooss, p. 203, fig. 1.
1954 *Cepaea* cf. *renevieri* (Maillard): Zöbelein, p. 156.
2015a *Palaeotachea renevieri* (Maillard): Salvador *et al.*, p. 261, figs. 4A-B.
2015b *Palaeotachea renevieri* (Maillard): Salvador *et al.*, p. 208, figs. 2R-T.
2016 *Palaeotachea renevieri* (Maillard): Salvador *et al.*, p. 137, figs. 3D-F.

**Material examined.** Oggenhausen 1: SMNS 66453 (one spc.), 66456 (three spc.), 66457 (two spc.), 66840 (three spc.), 101369 (two spc.), 101370 (three spc.), 101371 (four spc.), 101372 (one spc.). Oggenhausen 2: SMNS 101368 (one spc.).
**Dimensions.** 4 whorls, H = 10.0 – 12.0 mm, D = 14.9 – 17.4 mm.
**Remarks.** *Palaeotachea renevieri* can be easily identified by its small size, small circular aperture and somewhat flattened shell profile with a faint keel. On two specimens (SMNS 101368 and 101372) it is possible to observe vestiges of colored parallel spiral bands under UV light. The former shows a trifasciate pattern with very fine spiral bands: the topmost one on the middle to upper portion of the whorl, the other two regularly spaced on the basal portion of whorl. The latter exhibits a fourth band, positioned on the upper portion of the whorl, above all others.

Berz & Jooss (1927) described a new variety of this species with the poorly preserved material from Oggenhausen, namely *Palaeotachea renevieri coniuncta*, diagnosed by a slightly larger size, more flattened profile and a smaller and rounder aperture. Furthermore, Berz & Jooss (1927: p. 203) state that the two forms are connected by many intermediates and are hard to distinguish. These characters are clearly insufficient to diagnose two subspecies. Thus, we treat *P. renevieri coniuncta* as a synonym of the nominate *P. renevieri*. The species is known from the Middle and Late Miocene of southern Germany and Switzerland (Wenz, 1923; Zöbelein, 1954).

### *Pseudochloritis* Boettger, 1909

**Type species.** *Helix incrassata* Klein, 1853.

### *Pseudochloritis incrassata* (Klein, 1853)
(Figures 2Q-S)

1846 *Helix inflexa* Klein, p. 71, pl. 1, fig. 12 [*non* von Zieten, 1832].
1853 *Helix incrassata* Klein, p. 208, pl. 5, fig. 6.
1923 *Tropidomphalus (Pseudochloritis) incrasstus incrassatus* (Klein): Wenz, p. 510.
1927 *Tropidomphalus (Pseudochloritis) incrasstus incrassatus* (Klein): Berz & Jooss, p. 202.
1976 *Tropidomphalus (Pseudochloritis) incrasstus incrassatus* (Klein): Schlickum, p. 16, pl. 4, fig. 56.
2006 *Tropidomphalus (Pseudochloritis)* cf. *incrassatus* (Klein): Kókay, p. 90, pl. 34, figs. 12-14.
2008 *Pseudochloritis incrassata* (Klein): Binder, p. 172, pl. 3, figs. 2-4, pl. 6, fig. 2.
2013 *Pseudochloritis incrassata* (Klein): Rasser *et al.*, p. 434, pl. 4, fig. 12.
2014 *Pseudochloritis incrassata* (Klein): Harzhauser *et al.*, p. 35, pl. 12, figs. 9-16, 19-24.
2015 *Pseudochloritis incrassata* (Klein): Höltke & Rasser, p. 1, figs. 4.3, 5.1, 6.11-6.12.
2015a *Pseudochloritis incrassata* (Klein): Salvador *et al.*, p. 261, figs. 4E-G.
2015b *Pseudochloritis incrassata* (Klein): Salvador *et al.*, p. 207, figs. 3A-C.

**Material examined.** Oggenhausen 1: SMNS 66213 (four spc.), 66657 (one spc.). Oggenhausen 2: SMNS 101377 (one spc.).
**Dimensions.** 4½ – 4¾ whorls, H = 14.6 – 18.6 mm, D = 22.9 – 26.6 mm.
**Remarks.** This species can be identified by its depressed flattened spire, sculpture pattern, and the lightly bent body whorl (with a conspicuous constriction right before the aperture; "extralabial depression" *sensu* Binder, 2008). The protoconch sculpture pattern consists of fine striae, while the teleoconch pattern consists of coarse growth lines and regularly spaced and very shallow round pits

On one specimen (SMNS 101377) it is possible to observe vestiges of two parallel spiral bands on the middle portion of the body whorl under UV light. This bifasciate color pattern differs from the observations of Górka (2008: fig. 3), which reports two additional bands. Thus, this possibly indicates some degree of intraspecific variability, as seen in some recent helicids.

*Pseudochloritis incrassata* is known from the Middle Miocene of Poland (Górka, 2008), Austria, many localities in Germany (Binder, 2008) and perhaps Hungary (Kókay, 2006). Despite being traditionally placed in the Elonidae (*e.g.* Nordsieck, 2014), a recent revision (Höltke & Rasser, 2015) deems the genus to be more closely related to the helicid subfamily Ariantinae.

## Family HYGROMIIDAE Tryon, 1866

### *Urticicola* Lindholm, 1927

**Type species.** *Helix umbrosa* Pfeiffer, 1828.

### *Urticicola perchtae* Salvador, 2013
(Figure 2T)

2009 *Hygromiidae* gen. indet. sp. 2: Moser *et al.*, 2009, p. 50.
2009 *Leucochroopsis* sp.: Böttcher *et al.*, p. 241, figs. 13-14.
2013 *Urticicola perchtae* Salvador, p. 168, figs. 28-32.
2016 *Urticicola perchtae* Salvador: Salvador *et al.*, p. 138, figs. 3H-I.

**Material examined.** Oggenhausen 2: SMNS 68657 (one spc.), 101378 (one spc.).
**Dimensions.** SMNS 68657: H = 3.4 mm, D = 4.5 mm.
**Remarks.** The following characters allow the identification as *Urticicola perchtae*: whorl profile with a smooth but prominent keel-like angulation; depressed spire; teleoconch sculptured by regularly distributed and vertically elongated fine scales. As already remarked by Salvador (2013), the specimen from Oggenhausen 2 identified as *Leucochroopsis* sp. by Böttcher *et al.* (2009) actually belong to *Urticicola perchtae*. This species is presently known only from other two MN 5 localities, Sandelzhausen (type locality; Salvador, 2013) and Riedensheim (Salvador *et al.*, 2016), both in southeastern Germany.

### Superfamily PUNCTOIDEA Morse, 1864
### Family DISCIDAE Thiele, 1931 (1866)

### *Discus* Fitzinger, 1833

**Type species.** *Helix ruderata* Hartmann, 1821.

### *Discus pleuradrus* (Bourguignat, 1881)
(Figure 2U)

1881 *Helix pleuradra* Bourguignat, p. 53, pl. 3, figs. 67-72.
1923 *Gonyodiscus (Gonyodiscus) pleuradra pleuradra* (Bourguignat): Wenz, p. 341.
1942 *Gonyodiscus (Gonyodiscus) pleuradra pleuradra* (Bourguignat): Wenz & Edlauer, p. 93.
1967 *Discus (Discus) pleuradrus* (Bourguignat): Schütt, p. 213, fig. 16.
1976 *Discus (Discus) pleuradrus* (Bourguignat): Schlickum, p. 12, pl. 2, fig. 37.
1981 *Discus (Discus) pleuradrus* (Bourguignat): Lueger, p. 40, pl. 4, figs. 6-7.
2000 *Discus (Discus) pleuradra* (Bourguignat) [sic]: Fischer, p. 145, fig. 21.
2009 *Discus pleuradrus* (Bourguignat): Böttcher *et al.*, p. 239, figs. 2.10-2.11.
2013 *Discus pleuradrus* (Bourguignat): Rasser *et al.*, p. 439.
2014 *Discus pleuradrus* (Bourguignat): Harzhauser *et al.*, p. 29, pl. 9, figs. 8-13.
2014 *Discus pleuradrus* (Bourguignat): Salvador & Rasser, p. 195, figs. 32-33.
2015a *Discus pleuradrus* (Bourguignat): Salvador *et al.*, p. 264, figs. 4U-W.
2016 *Discus pleuradrus* (Bourguignat): Salvador *et al.*, p. 140, figs. 3M-N.

**Material examined.** Oggenhausen 2: SMNS 68655 (one spc.), 101671 (five spc.).
**Dimensions.** SMNS 68655: H = 2.0 mm, D = 3.5 mm.
**Remarks.** *Discus pleuradrus* is easily identified by its discoid shell, with a step-like spire, a wide umbilicus and a lightly marked keel on the median-upper portion of the whorl, and by its shell sculpture. The protoconch is smooth and the teleoconch is sculptured by strong prosocline ribs. The species is known from the entire Miocene of Central and West Europe (Böttcher *et al.*, 2009). Nevertheless, Early and Late Miocene records could represent different species, as argued by Moser *et al.* (2009). Thus, *D. pleuradrus* could be restricted to the Middle Miocene of France, southern Germany, and Austria (Harzhauser *et al.*, 2014).

### Superfamily PUPILLOIDEA Turton, 1831
### Family CHONDRINIDAE Steenberg, 1925

### *Granaria* Held, 1838

**Type species.** *Pupa frumentum* Draparnaud, 1801.

### *Granaria* sp.
(Figure 2V)

**Material examined.** Oggenhausen 2: SMNS 101367 (two spc.), 101669 (three spc.).
**Dimensions.** SMNS 101367 (fragmentary specimen): H = 1.7 mm, D = 1.4 mm.
**Remarks.** These broken and badly preserved shell apexes can be attributed to the genus *Granaria* by their very characteristic conical shape and whorl profile. In one of the specimens, the teleoconch sculpture can be seen, consisting of very fine prosocline ribs, regularly distributed and spaced from each other by circa twice the rib's width. Nevertheless, identification beyond genus level remains impossible, since the apertural barriers are the most important diagnostic features in the family (Gittenberger, 1973; Höltke & Rasser, 2013). *Granaria* is a well-documented genus in the Central European Miocene (Höltke & Rasser, 2013).

### Family GASTROCOPTIDAE Pilsbry, 1918

### *Gastrocopta* Wollaston, 1878

**Type species.** *Pupa acarus* Benson, 1856.

### *Gastrocopta acuminata* (Klein, 1846)
(Figure 2W)

1846 *Pupa acuminata* Klein, p. 75, pl. 1, fig. 19.
1923 *Gastrocopta (Albinula) acuminata acuminata* (Klein): Wenz, p. 916.
1999 *Gastrocopta acuminata* (Klein): Stworzewicz, p. 161, figs. 56-58).
2000 *Gastrocopta (Albinula) acuminata* (Klein): Manganelli & Giusti, p. 60, pl. 1, figs. 1-6, pl. 2, figs. 1-7.
2015 *Gastrocopta acuminata* (Klein): Salvador, p. 42, fig. 7.
2016 *Gastrocopta acuminata* (Klein): Salvador *et al.*, p. 140, fig. 3P.

**Material examined.** Oggenhausen 2: SMNS 101675 (two spc.).
**Dimensions.** SMNS 101675: H = 2.6 mm.
**Remarks.** *Gastrocopta acuminata* is diagnosed by its larger size, when compared with coeval congeners, and by the shape of its bifid anguloparietal lamella. It is known from the Middle Miocene to Late Pliocene (and maybe Early Pleistocene) of Europe (Stworzewicz, 1999; Manganelli & Giusti, 2000). Unfortunately, the report of *G.* aff. *acuminata* of Berz & Jooss (1927: p. 206) for Oggenhausen 1 could not be confirmed, as the material seems to be missing.

### *Gastrocopta nouletiana* (Dupuy, 1850)
(Figure 2X)

1850 *Pupa Nouletiana* Dupuy, p. 309, pl. 15, fig. 6.
1923 *Gastrocopta (Sinalbinula) nouletiana nouletiana* (Dupuy): Wenz, p. 930.
1999 *Gastrocopta nouletiana* (Dupuy): Stworzewicz, p. 163, figs. 59-61.
2009 *Gastrocopta* cf. *nouletiana* (Dupuy): Böttcher *et al.*, p. 241, fig. 2/12.
2015 *Gastrocopta nouletiana* (Dupuy): Salvador, p. 43, figs. 8-11.

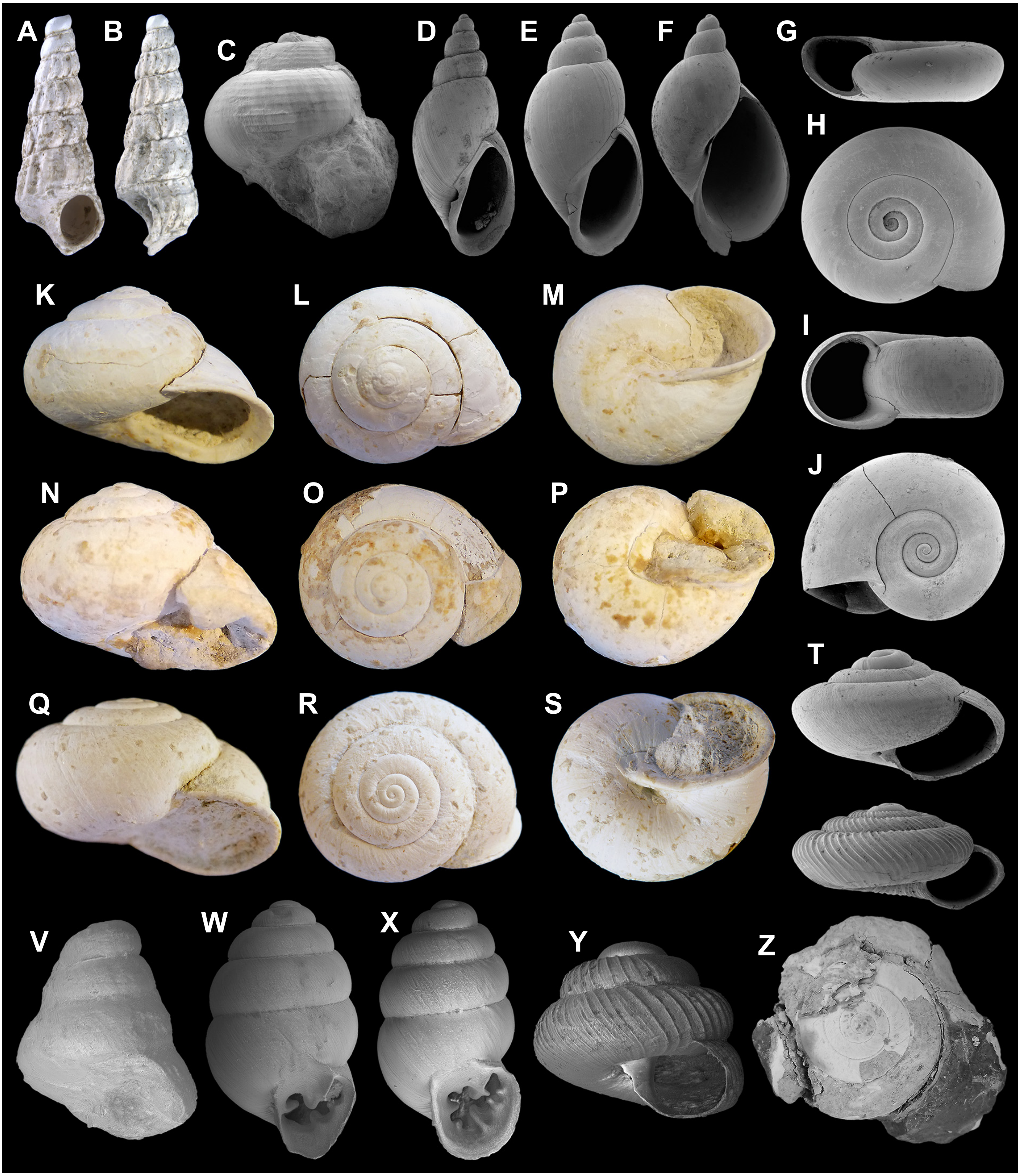

**Figure 2. A-B**, *Tinnyea escheri*, juvenile or fragmentary (SMNS 68388; H = 13.7 mm). **C**, *Pomatias conicus*, juvenile or fragmentary (SMNS 68041; H = 5.9 mm, D = 5.7 mm). **D**, *Galba dupuyiana*, slender form (SMNS 68651; H = 6.5 mm). **E**, *Galba dupuyiana*, broad form (SMNS 68650; H = 6.5 mm). **F**, *Lymnaea* cf. d*ilatata*, juvenile or fragmentary (SMNS 68652; H = 7.2 mm). **G-H**, *Gyraulus applanatus* (SMNS 68654; D = 6.0 mm). **I-J**, *Planorbarius mantelli* (SMNS 68653; H = 3.9 mm, D = 7.7 mm). **K-M**, *Palaeotachea renevieri* (SMNS 101368; D = 16.4 mm). **N-P**, *Megalotachea silvana* (SMNS 101374; D = 21.1 mm). **Q-S**, *Pseudochloritis incrassata* (SMNS 66213; D = 22.9 mm). **T**, *Urticicola perchtae* (SMNS 68657; H = 3.4 mm, D = 4.5 mm). **U**, *Discus pleuradrus* (SMNS 68655; H = 2.0 mm, D = 3.5 mm). **V**, *Granaria* sp., spire apex (SMNS 101367; H = 1.7 mm, D = 1.4 mm). **W**, *Gastrocopta acuminata* (SMNS 101675; H = 2.6 mm). **X**, *Gastrocopta nouletiana* (SMNS 1016764; H = 2.1 mm). **Y**, ?*Truncatellina* sp. (SMNS 101676; H = 0.8 mm, D = 0.9 mm). **Z**, *Archaeozonites costatus* (SMNS 65617; D = 25.8 mm).

2016 *Gastrocopta nouletiana* (Dupuy): Salvador *et al.*, p. 140, figs. 3Q-R.

**Material examined.** Oggenhausen 2: SMNS 68656 (one spc.), 101674 (ten spc.).
**Dimensions.** SMNS 1016764: H = 2.1 mm.
**Remarks.** The present specimens compare well to *Gastrocopta nouletiana*, by their slender shell and number and shape of their apertural barriers (totaling seven): suprapalatal tooth, upper palatal tooth, lower palatal tooth, basal tooth, columellar lamella, infraparietal lamella and anguloparietal lamella. The anguloparietal lamella has an overall bifid aspect, with the angular lamella more vertically positioned and the parietal lamella folded towards the outer lip. *Gastrocopta nouletiana* is common in the European Miocene and shows some variability in the strength of the apertural barriers, with the weaker ones eventually absent (Salvador, 2015).

### Family VERTIGINIDAE Fitzinger, 1833

### *Truncatellina* Lowe, 1852

**Type species.** *Pupa linearis* Lowe, 1852.

### ?*Truncatellina* sp.
(Figure 2Y)

**Material examined.** Oggenhausen 2: SMNS 101676 (one spc.).
**Dimensions.** SMNS 101676 (fragmentary specimen): H = 0.8 mm, D = 0.9 mm.
**Remarks.** Only a single spire apex was found. The shell size, overall shape of the whorls and teleoconch sculpture are very reminiscent of *Truncatellina*, a widespread genus in the European Miocene. However, a more precise identification is impossible.

### Superfamily ZONITOIDEA Mörch, 1864
### Family ZONITIDAE Mörch, 1864

### *Archaeozonites* Sandberger, 1872

**Type species.** *Archaeozonites subverticillus* Sandberger, 1875.

### *Archaeozonites costatus* Sandberger, 1875
(Figure 2Z)

1875 *Archaeozonites costatus* Sandberger, p. 604.
1923 *Zonites (Aegopis) costatus* (Sandberger): Wenz, p. 254.
1927 *Zonites (Aegopis) costatus costatus* (Sandberger): Berz & Jooss, p. 202.
1976 *Archaeozonites costatus* Sandberger: Schlickum, p. 18, pl. 5, fig. 66.
2002 *Miozonites costatus* (Sandberger): Binder, p. 168, pl. 1, figs. 14-16, pl. 3, fig. 8, pl. 7, fig. 3, pl. 8, fig. 4.
2006 *Aegopis costatus* (Sandberger): Kókay, p. 77, pl. 29, figs. 11-12.
2007 *Miozonites costatus* (Sandberger): Jost *et al.*, p. 312.
2013 *Archaeozonites costatus* Sandberger: Rasser *et al.*, p. 440.
2014 *Miozonites costatus* (Sandberger): Harzhauser *et al.*, p. 33, pl. 10, figs. 13-19.

**Table 1.** Species recorded for each site (Ogg. 1: Oggenhausen 1; Ogg. 2: Oggenhausen 2), alongside their identification in the works of Berz & Jooss (1927) and Böttcher *et al.* (2009). A "u" (for unconfirmed) indicates species reported by Berz & Jooss (1927) for which the original material could not be found.

| Species | Site | | Former species identification | |
|---|---|---|---|---|
| | Ogg. 1 | Ogg. 2 | Berz & Jooss (1927) | Böttcher *et al.* (2009) |
| CAENOGASTROPODA | | | | |
| *Pomatias conicus* | x | | *Tudorella conica conica* | — |
| *Tinnyea lauraea* | x | | *Melanatria escheri turrita* | — |
| HYGROPHILA | | | | |
| *Galba dupuyiana* | | x | — | *Galba dupuyiana* |
| *Gyraulus applanatus* | | x | — | *Anisus* sp. |
| *Lymnaea cf. dilatata* | | x | — | *Radix* sp. |
| *Planorbarius mantelli* | | x | — | *Planorbarius cornu* |
| STYLOMMATOPHORA | | | | |
| *Archaeozonites* sp. | x | | *Zonites (Aegopis) costatus costatus* | — |
| *Discus pleuradrus* | | x | — | *Discus pleuradrus* |
| *Gastrocopta acuminata* | u | x | *Gastrocopta* aff. *acuminata acuminata* | — |
| *Gastrocopta nouletiana* | | x | — | *Gastrocopta* cf. *G. nouletiana* |
| *Granaria* sp. | | x | — | — |
| *Megalotachea silvana* | x | x | *Cepaea eversa larteti, Cepaea sylvana sylvana* [sic] | *Cepaea* sp. |
| *Palaeotachea renevieri* | x | x | *Cepaea renevieri coniuncta* | — |
| *Pseudochloritis incrassata* | x | x | *Tropidomphalus (Pseudochloritis) incrasstus incrassatus* | — |
| *Triptychia kleini* | u | | *Triptychia (Triptychia) grandis* | — |
| ?*Truncatellina* sp. | | x | — | — |
| *Urticicola perchtae* | | x | — | *Leucochroopsis* sp. |

2015a *Archaeozonites costatus* Sandberger: Salvador *et al*., p. 259, figs. 3Q-R.
2015b *Archaeozonites costatus* Sandberger: Salvador *et al*., p. 206, figs. 2O-P.

**Material examined.** Oggenhausen 1: SMNS 65617 (1 spc.).
**Remarks.** The single specimen compares well with *A. costatus* by its broad conical spire, flattened protoconch (~1 whorl, sculptured by fine riblets that grow coarser towards teleoconch), teleoconch sculptured by numerous strong prosocline ribs, flattened whorl profile and prominent keel on body whorl. The species is known from the Early and Middle Miocene of Central Europe, being rather common in the Silvana-beds of southern Germany (Schlickum, 1976; Kókay, 2006). In its original description, *A. costatus* was not figured nor properly described (Sandberger, 1875). Thus, Lueger (1981) expressed doubts as to the definition of this species. Nevertheless, the present specimen compares well to later descriptions by Gottschick & Wenz (1916, 1920).

## DISCUSSION

Overall, the Oggenhausen molluscan fauna (Table 1) is rather scarce, presenting more species than several deposits known in the literature (*e.g.* Wenz, 1923), but being much poorer when compared to the large lakes of the German Miocene, such as Randeck Maar, Sandelzhausen, Riedensheim and Steinheim (*e.g.* Finger, 1998; Salvador, 2015; Salvador *et al*., 2015a, 2016). There could be some degree of preservation bias in Oggenhausen 2, since the more extensive and careful collection undertook in this locality did not managed to recover microgastropods, which are very common in other German OSM deposits (*e.g.* Salvador *et al*., 2016).

As already remarked by Berz & Jooss (1927), the snail fauna from Oggenhausen 1 is unusual for its lack of freshwater species, with the exception of *Tinnyea lauraea*. This fact, when allied to the lack of microgastropods (with the possible exception of *Gastrocopta* aff. *acuminata*) and the poor and often fragmentary preservation of the larger species, led Berz & Jooss (1927) to propose rough transport from terrestrial to freshwater sites. Oggenhausen 2, on the other hand, shows a much better preservation, and also freshwater taxa (*Lymnaea*, *Galba*, *Gyraulus* and *Planorbarius*) usually found in other German OSM localities (see also Böttcher *et al*., 2009).

Böttcher *et al.* (2009) proposed that the deposits of Oggenhausen 2 could be interpreted as a shallow lake or an oxbow lake formed by the river that deposited the "Oggenhausen-Sande" from Oggenhausen 1, surrounded by lush vegetation. However, the scarce snail fauna found in this deposit do not add much information beyond this. The genera recorded from the sites are not very useful for a paleoecological analysis, because their Recent representatives are not strongly related to any particular environment. Overall, the freshwater snail genera are consistent with slow-flowing or stagnant waters, while the terrestrial *Discus* and *Urticicola* are consistent with lusher and more humid vegetation (*e.g.* Lueger, 1981; Kerney *et al*., 1983; Welter-Schultes, 2012).

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RESEARCH PAPER

# Early Miocene continental gastropods from new localities of the Molasse Basin in southern Germany

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**Abstract** Here, we present the continental aquatic and terrestrial gastropods found in samples of 11 new boreholes in the Molasse Basin, southern Germany. The samples come from the Lower Freshwater Molasse (USM), the Upper Brackish Molasse (OBM; Grimmelfingen and Kirchberg Formations) and the Upper Freshwater Molasse (OSM). The studied segments of these lithostratigraphical units represent the beginning of the lower Miocene (USM), and the uppermost lower Miocene (OBM, OSM). Twenty-four species of terrestrial and freshwater gastropods are reported here, belonging to the families Neritidae, Melanopsidae, Pachychilidae, Bithyniidae, Hydrobiidae, Truncatellidae(?), Viviparidae, Valvatidae(?), Lymnaeidae, Planorbidae, Carychiidae, Zonitidae, Helicidae, Hygromiidae and Discidae(?). We provide remarks on the taxonomy of some of the studied species, including a revision of *Theodoxus cyrtocelis*, *T. obstusangula* and *T. sparsus* (the latter can be considered a synonym of *T. cyrtocelis*). Finally, we present a paleoecological interpretation for the USM, OBM and OSM based on the gastropod fauna.

**Keywords** Gastropoda · Grimmelfingen Formation · Kirchberg Formation · Lower Freshwater Molasse · Upper Brackish Molasse · Upper Freshwater Molasse

**Kurzfassung** Basierend auf den Proben von 11 in den letzten Jahren durchgeführten Bohrungen im süddeutschen Molassebecken wird die kontinentale aquatische und terrestrische Gastropodenfauna neu bearbeitet. Das Material stammt aus Proben der Unteren Süßwassermolasse (USM), der Oberen Brackwassermolasse (OBM; Grimmelfingen und Kirchberg Formationen) und der Oberen Süßwassermolasse (OSM). Die hier bearbeiteten Abschnitte dieser lithostratigraphischen Einheiten sind in das unterste Unter-Miozän (USM) bzw. in das oberste Unter-Miozän (OBM, OSM) einzustufen. Insgesamt werden 24 Arten kontinentaler Gastropoden aus den Familien Neritidae, Melanopsidae, Pachychilidae, Bithyniidae, Hydrobiidae, Truncatellidae(?), Viviparidae, Valvatidae(?), Lymnaeidae, Planorbidae, Carychiidae, Zonitidae, Helicidae, Hygromiidae und Discidae(?) beschrieben. Die Taxonomie einiger dieser Arten wird kritisch beleuchtet und die Arten der Gattung *Theodoxus* (*T. cyrtocelis*, *T. obstusangula*, *T. sparsus*) warden revidiert, *T. sparsus* wird als Synonym von *T. cyrtocelis* interpretiert. Darüber hinaus wird auf der Grundlage der Gastropodenfauna eine paläoökologische Interpretation für die USM, OBM und OSM gegeben.

**Schlüsselwörter** Gastropoda · Grimmelfingen Formation · Kirchberg Formation · Untere Süßwassermolasse · Obere Brackwassermolasse · Obere Süßwassermolasse

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## Introduction

Numerous samples from the cores of 11 boreholes located in the Molasse Basin of Bavaria, southern Germany (Fig. 1), have recently been investigated in the course of a research program of the Bayerisches Landesamt für Umwelt (project "Informationsoffensive Oberflächennahe Geothermie"). The sampled lithostratigraphic units are known as the Lower Freshwater Molasse (USM), the Upper Brackish Molasse (OBM, Grimmelfingen and Kirchberg Formations [Fms.]) and the Upper Freshwater Molasse (OSM, Fig. 2). The studied samples from the USM are dated from the lowermost Miocene (Aquitanian), while those from the OBM and the OSM correspond to the uppermost lower Miocene (upper Burdigalian).

Whereas the molluscan fauna from the USM has not yet been studied, several works are available for the OBM and USM including the pioneering works of nineteenth century paleontologists (e.g., Krauss 1852), the later works of W. R. Schlickum in the 1960s and 1970s, and some works dedicated to special aspects such as ontogenetic strategies (Kowalke and Reichenbacher 2005), biogeographic distribution (e.g., Reichenbacher 1993) or community studies (Schneider and Prieto 2011). The newly available material from the drilling research program mentioned above provides a unique opportunity to present a comprehensive taxonomical study of all the brackish, freshwater and terrestrial gastropods from the USM, OBM and OSM, and allows new paleoecological considerations. It was also possible to include type material for some species in order to achieve a better understanding of their taxonomy.

## Geological setting

The boreholes are situated in the western to central part of the Molasse Basin (Fig. 1), which is part of the North Alpine Foreland Basin and belongs to the Paratethys realm.

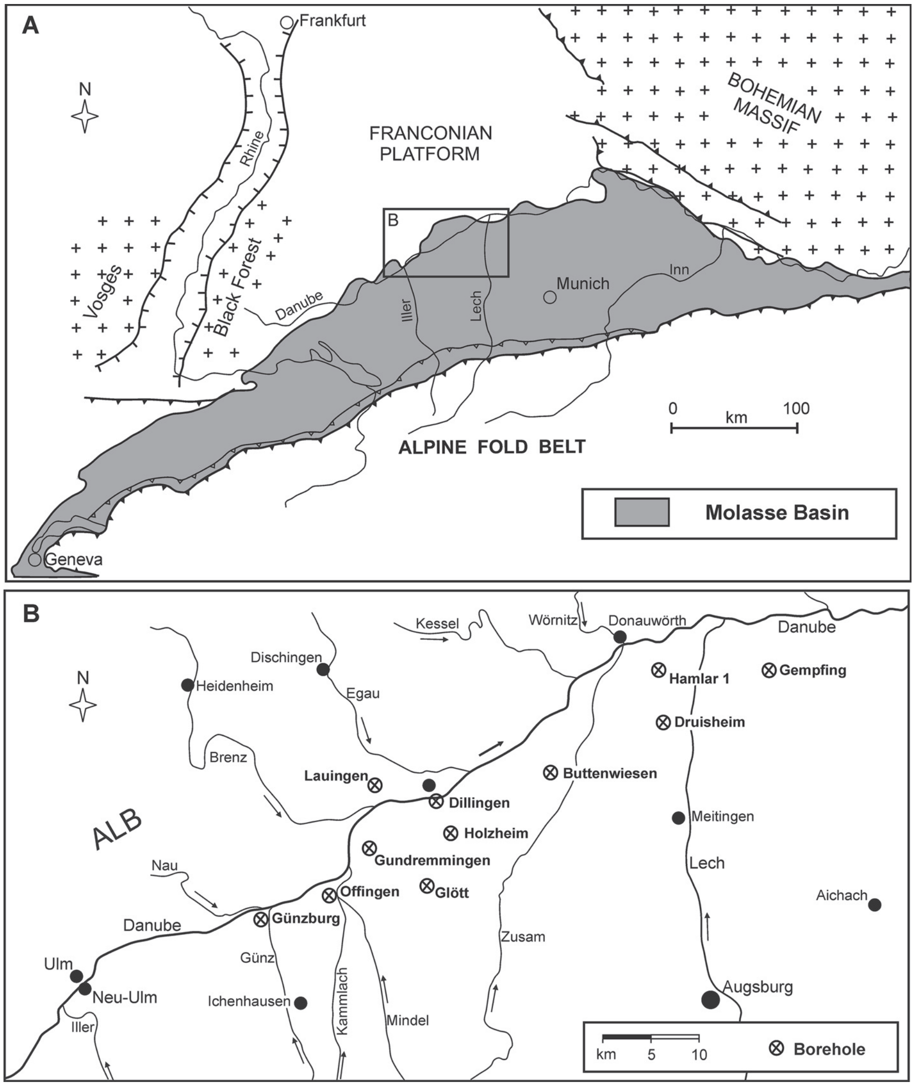


**Fig. 1** Map showing the localities studied in the present work. **a** Schematic map of the Molasse Basin (modified after Jin et al. 1995). **b** Geographic locations of the boreholes

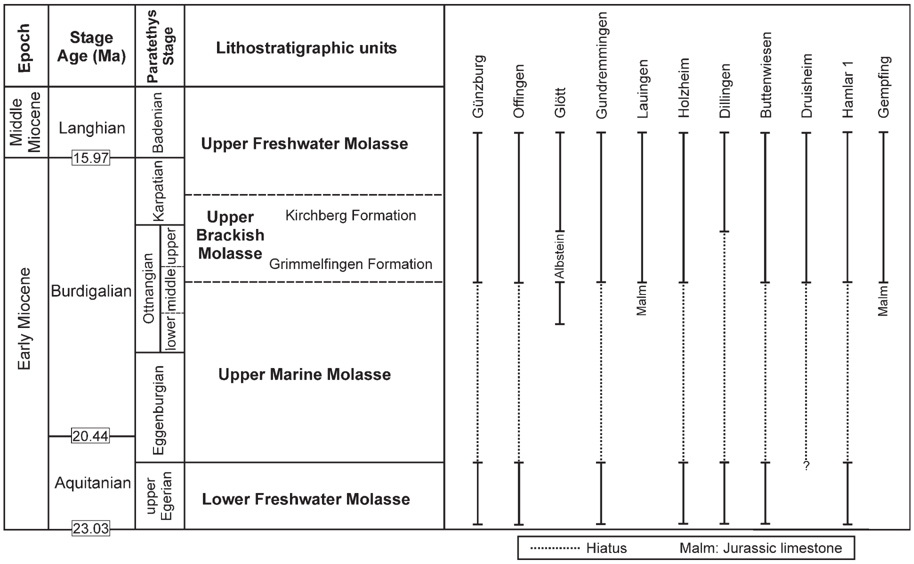


**Fig. 2** Miocene lithostratigraphic units in the south German Molasse Basin (after Doppler et al. 2005; Reichenbacher et al. 2013) and stratigraphic range of drill cores. *Dotted lines* indicate stratigraphic units not present in the drill cores

In the German segment of the North Alpine Foreland Basin, the Molasse succession as a whole is divided into two transgressive–regressive megacycles, which are separated by an unconformity (e.g., Lemcke 1988; Bachmann and Müller 1992; Schwerd et al. 1996; Doppler et al. 2005). The first megacycle, spanning the lower Oligocene (Rupelian) to lowermost Miocene (Aquitanian), comprises the Lower Marine Molasse, the Lower Brackish Molasse, and the USM. The second megacycle includes the Upper Marine Molasse (OMM), the OBM and OSM deposits and is late Early Miocene (latest Aquitanian and Burdigalian) to early Late Miocene (Tortonian) in age.

This study focuses on the USM, OBM (Grimmelfingen and Kirchberg Formations) and OSM gastropods (note that, here, we opt for the more widely used German abbreviations; USM: "Untere Süßwassermolasse"; OBM: "Obere Brackwassermolasse"; OSM: "Obere Süßwassermolasse"; Fig. 2). The USM sediments of the drill cores have yielded partially rich fossil assemblages with charophytes, gastropods, ostracods, fish otoliths and small mammal teeth, which are most probably late Egerian (earliest Miocene, Aquitanian) in age (unpublished data).

The Grimmelfingen and Kirchberg Formations are generally summarized as OBM. The Grimmelfingen Fm. overlies discordantly the USM (Fig. 2) and is between 7 and 41 m thick. This discordancy is due to the incision of a river (Graupensand River) that extended along the northern margin of the Southwest German Molasse Basin and eroded the entire OMM and partly also the upper USM in this area (Kiderlen 1931; Reichenbacher et al. 1998). The Grimmelfingen Fm. represents deposition of the Graupensand River and consists of fine- to coarse-grained sands that are predominantly carbonate- and fossil-free; only a few beds contain mollusks, fish teeth and charophytes (Reichenbacher et al. 1998). The thick marls of the Kirchberg Fm. (up to 22 m) overlie the Grimmelfingen Fm. without a discontinuity. Typically, these marls contain rich and diverse fossil assemblages with bivalves, gastropods, ostracods, fish otoliths and charophytes that allow for a subdivision into the brackish–marine lower Kirchberg Fm. and the brackish–lacustrine upper Kirchberg Fm. (Reichenbacher 1989; Doppler 2011; Reichenbacher et al. 2013).

Reichenbacher et al. (2013) have suggested an upper lower Miocene (upper Burdigalian) age for the OBM sediments, based on a combination of bio-, litho- and magnetostratigraphy, with the Kirchberg Fm. representing the uppermost Burdigalian (lower Karpatian). The OBM/OSM transition is gradual in all drill cores. In most of the cores, only the lowermost OSM sediments, which are middle Karpatian in age (Reichenbacher et al. 2013), contain few freshwater fossils and rare brackish microfossils.

## Materials and methods

Our new material has been assembled from the cores of several boreholes drilled under the auspices of the Bavarian Environment Agency (Landesamt für Umwelt) between 2010 and 2013 (Offingen 1, Glött 1, Gundremmingen 1, Holzheim 1, Dillingen 1, Buttenwiesen 1, Druisheim 1, Hamlar 1) as well as from the boreholes "Günzburg Brunnen 3 neu", "Vogelhölzl N Lauingen" and "WWA Donauwörth, Kernbohrung Gempfing W4".

Core samples were processed by soaking in hydrogen peroxide solution for several hours, washing through sieves of 63-, 200- and 400-µm mesh size, and drying at a temperature of 40 °C. Identification of USM, OBM and OSM in borehole segments and samples has been conducted based on litho and biofacies as well as taxonomic and biostratigraphic analyses involving presence/absence of index taxa and characteristic fossil assemblages (including charophytes, bivalves, gastropods, ostracods, fish otoliths and mammal teeth). Details on the boreholes Hamlar 1, Druisheim 1 and Gempfing W4 are available from Reichenbacher et al. (2013); publications dealing with the other boreholes are in preparation. The total numbers of samples and the number of gastropod-yielding samples that were the basis for this study can be found in Online Supplementary Appendix 1. All cores are stored in the archives of the Bavarian Environment Agency (Landesamt für Umwelt) in Hof.

The fossil material is housed in the micropaleontology collection (Mikropaläontologische Sammlung) of the Bayerisches Landesamt für Umwelt in Munich, Germany, under the single record number LfU-SPR2014. The numbers for the figured material received additional digits; the remainder can be identified (species, locality, height in sediment) via labels. Below, we indicate the occurrence of each species regarding the borehole localities and main stratigraphic units; for the detailed stratigraphical position of each species in each site/borehole, please refer to the tables in Online Supplementary Appendix 1.

Gastropod classification follows Bouchet et al. (2005), with further modifications pointed out by Nordsieck (2014) for the European fossil land snails. All species found in the material are figured and further data on their diagnostic features is provided in the remarks section of each; full descriptions are provided only when required for further remarks on the species' taxonomy.

The following abbreviations are used throughout the article. Institutional: LfU, Bayerisches Landesamt für Umwelt (Hof, Germany); MUWI, Naturwissenschaftliche Sammlung des Museums Wiesbaden (Wiesbaden, Germany); NHMW, Naturhistorisches Museum Wien (Vienna, Austria); SMNS, Staatliches Museum für Naturkunde Stuttgart (Stuttgart, Germany). Shell measurements: H, shell height; D, shell width (diameter); h, aperture/operculum length; d, aperture/operculum width. The specimens were measured either with a digital caliper or with the aid of computer software (Leica Application Suite [LAS] v.3.8.0 and ImageJ). Stratigraphic units: USM, Lower Freshwater Molasse; OBM, Upper Brackish Molasse; OSM, Upper Freshwater Molasse.

## Systematic paleontology

Phylum **Mollusca**, 1758
Class **Gastropoda** Cuvier, 1795
**Neritimorpha** Golikov and Starobogatov, 1975
Superfamily **Neritoidea** Rafinesque, 1815
Family **Neritidae** Rafinesque, 1815
Genus ***Theodoxus*** Montfort, 1810
***Theodoxus cyrtocelis*** (Krauss, 1852)
Figure 3a–g.

*1852 *Neritina cyrtocelis* Krauss: p. 145.
*1852 *Neritina sparsa* Krauss: p. 145.
1929 *Theodoxus (Theodoxus) cyrtocelis cyrtocelis* – Wenz: p. 2991.
1929 *Theodoxus (Theodoxus) cyrtocelis sparsus* – Wenz: p. 2992.
1963 *Theodoxus (Theodoxus) cyrtocelis cyrtocelis* – Schlickum: p. 2.
1964 *Theodoxus (Theodoxus) cyrtocelis* – Schlickum: p. 4, pl. 1, figs. 3–6.
1966 *Theodoxus (Theodoxus) cyrtocelis* – Schlickum: p. 3, pl. 12, figs. 1–5.
1970a *Theodoxus (Theodoxus) cyrtocelis* – Schlickum: p. 146, pl. 10, figs. 3–4.
1970b *Theodoxus cyrtocelis* – Schlickum: p. 162.
1970c *Theodoxus cyrtocelis* – Schlickum: p. 176, pl. 3, Fig. 1.
1989 *Theodoxus cyrtocelis cyrtocelis* – Reichenbacher: p. 144, pl. 1, figs. 1–2.
1993 *Theodoxus cyrtocelis cyrtocelis* – Reichenbacher: Tables 7, 13.
2005 *Theodoxus cyrtocelis* – Kowalke and Reichenbacher: p. 617, figs. 4.3–4.7
2014 *Theodoxus (Theodoxus) cyrtocelis* – Neubauer et al.: supplementary material 1.
2014 *Theodoxus (Theodoxus) cyrtocelis sparsus* – Neubauer et al.: supplementary material 1.

*Occurrence* USM: Gundremmingen. OBM (Kirchberg Fm.): Buttenwiesen, Druisheim, Gempfing, Günzburg, Hamlar 1, Holzheim, Lauingen. OSM: Glött (immediately above the boundary with the Kirchberg Fm., so it could represent reworked material).

*Description* Shell with few quickly growing whorls. Protoconch ($\sim$1 whorl) smooth, rounded, large (relative to whole shell); transition to teleoconch clearly marked. Teleoconch sculptured by well-marked growth lines. Shell color from almost completely brown to almost completely white, with numerous patterns of white and brown dots and blotches. Suture shallow, but well-marked. Whorl profile convex. Apex immersed to weakly raised. Peristome simple, sharp. Aperture D-shaped, with a large callus pad, which may show several very faint furrows (likely increasing with age). Operculum D-shaped, typical for genus, with an internal scimitar-shaped ridge.

*Remarks* The present specimens compare very well to *T. cyrtocelis*, a species originally described from the Kirchberg Fm. (Krauss 1852). The type series (SMNS

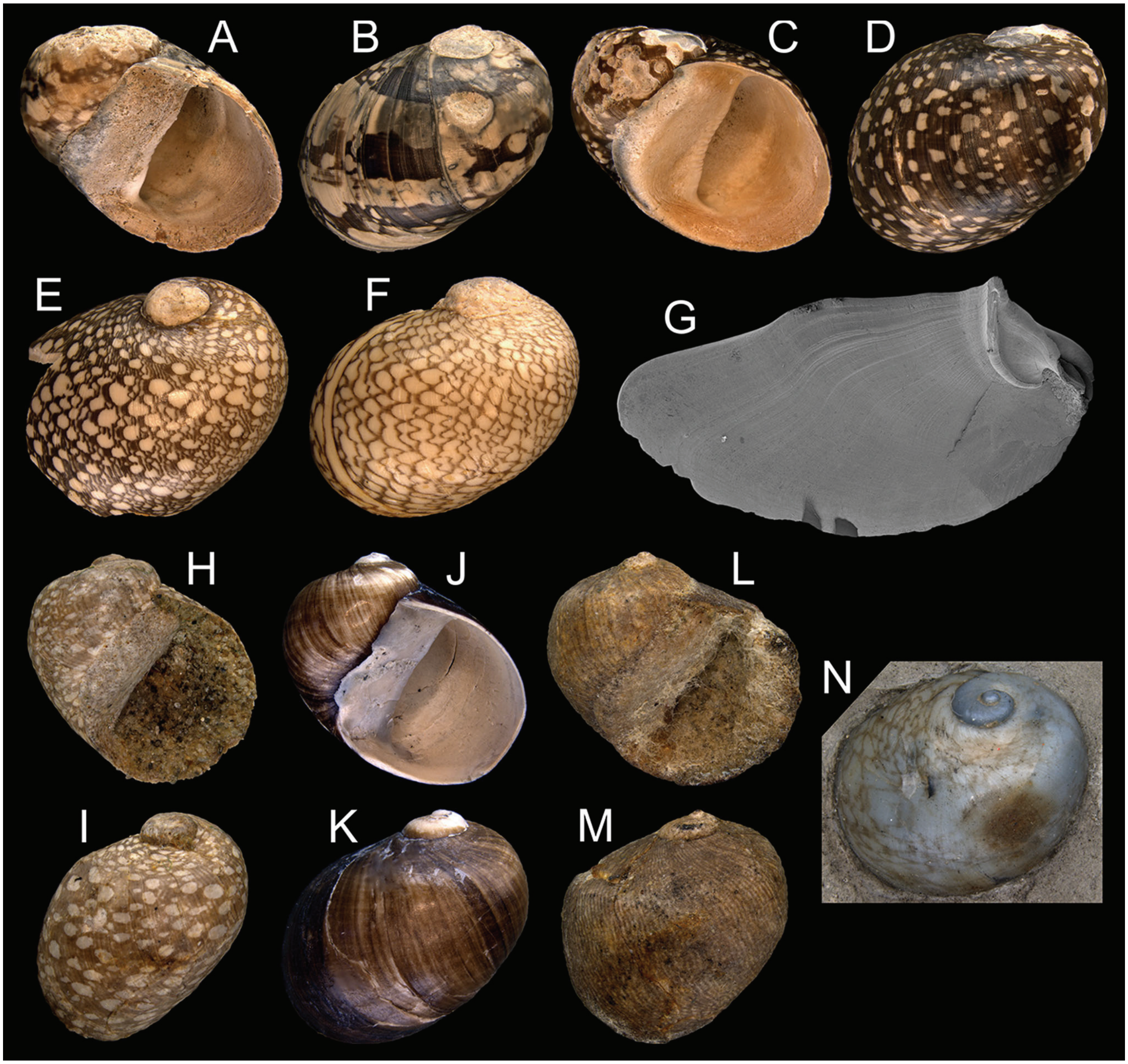


**Fig. 3** Aquatic gastropods. **a**, **b** *Theodoxus cyrtocelis*, in apertural and dorsal views, respectively (LfU-SPR2014-015; Hamlar 1, OBM, Kirchberg Fm.; $H = 6.7$ mm, $D = 7.4$ mm). **c**, **d** *Theodoxus cyrtocelis*, in apertural and dorsal views, respectively (LfU-SPR2014-016; Hamlar 1, OBM, Kirchberg Fm.; $H = 6.4$ mm, $D = 6.6$ mm). **e** *Theodoxus cyrtocelis*, dorsal to apical view (LfU-SPR2014-017 spcm. #1; Hamlar 1, OBM, Kirchberg Fm.; $H = 5.0$ mm, $D = 4.9$ mm). **f** *Theodoxus cyrtocelis*, dorsal view (LfU-SPR2014-017 spcm. #2; Hamlar 1, OBM, Kirchberg Fm.; $H = 4.5$ mm, $D = 5.0$ mm). **g** *Theodoxus cyrtocelis*, operculum (LfU-SPR2014-021; Buttenwiesen, OBM, Grimmelfingen Fm.; $H = 4.6$ mm, $D = 2.4$ mm). h, i *Theodoxus cyrtocelis*, syntype, in apertural and dorsal views, respectively (SMNS 25291/2005; Kirchberg an der Iller, OBM, Kirchberg Fm.; $D = 7.5$ mm). **j**, **k** *Theodoxus obtusangula*, in apertural and dorsal views, respectively (LfU-SPR2014-014; Buttenwiesen, OBM, Kirchberg Fm.; $H = 5.0$ mm, $D = 4.9$ mm). **l**, **m** *Theodoxus obtusangula*, syntype, in apertural and dorsal views, respectively (SMNS 25294/2005; Kirchberg an der Iller, OBM, Kirchberg Fm.; $D = 8.1$ mm). **n** *Theodoxus sparsus*, syntype, in dorsal to apical view (SMNS 25300/2005; Kirchberg an der Iller, OBM, Kirchberg Fm.; $D = 5.7$ mm)

25291/2005; 17 specimens; Fig. 3h, i) of this species show a good range of variation in color pattern (from completely brown shells to white and brown to almost completely white) and overall shell shape (e.g., higher or lower spires, rounder or slenderer shells). The same variation of shape (mainly regarding higher or lower spires, see below) and an even greater variation in color pattern can be seen in the present specimens. *Theodoxus* species are remarkable for exhibiting this kind of variation, as reported for many recent representatives of the genus (e.g., Heller 1979; Bandel 2001; Anistratenko 2005; Glöer and Pešic 2015).

The opercula found (Fig. 3g) come from samples including only *T. cyrtocelis* (Hamlar 1), so they can be reasonably assigned to this species.

Krauss (1852) described another *Theodoxus* species from the Kirchberg Fm., namely *T. sparsus*, which he defined by a flattened spire and gray color (syntypes: SMNS 253000/2005, 7 specimens; Fig. 3n). We consider here *T. sparsus* a synonym of *T. cyrtocelis* for the following reasons. The gray color seen in Krauss' shells is the same as the rock matrix and is probably a preservation artifact; one of the syntypes actually is white and brown, like typical *T. cyrtocelis*. The flattened spires can be considered as variation in overall shell shape, as known from recent *Theodoxus* species (e.g., Elkarmi and Ismail 2005; Glöer and Pešic 2015). Moreover, some syntypes of *T. sparsus* have more pronounced spires while some syntypes of *T. cyrtocelis* (SMNS 25291/2005) have flattened spires. Finally, the overall impression of a more flattened spire profile can be the result of all specimens of *T. sparsus* being either juvenile or fragmentary shells. As seen in the recent *T. macri* (Sowerby, 1849), for instance, the overall shell shape and its proportions depend on age: the shells become taller, changing the impression of a flattened spire to a more prominent one, as the animals grow older and larger and, thus, add more whorls (Elkarmi and Ismail 2005).

***Theodoxus obtusangula*** (Krauss, 1852).
Figure 3j, k.
*1852 *Neritina obtusangula* Krauss: p. 145.
1929 *Theodoxus (Theodoxus) cyrtocelis obtusangulus* [sic] – Wenz: p. 2992.
2014 *Theodoxus (Theodoxus) cyrtocelis obtusangulus* [sic] – Neubauer et al.: supplementary material 1.

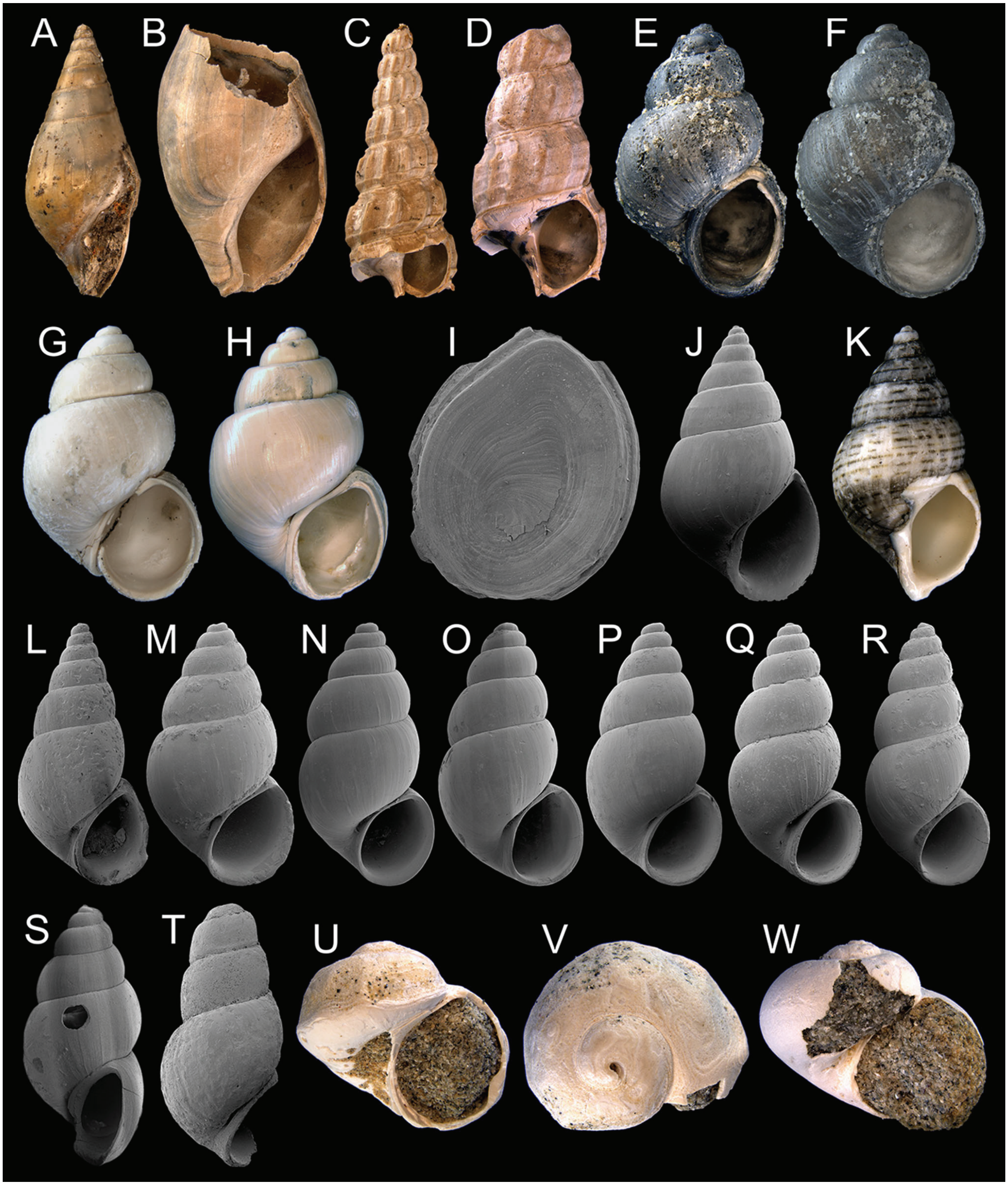
*Occurrence* OBM (Kirchberg Fm.): Buttenwiesen, Günzburg.

*Description* Shell small, neritiform, with few regularly growing whorls (but with a sudden expansion after ~2¼ whorls). Protoconch (~1 whorl) smooth, relatively smaller than in congeners; transition to teleoconch clear. Teleoconch sculptured by well-marked growth lines. Shell color uniformly brown (a single specimen displays round white dots, similar to *T. cyrtocelis*). Suture shallow, but well-marked. Whorl profile slightly flattened, with well-defined angulation on upper portion of whorl. Apex raised. Peristome simple, sharp. Aperture D-shaped, with large columellar region.

*Remarks* *Theodoxus obtusangula* is the third *Theodoxus* species described by Krauss (1852) from the Kirchberg Fm. (holotype: SMNS 106414; Fig. 3l, m). When compared to *T. cyrtocelis*, this species has a smaller protoconch, a smaller width of the initial whorls (which are also more tightly coiled and more regularly growing, but expanding suddenly around 2¼ whorls), a slightly larger number of whorls, a well-defined angulation on upper portion of whorl (which gives the species its name), a usually uniformly brown color (Krauss had only one specimen, but this seems to hold true for the present specimens with a single exception; see description above) and stronger and more well-marked growth lines. As such, with the presently available material, *T. obtusangula* seems to be a clearly distinct species.

The species epithet is derived from the Latin word "*angulus*" (=an angle). As such, "*angula*" is still a substantive with a variant gender ending and is, therefore, not declensable.

**Fig. 4** Aquatic gastropods. **a** *Melanopsis impressa*, spire apex fragment, apertural view (LfU-SPR2014-007; Offingen, OBM, Kirchberg Fm.; $H = 6.0$ mm). **b** *Melanopsis impressa*, aperture fragment (LfU-SPR2014-008; Hamlar 1, OBM, Kirchberg Fm.; $H = 10.9$ mm). **c** *Tinnyea escheri*, apertural view (LfU-SPR2014-004; Lauingen, OBM, Kirchberg Fm.; $H = 9.7$ mm). **d** *Tinnyea escheri*, apertural view (LfU-SPR2014-005; Hamlar 1, OBM, Kirchberg Fm.; $H = 12.1$ mm). **e** *Bithynia glabra*, apertural view (LfU-SPR2014-020; Glött, OBM, Kirchberg Fm.; $H = 9.1$ mm). **f** *Bithynia glabra*, apertural view (LfU-SPR2014-020; Glött, OBM, Kirchberg Fm.; $H = 8.1$ mm). **g** *Bithynia glabra*, apertural view (LfU-SPR2014-019 spcm. #1; Buttenwiesen, OBM, Kirchberg Fm.; $H = 8.9$ mm). **h** *Bithynia glabra*, specimen more akin to *B. dunkeri*, apertural view (LfU-SPR2014-019 spcm. #2; Buttenwiesen, OBM, Kirchberg Fm.; $H = 9.4$ mm). **i** *Bithynia glabra*, operculum (LfU-SPR2014-040; Druisheim, OBM, Kirchberg Fm.; $H = 4.2$ mm, $D = 3.5$ mm). **j** *Ctyrokya conoidea*, apertural view (LfU-SPR2014-037; Hamlar 1, OBM, Kirchberg Fm.; $H = 4.1$ mm). **k** *Ctyrokya conoidea*, with preserved color pattern, apertural view (LfU-SPR2014-013; Hamlar 1, OBM, Kirchberg Fm.; $H = 3.5$ mm). **l** *Hydrobia semiconvexa*, apertural view (LfU-SPR2014-031; Hamlar 1, OBM, Kirchberg Fm.; $H = 5.0$ mm). **m** *Nematurella bavarica*, apertural view (LfU-SPR2014-047 spcm.. #1; Günzburg, OBM, Kirchberg Fm.; $H = 3.9$ mm). **n** *Nematurella bavarica*, apertural view (LfU-SPR2014-042 spcm.. #1; Druisheim, OBM, Grimmelfingen Fm.; $H = 3.6$ mm). **o** *Nematurella bavarica*, apertural view (LfU-SPR2014-029; Lauingen, OBM, Kirchberg Fm.; $H = 4.2$ mm). **p** *Nematurella bavarica*, apertural view (LfU-SPR2014-042 spcm.. #2; Druisheim, OBM, Grimmelfingen Fm.; $H = 3.6$ mm). **q** *Nematurella bavarica*, apertural view (LfU-SPR2014-043; Hamlar 1, OBM, Kirchberg Fm.; $H = 4.3$ mm). **r** *Nematurella bavarica*, apertural view (LfU-SPR2014-047 spcm.. #2; Günzburg, OBM, Kirchberg Fm.; $H = 4.2$ mm). **s** *Nematurella bavarica*, in apertural to lateral view, showing circular hole, likely a predation mark (LfU-SPR2014-041; Buttenwiesen, OBM, Kirchberg Fm.; $H = 3.5$ mm). **t** ?*Truncatella* sp., apertural view (LfU-SPR2014-009; Hamlar 1, OBM, Kirchberg Fm.; $H = 4.2$ mm). **u**, **v** *Viviparus* cf. *suevicus*, in apertural and apical views, respectively (LfU-SPR2014-002, spcm. #1; Druisheim, OBM, Grimmelfingen Fm.; $H = 8.6$ mm, $D = 9.9$ mm). **w** ?*Valvata* sp., apertural view (LfU-SPR2014-001; Druisheim, OBM, Grimmelfingen Fm.; $H = 7.0$ mm, $D = 8.7$ mm) ▶



**Caenogastropoda** Cox, 1966
Superfamily **Cerithioidea** Fleming, 1822
Family **Melanopsidae** H. Adams and Adams, 1854
Genus ***Melanopsis*** Férussac, 1807

***Melanopsis impressa*** Krauss, 1852
Figure 4a, b.
*1852 *Melanopsis impressa* Krauss: p. 143, pl. 3, fig. 3.
1872 *Melanopsis impressa* – Sandberger: pl. 31, fig. 8.

1872 *Melanopsis impressa* – Sandberger: p. 558.
1964 *Melanopsis impressa impressa* – Schlickum: p. 11, pl. 2, figs. 23–25.
1966 *Melanopsis impressa impressa* – Schlickum: p. 325, pl. 13, fig. 25.
1970a *Melanopsis impressa impressa* – Schlickum: p. 148, pl. 10, fig. 5.
1970b *Melanopsis impressa impressa* – Schlickum: p. 160.
1973 *Melanopsis impressa impressa* – Steininger et al.: p. 404, pl. 4, figs. 6–7.
1989 *Melanopsis impressa impressa* – Reichenbacher: p. 174, pl. 2, fig. 6.
1993 *Melanopsis impressa impressa* – Reichenbacher: Tables 6, 13.
2001 *Melanopsis impressa* – Harzhauser and Kowalke: p. 360, figs. 3.6–3.8.
2005 *Melanopsis impressa impressa* – Kowalke and Reichenbacher: p. 830, figs. 8.3–8.5.
2014 *Melanopsis impressa* – Neubauer et al.: supplementary material 1.

*Occurrence* OBM (Grimmelfingen Fm.): Günzburg. OBM (Kirchberg Fm.): Buttenwiesen, Druisheim, Glött, Günzburg, Hamlar 1, Holzheim, Offingen.

*Remarks* The shells have a very flat whorl profile, a slightly incised suture, a simple and sharp peristome and an elongated aperture, with a callus on the columellar and palatal regions; furthermore, the base of the aperture's columellar region is folded, encircling the central coiling axis of the shell and slightly bent inwards. These features (especially the characteristic aperture, present even in juvenile specimens, such as the syntypes SMNS 106400) makes the species easily identifiable in the material. As already reported by Kowalke and Reichenbacher (2005), the width of the spire in this species is slightly variable: shells with slender spires are more common, but some shells show wider and bulkier spires.

*Melanopsis impressa* is common in estuarine environments from the Miocene of the Paratethys and Mediterranean (Harzhauser and Kowalke 2001); it was originally described from the Kirchberg Fm. of Kirchberg an der Iller (Krauss 1852).

Family **Pachychilidae** P. Fischer and Crosse, 18
Genus ***Tinnyea*** Hantken, 1887
***Tinnyea lauraea*** (Mathéron, 1843)
Figure 4c, d

*1843 *Melania lauraea* Mathéron: p. 291, pl. 36, figs. 23–24.
1927 *Melanatria escheri turrita* – Berz and Jooß: p. 206.
1953 *Brotia (Tinnyea) escheri* – Papp: p. 128, pl. 3, fig. 29.
1976 *Brotia (Tinnyea) escheri* – Schlickum: p. 4, pl. 1, fig. 9.
2000 *Brotia (Tinnyea) escheri* – Mikuž and Pavšič: p. 44, pl. 1, figs. 1–8.

*Occurrence* OBM (Kirchberg Fm.): Buttenwiesen, Druisheim, Günzburg, Hamlar 1, Lauingen.

*Remarks* Despite the very fragmentary nature of the present material, the species' turriform shell and characteristic teleoconch sculpture (very strong opisthocline and slightly curved axial ribs on first whorls and both axial ribs and spiral cords on the remaining whorls) allow the identification. According to Harzhauser et al. (2002), the species has a broad range of morphological plasticity, as usually seen in recent Pachychilidae.

*Tinnyea lauraea* is known in the fossil record of Central Europe from the Oligocene to the Pliocene (Harzhauser et al. 2002). This large time span suggests that this is a still unresolved species complex (Kadolsky 1995)

Superfamily **Truncatelloidea** Gray, 1840
Family **Bithyniidae** Gray, 1857
Genus ***Bithynia*** Leach, 1818
***Bithynia glabra*** (von Zieten, 1830)
Figure 4e, i

*1830 *Cyclostoma glabrum* von Zieten: p. 42, pl. 31, fig. 9.
1852 *Paludina tentaculata* – Krauss: p. 140.
*1872 *Bythynia* [sic] *gracilis* – Sandberger: pl. 28, figs. 16–16a.
1875 *Bythynia* [sic] *gracilis* – Sandberger: p. 561.
1964 *Bithynia glabra* – Schlickum: p. 9.
1966 *Bithynia dunkeri* – Schlickum: p. 324, pl. 12, figs. 19–21.
1966 *Bithynia glabra* – Schlickum: p. 324, pl. 12, fig. 22.
1989 *Bithynia* cf. *glabra* – Reichenbacher: p. 144, pl. 1, fig. 4.
1989 *Bithynia dunkeri* – Reichenbacher: p. 144, pl. 1, figs. 6–7.
1993 *Bithynia dunkeri* – Reichenbacher: Tables 6–7.
1993 *Bithynia glabra* – Reichenbacher: Table 13.
2005 *Bithynia* cf. *glabra* – Kowalke & Reichenbacher: p. 629, figs. 8.1–8.2.
2014 *Bithynia glabra* – Neubauer et al.: supplementary material 1.

*Occurrence* USM: Offingen. OBM (Grimmelfingen Fm.): Buttenwiesen, Dillingen, Günzburg. OBM (Kirchberg Fm.): Buttenwiesen, Dillingen, Druisheim, Gempfing, Glött, Günzburg, Hamlar 1, Holzheim, Lauingen, Offingen. OSM: Buttenwiesen, Dillingen, Gempfing, Glött, Gundremmingen, Hamlar 1, Holzheim, Offingen.

*Description* Shell small, conical, imperforate. Protoconch smooth (~1 whorl), rounded; transition to teleoconch not clearly marked. Teleoconch smooth, except for growth lines. Whorl profile strongly convex. Suture deep. Aperture oval, pointed on the meeting of palatal and parietal regions. Peristome thickened, complete. Operculum with concentric growth pattern and central nucleus.

*Remarks* Two species of *Bithynia* have been described for the OBM: *B. dunkeri* Gude, 1913, from the Kirchberg Fm. (but also occurring in the OSM), and *B. glabra* (von Zieten, 1830), from the Grimmelfingen and Kirchberg Fms. Schlickum (1966) notes that *B. glabra* substitutes *B. dunkeri* in the younger layers of the Kirchberg Fm. at Leipheim.

There is some confusion in the literature about the identification of these two species. When only the early whorls are present, it is impossible to distinguish between them, while the adults differ according to the original descriptions and later revision by Sandberger (1875): *Bithynia dunkeri* has a broader shell, more flattened whorls, a proportionately larger body whorl (and thus proportionately smaller spire) and a larger and more angular aperture; *Bithynia glabra* is identified by its slenderer shell, proportionately smaller body whorl and very convex whorls. However, this distinction might not be as clear-cut as previously supposed.

In the present material, there seems to be a gradation of forms from a more slender shell (i.e., more akin to *B. glabra*; Fig. 4e) to a broader one (i.e., more akin to *B. dunkeri*; Fig. 4h), with intermediate forms between them (Fig. 4f, g). As such, the two described species could be simply extreme forms in a continuum; moreover, the protoconch size and its overall shape seem to be the same throughout this continuum in the present material. There is not a clear case of substitution of one species for the other through the sedimentary layers; both forms are equally found throughout the Kirchberg Fm. (the only stratigraphical unit for which we have completely preserved specimens). Nevertheless, the present material is too scarce and poorly preserved to delve deeper into this matter. A throrough taxonomical revision of these two species is urgently needed, with examination of the available type material and a large sample of topotypes. Meanwhile, we prefer here the more cautious approach of a classification as *B. glabra*, the older name.

Family **Hydrobiidae** Stimpson, 1865
Genus ***Ctyrokya*** Schlickum, 1965
***Ctyrokya conoidea*** (Krauss, 1852)
Figure 4j, k.

*1852 *Paludina conoidea* Krauss: p. 141, pl. 3, fig. 1 [non *Paludina conoidea* de Reyniès, 1844: 4; Küster, 1852: 43, pl. 9, figs. 3–7].
1965 *Ctyrokya conoidea* – Schlickum: p. 101.
1973 *Ctyrokya conoidea* – Steininger et al.: p. 397, pl. 3, fig. 5.
1989 *Ctyrokya conoidea* – Reichenbacher: p. 144, pl. 2, fig. 4.
2005 *Ctyrokia conoidea* [sic] – Kowalke and Reichenbacher: p. 621, figs. 6.8–6.10.
2014 *Ctyrokya conoidea* – Neubauer et al.: supplementary material 1.

*Occurrence* OBM (Kirchberg Fm.): Buttenwiesen, Druisheim, Günzburg, Hamlar 1, Holzheim, Lauingen, Offingen. OSM: Gundremmingen (at the lowermost layer, could be reworked material from older layers).

*Remarks* The shell is conical-elongated and broad, with a flat whorl profile, a proportionately large body whorl, a large ellipsoid aperture, an incomplete peristome and a dome-shaped and prominent smooth protoconch (of ca. 1¾ whorl) transitioning abruptly to a smooth teleoconch (except for growth lines). The color pattern was apparently preserved in some specimens (Fig. 4k) and consists of numerous intermittent dark spiral stripes.

The broad conical spire of the present specimens, with flat whorls and a large aperture, compare well to the syntypes of *C. conoidea* (SMNS 106373), a species described by Krauss (1852) from the Kirchberg Fm. Schlickum (1965) erected the genus *Ctyrokya* and included this species, but the validity of this genus remains a matter for future revisionary work. As pointed out by Salvador et al. (in press), the substitution of the junior primary homonym is not mandatory if the conditions of Article 23.9.5 ICZN are met.

Two further species of *Ctyrokya* have been reported from the Kirchberg Fm., namely *C. hoelzli* (Schlickum, 1964) and *C. zoebeleini* Schlickum, 1970a, b, c, d (Kowalke and Reichenbacher 2005), but they were not found in the present material.

Genus ***Hydrobia*** Hartmann, 1821
***Hydrobia semiconvexa*** Sandberger, 1875
Figure 4l

1852 *Litorinella acuta* – Krauss: p. 142 [non *Cyclostoma acutum* Draparnaud, 1805].
*1875 *Hydrobia semiconvexa* Sandberger: p. 561.
1971 *Hydrobia semiconvexa* – Schlickum: p. 571, pl. 1, figs. 2–3.
1973 *Hydrobia semiconvexa* – Steininger et al.: p. 391, pl. 2, fig. 2.
1989 *Hydrobia semiconvexa* – Reichenbacher: pl. 2, fig. 8.
1993 *Hydrobia semiconvexa* – Reichenbacher: p. 290.
2005 *Hydrobia* cf. *semiconvexa* – Kowalke and Reichenbacher: p. 619, figs. 5.3–5.4.

*Occurrence* OBM (Kirchberg Fm.): Buttenwiesen, Gempfing, Günzburg, Hamlar 1, Holzheim, Lauingen.

*Remarks* The narrow and conical-elongated shell, with a prominent smooth protoconch (of ca. 1 whorl), a small ellipsoid aperture and a complete peristome, compares well with the type specimens of *H. semiconvexa* (housed at the MUWI). This species was originally described from the Kirchberg Fm. from Illerkirchberg (Krauss 1852; Sandberger 1875).

However, the present specimens also compare reasonably well to the syntypes *H. frauenfeldi* (Hörnes, 1856) (NHMW 1846/0037/0456), but have a somewhat more elongated aperture. This species was originally described from Sarmatian sediments at Hauskirchen, Austria (Hörnes 1856; Harzhauser and Piller 2004), but is also known from the OBM of the Oncophora Basin, which neighbors the Kirchberg Basin (Schlickum 1964; Reichenbacher 1993; Kowalke and Reichenbacher 2005). A possible synonymy between these two species should be further investigated.

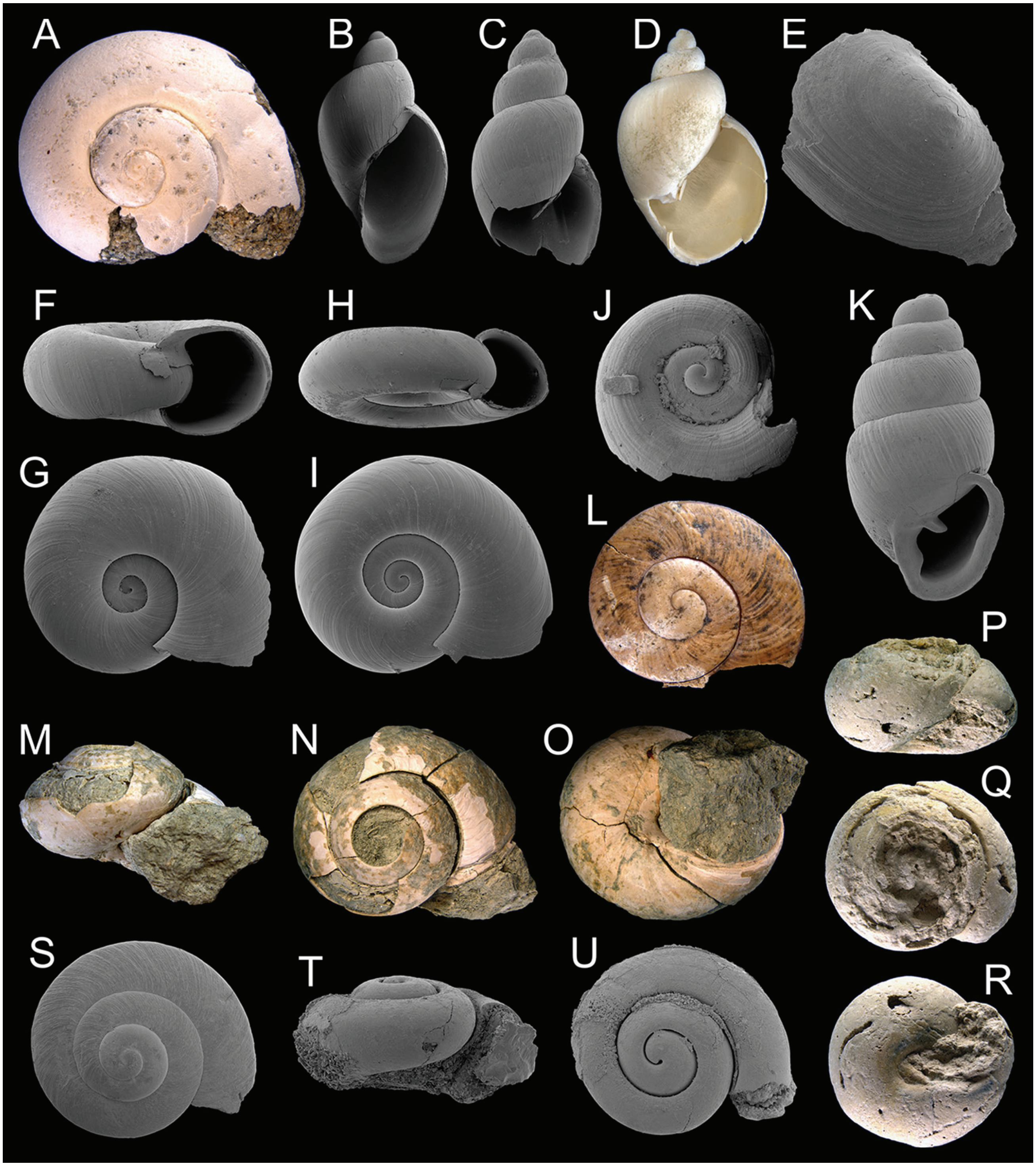
Genus ***Nematurella*** Sandberger, 1875
***Nematurella bavarica*** Sandberger, 1875
Figure 4m–s.
*1875 *Hydrobia bavarica* Sandberger: p. 576.
*1960 *Nematurella schuetti* Schlickum: p. 211, pl. 19, fig. 12.
1961 *Nematurella bavarica* – Schlickum: p. 57.
1963 *Nematurella scholli* – Schlickum: p. 3.
1966 *Nematurella zilchi* – Schlickum: p. 223, pl. 12, figs. 9–18.
1971 *Nematurella convexula* – Schlickum: pl. 1, fig. 5.
1973 *Nematurella scholli* – Steininger et al.: p; 391, pl. 2, Fig. 5.
1973 *Nematurella convexula* – Steininger et al.: p. 392, pl. 2, fig. 8.
1973 *Nematurella zilchi* – Steininger et al.: p. 393, pl. 2, fig. 10.
1989 *Nematurella convexula* – Reichenbacher: p. 144, pl. 1, fig. 2.
1989 *Nematurella zilchi* – Reichenbacher: p. 144, pl. 2, fig. 1.
1989 *Nematurella* cf. *bavarica* – Reichenbacher: p. 144, pl. 2, fig. 3.
2005 *Nematurella bavarica* – Kowalke and Reichenbacher: p. 623, figs. 7.3–7.5.
2005 *Nematurella convexula* – Kowalke and Reichenbacher: p. 627, figs. 5.9–5.10.
2014 *Nematurella bavarica* – Neubauer et al.: supplementary material 1.
2014 *Nematurella convexula* – Neubauer et al.: supplementary material 1.
2014 *Nematurella zilchi* – Neubauer et al.: supplementary material 1.

**Fig. 5** Aquatic and terrestrial gastropods. **a** ?*Valvata* sp., apical view (LfU-SPR2014-001; Druisheim, OBM, Grimmelfingen Fm.; $H = 7.0$ mm, $D = 8.7$ mm). **b** *Stagnicola armaniacensis*, apertural view (LfU-SPR2014-028; Offingen, OBM, Kirchberg Fm.; $H = 3.9$ mm). **c** *Stagnicola praebouilleti*, apertural view (LfU-SPR2014-026; Buttenwiesen, OBM, Grimmelfingen Fm.; $H = 2.1$ mm). **d** *Lymnaea dilatata*, apertural view (LfU-SPR2014-018; Buttenwiesen, OBM, Kirchberg Fm.; $H = 6.1$ mm). **e** *Ferrissia* cf. *wittmanni*, apical view (LfU-SPR2014-025; Offingen, OBM, Kirchberg Fm.; $H = 4.0$ mm, $D = 2.6$ mm). **f** *Gyraulus albertanus*, apertural view (LfU-SPR2014-034 spcm. #1; Offingen, OBM, Kirchberg Fm.; $H = 1.1$ mm, $D = 2.3$ mm). **g** *Gyraulus albertanus*, umbilical view (LfU-SPR2014-034 spcm. #2; Offingen, OBM, Kirchberg Fm.; $D = 2.0$ mm). **h** *Gyraulus applanatus*, apertural view (LfU-SPR2014-035; Buttenwiesen, OBM, Kirchberg Fm.; $H = 0.7$ mm, $D = 2.2$ mm). **i** *Gyraulus applanatus*, umbilical view (LfU-SPR2014-036; Offingen, OBM, Kirchberg Fm.; $D = 2.4$ mm). **j** *Planorbarius mantelli*, apical view (LfU-SPR2014-039; Offingen, OBM, Kirchberg Fm.; $D = 2.6$ mm). **k** *Carychium* cf. *galli*, apertural view (LfU-SPR2014-022; Buttenwiesen, OBM, Grimmelfingen Fm.; $H = 1.7$ mm). **l** *Archaeozonites* sp., apical view (LfU-SPR2014-006; Offingen, OBM, Kirchberg Fm.; $D = 6.1$ mm). **m–o** *Megalotachea* cf. *silvana*, in apertural, apical and umbilical view, respectively (LfU-SPR2014-011; Glött, OSM; $H = 14.9$ mm, $D = 23.4$ mm). **p–r** *Palaeotachea* sp., in apertural, apical and umbilical view, respectively (LfU-SPR2014-010; Dillingen, USM; $H = 8.6$ mm, $D = 14.8$ mm). **s** *Leucochroopsis* sp., apical view (LfU-SPR2014-024; Buttenwiesen, OBM, Grimmelfingen Fm.; $D = 4.3$ mm). **t, u** ?*Discus* sp., in apertural and apical view, respectively (LfU-SPR2014-023; Gundremmingen, USM; $H = 0.9$ mm, $D = 1.5$ mm)

*Occurrence* OBM (Grimmelfingen Fm.): Buttenwiesen, Günzburg. OBM (Kirchberg Fm.): Buttenwiesen, Dillingen, Druisheim, Gempfing, Glött, Günzburg, Hamlar 1, Holzheim, Lauingen, Offingen. OSM: Buttenwiesen, Gempfing, Glött, Gundremmingen.

*Description* Shell small, conical-elongated. Protoconch (~1 whorl) prominent, rounded, dome-shaped, smooth; transition to teleoconch clearly marked. Teleoconch smooth, except for growth lines. Whorl profile convex. Suture deep. Aperture ellipsoid. Peristome complete, slightly thickened. Umbilicus narrow, shallow.

*Remarks* Several species of *Nematurella* have been described from the OBM of the Kirchberg Basin and the neighboring Oncophora Basin (e.g., Schlickum 1960; Schlickum and Strauch 1967; Kowalke and Reichenbacher 2005). The first one to be described was *N. bavarica*, from the lowermost OSM of Günzburg, with no figure and just a very brief description (Sandberger 1875). Analyzing what is possibly original material from Sandberger, Schlickum (1961) synonymized one of his species, *N. schuetti*, with *N. bavarica*. The figured type material of these many species seem to be often indistinguishable from one another (e.g., Schlickum 1960) and are usually what would be perceived as a continuum of variation of a single species. Hydrobiids are remarkable in intraspecific conchological variability,



both hereditary and ecophenotypic (e.g., Dillon 2000; Haase 2003; Vuolo et al. 2011).

This continuum of variation in shell shape is exactly what is seen in the present material (Fig. 4m–r): the specimens are all within a reasonable shell height range of 3.6–4.3 mm (the protoconch of the *Nematurella* "species" are also within a narrow and overlapping range; see Kowalke and Reichenbacher 2005) and range from slender to broad spires, from 4 to 5 whorls, from a deep suture (and, thus, more convex whorls) to a shallower suture (and more flattened whorls), etc. All these extremes, of course, are accompanied by a series of intermediate forms in all the stratigraphical units where they occur. For example, the specimens of Fig. 4n would represent what is commonly identified as *N. zilchi* Schlickum, 1960 in the literature, while those of Fig. 4q, r would be *N. convexula* Schlickum and Strauch 1967; finally, those of Fig. 4o, p are clear intermediates that could be identified as either *N. zilchi* or *N. convexula*. The broader shell of Fig. 4m is what corresponds to typical *N. bavarica*. A future (and sorely needed) revision of this species complex should take into account this variability and intermediate forms, besides conducting a thorough analysis of the type material.

Moreover, shell growth after breakage or abnormal growth on the body whorl are rather commonly found in the material and are responsible for alterations in overall shell shape and proportions (for instance, fewer whorls, a more truncated body whorl or a slightly detached aperture); these changed features seem to have been sometimes used for the diagnosis of new species of *Nematurella* (e.g., Schlickum 1960).

*Trace fossils* Some specimens of *N. bavarica* (e.g., Fig. 4s) and a single specimen of *Stagnicola armaniacensis* (Noulet, 1857), described further below, show a circular hole on their body whorls (a single specimen of *N. bavarica* shows two neighboring holes). These holes are the same as those reported by Rasser and Covich (2014) for the freshwater snails from Steinheim (Middle Miocene, SW Germany), related to predation by *Tinca* Cuvier, 1817 (Actinopterygii: Cyprinidae). The teeth of *Tinca* sp. described from the Kirchberg Fm. (Reichenbacher 1988: pl. 1, figs. 10–11) actually belong to another cyprinid, *Palaeocarassius* Obrhelová, 1970 (see Böhme 2010: Fig. 5a–c), but others cyprinids present in the Kirchberg Fm. (Reichenbacher 1988; Reichenbacher et al. 2004; Schulz-Mirbach and Reichenbacher 2006) could be responsible for these marks. These ichnofossils are studied in more detail by Rasser et al. (in press).

Family **Truncatellidae** Gray 1840
Genus ***Truncatella*** Risso, 1826
**?*Truncatella* sp.**
Figure 4t.

*Occurrence* OBM (Kirchberg Fm.): Hamlar 1.

*Description* Shell conical-elongated, with 4 whorls; imperforate; regularly and slowly growing first whorls; body whorl expanded. Protoconch large, rounded, dome-shaped. Shell sculpture cannot be observed due to poor preservation. Whorls profile slightly convex. Suture well-marked but not incised. Aperture oval, elongated diagonally. Peristome complete.

*Remarks* The single, poorly preserved, juvenile specimen can be distinguished from all the other species described herein by its large and dome-shaped protoconch and its pattern of growth, with the first whorls regularly growing and slowly increasing in width and an expanded body whorl. This specimen is very reminiscent of the genus *Truncatella*. However, its spire is slightly more conical than usual for the genus, though this could be due to the specimen being sub-adult. A more precise identification is not possible at present. Few fossil *Truncatella* species are known from western and central Europe, but the genus has records from the Paleocene to the Pliocene (Wenz 1928; Glibert 1973; Lozouet et al. 2001).

Superfamily **Viviparoidea** Gray, 1847

Family **Viviparidae** Gray, 1847
Genus ***Viviparus*** Montfort, 1810
***Viviparus* cf. *suevicus*** Wenz, 1919
Figure 4u, v

*Occurrence* OBM (Kirchberg Fm.): Druisheim.

*Remarks* Despite the poor preservation, the present specimens can be assigned to the genus *Viviparus* based on their size, the very characteristic shape of the first whorls and teleoconch sculpture pattern. *Viviparus suevicus* is the only species of the genus recorded so far from the Kirchberg Fm. (which is also its type stratum; type locality: Kirchberg an der Iller; Krauss 1852; holotype: SMNS 106437).

**Heterobranchia** Gray 1840
Superfamily **Valvatoidea** Gray 1840
Family **Valvatidae** Gray 1840
Genus ***Valvata*** Müller, 1773
**?*Valvata* sp**
Figures 4w, 5a

*Occurrence* OBM (Kirchberg Fm.): Druisheim, Offingen.

*Remarks* The overall shell shape (depressed trochiform, with round whorls rapidly growing in size, circular aperture and narrow umbilicus) and protoconch size and rounded shape seem consistent with the genus *Valvata*. The poor preservation prevents the observation of the protoconch sculpture, which is very characteristic for the genus (Binder 1967; Riedel 1993), precluding a more definitive generic assignment.

**Pulmonata** Cuvier, 1814.
**Basommatophora** Keferstein in Bronn, 1864
Superfamily **Lymnaeoidea** Rafinesque, 1815
Family **Lymnaeidae** Rafinesque, 1815
Genus ***Stagnicola*** Jeffreys, 1830
***Stagnicola armaniacensis*** (Noulet, 1857)
Figure 5b.

*1852 *Limnaea armaniacensis* Noulet: p. 22.
1923 *Galba (Galba) armaniacensis armaniacensis* – Wenz: p. 1351.
1964 *Stagnicola (Stagnicola) armaniacensis* – Schlickum: p. 13, pl. 2, fig. 31.
1989 *Stagnicola armaniacensis* – Reichenbacher: p. 174, pl. 2, fig. 7.
1993 *Stagnicola armaniacensis* – Reichenbacher: Tables 7, 11–13.
2005 *Stagnicola armaniacensis* – Kowalke and Reichenbacher: p. 631, figs. 9.6–9.7.
2014 *Stagnicola armaniacensis* – Harzhauser et al.: 11, pl. 2, figs. 4–11.
2014 *Stagnicola armaniacensis* – Neubauer et al.: supplementary material 1.

*Occurrence* USM: Gundremmingen, Offingen. OBM (Grimmelfingen Fm.): Buttenwiesen, Günzburg, Offingen. OBM (Kirchberg Fm.): Buttenwiesen, Dillingen, Glött, Günzburg, Holzheim, Lauingen, Offingen. OSM: Gempfing, Gundremmingen, Holzheim, Offingen.

*Remarks* The small and wide lymnaeid shells, with few quickly growing whorls, a deep suture and an elongated oval aperture, can be identified as *S. armaniacensis*. This species was originally described from the Middle Miocene (late Burdigalian/Langhian) of France and is very common in coeval deposits of Central Europe (Harzhauser et al. 2014).

***Stagnicola praebouilleti*** Schlickum, 1970a, b, c, d
Figure 5c

1964 *Stagnicola (Stagnicola?) bouilleti* – Schlickum: p. 14, pl. 2, fig. 32 [non Michaud].
*1970d *Stagnicola praebouilleti* Schlickum: p. 92, figs. 12–17.
1973 *Stagnicola (Stagnicola) praebouilleti* – Steininger et al.: p. 451, pl. 9, fig. 10.
1993 *Stagnicola praebouilleti* – Reichenbacher: Table 13.
2005 *Stagnicola praebouilleti* – Kowalke and Reichenbacher: p. 631, figs. 9.8–9.9.
2014 *Stagnicola praebouilleti* – Neubauer et al. 2014: supplementary material 1.

*Occurrence* OBM (Grimmelfingen Fm.): Buttenwiesen. OBM (Kirchberg Fm.): Buttenwiesen.

*Remarks* The forms known as *S. praebouilleti*, originally described from the Bavarian "Oncophora Beds" (now "Rzehakia Beds", OBM), can be distinguished from *S. armaniacensis* by its slender shell and taller spire, deeper suture and by usually having at least one additional half whorl.

Genus ***Lymnaea*** Lamarck, 1799
***Lymnaea dilatata*** (Noulet, 1854)
Figure 5d.

*1854 *Limnea dilatata* Noulet: p. 107.
2000 *Lymnaea dilatata* – Fischer: p. 136, figs. 1–2.
2002 *Lymnaea dilatata* – Binder: p. 165, pl. 1, fig. 7a.
2004 *Lymnaea dilatata* – Binder: p. 192, pl. 1, fig. 7.
2005 *Lymnaea dilatata* – Kowalke and Reichenbacher: p. 630, figs. 9.4–9.5.
2014 *Lymnaea dilatata* – Salvador and Rasser: p. 189, figs. 8–9.
2014 *Radix dilatata* – Neubauer et al.: supplementary material 1.

*Occurrence* USM: Gundremmingen, Offingen. OBM (Grimmelfingen Fm.): Buttenwiesen. OBM (Kirchberg Fm.): Buttenwiesen, Glött, Hamlar 1, Holzheim, Lauingen, Offingen. OSM: Gempfing, Offingen.

*Remarks* Although only shell apexes remain, the specimens can be confidently assigned to *Lymnaea dilatata*. This species is diagnosed by its large size, its overall acuminated (although rather blunt on its very top) and proportionately short spire and the rapidly growing whorls. Originally described from Sansan (MN 6, France; see Fischer 2000), *L. dilatata* is known from the whole Middle Miocene of West and Central Europe (Binder 2004).

Some (if not all) specimens previously described from the Kirchberg Fm. and overlying OSM as *Radix socialis dilatata* by Schlickum (1964, 1966) and Reichenbacher (1989, 1993) probably belong to *Radix socialis* (von Zieten, 1830), identifiable by its diagnostic proportionally very minute spire (when compared to the large body whorl; e.g., Salvador and Rasser 2014).

Superfamily **Planorboidea** Rafinesque, 1815
Family **Planorbidae** Rafinesque, 1815
Genus ***Ferrissia*** Walker, 1903
***Ferrissia* cf. *wittmanni*** (Schlickum, 1964)
Figure 5e

*Occurrence* OBM (Grimmelfingen Fm.): Buttenwiesen. OBM (Kirchberg Fm.): Buttenwiesen, Günzburg, Lauingen, Offingen.

*Remarks* These cap-shaped and elliptical shells, with a longitudinally central apex, compare well to *F. wittmanni*, a species originally described as *Ancylus wittmanni* from the uppermost "Rzehakia Beds" (previously known as "Oncophora Beds"; see also Kowalke and Reichenbacher 2005: p. 631, figs. 9.10–9.12). The species is well known from the Kirchberg Fm. (Schlickum 1966; Reichenbacher 1989, 1993) and its stratigraphic equivalents in upper Bavaria (Schlickum 1970a, b, c, d). Furthermore, *F. wittmanni* occurs in the middle Miocene (Sarmatian) of Austria and Hungary (Harzhauser and Kowalke 2002). Nevertheless, the typical axial sculpture (Kowalke and Reichenbacher 2005) could not be observed in the present specimens, preventing a more definitive identification.

Genus **Gyraulus** Charpentier, 1837
***Gyraulus albertanus*** (Clessin, 1877)
Figure 5f, g

*1877 *Planorbis albertanus* Clessin: p. 40.
1923 *Gyraulus (Gyraulus) albertanus* – Wenz: p. 1541.
1972 *Gyraulus (Gyraulus) albertanus* – Gall: 16.
2004 *Gyraulus* sp. B – Reichenbacher et al.: p. 76, pl. 1, fig. 6.
2009 *Menetus* (*Dilatata*) *albertanus* – Moser et al.: p. 46.
2014 *Gyraulus albertanus* – Neubauer et al.: supplementary material 1.
2014 *Gyraulus albertanus* – Salvador and Rasser: p. 191, figs. 12–15.

*Occurrence* OBM (Grimmelfingen Fm.): Offingen. OBM (Kirchberg Fm.): Holzheim, Offingen. OSM: Offingen.

*Remarks* This species is distinguished from its coeval congeners by its slightly larger size, more rounded shell profile, quickly growing whorls and large round aperture. It was originally described from Undorf (MN 5, SE Germany; Clessin 1877) and is additionally known from Adelschlag (MN 5, SE Germany; Reichenbacher et al. 2004, as *Gyraulus* sp.) and several other OSM localities (Salvador and Rasser 2014). To our knowledge, this is the first record of *G. albertanus* for the Grimmelfingen and Kirchberg Formations and thus, the earliest for the species.

***Gyraulus applanatus*** (Thomä, 1845)
Figure 5h, i

*1845 *Planorbis applanatus* Thomä: p. 150.
*1851 *Planorbis dealbatus* Braun: p. 1134.
1923 *Gyraulus (Gyraulus) trochiformis applanatus* – Wenz: p. 1579.
1923 *Gyraulus (Gyraulus) trochiformis dealbatus* – Wenz: p. 1591.
1964 *Gyraulus trochiformis dealbatus* – Schlickum: p. 15, pl. 2, fig. 35.
1970a *Gyraulus trochiformis applanatus* – Schlickum: p. 148, pl. 10, fig. 6.
1970c *Gyraulus trochiformis applanatus* – Schlickum: p. 180.
1973 *Gyraulus trochiformis dealbatus* – Steininger et al.: p. 451, pl. 9, fig. 11a–b.
1989 *Gyraulus trochiformis dealbatus* – Reichenbacher: p. 172, pl. 1, fig. 11.
1993 *Gyraulus trochiformis dealbatus* – Reichenbacher: Tables 6–7, 13.
1995 *Gyraulus dealbatus* – Kadolsky: p. 40, fig. 47.
2004 *Gyraulus dealbatus* – Binder: p. 193, pl. 2, figs. 1a–c.
2004 *Gyraulus* sp. A – Reichenbacher et al.: p. 76, pl. 1, figs. 4–5.
2004 *Gyraulus* sp. C – Reichenbacher et al.: p. 76, pl. 1, fig. 7.
2005 *Gyraulus applanatus* – Kowalke and Reichenbacher: p. 631, figs. 9.1–9.3.
2006 *Gyraulus applanatus* – Kókay: p. 56, pl. 19, Figs. 13–14.
2006 *Gyraulus trochiformis dealbatus* – Kókay: p. 57, pl. 19, fig. 15.
2014 *Gyraulus applanatus* – Neubauer et al.: supplementary material 1.
2014 *Gyraulus dealbatus* – Neubauer et al.: supplementary material 1.
2014 *Gyraulus dealbatus* – Salvador and Rasser: p. 192, figs. 16–23.

*Occurrence* USM: Gundremmingen, Offingen. OBM (Grimmelfingen Fm.): Buttenwiesen, Offingen. OBM (Kirchberg Fm.): Buttenwiesen, Dillingen, Druisheim, Glött, Günzburg, Hamlar 1, Holzheim, Lauingen, Offingen. OSM: Gempfing, Glött.

*Remarks* The present specimens show the common conchological variation reported for *G. applanatus* in several German sites, including the Kirchberg Fm. and OSM (Gottschick and Wenz 1916; Kowalke and Reichenbacher 2005; Salvador and Rasser 2014): two extremes, the typical *G. applanatus* and the typical *G. dealbatus*, with numerous intermediate forms. The typical *G. applanatus* has a flattened shell, regularly growing whorls, more closely packed together, with a well-marked angulation on the laterobasal portion of the body whorl, and a smaller aperture, shaped as an arrowhead. The other extreme, commonly called *G. dealbatus* in the literature, has a more rounded shell profile, with rapidly growing whorls, a faint angulation on its median portion and a larger aperture. This variation, linked by numerous intermediate forms, led Kowalke and Reichenbacher (2005) to synonymize the two species, a decision which is followed here.

Genus **Planorbarius** Duméril, 1806
***Planorbarius mantelli*** (Dunker, 1848)
Figure 5j.

*1848 *Planorbis Mantelli* Dunker: p. 159, pl. 21, figs. 27–29.
1966 *Planorbarius cornu* – Schlickum: p. 326, pl. 13, fig. 27.
1970a *Planorbarius cornu* – Schlickum: p. 149, pl. 10, fig. 7.
1989 *Planorbarius cornu* – Reichenbacher: p. 172, pl. 1, Fig. 10.
1993 *Planorbarius cornu* – Reichenbacher: Tables 6–7, 13.

2004 *Planorbarius cornu* – Binder: p. 193, pl. 2, figs. 2–3.
2004 *Planorbarius* sp. – Reichenbacher et al.: p. 76, pl. 1, figs. 1–3.
2006 *Planorbarius cornu cornu* – Kókay: p. 58, pl. 20, fig. 6.
2009 *Planorbarius cornu cornu* – Böttcher et al.: p. 239, figs. 2.4–2.6.
2014 *Planorbarius mantelli* – Harzhauser et al.: p. 15, pl. 3, figs. 5, 7–13, 15–16.
2014 *Planorbarius mantelli* – Neubauer et al., 2014: supplementary material 1.
2014 *Planorbarius cornu* – Salvador and Rasser: p. 193, figs. 26–28.

*Occurrence* USM: Gundremmingen. OBM (Grimmelfingen Fm.): Buttenwiesen. OBM (Kirchberg Fm.): Buttenwiesen, Dillingen, Druisheim, Glött, Günzburg, Holzheim, Lauingen, Offingen. OSM: Buttenwiesen, Dillingen, Holzheim, Offingen.

*Remarks* Only the first whorls and fragments of later whorls are preserved. The shell size, shape and unique sculpture (protoconch of ca. 1 whorl sculptured by spiral lines of regularly organized circular pits, transitioning abruptly to a teleoconch sculptured by spiral striae on first ca. 1½ whorl and smooth on the rest, except for growth lines) enable the identification as *P. mantelli*. This species is known from the late Early Miocene to the Late Miocene of Central Europe (Harzhauser et al. 2014). Specimens of *P. mantelli* from these localities and ages are usually referred to as *P. cornu* (Brongniart, 1810), a form from the Late Oligocene to Early Miocene. These hard to diagnose species are part of a complex that is in urgent need of revision.

**Eupulmonata** Haszprunar and Huber, 1990
Superfamily **Ellobioidea** Pfeiffer, 1854
Family **Carychiidae** Jeffreys, 1830
Genus ***Carychium*** O.F. Müller, 1773
***Carychium* cf. *galli*** Salvador, 2015
Figure 5k.

*Occurrence* OBM (Grimmelfingen Fm.): Buttenwiesen.

*Remarks* The single specimen available shows a minute pupiform to fusiform shell, with a slightly acuminated spire (but with blunt apex) and its greatest width on the body whorl. The dome-shaped protoconch (ca. 1½ whorl) transitions abruptly to a teleoconch sculptured by fine prosocline axial riblets. The trapezoid aperture has a faint parietal callus, a strong oblique columellar lamella, a narrow parietal lamella and a very faint median palatal tooth.

The present specimen compares well to the overall morphology of *C. galli*, a species described from the OSM site of Sandelzhausen (SE Germany; Salvador, 2015) and also known from the MN 5 locality of Riedensheim (Salvador et al. unpublished data). The present specimen has weaker apertural barriers (especially the palatal tooth) when compared to *C. galli*, but intraspecific variation in such features is well known in the genus (Strauch 1977; Stworzewicz 1999). The most characteristic feature of this species is the simple internal lamella (Salvador 2015). Nevertheless, to observe this feature, the specimen would have to be broken, which we opted not to do.

The externally similar species *C. nouleti* Bourguignat, 1857 (and its likely synonym *C. gibbum* Sandberger, 1875; Strauch 1977; Harzhauser et al. 2014) differs from *C. galli* mainly by having a sinuous internal lamella (Salvador 2015). Other useful diagnostic characters of *C. galli* are usually a more slender and smaller shell, a more defined and spaced axial sculpture and a more angular shape of the peristome (Salvador 2015).

If the present identification is later confirmed, this would be the earliest known record of *C. galli*. Furthermore, previous reports of *C. nouleti* from the uppermost parts of the Kirchberg Fm. and "Rzehakia Beds" (previously known as "Oncophora Beds"; Schlickum 1964, 1966) could actually represent *C. galli*.

**Stylommatophora** A. Schmidt, 1855
Superfamily **Zonitoidea** Mörch, 1864
Family **Zonitidae** Mörch, 1864
Genus ***Archaeozonites*** Sandberger, 1872
***Archaeozonites* sp.**
Figure 5l

*Occurrence* OBM (Grimmelfingen Fm.): Buttenwiesen. OBM (Kirchberg Fm.): Offingen.

*Remarks* Only fragmentary shell apexes remain, but the combination of its helicoid-like size and shape, flattened first whorls and the characteristic teleoconch sculpture (well-marked prosocline ribs) allows for the identification as *Archaeozonites*, a common member of land snail assemblages in the Central European Oligocene and Miocene (e.g., Kadolsky 2008b; Salvador and Rasser 2014).

Superfamily **Helicoidea** Rafinesque, 1815
Family **Helicidae** Rafinesque, 1815
Genus ***Megalotachea*** Pfeffer, 1930
***Megalotachea* cf. *silvana*** (Klein, 1853)
Figure 5m–o

*Occurrence* OBM (Grimmelfingen Fm.): Buttenwiesen. OBM (Kirchberg Fm.): Glött, Holzheim, Lauingen, Offingen. OSM: Dillingen, Gempfing, Glött, Holzheim, Offingen.

*Remarks* The specimens from the OSM layers are very reminiscent of *M. silvana*, a common species from the

Silvana beds (previously classified in the genus *Cepaea* Held, 1838; e.g., Schlickum 1976; Reichenbacher 1989). Nevertheless, due to their larger size and deformation due to sub-optimal preservation, we prefer here a more cautious classification. Moreover, the specimens from the OBM layers comprise fragmentary early whorls and may belong to another species.

Vestiges of a color pattern can be seen under UV light, consisting of three spiral bands on the whorl surface above the faint angulation and two additional spiral bands below it.

Genus ***Palaeotachea*** Jooss, 1912
***Palaeotachea* sp**
Figure 5p–r

*Occurrence* USM: Dillingen, Gundremmingen, Offingen.

*Remarks* Due to the poor preservation of the present specimens, they cannot be identified beyond genus level. These specimens, all from the USM, are much smaller than the *M.* cf. *silvana* found in the OSM layers. They also apparently have a proportionately much smaller aperture and a greater constriction in the body whorl immediately preceding the aperture. By the shells' size and overall shape, as well as the age of the sediments, the present specimens likely belong to *P. subsulcosa* (Thomä, 1845).

Family **Hygromiidae** Tryon, 1866
Genus ***Leucochroopsis*** Boettger, 1909
***Leucochroopsis* sp.**
Figure 5s.

*Occurrence* OBM (Grimmelfingen Fm.): Buttenwiesen. OBM (Kirchberg Fm.): Offingen.

*Remarks* The material can be identified as *Leucochroopsis* by its size, depressed spire, whorls regularly increasing in size and characteristic sculpture: protoconch (ca. 1¼ whorl) sculptured by fine parallel striae, transitioning abruptly to a teleoconch sculptured by fine, regularly distributed, well-marked papillae, which, together with the growth lines, give the impression of prosocline axial striae. Identification beyond genus level is not possible, but there are records of *L. francofurtana* (Wenz, 1919) for the OBM (Schlickum 1964; Reichenbacher 1989).

Superfamily **Punctoidea** Morse, 1864
Family **Discidae** Thiele, 1931
Genus ***Discus*** Fitzinger, 1833
**?*Discus* sp**
Figure 5t, u

*Occurrence* USM: Gundremmingen.

*Remarks* The small size and overall shape of the shell (discoid, with low spire, whorls regularly growing, and wide umbilicus) seem to point to the genus *Discus*, well-known from the German Miocene. Unfortunately, the poor preservation prevents a precise identification, since the characteristic sculpture pattern was not preserved. The present specimen could represent *Discus pleuradrus* (Bourguignat, 1881), originally described from Sansan (MN 6; France), but known from the entire Miocene of Central and Western Europe (Böttcher et al. 2009). However, as pointed out by previous authors, early and late Miocene records could represent different species and, thus, *D. pleuradrus* would be restricted to the middle Miocene (Moser et al. 2009; Harzhauser et al. 2014).

## Discussion

Continental mollusks, especially land snails, often show on the generic level preference for one type of habitat (Barker 2001; Cook 2001; Pearce and Örstan 2006). Therefore, ecological data from recent genera are often used as a guide for paleoecological inferences of congeneric fossil species (e.g., Albesa et al. 1997; Moser et al. 2009). Below, we present an analysis regarding each major stratigraphical unit; Table 1 lists the occurrence of each species in these units. Since the sites are all close to each other (Fig. 1), they are treated together; nevertheless, some localities (or group of localities) receive further comments separately when appropriate.

*USM* The molluscan fauna recovered from the USM layers is rather poor, which could be a reflection of the low amounts of fossil-bearing samples available. As expected, it is composed mainly of freshwater snails (Table 1). The habitats preferred by their living congeners are richly vegetated standing or slowly flowing waters, sometimes even temporary water bodies (Welter-Schultes 2012). The land snails recovered are ?*Discus* sp., whose rather uncertain identity precludes the use in a paleoenvironmental analysis, and *Palaeotachea* sp., which should thrive in a rather broad range of habitats (hot humid temperate to sub-tropical, in reasonably well-vegetated areas).

Only a few previous studies have dealt with the paleoecological interpretation of the USM (e.g., Reichenbacher and Weidmann 1992; Reichenbacher 1996; Schäfer 2005, 2011; Weidmann et al. 2014). All these studies were based on fossil assemblages found in the westernmost Molasse Basin, i.e., in western Switzerland and Haute Savoie, and gastropods have not been considered. However, the suggestion of heterogenous lacustrine and terrestrial habitats with some periods of drought from time to time indicated by the above-mentioned studies (based on charophytes, ostracods, fish otoliths and mammal remains) fits with the interpretation presented here based on the gastropods.

**Table 1** List of all species found in the present material and their general stratigraphical occurrence (considering all localities together)

| Species | OSM | OBM | | | USM |
|---|---|---|---|---|---|
| | | uKF | lKF | GF | |
| Neritimorpha | | | | | |
| *Theodoxus cyrtocelis* | X | X | X | X | X |
| *Theodoxus obtusangula* | | | X | | |
| Caenogastropoda | | | | | |
| *Melanopsis impressa* | | X | X | | |
| *Tinnyea lauraea* | | X | X | | |
| *Bithynia glabra* | X | X | X | X | X |
| *Ctyrokya conoidea* | ? | X | X | | |
| *Hydrobia semiconvexa* | | X | X | | |
| *Nematurella bavarica* | ? | X | X | X | |
| ?*Truncatella* sp. | | | X | | |
| *Viviparus* cf. *suevicus* | | | X | | |
| Heterobranchia | | | | | |
| ?*Valvata* sp. | | X | X | | |
| Pulmonata | | | | | |
| *Stagnicola armaniacensis* | X | X | X | X | X |
| *Stagnicola praebouilleti* | | X | | X | |
| *Lymnaea dilatata* | X | X | | X | X |
| *Ferrissia* cf. *wittmanni* | | X | | X | |
| *Gyraulus albertanus* | X | X | | X | |
| *Gyraulus applanatus* | X | X | X | X | X |
| *Planorbarius mantelli* | X | X | X | X | X |
| *Carychium* cf. *galli* | | | | X | |
| *Archaeozonites* sp. | | X | | | |
| *Megalotachea* cf. *silvana* | X | X | | X | |
| *Palaeotachea* sp. | | | | | X |
| *Leucochroopsis* sp. | | X | | | |
| ?*Discus* sp. | | | | X | X |

The presence of *Nematurella bavarica* and *Ctyrokya conoidea* in the OSM is interpreted as reworked material from older OBM layers (see "Discussion")

*GF* Grimmelfingen Formation, *lKF* lower Kirchberg Formation; *OBM* Upper Brackish Molasse, *OSM* Upper Freshwater Molasse; uKF upper Kirchberg Formation, *USM* Lower Freshwater Molasse

*OBM (Grimmelfingen Fm.)* These beds have fauna more typical of freshwater environments, as indicated by the richness and abundance of freshwater species: *Bithynia, Theodoxus* and the basommatophoran pulmonates (Table 1; despite being preferentially freshwater species, some recent congeners of the operculate snails can withstand slightly brackish waters). The hydrobiids, despite being considered more typical brackish water snails (especially the genus *Nematurella*), are also commonly found in fully freshwater environments (e.g., Welter-Schultes 2012). Kadolsky (2008a) even raised the possibility that some Miocene hydrobiids could actually belong to the conchological identical genus *Heleobia* Stimpson, 1865 (family Cochliopidae Tryon, 1866), which is more typically found in freshwater (although also occurring in brackish environments).

Almost all previous reports on the paleoenvironment of the Grimmelfingen Fm. refer to marine or brackish faunal elements found in the base of this formation (Reichenbacher et al. 1998, 2013; Sach and Heizmann 2001). Only *Viviparus* and the bivalve *Rzehakia* Korobkov, 1954 have already been reported from the upper parts of the Grimmelfingen Fm. (Reichenbacher 1989, 1993). The freshwater and terrestrial gastropod species described here are, thus, the first record for the Grimmelfingen Fm. The gastropods indicate that the environment may have been much less brackish and estuarine than previously thought. The environment of these layers could be freshwater or of very low salinity levels.

On land, the presence of the hygrophilous land snail *Carychium* is a fair indicative of humid and usually well-vegetated areas near a water body (Welter-Schultes 2012). A single specimen of *Carychium* cf. *galli* was found in Buttenwiesen, but the fragile and diminutive shells of the genus makes preservation and/or recovery difficult (and this locality is the one with the better-preserved specimens). *Archaeozonites* and *Leucochroopsis* are also considered indicatives of humid forests (Lueger 1981).

*OBM (lower Kirchberg Fm.)* The molluscan fauna of the lower Kirchberg Fm. is very different to that of the Grimmelfingen Fm., likely indicating changes in the environmental conditions. These beds "lose" much of their pulmonate aquatic fauna and show the richest operculate snail fauna (i.e., non-pulmonates) of all layers studied here (Table 1).

*Theodoxus* (which occurs in considerable numbers in the Kirchberg Fm.) and *Viviparus* are typical of freshwater environments, although a few recent species can also be found in low salinity waters (Bandel, 2001; Glöer and Meier-Brook 2003; Zettler et al. 2004; Bunje 2005; Welter-Schultes 2012). *Tinnyea lauraea* have been found in both freshwater and oligohaline sediments (Kadolsky 1995; Kowalke 2004; Kókay 2006). The more typical brackish fauna of the lower Kirchberg Fm. includes the hydrobiids (although with reservations, as explained above), possibly ?*Truncatella* sp. and several brackish water bivalves (not studied here, but known from previous reports, e.g., Schlickum 1963; Reichenbacher 1989).

The environment of the lower Kirchberg Fm. is thus interpreted as low brackish to brackish (with a salinity level still allowing the scarce pulmonates, *Bithynia*, *Theodoxus*, *Viviparus* and ?*Valvata* to thrive). This assumption is consistent with the suggestion of a brackish environment based on the fish fauna (Reichenbacher 1993).

*Melanopsis impressa*, in particular, is an index for strong fluvial influx (Harzhauser and Kowalke 2001). The fragmented nature of the shells of *M. impressa* from Agapi (early Miocene, Greece) was deemed by Harzhauser and Kowalke (2001) as a sign that the sedimentation area was far from the more energetic environments where the species usually occurs. This is similar to what is seen in the present specimens, although breakage could have happened during sample processing.

A single specimen of ?*Truncatella* sp. was found in the locality "Hamlar 1". The recent *Truncatella subcylindrica* (Linnaeus, 1767) lives in the marine supralittoral, usually out of the water on algae or burrowed in the sand and it can survive through long periods of submersion (Welter-Schultes 2012). Since only a single specimen of dubious identification was found, its use in a paleoecological analysis must remain tentative. Its poor preservation could indicate that it was carried from the littoral by some currents. Nevertheless, a unique occurrence of a foraminifera layer intercalated into the "regular" Kirchberg Fm. (Reichenbacher et al. 2013: Fig. 5) was found in the locality "Hamlar 1", which could indicate a rapid small-scale transgression. Another (less likely) possibility is that this ?*Truncatella* sp. could respresent a fully terrestrial species, a trait known to have evolved repeatedly in *Truncatella* and other truncatellids (Rosenberg 1996).

*OBM (upper Kirchberg Fm.)* Overall, the layers of the upper Kirchberg Fm. have a fauna of operculate snails similar to the lower levels, but, at the same time, have a more diverse basommatophoran fauna. As in the Grimmelfingen Fm., this should indicate a fully or nearly freshwater environment. A similar assumption has previously been presented based on the microfossil assemblages and especially the fish otoliths, which were found to be indicative for a mesohaline to oligohaline environment in the upper Kirchberg Fm. (Reichenbacher 1989, 1993). The presence of the land snails *Archaeozonites* and *Leucochroopsis* would again indicate humid forests in the surrounding area.

The freshwater snails of the northeasternmost boreholes (Druisheim, Gempfing and Hamlar 1; Fig. 1) seem to present a different composition than the other localities. In the lower Kirchberg Fm., the faunas are very similar (Table 2), except for the occurrence of two additional species in the NE localities that are more commonly related to freshwater: ?*Valvata* sp. and *Viviparus* cf. *suevicus*. In the upper Kirchberg Fm., however, the NE localities show a much less diverse typical freshwater fauna, with only two pulmonates recorded (Table 2). The other localities have records of seven pulmonate species and also ?*Valvata* sp. As such, it is plausible that the SW localities possessed fully or nearly freshwater environments, probably due to local fluvial influx, while the NE localities would have retained slightly more brackish environments (similar to the lower Kirchberg Fm.).

**Table 2** List of the freshwater species found in the northeastern localities (NE; Druisheim, Gempfing and Hamlar 1; see also Fig. 1) and the remaining southwestern localities (SW)

| Species | SW | | NE | |
|---|---|---|---|---|
| | uKF | lKF | uKF | lKF |
| *Theodoxus cyrtocelis* | X | X | X | X |
| *Theodoxus obtusangula* | | X | | |
| *Melanopsis impressa* | X | X | X | X |
| *Tinnyea lauraea* | | X | X | X |
| *Bithynia glabra* | X | X | X | X |
| *Ctyrokya conoidea* | X | X | X | X |
| *Hydrobia semiconvexa* | X | | | X |
| *Nematurella bavarica* | X | X | X | X |
| ?*Truncatella* sp. | | | | X |
| *Viviparus* cf. *suevicus* | | | | X |
| ?*Valvata* sp. | X | | | X |
| *Stagnicola armaniacensis* | X | X | | |
| *Stagnicola praebouilleti* | X | | | |
| *Lymnaea dilatata* | X | | X | |
| *Ferrissia* cf. *wittmanni* | X | | | |
| *Gyraulus albertanus* | X | | | |
| *Gyraulus applanatus* | X | X | X | X |
| *Planorbarius mantelli* | X | X | | X |

lKF *lower Kirchberg Formation*, uKF upper Kirchberg Formation

Finally, one unusual occurrence noted in the present material is the record of *Ctyrokya conoidea* for the upper Kirchberg Fm. of some localities (see Online Supplementary Appendix 1), since previous reports restrict this species to the lower Kirchberg Fm. (e.g., Schlickum 1966; Reichenbacher 1989). This means that *C. conoidea* survived the transition in some localities. In Offingen, the species is only recorded from the most basal layers of the upper Kirchberg Fm. and, thus, managed to survive only for a brief time. However, in other localities such as Buttenwiesen, *C. conoidea* thrived for longer, disappearing only towards the end of the Kirchberg Fm.

*OSM* In the OSM layers, most of the operculate snails disappear from the record, causing the diversity of aquatic species to greatly decrease. This is consistent with other faunas from German localities (e.g., Salvador and Rasser 2014), which can be very abundant in sheer number of freshwater specimens, but rather poor in richness of freshwater species (composed mainly of pulmonates). The same pattern is seen in the otolith-based fish fauna from the lowermost OSM: few freshwater and/or euryhaline species are present, often represented by numerous specimens (e.g., Reichenbacher et al. 2004; Reichenbacher and Prieto 2006).

As in the USM, discussed above, most of the species present in the OSM prefer richly vegetated standing or slow-moving waters. The possibly brackish water species *Nematurella bavarica* and *Ctyrokya conoidea* recorded from basal layers of some OSM localities (see Online Supplementary Appendix 1) very likely represent reworked material from older OBM layers.

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**Article**

# New gastropod assemblages from the Early/Middle Miocene of Riedensheim and Adelschlag-Fasanerie, southern Germany

**Rodrigo B. Salvador, Jérôme Prieto, Christoph Mayr and Michael W. Rasser**

With 4 figures, 1 table and 2 appendices

**Abstract:** This work presents a taxonomic study and paleoecological reconstructions of the continental gastropod assemblages from two new Miocene localities in the German part of the North Alpine Foreland Basin, Bavaria. Riedensheim (next to the town of Rennertshofen) and Fasanerie (next to the town of Adelschlag). The fossil rich deposits belong to the Upper Freshwater Molasse (OSM), correlated to the regional biostratigraphic unit C+D (Burdigalian/Langhian; MN 5 in the European mammal Neogene zone). 17 gastropod species (almost exclusively pulmonates) were found in Adelschlag-Fasanerie and 35 species in Riedensheim. 13 species are shared by both assemblages. Of these, the following species have their distribution expanded in Germany: *Azeca peneckei*, *Carychium (Carychium) galli*, *Vitrea ammoni* and *Urticicola perchtae*; and possibly also *Stagnicola* cf. *praebouiletti* and *Truncatellina* cf. *pantherae*. Paleoecological reconstructions indicate a rich freshwater gastropod community in Riedensheim, with a well-vegetated area immediately surrounding the water body (which diminished in size with time), and a surrounding environment dominated by humid forest. The fauna from Adelschlag-Fasanerie, which was much impoverished in comparison, might represent flood plain and fluvial channel deposits. Finally, a comparison to the molluscan faunas of coeval and nearby localities (Adelschlag, Attenfeld, Sandelzhausen and Undorf) is provided.

**Key words:** Burdigalian/Langhian, Caenogastropoda, Karpatian/Badenian, Pulmonata, Upper Freshwater Molasse.

## 1. Introduction

The North Alpine Foreland Basin (NAFB) is well known for its rich and diverse Miocene fossil record. Its youngest part, the Upper Freshwater Molasse ("Obere Süßwassermolasse", in German; abbreviated OSM), contains a large number of vertebrate-bearing localities (e.g., Heissig 1997; Kälin & Kempf 2009; Abdul-Aziz et al. 2010; Böhme & Ilg 2003). The invertebrate fossils, however, have usually received less attention, despite the importance of mollusks in paleoenvironmental reconstructions and biostratigraphy (e.g., Harzhauser et al. 2008; Moser et al. 2009a).

Fossil samples were recently collected from two new Miocene Bavarian localities: Riedensheim (in the municipality of Rennertshofen) and Fasanerie (in the municipality of Adelschlag). These two sites are not accessible anymore, but have delivered rich fossil assemblages presently under study. A first taxonomical contribution dealing with the continental gastropods and their paleoecological and biostratigraphic context is presented here.

## 2. Geological setting

The two fossil sites presented in this paper, Riedensheim and Adelschlag-Fasanerie, belong to the OSM. Geographically, they are located at the northern margin of the basin at the border to the Franconian Alb (Fig. 1). Rich vertebrate and invertebrate faunas were recently discovered at both localities.

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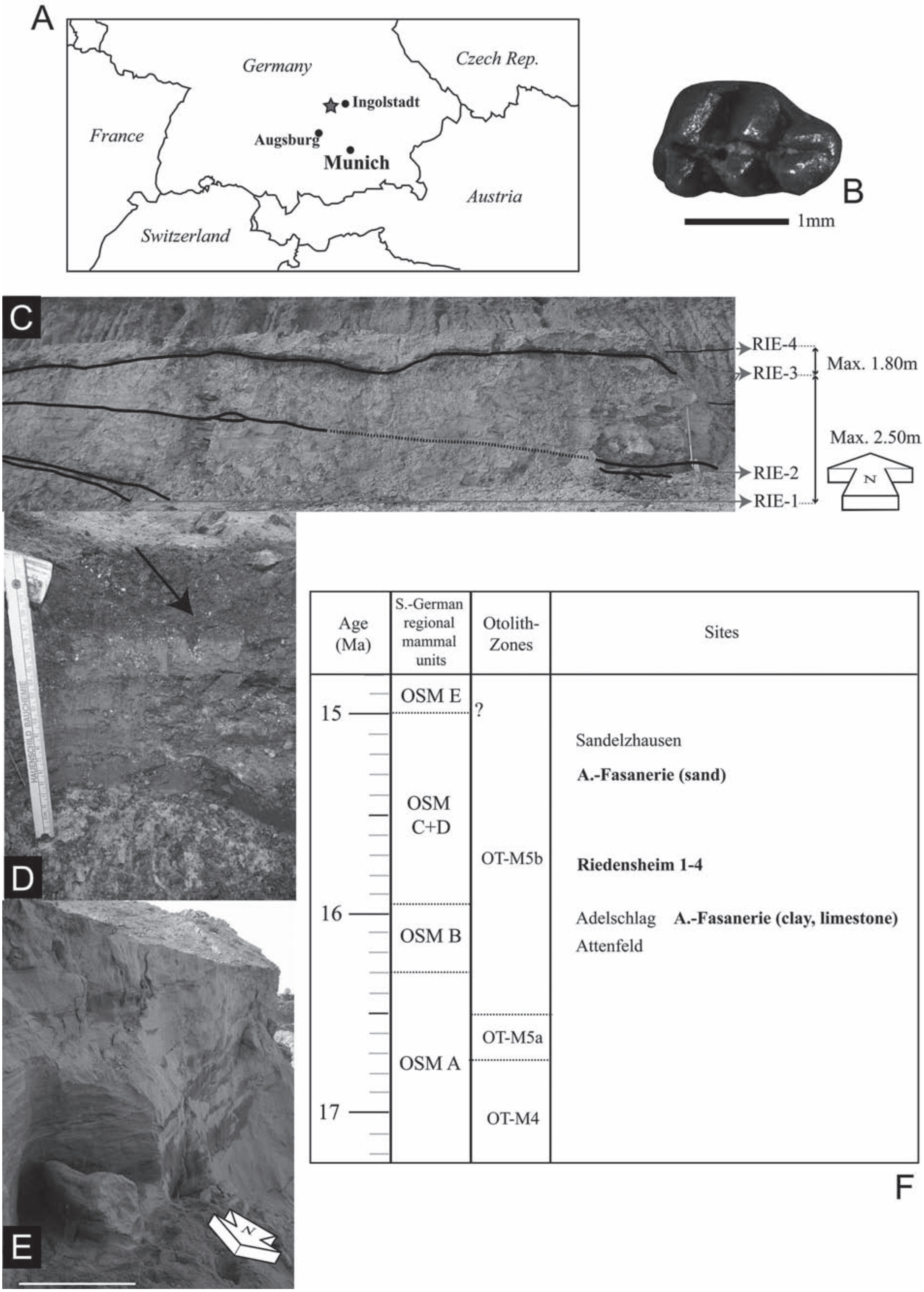
A
Germany
Czech Rep.
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Max. 2.50m
RIE-2
RIE-1
N
D
HAUENSCHILD BAUCHEMIE
E
N
Age (Ma)
S.-German regional mammal units
Otolith-Zones
Sites
15
16
17
OSM E
?
OSM C+D
OSM B
OSM A
OT-M5b
OT-M5a
OT-M4
Sandelzhausen
A.-Fasanerie (sand)
Riedensheim 1-4
Adelschlag
A.-Fasanerie (clay, limestone)
Attenfeld
F

**Fig. 1.**

### 2.1. Adelschlag-Fasanerie

The sand pit was located at the hamlet Fasanerie (48°51' N, 11°12' E) northwest of the town of Adelschlag. The pit is presently filled up and excavations are not possible anymore. It was in the paleontological limelight in 2012 due to the discovery of a well-preserved skull of the proboscidean *Gomphotherium* Burmeister, 1837. An intensive study of the deposits followed, leading, among other works, to the sampling of the molluscs studied herein (Sauer 2013). Most of the gastropods presented here stem from one of the deepest exposed layers (location A in Sauer 2013), an approximately 12 cm thick layer of reddish to brownish clay (named here as "Adelschlag-Fasanerie clay"). This layer was unconformably overlain by sandy and vertebrate-rich strata which provided also some rare and fragile, but complete, gastropod specimens (named here as "Adelschlag-Fasanerie sand"). Finally evidence of gastropod-enriched freshwater limestones in the profile is provided by displaced blocks (named here as "Adelschlag-Fasanerie limestone"). According to earlier observations by one of the authors (CM), these limestones occurred below the clay deposits in adjacent pits and therefore form the base of the reported sedimentary sequence.

### 2.2. Riedensheim

The pit "Riedensheim III" of the company Hoffmann Mineral was recently opened for mining of siliceous earth. It is located 650 m north of the small town of Riedensheim (48°45'N, 11°07'E), and 6.5 km northwest of Neuburg on the Danube. Several meters of Miocene sand and marls were exposed below Quaternary loess loams. The strata laid unconformably on Cretaceous siliceous earth and sandstones of the Upper Cretaceous Wellheim Formation (Schneider et al. 2013). Due to the progression of mining, the strata have been removed in the meantime. Four gastropod-enriched marly layers were sampled in 2014. Although post-depositional karst phenomena disturbed the horizontal layering of the strata, the samples studied here could be ordered from the bottom (layer Riedensheim 1) to the top (layer Riedensheim 4) (Fig. 1). The layer Riedensheim 2 had a laterally changing facies; its eastern part was more sandy while the western part was marly. As the horizon could be clearly tracked through the whole section despite of facial changes, all findings from this layer were merged under the label Riedensheim 2. The gastropods presented here stem from layers 1, 2 (including the sandy facies) and 4.

### 2.3. Biostratigraphy

The biozonation of the German Upper Freshwater Molasse is based on the presence/absence of mammalian taxa (e.g., Dehm 1955; Heissig 1997; Böhme et al. 2002; Abdul-Aziz et al. 2008, 2010). The rodent species, in particular, are of first importance for detailed biostratigraphy in this area. Seven faunal units (OSM A to F) are now defined for the Older and Middle Series (*sensu* Dehm 1955), and have their equivalents in the taxon range-based zonation of the Swiss part of the NAFB (Kälin & Kempf 2009).

#### 2.3.1. Adelschlag-Fasanerie

At present, no biostratigraphically significant mammalian fossil has been obtained from the location A, but fish otoliths correlate it to the later part of the otolith zone OT-M5 (Reichenbacher, personal communication in Sauer 2013). The mammals obtained from the sand unconformably overlying this level correlate to the OSM C+D (Sauer 2013). The rare isolated teeth of the cricetid rodent *Megacricetodon* aff. *bavaricus* Fahlbusch, 1964 are clearly larger than the tooth recorded from Langenmoosen (OSM B), and more similar to what was observed in Sandelzhausen, for instance (OSM C+D).

The few *Megacricetodon* Fahlbusch, 1964 remains documented in Adelschlag (see also below), a local-

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**Fig. 1. A** – Map showing the localities of Adelschlag-Fasanerie and Riedensheim (red star). **B** – Left upper first molar of Megacricetodon aff. bavaricus (Riedensheim 4). **C** – View of the gastropod-rich layers from Riedensheim (RIE-4 and part of RIE-3 are in a second exposure in the background). **D.** Adelschlag-Fasanerie, locality A (the arrow indicates the sampled layer). **E** – Adelschlag-Fasanerie sand, during the excavation of the *Gomphotherium* skull (scale: 1 m). **F** – Biostratigraphic correlation of Adelschlag-Fasanerie (abbreviated "A.-Fasanerie") and Riedensheim, as well as the localities discussed in the text. Undorf is not considered because of the lack of sufficient biostratigraphic information, but the presence of the rodent *Keramidomys* allows the exclusion of OSM A. The correlations follow Reichenbacher et al. (2013).

ity sampled in the 1950s (at approximatively the same height above sea level as Adelschlag-Fasanerie but 1.8 km distant), do not contradict an assignment to the OSM B or early OSM C+D. The two teeth found there belonging to m2 and m3 are unfortunately not of high biostratigraphic value and belong to the uppermost size range, similar to the tooth from Langenmoosen (OSM B). They also fall within the variation range from Roßhaupten (base of OSM C+D, after HEISSIG 1997; for measurements, see FAHLBUSCH 1964). The fossils obtained from Roßhaupten are derived from dark, organic rich, sandy marl rich in gastropods (REICHENBACHER et al. 2004). This lithological description resembles the observations made at the location A (sensu SAUER 2013) from Adelschlag-Fasanerie. Therefore, the duration of the hiatus between the marly deposits and the erosive base of the sand in Adelschlag-Fasanerie cannot be precisely determined.

#### 2.3.2. Riedensheim

At present, the few findings of mammal fossils do not allow for a precise biostratigraphic assignment of this locality. The uppermost layer Riedensheim 4 yielded a first upper molar of *Megacricetodon* aff. *bavaricus* (Fig. 1B). Its size (2 mm x 1.23 mm) is in the lower range of specimens from the Sandelzhausen locality (WESSELS & REUMER 2009) and, thus, allows for a preliminary correlation to the OSM C+D. Based on this specimen only, a more precise relative dating of Riedensheim 4 is not possible. Vertebrate-enriched layers have been recently sampled in the sandy layers underlying the deposits considered herein, as well as a marly layer that cannot be confidently correlated to any of the layers discussed herein. While lacking gastropods, the large amount of *Megacricetodon* teeth found allows us to correlate the beginning of the sedimentation in Riedensheim to the base of OSM C+D. All four available M1 teeth are clearly smaller than the tooth from Riedensheim 4. For this reason it is reasonable to correlate the layers 1-4 to the first half of the OSM C+D (Fig. 1).

The absolute dating of the pre-Riesian OSM deposits is a much-debated subject. While ABDUL-AZIZ et al. (2010) propose an age roughly ranging from 15.8 to 17.1 Ma (mostly Karpatian), other studies consider these dates are somewhat too old (REICHENBACHER et al. 2013 and references therein), and define the biozone between ca. 15 and 16 Ma (Badenian). Regarding these discrepancies and the lack of sufficient material in the gastropod-enriched layers, a more precise dating is presently not possible.

### 2.4. Additional information on the studied OSM localities

The faunal composition of several neighboring and nearly coeval localities are compared to the localiteiy of Riedensheim and Adelschlag-Fasanerie. The following preliminary biostratigraphic succession is suggested (from the oldest to the youngest): Attenfeld, Adelschlag/Adelschlag-Fasanerie clay, Adelschlag-Fasanerie sand/Riedensheim 1-4, Sandelzhausen. The Undorf localities cannot be arranged in this system due to the uncertainties mentioned below.

#### 2.4.1. Adelschlag

As noted before, the Adelschlag locality is geographically very close to Adelschlag-Fasanerie, and might be a stratigraphical equivalent to the marly part of the latter. Emending MAYR (1979), REICHENBACHER et al. (2004) proposed a slightly younger stratigraphic age of Adelschlag with regard to Attenfeld. Their proposal is based on the evolutionary stage of the dormouse *Miodyromys* KRETZOI, 1943 compared to the representatives of the OSM B, more precisely from Langenmoosen. The gastropods reported by REICHENBACHER et al. (2004) from this locality are revised in the present work, based on SEM images (Appendix 2: Table 1). Nearly all gastropod species are freshwater taxa; a single terrestrial species was reported.

#### 2.4.2. Attenfeld

The clay pit is situated approximately 4 km north of Neuburg (REICHENBACHER et al. 2004), and is thus close to Riedensheim. The locality can be correlated to OSM B. As above, the gastropods listed by REICHENBACHER et al. (2004) were re-identified (Appendix 2: Table 1). Only freshwater snails are known from this locality.

#### 2.4.3. Sandelzhausen

The molluscan fauna from Sandelzhausen was studied by GALL (1972) and MOSER et al. (2009a) and revised by SALVADOR (2013a, 2013b, 2015) and SALVADOR & RASSER (2014). The locality has been intensively excavated and studied, and a rich literature dealing with the taxonomy of the fossils, their age and paleoecology, as well as the geology of the site, is now available (see MOSER et al. 2009b, and references therein for an overview). Sandelzhausen correlates to OSM C+D.

#### 2.4.4. Undorf

The molluscan fauna from Undorf (near Regensburg) was studied by CLESSIN (1877, 1885, 1892, 1911) and never revised, although a single species was later described by Falkner (1974). Clessin presented a profile of the mollusk-bearing locality (Clessin 1911), but without clearly mentioning the exact location. It is thus difficult to correlate these data with the small mammal finds from Undorf reported by Fahlbusch (1964). The literature also reports fossil vertebrates excavated along the railway track, with a large diversity of large mammals and other vertebrates (e.g., Rinnert 1956). The small mammal finds do not help much with the relative dating, because the stratigraphical ranges of the species are too long (*Democricetodon* Fahlbusch, 1964, *Eumyarion* Thaler, 1966, *Keramidomys* Hartenberger, 1966, *Neocometes similis* Fahlbusch, 1966; Fahlbusch 1975; Schötz 1981; Prieto 2010). It should be noted that many taxa from Undorf described by Clessin (1877, 1885, 1892, 1911) were considered doubtful by Wenz (1923-1930) and are therefore excluded from the present faunal composition analysis. The single new species described later (*Spermodea candida* Falkner, 1974) was also excluded, since it is not known if it is syonymous with one of Clessin's species (Clessin 1877, 1885, 1892, 1911).

## 3. Material and methods

All the gastropod material found in the new localities of Adelschlag-Fasanerie and Riedensheim is reported here. The sediments were screen-washed (smallest sieve 0.4 mm) after dissolution in a low concentrated $H_2O_2$ solution. The specimens are housed at the collections of the Bayerische Staatssammlung für Paläontologie und Geologie (BSPG; Munich, Germany) and the Staatliches Museum für Naturkunde Stuttgart (SMNS; Stuttgart, Germany). The material analyzed is fully listed in Appendix 1.

The classification used here follows Bouchet et al. (2005) and Nordsieck (2014). All species found are figured. Further data on their diagnostic features is provided on the discussion section of each species. Specimens were measured either with a digital caliper or with the aid of computer software (Leica Application Suite [LAS] v.3.8.0 and ImageJ). The following abbreviations are used throughout the article for shell measurements: H = shell height; D = shell greatest diameter; h = operculum height; w = operculum width.

## 4. Systematic Paleontology

Caenogastropoda
Superfamily Littorinoidea
Family Pomatiidae
Genus *Pomatias* Studer, 1789

*Pomatias* sp.
(Fig. 2A)

**Occurrence:** Riedensheim 2 (1 operculum).

**Discussion:** This single ellipsoid operculum presenting a sub-central nucleus and spiral growth pattern is consistent with the genus *Pomatias*. Classification beyond genus level is not possible.

Superfamily Truncatelloidea
Family Bithyniidae
Genus *Bithynia* Leach, 1818
*Bithynia* sp.
(Figs. 2B-C)

**Occurrence:** Adelschlag-Fasanerie sand (6 opercula), Riedensheim 1 (6 opercula) and Riedensheim 2 (1 specimen + 1 operculum).

**Discussion:** A single shell fragment and some opercula remains. The sturdy shell with strongly convex whorls and the tear-shaped operculum (with a central nucleus and concentric growth pattern) are consistent with the genus *Bithynia*, but do not allow further classification.

Family Hydrobiidae
Genus *Pseudamnicola* Paulucci, 1878
*Pseudamnicola suevicus* (Gottschick, 1928)
(Fig. 2D)

1928 *Amnicola suevica* Gottschick, p. 148, pl. 2, figs. 7a-c.
1976 *Pseudamnicola convexa suevica* [sic]. – Schlickum, p. 3, pl. 1, fig. 6.
2014 *Pseudamnicola convexa suevica* [sic]. – Neubauer et al., supplementary material 1.

**Occurrence:** Adelschlag-Fasanerie clay (16 specimens), Riedensheim 4 (>30 specimens).

**Discussion:** This genus can be identified by its hydrobiid shell with few whorls, with rapidly-expanding whorls and a large oval aperture; the adults are of a very small size. The present specimens compare very well to the syntypes of *Pseudamnicola suevicus* (SMNS 15817), a species known only from Zwiefaltendorf (MN 5-6, Germany; Schlickum 1976). This species is often treated as a subspecies of *Pseudamnicola convexus* (Sandberger, 1875), which was originally described from Ehingen (MN 5, Germany; also reported from other localities in Central Europe), but is insufficiently defined. *Pseudamnicola convexus* may well be the senior name for this species, but addressing this issue is beyond the scope of the present work.

The genus *Pseudamnicola* should be treated as masculine, following *Amnicola* Gould & Haldeman, 1840 (Falkner et al. 2002).

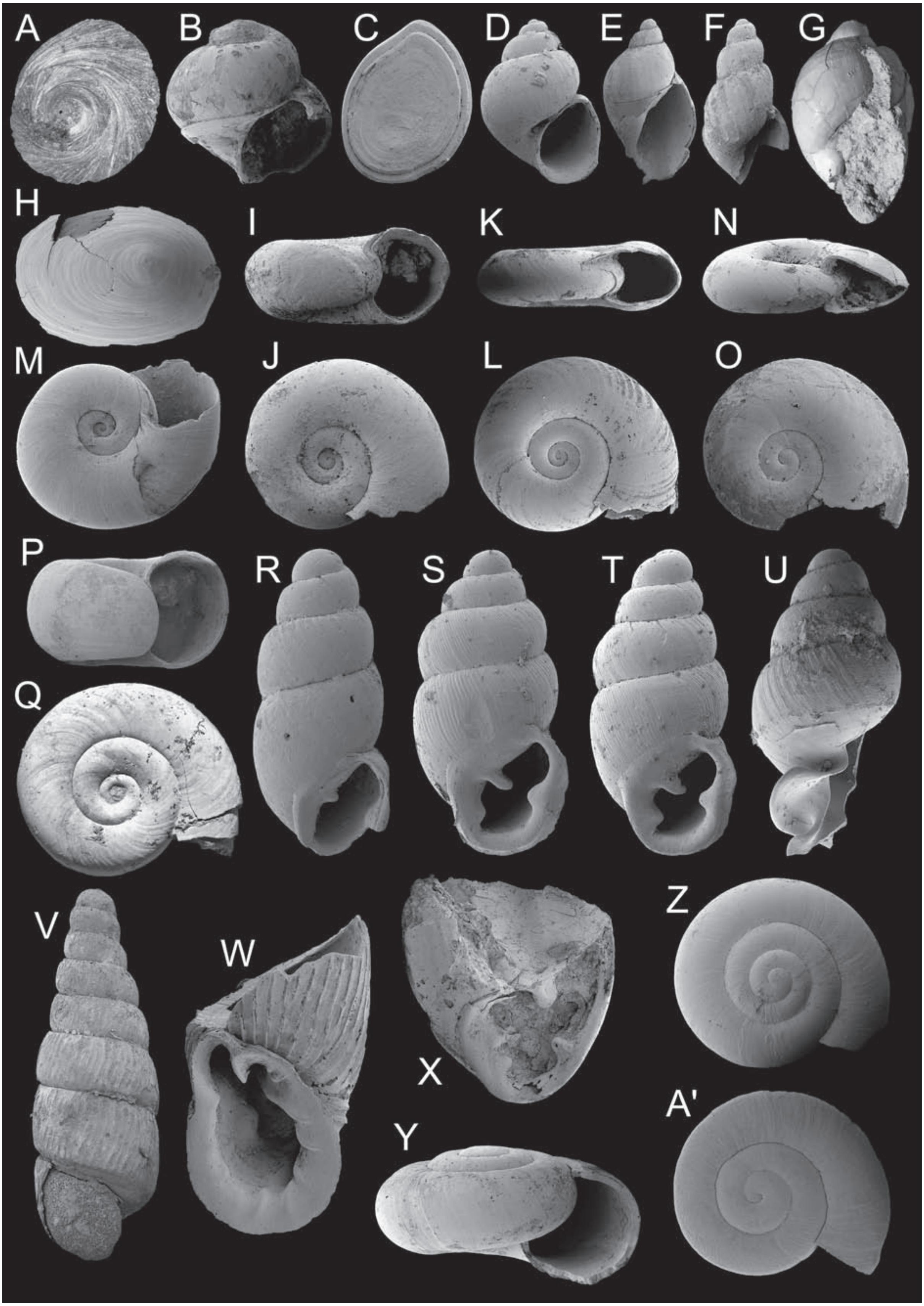

**Fig. 2.**

### Pulmonata
### Hygrophila
### Superfamily Lymnaeoidea
### Family Lymnaeidae
### Genus *Galba* Schrank, 1803
### *Galba dupuyiana* (Noulet, 1854)
### (Fig. 2E)

1854 *Limnea Dupuyiana* Noulet, p. 108.
1872 *Limneus Laurillardianus* Sandberger, pl. 28, figs. 27-27b [non *laurillardianus* Noulet 1854].
1875 *Limneus Dupuyianus*. – Sandberger, p. 543.
1923 *Radix (Radix) dupuyana* [sic]. – Wenz, p. 1242.
2000 *Galba* (*Galba*) *dupuyiana*. – Fischer, p. 135, fig. 4.
2006 *Galba dupuyana* [sic]. – Kókay, p. 50, pl. 16, figs. 14-16.
2009 *Galba dupuyiana*. – Böttcher et al., p. 239, figs. 2/1-2.
2014 *Galba dupuyiana*. – Neubauer et al., supplementary material 1.
2014 *Galba dupuyiana*. – Salvador & Rasser, p. 188, figs. 1-7.

**Occurrence:** Adelschlag-Fasanerie clay (>30 specimens), Riedensheim 1 (>30 specimens), Riedensheim 2 (>40 specimens) and Riedensheim 4 (>50 specimens).

**Discussion:** The present specimens compare well to *G. dupuyiana,* with large, round and rapidly-expanding whorls. The species was originally described from Sansan (MN6, France; Fischer 2000), but is known throughout the Middle Miocene of Western and Central Europe (Kókay 2006). There are two distinct extreme morphological varieties (a broader and a slender form) of this species known from other coeval sites in Germany (Böttcher et al. 2009; Salvador & Rasser 2014), but in the present material only the broader form is present.

### Genus *Stagnicola* Jeffreys, 1830
### *Stagnicola* cf. *praebouiletti* (Schlickum, 1970c)
### (Fig. 2F)

1964 *Stagnicola (Stagnicola?) bouiletti*. – Schlickum, p. 14, pl. 2, fig. 32 [non Michaud 1835].
1970c *Stagnicola praebouiletti* Schlickum, p. 92, figs. 12-17.
1973 *Stagnicola (Stagnicola) praebouiletti*. – Steininger et al., p. 451, pl. 9, fig. 10.
1993 *Stagnicola praebouiletti*. – Reichenbacher, table 13.
2005 *Stagnicola praebouiletti*. – Kowalke & Reichenbacher, p. 631, figs. 9.8-9.9.
2014 *Stagnicola praebouiletti*. – Neubauer et al., supplementary material 1.

**Occurrence:** Riedensheim 2 (1 specimen).

**Discussion:** This single specimen has a very slender lymnaeiform shell, with a tall spire, tall whorls, deep suture and regularly growing whorls. The material is poorly preserved, but it compares well to *Stagnicola praebouiletti*, a species originally described from the Bavarian Oncophora Beds (from the Upper Brackish Molasse, or OBM). Due to the younger age and fragmentary nature of the present specimen, this identification remains tentative.

### Genus *Lymnaea* Lamarck, 1799
### *Lymnaea dilatata* Noulet, 1854
### (Fig. 2G)

**Fig. 2.** Fossil gastropods. **A** – *Pomatias* sp., operculum (BSPG 2014 XIX 095; Riedensheim 2; h = 4.6 mm, w = 4.0 mm). **B** – *Bithynia* sp. (BSPG 2014 XIX 039; Riedensheim 2; H = 1.7 mm, D = 1.6 mm). **C** – *Bithynia* sp., operculum (BSPG 2014 XIX 012; Riedensheim 1; h = 2.7 mm, w = 2.1 mm). **D** – *Pseudamnicola suevicus* (BSPG 2014 XIX 086; Riedensheim 4; H = 1.8 mm, D = 1.2 mm). **E** – *Galba dupuyiana* (BSPG 2014 XIX 061; Riedensheim 4; H = 4.8 mm). **F** – *Galba* cf. *praebouiletti* (BSPG 2014 XIX 037; Riedensheim 2; H = 3.6 mm). **G** – *Lymnaea dilatata* (BSPG 2013 XXVI; Adelschlag-Fasanerie; H = 22.9 mm). **H** – *Ferrissia deperdita* (BSPG 2014 XIX 009; Riedensheim 1; H = 3.3 mm, D = 2.3 mm). **I** – *Gyraulus albertanus* (BSPG 2014 XIX 054; Riedensheim 4; H = 1.2 mm, D = 2.6 mm). **J** – *Gyraulus albertanus* (BSPG 2014 XIX 080; Riedensheim 4; D = 2.9 mm). **K** – *Gyraulus applanatus* (BSPG 2014 XIX 075; Riedensheim 4; H = 1.1 mm, D = 3.2 mm). **L** – *Gyraulus applanatus* (BSPG 2014 XIX 060; Riedensheim 4; D = 3.0 mm). **M** – *Gyraulus applanatus*, specimen with predation mark (BSPG 2014 XX 004; Adelschlag-Fasanerie; D = 2.2 mm). **N** – *Hippeutis subfontanus* (BSPG 2014 XIX 055, spcm. #1; Riedensheim 4; H = 0.6 mm, D = 1.8 mm). **O** – *Hippeutis subfontanus* (BSPG 2014 XIX 055, spcm. #2; Riedensheim 4; D = 1.6 mm). **P** – *Planorbarius cornu* (BSPG 2014 XIX 079, spcm. #1; Riedensheim 4; H = 3.4 mm, D = 5.8 mm). **Q** – *Planorbarius cornu* (BSPG 2013 XXVI; Adelschlag-Fasanerie; D = 21.2 mm). **R** – *Carychium eumicrum* (BSPG 2014 XIX 083; Riedensheim 4; H = 1.2 mm). **S** – *Carychium galli* (BSPG 2014 XIX 087, spcm. #1; Riedensheim 4; H = 1.6 mm). **T** – *Carychium galli* (BSPG 2014 XIX 087, spcm. #2; Riedensheim 4; H = 1.7 mm). **U** – *Carychium nouleti*, broken specimen showing sinuous internal lamella (BSPG 2014 XX 001; Adelschlag-Fasanerie; H = 1.4 mm). **V** – *Pseudidyla moersingensis* (BSPG 2014 XIX 042; Riedensheim 2; H = 6.4 mm). **W** – *Pseudidyla moersingensis*, aperture fragment (BSPG 2014 XIX 066; Riedensheim 4; H = 3.3 mm, D = 1.8 mm). **X** – *Azeca peneckei*, aperture fragment (BSPG 2014 XIX 064; Riedensheim 4; H = 2.4 mm, D = 2.1 mm). **Y** – *Vitrea ammoni* (BSPG 2014 XIX 059; Riedensheim 4; H = 1.7 mm, D = 3.1 mm). **Z** – *Vitrea ammoni* (BSPG 2014 XIX 085; Riedensheim 4; D = 3.6 mm). **A'** – *Pseudochloritis* sp., spire apex fragment (BSPG 2014 XIX 021; Riedensheim 2; D = 8.3 mm).

1854 *Limnea dilatata* Noulet, p. 107.
1923 *Radix (Radix) socialis dilatata*. – Wenz, p. 1277.
2000 *Lymnaea dilatata*. – Fischer, p. 136, figs. 1-2.
2006 *Radix dilatata*. – Kókay, p. 52, pl. 17, fig. 14.
2014 *Radix dilatata*. – Neubauer et al., supplementary material 1.
2014 *Lymnaea dilatata*. – Salvador & Rasser, p. 189, figs. 8-9.

**Material examined:** BSPG 2013 XXVI (8 spcm.); 2014 XIX 007 (14 spcm.), XIX 040 (1 spcm.), XIX 049 (4 spcm.), XIX 071 (15 spcm). SMNS 101695 (1 spcm.).

**Occurrence:** Adelschlag-Fasanerie limestone (8 specimens), Riedensheim 1 (14 specimens), Riedensheim 2 (1 specimen) and Riedensheim 4 (19 specimens).

**Discussion:** *Lymnaea dilatata* is diagnosed by its large lymaneid shell, with an acuminated and proportionately small spire, rapidly-expanding and slightly convex whorls, a somewhat oval body whorl and a large ellipsoid aperture. This species is known from the entire Miocene of Western and Central Europe (Binder 2004; Kókay 2006).

### Superfamily Planorboidea
### Family Planorbidae
### Genus *Ferrissia* Walker, 1903
### *Ferrissia deperdita* (Desmarest, 1814)
(Fig. 2H)

1814 *Ancylus deperditus* Desmarest, p. 19, pl. 1, fig. 14.
1923 *Pseudancylus deperditus deperditus*. – Wenz, p. 1692.
1976 *Ferrissia deperdita*. – Schlickum, p. 7, pl. 1, fig. 20.
2006 *Ferrissia deperdita*. – Kókay, p. 60, pl. 20, fig. 15, pl. 21, fig. 1.
2014 *Ferrissia deperdita*. – Harzhauser et al., p. 17, pl. 5, figs. 1, 2, 5, 12,
2014 *Ferrissia deperdita*. – Neubauer et al., supplementary material 1.
2014 *Ferrissia deperdita*. – Salvador & Rasser, p. 191, fig. 11.

**Occurrence:** Riedensheim 1 (2 specimens) and Riedensheim 2 (1 specimen).

**Discussion:** The present specimens show a shell apex slightly bent to the side; the cap-like protoconch is smooth, gradually transitioning to the teleoconch, which bears well-marked growth lines. Given this pattern and age, the specimens compare well to *F. deperdita*, a species known from the Middle Miocene of Hungary, Austria, southern Germany, Switzerland and France (Schlickum 1976; Kókay 2006; Harzhauser et al. 2014).

### Genus *Gyraulus* Charpentier, 1837
### *Gyraulus albertanus* (Clessin, 1877)
(Figs. 2I-J)

1877 *Planorbis albertanus* Clessin, p. 40.
1923 *Gyraulus (Gyraulus) albertanus*. – Wenz, p. 1541.
1972 *Gyraulus (Gyraulus) albertanus*. – Gall, p. 16.
2009a *Menetus* (*Dilatata*) *albertanus*. – Moser et al., p. 46.
2014 *Gyraulus albertanus*. – Neubauer et al., supplementary material 1.
2014 *Gyraulus albertanus*. – Salvador & Rasser, p. 191, figs. 12-15.

**Occurrence:** Adelschlag-Fasanerie clay (>20 specimens), Riedensheim 1 (15 specimens), Riedensheim 2 (>30 specimens) and Riedensheim 4 (>20 specimens).

**Description:** Shell diminutive, pseudodextral, planispiral; shell height ~1/2 shell width. Protoconch (~1¼ whorl) sculptured by faint spiral striae; transition to teleoconch unclear. Teleoconch smooth, except for numerous very well-marked growth lines. Spire depressed. Suture very deep. Whorls rapidly growing. Aperture rounded. Peristome simple, sharp. Umbilicus wide, deep.

**Discussion:** *Gyraulus albertanus*, when compared to coeval congeners, is diagnosed by its proportionately larger size (shell height ca. half the shell diameter), a more overall rounded shell profile, quickly growing whorls and a large and round aperture. The species is known from several Early/Middle Miocene OSM localities (e.g., Clessin 1877; Salvador & Rasser 2014).

### *Gyraulus applanatus* (Thomae, 1845)
(Figs. 2K-M)

1845 *Planorbis applanatus* Thomae, p. 150.
1851 *Planorbis dealbatus*. – Braun, p. 1134.
1923 *Gyraulus (Gyraulus) trochiformis applanatus*. – Wenz, p. 1579.
1923 *Gyraulus (Gyraulus) trochiformis dealbatus*. – Wenz, p. 1591.
1964 *Gyraulus trochiformis dealbatus*. – Schlickum, p. 15, pl. 2, fig. 35.
1970a *Gyraulus trochiformis applanatus*. – Schlickum, p. 148, pl. 10, fig. 6.
1970b *Gyraulus trochiformis applanatus*. – Schlickum, p. 180.
1973 *Gyraulus trochiformis dealbatus*. – Steininger et al., p. 451, pl. 9, fig. 11a-b.
1989 *Gyraulus trochiformis dealbatus*. – Reichenbacher, p. 172, pl. 1, fig. 11.
1995 *Gyraulus dealbatus*. – Kadolsky, p. 40, fig. 47.
2004 *Gyraulus dealbatus*. – Binder, p. 193, pl. 2, figs. 1a-c.
2005 *Gyraulus applanatus*. – Kowalke & Reichenbacher, p. 631, figs. 9.1-9.3.
2006 *Gyraulus applanatus*. – Kókay, p. 56, pl. 19, figs. 13-14.
2006 *Gyraulus trochiformis dealbatus*. – Kókay, p. 57, pl. 19, fig. 15.
2014 *Gyraulus applanatus*. – Neubauer et al., supplementary material 1.
2014 *Gyraulus dealbatus*. – Neubauer et al., supplementary material 1.

2014 *Gyraulus dealbatus*. – Salvador & Rasser, p. 192, figs. 16-23.

**Occurrence:** Adelschlag-Fasanerie clay (>80 specimens), Adelschlag-Fasanerie sand (8 specimens), Riedensheim 1 (>20 specimens), Riedensheim 2 (>50 specimens) and Riedensheim 4 (>120 specimens).

**Discussion:** The present specimens are well within the common conchological variation of *G. applanatus*, reported for several sites in Germany (Gottschick & Wenz 1916; Kowalke & Reichenbacher 2005; Salvador & Rasser 2014). There are two extreme forms, the typical *G. applanatus* (flattened shell, regularly growing whorls, more closely packed together, with a well-marked carina on the laterobasal portion of the body whorl, and a smaller aperture, shaped as an arrowhead) and the typical *G. dealbatus* (Braun, 1851) (with a more rounded shell profile, with rapidly growing whorls, a faint keel on its median portion and a larger aperture), with all intermediate steps. As such, Kowalke & Reichenbacher (2005) synonymized the two species, a decision which is followed here.

### Genus *Hippeutis* Charpentier, 1837
### *Hippeutis subfontanus* (Clessin, 1877)
### (Figs. 2N-O)

1877 *Planorbis (Hippeutis) subfontanus* Clessin, p. 39.
1923 *Hippeutis (Hippeutis) subfontanus subfontanus*. – Wenz, p. 1648.
1976 *Hippeutis subfontaneus subfontaneus* [sic]. – Schlickum, p. 6, pl. 1, fig. 17.
2014 *Hippeutis subfontanus*. – Neubauer et al., supplementary material 1.

**Occurrence:** Riedensheim 4 (5 specimens).

**Discussion:** The genus *Hippeutis* is easily recognizable by its flattened and angular shell profile (it is round in early whorls, though), slightly incised suture and arrowhead-shaped aperture. The present specimens compare well with *H. subfontanus* (syntypes SMNS 106434), a species known from coeval and nearby localities from the Silvana Beds (“Silvanaschichten”, in German) of the OSM (Wenz 1923; Schlickum 1976).

### Genus *Planorbarius* Duméril, 1806
### *Planorbarius cornu* (Brongniart, 1810)
### (Figs. 2P-Q)

1810 *Planorbis cornu* Brongniart, p. 371, pl. 22, fig. 6.
1923 *Coretus cornu cornu*. – Wenz, p. 1426.
1966 *Planorbarius cornu*. – Schlickum, p. 326, pl. 13, fig. 27.
1970a *Planorbarius cornu*. – Schlickum, p. 149, pl. 10, fig. 7.
1989 *Planorbarius cornu*. – Reichenbacher, p. 172, pl. 1, fig. 10.
2004 *Planorbarius cornu*. – Binder, p. 193, pl. 2, figs. 2-3.
2006 *Planorbarius cornu cornu*. – Kókay, p. 58, pl. 20, fig. 6.
2009 *Planorbarius cornu cornu*. – Böttcher et al., p. 239, figs. 2.4-2.6.
2014 *Planorbarius cornu*. – Neubauer et al., supplementary material 1.
2014 *Planorbarius cornu*. – Salvador & Rasser, p. 193, figs. 26-28.

**Occurrence:** Adelschlag-Fasanerie limestone (>30 specimens), Adelschlag-Fasanerie clay (>40 specimens), Adelschlag-Fasanerie sand (5 specimens), Riedensheim 1 (>20 specimens), Riedensheim 2 (>30 specimens) and Riedensheim 4 (>50 specimens).

**Discussion:** Despite the fact that, for the vast majority of the present specimens, only the first whorls are preserved, the shell characteristic shape and unique sculpture enables the identification as *P. cornu*. This characteristic sculpture consists of a protoconch (ca. 1 whorl) sculptured by spiral lines of regularly organized circular pits (giving the impression of a reticulated pattern under light microscopy), transitioning abruptly to the teleoconch, which is sculptured by spiral striae on the first ca. 1½ whorl and smooth on the rest (except for growth lines).

*Planorbarius cornu* is especially abundant in the OSM and the sturdy nucleus of its shell favors preservation. The species is known from a long time span, ranging from the Middle Eocene to the Late Miocene of France, Germany and the Czech Republic (Schlickum 1970a; Kókay 2006), which likely indicates an agglomerate of species under the same name. As such, until this species complex has received a much-needed revisionary work, this species is better classified as *P. cornu* sensu lato.

### Eupulmonata
### Superfamily Ellobioidea
### Family Ellobiidae
### Genus *Carychium* O.F. Müller, 1773
### *Carychium eumicrum* Bourguignat, 1857
### (Fig. 2R)

1857 *Carychium eumicrum* Bourguignat, p. 253.
1923 *Carychium eumicron eumicron* [sic]. – Wenz, p. 1187.
1977 *Carychium (Carychiella) eumicron* [sic]. – Strauch, p. 159, pl. 14, figs. 13-15, pl. 17, fig. 53, pl. 19, fig. 76.
1999a *Carychium eumicrum*. – Stworzewicz, p. 264, figs. 5-6.
2006 *Carychium (Carychiella) eumicron eumicron* [sic]. – Kókay, p. 48, pl. 16, fig. 5.
2014 *Carychium eumicrum*. – Harzhauser et al., p. 19, pl. 6, figs. 6, 7, 10.
2015 *Carychium (Carychiella) eumicron* [sic]. – Salvador, p. 38, fig. 1.

**Occurrence:** Riedensheim 4 (5 specimens).

**Description:** Shell diminutive, pupiform to fusiform, narrow. Protoconch (~1 whorl) dome-shaped, smooth; transition to teleoconch unclear. Teleoconch smooth, except by fine growth lines. Whorl profile convex. Suture well-marked, deep. Aperture ellipsoid; parietal lamella well-marked; median palatal tooth very faint. Peristome narrow, very weakly reflexed. Umbilicus rimate, very shallow.

**Discussion:** *Carychium eumicrum* is easily diagnosed by its much smaller size than other Carychiinae. Other diagnostic characters include a much slenderer shell, a lack of teleoconch sculpture, a less developed aperture (with a narrow and very weakly reflexed peristome) and the apertural dentition (with a well-marked parietal lamella and a very faint median palatal tooth). This species is known from Central Europe from the Late Oligocene to Middle Miocene (Strauch 1977; Stworzewicz 1999a).

### *Carychium (Carychium) galli* Salvador, 2015
### (Figs. 2S-T)

2015 *Carychium (Carychium) galli*. – Salvador, p. 39, figs. 2-4.

**Occurrence:** Adelschlag-Fasanerie clay (12 specimen), Riedensheim 1 (2 specimens), Riedensheim 2 (7 specimens) and Riedensheim 4 (>100 specimens).

**Discussion:** This species was previously known only from its type locality in Sandelzhausen (MN 5), Germany. It is diagnosed mainly by displaying a simple internal lamella (columellar apparatus) (Salvador 2015). This species is similar to *Carychium nouleti* Bourguignat, 1857, known from many Miocene localities throughout Central Europe, which can be distinguished mainly by bearing a sinuous internal lamella (Strauch 1977; Stworzewicz 1999a). Other useful diagnostic characters of *C. galli* are a usually slenderer and smaller shell, the more defined and spaced axial sculpture, the more angular shape of the peristome and a strong and distinct palatal tooth (Salvador 2015). The presence of a simple vs. sinuous internal lamella is an important character for taxonomy, separating two large subgeneric groups (Strauch 1977).

The presents specimens, though low in number, show a similar variation in overall shell shape as seen in Sandelzhausen (Salvador 2015), going from a broader form to a narrower one, with many intermediate forms. Both fossil and recent *Carychium* species are known for a large amount of conchological variability in overall shell shape and in the whorls' height and relative proportions (Bulman 1990; Stworzewicz 1999a).

### *Carychium (Saraphia) nouleti* Bourguignat, 1857
### (Fig. 2U)

1857 *Carychium nouleti* Bourguignat, figs. 9-10.
1923 *Carychium nouleti nouleti*. – Wenz, p. 1195.
1923 *Carychium nouleti gibbum*. – Wenz, p. 1197.
1977 *Carychium (Saraphia) nouleti*. – Strauch, p. 162, pl. 15, figs. 24-27, pl. 18, fig. 61, pl. 20, fig. 83.
1999a *Carychium nouleti*. – Stworzewicz, p. 269, figs. 19-22.

**Occurrence:** Adelschlag-Fasanerie clay (6 specimens).

**Discussion:** These few larger specimens of *Carychium* are reminiscent of the shells of *C. nouleti* reported from the Middle Miocene of Opole, Poland (Strauch 1977), in both size and overall shape. Shell shape is somewhat reminiscent of the smaller *C. galli*, but the clearest diagnostic feature is the sinuous internal lamella (columellar apparatus) (see also the discussion of *C. galli* above). The species is known throughout the Miocene of Europe and Algeria (Strauch 1977).

## Stylommatophora
## Superfamily Clausilioidea
## Family Clausiliidae
## Genus *Pseudidyla* Boettger, 1877
### *Pseudidyla moersingensis* (Boettger, 1877)
### (Figs. 2V-W)

1877 *Clausilia (Pseudidyla) mörsingensis* Boettger, p. 89, pl. 3, figs. 32-34.
1923 *Pseudidyla moersingensis moersingensis*. – Wenz, p. 791.
1981 *Pseudidyla moersingensis*. – Nordsieck, p. 107.
2007 *Pseudidyla moersingensis*. – Nordsieck, p. 136.
2015 *Pseudidyla moersingensis*. – Salvador, p. 47, figs. 19-22.

**Occurrence:** Riedensheim 1 (9 specimens), Riedensheim 2 (>20 specimens) and Riedensheim 4 (>100 specimens).

**Discussion:** The present material consists of spire and aperture fragments. The shell is sinistral, with an acuminated apex; the protoconch (ca. 2 whorls) is rounded and smooth, transisitioning abruptly to a teleoconch sculpture by well-marked sinuous axial ribs that become stronger towards the aperture; the body whorl is non-apostrophic, with two crests on its basal surface (the lower one stronger than the upper) and a slight furrow between them; the aperture is roughly oval, with a small rounded area between parietal lamella and palatal region; the peristome is greatly reflexed.

The following apertural barriers are always present: a strong and vertical parietal lamella; a columellar lamella (leading to the clausilium); a basal lamella (beginning deeper on the body whorl inner surface); two folds preceding the columellar lamellar and one fold preceding basal lamella; a principal lamella (deeper on the body whorl's inner palatal surface). Other apertural barriers are not always present, such as one to two basal folds, one supracolumellar fold and one infraparietal fold. Weak fold-like marks are sometimes present on the palatal region.

Due to the overall shell profile and especially the apertural shape and barriers, the specimens can be identified as

*Pseudidyla moersingensis*. This species is known from the late Early to early Late Miocene of Germany (Nordsieck 1981).

### Superfamily Cochlicopoidea
### Family Cochlicopidae
### Genus *Azeca* Fleming, 1828
### *Azeca peneckei* Andreae, 1892
### (Fig. 2X)

1891 *Azeca Boettgeri* Penecke, p. 364, pl. 21, figs. 8a-b [*non* Andreae 1884].
1892 *Azeca peneckei* Andreae, p. 435.
1923 *Azeca peneckei*. – Wenz, p. 1095.
2014 *Azeca peneckei*. – Harzhauser et al., p. 20, pl. 6, figs. 8, 11, 13-14.

**Occurrence:** Riedensheim 4 (>30 specimens).

**Discussion:** Although the specimens are fragmentary, several entirely preserved apertures permit identification to species level. The triangular aperture (columellar and parietal regions of peristome meet at an angle of ca. 90°) with a complete and thickened peristome, alongside the dentition of the present specimens (with four teeth), is diagnostic for *Azeca peneckei* (Harzhauser et al. 2014b). This dentition consists of a median parietal tooth, a low palatal tooth and two columellar teeth; the parietal tooth is stronger than the others, which are all of similar size.

*Azeca peneckei* was previously known only from the early Middle Miocene of the Rein Basin, Austria (Harzhauser et al. 2014b). The palatal tooth seems to be stronger in the specimens from the Rein Basin, but this could represent intraspecific morphological variation. As such, the present record considerably expands the distribution of the species.

### Superfamily Gastrodontoidea
### Family Pristilomatidae
### Genus *Vitrea* Fitzinger, 1833
### *Vitrea ammoni* (Clessin, 1894)
### (Figs. 2Y-Z)

1894 *Hyalina Ammoni* Clessin, p. 29.
1923 *Vitrea ammoni*. – Wenz, p. 292.

**Occurrence:** Riedensheim 1 (1 specimen), Riedensheim 2 (3 specimens) and Riedensheim 4 (>80 specimens).

**Discussion:** The present material compares well to the original description and syntypes (SMNS 106363, 106364) of *V. ammoni*, a species known only from the geographically close and likely coeval site of Undorf (Wenz 1923). These syntypes, however, seem to belong to several species (and maybe even genera), as remarked by Clessin (1894) himself. The present material compares well to a syntype which was alone in the lot (SMNS 106364) and thus likely is the one to which the original description refers to.

### Superfamily Helicoidea
### Family Helicidae
### Genus *Pseudochloritis* Boettger, 1909
### *Pseudochloritis* sp.
### (Fig. 2A')

**Occurrence:** Riedensheim 1 (9 specimens), Riedensheim 2 (5 specimens) and Riedensheim 4 (11 specimens).

**Discussion:** Identification as *Pseudochloritis* is possible due to the characteristic flattened early whorls and sculpture (protoconch of ca. 1¼ whorl, large in relation to following whorl, sculptured by fine striae dotted with weak papillae, transitioning gradually to the teleoconch, which is sculptured by thickened growth lines and irregular weak furrows, with regularly arranged papillae). It is impossible to proceed further than genus level in the identification, but *P. incrassata* (Klein 1853) is very commonly found in coeval sites (e.g., Salvador 2013; Salvador et al. 2015b).

### Genus *Megalotachea* Pfeffer, 1930
### *Megalotachea silvana* (Klein, 1853)
### (Figs. 3A-C)

1853 *Helix silvana* Klein, p. 205, pl. 5, fig. 2.
1923 *Cepaea silvana silvana*. – Wenz, p. 667.
1976 *Cepaea silvana silvana*. – Schlickum, p. 17, pl. 4, figs. 62-63.
1989 *Cepaea silvana silvana*. – Reichenbacher, p. 165, pl. 2, figs. 17-19.
2006 *Cepaea silvana*. – Kókay, p. 93, pl. 36, figs. 2-3.
2013 *Cepaea silvana*. – Rasser et al., p. 440.

**Occurrence:** Adelschlag-Fasanerie sand (1 specimen).

**Remarks:** The present specimen conforms well to *M. silvana* (syntype SMNS 22738) in size and overall shell shape and proportions. This species is very common in the OSM, lending its name to the Silvana Beds.

### Genus *Palaeotachea* Jooss, 1912
### *Palaeotachea renevieri* (Maillard, 1892)
### (Figs. 3D-F)

1892 *Helix (Macularia) Renevieri* Maillard, p. 43, pl. 3, fig. 18.
1923 *Cepaea renevieri*. – Wenz, p. 652.
1954 *Cepaea* cf. *renevieri*. – Zöbelein, p. 156.

**Occurrence:** Adelschlag-Fasanerie sand (1 specimen).

**Remarks:** This species is identified by its small size, small circular aperture, flattened shell profile and faint keel. *Palaeotachea renevieri* is known from the Middle and Late Miocene of southern Germany and Switzerland (Wenz 1923; Zöbelein 1954).

### *Megalotachea* vel *Palaeotachea* sp.

**Occurrence:** Riedensheim 1 (1 specimen) and Riedensheim 4 (4 specimens).

**Discussion:** Some few fragments of spire apexes from the Riedensheim locality cannot be assigned precisely to either *Megalotachea* or *Palaeotachea*. Both genera occur in Adelschlag-Fasanerie (see above), but there are no complete specimens from Riedensheim.

### Family Hygromiidae
### Genus *Leucochroopsis* Boettger, 1908
### *Leucochroopsis* sp.
(Fig. 3G)

**Occurrence:** Riedensheim 2 (5 specimens) and Riedensheim 4 (5 specimens).

**Remarks:** The assignment of the present fragmentary specimens to the genus *Leucochroopsis* is possible by the following characters: a depressed conical spire; the rounded basal portion of the shell; regularly growing and smoothly keeled whorls; a crescent-shaped aperture; and teleoconch sculpture pattern (fine regularly distributed scales, giving the impression of prosocline axial striae). Further identification in the species level is not possible, but the present specimens are reminiscent (in overall shell shape and proportions) of *L. kleinii* (Klein, 1847), a common species in the German Silvana Beds.

### Genus *Urticicola* Lindholm, 1927
### *Urticicola perchtae* Salvador, 2013b
(Figs. 3H-I)

2009a *Hygromiidae* gen. indet. sp. 2. – Moser et al., p. 50.
2009 *Leucochroopsis* sp. – Böttcher, p. 241, figs. 13-14.
2013b *Urticicola perchtae* Salvador, p. 168, figs. 28-32.

**Occurrence:** Riedensheim 4 (2 specimens).

**Discussion:** The profile of the whorls (with a smooth but prominent keel-like angulation), the depressed spire and the teleoconch sculpture (regularly distributed and vertically elongated fine scales), allow the identification as *Urticicola perchtae*. The species was previously known only from the German fossil outcrops of Sandelzhausen (type locality) and Oggenhausen (Salvador 2013b), coeval with Riedensheim.

### Superfamily Limacoidea
### Family Agriolimacidae
### Genus *Deroceras* Rafinesque, 1820
### *Deroceras* sp.
(Fig. 3J)

**Occurrence:** Adelschlag-Fasanerie sand (4 specimens), Riedensheim 2 (1 specimen) and Riedensheim 4 (4 specimens).

**Remarks:** Slug shells are vestigial and internal, having a very limited taxonomic value. Nevertheless, the present material (oval shell, with nucleus lightly bent laterally and concentric well-marked growth lines) compare well to specimens of the genus *Deroceras*. As remarked by Harzhauser et al. (2014), the genus is present in Europe since the Miocene, but the fossils are often identified as either *Limax* Linnaeus, 1758 or *Milax* Gray, 1855.

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**Fig. 3.** Fossil gastropods. **A-C** – *Megalotachea silvana* (BSPG 2013 XXVI; Adelschlag-Fasanerie; H = 16.2 mm, D = 25.4 mm). **D-F** – *Palaeotachea renevieri* (BSPG 2013 XXVI; Adelschlag-Fasanerie; H = 12.5 mm, D = 16.7 mm). **G** – *Leucochroopsis* sp. (BSPG 2014 XIX 038; Riedensheim 2; H = 2.2 mm, D = 3.1 mm). **H** – *Urticicola perchtae* (BSPG 2014 XIX 063; Riedensheim 4; H = 2.1 mm, D = 3.1 mm). **I** – *Urticicola perchtae* (BSPG 2014 XIX 088; Riedensheim 4; D = 3.5 mm). **J** – *Deroceras* sp. (BSPG 2014 XIX 096; Riedensheim 2; H = 4.5 mm, D = 3.3 mm). **K** – *Vitrina suevica* (BSPG 2014 XIX 065; Riedensheim 4; H = 1.7 mm, D = 3.1 mm). **L** – *Vitrina suevica* (BSPG 2014 XIX 093; Riedensheim 4; D = 2.3 mm). **M** – *Discus pleuradrus* (BSPG 2014 XIX 084, spcm. #1; Riedensheim 4; H = 1.9 mm, D = 3.9 mm). **N** – *Discus pleuradrus* (BSPG 2014 XIX 084, spcm. #2; Riedensheim 4; D = 3.2 mm). **O** – *Granaria* sp. (BSPG 2014 XIX 091; Riedensheim 4; H = 1.7 mm, D = 1.6 mm). **P** – *Gastrocopta acuminata* (BSPG 2014 XIX 082; Riedensheim 4; H = 2.6 mm). **Q** – *Gastrocopta nouletiana* (BSPG 2014 XIX 077, spcm. #1; Riedensheim 4; H = 1.9 mm). **R** – *Gastrocopta nouletiana* (BSPG 2014 XIX 077, spcm. #2; Riedensheim 4; H = 2.2 mm). **S** – *Strobilops costata* (BSPG 2014 XIX 057; Riedensheim 4; H = 1.5 mm, D = 2.3 mm). **T** – *Strobilops uniplicata* (BSPG 2014 XIX 041; Riedensheim 2; H = 1.1 mm, D = 2.0 mm). **U** – *Negulopsis lineolata* (BSPG 2014 XIX 094; Riedensheim 4; H = 1.2 mm). **V** – *Truncatellina* cf. *pantherae* (BSPG 2014 XIX 089; Riedensheim 4; H = 1.0 mm, D = 0.9 mm).

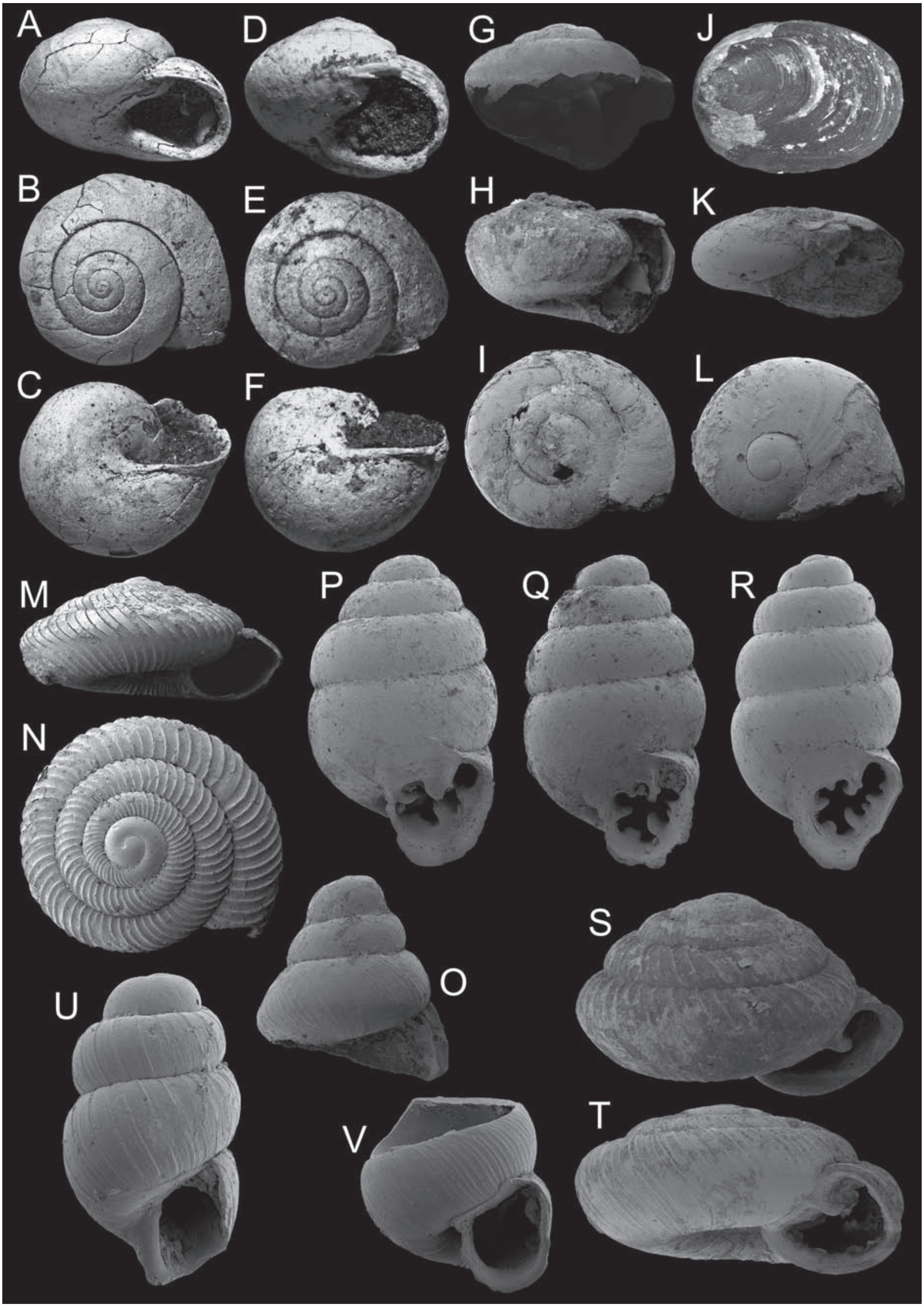

**Fig. 3.**

### Family Vitrinidae
### Genus *Vitrina* Draparnaud, 1801
### *Vitrina suevica* Sandberger, 1872
### (Figs. 3K-L)

1872 *Vitrina suevica* Sandberger, pl. 29, figs. 27a-b.
1875 *Vitrina suevica*. – Sandberger, p. 602.
1923 *Vitrina suevica suevica*. – Wenz, p. 219.
1967 *Vitrina (Vitrina) suevica suevica*. – Schütt, p. 213, fig. 17.

**Occurrence:** Riedensheim 4 (2 specimens).

**Discussion:** The present specimens have a discoidal shell, with a flattened spire and rapidly expanding whorls, a slightly incised suture and a protoconch (ca. 1 whorl) sculptured by spiral rows of punctae, which gradually transitions to a smooth teleoconch. They compare well to *Vitrina suevica* (holotype SMNS 106439). This species is known from a few Middle Miocene sites of southern Germany (Schütt 1967).

### Superfamily Punctoidea
### Family Discidae
### Genus *Discus* Fitzinger, 1833
### *Discus pleuradrus* (Bourguignat, 1881)
### (Figs. 3M-N)

1881 *Helix pleuradra* Bourguignat, p. 53, pl. 3, figs. 67-72.
1923 *Gonyodiscus (Gonyodiscus) pleuradra pleuradra*. – Wenz, p. 341.
1942 *Gonyodiscus (Gonyodiscus) pleuradra pleuradra*. – Wenz & Edlauer, p. 93.
1967 *Discus (Discus) pleuradrus*. – Schütt, p. 213, fig. 16.
1976 *Discus (Discus) pleuradrus*. – Schlickum, p. 12, pl. 2, fig. 37.
1981 *Discus (Discus) pleuradrus*. – Lueger, p. 40, pl. 4, figs. 6-7.
2000 *Discus (Discus) pleuradra* [sic]. – Fischer, p. 145, fig. 21.
2004 *Discus pleuradrus*. – Harzhauser & Binder, p. 22, pl. 7, figs. 9-11.
2006 *Discus pleuradrus*. – Kókay, p. 75, pl. 28, figs. 3-4.
2009 *Discus pleuradrus*. – Böttcher et al., p. 239, figs. 2.10-2.11.
2013 *Discus pleuradrus*. – Rasser et al., p. 439.
2014 *Discus pleuradrus*. – Salvador & Rasser, p. 195, figs. 32-33.

**Occurrence:** Adelschlag-Fasanerie clay (12 specimens), Riedensheim 2 (4 specimens) and Riedensheim 4 (>80 specimens).

**Discussion:** The present specimens show a discoid shell, with a low spire, regularly increasing whorls, a faint keel on median-upper portion of the body whorl and a wide umbilicus; the protoconch (ca. 1½ whorl) is flat and smooth, transitioning abruptly to the teleoconch, which is sculptured by strong prosocline ribs. The specimens compare well with *D. pleuradrus*, a species known from the entire extent of the Miocene in Central and Western Europe, being especially common in the OSM (Kókay 2006; Böttcher et al. 2009). Early and Late Miocene records could actually belong to other species, as remarked by Moser et al. (2009a), thus restricting *D. pleuradrus* to the Middle Miocene of France, southern Germany and Austria (Harzhauser et al. 2014). Further revision is needed for this species complex.

### Superfamily Pupilloidea
### Family Chondrinidae
### Genus *Granaria* Held, 1838
### *Granaria* sp.
### (Fig. 3O)

**Occurrence:** Adelschlag-Fasanerie clay (2 specimens), Riedensheim 2 (1 specimen) and Riedensheim 4 (10 specimens).

**Discussion:** The conical acuminated spire, regular whorl growth, convex whorls and the sculpture pattern (round and smooth protoconch of ca. 1½ whorl, transitioning abruptly to teleoconch, which is sculptured by very fine prosocline ribs) indicate the genus *Granaria* (Höltke & Rasser 2013). Spires of *Granaria* are very common in coeval sites (e.g., Salvador 2015; Salvador et al. 2015a). Since no aperture was preserved, a more precise identification is impossible.

### Family Gastrocoptidae
### Genus *Gastrocopta* Wollaston, 1878
### *Gastrocopta acuminata* (Klein, 1846)
### (Fig. 3P)

1846 *Pupa acuminata* Klein, p. 75, pl. 1, fig. 19.
1923 *Gastrocopta (Albinula) acuminata acuminata*. – Wenz, p. 916.
1999b *Gastrocopta acuminata*. – Stworzewicz, p. 161, figs. 56-58.
2000 *Gastrocopta (Albinula) acuminata*. – Manganelli & Giusti, p. 60, pl. 1, figs. 1-6; pl. 2, figs. 1-7.
2015 *Gastrocopta acuminata*. – Salvador, p. 42, fig. 7.

**Occurrence:** Adelschlag-Fasanerie clay (4 specimens), Riedensheim 2 (2 specimens) and Riedensheim 4 (>40 specimens).

**Discussion:** The present specimens compare well to *G. acuminata* (syntypes SMNS 106361), diagnosed by a proportionately larger size than other coeval congeners and the shape of the anguloparietal lamella. The species occurs from the Middle Miocene to the Late Pliocene and perhaps even the Early Pleistocene (Stworzewicz 1999b; Manganelli & Giusti 2000).

### *Gastrocopta nouletiana* (Dupuy, 1850)
### (Figs. 3Q-R)

1850 *Pupa Nouletiana* Dupuy, p. 309, pl. 15, fig. 6.
1923 *Gastrocopta (Sinalbinula) nouletiana nouletiana*. – Wenz, p. 930.
1999b *Gastrocopta nouletiana*. – Stworzewicz, p. 163, figs. 59-61.
2015 *Gastrocopta nouletiana*. – Salvador, p. 43, figs. 8-11.

**Occurrence:** Riedensheim 4 (>100 specimens).

**Discussion:** The present specimens compare well to *G. nouletiana*, a frequent species throughout the Miocene European fossil record. The shells show some variation in overall shape, from more ovate (Fig. 3Q) to more slender ones (Fig. 3R), similar to what has been reported for other sites (e.g., Salvador 2015). The number and strength of the apertural barriers also vary, as common in the family; the total number of apertural barriers is usually eight in Riedensheim and seven in Adelschlag-Fasanerie (they lack the interpalatal tooth). The present apertural barriers are: suprapalatal tooth, upper palatal tooth, interpalatal tooth, lower palatal tooth, basal tooth, columellar lamella, infraparietal lamella, anguloparietal lamella (bifid, composed by a large and thick angular lamella, vertically positioned, and a narrow parietal lamella, folded towards the outer lip).

## Family Strobilopsidae

### Genus *Strobilops* Pilsbry, 1893

### *Strobilops costata* (Clessin, 1877)

(Fig. 3S)

1877 *Strobilus costatus* (Sandberger MS) Clessin, p. 37.
1885 *Strobilus bilamellatus* Clessin, p. 79.
1915 *Strobilops (Strobilops) costata*. – Wenz, p. 79, textfig. 7, pl. 9, figs. 15-16.
1923 *Strobilops (Strobilops) costata*. – Wenz, p. 1041.
1967 *Strobilops (Strobilops) costata*. – Schütt, p. 213, fig. 15.
1999b *Strobilops costata*. – Stworzewicz, p. 152, figs. 34-37.
2006 *Strobilops costata*. – Kókay, p. 72, pl. 26, figs. 11-13.
2006 *Strobilops costata bilamellata*. – Kókay, p. 72, pl. 26, figs. 14-15.

**Occurrence:** Riedensheim 4 (8 specimens).

**Discussion:** The present specimens have a conical-depressed shell, with whorls regularly growing, a slit-shaped aperture (bearing a strong median parietal tooth), a complete thickened and greatly reflexed peristome and a wide and deep umbilicus; the protoconch (ca. 1¼ whorl) is smooth and flattened, abruptly transitioning to the teleoconch, which is sculptured by strong widely spaced prosocline ribs. They compare well to *S. costata*, a species known from the Miocene of Central Europe (type locality Undorf) and reported to have some degree of morphological variation (Stworzewicz 1999b). The species *S. bilamellatus*, also from Undorf, is considered a synonym of *S. costata* (Wenz, 1915).

### *Strobilops uniplicata* (Braun *in* Walchner, 1851)

(Fig. 3T)

1851 *Helix uniplicata* Braun *in* Walchner, p. 1138.
1885 *Strobilus planus* Clessin, p. 80, pl. 7, fig. 8.
1923 *Strobilops (Strobilops) uniplicata plana*. – Wenz, p. 1059.
1976 *Strobilops uniplicata plana*. – Schlickum, p. 11, pl. 2, fig. 31.
1999b *Strobilops uniplicata*. – Stworzewicz, p. 156, figs. 44-45.
2006 *Strobilops uniplicata plana*. – Kókay, p. 71, pl. 26, figs. 7-8.

**Occurrence:** Riedensheim 2 (1 specimen).

**Discussion:** The present specimens have a discoid shell, with regularly growing whorls, a circular aperture (with a strong median parietal tooth), a complete thickened and reflexed peristome and a wide and deep umbilicus; the protoconch (ca. 1¼ whorl) is smooth and flattened, transitioning abruptly to the teleoconch, which is sculptured by well-marked prosocline ribs. They compare well to *S. uniplicata*, a species known from the Late Oligocene to the Middle Miocene of Central Europe (Stworzewicz 1999b). The species *S. plana* (from Undorf) is a subspecies of *S. uniplicata*.

## Family Vertiginidae

### Genus *Negulopsis* Nordsieck, 2014

### *Negulopsis lineolata* (Sandberger, 1872)

(Fig. 3U)

1843 *Bulimus lineolatus* A. Braun, p. 149 [*nomen nudum*].
1851 *Bulimus lineolatus* A. Braun, p. 1137 [*nomen nudum*].
1858 *Pupa cryptodus* "Braun" Sandberger, livr. 1, pl. 5, figs. 13-13c [non *Pupa cryptodonta* A. Braun 1843; *cryptodus* Sandberger is an unjustified emendation].
1858 *Pupa suturalis*. – Sandberger, livr. 1, pl. 6, figs. 1-1a [non *Bulimus suturalis* A. Braun 1851].
1858 *Pupa (Pupilla) suturalis* "Braun" Sandberger, livr. 2, p. 54 [non *Bulimus suturalis* A. Braun 1851].
1872 *Pupa lineolata* Sandberger, pl. 23, figs. 12-12b.
1872 *Pupa lineolate*. Sandberger, p. 397, p. 438.
1919 *Negulus suturalis gracilis* Gottschick & Wenz, p. 9, pl. 1, figs. 12-13.
1923 *Negulus suturalis suturalis*. – Wenz, p. 1024 [non A. Braun 1851].
1923 *Negulus suturalis gracilis*. – Wenz, p. 1027.
1999b *Negulus suturalis*. – Stworzewicz, p. 146, figs. 23-25 [non A. Braun 1851].
2004 *Negulus gracilis*. – Harzhauser & Binder, p. 126, pl. 6, figs. 9-10.
2008 *Negulus gracilis*. – Harzhauser et al., p. 50, fig. 5.4.
2014 *Negulopsis suturalis*. – Nordsieck, p. 175, fig. 13 [non A. Braun 1851].
2015a *Negulus suturalis*. – Salvador et al., p. 266, fig. 5C [non A. Braun 1851].

**Occurrence:** Riedensheim 4 (1 specimen).

**Remarks:** The very characteristic sculpture of this minute cylindrical-pupiform Miocene snail allows the identification as the species normaly referred to as "*Negulus suturalis*" in the literature (Stworzewic 1999b; Harzhauser et al. 2008; see the nomenclatural remarks below). The two Miocene fossil species occurring in Germany are "*N. suturalis*" and *N. gracilis*; the latter was originally described as a subspecies of the previous. Harzhauser & Binder (2004) consider both species valid (based on whorl convexity and aperture height), using the name "*N. suturalis*" for Late Oligocene to Early Miocene forms and *N. gracilis* for Middle to Late Miocene forms. Stworzewicz (1999b), on a more throurough analysis, found no morphological differences between them and treat them as synonyms; a decision which is followed here. The new genus *Negulopsis* was recently created to allocate the European fossil species of *Negulus* (Nordsieck 2014), widespread from the Eocene to Pliocene (Zilch 1959-1960; Esu et al. 1993). Recent *Negulus* is exclusively African (Bruggen 1994).

**Nomenclature:** Sandberger (1875: 397) stated clearly and convincingly that A. Braun named this species *Pupa lineolata*, and that he applied the name *Bulimus suturalis* to the species *Acicula limbata* Reuss, 1849 [but actually to *A. filifera* Sandberger, 1862, which Sandberger (1875) synonymized with *A. limbata*]. Wenz (in Fischer & Wenz, 1912) reinstated the name *suturalis* without providing any justification (there or in his subsequent publications); all later authors seem to have followed him uncritically. Sandberger (1872) made the name *lineolatus* available by providing a figure with a legend. *Bulimus suturalis* is available from A. Braun (1851) and is synonymous with *A. filifera*.

Finally, Nordsieck (2014) defined the type species of the genus based on a misidentification, as explained above. As such, the type species of the genus *Negulopsis* Nordsieck, 2014 is now fixed (under Article 70.3 ICZN) as *Pupa lineolata* Sandberger, 1872, misidentified as *Pupa suturalis* Sandberger, 1858 in the original designation by Nordsieck (2014).

### Genus *Truncatellina* Lowe, 1852
### *Truncatellina* cf. *pantherae* Harzhauser & Neubauer *in* Harzhauser et al., 2014
### (Fig. 3V)

2014 *Truncatellina pantherae* Harzhauser & Neubauer *in* Harzhauser et al., 25, pl. 8, figs. 3-4, 13.

**Occurrence:** Riedensheim 4 (3 specimens).

**Discussion:** The present specimens can be assigned to the genus *Truncatellina* by the minute size, overall shape of the whorls, their growth pattern and sculpture (teleoconch sculptured by fine prosocline ribs), and the rounded trapezoid aperture, with a complete reflexed peristome. The identification beyond genus level is complicated by the fragmentary nature of the material. Nevertheless, the lack of apertural barriers seems to indicate *T. pantherae*. The single preserved aperture is somewhat narrower than in *T. pantherae*, but this could represent morphological variation.

### Genus *Vertigo* O.F. Müller, 1773
### *Vertigo angulifera* Boettger, 1884
### (Fig. 4A)

1884 *Vertigo (Alaea) angulifera* Boettger, p. 271, pl. 4, figs. 10a-c.
1923 *Vertigo (Vertilla) angulifera angulifera*. – Wenz, p. 1006.
1967 *Vertigo (Vertilla) angulifera angulifera*. – Schütt, p. 207, fig. 9.
1998 *Vertigo angulifera*. – Finger, p. 44, pl. 9, fig. H.
1999b *Vertigo angulifera*. – Stworzewicz, p. 144, fig. 18.
2008 *Vertigo angulifera*. – Harzhauser et al., p. 50, figs. 5.7-5.8.
2014 *Vertigo angulifera*. – Harzhauser et al., p. 23, pl. 8, figs. 5-7.

**Occurrence:** Riedensheim 4 (13 specimens).

**Discussion:** The present specimens compare well in overall shell shape and apertural shape and barriers with *V. angulifera*. The minute ovate shell has a smooth protoconch (ca. 1¼ whorl), transitioning rather abruptly to a teleoconch sculptured by very fine prosocline ribs; the aperture is rounded trapezoid, with a weakly marked sinulus (on the meeting of parietal and palatal regions of peristome) and four apertural lamellae (palatal, columellar, parietal and angular). *Vertigo angulifera* is known from the Early and Middle Miocene of Central Europe (Harzhauser et al. 2014).

### *Vertigo callosa* (Reuss, 1849)
### (Fig. 4B)

1849 *Pupa callosa* Reuss, p. 30, pl. 3, fig. 7.
1923 *Vertigo (Vertigo) callosa*. – Wenz, p. 983.
1999b *Vertigo callosa*. – Stworzewicz, p. 137, figs. 6-7.
2015 *Vertigo callosa*. – Salvador, p. 45, figs. 17-18.

**Occurrence:** Adelschlag-Fasanerie clay (2 specimens).

**Discussion:** The present specimens compare well to the typical *Vertigo callosa*, a commonly found fossil that ranges from the Late Oligocene to the Late Miocene of Central Europe (Stworzewicz 1999b). This species is known for a large conchological variability in size, overall shell shape, aperture shape, and number and strength of the apertural barriers (Stworzewicz 1999b; Salvador 2015). The present specimens have a rounded triangular to trapezoid aperture, with six apertural barriers, namely: parietal lamella, angular lamella, upper palatal tooth, lower palatal tooth, basal tooth, columellar lamella; the angular lamella and upper palatal tooth are in close proximity to each other, forming a circular sinulus.

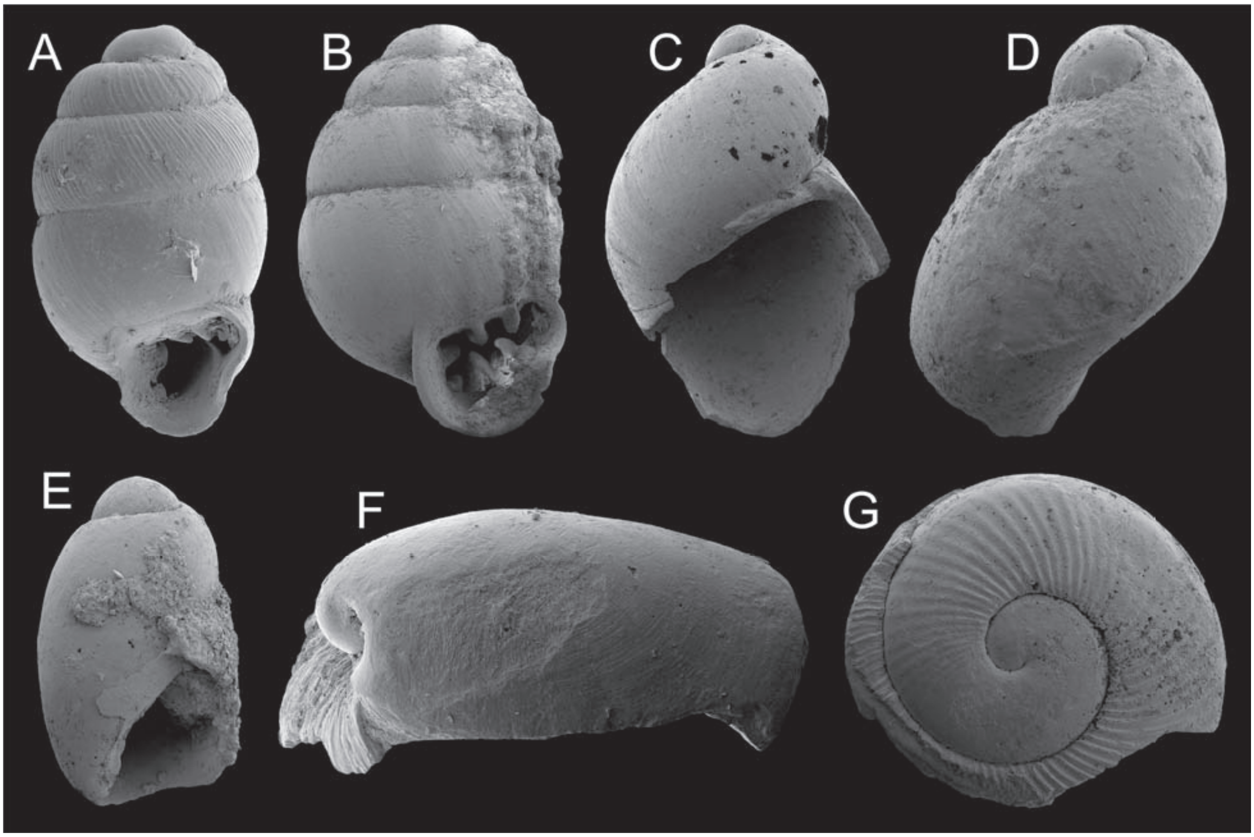

**Fig. 4.** Fossil gastropods. **A** – *Vertigo angulifera* (BSPG 2014 XIX 092; Riedensheim 4; H = 1.4 mm). **B** – *Vertigo callosa* (BSPG 2014 XX 009; Adelschlag-Fasanerie; H = 1.7 mm). **C** – *Oxyloma minima* (BSPG 2014 XIX 056; Riedensheim 4; H = 2.5 mm). **D** – *Oxyloma minima* (BSPG 2014 XIX 078; Riedensheim 4; H = 2.5 mm). **E** – *Pseudoleacina* sp. (BSPG 2014 XIX 058; Riedensheim 4; H = 2.0 mm, D = 1.2 mm). **F** – *Testacella* sp. (BSPG 2014 XIX 081; Riedensheim 4; H = 2.5 mm). **G** – *Archaeozonites* sp., shell apex fragment (BSPG 2014 XIX 062; Riedensheim 4; D = 2.6 mm).

### Superfamily Succineoidea
### Family Succineidae
### Genus *Oxyloma* Westerlund, 1885
### *Oxyloma minima* (Klein, 1853)
(Figs. 4C-D)

1853 *Succinea minima* Klein, p. 205.
1923 *Succinea (Amphibina) minima minima*. – Wenz, p. 893.
1976 *Succinea (Hydrotropa?) mínima*. – Schlickum, p. 11, pl. 2, fig. 34.
2006 *Succinea minima*. – Kókay, p. 74, pl. 27, fig. 13.
2013b *Succinea minima*. – Salvador, p. 158, figs. 1-2.
2014 *Oxyloma mínima*. – Harzhauser et al., p. 27, pl. 9, figs. 1-2, 6.

**Occurrence:** Adelschlag-Fasanerie clay (2 specimens), Riedensheim 4 (8 specimens).

**Discussion:** *Oxyloma minima* (syntypes SMNS 106410) is easily identified in fossil samples by its succineiform shell, small size, whorls growth pattern and incised suture. The species is known from several localities throughout the Miocene of Central Europe (Kókay 2006).

### Superfamily Testacelloidea
### Family Oleacinidae
### Genus *Pseudoleacina* Wenz, 1914
### *Pseudoleacina* sp.
(Fig. 4E)

**Occurrence:** Riedensheim 4 (1 specimen).

**Discussion:** The rounded and slightly bulbous protoconch, the convex but nearly straight whorl profile and elongated aperture (with a prominently acuminated meeting of the parietal and palatal regions) are together reminiscent of the genus *Pseudoleacina*. Further identification is not possible.

### Family Testacellidae

### Genus *Testacella* Draparnaud, 1801

### *Testacella* sp.

(Fig. 4F)

**Occurrence:** Riedensheim 4 (3 specimens).

**Discussion:** The vestigial ear-shaped shells of *Testacella* are very characteristic, bearing a pointed apex, quickly growing whorls, well-marked growth lines and an oval and elongated aperture, with thickened parietal and columellar regions. Only juvenile specimens were found in the present material, precluding identification to species level. Nevertheless, the overall shell shape (with a low shell and a pointed but curved apex) is reminiscent of *Testacella schuetti* Schlickum 1967, a species known from a few Middle Miocene localitites of Austria and SE Germany (Harzhauser et al. 2008; Salvador 2014).

### Superfamily Zonitoidea

### Family Zonitidae

### Genus *Archaeozonites* Sandberger, 1872

### *Archaeozonites* sp.

(Fig. 4G)

**Occurrence:** Riedensheim 2 (2 specimens) and Riedensheim 4 (6 specimens).

**Discussion:** Only apical fragments are present; nevertheless, they show the main diagnostic features of the genus *Archaeozonites* (strong prosocline ribs, flattened whorl profile and weakly marked suture), allowing at least for genus level identification. The genus is known in Europe from the Middle Eocene to the Late Pliocene (Zilch 1959-1960).

## 5. Discussion

The sedimentology of the outcrops offers the main clues about the paleoenvironment, but non-marine gastropods can help refine environmental reconstructions. Land snails, in particular, often show on the generic level a preference for one type of habitat (Barker 2001; Cook 2001; Pearce & Örstan 2006). As such, it is common for paleoecological reconstructions to use ecological data from Recent land snail genera as a guide for reconstructing the habitats of congeneric fossils (e.g., Albesa et al. 1997; Moser et al. 2009a). Some remarks concerning the gastropod paleohabitats in the Miocene sites of Riedensheim and Adelschlag-Fasanerie are thus given.

### 5.1. Riedensheim

The gastropod-bearing marly sediments are superimposed on fluvial sandy deposits that incised into the Cretaceous Wellheim Formation. The dark fossil-bearing layers are intercalated in olive-grey marls and silts containing centimeter-sized carbonate concretions and larger blocks of Cretaceous rocks up to ca. 30 cm in size. Thus, the fossil-bearing strata Riedensheim 1 to 4 probably represent oxbow lakes in which the aquatic gastropods lived and the land snails were deposited at river highstands or during flash floods. These are intercalated by floodplain deposits with possible pedogenic features (carbonate concretions). The large blocks indicate the existence of steep slopes in the vicinity that may have provided the more open area habitats needed by some of the snail species (see below).

In Riedensheim there seems to have been a rich freshwater gastropod community living in stagnant or slow moving permanent waters (such as oxbows), a well-vegetated area immediately surrounding it, and an environment dominated by humid woods beyond that (eventual patches of more open rocky or grassland areas should have existed beyond that). This reconstruction is explored in more detail below.

Regarding the freshwater environment, most of the Recent congeners can be found in many different environments, but they share a preference for richly vegetated, slow moving or standing water (Welter-Schultes 2012). The appearance of *Hippeutis* in the topmost layer of the fossil-bearing strata, as well as the upward increase in land snail diversity, could point to shallowing.

Both *Carychium* and *Oxyloma* species are hygrophilous, living in very humid forests and meadows. Moreover, *Oxyloma* can be usually found in the reed belt surrounding water bodies (Welter-Schultes 2012). The abundance of the diminutive and fragile *Carychium galli* seems to point to a very richly vegetated and humid area. *Oxyloma minima*, which also has a remarkably fragile shell, was also found relatively frequently.

When comparing the composition of the molluscan fauna across the three different layers in Riedensheim (Table 1), it is possible to see an increase in terrestrial species richness from layers 1 to 4. This could be related to increasingly hospitable habitats for the land snails in the vicinities of the water body, to the shrinking and shallowing of the water body as mentioned above or to more frequent flood events.

The vast majority of land snail species in the Riedensheim fauna are inhabitants of humid forests, in particular *Discus* and *Vitrina* (Kerney et al. 1983; Welter-Schultes 2012). Furthermore, Recent *Negulus* species are only known from tropical African forests (Bruggen

**Table 1.** Occurrence of fossil gastropod species (and total number of specimens recovered) on each site and layer (an "*" indicates that the number refers to opercula). The horizontal blank lines delimitates the groups Caenogastropoda, Basommatophora and Eupulmonata, in this order. Species are listed in the same order they appear on the text.

| | Adelschlag-Fasanerie | | | Riedensheim | | |
|---|---|---|---|---|---|---|
| Species | limestone | clay | sand | 1 | 2 | 4 |
| *Pomatias* sp. | | | | | 1* | |
| *Bithynia* sp. | | | 6* | 6* | 1* + 1 | |
| *Pseudamnicola suevicus* | | 16 | | | | >30 |
| | | | | | | |
| *Galba dupuyiana* | | >30 | | >30 | >40 | >50 |
| *Stagnicola* cf. *praebouiletti* | | | | | 1 | |
| *Lymnaea* cf. *dilatata* | 8 | | | 14 | 1 | 19 |
| *Ferrissia deperdita* | | | | 2 | 1 | |
| *Gyraulus albertanus* | | >20 | | 15 | >30 | >20 |
| *Gyraulus applanatus* | | >80 | 8 | >20 | >50 | >120 |
| *Hippeutis subfontanus* | | | | | | 5 |
| *Planorbarius cornu* | >30 | >40 | 5 | >20 | >30 | >50 |
| | | | | | | |
| *Carychium eumicrum* | | | | | | 5 |
| *Carychium galli* | | 12 | | 2 | 7 | >100 |
| *Carychium nouleti* | | 6 | | | | |
| *Pseudidyla moersingensis* | | | | 9 | >20 | >100 |
| *Azeca peneckei* | | | | | | >30 |
| *Vitrea ammoni* | | | | 1 | 3 | >80 |
| *Pseudochloritis* sp. | | | | 9 | 5 | 11 |
| *Megalotachea silvana* | | | 1 | | | |
| *Palaeotachea renevieri* | | | 1 | | | |
| *Megalotachea* vel. *Palaeotachea* | | | | 1 | | 4 |
| *Leucochroopsis* sp. | | | | | 5 | 5 |
| *Urticicola perchtae* | | | | | | 2 |
| *Deroceras* sp. | | | 4 | | 1 | 4 |
| *Vitrina suevica* | | | | | | 2 |
| *Discus pleuradrus* | | 12 | | | 4 | >80 |
| *Granaria* sp. | | 2 | | | 1 | 10 |
| *Gastrocopta acuminata* | | 4 | | | 2 | >40 |
| *Gastrocopta nouletiana* | | | | | | >100 |
| *Strobilops costata* | | | | | | 8 |
| *Strobilops uniplicata* | | | | | 1 | |
| *Negulopsis lineolata* | | | | | | 1 |
| *Truncatellina* cf. *pantherae* | | | | | | 3 |
| *Vertigo angulifera* | | | | | | 13 |
| *Vertigo callosa* | | 2 | | | | |
| *Oxyloma minima* | | 2 | | | | 8 |
| *Pseudoleacina* sp. | | | | | | 1 |
| *Testacella* sp. | | | | | | 3 |
| *Archaeozonites* sp. | | | | | 2 | 6 |

1994), but it is unclear how closely it is related to it *Negulopsis* and if an ecological comparison can be made. Some of the fossil genera are also supposed to inhabit humid forest, also tending towards warm environments, such as *Pseudoleacina*, *Pseudidyla*, *Leucochroopsis* and *Archaeozonites* (Lueger 1981; Harzhauser & Binder 2004; Harzhauser & Tempfer 2004; Nordsieck 2007). Other species can live both in forests and shrublands, provided it is a humid environment, such as those of the genera *Pomatias*, *Azeca* and *Testacella* (Kerney & Cameron 1979; Barker & Efford 2004; Welter-Schultes 2012; Rowson et al. 2014).

Nevertheless, three genera are indicative of drier and more open habitats: *Granaria* and *Truncatellina*, which thrive on calcareous rocks and on meadows (Welter-Schultes 2012; Höltke & Rasser 2013), and supposedly the fossil genus *Pseudochloritis*, whose shell is considered an adaptation for reducing water loss (Moser et al. 2009a). The scarcity and poor preservation of these taxa, hovewer, indicate that such open habitats would be located further away from the deposits.

Finally, some recent genera (*Vitrea*, *Urticicola*, *Vertigo*, *Gastrocopta* and *Strobilops*) have too broad a range of habitats (Welter-Schultes 2012) to be useful for a paleoenvironmental analysis (the latter two do not even have living native representatives in Europe). The slug *Deroceras* is also known from a broad range of habitats, including disturbed ones, provided they are humid (Rowson et al. 2014).

It is also interesting to note the presence of two carnivorous species in the studied fauna. *Pseudoleacina* is a fossil genus, but its species likely were malacophagous, as are the remainder of the oleacinids (Barker & Efford 2004). Recent *Testacella* feed mainly on earthworms, but gastropods and centipedes are also part of their diet (Barker & Efford 2004; Rowson et al. 2014). These two gastropods would surely have a broad range of prey to choose from in Riedensheim. No clear signs of predation by other malacophagous animals (such as holes on the shell, breakage followed by shell repair or anomalous growth etc.) were found in the present material.

## 5.2. Adelschlag-Fasanerie

The sedimentology of the basal layers of the sand pit points to a carbonate-rich freshwater lake. The initial lacustrine limestone precipitated during this phase was not exposed during sampling (it was seen only as a pile of rubble in one corner of the pit), which may explain the low diversity of the recorded fauna as a sampling bias. Later, argillaceous sediments including the reddish to brownish clay were deposited, presumably indicating an increasingly shallow water body. A poorly sorted sandy gravel layer containing limonitic wood and bone debris marks the transition to the sandy layers overlying this deposit. The depositional system thus indicates the rapid transition from a flood plain environment to fluvial channel deposits.

The freshwater fauna is clearly dominated by *Gyraulus applanatus*, with comparatively few representatives of the other species. A considerable proportion of specimens of *G. applanatus* bear marks of shell breakage and further growth (Fig. 2M), which are commonly interpreted as the survival of these individuals after predation attempts. The pulmonate aquatic fauna is consistent with both temporary and perennial water bodies, but the presence of *Pseudamnicola* points to a perennial water body during the clay layer (Table 1). The impoverished aquatic fauna of the sand layer is consistent with the transition to fluvial channel deposits. As in Riedensheim, the presence of the hygrophilous genera *Carychium* and *Oxyloma* seem to indicate a well-vegetated area surrounding the water body. The remaining of the terrestrial fauna is not very useful for paleoecological analysis, but *Discus* at least is a reasonable indicator for humid forests.

## 5.3. Faunal composition

Comparing the overall faunas, 13 of the 17 species occurring in Adelschlag-Fasanerie are also known from Riedensheim (which has 35 species, considering all layers; Table 1). Given the possible biostratigraphic correlation explained above (OSM C+D), the most obvious comparison of these presently described snail faunas would be with the geographically close and nearly coeval localities of Adelschlag, Attenfeld, Sandelzhausen and Undorf (see also Table 2 of Appendix 2).

Riedensheim shares ca. 60% of its snail species with Sandelzhausen (reinterpreting the records of the genera *Limax* and *Milax* as *Deroceras* sp., as explained above), but only ca. 45% with Undorf. Similarly, Adelschlag-Fasanerie shares 12 of its species with Sandelzhausen and only eight with Undorf. As such, the presently studied faunas seem to have a greater affinity with Sandelzhausen. The species that occur only in Riedensheim and not in Sandelzhausen (*Negulopsis lineolata*, *Truncatellina* cf. *pantherae*, *Vertigo angulifera* and *Vitrea ammoni*) do not provide much information with respect to the paleoecological analysis. In contrast, species occurring only in Sandelzhausen, indicate a much more diverse freshwater environment (see also Moser et al. 2009b; Salvador & Rasser 2014).

Finally, the faunas of Adelschlag and Attenfeld (see the revised identification on Table 1 of Appendix 2) are restricted to freshwater species, all of which occur in Adelschlag-Fasanerie and/or Riedensheim. The comparison with these faunas underlines the expected affinities given the geographic and stratigraphic proximity of these two localities. The single terrestrial species found (*Opeas minutum* from Adelschlag) is recorded only from Undorf among the further localities discussed here.

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## Appendix 1

### List of analyzed material

All the material from Riedensheim and Adelschlag-Fasanerie available for each species is listed here. The order in which the species are presented below is the same as they appear in the main body of the text. Institutional abbreviations: BSPG = Bayerische Staatssammlung für Paläontologie und Geologie (Munich, Germany); SMNS = Staatliches Museum für Naturkunde Stuttgart (Stuttgart, Germany).

***Pomatias* sp.:** BSPG 2014 XIX 095 (1 operculum).

***Bithynia* sp.:** BSPG 2014 XIX 012 (4 opercula), XIX 039 (1 spcm., 1 operculum), XX 014 (2 opercula), XX 018 (3 opercula). SMNS 101684 (2 opercula), 101717 (1 operculum).

***Pseudamnicola suevicus* (Gottschick, 1928):** BSPG 2014 XIX 086 (~20 spcm.), XX 003 (6 spcm.), XX 020 (4 spcm.). SMNS 101687 (6 spcm.), 101693 (6 spcm.).

***Galba dupuyiana* (Noulet, 1854):** BSPG 2014 XIX 010 (~30 spcm.), XIX 018 (~30 spcm.), XIX 022 (5 spcm.), XIX 034 (7 spcm.), XIX 037 (1 spcm.), XIX 061 (~20 spcm.), XIX 067 (~20 spcm.), XX 010 (~30 spcm.). SMNS 101699 (8 spcm.).

***Stagnicola* cf. *praebouiletti* (Schlickum, 1970c):** BSPG 2014 XIX 037 (1 spcm.).

***Lymnaea dilatata* Noulet, 1854:** BSPG 2013 XXVI (8 spcm.); 2014 XIX 007 (14 spcm.), XIX 040 (1 spcm.), XIX 049 (4 spcm.), XIX 071 (15 spcm). SMNS 101695 (1 spcm.).

***Ferrissia deperdita* (Desmarest, 1814):** BSPG 2014 XIX 009 (2 spcm.), XIX 015 (1 spcm.).

***Gyraulus albertanus* (Clessin, 1877):** BSPG 2014 XIX 001 (10 spcm.), XIX 014 (~30 spcm.), XIX 035 (2 spcm.), XIX 054 (4 spcm.), XIX 080 (~20 spcm.), XX 005 (~20 spcm.). SMNS 101683 (5 spcm.), 101708 (3 spcm.).

***Gyraulus* applanatus (Thomae, 1845):** BSPG 2014 XIX 002 (~20 spcm.), XIX 020 (~50 spcm.), XIX 029 (~40 spcm.), XIX 060 (~40 spcm.), XIX 075 (>50 spcm.), XX 004 (>50 spcm.), XX 016 (8 spcm.). SMNS 101686 (~30 spcm.), 101694 (~30 spcm.), 101706 (12 spcm.), 101709 (3 spcm.).

***Hippeutis subfontanus* (Clessin, 1877):** BSPG 2014 XIX 055 (3 spcm.), XIX 068 (1 spcm.). SMNS 101704 (1 spcm.).

***Planorbarius cornu* (Brongniart, 1810):** BSPG 2013 XXVI (~30 spcm.); 2014 XIX 008 (~20 spcm.), XIX 016 (8 spcm.), XIX 025 (6 spcm.), XIX 030 (~20 spcm.), XIX 053 (>50 spcm.), XIX 079 (>50 spcm.), XX 011 (~40 spcm.), XX 013 (1 spcm.), XX 017 (5 spcm.). SMNS 101685 (2 spcm.).

***Carychium eumicrum* Bourguignat, 1857:** BSPG 2014 XIX 083 (3 spcm.). SMNS 101702 (2 spcm.).

***Carychium (Carychium) galli* Salvador, 2015:** BSPG 2014 XIX 005 (2 spcm.), XIX 017 (4 spcm.), XIX 052 (6 spcm.), XIX 087 (>50 spcm.), XX 007 (7 spcm.). SMNS 101690 (5 spcm.), 101698 (~40 spcm.), 101707 (3 spcm.), 101713 (7 spcm.).

***Carychium nouleti* Bourguignat, 1857:** BSPG 2014 XX 001 (1 spcm.), XX 019 (1 spcm.). SMNS 101719 (4 spcm.).

***Pseudidyla moersingensis* (Boettger, 1877):** BSPG 2014 XIX 006 (9 spcm.), XIX 013 (16 spcm.), XIX 026 (1 spcm.), XIX 042 (9 spcm.), XIX 066 (~40 spcm.), XIX 074 (>50 spcm.). SMNS 101697 (12 spcm.).

***Azeca peneckei* Andreae, 1892:** BSPG 2014 XIX 064 (~20 spcm.), XIX 073 (14 spcm.).

***Vitrea ammoni* (Clessin, 1892):** BSPG 2014 XIX 011 (1 spcm.), XIX 027 (3 spcm.), XIX 059 (~20 spcm.), XIX 085 (~30 spcm.). SMNS 101703 (12 spcm.), 101715 (15 spcm.).

***Pseudochloritis* sp.:** BSPG 2014 XIX 003 (9 spcm.), XIX 021 (4 spcm.), XIX 031 (1 spcm.), XIX 072 (11 spcm.).

***Megalotachea silvana* (Klein, 1853):** BSPG 2013 XXVI (1 spcm.).

***Palaeotachea renevieri* (Maillard, 1892):** BSPG 2013 XXVI (1 spcm.).

***Megalotachea* vel *Palaeotachea* sp.:** BSPG 2014 XIX 004 (1 spcm.), XIX 045 (2 spcm.), XIX 076 (2 spcm.).

***Leucochroopsis* sp.:** BSPG 2014 XIX 023 (1 spcm.), XIX 038 (4 spcm.), XIX 050 (4 spcm.), XIX 090 (1 spcm.).

***Urticicola perchtae* Salvador, 2013b:** BSPG 2014 XIX 063 (1 spcm.), 2014 XIX 088 (1 spcm.).

***Deroceras* sp.:** BSPG 2014 XIX 096 (1 spcm.), XIX 097 (2 spcm.), XX 015 (2 spcm.). SMNS 101716 (2 spcm.), 101718 (2 spcm.).

***Vitrina suevica* Sandberger, 1872:** BSPG 2014 XIX 065 (1 spcm.), XIX 093 (1 spcm.).

***Discus pleuradrus* (Bourguignat, 1881):** BSPG 2014 XIX 024 (1 spcm.), XIX 033 (3 spcm.), XIX 043 (~30 spcm.), XIX 084 (~30 spcm.), XX 012 (12 spcm.). SMNS 101696 (~20 spcm.).

***Granaria* sp.:** BSPG 2014 XIX 036 (1 spcm.), XIX 044 (4 spcm.), XIX 091 (6 spcm.), XX 008 (2 spcm.).

***Gastrocopta acuminata* (Klein, 1846):** BSPG 2014 XIX 019 (1 spcm.), XIX 028 (1 spcm.), XIX 051 (9 spcm.), XIX 082 (~20 spcm.), XX 002 (4 spcm.). SMNS 101705 (13 spcm.), 101714 (3 spcm.).

***Gastrocopta nouletiana* (Dupuy, 1850):** BSPG 2014 XIX 048 (~30 spcm.), XIX 077 (~30 spcm.). SMNS 101700 (~20 spcm.), 101712 (~20 spcm.).

***Strobilops costata* (Clessin, 1877):** BSPG 2014 XIX 057 (2 spcm.), XIX 070 (4 spcm.). SMNS 101692 (1 spcm.), 101711 (1 spcm.).

***Strobilops uniplicata* (Braun *in* Walchner, 1851):** BSPG 2014 XIX 041 (1 spcm.).

***Negulopsis lineolata* (Sandberger, 1872):** BSPG 2014 XIX 094 (1 spcm.).

***Truncatellina* cf. *pantherae* Harzhauser & Neubauer *in* Harzhauser et al., 2014:** BSPG 2014 XIX 089 (3 spcm.).

***Vertigo angulifera* Boettger, 1884:** BSPG 2014 XIX 047 (1 spcm.), XIX 092 (7 spcm.). SMNS 101701 (5 spcm.).

***Vertigo callosa* (Reuss, 1849):** BSPG 2014 XX 009 (1 spcm.). SMNS 101688 (1 spcm.).

***Oxyloma minima* (Klein, 1853):** BSPG 2014 XIX 056 (1 spcm.), XIX 078 (3 spcm.), XX 006 (1 spcm.). SMNS 101689 (1 spcm.), 101691 (3 spcm.), 101710 (1 spcm.).

***Pseudoleacina* sp.:** BSPG 2014 XIX 058 (1 spcm.).

***Testacella* sp.:** BSPG 2014 XIX 046 (1 spcm.), XIX 081 (2 spcm.).

***Archaeozonites* sp.:** BSPG 2014 XIX 032 (2 spcm.), XIX 062 (2 spcm.), XIX 069 (4 spcm.).

## Appendix 2

**Table 1.** Gastropod species reported by Reichenbacher et al. (2004) for the localities of Adelschlag and Attenfeld. The SEM images provided by these authors were used to offer a revised identification of the species (unfortunately, they did not figure *Bithynia* sp.).

| Reichenbacher et al. (2004) | Revised identification | Adelschlag | Attenfeld |
|---|---|---|---|
| *Belgrandiella*? sp. | *Pseudamnicola suevicus* | X | |
| *Bithynia* sp. | (not figured) | X | |
| *Lymnaea* sp. | *Galba dupuyiana* | X | X |
| *Omphiscola* sp. | *Opeas minutum* | X | |
| *Radix* sp. | *Lymnaea dilatata* | X | X |
| *Ferrissia* sp. | *Ferrissia deperdita* | X | X |
| *Gyraulus* sp. A | *Gyraulus applanatus* | X | X |
| *Gyraulus* sp. B | *Gyraulus albertanus* | X | |
| *Gyraulus* sp. C | *Gyraulus applanatus* | X | |
| *Hippeutis* sp. | *Hippeutis subfontanus* | X | |
| *Planorbarius* sp. | *Planorbarius cornu* | X | X |

**Table 2.** Occurrence of gastropod species in the following localities: Adelschlag (Adels.), Adelschlag-Fasanerie (Ad.-Fasan.), Attenfeld (Atten.), Riedensheim, Sandelzhausen and Undorf. Species occurrence for Adelschlag and Attenfeld as reported by Reichenbacher et al. (2004) and revised here (Appendix: Table 1); for Sandelzhausen as reported by Salvador (2013a, b, c) and Salvador & Rasser (2014); for Undorf by Clessin (1911), excluding dubious taxa (*sensu* Wenz 1923). Division of layers for Sandelzhausen follow Moser et al. (2009a); a "?" indicates that the precise layer of origin is unknown.

| **Species** | **Adels.** | **Adelschlag-Fasanerie** | | | **Atten.** | **Riedensheim** | | | **Sandelzhausen** | | **Undorf** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | **limestone** | **clay** | **sand** | | **1** | **2** | **4** | **B-C2** | **C3-D1** | |
| *Acanthinula trochulus* | | | | | | | | | | | x |
| *Acicula isselii* | | | | | | | | | | | x |
| *Archaeozonites costatus* | | | | | | | | | | | x |
| *Archaeozonites* sp. | | | | | | | x | x | x | x | |
| *Argna praeambula* | | | | | | | | | | | x |
| *Argna pseudoennea* | | | | | | | | | | | x |
| *Azeca peneckei* | | | | | | | | x | | | |
| *Bithynia gracilis* | | | | | | | | | | | x |
| *Bithynia* sp. | x | | | x | | x | x | | | x | |
| *Carychium eumicrum* | | | x | | | | | x | ? | ? | x |
| *Carychium galli* | | | | | | x | x | x | | x | |
| *Carychium nouleti* | | | x | | | | | | | | x |
| *Deroceras* sp. | | | | x | | | x | x | ? | ? | x |
| *Discus pleuradrus* | | | x | | | | x | x | | x | |
| *Discus undorfensis* | | | | | | | | | | | x |
| *Emarginaria schaefferiana* | | | | | | | | | | | x |
| Endodontidae indet. | | | | | | | | | | x | |
| *Ferrissia deperdita* | x | | | | x | x | x | | x | | x |
| *Galba dupuyiana* | x | | x | | x | x | x | x | x | x | |
| *Gastrocopta acuminata* | | | x | | | | x | x | | x | x |
| *Gastrocopta nouletiana* | | | | | | | | x | x | x | x |
| *Granaria grossecostata* | | | | | | | | | x | x | |
| *Granaria* sp. | | | x | | | | x | x | x | x | |
| *Gyraulus albertanus* | x | | x | | | x | x | x | x | x | |
| *Gyraulus applanatus* | x | | x | x | x | x | x | x | | x | x |
| *Helicodonta involuta* | | | | | | | | | | | x |
| *Helicodonta* sp. | | | | | | | | | ? | ? | |
| *Hippeutis subfontanus* | x | | | | | | | x | | | x |
| *Hippeutis* sp. | | | | | | | | | | x | |
| *Janulus supracostatus* | | | | | | | | | ? | ? | x |
| *Klikia coarctata* | | | | | | | | | | x | |
| *Klikia giengensis* | | | | | | | | | | | x |
| *Leucochroopsis kleini* | | | | | | | | | | x | x |
| *Leucochroopsis* sp. | | | | | | | x | x | | | |
| *Lucilla subteres* | | | | | | | | | x | | x |
| *Lymnaea dilatata* | x | x | | | x | x | x | x | x | x | x |
| *Megalotachea eversa* | | | | | | | | | x | x | |
| *Megalotachea silvana* | | | | x | | | | | | | x |
| *Megalotachea sylvestrina* | | | | | | | | | x | x | |
| *Negulopsis lineolata* | | | | | | | | x | | | x |

| Species | Adels. | Adelschlag-Fasanerie | | | Atten. | Riedensheim | | | Sandelzhausen | | Undorf |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | limestone | clay | sand | | 1 | 2 | 4 | B-C2 | C3-D1 | |
| *Opeas minutum* | x | | | | | | | | | | x |
| *Orcula* sp. | | | | | | | | | | | x |
| *Oxychilus subnitens* | | | | | | | | | | | x |
| *Oxyloma minima* | | | x | | | | | x | | x | x |
| *Palaeoglandina porrecta* | | | | | | | | | | | x |
| *Palaeoglandina* sp. | | | | | | | | | x | x | |
| *Palaeotachea renevieri* | | | | x | | | | | | | |
| *Palaina dietzi* | | | | | | | | | | | x |
| *Planorbarius cornu* | x | x | x | x | x | x | x | x | x | x | x |
| *Platyla alta* | | | | | | | | | | | x |
| *Platyla diezi* | | | | | | | | | | | x |
| *Platyla flachi* | | | | | | | | | | | x |
| *Pomatias consobrina* | | | | | | | | | | | x |
| *Pomatias* sp. | | | | | | | x | | x | | |
| *Pseudamnicola suevicus* | x | | x | | | | | x | | | |
| *Pseudidyla moersingensis* | | | | | | x | x | x | x | x | x |
| *Pseudochloritis incrassata* | | | | | | | | | x | x | x |
| *Pseudochloritis* sp. | | | | | | x | x | x | | | |
| *Pseudoleacina* sp. | | | | | | | | x | | | |
| *Pyramidula* sp. | | | | | | | | | ? | ? | |
| *Radix socialis* | | | | | | | | | | x | |
| *Segmentina lartetii* | | | | | | | | | | x | x |
| *Serrulina clessini* | | | | | | | | | | | x |
| *Stagnicola* cf. *praebouiletti* | | | | | | | x | | | | |
| *Strobilops costata* | | | | | | | | x | | | x |
| *Strobilops* sp. | | | | | | | | | x | | |
| *Strobilops uniplicata* | | | | | | | x | | | | x |
| *Testacella* sp. | | | | | | | | x | | | |
| *Testacella zellii* | | | | | | | | | x | | x |
| *Theodoxus* sp. | | | | | | | | | | x | |
| *Triptychia bacillifera* | | | | | | | | | | | x |
| *Triptychia kleini* | | | | | | | | | | | x |
| *Triptychia* sp. | | | | | | | | | x | x | |
| *Truncatellina lentilii* | | | | | | | | | | | x |
| *Truncatellina* cf. *pantherae* | | | | | | | | x | | | |
| *Urticicola perchtae* | | | | | | | | x | | x | |
| *Vallonia lepida* | | | | | | | | | | x | x |
| *Valvata* sp. | | | | | | | | | | x | |
| *Vertigo angulifera* | | | | | | | | x | | | |
| *Vertigo callosa* | | | x | | | | | | x | x | x |
| *Vertigo flexidens* | | | | | | | | | | | x |
| *Vitrea ammoni* | | | | | | x | x | x | | | x |
| *Vitrea subdiaphana* | | | | | | | | | | | x |
| *Vitrina suevica* | | | | | | | | x | | x | x |
| *Zonitoides boettgerianus* | | | | | | | | | | | x |

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**Article**

# Fossil gastropods from Miocene Lake Randeck Maar and its hinterland (SW Germany)

**Rodrigo B. Salvador, Michael W. Rasser, and Olaf Höltke**

With 5 figures and 1 table

**Abstract:** The Randeck Maar lake sediments from southwestern Germany were deposited during the late Early to early Middle Miocene (mammal zone MN 5). Although historically well known as an important fossil Lagerstätte, there are few works that have dealt specifically with the fossil gastropods (no bivalves have ever been found). A revision is presented herein of all the material available from the site, both from historical museum collections and from new excavations, figuring much of these gastropods for the first time. The snail fauna of the Randeck Maar now comprises a total 32 continental gastropod species, among which only four are freshwater: *Lymnaea* cf. *dilatata*, *Ferrissia deperdita*, *Gyraulus kleini* and *Planorbarius cornu*. The terrestrial snail fauna consist mostly of land-dwelling pulmonates, being dominated by the following species: *Pomatias conicus* (the only operculate snail in the fauna), *Cochlicopa loxostoma*, *Granaria* sp. and *Praeoestophorella phacodes*. Finally, the following species are reported for the first time from Randeck Maar: Clausiliinae indet., *Triptychia kleini*, *Palaeotachea renevieri*, *Deroceras* sp., *Milax* sp., *Gastrocopta sandbergeri*, *Testacella zellii*. Such a diverse snail fauna might help elucidate paleoecological questions regarding the Randek Maar lake and its hinterland.

**Key words:** Gastropoda, Caenogastropoda, Pulmonata, Early/Middle Miocene, lake paleoenvironments, MN 5 European Mammal Neogene zone.

## 1. Introduction

The Randeck Maar lake sediments were deposited during the "Mid-Miocene Climatic Optimum" that lasted from ca. 17 to 15 Ma bp (late Early/early Middle Miocene, mammal zone MN5), which was the last time interval favorable for a thermophilous fauna and flora in Europe and a time of increased seasonality (Fig. 1; Zachos et al. 2001; Böhme et al. 2011). A paleoenvironmental reconstruction based on 363 taxa provided a relatively detailed picture of the various habitats of the Randeck Maar and its environs (Rasser et al. 2013).

Although historically well known as an important fossil Lagerstätte (*e.g.*, Schweigert & Bechly 2001), there are few works that have dealt specifically with the gastropods from Randeck Maar (no bivalves have ever been found). Both Ehrat & Jooss (1921) and Seemann (1926) offered a list of species in addition to indicating the facies in which they occur, but without describing or figuring the snails. More recently, Rasser et al. (2013) offered a preliminary identification of the material (also figuring some specimens), but within the context of a broader paleoenvironmental analysis in which the mollusks were not the main focus. A revision of all available gastropod material from the Randeck Maar is thus presented here. Many of the species are here recorded as well as figured for the first time for the Randeck Maar.

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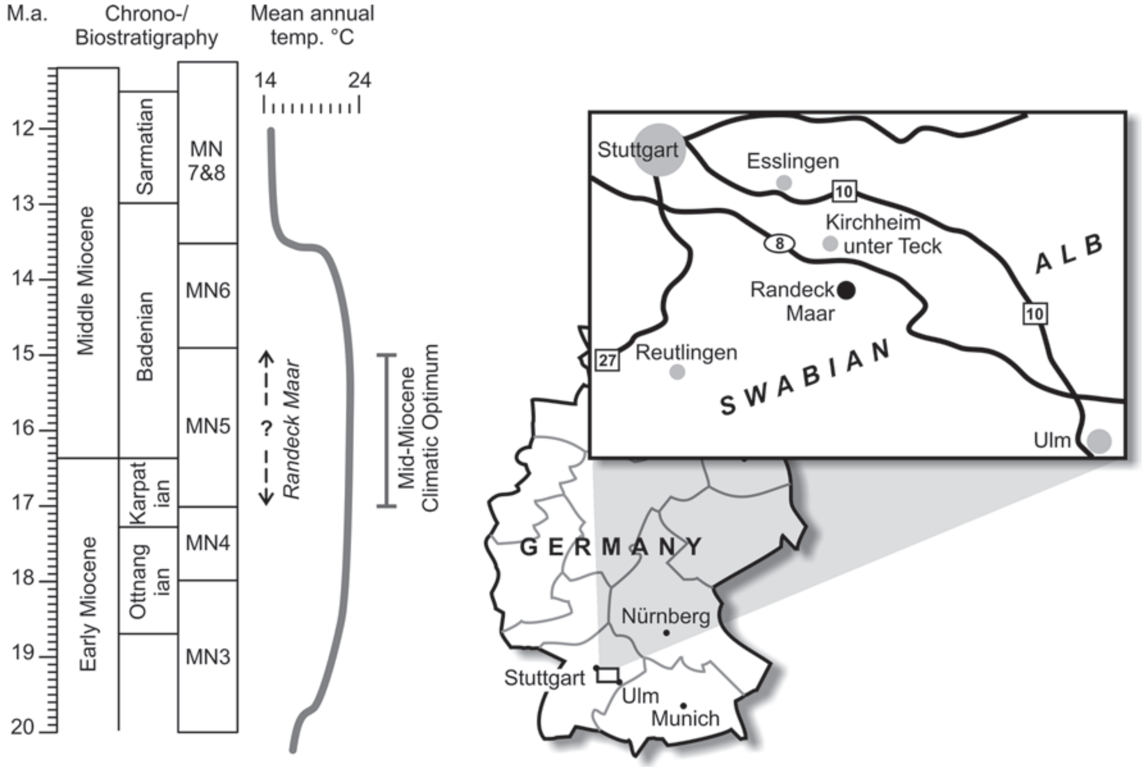

**Fig. 1.** Geography and stratigraphy of the Randeck Maar.

## 2. Geological setting

The Randeck Maar in SW Germany at the northern margin of the Swabian Alb (Fig. 1) belongs to a large volcanic area that was active during the Early/Middle Miocene, and was formed by a phreatomagmatic explosion (Lorenz 1979). No radiometric data exist so far (Krochert et al. 2009), but small mammals indicate a MN 5 age (following the European Mammal Neogene zone), *i.e.*, latest Early Miocene to earliest Middle Miocene (Fig. 1; Heizmann 1983; Rasser et al. 2013). Due to its volcanogenic origin, a crater with a diameter of ca. 1800 m, steep slopes and a crater rim was formed. The resulting lake lacked tributaries and therefore represented a protected setting with a topographic relief of ca. 220 m and water depths of up to ca. 130 m (Rasser et al. 2013, 2014). Today, ca. 60 m of lake sediments are preserved.

Jankowski (1981) separated three consecutive lake stages (Fig. 2). The first one appeared immediately after maar formation. It starts with an alluvial stage with reworked vulcanites, followed by a brackish and lacustrine-eutrophic lake stage. The latter comprises bituminous laminites (dysodil) in the deepest parts, calcareous and marly laminites (“Süßwasserkalk” in the older German literature) in the more marginal parts as well as littoral limestones and dolomites. The third lake stage is characterized by massive, fossiliferous freshwater limestones.

Most of the terrestrial gastropods originate from the reworked vulcanites, generally referred to as “light tuffite” (*i.e.*, yellowish to brownish; “heller/gelber Tuff” in the German literature) and “dark tuffite” (*i.e.*, grayish to black; “dunkler/schwarzer Tuff” in the German literature). Ehrat & Jooss (1921) assumed that these two types of tuffites were formed during two different eruptive events. Later studies, starting with Seemann (1926) suggested, however, that they are two different, synchronous facies types. While the dark tuffite contains both terrestrial and freshwater snails, the light tuffites contain almost only terrestrial snails (Ehrat & Joss 1921; Seemann 1926). Seemann (1926) suggested that the dark tuffite formed in the deepest part of the earliest maar stage under permanent water cover, while the light tuffite formed subaerially in a more marginal position. The calcareous laminites,

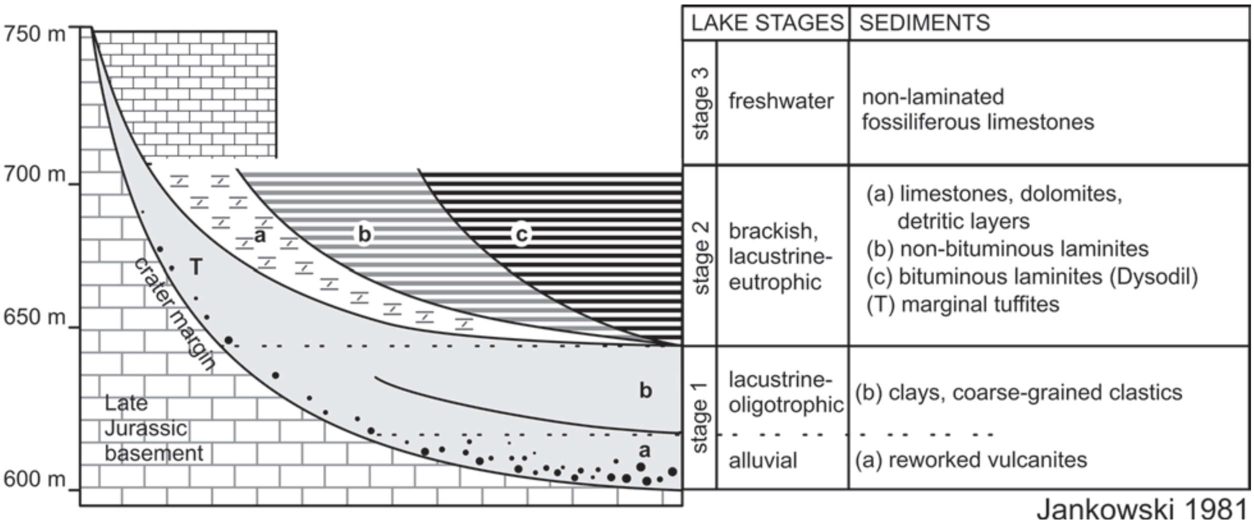

**Fig. 2.** Schematic cross section through the Randeck Maar sediments after Jankowski (1981). A "T" indicates the position of the light and dark tuffites. See Table 1 for the distribution of snails in the different facies types.

all of which are aquatic sediments, are dominated by aquatic gastropods (Rasser et al. 2013).

## 3. Material and methods

Various excavations in the Randeck Maar have taken place since the middle of the 19th century and are continued until today (Rasser et al. 2014). Most of the available gastropods originate from excavations lacking sufficient documentation, which makes the attribution to certain facies/habitat types difficult (Rasser et al. 2013). All the molluscan material from the Randeck Maar is housed at the collection of the Staatliches Museum für Naturkunde Stuttgart (SMNS; Stuttgart, Germany), with some additional material housed at the Urweltmuseum Hauff (UHH; Holzmaden, Germany). All available specimens (ca. 2000) were analyzed; the list of examined material can be found in Appendix 1 (additional material consisting of unidentifiable fragments or external molds is not listed). Unfortunately, part of the historical material is lost and the presence of one species previously reported for the site (Ehrat & Jooss 1921; Wenz 1923; Seemann 1926), namely *Joossia insignis* (von Zieten), could not be confirmed. Selected specimens were examined by scanning electronic microscopy (SEM) in the SMNS. Shell measurements abbreviations: H = shell length; D = shell greatest width; h = aperture height; d = aperture width.

As far as the taxonomy is concerned, Bouchet et al. (2005) are followed, with further modifications pointed out by Nordsieck (2014) regarding the fossil land snail fauna, and by Thompson (2010), moving the Euglandininae from the Oleacinidae to the Spiraxidae.

Finally, inconsistencies in the precise naming of gastropod taxonomic ranks in the text and figure captions in Rasser et al. (2013) are cleared up. This is the case for: (1) *Cochlicopa subrimata* and *Cochlicopa subrimata loxostoma*; (2) *Tropidomphalus (Pseudochloritis) incrassata* [sic] and *Pseudochloritis incrassata*; (3) *Discus* sp. and *Discus pleuradrus*; (4) *Granaria* ?*schuebleri* and *Granaria* sp. The reasons for preferring one name over the other in this paper are explained in the text.

## 4. Systematics

Caenogastropoda
Superfamily Littorinoidea
Family Pomatiidae
Genus *Pomatias* Studer, 1789
*Pomatias conicus* (Klein, 1853)
(Fig. 3A)

*Cyclostoma conicum* Klein, 1853: 217 (pl. 5, fig. 14).
*Tudora conica*: Ehrat & Jooss, 1921: 3.
*Tudorella conica conica*: Wenz, 1923: 1820; Seemann, 1926: 90; Berz & Jooss, 1927: 206.
*Pomatias conicus conicus*: Papp & Thenius, 1953: 21 (pl. 3, fig. 7).
*Tudorella conica*: Schlickum, 1976: 3 (pl. 1, fig. 2-3).
*Pomatias conica*: Lueger, 1981: 10 (pl. 1, figs. 11-12, pl. 6, fig. 3); Kókay, 2006: 33 (pl. 4, fig. 4); Rasser et al., 2013: 440 (pl. 4, fig. 11).
*Pomatias conicus*: Harzhauser & Kowalke, 2002: 70 (pl.

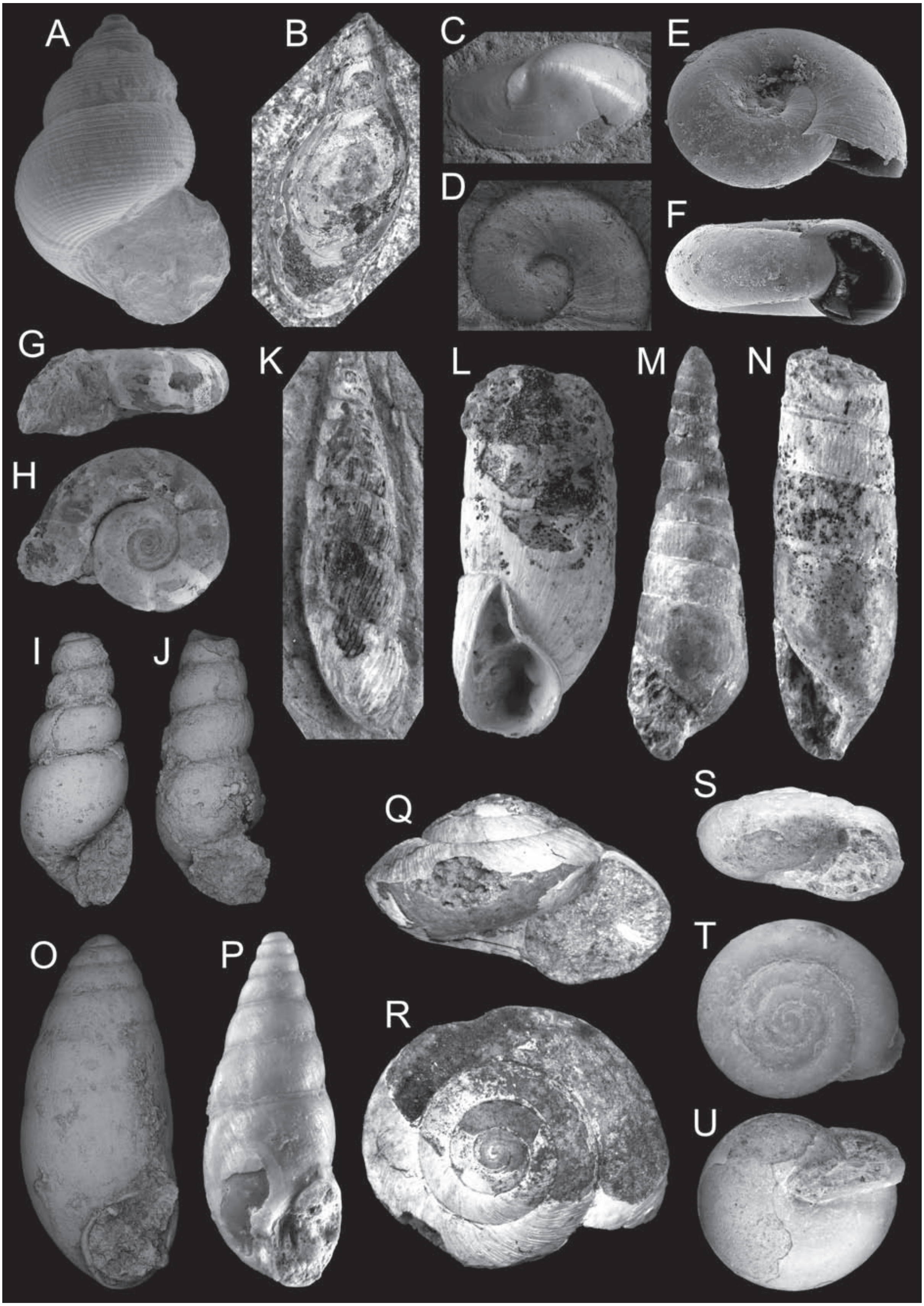

**Fig. 3.** Gastropods of the Randeck Maar.

**Table 1.** Distribution of the gastropod species of Randeck Maar in the different facies types. 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); **MLs,** marginal limestones and marls (stage 2a); **CL,** calcareous laminites (stage 2b); **Dys,** dysodil (stage 2c).

| **Species** | **DT** | **BT** | **MLs** | **CL** | **Dys** |
|---|---|---|---|---|---|
| *Apula coarctata* | | 65 | 7 | | |
| *Archaeozonites costatus* | | 1 | 11 | | |
| Clausiliidae indet. | | | 33 | | |
| *Cochlicopa loxostoma* | 1 | 254 | 5 | | |
| *Deroceras* sp. | | | 3 | | |
| *Discus pleuradrus* | | 7 | 4 | | |
| *Ferrissia deperdita* | 4 | | 38 | 33 | 1 |
| *Gastrocopta* cf. *acuminata* | | 1 | | | |
| *Gastrocopta sandbergeri* | | 1 | | | |
| *Granaria* sp. | | 218 | 48 | 3 | |
| *Gyraulus kleini* | 2 | | 11 | 50 | 3 |
| *Helicodonta involuta* | | 18 | 1 | | |
| *Leucochroopsis kleini* | 7 | 91 | 22 | 2 | |
| *Lymnaea* cf. *dilatata* | 13 | 1 | 9 | 45 | |
| *Megalotachea silvana* | ? | 23 | 6 | | |
| *Milax* sp. | | | 1 | | |
| *Negulus suturalis* | | 1 | | | |
| *Opeas* cf. *minutum* | | 8 | | | |
| *Palaeoglandina gracilis* | 1 | 3 | | | |
| *Palaeomastus filocinctus* | | 1 | | | |
| *Palaeotachea renevieri* | | 25 | | | |
| *Planorbarius cornu* | 8 | | 47 | 40 | 1 |
| *Pomatias conicus* | 2 | 167 | 76 | | |
| *Praeoestophorella phacodes* | | 219 | 1 | | 1 |
| *Pseudochloritis incrassata* | | 24 | | | |
| *Pseudoleacina eburnea* | | 68 | | | |
| *Testacella zellii* | | | 10 | | |
| *Triptychia kleini* | | | 1 | | |
| *Triptychia randeckiana* | | 4 | 31 | | |
| ?*Truncatellina sp.* | | 6 | | | |
| *Vallonia* cf. *lepida* | | 2 | | | |
| *Vitrina suevica* | | 29 | | | |

10, figs. 6-8).
*Pomatias conicum*: Harzhauser & Binder, 2004: 7 (pl. 1, figs. 7-11).

**Stratigraphic occurrence:** dark tuffites, light tuffites, marginal limestones and marls (Fig. 2; Table 1).

**Description:** Shell small, trochiform; shell width ~2/3 its length. Protoconch (1¾ whorl) rounded, smooth; transition to teleoconch clear. Teleoconch sculpture reticulated, with stronger spiral ribs and weaker axial ribs; distance between spiral ribs equal to twice their width; distance between axial ribs roughly equal to their width. Whorls profile greatly convex. Suture deep, slightly oblique (diagonal) to columellar axis. Body whorl ~2/3 shell length. Aperture sub-circular, slightly prosocline; aperture ~2/5 shell length, ~3/5 shell width. Peristome simple. Operculum round, with spiral growth.

**Measurements (in mm):** 4¾-5 whorls; H = ~11.5; D = ~7.5; h = ~4.9; d = ~4.4.

**Remarks:** *Pomatias conicus* has sometimes been classified in *Tudorella* Fischer, 1885, a very closely related genus and possibly a synonym, but the taxonomy of these genera remains unclear (Welter-Schultes 2012). As such, a more cautious classification in the genus *Pomatias* is preferred here. *Pomatias conicus* is a common species in the Central European fossil record, occurring in the Middle to Late Miocene of Hungary, Austria and the Silvana-beds ("Silvanaschichten") of south-western Germany and Switzerland (Klein 1853; Harzhauser & Binder 2004; Kókay 2006).

### Pulmonata
### Hygrophila
### Superfamily Lymnaeoidea
### Family Lymnaeidae
### Genus *Lymnaea* Lamarck, 1799
### *Lymnaea* cf. *dilatata* (Noulet, 1854)
### (Fig. 3B)

*Limnea dilatata* Noulet, 1854: 107.
*Limnaea (Radix) dilatata*: Ehrat & Jooss, 1921: 4.
*Radix (Radix) socialis dilatata*: Wenz, 1923: 1277; Seemann, 1926: 92.
*Lymnaea turrita turrita*: Seemann, 1926: 90.

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**Fig. 3.** Gastropods of the Randeck Maar.
**A –** *Pomatias conicus* (SMNS 101155; H = 11.5 mm). **B –** *Lymnaea* cf. *dilatata*, dorsal view of juvenile specimen embedded in the matrix (SMNS 101224; H = 22.5 mm). **C –** *Ferrissia deperdita*, specimen embedded in the matrix (SMNS 101641; H = 4.6 mm; D = 9.4 mm). **D –** *Gyraulus kleini*, protoconch detail (SMNS 101624). **E-F –** *Gyraulus kleini* (SMNS 100789; H = 0.6, D = 1.3 mm). **G-H –** *Planorbarius cornu*, slightly deformed juvenile specimen (SMNS 101195; H = 9.1, D = 22.1 mm). **I –** *Opeas* cf. *minutum* (SMNS 67044; H = 4.3 mm). **J –** *Opeas minutum* (SMNS 101393; H = 6.9 mm). **K –** Clausiliinae indet., specimen embedded in the matrix (SMNS 101163; H = 11.9 mm, D = 3.1 mm). **L –** *Triptychia kleini*, incomplete specimen (SMNS 101217; H = 18.7 mm, D = 7.8 mm). **M –** *Triptychia randeckiana*, incomplete specimen (lectotype; SMNS 101212; H = 16.3 mm, D = 4.7 mm). **N –** *Triptychia randeckiana*, incomplete specimen (paralectotype; SMNS 101213; H = 17.2 mm, D = 5.3 mm). **O –** *Cochlicopa loxostoma* (SMNS 100794; H = 5.5 mm). **P –** *Palaeomastus filocinctus* (SMNS 101430; H = 12.2 mm, D = 4.6 mm). **Q-R –** *Archaeozonites costatus* (SMNS 101489; D = 16.2 mm). **S-U –** *Apula coarctata* (SMNS 100797; D = 8.4 mm).

*Radix (Radix) socialis socialis*: Seemann, 1926: 90.
*Lymnaea dilatata*: Fischer, 2000: 136 (figs. 1-2).
*Radix dilatata*: Kókay, 2006: 52 (pl. 17, fig. 14).
Lymnaeidae indet.: Rasser et al., 2013: 435 (pl. 4, fig. 4).

**Stratigraphic occurrence:** dark tuffites, light tuffites, marginal limestones and marls, calcareous laminites (Fig. 2; Table 1).

**Description:** Shell large, lymnaeiform; spire acuminated, proportionately small. Protoconch (~1½ whorl) rounded, smooth; transition to teleoconch unclear. Teleoconch smooth, except for growth lines. Suture well-marked. Whorls profile slightly convex. Body whorl proportionately large. Peristome simple. Umbilicus imperforate.

**Measures (in mm):** estimated: 5-5½ whorls; H = ~40.0.

**Remarks:** As noted by Rasser et al. (2013), the lymnaeid specimens show a very poor preservation, being usually completely compressed and flattened (to the point that some were previously identified as bivalves in the SMNS collection) and making identification very tentative. Nevertheless, a few better preserved specimens are very reminiscent of *Lymnaea dilatata*, diagnosed by its acuminated and proportionately short spire and the proportionately large body whorl. This species was originally described from Sansan (MN6, France; Fischer 2000), but it is known from the whole Miocene of West and Central Europe (Binder 2004; Kókay 2006). Some authors (*e.g.*, Wenz 1923; Kókay 2006) have placed *L. dilatata* in the genus *Radix* Montfort, but, as argued by Fischer (2000), it clearly belongs to *Lymnaea*.

## Superfamily Planorboidea
## Family Planorbidae
## Genus *Ferrissia* Walker, 1903
### *Ferrissia deperdita* (Desmarest, 1814)
(Fig. 3C)

*Ancylus deperditus* Desmarest, 1814: 19 (pl. 1, fig. 14); Schlickum, 1964: 17.
*Pseudaucylus deperditus deperditus*: Wenz, 1923: 1692.
*Ferrissia deperdita*: Schlickum, 1976: 7 (pl. 1; fig. 20); Kókay, 2006: 60 (pl. 20, fig. 15, pl. 21, fig. 1); Rasser et al., 2013: 439 (pl. 4, fig. 2); Harzhauser et al., 2014b: 17 (pl. 5, figs. 1, 2, 5, 12).

**Stratigraphic occurrence:** dark tuffites, marginal limestones and marls, calcareous laminites, dysodil (Fig. 2; Table 1).

**Description:** Shell diminutive, cap-shaped, elliptical. Shell apex slightly bent laterally. Protoconch cap-like, smooth; transition to teleoconch unclear. Teleoconch smooth, but with well-marked growth lines.

**Measures (in mm):** H = ~5.1; D = ~7.0.

**Remarks:** The apex pointing towards the right is a clear indication for the Genus *Ferrissia*. The specimens compare fittingly with *F. deperdita*, a species known from the Middle Miocene of Central Europe (Schlickum 1976; Kókay 2006; Harzhauser et al. 2014b). Another common Middle Miocene species is *F. wittmanni* (Schlickum 1964), which is slightly larger than *F. deperdita*. Some specimens from Randeck Maar (*e.g.*, SMNS 101243) are larger and have slightly more pointed apices, being thus very reminiscent of *F. wittmanni*. This could be due to the deformation of the species during fossil diagenesis, since they do not appear to show the distinctive sculpture of this species.

## Genus *Gyraulus* Charpentier, 1837
### *Gyraulus kleini* (Gottschick & Wenz, 1916)
(Figs. 3D-F)

*Gyraulus multiformis kleini* Gottschick & Wenz, 1916: 101.
*Gyraulus* (*Gyraulus*) *trochiformis kleini*: Wenz, 1923: 1595.
*Gyraulus kleini*: Rasser et al., 2013: 439 (pl. 4, fig. 1).

**Stratigraphic occurrence:** dark tuffites, marginal limestones and marls, calcareous laminites, dysodil (Fig. 2; Table 1).

**Description:** Shell diminutive, pseudodextral, planispiral, flattened. Spire depressed. Protoconch (~1 whorl) sculpture by circa 13 spiral cords; transition to teleoconch clear. Teleoconch smooth, except for growth lines. Suture deep, well-marked. Whorls somewhat rapidly growing, especially body whorl. Body whorl with smooth keel on its lower-median portion. Aperture ellipsoid, slightly inclined diagonally. Umbilicus wide, shallow.

**Remarks:** Most specimens are flattened due to sediment compaction and poorly preserved. Only one specimen with a sufficiently preserved protoconch could be found (Fig. 6). The protoconch sculpture consisting of spiral cords (cf. Nützel & Bandel 1992; Finger 1998), as well as the general shape (Gottschick & Wenz 1916), allows the identification as *G. kleini*.

## Genus *Planorbarius* Duméril, 1806
### *Planorbarius cornu* (Brongniart, 1810)
(Figs. 3G-H)

*Planorbis cornu* Brongniart, 1810: 371 (pl. 22, fig. 6).
*Coretus cornu cornu*: Wenz, 1923: 1426.
*Planorbis cornu mantelli*: Ehrat & Jooss, 1921: 4.
*Coretus cornu mantelli*: Seemann, 1926: 92.
*Planorbarius cornu*: Schlickum, 1970: 149 (pl. 10, fig. 7); Binder, 2004: 193 (pl. 2, figs. 2-3).
*Planorbarius cornu cornu*: Kókay, 2006: 58 (pl. 20, fig. 6); Böttcher et al., 2009: 239 (figs. 2/4-6).
*Planorbarius* cf. *mantelli*: Rasser et al., 2013: 439 (pl. 4, fig. 3).

**Stratigraphic occurrence:** dark tuffites, marginal limestones and marls, calcareous laminites, dysodil (Fig. 2; Table 1).

**Description:** Shell large, sinistral, planispiral; shell height ~1/3 shell width. Spire very depressed. Suture deep, well-marked. Whorls regularly growing. Aperture rounded. Umbilicus very wide, deep. Unfortunately, due to poor preservation, proto- and teleoconch sculpture cannot be observed.

**Remarks:** The conchological features (size, proportions and overall shape) of the present specimens compare well with *Planorbarius cornu*, a morphologically variable species known from the Middle Eocene to the Late Miocene of France, Germany and Czech Republic (Kókay 2006). It is especially abundant in the OSM of southern Germany (Schlickum 1970). The long time span of this species likely indicates that it may actually represent an agglomerate of species. The exclusively Miocene species, *P. mantelli* (Dunker, 1848), is often considered either a synonym or a subspecies of *P. cornu*, but could be a valid taxon (Harzhauser et al. 2014b). This species complex needs a thorough revision and, thus, the more conservative classification of the present specimens as *P. cornu* is used here.

### Stylommatophora
### Superfamily Achatinoidea
### Family Subulinidae
### Genus *Opeas* Albers, 1850
### *Opeas* cf. *minutum* (Klein, 1853)
### (Figs. 3I-J)

*Opeas minutum*: Seemann, 1926: 92.
Subulinidae indet.: Rasser et al., 2013: 440 (pl. 4, fig. 14).

**Stratigraphic occurrence:** light tuffites (Fig. 2; Table 1).

**Description:** Shell small, conical-elongated, with regularly growing whorls; shell width ~2/5 its length. Protoconch large, rounded, dome-shaped, apparently smooth; transition to teleoconch unclear. Teleoconch apparently smooth. Whorls profile slightly convex. Suture well-marked but not too deep, oblique (diagonal) to columellar axis. Body whorl ~1/2 shell length. Aperture rounded trapezoid, orthocline; aperture width ~1/2 its length; aperture ~2/5 shell length, ~1/2 shell width.

**Remarks:** *Opeas minutum* is known from the Early/Middle Miocene of Hungary and Austria (and possibly Ukraine) and is especially widespread in the Silvana-beds (“Silvanaschichten”) of south-western Germany and Switzerland (Schlickum 1976; Kókay 2006; Harzhauser et al. 2014b). Despite the species’ supposed small size, some specimens (*e.g.*, Fig. 12) show a larger size with a greater whorl count, raising two possibilities: (1) the larger specimens could represent a second species; or (2) the smaller ones could be juveniles or broken shell apices of an overall larger species. Unfortunately, due to the paucity of specimens and their poor preservation, this question cannot be answered for now.

Recent Subulinidae are absent from Europe (except for introduced species), displaying a tropical and subtropical worldwide distribution and being especially diverse in Africa and South America (*e.g.*, Schileyko 1999; Simone 2006). Considering its recent disitbution, this group can be expected to have thrived in the warm climate attributed to the Middle Miocene of Central Europe (*e.g.*, Esu 1999).

### Superfamily Clausilioidea
### Family Clausiliidae
### Subfamily Clausiliinae
### Clausiliinae indet.
### (Fig. 3K)

**Stratigraphic occurrence:** marginal limestones and marls (Fig. 2; Table 1).

**Description:** Shell sinistral, multispiral, elongated fusiform; greater width on penultimate whorl. Protoconch (~2 whorls) rounded, smooth; transition to teleoconch clear. Teleoconch sculptured by strong lightly sinuous and slightly prosocline parallel axial ribs, stronger on last whorls; distance between ribs roughly twice width of rib. Whorls profile convex. Suture deep, well-marked, oblique (diagonal) to columellar axis. Peristome apparently reflexed.

**Remarks:** Although clearly a Clausiliinae, a more precise determination of the present specimen is not possible. The aperture, the main diagnostic feature in the family (Nordsieck 2007), cannot be analyzed.

### Family Filholiidae
### Genus *Triptychia* Sandberger, 1876
### *Triptychia kleini* Schnabel, 2006
### (Fig. 3L)

*Clausilia grandis* Klein, 1846 [*non* Rössmassler, 1838]: 73 (pl. 1, fig. 16).
*Triptychia (Triptychia) grandis*: Wenz, 1923: 808.
*Triptychia kleini kleini*: Schnabel, 2006b: 147 (pl. 3, figs. 32-34).

**Stratigraphic occurrence:** marginal limestones and marls (Fig. 2; Table 1).

**Description:** Shell multispiral, narrow, elongated vertically. Teleoconch sculptured by prosocline very fine parallel axial ribs; distance between ribs roughly equal to rib width. Whorl profile flattened. Suture deep, well-marked, slightly incised, greatly oblique (diagonal) to columellar axis. Aperture round with a pronounced vertically elongated palatal region (sinulus). Aperture with parietal lamella, upper columellar lamella and lower columellar lamella. Peristome reflexed. Umbilicus imperforate.

**Remarks:** The single specimen from Randeck Maar, despite its incomplete preservation, compares well with *T. kle-*

*ini*, mainly by its size, teleoconch sculpture, whorl profile and aperture shape. *Triptychia kleini* is a new name coined by Schnabel (2006b) to replace the invalid *T. grandis*. The species occurs in many localities from the Silvana-beds of southern Germany (Schnabel 2006b).

### *Triptychia randeckiana* (Kranz, 1908)
### (Figs. 3M-N)

*Clausilia randeckiana* Kranz, 1908: 590 (fig. 2).
*Triptychia (Eutriptychia) randeckiana*: Ehrat & Jooss, 1921: 3.
*Triptychia randeckensis*: Wenz, 1923: 818.
*Triptychia (Triptychia) randeckensis*: Seemann, 1926: 92.
*Triptychia (Triptychia) randeckiana*: Schnabel, 2006b: 165 (pl. 7, fig. 86).
*Triptychia* sp.: Rasser et al., 2013: 440.

**Stratigraphic occurrence:** light tuffites, marginal limestones and marls (Fig. 2; Table 1).

**Description:** Shell multispiral, with closely packed whorls. Protoconch (1¾ whorl) acuminated, apparently smooth on first ¾ whorl and sculptured by very fine parallel axial striae on the remaining whorl; transition to teleoconch clear. Teleoconch sculptured by slightly prosocline parallel axial ribs, weaker on first whorls but becoming stronger on later whorls. Whorls profile flat. Suture deep, well-marked, greatly oblique (diagonal) to columellar axis. Aperture apparently oval.

**Measurements (in mm):** SMNS 101212 (lectotype, incomplete specimen; Fig. 15): 10½ whorls; H = 16.3; D = 4.7. SMNS 101213 (paralectotype, incomplete specimen; Fig. 16): H = 17.2; D = 5.3.

**Remarks:** *Triptychia randeckiana* was described from Randeck Maar (type stratum: light tuffite) and, despite the material being very fragmentary and the apertural region being unknown, it was deemed a valid species in the revisionary work of Schnabel (2006b). The main diagnostic features of this species are: a small size, a slender spire and relatively coarse uniform ribs (Schnabel 2006b). It is presently known only from its type locality, but here it is recorded for the two additional facies of Randeck Maar.

Schnabel (2006b) states that the whereabouts of the type material is unknown, but the labels of some specimens from the Jooss collection housed at the SMNS clearly states that they are the originals from Kranz (1908). The type series consists of 3 specimens (plus the external mold or impression of one) and therefore the best preserved is defined here as a lectotype (Fig. 15); the remaining specimens are, thus, paralectotypes.

## Superfamily Cochlicopoidea
## Family Cochlicopidae
### Genus *Cochlicopa* Férussac, 1821
### *Cochlicopa loxostoma* (Klein, 1853)
### (Fig. 3O)

*Achatina loxostoma* Klein, 1853: 214 (pl. 5, fig. 12).
*Cochlicopa subrimata loxostoma*: Wenz, 1923: 1107; Seemann, 1926: 90; Papp & Thenius, 1954: 21 (pl. 4, fig. 7a-c); Lueger, 1981: 16 (pl. 1, fig. 4); Rasser et al., 2013: 440 (pl. 4, fig. 6).
*Cochlicopa subrimata*: Rasser et al., 2013: 434 (pl. 4, fig. 6).

**Stratigraphic occurrence:** dark tuffites, light tuffites, marginal limestones and marls (Fig. 2; Table 1).

**Description:** Shell diminutive, oval, elongated, with regularly growing whorls. Protoconch round, smooth; transition to teleoconch unclear. Teleoconch smooth. Whorl profile flattened. Suture weak, shallow (especially on last whorls). Body whorl large, ~1/2 shell length. Aperture rounded trapezoid; parietal callus light. Peristome simple, lightly thickened. Umbilicus imperforate.

**Measurements (in mm):** 6 whorls; H = ~6.0; D = ~2.5.

**Remarks:** *Cochlicopa loxostoma* is commonly considered a subspecies of *C. subrimata* (Reuss *in* Reuss & Meyer, 1849), which would occur from the Late Oligocene to the early Late Miocene of France and Central Europe (when counting all its numerous subspecies; Wenz 1923). As recently shown by Harzhauser et al. (2014a), the shells of *C. subrimata* from the type locality differ from those of other localities and ages.

The present specimens are closely reminiscent of *C. loxostoma* Klein (1853) from the Upper Freshwater Molasse (OSM) in Germany, differing greatly from the topotypes (Harzhauser et al. 2014a) of *C. subrimata* by their much wider aperture, higher in the columellar region.

## Superfamily Enoidea
## Family Enidae
### Genus *Palaeomastus* Nordsieck, 2014
### *Palaeomastus filocinctus* (Reuss, 1861)
### (Fig. 3P)

*Bulimus (Chondrus) filocinctus* Reuss, 1861: 69 (pl. 2, fig. 5).
*Buliminus (Petraeus) filocinctus*: Klika, 1891: 68 (fig. 63).
*Ena (Napaeus) filocincta*: Wenz, 1923: 1075.
*Ena (Napaeus)* n. sp. Seemann, 1926: 92.
*Ena (Napaeus) schützei* Jooss & Seemann *in* Seemann, 1926 [*nomen nudum*]: 92 (footnote).
*Napaeus* sp.: Rasser et al., 2013: 449.
*Mastus filocinctus*: Harzhauser et al., 2014a: 842 (figs. 6E-G).

**Stratigraphic occurrence:** light tuffites (Fig. 2; Table 1).

**Description:** Shell small, multispiral, slender, conico-fusiform; 7½ whorls; shell width ~2/5 shell length. Spire angle ~35º. Protoconch (~1½ whorls) round, apparently smooth; transition to teleoconch clear. Teleoconch sculptured by fine but well-marked, regularly arranged and closely spaced, prosocline growth lines. Presence of a spiral band-like thickening on upper portion of whorls, adjacent to suture. Whorls regularly growing; body whorl high (~1/2 shell length). Whorl profile flattened (except for first two convex whorls). Suture shallow, but well-marked. Aperture oval (unfortunately, not completely preserved). Umbilicus rimate.

**Remarks:** The specimen's original label states that the name of this (supposedly new) gastropod would be *Ena* (*Napeus*) *schützei* Jooss & Seemann. Jooss & Seemann makes reference to this new species in a footnote in Seemann (1926), but neither presenting a description nor figuring the only known specimen. The footnote simply stated that a more detailed treatment of the species would soon follow in the journal Archiv für Molluskenkunde, which seems to have never happened, either in this or in other journals. As such, the name *Ena schützei* fails to comply with Article 12 of the ICZN (4th edition; International Commission on Zoological Nomenclature 1999) and may be thus considered a *nomen nudum*.

All the fossil species of *Napaeus* Albers, 1850, from the Early Oligocene to the Early Miocene, have been included in a new genus, *Palaeomastus*, by Nordsieck (2014). The present specimen compares fittingly with *P. filocinctus*, known only from Tuchořice (Early Miocene, MN 3, Czech Republic; Harzhauser et al. 2014a). It is easily diagnosed by its slender shell, with a thickened spiral band on the suture region, and a high body whorl, of circa half the shell length (Klika 1891; Harzhauser et al. 2014a). Thus, the present record greatly expands the stratigraphical and geographical occurrence of this species.

## Superfamily Zonitoidea
## Family Zonitidae
## Genus *Archaeozonites* Sandberger, 1873
### *Archaeozonites costatus* Sandberger, 1876
### (Figs. 3Q-R)

*Archaeozonites costatus*: Sandberger, 1876: 604; Schlickum, 1976: 18 (pl. 5, fig. 66); Rasser et al., 2013: 440.
*Zonites (Aegopis) costatus*: Ehrat & Jooss, 1921: 3; Wenz, 1923: 254; Seemann, 1926: 91.
*Aegopis costatus*: Kókay, 2006: 77 (pl. 29, figs. 11-12).
*Miozonites costatus*: Binder, 2002: 168 (pl. 1, figs. 14-16, pl. 3, fig. 8, pl. 7, fig. 3, pl. 8, fig. 4); Jost et al., 2007: 312; Harzhauser et al., 2014b: 33 (pl. 10, figs. 13-19).

**Stratigraphic occurrence:** light tuffites, marginal limestones and marls (Fig. 2; Table 1).

**Description:** Shell medium-sized, helicoid, with broad conical spire and regularly growing whorls. Protoconch (~1 whorl) flattened, sculptured by fine riblets that grow coarser towards teleoconch. Teleoconch sculptured by numerous strong parallel prosocline ribs; distance between ribs equal to rib's width; ribs apparently absent on lower portion of whorls. Suture weakly marked. Whorls profile flattened; body whorl with a strong keel. Aperture oval, pointed on palatal region due to keel. Umbilicus broad, deep.

**Remarks:** *Archaeozonites costatus* is known from the Early and Middle Miocene of Central Europe (Kókay 2006; Harzhauser et al. 2014b), being common in the Silvana-beds ("Silvanaschichten") of southwestern Germany (MN5-6; Schlickum 1976). The species was originally described from the German locality of Mörsingen by Sandberger (1876), but without being figured; as such, Lueger (1981) expresses doubts as to its definition. Nevertheless, the present specimens compare fittingly to the descriptions given by Gottschick & Wenz (1916, 1920). Another coeval species, *A. subcostatus* Sandberger, 1876, is considered a synonym or a subspecies of *A. costatus* (Wenz 1923; Baumberger 1927).

## Superfamily Helicoidea
## Family Elonidae
## Genus *Apula* Boettger, 1909
### *Apula coarctata* (Klein, 1853)
### (Figs. 3S-U)

*Helix coarctata* Klein, 1853: 206 (pl. 5, fig. 6).
*Klikia (Apula) coarctata coarctata*: Wenz, 1923: 534; Seemann, 1926: 92.
*Klikia (Apula) coarctata*: Ehrat & Jooss, 1921: 3; Schlickum, 1976: 17 (pl. 4, fig. 60); Kókay, 2006: 92.
*Klikia coarctata*: Rasser et al., 2013: 440 (pl. 4, fig. 9); Salvador, 2013b: 161 (figs. 6-9).
*Apula coarctata*: Harzhauser et al., 2014b: 34 (pl. 11, figs. 5-8, 21).

**Stratigraphic occurrence:** light tuffites, marginal limestones and marls (Fig. 2; Table 1).

**Description:** Shell small, depressed. Protoconch blunt, wide, apparently smooth; transition to teleoconch unclear. Teleoconch sculpture unpreserved, but faint markings give impressions of fine axial striae; Salvador (2013b) reported that regularly distributed fine papillae gave the impression of axial striae in specimens from Sandelzhausen (MN5; Germany). Whorls' profile slightly convex. Suture well-marked, moderately deep. Whorls regularly increasing in size. Body whorl with very faint keel. Body whorl with conspicuous constriction right before the aperture ("extralabial depression" *sensu* Binder, 2008), which is slightly turned down. Aperture crescent-shaped. Peristome greatly reflexed. Umbilicus covered.

**Measurements (in mm):** 4½ whorls; H = 5.3; D = 8.7; h = ~3.1; d = ~2.3.

**Remarks:** Despite the type material of this species being lost and that different subspecies have been designated through the years (Lueger 1981), the present material compares fittingly with the original description of *A. coarctata* and topotypes available at the SMNS. *Apula coarctata* was described from the Silvana-beds of southwestern Germany (MN 5-6; Schlickum 1976) and is a widespread species in the central European Miocene (Harzhauser et al. 2014b).

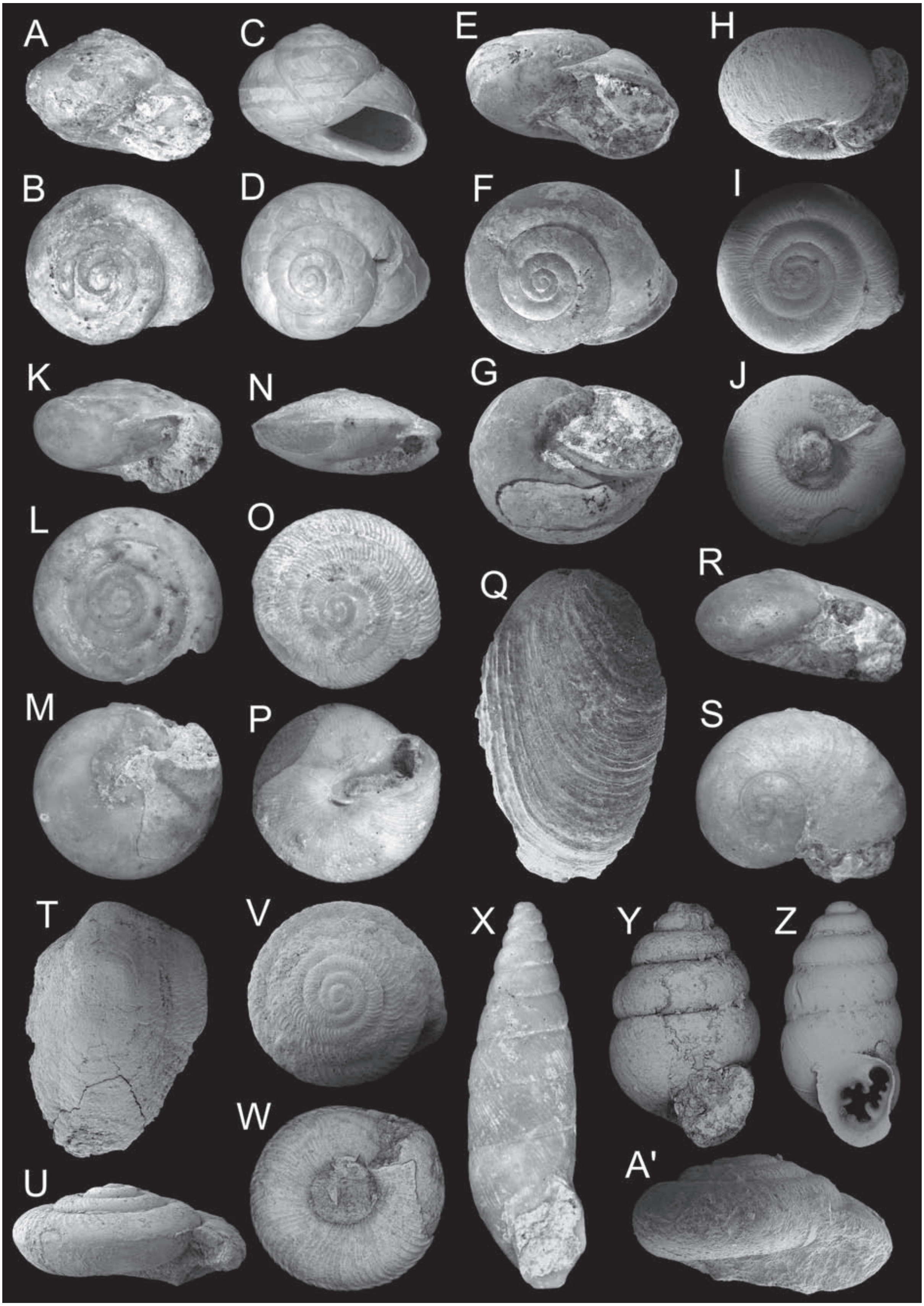

**Fig. 4.** Gastropods of the Randeck Maar (cont.).

## Genus *Pseudochloritis* Boettger, 1909
## *Pseudochloritis incrassata* (Klein, 1853)
(Figs. 4E-G)

*Helix inflexa* Klein, 1847 [*non* von Zieten, 1832]: 71 (pl. 1, fig. 12).
*Helix incrassata* Klein, 1853: 208 (pl. 5, fig. 6).
*Tropidomphalus (Pseudochloritis) incrasstus incrassatus*: Wenz, 1923: 510; Seemann, 1926: 91; Schlickum, 1976: 16 (pl. 4, fig. 56).
*Oxychilus subnitens subnitens*: Seemann, 1926: 91.
*Oxychilus subnitens recedens*: Seemann, 1926: 91.
*Tropidomphalus (Pseudochloritis) incrassatus*: Kókay, 2006: 90 (pl. 34, figs. 12-14).
*Pseudochloritis incrassata*: Binder, 2008: 172 (pl. 3, figs. 2-4, pl. 6, fig. 2); Rasser et al., 2013: 434 (pl. 4, fig. 12); Harzhauser et al., 2014: 35 (pl. 12, figs. 9-16, 19-24).
*Tropidomphalus (Pseudochloritis) incrassata* [sic]: Rasser et al., 2013: 440.

**Stratigraphic occurrence:** light tuffites (Fig. 2; Table 1).

**Description:** Shell medium-sized, helicoid, with flattened spire; 4 whorls; shell length ~2/3 its width. Protoconch flattened, large in relation to following whorl. Teleoconch sculptured by fine parallel axial ribs. Whorls profile convex. Suture deep, well-marked. Body whorl slightly bent downwards, with conspicuous constriction right before the aperture ("*extralabial depression*" sensu Binder 2008). Aperture markedly prosocline. Peristome reflexed. Well-marked callus on parietal region of aperture. Umbilicus narrow. Poor preservation precludes clear definition of protoconch and sculpture and apertural region.

**Remarks:** *Pseudochloritis* was considered a subgenus of *Tropidomphalus* Pilsbry, 1895, but was recently elevated to genus status by Binder (2008). *Pseudochloritis incrassata* is known from the Middle Miocene of Poland (Górka 2008), Austria, many localities in Germany (Binder 2008) and perhaps also Hungary (Kókay 2006). Some protoconchs and spire tops of *P. incrassata* (identifiable by their shape, whorl pattern and sculpture) were identified as *Oxychilus subnitens* (Klein 1853) by Seemann (1926), as seen in the SMNS specimens' labels.

## Family Helicidae
## Genus *Palaeotachea* Jooss, 1912

## *Palaeotachea renevieri* (Maillard, 1892)
(Figs. 4A-B)

*Helix (Macularia) Renevieri* Maillard, 1892: 43 (pl. 3, fig. 18).
*Cepaea renevieri*: Wenz, 1923: 652.
*Cepaea* cf. *renevieri*: Zöbelein, 1954: 156.

**Stratigraphic occurrence:** light tuffites (Fig. 2; Table 1).

**Description:** Shell small, helicoid, with overall flattened profile and very faint keel; 4½ whorls; whorls quickly but regularly growing; shell length ~2/3 its width. Protoconch flattened. Suture well-marked. Body whorl slightly bent downwards near the aperture. Aperture small, prosocline, circular. Peristome lightly thickened and slightly reflexed. Umbilicus imperforate.

**Remarks:** *Palaeotachea renevieri* can be easily identified by its small size, a small circular aperture and a somewhat flattened shell profile with a faint keel. The species is known from the Middle and Late Miocene of Southern Germany and Switzerland (Wenz 1923; Zöbelein 1954).

## Genus *Megalotachea* Pfeffer, 1930
## *Megalotachea silvana* (Klein, 1853)
(Figs. 4C-D)

*Helix silvana* Klein, 1853: 205 (pl. 5, fig. 2).
*Cepaea dentula*: Ehrat & Jooss, 1921: 3.
*Cepaea silvana silvana*: Wenz, 1923: 667; Seemann, 1926: 92; Schlickum, 1976: 17 (pl. 4, figs. 62-63); Reichenbacher, 1989: 165 (pl. 2, figs. 17-19).
*Cepaea silvana*: Kókay, 2006: 93 (pl. 36, figs. 2-3); Rasser et al., 2013: 440.

**Stratigraphic occurrence:** light tuffites, marginal limestones and marls (Fig. 2; Table 1). The record of ?*Cepaea sylvestrina geniculata* of Seemann (1926) in the dark tuffites might be *M. silvana*.

**Description:** Shell medium-sized, helicoid; whorls quickly but regularly growing. Protoconch flattened, smooth; transition to teleoconch unclear. Teleoconch smooth. Suture well-marked. Body whorl slightly bent downwards. Aperture prosocline, crescent-shaped; callus faint. Peristome markedly thickened and reflexed. Umbilicus imperforate.

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**Fig. 4.** Gastropods of the Randeck Maar (cont.).
**A-B –** *Palaeotachea renevieri* (SMNS 101311; H = 11.0 mm; D = 15.3 mm). **C-D –** *Megalotachea silvana* (SMNS 101237; D = 25.4 mm). **E-G –** *Pseudochloritis incrassata* (SMNS 100800; H = 16.6 mm; D = 26.8 mm). **H –** *Helicodonta involuta* (SMNS 101210; D = 5.7 mm). **I –** *Helicodonta involuta* (SMNS 101388; D = 5.6 mm). **J –** *Helicodonta involuta* (SMNS 101386; D = 5.3 mm). **K-M –** *Leucochroopsis kleinii* (SMNS 100798; D = 8.7 mm). **N-P –** *Praeoestophorella phacodes* (SMNS 100793; D = 6.7 mm). **Q –** *Deroceras* sp. (SMNS 101511; H = 5.9 mm, D = 3.7 mm). **R-S –** *Vitrina suevica* (SMNS 101184; D = 7.8 mm). **T –** *Milax* sp. (SMNS 101518; H = 3.4 mm, D = 2.4 mm). **U –** *Discus pleuradrus* (SMNS 100795; D = 3.5 mm). **V –** *Discus pleuradrus* (SMNS 101445; D = 4.4 mm). **W –** *Discus pleuradrus* (SMNS 101447; D = 5.0 mm). **X –** *Granaria* sp. (SMNS 101437; H = 10.6 mm). **Y –** *Gastrocopta* cf. *acuminata* (SMNS 67387; H = 2.5 mm). **Z –** *Gastrocopta sandbergeri* (SMNS 67410; H = 2.6 mm). **A' –** *Vallonia* cf. *lepida* (SMNS 101185; H = 1.2 mm, D = 2.0 mm).

Vestiges of colored spiral bands (trifasciate pattern) can be seen under UV light on body whorl: the topmost one on the middle to upper portion of the body whorl, the other two regularly spaced on the basal portion of whorl, with the bottom one being wider (almost twice the width of the others). Peristome also bears vestige of coloration.

**Remarks:** The present specimen conforms well to *M. silvana*. This is mainly due to its more rounded aperture, only slightly elongated laterally, and the greatly reflexed peristome. *Megalotachea silvana* was originally considered a variety of *M. sylvestrina* (Schlotheim 1820), another very similar species from the Middle and Late Miocene of Central Europe. Recently, Nordsieck (2014) suggested the separation of Miocene forms in the genera *Megalotachea* and *Paleotachea*. Morphological variability in recent *Cepaea* Held, 1838 species is often considerably high, so exact delimitation of fossil species and genera can be problematic.

On some specimens (*e.g.*, SMNS 101237) it is possible to observe under UV light a trifasciate pattern of colored spiral bands. This pattern occurs in recent *Cepaea* species and was found to be the commonest one in Miocene *M. sylvestrina* from Poland (MN 7-8; Górka 2008), being also found in *M. sylvestrina* and *P. renevieri* from other southern German Early/Middle Miocene sites (*e.g.*, Salvador 2013b).

### Family Helicodontidae
### Genus *Helicodonta* Férussac, 1821
### *Helicodonta involuta* (Thomae, 1845)
### (Figs. 4H-J)

*Helix involuta* Thomae, 1845: 144 (pl. 2, fig. 8).
*Helix* (*Trigonostoma*) *involuta*: Sandberger, 1876: 376 (pl. 22, fig. 17-17d).
*Helix* (*Trigonostoma*) *scabiosa*: Sandberger, 1876: 377.
*Helix (Trigonostoma) involuta var. Scabiosa*: Jooss, 1902: 304.
*Helicodonta* (*Helicodonta*) *involuta* var. *angitorta* Jooss, 1912: 34 (pl. 2, fig. 3-3a).
*Helicodonta (Helicodonta) involuta involuta*: Wenz, 1923: 447
*Helicodonta (Helicodonta) involuta angitorta*: Gottschick & Wenz, 1920: 46; Wenz, 1923: 452.
*Helicodonta involuta scabiosa*: Ehrat & Jooss, 1921: 3.
*Helicodonta (Helicodonta) involuta scabiosa*: Wenz, 1923: 452; Seemann, 1926: 91.
*Protodrepanostoma nordsiecki* Falkner, 1986: 121 (pl. 17, figs. 9-10).
*Helicodonta involuta*: Rasser et al., 2013: 440.

**Stratigraphic occurrence:** light tuffites, marginal limestones and marls (Fig. 2; Table 1).

**Description:** Shell small, discoid, with greatly depressed spire. Protoconch (apparently ~1½ whorls) flattened, apparently smooth; transition to teleoconch apparently clear. Teleoconch sculptured by very fine parallel orthocline axial ribs; distance between ribs equal to width of rib. Suture well-marked. Whorl profile convex; whorls closely packed together, growing regularly. Body whorl bent down on apertural region. Aperture oval, narrow, prosocline. Peristome slightly reflexed. Umbilicus wide, deep.

**Measurements (in mm):** 4¼-4½ whorls; H = ~2.8; D = ~4.9.

**Remarks:** *Helicodonta involuta* was originally described by Thomae (1845) from the Late Oligocene/Early Miocene of Hochheim am Main, Germany. Later, Sandberger (1976) described *Helicodonta scabiosa* from the Early/Middle Miocene of the North Alpine Foreland Basin, remarking that its status as a distinct species from *H. involuta* was uncertain. Jooss (1902) considered *H. scabiosa* simply as a variety of *H. involuta* and later (Jooss 1912) described yet another form, namely *H. involuta angitorta*, from Steinheim am Albuch, Germany. All these varieties were later considered subspecies of *H. involuta* (Gottschick & Wenz 1920; Wenz 1923) and the distinction among them is very difficult. Falkner (1986) described yet another species, *H. nordsiecki*, considered a synonym of *H. involuta* in the revision of Manganelli & Giusti (2000a). *Helicodonta involuta* thus seem to display a broad range of intraspecific variability in shell morphology. It occurs from the Late Oligocene to the early Late Miocene.

### Family Hygromiidae
### Genus *Leucochroopsis* Boettger, 1908
### *Leucochroopsis kleinii* (Klein, 1847)
### (Figs. 4K-M)

*Helix kleinii* Klein, 1847: 69 (pl. 1, fig. 8).
*Trichia (Leucochroopsis) kleini kleini* [sic]: Wenz, 1923: 429; Seemann, 1926: 91.
*Leucochroopsis kleini kleini* [sic]: Gall, 1972: 9.
*Leucochroopsis kleini* [sic]: Schlickum, 1976: 15 (pl. 3, fig. 52); Harzhauser & Binder: 2004: 25 (pl. 11, figs. 8-10); Rasser et al., 2013: 440 (pl. 4, fig. 10).
*Leucochroopsis kleinii*: Salvador, 2013b: 166 (figs. 26-27); Harzhauser et al. (2014b): 35 (pl. 11, figs. 12-14).

**Stratigraphic occurrence:** dark tuffites, light tuffites, marginal limestones and marls, calcareous laminites (Fig. 2; Table 1).

**Description:** Shell small, with a depressed conical spire and a rounded inferior portion. Protoconch (~1¼ whorl) blunt, sculptured by fine parallel striae; transition to teleoconch clear. Teleoconch sculptured by fine regularly distributed well-marked scales, giving the impression of prosocline axial striae; growth lines can sometimes be more marked. Whorls' profile convex. Suture well-marked. Whorls regularly increasing in size. Whorls with a smooth keel-like angulation. Aperture crescent-shaped and slightly prosocline. Peristome lightly reflexed. Umbilicus rimate.

**Measurements (in mm):** 4½-5 whorls; H = ~5.0; D = ~8.5; h = ~3.9; d = ~2.9.

**Remarks:** *Leucochroopsis kleinii* is known from the Middle Miocene of the Silvana-beds ("Silvanaschichten"), Germany, to the Late Miocene of Vienna Basin (Schlickum 1976; Harzhauser & Binder 2004). The status of the genus and its species has been recently called into question (Moser et al. 2009), but the present specimens compare well with the original material from Klein (1847), housed at the SMNS. A full revision of this species is currently in preparation. The specimens from Randeck Maar show some morphological variation, from forms with a more flattened spire to forms with a higher, more conical one.

### Family Trissexodontidae
### Genus *Praeoestophorella* Pfeffer, 1930
### *Praeoestophorella phacodes* (Thomae, 1845)
### (Figs. 4N-P)

*Helix phacodes* Thomae, 1845: 142 (pl. 2, fig. 8).
*Oestophora phacodes subphacodes*: Ehrat & Jooss, 1921: 3.
*Caracollina phacodes phacodes*: Wenz, 1923: 461.
*Caracollina phacodes barreri*: Seemann, 1926: 91.
*Caracollina phacodes*: Rasser et al., 2013: 439 (pl. 4, fig. 5).
*Praeoestophorella phacodes*: Harzhauser et al., 2014a: 887.

**Stratigraphic occurrence:** light tuffites, marginal limestones and marls, dysodil (Fig. 2; Table 1).

**Description:** Shell small, lenticular, with regularly growing whorls. Protoconch (~1¼ whorl) flattened, apparently smooth; transition to teleoconch clear. Teleoconch sculptured by well-marked sinuous parallel prosocline axial ribs; distance between ribs roughly equal to twice the rib's width; ribs are stronger above the keel. Whorl profile flattened. Suture well-marked (especially on first whorls), but not too deep. Body whorl with strong angular keel, demarcating two regions in the shell: a low conical spire and a rounded basal portion. Body whorl slightly bent downwards near the apertural region. Aperture narrow, elongated, slit-like. Peristome slightly reflexed. Umbilicus rimate.

**Measurements (in mm):** 5 whorls; H = ~3.6: D = ~7.6; h = ~2.0; d = ~1.0.

**Remarks:** The present specimens compare well with typical *P. phacodes*, a species originally described from the Late Oligocene of Hochheim am Main, Germany (Thomae 1845). Sandberger (1870-1876) mentioned that specimens from other German localities (Mörsingen, Hausen and Hepsisau) were smaller, with a flatter base and fewer and broader ribs. As such, numerous subspecies of *P. phacodes* have been described (Wenz 1923), but their validity should be the aim of a revisionary work.

### Superfamily Limacoidea
### Family Agriolimacidae
### Genus *Deroceras* Rafinesque, 1820
### *Deroceras* sp.
### (Fig. 4Q)

**Stratigraphic occurrence:** marginal limestones and marls (Fig. 2; Table 1).

**Description:** Shell small, vestigial, oval; shell width ~2/3 length. Nucleus slightly bent laterally. Growth marks concentric, well-marked.

**Remarks:** The shells of slugs are vestigial and internal and thus of very limited taxonomical value; therefore, the identification of the present material cannot proceed further than genus level. As remarked by Harzhauser et al. (2014), *Deroceras* is known in the European fossil record since the Miocene, but it is often identified as *Limax* Linnaeus or *Milax* Gray.

### Family Vitrinidae
### Genus *Vitrina* Draparnaud, 1801
### *Vitrina suevica* Sandberger, 1876
### (Figs. 4R-S)

*Vitrina Suevica* Sandberger, 1876: 602 (pl. 29, figs. 27-27b).
*Vitrina suevica suevica*: Wenz, 1923: 219; Seemann, 1926: 91.
*Vitrina (Vitrina) suevica suevica*: Schütt, 1967: 213 (fig. 17).
*Vitrina* cf. *suevica*: Rasser et al., 2013: 440.
"*Vitrina*" *suevica*: Nordsieck, 2014: 165.

**Stratigraphic occurrence:** light tuffites (Fig. 2; Table 1).

**Description:** Shell small, discoid, with depressed spire and few rapidly expanding whorls; shell length ~1/2 its width. Protoconch (~1¼ whorl) sculpture by spiral rows of puncta; transition to teleoconch unclear. Teleoconch smooth, except for growth lines. Suture well-marked but not too deep. Body whorl very large, almost 3/4 of shell width. Aperture oval, prosocline. Peristome simple. Umbilicus very narrow.

**Measurements (in mm):** 2¼-2½ whorls; H = ~6.5; D = ~3.5.

**Remarks:** The shells of vitrinids do not contain many useful taxonomical characters. Nevertheless, the protoconch shape and the pattern of whorl expansion allow for a reasonable classification of Randeck Maar's specimens as *V. suevica* (holotype: SMNS 37598/2005), a species known from other Middle and Late Miocene (MN 5-8) sites of Germany and Austria (Schütt 1967). Other unconfirmed records of the species stem from the younger Austrian sites of Richardhof (MN 9-10; Harzhauser & Binder 2004) and Graktorn Basin (MN 7-9, identified as *Oligolimax* cf. *suevica*; Harzhauser et al. 2008). Recently, Nordsieck (2014) has called to attention that the generic allocation of Tertiary vitrinids is unclear and that *V. suevica* could belong either to *Vitrina* or *Phenacolimax* Stabile, 1859.

### Superfamily Parmacelloidea
### Family Milacidae
### Genus *Milax* Gray, 1855
### *Milax* sp.
(Fig. 4T)

**Stratigraphic occurrence:** marginal limestones and marls (Fig. 2; Table 1).

**Description:** Shell diminutive, vestigial, oval, markedly convex; shell width ~2/3 length. Nucleus central, high. Shell with fine concentric growth lines. Shell edge irregular.

**Remarks:** The shells of milacids are vestigial and internal, precluding reliable identification beyond genus level. *Milax* is known in Europe from the Early Oligocene onwards, with a doubtful Late Eocene record (Zilch 1959-1960).

### Superfamily Punctoidea
### Family Discidae
### Genus *Discus* Fitzinger, 1833
### *Discus pleuradrus* (Bourguignat, 1881)
(Figs. 4U-W)

*Helix pleuradra* Bourguignat, 1881: 53 (pl. 3, figs. 67-72).
*Gonyodiscus (Gonyodiscus) pleuradra pleuradra*: Wenz, 1923: 341; Wenz & Edlauer, 1942: 93.
*Gonyodiscus euglyphoides*: Ehrat & Jooss, 1921: 4.
*Gonyodiscus (Gonyodiscus) costulatostriatus*: Seemann, 1926: 91.
*Gonyodiscus (Gonyodiscus) euglyphoides euglyphoides*: Seemann, 1926: 91.
*Discus (Discus) pleuradrus*: Schütt, 1967: 213 (fig. 16); Schlickum, 1976: 12 (pl. 2, fig. 37); Lueger, 1981: 40 (pl. 4, figs. 6-7).
*Discus (Discus) pleuradra* [sic]: Fischer, 2000: 145 (fig. 21).
*Discus pleuradrus*: Böttcher et al., 2009: 239 (figs. 2/10-11); Rasser et al., 2013: 439; Harzhauser et al., 2014b: 29 (pl. 9, figs. 8-13).
*Discus* sp.: Rasser et al., 2013: 434 (pl. 4, fig. 7).

**Stratigraphic occurrence:** light tuffites, marginal limestones and marls (Fig. 2; Table 1).

**Description:** Shell diminutive, discoid, with low spire. Protoconch (~1½ whorl) flat, smooth; transition to teleoconch clear. Teleoconch sculpture by strong parallel prosocline ribs; distance among ribs equal to twice rib width. Whorl profile convex. Suture well-marked. Whorls regularly growing. Body whorl with faint keel on median-upper portion. Umbilicus wide.

**Measurements (in mm):** 5½ whorls; H = ~2.4; D = ~4.0.

**Remarks:** The present specimens compare well with *D. pleuradrus*. This species was originally described from Sansan (MN6), France (Bourguignat 1881), and is supposedly known from the entire Miocene of Central and Western Europe (Böttcher et al. 2009). Still, Early and Late Miocene records could actually represent different species (Moser et al. 2009), thus restricting *D. pleuradrus* to the Middle Miocene of France, southern Germany, and Austria (Harzhauser et al. 2014b).

### Superfamily Pupilloidea
### Family Chondrinidae
### Genus *Granaria* Held, 1838
### *Granaria* sp.
(Fig. 4X)

*Abida subfusiformis randeckiana* Jooss & Seemann *in* Seemann, 1926 [*nomen nudum*]: 92 (footnote).
*Granaria* ?*schuebleri*: Rasser et al., 2013: pl. 4, fig. 8.
*Granaria* sp.: Rasser et al., 2013: 449.

**Stratigraphic occurrence:** light tuffites, marginal limestones and marls, calcareous laminites (Fig. 2; Table 1).

**Description:** Shell small, narrow, multispiral, pupiform, with conical, acuminated spire top. Protoconch (~1¼ whorl) rounded, smooth; transition to teleoconch clear. Teleoconch sculptured by regularly distributed, very fine greatly prosocline ribs; distance between ribs approximately equal to rib width. Whorl profile slightly convex. Suture deep. Body whorl large; about ~2/5 shell height. Aperture rounded quadrangular. Peristome reflexed. Umbilicus imperforate.

**Measurements (in mm):** H = ~5.0; D = ~2.5.

**Remarks:** Seeman (1926) presents these specimens as *Abida subfusiformis randeckiana* nov. var. Jooss & Seemann, in the same manner as explained for *Napaeus* above and, thus this designation constitutes another *nomem nudum*. Identification beyond genus level is not possible with the present specimens, since the most important taxonomical characters (the aperture and its barriers; Gittenberger 1973; Höltke & Rasser 2013) cannot be seen. Nevertheless, as remarked by Rasser et al. (2013), the shell overall morphology and sculpture is very reminiscent of *G. schuebleri* (Klein 1847), a species known from much younger sediments, from the Middle to Late Miocene of Germany, starting at the MN 7 age (Höltke & Rasser 2013).

### Family Gastrocoptidae
### Genus *Gastrocopta* Wollaston, 1878
### *Gastrocopta* cf. *acuminata* (Klein, 1846)
(Fig. 4Y)

*Leucochila acuminata*: Ehrat & Jooss, 1921: 4.
*Gastrocopta (Albinula) acuminata acuminata*: Seemann, 1926: 92.

**Stratigraphic occurrence:** light tuffites (Fig. 2; Table 1).

**Description:** Shell diminutive, ovate, with slightly acuminated spire and greatest width on body whorl; 4½ whorls. Protoconch rounded, smooth; transition to teleoconch unclear. Whorl profile convex. Suture well-marked, deep. Aperture rounded triangular. Peristome reflexed. Umbilicus very narrow, deep.

**Remarks:** The single specimen from Randeck Maar consist of an internal mold, making a precise identification difficult. Nevertheless, its large size, alongside the overall shell shape, is very reminiscent of *G. acuminata*, as recently revised by Manganelli & Giusti (2000b). This species is commonly found in the European fossil record, occurring from the Early/Middle Miocene (MN 5) to the Late Pliocene and perhaps even the Early Pleistocene (Stworzewicz 1999).

### *Gastrocopta sandbergeri* Stworzewicz & Prisyazhnyuk, 2006
### (Fig. 4Z)

*Pupa (Vertigo) suevica* Sandberger, 1876 [*nomen nudum*]: 654.
*Gastrocopta suevica*: Stworzewicz, 1999: 164 (fig. 62).
*Gastrocopta sandbergeri* Stworzewicz & Prisyazhnyuk, 2006: 167 (figs. 1, 2A-E).

**Stratigraphic occurrence:** light tuffites (Fig. 2; Table 1).

**Description:** Shell diminutive, elongated ovate; 5 whorls. Protoconch rounded, smooth; transition to teleoconch unclear. Whorl profile convex. Suture well-marked, deep. Teleoconch smooth, except for growth lines. Body whorl and penultimate of roughly equal size. Aperture rounded triangular. Peristome greatly reflexed. Apertural barriers totaling eight: suprapalatal tooth, upper palatal tooth, interpalatal tooth, lower palatal tooth, basal tooth, columellar lamella, infraparietal lamella, anguloparietal lamella. Infraparietal lamella and/or the suprapalatal tooth lacking in some specimens. Anguloparietal lamella with overall bifid aspect: angular lamella vertically positioned, large, thick; parietal lamella narrow, folded towards the outer lip. After the anguloparietal lamella, the strongest barrier is the lower palatal tooth. Umbilicus very narrow, deep.

**Remarks:** The single specimen from Randeck Maar compares well with *G. sandbergeri*, mainly due to its large shell height and overall elongated shell shape. The dentition is also very similar, albeit the present specimen has one tooth more (the interpalatal) than typical *G. sandbergeri* (Stworzewicz & Prisyazhnyuk 2006). This teeth pattern is known in *G. nouletiana* (Dupuy 1850), a Middle Miocene species that is usually slightly smaller and more rounded than *G. sandbergeri*. Nevertheless, *G. nouletiana* seems to be very variable and Salvador (2013a) has pointed out the possibility that *G. sandbergeri* would be one of the extremes in shell form of *G. nouletiana* and hence, its synonym.

*Gastrocopta sandbergeri* is known only from Bełchatów (type locality; MN5, Poland) and Steinheim am Albuch (MN7-8, Germany); this name was coined to replace the old *G. suevica*, a *nomem nudum* (Stworzewicz & Prisyazhnyuk 2006).

## Family Valloniidae
### Genus *Vallonia* Risso, 1826
### *Vallonia* cf. *lepida* (Reuss, 1849)
### (Figs. 4A’, 5A)

*Helix lepida* Reuss, 1849: 24 (pl. 2, fig. 4).
*Helix (Vallonia) subpulchella* Sandberger, 1876: 544 (pl. 29, figs. 3a-c).
*Vallonia lepida lepida*: Wenz, 1923a: 903.
*Vallonia* cfr. *subcyclophorella*: Ehrat & Jooss, 1921: 3.
*Vallonia lepida*: Gerber, 1996: 88 (figs. 3d, 29a-g, 30a-d, 31a-f, 32a-c, 33); Moser et al., 2009: 47; Salvador, 2013a: figs. 15-16; Harzhauser et al., 2014a: 846 (figs. 7L-Q); Harzhauser et al., 2014b: 22 (pl. 7, figs. 5-6, 9).
*Vallonia* cf. *subpulchella*: Rasser et al., 2013: 440.

**Stratigraphic occurrence:** light tuffites (Fig. 2; Table 1).

**Description:** Shell diminutive; spire flat, depressed; 3¾ whorls; shell length ~3/5 its width. Whorls regularly growing; whorls profile convex. Suture deep, well-marked, perpendicular to columellar axis (except for aperture region, which is slightly tilted towards base). Aperture prosocline. Umbilicus wide. Poor preservation precludes clear definition of protoconch and aperture. Even so, in a small portion of the body whorl, it can be seen that the teleoconch is smooth but marked with coarse growth lines.

**Remarks:** The overall shell shape and size, number and shape of whorls, and the smooth teleoconch with coarse growth lines, is very reminiscent of *Vallonia lepida*, a long-lived (Oligocene–Pliocene) species from Europe and likely Asia, but the poor preservation of the protoconch and aperture precludes a more precise determination (Harzhauser & Kowalke 2002; Harzhauser et al. 2008, 2014a, 2014b). Another Central European Miocene species is *V. subpulchella* (Sandberger 1876), which has recently been considered a synonym of *V. lepida* by Gerber (1996), since there seems to be no clear morphological characters to distinguish them. Gerber (1996) points out that it is common practice to identify older forms (Middle Oligocene to Early Miocene) as *V. lepida* and younger forms (Middle to Late Miocene) as *V. subpulchella*. Moreover, recently Harzhauser et al. (2014a) pointed out that there may be differences in protoconch structure and that a differentiation of these species might be possible upon further revision.

## Family Vertiginidae
### Genus *Truncatellina* Lowe, 1852
### ?*Truncatellina* sp.
### (Fig. 5B)

*Pupilla (Primipupilla) iratiana iratiana*: Seemann, 1926: 92.

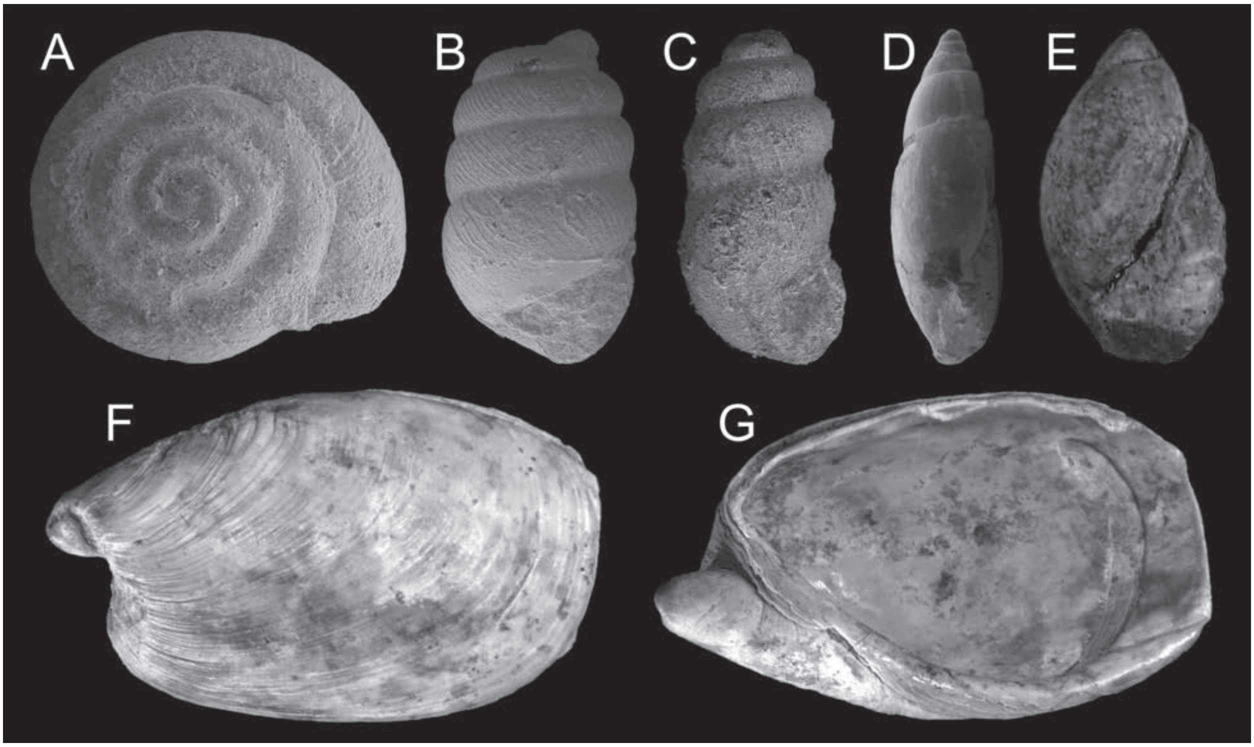

**Fig. 5.** Gastropods of the Randeck Maar (cont.).
**A –** *Vallonia* cf. *lepida* (SMNS 101185; H = 1.2 mm, D = 2.0 mm). **B –** ?*Truncatellina* sp. (SMNS 101181; H = 2.1 mm, D = 1.2 mm). **C –** *Negulus suturalis* (SMNS 101187; H = 1.5 mm, D = 0.7 mm). **D –** *Pseudoleacina eburnea* (SMNS 101164; H = 14.6 mm). **E –** *Palaeoglandina gracilis* (SMNS 101429; H = 40.0 mm, D = 21.0 mm). **F-G –** *Testacella zellii* (SMNS 101510; H = 10.3 mm, D = 6.0 mm).

**Stratigraphic occurrence:** light tuffites (Fig. 2; Table 1).

**Description:** Shell diminutive, pupiform; 5 whorls; shell width ~1/2 its length. Protoconch rounded, dome-shaped, much narrower than teleoconch, giving the spire top a starkly tapering profile. Whorls profile convex. Suture deep, well-marked, almost perpendicular to columellar axis. Teleoconch sculptured by very weak and greatly prosocline ribs. Aperture sub-circular, apparently orthocline. Poor preservation precludes clear definition of protoconch and aperture, but there seems to be a small and very shallow furrow on the external portion of the aperture's middle palatal region.

**Remarks:** These specimens show an overall shell morphology that is very widespread in the Pupilloidea, more precisely in the families Pupillidae (especially the genus *Pupilla* Fleming, 1828) and Vertiginidae. The shape and proportion of the whorls and the suture nearly perpendicular to the columellar axis, however, can narrow down the possibilities of identification. Moreover, one specimen (SMNS 47992/2007) shows a small and very shallow furrow on the external portion of the aperture's middle palatal region, a feature which is more akin to vertiginids. Overall, the specimens are very reminiscent of the genus *Truncatellina*.

### Genus *Negulus* Boettger, 1889
### *Negulus suturalis* (Sandberger, 1858)
### (Fig. 5C)

*Bulimus lineolatus* A. Braun, 1843: 149. [*nomen nudum*]
*Pupa suturalis* Sandberger, 1858: 54 (pl. 5, fig. 13; pl. 6, figs. 1-1a).
*Negulus suturalis gracilis* Gottschik & Wenz, 1919: 9 (pl. 1, figs. 12-13); Wenz, 1923: 1027.
*Negulus suturalis suturalis*: Wenz, 1923: 1024; Kókay, 2006: 61 (pl. 21, figs 12-13).
*Truncatellina* cfr. *lentilli*: Seemann, 1926: 92.
*Negulus suturalis*: Stworzewicz, 1999: 146 (figs. 23-25); Binder, 2002: 168 (text-figs. 6a-b, pl. 1, fig. 10); Harzhauser et al., 2014a: 854 (figs. 8K-N).
*Negulus gracilis*: Harzhauser & Binder, 2004: 126 (pl. 6, figs. 9-10); Harzhauser et al., 2008: 50 (fig. 5.4).
*Negulus* cf. *suturalis*: Rasser et al., 2013: 449.

**Stratigraphic occurrence:** light tuffites (Fig. 2; Table 1).

**Description:** Shell diminutive, cylindrical-pupiform but with slightly tapering apex; 4 whorls; shell width ~1/2 its length. Protoconch rounded, dome-shaped. Teleoconch sculptured by strong, widely spaced, prosocline axial ribs. Whorls profile very convex. Suture deep, well-marked, oblique (diagonal) to columellar axis. Aperture sub-circular, orthocline. Poor preservation precludes clear definition of protoconch and aperture.

**Remarks:** The genus can be confidently determined based on shell size and shape, and on the number, shape, proportion and expansion rate of the whorls (a very limited number is diagnostic of the genus; Bruggen 1994). Moreover, the very characteristic sculpture of Miocene forms (Stworzewic 1999; Harzhauser et al. 2008) can be seen in one of the present specimens (SMNS 101187; Fig. 53), although only under SEM examination. The two Miocene fossil species occurring in Germany are *N. suturalis* and *N. gracilis* Gottschick & Wenz, 1919, the latter being first described as a subspecies of the previous. Harzhauser & Binder (2004) consider both as valid species, based on whorl convexity and aperture height; they use *N. suturalis* for Late Oligocene to Early Miocene forms and *N. gracilis* for Middle Miocene (Early Sarmatian) to Late Miocene forms. Stworzewicz (1999), however, found no morphological differences between the species and treat them as synonyms; a decision followed here. *Negulus* is a very widespread genus throughout Europe, ranging from the Eocene to Pliocene (Zilch 1959-1960; Esu et al. 1993).

### Superfamily Testacelloidea
### Family Oleacinidae
### Genus *Pseudoleacina* Wenz, 1914
### *Pseudoleacina eburnea* (Klein, 1853)
### (Fig. 5D)

*Glandina (Achatina) eburnea* Klein, 1853: 213 (pl. 5, fig. 10).
*Poiretia (Pseudoleacina) eburnea*: Ehrat & Jooss, 1921: 4.
*Poiretia (Pseudoleacina) eburnea eburnea*: Wenz, 1923: 857; Seemann, 1926: 92.
*Pseudoleacina (Pseudoleacina) eburnea*: Lueger, 1981: 55 (pl. 5, figs. 15-16).
*Pseudoleacina eburnea*: Harzhauser & Binder, 2004: 22 (pl. 9, fig. 2); Rasser et al., 2013: 439 (pl. 4, fig. 13).

**Stratigraphic occurrence:** light tuffites (Fig. 2; Table 1).

**Description:** Shell small, fusiform, slim, with acuminated apex (bullet-shape); shell width ~1/3 its length. Protoconch large, rounded, dome-shaped, apparently smooth; transition to teleoconch unclear. Teleoconch sculptured by very fine parallel ribs that become slightly curved on body whorl, nearer to aperture. Whorls profile convex. Suture well-marked but not too deep, slightly incised, oblique (diagonal) to columellar axis, especially on the last whorls. Body whorl very large, ~2/3 shell length. Columella twisted, bent downwards. Aperture water-drop-shaped, prosocline, with palatal region greatly elongated vertically; aperture width ~1/2 its length; aperture ~1/2 shell length, ~2/3 shell width. Peristome simple. A faint callus may be present on columellar and parietal regions of aperture. Umbilicus imperforate.

**Measurements (in mm):** 5-5¼ whorls; H = ~12.5; D = ~4.2; h = ~5.7; d = ~2.7.

**Remarks:** The specimens from Randeck Maar fit very well the original description of *P. eburnea* from the contemporaneous German fossil site of Mörsingen (MN 5). The species is also recorded from Vienna Basin (MN9-10; Lueger 1981; Harzhauser & Binder 2004).

### Family Spiraxidae
### Genus *Palaeoglandina* Wenz, 1914
### *Palaeoglandina gracilis* (von Zieten, 1830)
### (Fig. 5E)

*Limnaea gracilis* von Zieten, 1830: 39 (pl. 30, fig. 3).
*Poiretia (Palaeoglandina) gracilis porrecta*: Ehrat & Jooss, 1921: 4; Seemann, 1926: 90.
*Poiretia (Palaeoglandina) gracilis gracilis*: Wenz, 1923: 839.
*Palaeoglandina gracilis*: Zilch, 1959-1960: 457 (fig. 1627).

**Stratigraphic occurrence:** dark tuffites, light tuffites (Fig. 2; Table 1).

**Description:** Shell large, broad, fusiform; greatest width on last whorl. Whorls' profile flattened. Suture well-marked. Teleoconch sculptured by regularly distributed, well-marked opistocline fine ribs; distance between ribs roughly equal to twice rib width. Whorls rapidly increasing in size. Aperture ellipsoid, vertically elongated. Peristome simple, sharp. Umbilicus imperforate.

**Remarks:** The present material compares well with *Palaeoglandina gracilis* by its size, broad shell, strong sculpture and elongated aperture. This species is known from the Late Oligocene to the Middle Miocene (MN7) of Central Europe (Salvador 2013b). The genus *Palaeoglandina* is known since the Paleocene, being widespread throughout Europe and becoming extinct in the Early Pleistocene (Zilch 1959-1960; Esu et al. 1993).

### Family Testacellidae
### Genus *Testacella* Draparnaud, 1801
### *Testacella zellii* Klein, 1853
### (Figs. 5F-G)

*Testacella zellii* Klein, 1853: 204 (pl. 5, fig. 1); Nardi & Bodon, 2011: 159 (table 3); Salvador, 2013b: 161 (fig. 5).
*Testacella zelli* [sic]: Wenz, 1923: 213; Schlickum, 1976: 15 (pl. 3, fig. 51).

**Stratigraphic occurrence:** marginal limestones and marls (Fig. 2; Table 1).

**Description:** Shell small, ear-shaped, vestigial; 1 whorl. Apex starkly pointed. Shell smooth, except for well-marked growth lines. Shell deep. Well marked keel near the apex.

Aperture water-drop shaped. Slight thickening of peristome on inner margin.

**Remarks:** The present specimens compares fittingly to *T. zellii*, a species known only from a few Lower/Middle Miocene sites of southern Germany (Schlickum 1976; Salvador 2013b).

## 5. Discussion

It was commonly held in the literature (Ehrat & Jooss 1921; Seemann 1926) that most of the terrestrial gastropods originated from the light and dark tuffites, which represent two synchronous facies (Seemann 1926). The present work largely agrees with these previous findings (Table 1). The dark tuffite contains only few terrestrial species, while all freshwater ones can be found in this facies. Likewise, most terrestrial species can be found in the light tuffite, which only contains a single freshwater snail. This agrees with the suggestion of Seemann (1926) that the dark tuffite formed under permanent water cover, while the light tuffite formed subaerially at the lake margin.

The marginal limestones, marls and laminite facies represent aquatic sediments (Rasser et al. 2013), but, despite being numerically dominated by freshwater species, a large portion of the terrestrial species can also be found in these facies. Moreover, a few species are restricted to these marginal facies, such as the slugs *Deroceras* sp. and *Milax* sp. and the semi-slug *Testacella zellii* (Table 1).

The Randeck Maar snail fauna comprises a total 32 species of continental snails, among which four are freshwater. This relatively low diversity of aquatic taxa might be due to extreme water chemistry (Rasser et al. 2013), which may also explain the lack of other freshwater snails such as hydrobiids, common in other European Miocene fossil faunas. *Lymnaea* cf. *dilatata* is the most common species and it can form mass occurrences together with *Ferrissia deperdita*. *Gyraulus kleini* is also extremely abundant (probably the most numerous species in the field) and may also form mass occurrences, but, since their preservation is often in very poor, they are probably underrepresented in collections. *Planorbarius cornu* is particularly scarce.

The terrestrial snail fauna is dominated by *Pomatias conicus* (curiously the only operculate snail in the Randeck Maar fauna), *Cochlicopa loxostoma*, *Granaria* sp. and *Praeoestophorella phacodes*. The latter two are species commonly found in exposed rocky substrates, such as the limestones that weere present around the Randeck Maar lake (Rasser et al. 2013). The Randeck Maar snail fauna is quite diverse and many taxa can be compared with well-known extant relatives. Ecological data from recent genera can thus be used as a guide for paleoecological inferences of congeneric fossil species, especially for land snails (*e.g.*, Albesa et al. 1997; Moser et al. 2009). An in-depth study on this subject is in preparation by the authors.

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# Appendix 1

## List of analyzed material

Here is listed all the material from Randeck Maar available for each species. The order in which the species are presented below is the same as they appear in the main body of the text. **Institutional abbreviations: UHH,** Urweltmuseum Hauff (Holzmaden, Germany); **SMNS,** Staatliches Museum für Naturkunde Stuttgart (Stuttgart, Germany).

***Pomatias conicus* (Klein, 1853):** SMNS 101152 (14 spcm.), 101153 (5 spcm.), 101154 (12 spcm.), 101155 (19 spcm.), 101156 (1 spcm.), 101157 (1 operculum), 101158 (3 spcm.), 101159 (3 spcm.), 101160 (1 spcm.), 101161 (18 spcm., 1 operculum), 101162 (2 spcm.), 101176 (1 spcm.), 101177 (1 spcm.), 101188 (1 spcm.), 101189 (1 operculum), 101190 (1 spcm.), 101208 (20 spcm), 101216 (3 spcm.), 101255 (1 spcm.), 101334 (1 spcm.), 101352 (2 spcm.), 101353 (numerous external molds), 101354 (numerous external molds), 101381 (1 spcm.), 101382 (2 spcm.), 101383 (3 spcm.), 101384 (23 spcm.), 101442 (1 spcm.), 101506 (1 spcm.), 101507 (3 spcm.), 101512 (25 spcm., >200 opercula), 101516 (21 spcm., ~50 opercula). UHH 748 (>70 spcm.).

***Lymnaea* cf. *dilatata* (Noulet, 1854):** SMNS 101223 (1 spcm), 101224 (2 spcm), 101225 (1 spcm), 101226 (2 spcm), 101227 (1 spcm), 101228 (1 spcm), 101229 (5 spcm), 101230 (1 spcm), 101231 (3 spcm), 101232 (2 spcm), 101233 (1 spcm), 101234 (6 spcm), 101235 (12 spcm), 101236 (2 spcm), 101280 (1 spcm.), 101281 (3 spcm.), 101282 (1 spcm.), 101283 (1 spcm.), 101284 (3 spcm.), 101285 (1 spcm.), 101286 (1 spcm.), 101287 (1 spcm.), 101288 (9 spcm.), 101289 (3 spcm.), 101290 (2 spcm.), 101291 (4 spcm.), 101292 (1 spcm.), 101293 (4 spcm.), 101294 (3 spcm.), 101295 (1 spcm.), 101296 (1 spcm.), 101297 (1 spcm.), 101328 (2 spcm.), 101330 (2 spcm.), 101331 (1 spcm.), 101332 (1 spcm.), 101340 (2 spcm.), 101341 (1 spcm.), 101347 (1 spcm.), 101349 (1 spcm.), 101350 (2 spcm.), 101351 (1 spcm.), 101359 (6 spcm.), 101405 (3 spcm.), 101406 (1 spcm.), 101407 (2 spcm.), 101408 (1 spcm.), 101409 (1 spcm.), 101410 (3 spcm.), 101448 (1 spcm.), 101449 (1 spcm.).

***Ferrissia deperdita* (Desmarest, 1814):** SMNS 68659 (~30 spcm.), 68660 (2 spcm.), 101235 (2 spcm), 101238 (1 spcm), 101239 (2 spcm), 101240 (1 spcm), 101241 (1 spcm), 101242 (1 spcm), 101243 (1 spcm), 101244 (1 spcm), 101245 (2 spcm), 101246 (1 spcm), 101247 (2 spcm), 101248 (1 spcm), 101262 (2 spcm), 101263 (1 spcm), 101264 (1 spcm), 101265 (1 spcm), 101266 (1 spcm), 101267 (1 spcm), 101268 (1 spcm), 101269 (1 spcm), 101270 (1 spcm), 101271 (1 spcm), 101272 (1 spcm), 101273 (1 spcm), 101274 (1 spcm), 101275 (1 spcm), 101276 (1 spcm), 101277 (1 spcm), 101278 (2 spcm), 101279 (1 spcm), 101298 (1 spcm), 101321 (1 spcm), 101322 (1 spcm), 101327 (3 spcm.), 101333 (1 spcm.), 101336 (3 spcm.), 101337 (1 spcm.), 101346 (1 spcm.), 101347 (1 spcm.), 101355 (2 spcm.), 101358 (1 spcm.), 101359 (14 spcm.).

***Gyraulus kleini* (Gottschick & Wenz 1916):** SMNS 68660 (2 spcm.), 100789 (5 spcm.), 101204 (1 spcm.), 101205 (>50 spcm.), 101355 (1 spcm.), 101517 (6 spcm.).

***Planorbarius cornu* (Brongniart, 1810):** SMNS 67838 (2 spcm.), 101195 (5 spcm.), 101196 (4 spcm.), 101197 (2 spcm.), 101198 (1 spcm.), 101199 (1 spcm.), 101200 (1 spcm.), 101201 (2 spcm.), 101202 (2 spcm.), 101209 (4 spcm.), 101299 (3 spcm.), 101300 (14 spcm.), 101313 (1 spcm.), 101314 (1 spcm.), 101315 (1 spcm.), 101316 (1 spcm.), 101317 (1 spcm.), 101318 (1 spcm.), 101319 (1 spcm.), 101323 (2 spcm.), 101324 (1 spcm.), 101325 (5 spcm.), 101326 (8 spcm.), 101327 (2 spcm.), 101329 (1 spcm.), 101335 (2 spcm.), 101338 (1 spcm.), 101339 (3 spcm.), 101342 (1 spcm.), 101343 (1 spcm.), 101344 (3 spcm.), 101345 (3 spcm.), 101348 (~15 spcm.), 101349 (1 spcm.), 101355 (1 spcm.), 101356 (4 spcm.), 101357 (6 spcm.), 101358 (1 spcm.), 101359 (1 spcm.), 101363 (1 spcm.).

***Opeas* cf. *minutum* (Klein, 1853):** SMNS 67044 (1 spcm.), 100802 (1 spcm.), 101206 (1 spcm.), 101393 (1 spcm.), 101394 (4 spcm.), 101395 (1 spcm.). UHH 748 (1 spcm., missing).

**Clausiliinae indet.:** SMNS 101163 (1 spcm.), 101392 (1 spcm.), 101503 (26 spcm.), 101514 (6 spcm.).

***Triptychia kleini* Schnabel, 2006:** SMNS 101217 (1 spcm.).

***Triptychia randeckiana* (Kranz, 1908):** SMNS 101212 (lectotype), 101213 (paralectotypes, 2 spcm.), 101178 (1 spcm.), 101179 (4 spcm.), 101207 (1 spcm.), 101220 (1 spcm.), 101221 (1 spcm.), 101222 (1 spcm.), 101515 (16 spcm.), 101521 (22 spcm.).

***Cochlicopa loxostoma* (Klein, 1853):** SMNS 67251 (4 spcm.), 100794 (60 spcm.), 101401 (2 spcm.), 101402 (26 spcm.), 101403 (1 spcm.), 101404 (1 spcm.), 101413 (41 spcm.), 101414 (1 spcm.), 101415 (1 spcm.), 101416 (23 spcm.), 101443 (19 spcm.), 101444 (1 spcm.). UHH 748 (>80 spcm.).

***Palaeomastus filocinctus* (Reuss, 1860):** SMNS 101430 (1 spcm.).

***Archaeozonites costatus* Sandberger, 1876:** SMNS 101192 (1 spcm.), 101193 (1 spcm.), 101194 (5 spcm.), 101489 (1 spcm.), 101490 (2 spcm.), 101508 (3 spcm.).

***Apula coarctata* (Klein, 1853):** SMNS 100797 (3 spcm.), 101450 (3 spcm.), 101467 (1 spcm.), 101468 (5 spcm.), 101469 (5 spcm.), 101470 (8 spcm.), 101471 (3 spcm.), 101472 (8 spcm.), 101473 (1 spcm.), 101474 (2 spcm.), 101488 (6 spcm.). UHH 748 (27 spcm.).

***Pseudochloritis incrassata* (Klein, 1853):** SMNS 100800 (4 spcm.), 101170 (1 spcm.), 101171 (1 spcm.), 101172 (2 spcm.), 101173 (1 spcm.), 101174 (1 spcm.), 101175 (7 spcm.), 101256 (1 spcm), 101476 (3 spcm.), 101483 (3 spcm.), 101500 (2 spcm.). UHH 748 (1 spcm.).

***Palaeotachea renevieri* (Maillard, 1892):** SMNS 101311 (7 spcm.), 101478 (3 spcm.), 101482 (1 spcm.), 101485

(6 spcm.), 101486 (1 spcm.), 101494 (1 spcm.), 101499 (5 spcm.), 101502 (2 spcm.).

***Megalotachea silvana*** **(Klein, 1853):** SMNS 101237 (1 spcm.), 101259 (4 spcm.), 101260 (1 spcm.), 101312 (1 spcm.), 101477 (1 spcm.), 101479 (1 spcm.), 101480 (1 spcm.), 101481 (5 spcm.), 101484 (1 spcm.), 101491 (5 spcm.), 101492 (2 spcm.), 101493 (1 spcm.), 101495 (1 spcm.), 101496 (2 spcm.), 101498 (2 spcm.), 101501 (6 spcm.). UHH 748 (4 spcm.).

***Helicodonta involuta*** **(Thomae, 1845):** SMNS 101210 (2 spcm.), 101385 (2 spcm.), 101386 (1 spcm.), 101387 (1 spcm.), 101388 (1 spcm.), 101389 (7 spcm.), 101390 (1 spcm.), 101418 (1 spcm.). UHH 748 (3 spcm.).

***Leucochroopsis kleinii*** **(Klein, 1847):** SMNS 100798 (16 spcm.), 101250 (1 spcm.), 101252 (1 spcm.), 101253 (6 spcm.), 101254 (2 spcm.), 101261 (1spcm.), 101360 (1 spcm.), 101361 (1 spcm.), 101420 (7 spcm.), 101421 (1 spcm.), 101422 (1 spcm.), 101423 (3 spcm.), 101424 (8 spcm.), 101425 (3 spcm.), 101426 (1 spcm.), 101427 (7 spcm.), 101428 (4 spcm.), 101487 (9 spcm.), 101504 (12 spcm.), 101509 (10 spcm.). UHH 748 (28 spcm.).

***Praeoestophorella phacodes*** **(Thomae, 1845):** SMNS 100793 (46 spcm.), 101211 (11 spcm.), 101215 (1 spcm.), 101258 (1 spcm.), 101362 (1 spcm.), 101398 (21 spcm.), 101399 (13 spcm.), 101400 (1 spcm.), 101411 (9 spcm.), 101412 (1 spcm.), 101419 (1 spcm.), 101441 (45 spcm.). UHH 748 (>70 spcm.).

***Deroceras*** **sp.:** SMNS 101511 (1 spcm.), 101519 (3 spcm.).

***Vitrina suevica*** **Sandberger, 1876:** SMNS 101183 (12 spcm.), 101184 (8 spcm.), 101191 (3 spcm.), 101397 (6 spcm.).

***Milax*** **sp.:** SMNS 101518 (1 spcm.).

***Discus pleuradrus*** **(Bourguignat, 1881):** SMNS 100795 (1 spcm.), 101445 (1 spcm.), 101446 (1 spcm.), 101447 (2 spcm.), 101475 (1 spcm.), 101520 (2 spcm.), 101667 (1 spcm.). UHH 748 (2 spcm.).

***Granaria*** **sp.:** SMNS 67461 (3 spcm.), 100796 (1 spcm.), 101216 (1 spcm.), 101218 (16 spcm.), 101251 (2 spcm.), 101320 (1 spcm.), 101431 (1 spcm.), 101432 (1 spcm.), 101433 (13 spcm.), 101434 (31 spcm.), 101435 (3 spcm.), 101436 (28 spcm.), 101437 (21 spcm.), 101438 (1 spcm.), 101439 (20 spcm.), 101440 (1 spcm.), 101505 (2 spcm.), 101513 (13 spcm.), 101522 (29 spcm.), 101720 (23 spcm.). UHH 748 (>60 spcm.).

***Gastrocopta*** **cf.** ***acuminata*** **(Klein, 1846):** SMNS 67387 (1 spcm.).

***Gastrocopta sandbergeri*** **Stworzewicz & Prisyazhnyuk, 2006:** SMNS 67410 (1 spcm.).

***Vallonia*** **cf.** ***lepida*** **(Reuss, 1849):** SMNS 101185 (1 spcm.); 101186 (1 spcm.).

**?*Truncatellina* sp.:** SMNS 101180 (1 spcm.), 101181 (3 spcm.), 101182 (1 spcm.), 101396 (1 spcm.).

***Negulus suturalis*** **(Sandberger, 1858):** SMNS 101187 (1 spcm.), 101203 (1 spcm.).

***Pseudoleacina eburnea*** **(Klein, 1853):** SMNS 67033 (1 spcm.), 100801 (1 spcm.), 101164 (5 spcm.), 101165 (2 spcm.), 101166 (9 spcm.), 101167 (2 spcm.), 101168 (1 spcm.), 101169 (12 spcm.), 101417 (14 spcm.). UHH 748 (21 spcm.).

***Palaeoglandina gracilis*** **(von Zieten, 1830):** SMNS 101214 (1 spcm.), 101257 (1 spcm.), 101429 (1 spcm.), 101497 (1 spcm.).

***Testacella zellii*** **Klein, 1853:** SMNS 101219 (1 spcm.), 101510 (9 spcm.).

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# THE FOSSIL CONTINENTAL MOLLUSKS IN THE UPPER FRESHWATER MOLASSE (MIDDLE MIOCENE) OF THE DISTRICTS OF BIBERACH, RAVENSBURG AND NEU-ULM, GERMANY

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ABSTRACT – The present work is a taxonomical study of the continental mollusks collected in several fossil outcrops in the districts of Biberach and Ravensburg (SE Baden-Württemberg state) and Neu-Ulm (SW Bavaria state), Germany, by one of the authors (V.J.S.) in the years 1983-2013. All these fossil sites are of Middle Miocene age (European Mammal Neogene zones MN 5 and MN 6) and belong to the Upper Freshwater Molasse ("Obere Süßwassermolasse" or OSM), in the North Alpine Foreland Basin of southern Germany. The molluscan fauna of these sites counts with 17 gastropod and three bivalve species: *Tinnyea laureae*, *Pomatias* sp., *Bithynia* sp., *Theodoxus* sp., *Galba* cf. *G. dupuyiana*, *Lymnaea dilatata*, *Gyraulus applanatus*, *Planorbarius cornu*, *Opeas minutum*, Clausiliidae indet., *Triptychia* sp., *Archaeozonites costatus*, *Klikia* sp., *Pseudochloritis incrassata*, *Palaeotachea renevieri*, *Megalotachea silvana*, *Deroceras* sp., *Margaritifera flabellata*, *Unio kirchbergensis* and *Sphaerium* aff. *S. rivicola*. Finally, a few paleoenvironmental remarks are offered.

**Key words:** Bivalvia, European Mammal Neogene Zones MN5 and MN 6, Gastropoda, OSM, Pulmonata.

RESUMO – O presente trabalho é um estudo taxonômico dos moluscos continentais coletados em diversos afloramentos fossilíferos nos distritos de Biberach e Ravensburg (SE do Estado de Baden-Württemberg) e Neu-Ulm (SO do Estado de Bayern), Alemanha, por um dos autores (V.J.S.) durante os anos 1983-2013. Tais afloramentos datam do Mioceno Médio (zonas neógenas de mamíferos europeus MN5 e MN 6), pertencendo ao grupo "Obere Süßwassermolasse" (OSM) da bacia Alpina do Norte. A malacofauna dessas localidades conta com 17 espécies de gastrópodes e três de bivalves: *Tinnyea laureae*, *Pomatias* sp., *Bithynia* sp., *Theodoxus* sp., *Galba* cf. *G. dupuyiana*, *Lymnaea dilatata*, *Gyraulus applanatus*, *Planorbarius cornu*, *Opeas minutum*, Clausiliidae indet., *Triptychia* sp., *Archaeozonites costatus*, *Klikia* sp., *Pseudochloritis incrassata*, *Palaeotachea renevieri*, *Megalotachea silvana*, *Deroceras* sp., *Margaritifera flabellata*, *Unio kirchbergensis* e *Sphaerium* aff. *S. rivicola*. Adicionalmente, são oferecidos alguns comentários sobre o paleoambiente das localidades estudadas.

**Palavras-chave:** Bivalvia, zonas neógenas de mamíferos europeus MN 5 e MN 6, Gastropoda, OSM, Pulmonata.

## INTRODUCTION

Sach (1999) described several Middle Miocene fossil sites in the district of Biberach, Baden-Württemberg state, SW Germany, with his main focus being the lithology, sedimentology, biostratigraphy and the fossil mammals of the region. This author also listed many mollusk-bearing sites, but, since they were not the objective of his study, he did not provide a formal treatment of them. These mollusks are also listed, but not described nor figured, in a recently published catalogue of Early/Middle Miocene fossil sites in southern Germany (Sach, 2014). This catalogue also brings species lists of a few other newly discovered mollusk-bearing fossil sites in the neighboring districts of Ravensburg, in Baden-Württemberg, and Neu-Ulm, in Bavaria State (Figure 1), preliminarily listed by Sach (2014). Herein is presented a taxonomical analysis of these fossil continental mollusks, which are represented by 17 gastropod and three bivalve species, alongside with some paleoenvironmental remarks.

## MATERIAL AND METHODS

The mollusk-bearing fossil sites in the districts of Biberach, Ravensburg and Neu-Ulm can be seen in Figure 1, as named by Sach (1999, 2014). The Middle Miocene fossil sites studied here are detailed below.

**Biberach District**

Wannenwaldtobel 1: 48º01’50.88’’N, 09º50’01.14’’E; boulder horizon of the Ries impact (“Brockhorizont” in the original), 603.5 m above sea level (a.s.l.); Mammal Neogene zones MN 5/6 (transition).

Wannenwaldtobel 2: coordinates as Wannenwaldtobel 1; calcareous marl and marlstone horizon (“Kalkmergel” in the original), 610.0 m a.s.l.; additional fine-sand horizon with bivalves (*Margaritifera flabellata*) at ~609 m a.s.l.; Mammal Neogene zones MN 5/6 (transition).

Tobel Oelhalde-Nord: 48º02’24.95’’N, 09º49’52.03’’E; two fine-grained sand horizons with reworked OSM components, 604.6 m and 612.5 m a.s.l.; Mammal Neogene zones MN 5/6 (transition).

Tobel Oelhalde-Süd: 48º02’16.08’’N, 09º49’47.06’’E; fine-sand horizon with reworked OSM components, 596.3 m a.s.l.; additional fine-grained sand horizon with bivalves (*Margaritifera flabellata*) at 600.2 m a.s.l.; Mammal Neogene zones MN 5/6 (transition).

Edelbeuren-Schlachtberg: 48º05’21.38’’N, 10º01’17.71’’E; two fine-grained sand horizons with reworked OSM components, ~583 m a.s.l.; Mammal Neogene zone MN 5.

Binnrot: 48º03’49.01’’N, 10º03’07.94’’E; fine-sand horizons with reworked OSM components, 571.3–572.7 a.s.l.; additional sandy horizon with bivalves (*Sphaerium* aff. *rivicola*) at ~577 m a.s.l.; Mammal Neogene zone MN 5.

Bonlanden: 48º04’03.71’’N, 10º04’11.04’’E; fine-sand horizon with reworked OSM components, 564.9 m a.s.l.; Mammal Neogene zone MN 6.

Edelbeuren-Maurerkopf: 48º05’40.82’’N, 10º01’51.93’’E; two fine-sand horizons with reworked OSM components, 559.5–563.0 m a.s.l.; Mammal Neogene zone MN 5.

Heselsberg (Ochsenhausen-Heselsberg): 48°04’11.19’’N, 9°57’23.48’’E; fine-gravel horizon (“Erolzheimer Sande” at “Baustelle Remmele” in the original) with reworked OSM components, ~607 m a.s.l.; and 48°04’05.33’’N, 9°57’27.72’’E; fine-sand horizon (“Baustelle Harsch” in the original) with reworked OSM components, ~620 m a.s.l.; Mammal Neogene zone MN 5 (both fossil sites).

Auttagershofen: 48º11’56.49’’N, 10º01’04.74’’E; calcareous marl horizon, ~531 m a.s.l.; Mammal Neogene zone MN 5.

**Ravensburg District**

Burgerbachtobel 1: 47º48’03.26’’, N 9º26’59.22’’E (close to the border of Ravensburg and Bodenseekreis districts); calcareous marl and fine-sand horizons with reworked OSM components, ~580 m a.s.l.; Mammal Neogene zone MN 6;

Schmalegger Tobel: 47º48’25.21’’, N 9º32’16.14’’E; fine-sand horizons with reworked OSM components, ~510 m above sea level; Mammal Neogene zone MN 6.

Lattentobel: 47º49’49.70’’, N 9º25’57.63’’E; fine-sand horizons with reworked OSM components, ~610 m; Mammal Neogene zone MN 6.

**Neu-Ulm District**

Altenstadt-Untereichen: 48º09’29.47’’N, 10º06’39.93’’E; fine-sand horizons with reworked OSM components, ~562–566 m a.s.l.; additional fine-sand horizon with bivalves (*Margaritifera flabellata*) at ~570 m a.s.l.; Mammal Neogene zone MN 5.

The largest portion of the fossil material studied here derives from the localities Wannenwaldtobel 2, Edelbeuren-Maurerkopf, Burgerbachtobel 1 and Altenstadt-Untereichen. Together, these four sites have so far yielded numerous fossils of mammals, other vertebrate groups, non-mollusk invertebrates (insects, crustaceans and ostracods) and plants (Sach, 1999, 2014). There are some additional sites in these districts that also bear mollusk fossils (Sach, 1999, 2014), but the material was too fragmentary and was not collected and thus, could not be studied here. As such, the records for the following sites could not be confirmed in the present work: Biberach: Awengen (*Lymnaea* sp., *Cepaea* sp.) and Oberstetten (*Cepaea* sp.); Ravensburg: Ibacher Tobel, Horber-/Staigertobel, Aichertobel and Weiler Sandkeller (*Unio* sp. vel *Margaritifera* sp.) and Höll-Tobel (?*Tropidomphalus* sp., *Margaritifera* cf. *flabellata*). The sites Schwendi-Tobel and Brunnentobel, in Ravensburg, despite harboring mollusks (Sach, 1999, 2014), were excluded from the present work, since their location and stratigraphical data remain unknown.

All the material from the above mentioned fossil sites, which is housed in the collection of the Staatliches Museum für Naturkunde Stuttgart (**SMNS**; Stuttgart, Germany), was analyzed for the present work. A list of the examined material follows each species description. The specimens were collected during the years of 1983 to 2013 by V.J. Sach; for more details, see Sach (1999). Systematic arrangements follow Bouchet *et al*. (2005) and Nordsieck (2014). Selected specimens were examined by scanning electronic microscopy (**SEM**) in the SMNS; shell measurements were obtained either with a digital caliper or with the aid of computer software. The following shell measurements abbreviations are used throughout the text: **H**, shell height; **D**, shell greatest width; **h**, operculum height; **L**, shell length (bivalves).

## GEOLOGICAL SETTING

All the studied fossil sites date from the Middle Miocene (European Mammal Neogene zones MN 5 and MN 6) and belong to the stratigraphical unit known as the Upper Freshwater Molasse (“Obere Süßwassermolasse” in German, or OSM). More specifically: four sites (Bonlanden, Burgerbachtobel 1, Lattentobel and Schmalegger Tobel) are deemed to belong to the MN 6 zone; three sites (Wannenwaldtobel 1+2, Tobel Oelhalde-Süd and Tobel Oelhalde-Nord) belong to the transitional period MN 5/6; the remaining sites date from the MN 5 zone. For a more thorough

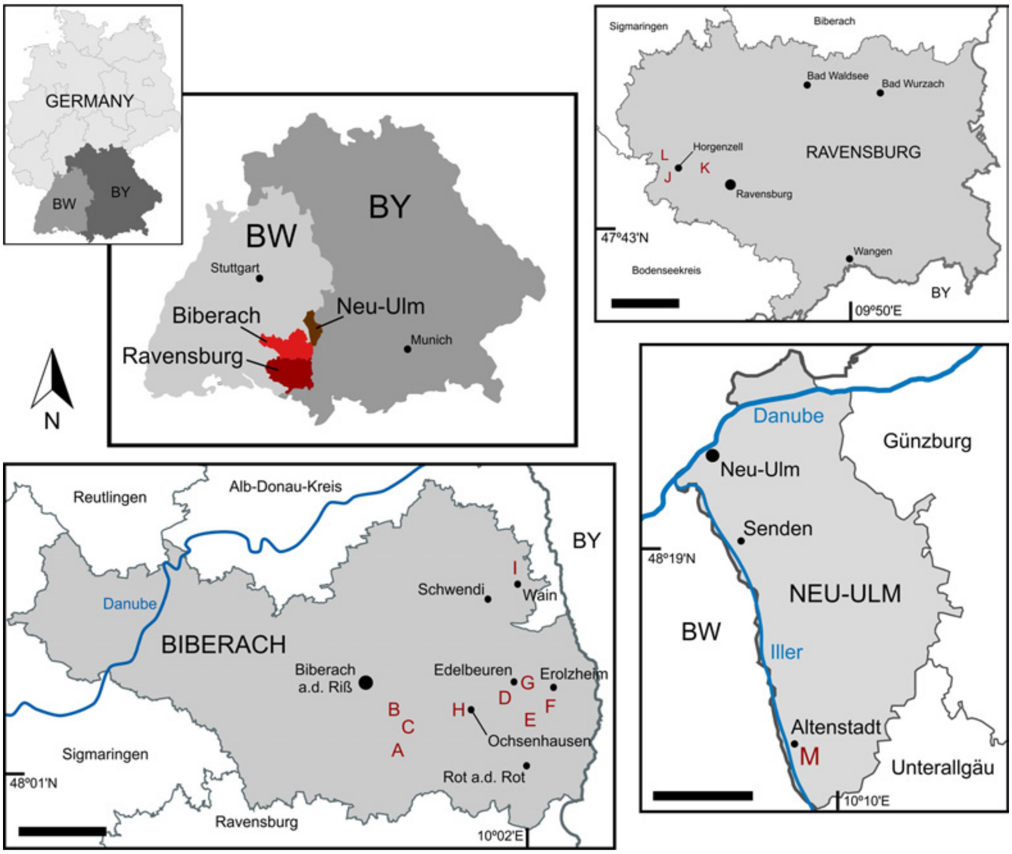

**Figure 1.** Map of the districts of Biberach and Ravensburg, Baden-Württemberg state (**BW**), and Neu-Ulm, Bavaria state (**BY**), Germany, indicating the Middle Miocene fossil sites (names according to Sach 1999, 2014). **A**, Wannenwaldtobel 1+2; **B**, Tobel Oelhalde-Nord; **C**, Tobel Oelhalde-Süd; **D**, Edelbeuren-Schlachtberg; **E**, Binnrot; **F**, Bonlanden; **G**, Edelbeuren-Maurerkopf; **H**, Heselsberg; **I**, Auttagershofen; **J**, Burgerbachtobel 1; **K**, Schmalegger Tobel; **L**, Lattentobel; **M**, Altenstadt-Untereichen. Scale bars = 10 km.

description of each fossil site, as well as the lithology of the fossiliferous sediments, their lithostratigraphic position and biostratigraphy, see Sach (1999, 2014) and Sach *et al*. (2003).

## SYSTEMATIC PALEONTOLOGY

Class GASTROPODA Cuvier, 1795
Clade CAENOGASTROPODA Cox, 1960
Superfamily CERITHIOIDEA Fleming, 1822
Family PACHYCHILIDAE P. Fischer & Crosse, 1892

*Tinnyea* Hantken, 1887

*Tinnyea lauraea* (Mathéron, 1843)
(Figures 2A-B)

1843 *Melania lauraea* Mathéron, p. 291, pl. 36, figs. 23-24.
1927 *Melanatria escheri turrita*: Berz & Jooss, p. 206.
1953 *Brotia* (*Tinnyea*) *escheri*: Papp, p. 128, pl. 3, fig. 29; Schlickum, 1976, p. 4, pl. 1, fig. 9; Mikuz & Pavsic, 2000, p. 44, pl. 1, figs. 1-8.
2014 *Brotia escheri*: Sach, p. 23.

**Material examined.** SMNS 101648 (seven specimens).
**Occurrence.** Altenstadt-Untereichen.
**Description.** Shell medium-sized to large, turreted, with regularly growing whorls. Protoconch not preserved. Teleoconch sculpture by parallel oblique axial ribs on first whorls (distance between axial ribs roughly twice their width) and by both axial and spiral cords on the remaining whorls (distance between cords roughly equal to three times their width). First spiral cord on each whorl stronger, with spike-like protuberances when it meets with axial ribs. Whorls profile convex. Suture well-marked, but not too deep.
**Discussion.** As pointed out by Kadolsky (1995), the name *T. escheri* (Brongniart, 1823) is a *nomen nudum*. The first valid name for the species is *T. laureae*. This species is known in the fossil record of Central Europe from the Oligocene to the Pliocene, but is rarer in the early and middle Miocene (Harzhauser *et al*., 2002). Nevertheless, it is known from the coeval nearby locality of Oggenhausen (Berz & Jooss, 1927).
**Paleoecological remarks.** This species is known from freshwater and oligohaline sediments (Kókay. 2006).

Superfamily LITTORINOIDEA Children, 1834
Family POMATIIDAE Newton, 1891

*Pomatias* Studer, 1789

*Pomatias* sp.

**Material examined.** SMNS 101678 (one operculum).
**Occurrence.** Burgerbachtobel 1.
**Discussion.** A single fragmentary operculum can be assigned to *Pomatias* by its spiral growth pattern, but identification beyond genus level is presently not possible.

Superfamily RISSOOIDEA Gray, 1847
Family BITHYNIIDAE Gray, 1857

*Bithynia* Leach, 1818

*Bithynia* sp.
(Figure 2C)

1999 *Bithynia* sp.: Sach, p. 24; Sach *et al*., 2003, p. 6; Sach, 2014, p. 27.

**Material examined.** SMNS 101539 (>100 operculum).
**Occurrence.** Edelbeuren-Maurerkopf.
**Discussion.** Only opercula remain; their overall shape and concentric growth pattern indicate the genus *Bithynia*, but identification at species level is impossible.
**Paleoecological remarks.** Recent *Bithynia* live in richly vegetated slow moving or standing waters, some are even found in temporary water bodies (Welter-Schultes, 2012).

Clade NERITIMORPHA Golikov & Starobogatov 1975
Family NERITIDAE Lamarck, 1809

*Theodoxus* Montfort, 1810

*Theodoxus* sp.
(Figure 2D)

2014 *Theodoxus crenulatus*: Sach, p. 25.

**Material examined.** SMNS 101649 (one specimen).
**Occurrence.** Altenstadt-Untereichen.
**Discussion.** The color pattern is preserved in this single fragment; this distinctive pattern allows the assignment to the genus *Theodoxus*. Despite a more precise identification at species level not being possible, it should be remarked that *Theodoxus crenulatus* (Klein, 1853) is a very common and widespread species in the middle and late Miocene of Central Europe and exhibits a great variation in color pattern (*e.g.* Harzhauser *et al*., 2012).
**Paleoecological remarks.** The habitat range of recent *Theodoxus* species is ample, so its use for paleoecological inferences is very limited; nevertheless, all species are intolerable to drought and seem to prefer rocky substrates (Bandel, 2001; Zettler *et al*., 2004; Bunje, 2005; Welter-Schultes, 2012).

PULMONATA Cuvier, 1814
Clade HYGROPHILA
Superfamily LYMNAEOIDEA Rafinesque, 1815
Family LYMNAEIDAE Rafinesque, 1815

*Galba* Schrank, 1803

*Galba* cf. *G. dupuyiana* (Noulet, 1854)
(Figure 2E)

1999 *Galba* sp.: Sach, p. 16; Sach *et al*., 2003, p. 9; Sach, 2014, p. 37.
1999 *Lymnaea* cf. *L. armaniacensis*: Sach, p. 24; Sach *et al*., 2003, p. 6; Sach, 2014, p. 27.

**Material examined.** SMNS 101540 (43 specimens), 101541 (one specimen), 101542 (one specimen), 101543 (one specimen), 101544 (eight specimens), 101545 (nine specimens).
**Occurrence.** Wannenwaldtobel 2, Edelbeuren-Maurerkopf and Auttagershofen.
**Description.** Shell small (H < 1 cm), lymnaeiform; shell width ~1/2 shell height. Transition proto- to teleoconch unclear. Teleoconch smooth, except for well-marked growth lines. Suture deep, well-marked. Whorls profile convex. Aperture oval, narrow, elongated. Peristome simple. Imperforate.
**Discussion.** Only broken and/or deformed spires remain in the present material, but they are reminiscent of *Galba dupuyiana*, a common species known throughout the middle Miocene of West and Central Europe (Kókay, 2006). The present specimens compare especially well with the taller and more elongated forms reported from the German early/middle Miocene sites of Oggenhausen and Sandelzhausen (Böttcher *et al*., 2009; Salvador & Rasser, 2014).
**Paleoecological remarks.** The single recent European species, *Galba truncatula* (O.F. Müller, 1774), inhabits both permanent and temporary water bodies, usually on the margins (Chapuis *et al*., 2007; Welter-Schultes, 2012).

*Lymnaea* Lamarck, 1799

*Lymnaea dilatata* (Noulet, 1854)
(Figures 2F-G)

1854 *Limnea dilatata* Noulet, p. 107.
1921 *Limnaea* (*Radix*) *dilatata*: Ehrat & Jooss, p. 4.
1923 *Radix* (*Radix*) *socialis dilatata*: Wenz, p. 1277; Seemann, 1926, p. 92.
1999 *Lymnaea dilatata*: Sach, p. 16; Fischer, 2000, p. 136, figs. 1-2; Binder, 2002, p. 165, pl. 1, fig. 7a; Sach *et al*., 2003, p. 6; Binder, 2004, p. 192, pl. 1, fig. 7; Kowalke & Reichenbacher, 2005, p. 630, figs. 9.4-9.5); Sach, 2014, p. 23; Salvador & Rasser, 2014, p. 189, figs. 8-9).
1999 *Lymnaea* sp.: Sach, p. 20.
1999 *Tudorella conica*: Sach, p. 24; Sach *et al*., 2003, p. 6.
2006 *Radix dilatata*: Kókay, p. 52, pl. 17, fig. 14; Neubauer *et al*., 2014, supplementary material 1.

**Material examined.** SMNS 101598 (~80 specimens), 101599 (~50 specimens), 101600 (one specimens), 101601 (three specimens), 101602 (one specimen), 101603 (two specimens), 101604 (six specimens), 101605 (three specimens), 101606 (one specimen), 101647 (seven specimens), 101680 (one specimen), 101682 (one specimen).

**Occurrence.** Wannenwaldtobel 2, Tobel Oelhalde-Süd, Bonlanden, Heselsberg, Edelbeuren-Maurerkopf, Burgerbachtobel 1 and Altenstadt-Untereichen.

**Description.** Shell large, lymnaeiform; spire acuminated, proportionately small. Transition proto- to teleoconch unclear. Teleoconch smooth, except for growth lines. Suture well-marked. Whorls profile slightly convex. Body whorl proportionately large. Peristome simple. Imperforate.

**Discussion.** *Lymnaea dilatata* is known from the whole Miocene of West and Central Europe (Binder, 2004; Kókay, 2006). Some authors (*e.g.* Wenz, 1923; Kókay, 2006) have placed the species in the genus *Radix* Montfort, 1810, but, as remarked by Fischer (2000), it is more reminiscent of *Lymnaea*. The single specimen previously identified as *Pomatias conicus* (Klein, 1853) by Sach (1999) and Sach *et al*. (2003) is a spire apex of *L. dilatata*.

**Paleoecological remarks.** Recent *Lymnaea* thrive in richly vegetated, shallow standing or slow-flowing waters, being commonly found in temporary water bodies (Glöer, 2002; Welter-Schultes, 2012).

### Superfamily PLANORBOIDEA Rafinesque, 1815
### Family PLANORBIDAE Rafinesque, 1815

### *Gyraulus* Charpentier, 1837

### *Gyraulus applanatus* (Thomae, 1845)
(Figures 2H-I)

1845 *Planorbis applanatus* Thomae, p. 150.
1851 *Planorbis dealbatus* Braun, p. 1134.
1923 *Gyraulus* (*Gyraulus*) *trochiformis applanatus*: Wenz, p. 1579.
1923 *Gyraulus* (*Gyraulus*) *trochiformis dealbatus*: Wenz, p. 1591.
1970a *Gyraulus trochiformis applanatus*: Schlickum, p. 148, pl. 10, fig. 6; Schlickum, 1970b, p. 180.
1964 *Gyraulus trochiformis dealbatus*: Schlickum, p. 15, pl. 2, fig. 35; Steininger *et al*., 1973, p. 451, pl. 9, figs. 11a,b; Reichenbacher, 1989, pl. 1, fig. 11; Kókay, 2006, p. 57, pl. 19, fig. 15.
2005 *Gyraulus applanatus*: Kowalke & Reichenbacher, p. 631, figs. 9.1-9.3; Kókay, 2006, p. 56, pl. 19, figs. 13-14; Neubauer *et al*., 2014, supplementary material 1.
1995 *Gyraulus dealbatus*: Kadolsky, p. 40, fig. 47; Binder, 2004, p. 193, pl. 2, figs. 1a-c; Neubauer *et al*., 2014, supplementary material 1; Salvador & Rasser, 2014, p. 192, figs. 16-23.

**Material examined.** SMNS 101544 (17 specimens), 101545 (~30 specimens), 101546 (~40 specimens), 101547 (one specimen).

**Occurrence.** Wannenwaldtobel 2 and Edelbeuren-Maurerkopf.

**Description.** Shell very small (D < 5 mm), pseudodextral, planispiral; shell height ~1/3 shell width. Protoconch sculpture not preserved; transition to teleoconch unclear. Teleoconch smooth, except for growth lines. Spire depressed. Suture deep, well-marked. Whorls somewhat rapidly growing, especially body whorl. Body whorl rounded, with very faint keel on median portion. Aperture arrowhead-shaped. Peristome simple, sharp. Umbilicus wide, shallow.

**Discussion.** The present specimens compare well with *Gyraulus applanatus* by the aperture shape, rapidly growing whorls and a rounded body whorl profile with a faint keel on its median portion. This species has not been reported by Sach (1999, 2014) for any of the localities. *Gyraulus applanatus* is known from the very early to middle Miocene of Germany and Austria (Gottschick & Wenz, 1916; Kadolsky, 1995; Binder, 2004; Kowalke & Reichenbacher, 2005). There is some morphological variation within this species and transitional forms between it and *G. dealbatus*, as reported by previous authors (Gottschick & Wenz, 1916; Kowalke & Reichenbacher, 2005; Salvador & Rasser, 2014). This led Kowalke & Reichenbacher (2005) to synonymize both species. The present specimens from Biberach are mostly juvenile or fragmentary; the small number of adult specimens does not seem to present much variation.

**Paleoecological remarks.** Recent *Gyraulus* are found in many habitats, limiting their use in paleoecological analysis. Still, they usually inhabit shallow richly-vegetated standing or slow-flowing waters, sometimes even temporary water bodies (Welter-Schultes, 2012).

### *Planorbarius* Duméril, 1806

### *Planorbarius cornu* (Brongniart, 1810)
(Figure 2J)

1810 *Planorbis cornu* Brongniart, p. 371, pl. 22, fig. 6.
1923 *Coretus cornu cornu*: Wenz, p. 1426.
1966 *Planorbarius cornu*: Schlickum, p. 326, pl. 13, fig. 27; Schlickum, 1970a, p. 149, pl. 10, fig. 7; Reichenbacher, 1989, p. 172, pl. 1, fig. 10; Binder, 2004, p. 193, pl. 2, figs. 2-3; Neubauer *et al*., 2014, supplementary material 1; Salvador & Rasser, 2014, p. 193, figs. 26-28.
1999 *Coretus* cf. *C. cornu*: Sach, p. 16.
1999 *Coretus* sp. Sach, p. 17.
2006 *Planorbarius cornu cornu*: Kókay, p. 58, pl. 20, fig. 6; Böttcher *et al*., 2009, p. 239, figs. 2.4-2.6.
2003 *Planorbarius* cf. *P. cornu*: Sach *et al*., p. 6; Sach, 2014, p. 23.

**Material examined.** SMNS 101571 (>100 specimens), 101572 (>100 specimens), 101573 (three specimens), 101574 (>100 specimens), 101575 (13 specimens), 101576 (one specimen), 101577 (two specimens), 101578 (one specimen), 101579 (one specimen), 101580 (four specimens), 101581 (five specimens), 101646 (eight specimens).

**Occurrence.** Wannenwaldtobel 2, Tobel Oelhalde-Nord, Tobel Oelhalde-Süd, Edelbeuren-Schlachtberg, Bonlanden, Edelbeuren-Maurerkopf and Altenstadt-Untereichen.

**Description.** Shell large, sinistral, planispiral; shell height ~1/3 shell width. Spire very depressed. Suture deep, well-marked. Whorls regularly growing. Whorl profile rounded. Aperture rounded. Umbilicus very wide, deep. Unfortunately, due to poor preservation, proto- and teleoconch sculpture cannot be observed.

**Discussion.** The present specimens, despite the poor preservation, compare well with *Planorbarius cornu*, a morphologically variable species known from the middle Eocene to the late Miocene of France, Germany (especially abundant in the OSM) and Czech Republic (Schlickum, 1970a; Kókay, 2006). As pointed out by Harzhauser *et al.* (2014), this long time span could indicate the presence of more than one species. Until this species complex has been the target of revisionary work, we prefer a more conservative identification as *P. cornu*.

**Paleoecological remarks.** Recent *Planorbarius* are found in typically richly-vegetated standing or slow-moving waters (Glöer, 2002; Welter-Schultes, 2012).

Clade STYLOMMATOPHORA A. Schmidt, 1855
Superfamily ACHATINOIDEA Swainson, 1840
Family SUBULINIDAE P. Fischer & Crosse, 1877

*Opeas* Albers, 1850

*Opeas minutum* (Klein, 1853)
(Figure 2K)

1853 *Bulimus minutus*: Klein, p. 212, pl. 5, fig. 9.
1923 *Opeas minutum*: Wenz, p. 872; Seemann, 1926, p. 92; Kókay, 2006, p. 80, pl. 30, fig. 16; Harzhauser *et al*., 2014, p. 28, pl. 9, figs. 3-5, 7.
1976 *Opeas* (*Opeas*) *minutum*: Schlickum, p. 14, pl. 3, fig. 46.

**Material examined.** SMNS 101551 (one specimen).

**Occurrence.** Edelbeuren-Maurerkopf.

**Description.** Shell small, with regularly growing whorls. Protoconch large, rounded, dome-shaped, apparently smooth; transition to teleoconch unclear. Teleoconch apparently smooth. Whorls profile slightly convex. Suture well-marked but not too deep.

**Discussion.** *Opeas minutum* is easily diagnosed by the small size of its subulinid shell. Although this single specimen is a spire apex, it compares extremely well with material from other Miocene fossil sites in Germany. The species is known from the early/middle Miocene of Hungary, Germany, Austria and Switzerland (Schlickum, 1976; Kókay, 2006; Harzhauser *et al*., 2014) and has not been reported by Sach (1999, 2014) for the present locality.

**Paleoecological remarks.** Recent *Opeas* are found in tropical and subtropical regions worldwide (Zilch, 1959-1960; Willig, 2013).

Superfamily CLAUSILIOIDEA J.E. Gray, 1855
Family CLAUSILIIDAE Gray, 1855

Clausiliidae indet.
(Figures 2L-M)

2003 Clausiliidae indet.: Sach *et al*., p. 6; Sach, 2014, p. 27.

**Material examined.** SMNS 101549 (one specimen), 101550 (four specimens).

**Occurrence.** Edelbeuren-Maurerkopf.

**Discussion.** The sinistral shell and rounded whorl profile (Figure 2L), as well as the sculpture pattern on the apertural fragment (Figure 2M), point to a clausiliid. Unfortunately, with the present material a more precise determination is not possible.

**Paleoecological remarks.** Nordsieck (2007) suggests that clausiliids up to the middle Miocene were mostly wood-dwelling animals, preferring humid and warm environments.

Family FILHOLIIDAE Wenz, 1923

*Triptychia* Sandberger, 1875

*Triptychia* sp.
(Figure 2N)

**Material examined.** SMNS 101548 (one specimen).

**Occurrence.** Edelbeuren-Maurerkopf.

**Description.** Shell sinistral, with conical profile. Protoconch dome-shaped; transition to teleoconch unclear. Teleoconch sculpture not preserved. Whorl profile slightly convex. Suture deep, well-marked, slightly incised.

**Discussion.** The conical sinistral shell with its flat whorl profile agrees very well with the genus *Triptychia*. Nevertheless, it is presently impossible to proceed further than this in the classification of the material.

**Paleoecological remarks.** It is usually suggested that filholiids were mostly wood-dwelling animals, preferring humid and warm forests (Schnabel, 2007, and references therein).

Superfamily ZONITOIDEA Mörch, 1864
Family ZONITIDAE Mörch, 1864

*Archaeozonites* Sandberger, 1872

*Archaeozonites costatus* Sandberger, 1875
(Figures 2O-P)

1875 *Archaeozonites costatus*: Sandberger, p. 604; Schlickum, 1976, p. 18, pl. 5, fig. 66; Rasser *et al*., 2013, p. 440.
1921 *Zonites* (*Aegopis*) *costatus*: Ehrat & Jooss, p. 3; Wenz, 1923, p. 254; Seemann, 1926, p. 91.
1999 *Valvata* sp.: Sach, p. 22; Sach, 2014, p. 31.
2006 *Aegopis costatus*: Kókay, p. 77, pl. 29, figs. 11-12.
2002 *Miozonites costatus*: Binder, p. 168, pl. 1, figs. 14-16, pl. 3, fig. 8, pl. 7, fig. 3, pl. 8, fig. 4; Harzhauser *et al*., 2014, p. 33, pl. 10, figs. 13-19.

**Material examined.** SMNS 101556 (three specimens), 101557 (one specimen), 101558 (one specimen), 101559 (three specimen).

**Occurrence.** Edelbeuren-Schlachtberg, Binnrot and Edelbeuren-Maurerkopf.

**Description.** Shell large (D > 2 cm), helicoid, with broad conical spire and regularly growing whorls. Protoconch (~1 whorl) flattened, sculptured by fine riblets that grow coarser towards teleoconch. Teleoconch sculptured by numerous strong parallel prosocline ribs; distance between ribs equal to rib's width; ribs apparently absent on lower portion of whorls. Suture weakly marked. Whorls profile flattened; body whorl with a strong keel. Aperture oval. Umbilicus broad, deep.

**Discussion.** Despite the somewhat distorted preservation of the body whorl and aperture, the present specimens compare fittingly with *Archaeozonites costatus*, a species known from the early and middle Miocene of Central Europe (Kókay, 2006) and common in the Silvana-beds ("Silvanaschichten") of southwestern Germany (MN 5-6; Schlickum, 1976). The single specimen of *Valvata* sp. reported by Sach (1999, 2014) is a misidentification of a fragment of *A. costatus*.

**Paleoecological remarks.** As a fossil genus, any paleoecological inference is tentative; still, Lueger (1981) considered that *Archaeozonites laticostatus* (Sandberger, 1885), also from the Miocene of Central Europe, lived under leaves or between rocks in moist forests.

### Superfamily HELICOIDEA Rafinesque, 1815
### Family ELONIDAE Gittenberger, 1977

### *Klikia* Pilsbry, 1895

### *Klikia* sp.
(Figure 2Q)

1999 *Klikia coarctata*: Sach, p. 24; Sach *et al*., 2003, p. 6; Sach, 2014, p. 27.

**Material examined.** SMNS 101552 (~85 specimens), 101645 (four specimens), 101681 (one specimen).

**Occurrence.** Edelbeuren-Maurerkopf, Heselsberg and Altenstadt-Untereichen.

**Description.** Shell medium-sized (D > 1 cm), depressed, multispiral. Suture well-marked, moderately deep. Whorls closely-packed, regularly increasing in size. Aperture crescent-shaped. Peristome reflexed.

**Discussion.** Despite the extremely poor preservation, the shell's discoid shape, size and the large number of narrowly coiled whorls indicate the genus *Klikia*. Nevertheless, identification beyond genus level is impossible.

**Paleoecological remarks.** Lueger (1981) suggested that species in this fossil genus preferred drier environments.

### Family HELICIDAE Rafinesque, 1815

### *Pseudochloritis* Boettger, 1909

### *Pseudochloritis incrassata* (Klein, 1853)
(Figures 3A-C)

1846 *Helix inflexa* Klein [*non* von Zieten, 1832], p. 71, pl. 1, fig. 12.
1853 *Helix incrassata* Klein, p. 208, pl. 5, fig. 6.
1923 *Tropidomphalus* (*Pseudochloritis*) *incrassatus incrassatus*: Wenz, p. 510; Seemann, 1926, p. 91; Schlickum, 1976, p. 16, pl. 4, fig. 56.
1980 *Tropidomphalus* (*Pseudochloritis*) *incrassatus incrassatus*: Gall, p. 59.
1999 *Tropidomphalus* sp.: Sach, p. 16; Sach *et al*., 2003, p. 9.
1999 *Tropidomphalus* aff. *zellii*: Sach, p. 21; Sach *et al*., 2003, p. 6; Sach, 2014, p. 23.
2006 *Tropidomphalus* (*Pseudochloritis*) *incrassatus*: Kókay, p. 90, pl. 34, figs. 12-14.
2008 *Pseudochloritis incrassata*: Binder, p. 172, pl. 3, figs. 2-4, pl. 6, fig. 2; Rasser *et al*., 2013, p. 434, pl. 4, fig. 12; Harzhauser *et al*., 2014, p. 35, pl. 12, figs. 9-16, 19-24; Höltke & Rasser, 2015, p. 1, figs. 4.3, 5.1-5.2, 6.11-6.12.
2008 *Tropidomphalus* (*Pseudochloritis*) *incrassatus*: Górka, p. 107, figs. 3.1-3.4.

**Material examined.** SMNS 101582 (28 specimens), 101583 (10 specimens), 101584 (one specimen), 101585 (four specimens), 101586 (five specimens), 101587 (three specimens), 101588 (one specimen), 101589 (one specimen), 101590 (one specimen), 101591 (two specimens), 101592 (one specimen), 101593 (two specimens), 101594 (two specimens), 101595 (two specimens), 101596 (two specimens), 101597 (>100 specimens), 101607 (one specimen), 101624 (three specimens), 101644 (eight specimens).

**Occurrence.** Wannenwaldtobel 1, Wannenwaldtobel 2, Tobel Oelhalde-Nord, Tobel Oelhalde-Süd, Edelbeuren-Schlachtberg, Binnrot, Edelbeuren-Maurerkopf, Heselsberg, Schmalegger Tobel and Altenstadt-Untereichen.

**Description.** Shell large (D > 2 cm), ~4½ whorls, helicoid to disc-shaped, with flattened spire. Protoconch (1¼ whorl) flattened, large in relation to following whorl; sculptured by fine striae dotted with weak papillae; transition to teleoconch unclear. Teleoconch sculptured by thickened growth lines and irregular weak furrows, with regularly arranged papillae. Suture deep, well-marked. Body whorl enlarged, slightly bent downwards, with conspicuous constriction right before the aperture ("extralabial depression" *sensu* Binder 2008). Aperture prosocline; no callus apparent. Peristome markedly thickened and reflexed, slightly covering umbilicus. Umbilicus narrow to wide.

**Discussion.** The present specimens conform well to *P. incrassata*, a species known from the middle Miocene of Central Europe (Binder, 2008; Salvador, 2014). There is some uncertainty regarding the position of this genus, which is either assigned to Helicidae (Ariantinae) or to Elonidae (Zilch, 1959–1960; Binder, 2008; Moser, *et al.*, 2009; Nordsieck, 2014; Höltke & Rasser, 2015).

**Paleoecological remarks.** Based on the bent down body whorl and prosocline aperture, Binder (2008) considered the shell an adaptation for ground-dwelling (by reducing water loss in drier environments). Similarly, Moser *et al.* (2009) suggested that the genus inhabited drier and more open habitats, having a "way of life like strong-shelled Balkanese representatives of Ariantinae".

### *Palaeotachea* Jooss, 1912

### *Palaeotachea renevieri* (Maillard, 1892)
(Figures 2R-T)

1892 *Helix* (*Macularia*) *renevieri* Maillard, p. 43, pl. 3, fig. 18.
1923 *Cepaea renevieri*: Wenz, p. 652.
1954 *Cepaea* cf. *C. renevieri*: Zöbelein, p. 156.
1999 *Cepaea* sp.: Sach, p. 23; Sach, 2014, p. 31.

**Material examined.** SMNS 101560 (34 specimens), 101561 (24 specimens), 101562 (three specimens), 101563 (one specimen), 101564 (two specimens), 101565 (two specimens), 101566 (three specimens), 101567 (one specimen), 101568 (one specimen), 101569 (five specimens), 101570 (four specimens).

**Occurrence.** Tobel Oelhalde-Nord, Tobel Oelhalde-Süd, Bonlanden, Edelbeuren-Maurerkopf, Heselsberg, Auttagershofen and Burgerbachtobel 1.

**Description.** Shell medium-sized (D > 1 cm), ~4¼ whorls, helicoid, with overall flattened profile and very faint keel; whorls quickly but regularly growing; shell length ~2/3 its width. Protoconch flattened; transition to teleoconch unclear. Suture well-marked. Body whorl slightly bent downwards near the aperture. Aperture small, prosocline, circular. Peristome lightly thickened and slightly reflexed. Imperforate. On one specimen (SMNS 101563) it is possible to observe, under UV light, vestiges of three colored fine parallel spiral bands, the topmost one on the middle to upper portion of the whorl, the other two regularly spaced on the basal portion of whorl.

**Discussion.** *Palaeotachea renevieri* can be identified by its small size, a small circular aperture, a thickened but not reflexed peristome and a somewhat flattened shell profile with a faint keel. The species is known from the middle and late Miocene of Southern Germany and Switzerland (Wenz, 1923; Zöbelein, 1954). The observed trifasciate banding pattern is recurrent in Miocene helicids (*e.g.* Górka, 2008; Salvador, 2013).

**Paleoecological remarks.** As a fossil genus, paleoecological implications are not possible. Recent *Cepaea* Held, 1838 and allied species inhabit a broad range of habitats (Welter-Schultes, 2012).

### *Megalotachea* Pfeffer, 1930

### *Megalotachea silvana* (Klein, 1853)
(Figures 2U-W)

1853 *Helix silvana* Klein, p. 205, pl. 5, fig. 2.
1923 *Cepaea silvana silvana*: Wenz, p. 667; Schlickum, 1976, p. 17, pl. 4, figs. 62-63; Reichenbacher, 1989, p. 165, pl. 2, figs. 17-19.
1999 *Cepaea silvana*: Sach, p. 16; Sach *et al.*, 2003, p. 6; Kókay, 2006, p. 93, pl. 36, figs. 2-3; Rasser *et al.*, 2013, p. 440; Sach, 2014, p. 23.

**Material examined.** SMNS 101608 (>100 specimens), 101609 (one specimen), 101610 (two specimens), 101611 (one specimen), 101612 (one specimen), 101613 (two specimens), 101614 (one specimen), 101615 (two specimens), 101616 (two specimens), 101617 (three specimens), 101618 (four specimens), 101619 (six specimens), 101620 (five specimens), 101621 (three specimens), 101622 (eight specimens), 101623 (34 specimens), 101625 (19 specimens), 101626 (35 specimens), 101627 (10 specimens), 101643 (16 specimens).

**Occurrence.** Wannenwaldtobel 1, Wannenwaldtobel 2, Tobel Oelhalde-Nord, Tobel Oelhalde-Süd, Edelbeuren-Schlachtberg, Binnrot, Bonlanden, Edelbeuren-Maurerkopf, Heselsberg, Auttagershofen, Burgerbachtobel 1 and Altenstadt-Untereichen.

**Description.** Shell large (D > 2 cm), 4¼-4½ whorls, helicoid; whorls regularly growing. Protoconch flattened, smooth; transition to teleoconch unclear. Teleoconch smooth, except for growth lines. Whorl profile flat on first whorls; more convex on later ones. Suture well-marked. Body whorl slightly bent downwards. Aperture prosocline, crescent-shaped; callus faint. Peristome markedly thickened and reflexed. Imperforate.

**Discussion.** The present specimens compare fittingly with *Cepaea silvana*, a common species in the German Early/Middle Miocene, mainly due to their more rounded aperture and their greatly reflexed peristome. The specimens show a broad size range: H = 14.9 ± 2.0 mm (max = 19.0 mm, min = 13.0 mm), D = 21.9 ± 1.9 mm (max = 28.0 mm, min = 19.2 mm). Still, the poor preservation of the fossils, with many internal molds and deformed specimens, precludes a precise description of morphological variation in other shell characters.

**Paleoecological remarks.** Same as *Palaeotachea renevieri*, above.

### Superfamily LIMACOIDEA Lamarck, 1801
### Family AGRIOLIMACIDAE H. Wagner, 1935

### *Deroceras* Rafinesque, 1820

### *Deroceras* sp.
(Figure 3D)

1999 *Limax* sp.: Sach, p. 16; Sach *et al.*, 2003, p. 6; Sach, 2014, p. 27.

**Material examined.** SMNS 101553 (eight specimens), 101554 (>100 specimens), 101555 (22 specimens), 101677 (~40 specimens).

**Occurrence.** Wannenwaldtobel 2, Edelbeuren-Maurerkopf and Burgerbachtobel 1.

**Description.** Shell small (H < 1 cm), vestigial, oval; shell width ~2/3 length. Nucleus slightly bent laterally; nucleus region higher than remainder of shell. Shell with marked concentric growth lines.

**Discussion.** The vestigial shells of slugs are of very limited

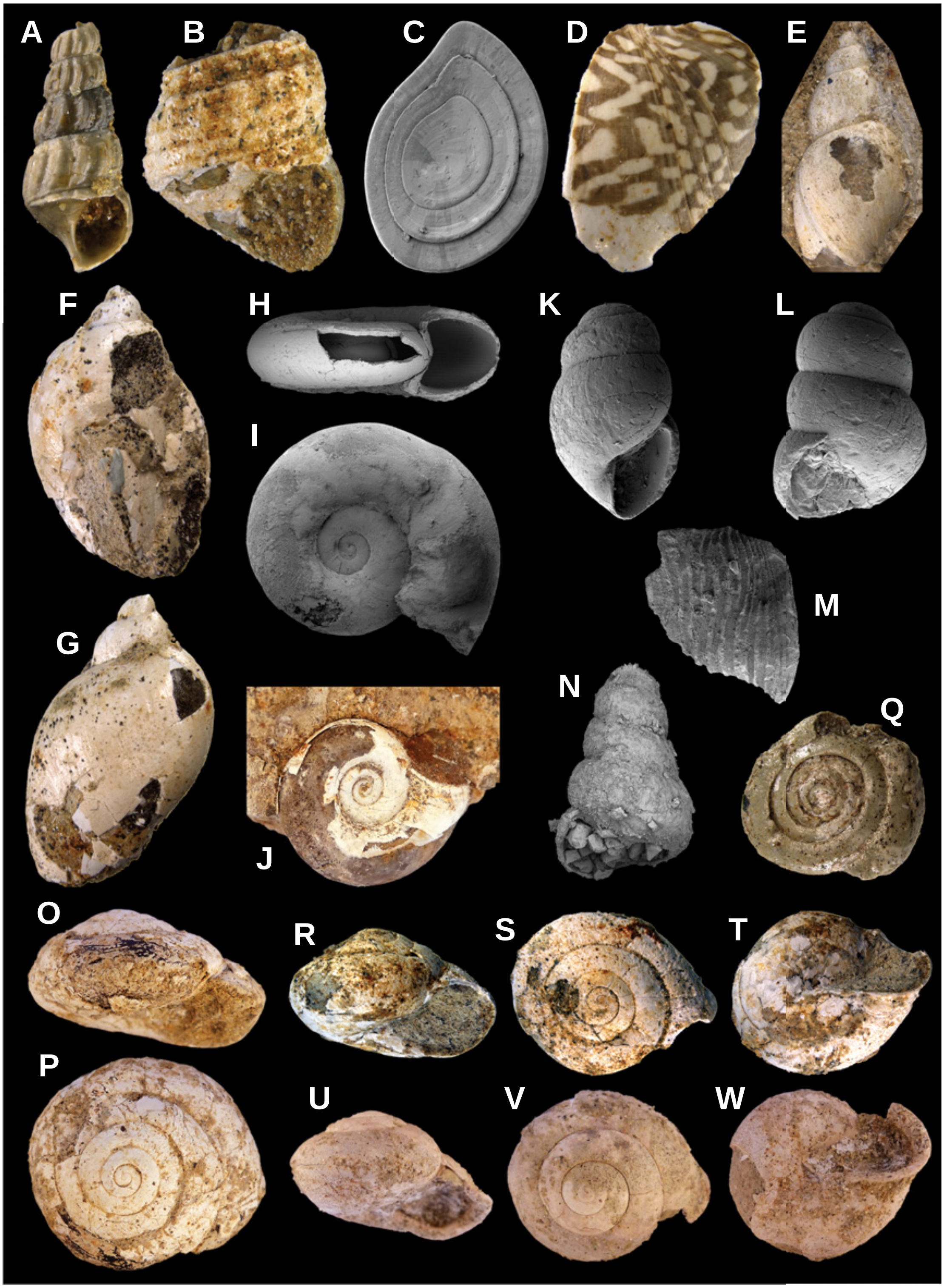

**Figure 2. A**, *Tinnyea lauraea* (SMNS 101648, specimen #1, from Altenstadt-Untereichen; H = 11.3 mm). **B**, *Tinnyea lauraea* (SMNS 101648, specimen #2, from Altenstadt-Untereichen; H = 16.0 mm). **C**, *Bithynia* sp., operculum (SMNS 101539, from Edelbeuren-Maurerkopf; h = 3.7 mm). **D**, *Theodoxus* sp. (SMNS 101649, from Altenstadt-Untereichen; fragment width = 4.5 mm). **E**, *Galba* cf. *G. dupuyiana* (SMNS 101540, from Wannenwaldtobel 2; H = 8.2 mm). **F-G**, *Lymnaea dilatata* (SMNS 101601, from Wannenwaldtobel 2; H = 17.8 mm, D = 11.1 mm). **H**, *Gyraulus applanatus* (SMNS 101546, specimen #1, from Wannenwaldtobel 2; D = 2.5 mm). **I**, *G. applanatus* (SMNS 101546, specimen #2, from Wannenwaldtobel 2; D = 2.9 mm). **J**, *Planorbarius cornu* (SMNS 101573, from Wannenwaldtobel 2; D = 19.0 mm). **K**, *Opeas minutum*, spire apex (SMNS 101551, from Edelbeuren-Maurerkopf; H = 1.8 mm). **L**, Clausiliidae indet., spire apex (SMNS 101550, from Edelbeuren-Maurerkopf; H = 0.7 mm). **M**, Clausiliidae indet., fragment of body whorl, apertural region (SMNS 101550, from Edelbeuren-Maurerkopf; fragment width = 2.1 mm). **N**, *Triptychia* sp., spire apex (SMNS 101548, from Edelbeuren-Maurerkopf; H = 2.6 mm). **O**-**P**, *Archaeozonites costatus* (SMNS 101559, from Edelbeuren-Schlachtberg; H = 17.3 mm, D = 27.0 mm). **Q**, *Klikia* sp. (SMNS 101552, from Edelbeuren-Maurerkopf; D = 11.2 mm). **R**-**T**, *Palaeotachea renevieri* (SMNS 101562, from Heselsberg; H = 11.2 mm, D = 17.1 mm). **U**-**W**, *Megalotachea silvana*, unusually large specimen (SMNS 101609, from Bonlanden; H = 19.0 mm, D = 28.0 mm).

taxonomical value and, therefore, identification of the present specimens cannot proceed further than genus level. As pointed by Harzhauser *et al*. (2014), fossil *Deroceras* are known since the Miocene, but are often identified as either *Limax* Linnaeus, 1758 or *Milax* Gray, 1855.

**Paleoecological remarks.** *Deroceras* is known from a broad range of habitats, from the more usual open grasslands to forests, including wetlands and anthropically disturbed areas (Welter-Schultes, 2012; Rowson *et al*., 2014).

Class BIVALVIA Linnaeus, 1758
Order UNIONOIDA Stoliczka, 1871
Family MARGARITIFERIDAE Henderson, 1929 (1910)

*Margaritifera* Schumacher, 1816

*Margaritifera flabellata* (Goldfuss, 1837)
(Figures 3E-G)

**Synonymy.** See Schneider & Prieto (2011) and complement:
1970 *Plicatibaphia flabellata*: Starobogatov, p. 61.
1999 *Unio* sp. vel *Margaritifera* sp.: Sach, p. 16; Sach *et al*., 2003, p. 6; Sach, 2014, p. 27.
2014 *Unio* sp. vel *Margaritifera* sp.: (in part) Sach, p. 81.
1999 *Margaritifera flabellata*: Sach, p. 20; Sach, 2014, p. 30.
2011 *Margaritifera* (*Pseudunio*) *flabellata*: Schneider & Prieto, p. 4, figs. 3-6.
2012 *Plicatibaphia bavarica*: Grim *et al*., p. 19, pl. 1.

**Material examined.** SMNS 101629 (three specimens), 101630 (five specimens), 101631 (two specimens), 101632 (three specimens), 101633 (seven specimens), 101634 (two specimens), 101635 (three specimens), 101636 (two specimens), 101637 (three specimens), 101638 (one specimen), 101639 (one specimen), 101640 (two specimens), 101656 (~10 specimens).

**Occurrence.** Wannenwaldtobel 2, Tobel Oelhalde-Nord, Tobel Oelhalde-Süd, Edelbeuren-Schlachtberg, Binnrot, Bonlanden, Edelbeuren-Maurerkopf, Heselsberg, Burgerbachtobel 1, Schmalegger Tobel, Lattentobel and Altenstadt-Untereichen.

**Description.** Valve elliptical to reniform; middle third of valve length slightly compressed in height; ~35% longer than taller. Shell inflated, width ~40% of total shell length. External surface frequently smooth, sometimes covered by traces of growth lines and deep and worn plicae at posterior margin of valves. Internal surface smooth, without scars preserved. Umbones wide and low, ~20% of total valve length and ~5% of total valve height, located between anterior and middle third of shell length. Ligament external, long and narrow, length ~60% of total shell length. Right hinge composed by two pseudocardinal teeth, disposed anteriorly to umbones axis, on a dental shelf; dental shelf triangular, located between anterior and dorsal shell margins; shape approximately fusiform; length ~60% of total valve height; anterior tooth long and narrow, length ~30% of dental shelf length, laminar, distanced from posterior tooth ~1.5 times its own width; posterior tooth short and rounded, ~1/2 anterior tooth total length. Left hinge with two pseudocardinal teeth, disposed anteriorly to umbones axis, on a dental shelf; dental shelf triangular, wide, length ~90% of total valve height; anterior tooth long, length same as dental shelf width, pyramidal, dorsal to middle portion wide and strong, middle and anterior portion laminar, away from posterior tooth *ca*. twice its own width; posterior tooth strong and wide, triangular and flat, length same as anterior tooth, greatest width ~10% total dental shelf length.

**Discussion.** *Margaritifera flabellata* is characteristic of the late Miocene in a wide range of Central European localities and shows a constancy of overall shell forms (Kókay, 2006; Schneider & Prieto, 2011). Moreover, this species shows some variety in shell ornamentation, which is deemed to be due to preservation issues rather than related to distinct environmental conditions (Schneider & Prieto, 2011).

**Paleoecological remarks.** Recent European *Margaritifera* species inhabit fast flowing and well oxygenated waters (Harzhauser & Tempfer, 2004), with the larger *M. auricularia* (Spengler, 1793) usually occurring in large rivers (Welter-Schultes, 2012). The fossil *M. flabellata* more closely resembles the recent *M. margaritifera* (Linnaeus, 1758), which usually is found in clear running waters (Welter-Schultes, 2012). Apparently, the conditions in the present sites during the Miocene were very favorable to *M. flabellata*: the species is widespread, occurring in nearly all the mollusk-bearing localities presented here (Table 1), reasonably abundant and reaches large sizes; moreover, there is an equal proportion of articulated and disarticulated specimens, indicating that the species is authochtonous. Given the environmental interpretation of the sites (Sach, 1999; see also discussion section below), *M. flabellata* seems to have had different preferences than its living relatives. Moreover, this species is also known from some paludal Miocene environments (Schneider & Prieto, 2011).

Family UNIONIDAE Fleming, 1828

*Unio* Philipsson, 1788

*Unio kirchbergensis* Krauss, 1852
(Figures 3J-K)

1852 *Unio kirchbergensis* Krauss, p. 152, figs. 5a-c; Pictet, 1855, p. 529; Lea, 1870, p. 65.
2014 *Unio* sp. vel *Margaritifera* sp.: (in part) Sach, p. 81.

**Material examined.** SMNS 101650 (one specimen).

**Occurrence.** Altenstadt-Untereichen.

**Description.** Valve elliptical, ~40% longer than taller. Valve width ~20% of total valve length. External surface mostly smooth, with traces of growth lines on middle and ventral portions. Internal surface smooth, without scars preserved. Umbones wide and low, ~25% of total valve length and ~5% of total valve height, located between anterior and middle third of length. Left hinge with two cardinal teeth disposed parallel

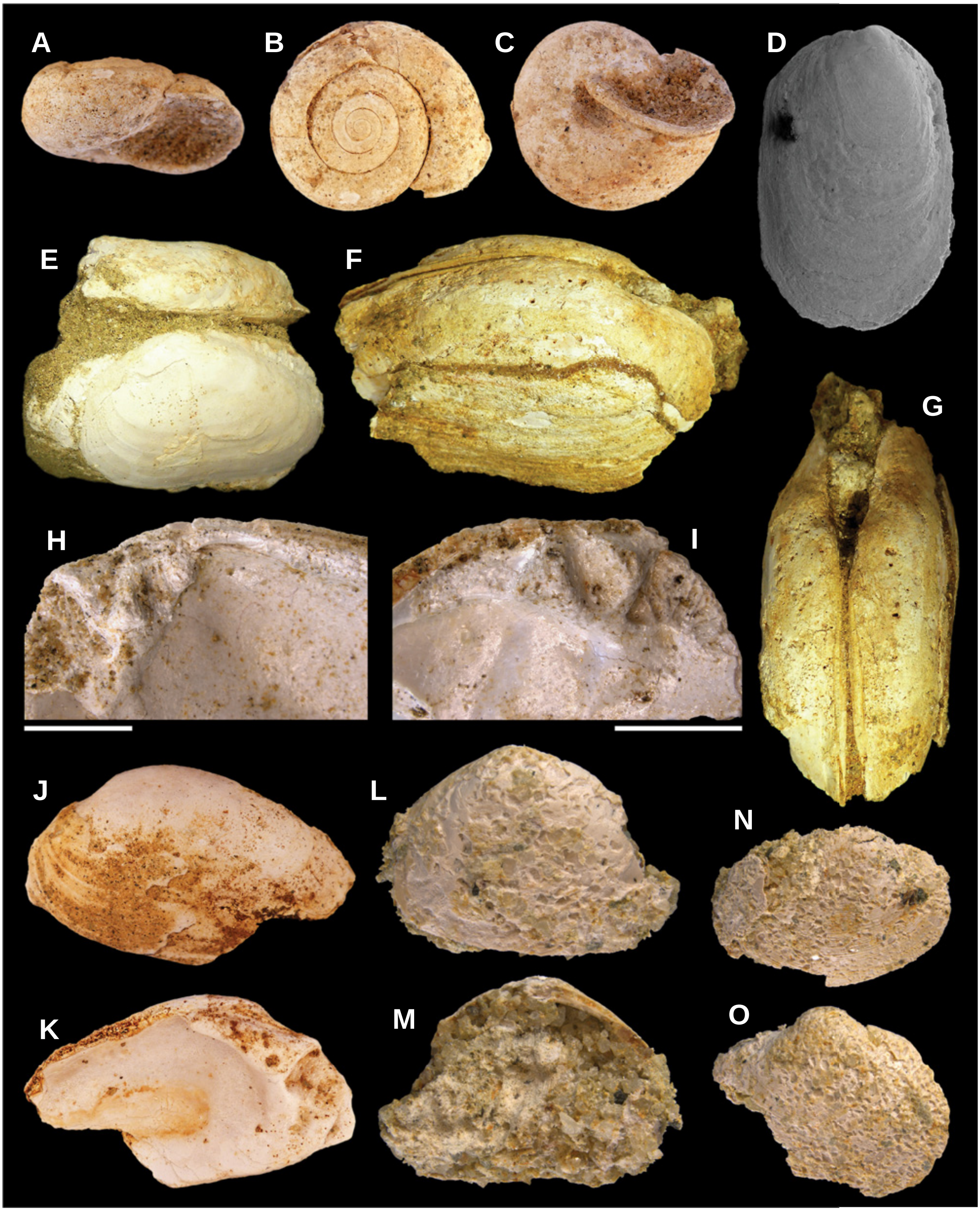

**Figure 3. A**-**C**, *Pseudochloritis incrassata* (SMNS 101585, from Edelbeuren-Schlachtberg; H = 15.3 mm, D = 26.0 mm). **D**, *Deroceras* sp. (SMNS 101554, from Edelbeuren-Maurerkopf; H = 9.5 mm, D = 6.1 mm). **E**, *Margaritifera flabellata*, left valve (SMNS 101656, from Altenstadt-Untereichen; L = 66.0 mm). **F-G**, *M. flabellata*, respectively, lateral (right valve) and dorsal view of closed specimen (SMNS 101632, from Edelbeuren-Schlachtberg; L = 65.1 mm). **H**, *M. flabellata*, detail of right hinge (SMNS 101633, specimen #1, from Edelbeuren-Schlachtberg; scale bar = 1 cm). **I**, *M. flabellata*, detail of left hinge (SMNS 101633, specimen #2, from Edelbeuren-Schlachtberg; scale bar = 1 cm). **J-K**, *Unio kirchbergensis*, respectively, external and internal view of left valve (SMNS 101650, from Altenstadt-Untereichen; L = 48.8 mm). **L-M**, *Sphaerium* aff. *S. rivicola*, respectively, external and internal view of left valve (SMNS 101628, specimen #1, from Binnrot; L = 7.7 mm). **N**, *Sphaerium* aff. *S. rivicola*, right valve (SMNS 101628, specimen #2, from Binnrot; L = 10.7 mm). **O**, *Sphaerium* aff. *S. rivicola*, right valve (SMNS 101628, specimen #3, from Binnrot; L = 10.3 mm).

to umbones axis, on a dental shelf. Dental shelf long and straight, length ~90% of total valve height, located between dorsal and anterior margins; shape follows that of valve's margins. Anterior tooth triangular, flat, ~35% shorter than dental shelf width, posterior end wider than anterior; touches posterior end of posterior tooth; greatest width ~30% of total dental shelf length; distant from posterior by roughly its own width. Posterior tooth long, wide; length equal to dental shelf width; greatest width ~55% of total dental shelf length.

**Discussion.**This single specimen is externally identical to a much worn *Margaritifera flabellata*, but the hinge is well-preserved and its proportions are very peculiar. The anterior tooth is very flat and triangular, while in *M. flabellata* it is pyramidal with disproportional sides. The posterior tooth is broad, occupying almost the entire posterior portion of the dental shelf area, while *M. flabellata* presents a posterior tooth with roughly half this size. The present specimen compares fittingly with the syntypes of *Unio kirchbergensis* (SMNS 25504/2005), a species known only from its type locality, Kirchberg an der Iller (southern Germany), from the late early Miocene Kirchberg Formation.

**Paleoecological remarks.** Recent *Unio* species have a wide range of habitats; nevertheless, they are more usually found in rivers, avoiding small water bodies, and do not tolerate desiccation (Welter-Schultes, 2012).

Order VENEROIDA H. Adams & A. Adams, 1856
Family SPHAERIIDAE Deshayes, 1855 (1820)

*Sphaerium* Scopoli, 1777

*Sphaerium* aff. *S. rivicola* (Lamarck, 1818)
(Figures 3L-O)

**Synonymy.** See Schneider & Prieto (2011) and complement:
1999 *Sphaerium* sp.: Sach, p. 22; Sach, 2014, p. 31.
2011 *Sphaerium* (*Amesoda*) *rivicola*: Schneider & Prieto, p. 9, figs. 7A-C.

**Material examined.** SMNS 101628 (four specimens).

**Occurrence.** Binnrot.

**Description.** Valve triangular to elliptical, ~30% longer than taller. Valves flattened, width ~10% of total shell length. External surface with growth lines. Internal surface not observable due to poor preservation. Umbones wide and low, prominent from shell outline, located on the middle of anterior portion of valve; ~25% valve total length and ~10% total valve height. Ligament external, long and narrow; ~50% total valve length. Hinge poorly preserved; cardinal tooth not observable; lateral tooth on middle portion of both sides of dorsal margin.

**Discussion.** Lueger (1979) reported the first Late Miocene record of this species from Vienna Basin, Austria, justifying his identification as *Sphaerium rivicola*, a recent species, due to the species' occurrence as Pleistocene fossils. Later, Schneider & Prieto (2011) reported the species from the Late Miocene of southern Germany. The present specimens are very similar in overall shape and proportions to those reported by Lueger (1979) and Schneider & Prieto (2011), being much more reminiscent of those reported by the latter. The present specimens are anteroventrally elongated, with less pronounced umbones, while Lueger's are nearly round, with a posterior carina and pronounced umbones. Conchological features apart, geographical and stratigraphical distributions are still problematic: *S. rivicola* is a recent European species. It is well know that recent freshwater bivalves can have broad geographical distributions, throughout rivers and others small water bodies (*e.g.* Pereira *et al*., 2014), but *ca*. 15 Ma separate the recent *S. rivicola* from the fossils. Therefore, here we prefer a more conservative classification of the present material, linking the present material to the specimens of Schneider & Prieto (2011), due to their shared similarity in conchological features and stratigraphical and geographical proximity. A thorough revision of all the available fossil material is necessary to a better definition of *Sphaerium* morphotypes occurring in the European Miocene.

**Paleoecological remarks.** The valves are poorly preserved and disarticulate and the numbers of specimens is too small for any taphonomical inference. Recent *Sphaerium* species show a remarkable tolerance to wide ranges of dissolved oxygen in water, from rapid and well-oxygenated waters to temporary and hypoxic water bodies (Cummings & Graf, 2010; Welter-Schultes, 2012).

## DISCUSSION

The poor preservation of part of the material studied here is problematic for taxonomy; therefore, for fragmentary and/or deformed specimens and internal molds identification could not proceed further than genus level (or family level for the clausiliid). Table 1 lists all the fossil sites in the districts of Biberach, Ravensburg and Neu-Ulm and the species found in each one. Table 1 also lists the abundance of each species for each site, but it should be noted that the collection of the molluscan specimens was not controlled for this and techniques for recovering microgastropods (usually abundant in other Miocene outcrops in southern Germany) were not used.

The species list presented here (Table 1) is consistent with those presented by Sach (1999, 2014). Nevertheless, some new occurrences were also noted here: *Gyraulus applanatus*, *Opeas minutum*, *Archaeozonites costatus*, *Palaeotachea renevieri*, *Triptychia* sp. and *Unio kirchbergensis*. Moreover, a few misidentifications listed by Sach (1999, 2014) and Sach *et al*. (2003) were rectified here: the single specimen previously identified as *Pomatias conicus* is a spire apex of *Lymnaea dilatata* and, likewise, the single specimen of *Valvata* sp. is a misidentification of a fragment of *Archaeozonites costatus*.

Sach (1999) presented a paleoenvironmental interpretation of the fossiliferous horizons of the Biberach district, proposing a large meandering river system surrounded by alluvial and gallery forests. This interpretation was based upon the cross-stratification lithology of the finely grained sandy sediments and on the evaluation of the fossil remains found, especially

**Table 1.** Molluscan species occurring in the middle Miocene fossil sites of the districts of Biberach, Ravensburg and Neu-Ulm. Fossil sites (names according to Sach, 1999, 2014): **A** Wannenwaldtobel 1 and 2; **B**, Tobel Oelhalde-Nord; **C**, Tobel Oelhalde-Süd; **D**, Edelbeuren-Schlachtberg; **E**, Binnrot; **F**, Bonlanden; **G**, Edelbeuren-Maurerkopf; **H**, Heselsberg; **I**, Auttagershofen; **J**, Burgerbachtobel 1; **K**, Schmalegger Tobel; **L**, Lattentobel; **M**, Altenstadt-Untereichen. Number of specimens found: **x**, 1-10 specimens; **xx**, 11-60 specimens; **xxx**, >60 specimens. An "**S**" indicates a species listed by Sach (1999, 2014) that could not be found in the SMNS collection (specimens were too fragmentary and were not collected or kept).

| | BIBERACH | | | | | | | | | RAVENSBURG | | | NEU-ULM |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | A | B | C | D | E | F | G | H | I | J | K | L | M |
| CAENOGASTROPODA | | | | | | | | | | | | | |
| *Bithynia* sp. | | | | | | | xxx | | S | | | | |
| *Pomatias* sp. | | | | | | | | | | x | | | |
| *Tinnyea laureae* | | | | | | | | | | | | | x |
| NERITIMORPHA | | | | | | | | | | | | | |
| *Theodoxus* sp. | | | | | | | | | | | | | x |
| HYGROPHILA | | | | | | | | | | | | | |
| *Galba* cf. *G. dupuyiana* | xxx | | | | | | x | | x | | | | |
| *Gyraulus applanatus* | xxx | | | | | | x | | | | | | |
| *Lymnaea dilatata* | x | | x | | | x | xxx | x | | x | | | x |
| *Planorbarius cornu* | x | x | x | x | | x | x | x | x | | | | x |
| STYLOMMATOPHORA | | | | | | | | | | | | | |
| *Archaeozonites costatus* | | | | x | x | | x | | | | | | x |
| Clausiliidae indet. | | | | | | | x | | | | | | |
| *Deroceras* sp. | x | | | S | | xx | xxx | | | xx | | | |
| *Klikia* sp. | | | | | | S | xxx | x | | S | | | x |
| *Megalotachea silvana* | xx | xx | xx | xx | x | xx | xxx | x | x | x | | | xx |
| *Opeas minutum* | | | | | | | x | | | | | | |
| *Palaeotachea renevieri* | | xx | xx | | | xx | xx | x | x | x | | | |
| *Pseudochloritis incrassata* | x | x | x | xx | x | | xxx | x | | S | x | | x |
| *Triptychia* sp. | | | | | | | x | | | | | | |
| BIVALVIA | | | | | | | | | | | | | |
| *Margaritifera flabellata* | x | x | x | x | x | x | x | x | | x | x | x | x |
| *Sphaerium* aff. *S. rivicola* | | | | | x | | | | | | | | |
| *Unio kirchbergensis* | | | | | | | | | | | | | x |

mammals, fishes, turtles and mollusks. Shells of freshwater mollusks would have been concentrated by the streams' waters, while periodical floods would have transported the shells of terrestrial snails from the neighboring area into the river system. The calcareous sediments (marls and freshwater limestones), however, were calmly deposited in the stagnant waters of ponds and small lakes. A very similar fluvial environment of meandering rivers, still water habitats and neighboring alluvial forests can also be assumed for the fossiliferous horizons in the districts of Ravensburg and Neu-Ulm.

The molluscan freshwater fauna, as already observed by Sach (1999), is consistent with rivers, oxbow lakes and ponds. *Bithynia* and the freshwater pulmonates indicate still or slow-flowing waters, including perhaps short-lived shallow water bodies. This is in accordance with the slow-flowing streams and ponds proposed by Sach (1999), with *Bithynia* and the freshwater pulmonates inhabiting the well vegetated areas close to the margins.

In the immediate vicinity of the water bodies, there were humid alluvial and gallery forests that went through periodical floods (Sach, 1999). These forests would have provided favorable conditions for the land snails (*Opeas*, the clausilioids and supposedly *Archaeozonites*) that prefer warmer and more humid environments. There is also indication, mainly based on plant and mammal remains, of drier forests and open areas (Sach, 1999), but, despite snails of such habitats being rather common in other German Miocene sites (*e.g.* Randeck Maar; Salvador *et al*., 2015), there is no such fauna in the present material. The two fossil genera *Pseudochloritis* and *Klikia* supposedly inhabited more exposed areas (Lueger, 1981; Binder, 2008; Moser *et al*., 2009) and they are very abundant in one of the sites studied here, namely Edelbeuren-Maurerkopf. These areas would be located farther away from the water bodies (and perhaps on raised ridges; Sach, 1999).

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# Paleobiogeography of Early/Middle Miocene terrestrial gastropods in Central Europe: a statistical approach using similarity indices

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## Abstract

Terrestrial gastropods are a common faunal element in continental Early/Middle Miocene fossil Lagerstätten of Europe. Although having lived during a time span that includes the Miocene Climatic Optimum and the devastating Ries/Steinheim meteorite impacts, the state of knowledge about their faunal composition and geographic distribution is surprisingly rare. The fauna of 28 different Early and Middle Miocene deposits of Central Europe (European Mammal Neogene zones MN 4 to MN 8) was compared using statistical methods (cluster and NMDS analyses). This includes 109 different species that have been identified so far. Most of the analysed deposits were part of the Miocene Paratethys and are today located in France, SW Germany (Baden-Württemberg state), SE Germany (Bavaria state), Austria, Poland, and Hungary. Cluster analyses resulted in 10 clusters. When plotted on a paleogeographic map, the majority of the clusters can be explained by the geographic situation and/or by the distribution in time. The remaining clusters cannot be fully explained so far, particularly certain "outliers", but some explanations are proposed here. Our results reveal the power of a solid taxonomic framework as a base for such studies; as such, more "basic" paleontological studies are required to strengthen future paleobiogeographical works.

**Keywords:** Cluster analysis, Helicidenmergel, NMDS analysis, OSM, Ries impact, Silvana-beds.

## 1. Introduction

Continental gastropods, especially those belonging to the Pulmonata, are a crucial faunal element in Miocene continental deposits. Despite their abundance in the European fossil record, however, only few attempts have been made to study them from a paleobiogeographical point of view. Esu (1999) described the land snail faunal changes throughout the Neogene, but only in relation to climatic changes and in a more descriptive and qualitative manner. Stworzewicz (1993) also carried on a qualitative analysis, focusing only on the terrestrial gastropods of Poland. Finally, Harzhauser & Mandic (2008) analyzed the faunal diversity of freshwater gastropods of Neogene lake systems in Central and Southern Europe, describing also the interrelationships of these lakes.

Following a similar course as these previous authors, we aim to fill some gaps in the paleobiogeographical knowledge of terrestrial gastropods and present a study of the Miocene land snail fauna of Central Europe. We focus on deposits that are sufficiently known and studied. This means basically the Middle Miocene outcrops, in special the stratigraphic group known as the Upper Freshwater Molasse ("Obere Süßwassermolasse", in German; abbreviated OSM). This age is of particular importance, since the "Mid-Miocene Climatic Optimum" (ca. 17–15 Ma; European Mammal Neogene zone MN 5) was the last time interval favorable for thermophilous fauna and flora in Europe and a time of increased seasonality (Zachos et al. 2001; Böhme et al. 2011). We compare the land snail faunas of twenty-eight distinct localities from the Middle Miocene of Poland, Hungary, Austria, Germany and France (Fig. 1), searching for similarities and differences. These localities were chosen according to their state of knowledge and the authors' own works. After an overall statistical analysis clustering these localities in groups, we offer more detailed explanations of some localities.

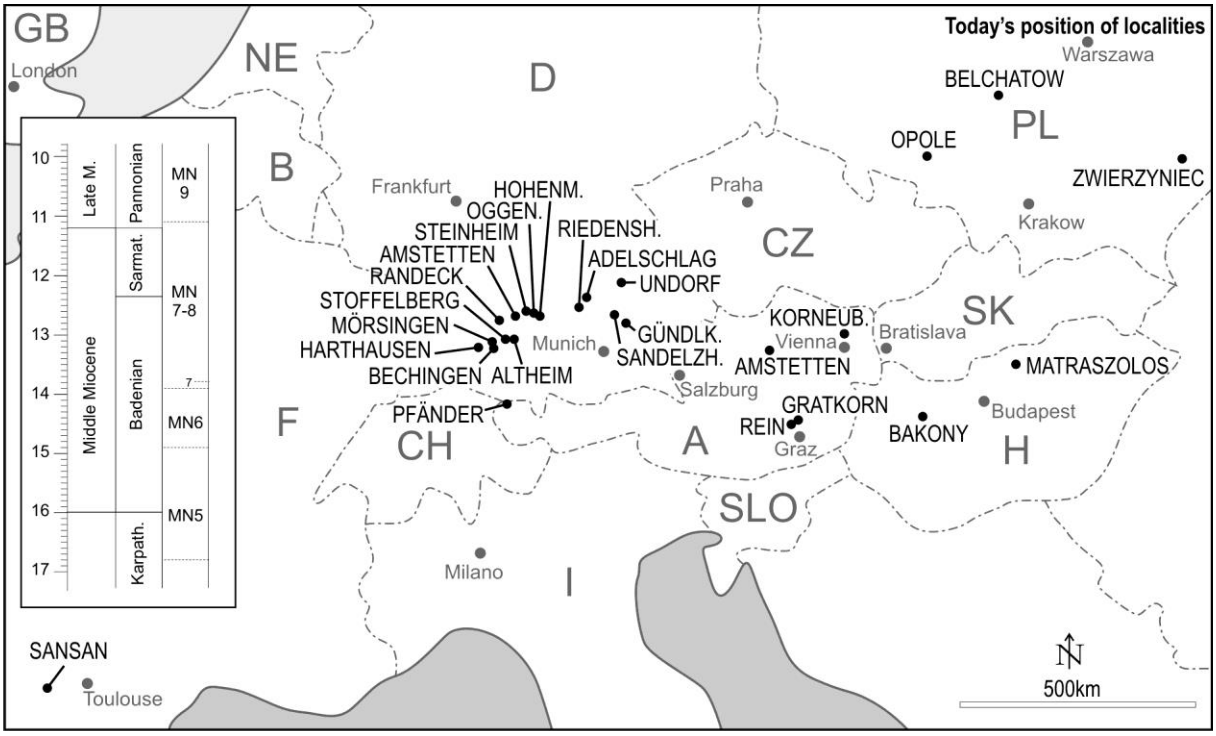

**Fig. 1**. Stratigraphy and localities. Mammal Neogene (MN) zones after Kälin & Kempf (2009).

## 2. Material and methods

Information on each fossil deposit and its respective land snail fauna is widely scattered throughout the literature. Unfortunately, several of these localities were never systematically examined and species lists are rarely present; or, when present, not entirely reliable. Apart from some very recent works, the literature is mostly dated from the end of the 19th century or beginning of the 20th century (mainly Wenz 1923), especially for the OSM.

Furthermore, for a locality to be chosen for the present analysis, it should count with at least eight different terrestrial gastropod species. This was deemed a good number for the biogeographical analysis and this choice implies that most known localities were left out, since they usually have just a few records of the most common species. There are two exceptions to this rule: Amstetten-Stubersheim and Harthausen auf der Scher, both in Germany (Fig. 1). Despite having only five species each, these localities were included because they are the best representatives in number of species of the Helicidenmergel stratigraphic unit (see below). Finally, the locality Zwiefaltendorf (Baden-Württemberg, South Germany) was excluded, since it is Miocene material reworked on Pleistocene gravel (Schlickum 1976).

### 2.1. Taxonomy

The systematic classification used here follows the most recent works for each locality (as listed on Tab. 1), with eventual updates of posterior taxonomic works. On a few cases, literature data was complemented with material from the collection of the Staatliches Museum für Naturkunde Stuttgart (SMNS; Stuttgart, Germany).

The generic assignment of many species has changed often over the past century and sometimes there are concurrent distinct opinions about this matter. Conveniently, our statistical methodology only compares taxa at the species level.

### 2.2. Stratigraphy

Data on stratigraphy and age of the Middle Miocene localities used here were also acquired from the literature (Tab. 1). The age of the localities range from the European Mammal Neogene zones MN 4–5 to MN 7–8, spanning the entire Middle Miocene. During this period, two meteorite impacts have occurred in southern Germany, the so-called Ries impact (ca. 14.7 Ma) and the less-known Steinheim event (Buchner et al. 2013; Buchner & Schmieder 2013).

For the following discussion, it is important to highlight two lithostratigraphic units: (1) the freshwater Silvana-beds (“Silvanaschichten”), within the OSM, dated from zone MN 5 (Esu 1999) and very rich in terrestrial gastropod fossils; and (2) the brackish-marine Helicidenmergel (“helicid marls”, also called “Marnes rouge”), within the Upper Marine Molasse (“Obere Meeresmolasse”, in German), dated from zones MN 4–5 (Jooss 1923; Berger et al. 2005; Geyer & Gwinner 2011).

**Table 1.** List of all localities used for the present analyses, with data on their stratigraphy and age. The references for the species list of each locality is also given (the full list can be found on the Appendix).

| Locality | Country | Stratigraphy / Age | References |
|---|---|---|---|
| Adelschlag-Fasanierie | Germany | OSM / MN 5 | Salvador et al., 2016 |
| Altheim (near Ehingen) | Germany | OSM (Silvana-beds) / MN 5 | Wenz, 1923; Gottschick, 1928; Seu, 1999 |
| Amstetten-Stubersheim | Germany | Helicidenmegel / MN 4-5 | Jooss, 1923; Schweigert, 1996; Berger et al., 2005 |
| Bakony Mts C | Hungary | Lower Badenian | Kókay, 2006 |
| Bakony Mts D | Hungary | Middle Badenian | Kókay, 2006 |
| Bakony Mts E | Hungary | Upper Badenian | Kókay, 2006 |
| Bakony Mts F | Hungary | Sarmatian | Kókay, 2006 |
| Bechingen | Germany | OSM (Silvana-beds) / MN 5 | Gottschick & Wenz, 1916; Esu, 1999; Salvador & Rasser, submitted |
| Bełchatów | Poland | MN 5-6 | Stworzewicz, 1995, 1999a, 1999b; Stworzewicz & Soltys, 1997; Stworzewicz & Prisyazhnyuk, 2006 |
| Gratkorn Basin | Austria | MN 7-8 | Harzhauser et al., 2008 |
| Gündlkofen | Germany | OSM / MN 5-6 | Salvador, 2014 |
| Harthausen auf der Scheer | Germany | Helicidenmegel / MN 4-5 | Jooss (1923); Schweigert (1996); Berger et al. (2005) |
| Oggenhausen | Germany | OSM (Silvana-beds) / MN 5 | Berz & Jooß, 1927; Böttcher et al., 2009; Salvador & Rasser, submitted |
| Hohenmemmingen | Germany | OSM (Silvana-beds) / MN 5 | Gottschick & Wenz, 1916; Esu, 1999; SMNS collection material |
| Korneuburg Basin | Austria | MN 5 | Daxner-Höck, 2001; Binder, 2002, 2003 |
| Lake Rein | Austria | Early Middle Miocene | Harzhauser et al., 2014 |
| Mátraszőlős | Hungary | MN 7 | Hír & Kókay, 2004 |
| Mörsingen | Germany | OSM (Silvana-beds) / MN 5 | Gottschick & Wenz, 1916; Wenz, 1923; Esu, 1999; Höltke, in preparation |
| Opole | Poland | MN 7 | Andreae, 1902, 1904; Wenz, 1923; Ginsburg, 1999 |
| Pfänder | Austria | OSM (Silvana-beds) / MN 5 | Jooss, 1910; Wenz, 1933, 1935; Esu, 1999 |
| Randeck Maar | Germany | OSM (Silvana-beds) / MN 5 | Salvador et al., 2015 |
| Riedensheim | Germany | OSM / MN 5 | Salavdor et al., 2016 |
| Sandelzhausen | Germany | OSM / MN 5 | Salvador, 2013a, 2013b, 2015; Salvador & Rasser, 2014 |
| Sansan | France | MN 6 | Fischer, 2000 |
| Steinheim | Germany | MN 7 | Gottschick & Wenz, 1919; Gottschick, 1919, 1920a, 1920b, 1920c, 1921; Wenz, 1923; Finger, 1998; Ginsburg, 1999; Höltke, in preparation |
| Stoffelberg (near Ehingen) | Germany | Silvana-beds, MN 5 | Wenz, 1923; Esu, 1999 |
| Undorf | Germany | Silvana-beds, MN 5 | Clessin, 1910, 1911; Fejar, 1999 |
| Zwierzyniec | Poland | MN 7-8 | Stworzewicz et al., 2013 |

### 2.3. Biogeographical Analysis

After all the land snail species of each localities were listed and had their taxonomical status checked, the dataset was subject to two types of analyses: (1) cluster analysis, and (2) non-metric multidimensional scaling (NMDS). For both types of analysis, two distinct similarity matrices, Kulczynski (1927) and Ochiai (1957), were used for the presence-absence data of the species in order to test for stability of the groupings. Trial with other indexes (not shown) all yielded very similar results. The analyses were carried out in PAST 2.17c (Hammer et al. 2001). Statistics are shown in Figs. 2 to 5, the respective paleogeography in Fig. 6.

## 4. Results

In total, 28 localities were selected according to the criteria outlined above (Table 1, Fig. 1), containing 109 different species. The taxa present in each locality are listed in the Appendix. The locality Bakony Mountains, in special, represents a long time span, so it was divided in six distinct sections (named “A” to “F”) according to the biostratigraphical occurrences given by Kókay (2006). Of these six sections, only the last four (the youngest) were in accordance with our selection criteria and, thus, were the only ones used in the analysis.

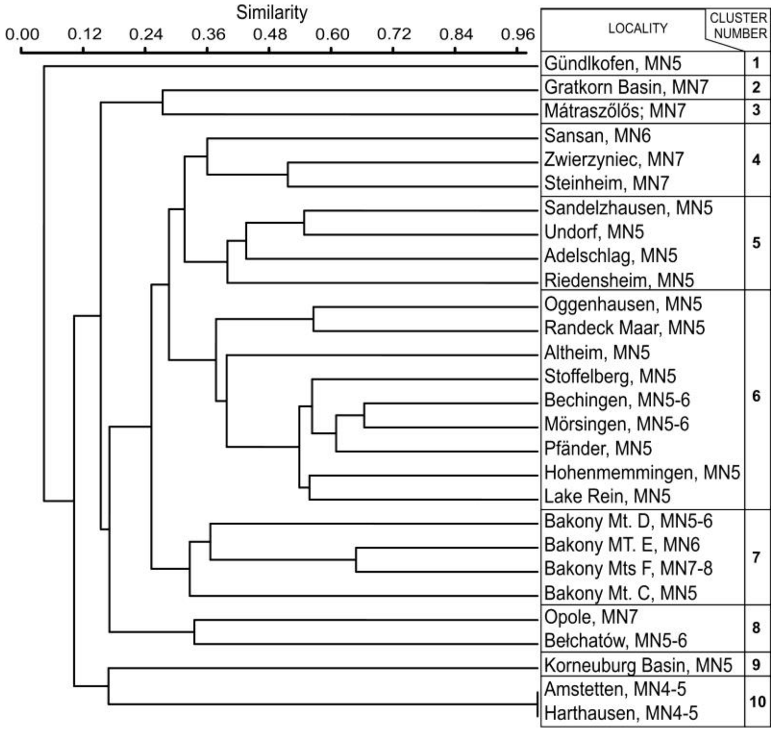

**Fig. 2**. Result of the cluster analysis using the Ochiai index. The numbers are clusters that are separated according to a similarity of 0.36. See Fig. 6 for the paleogeographic position of the respective clusters.

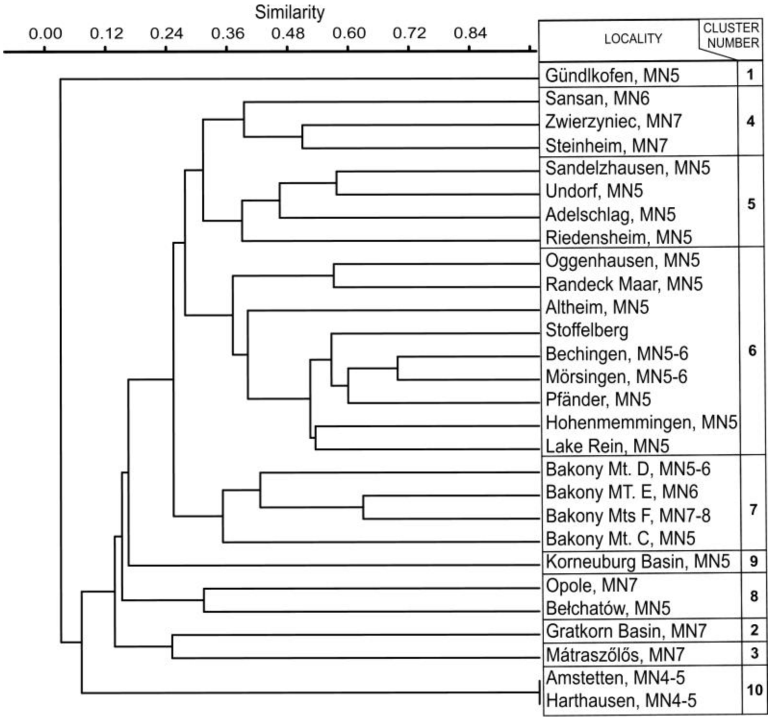

**Fig. 3**. Result of the cluster analysis using the Kulczynski index. Cluster numbering follows Fig. 2

The localities with the highest number of species are: Steinheim am Albuch (60) and Bakony Mounts E and Undorf (49 each). Apart from Amstetten-Stubersheim and Harthausen auf der Scher, explained above, the locality with the smallest number of species is Adelschlag-Fasanerie (8).

For both cluster (Figs. 2-3) and NMDS (Figs. 4-5) analyses, the same grouping patterns were recovered. The single exception is that Korneuburger Basin is isolated on its own "cluster" by the Kulczynski index (Fig. 3), while it is grouped with Amstetten-Stubersheim and Harthausen auf der Scher by the Ochiai index (Fig. 2). Figure 6 shows the clusters described below, plotted on a paleogeographic map (please refer to Figs. 1 and 3 for the locality names). This map gives an idea about the paleogeographic relationships between the localities.

The highest similarity indexes were retrieved for: (1) the two "Helicidenmergel" deposits of Amstetten-Stubersheim and Harthausen auf der Scher, with an index of 1.0; and (2) Mörsingen and Bechingen, geographically very close localities, with 0.72 Kulczynski index and 0.65 Ochiai index.

In order to obtain reasonable groupings, those localities with a similarity of more than 0.36 were summarized into clusters (Fig. 2). This resulted in 10 clusters that are characterized as follows:

Clusters #1 to #3 are three single localities. While Gratkorn Basin (#2) and Mátraszőlős (#3) show at least a certain similarity between them, the locality Gündlkofen (#1) is a complete statistical outlier. Cluster #4 contains three localities distributed from the very western to the very eastern part of our study area: Zwierzyniec (Poland), Steinheim (Germany) and Sansan (France). The shared feature that clusters these localities is the age (MN 6-7). Nevertheless, they are characterized by low similarities among them as well as in relation to the remaining localities.

Cluster #5 summarizes the MN 5 OSM localities from SE Germany (Bavaria state) and cluster #6 the MN 5 OSM localities from SW Germany (Baden-Württemberg state). These two clusters show a very high similarity. Cluster #5 is a relatively homogenous cluster, but curiously, Gündlkofen (also a MN 5 OSM Bavarian locality) falls outside the group and forms a cluster (#1) completely on its own. Sandelzhausen is within this cluster, but it appears somewhat isolated in the NMDS analyses (Figs. 4-5). Cluster #6 is also rather homogenous. The only surprising aspect is that Lake Rein, from the MN 5 of SE Austria, falls inside it.

Although containing different stratigraphic levels, the Bakony Mountains localities forms a single cluster (#7). Cluster #8 contains two localities from the Polish Lowlands of different ages. Cluster #9 contains only the locality Korneuburg Basin, which is placed differently in the cluster analyses with distinct indexes (compare Figs. 2 and 3). Finally, cluster #10 contains the two localities show the highest similarity of our analysis. Remarkably, they are the stratigraphically oldest ones from the “Helicidenmergel”.

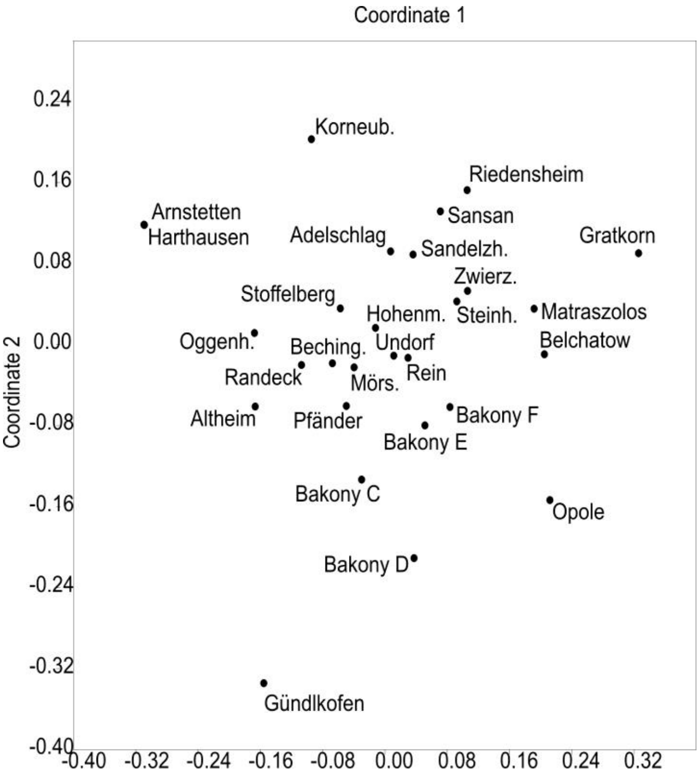

**Fig. 4**. Result of the NMDS analysis using the Ochiai index.

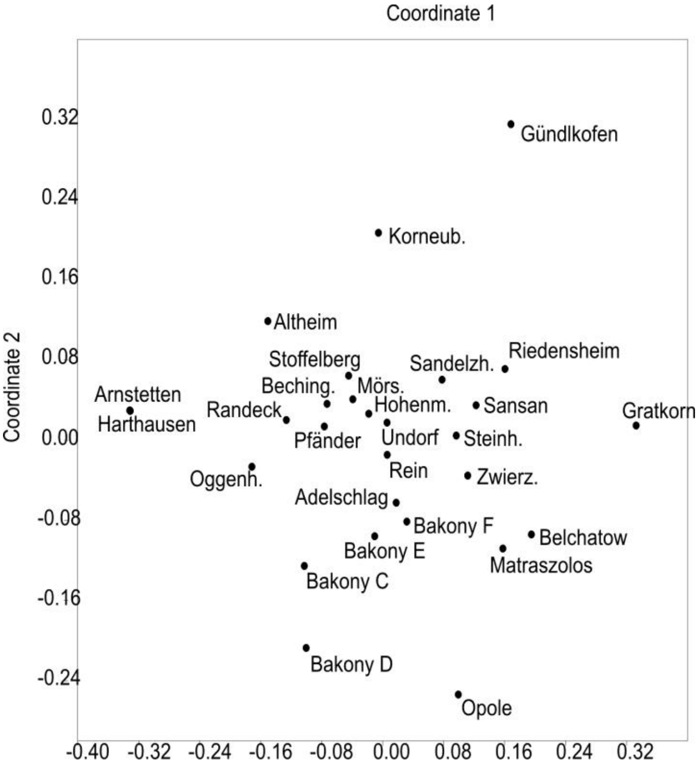

**Fig. 5**. Result of the NMDS analysis using the Kulczynski index.

## 5. Discussion

Both cluster (Figs. 2-3) and NMDS (Figs. 4-5) analyses reached basically the same groupings, independent of the index used. Considering the stratigraphic (Table 1) and paleogeographic (Fig. 6) similarities, some of these groupings were reasonably expected, like: (1) all the OSM deposits of SE Germany (#5) and SW Germany (#6), respectively, are clustered together; (2) all the layers of the Bakony Mountains (#7); (3) Amstetten-Stubersheim and Harthausen auf der Scher forming a solid group (#10, index = 1.0), since both are coeval and the only representatives of the Helicidenmergel among the studied localities; (4) Gratkorn Basin (Austria) and Mátraszőlős (Hungary) are separate clusters, but show a certain degree of similarity (they are coeval and reasonably close geographically); (5) Opole and Bełchatów (#8), both in Poland, bear some similarities, despite not being coeval.

In order to better understand the potential factors that caused clusters and outgroups, some of the exceptions and unexpected groupings are discussed below in more detail. Our discussion focuses on localities that are best studied in general, and/or are familiar from the authors' studies.

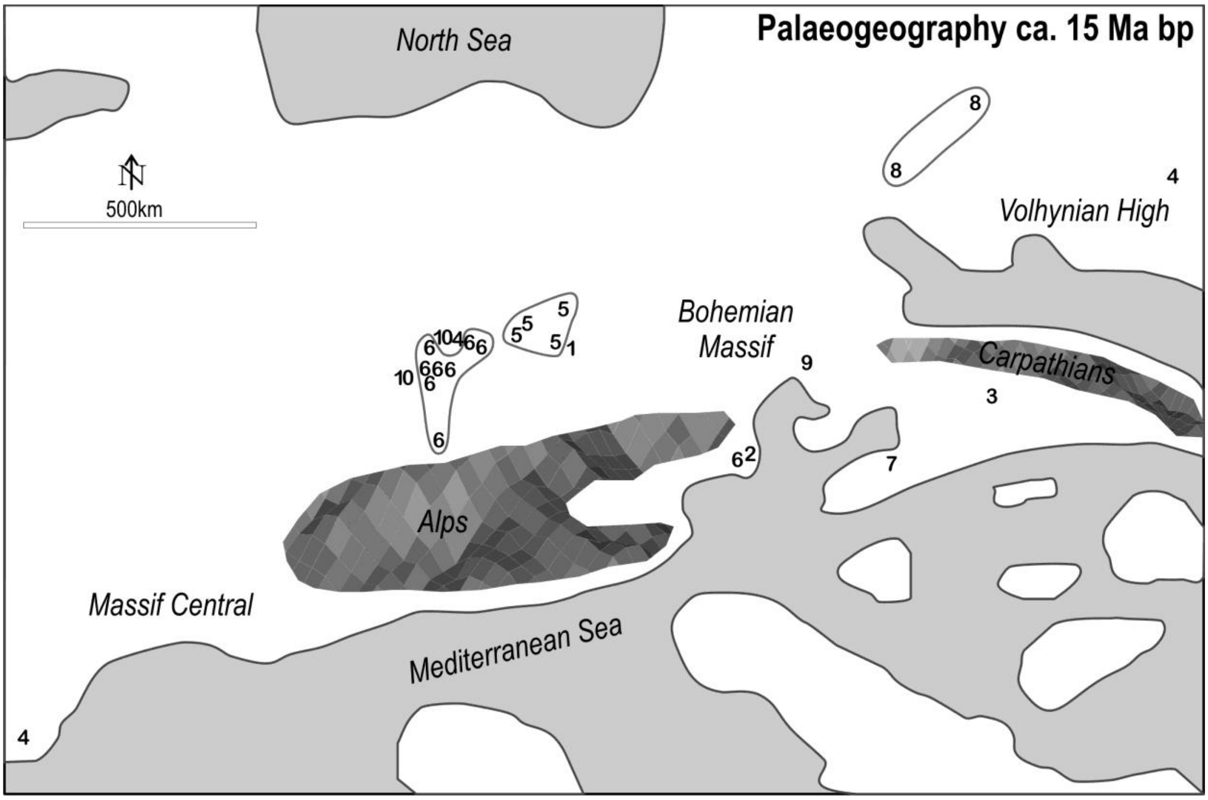

**Fig. 6**. Paleogeographic map with the position of the studied localities and the respective cluster numbers (as given on Fig. 3). Map modified after Rasser & Harzhauser (2008).

### 5.1. Bakony Mountains

Remarkably, the separate stratigraphic levels of the Bakony Mountains form a single cluster on its own (#7). An explanation for this might be the paleogeographic position, because Bakony was part of the Transdanubian Range, which was a separate geodynamic unit. The cluster is most similar to the OSM clusters #5 and #6, which agrees with the suggestion of Kókay (2006) of a paleobiogeographic relationship between these areas.

With respect to the land snail fauna, Kókay (2006) reports only one noticeable change in taxa composition across the layers. This happens in Layer C, where six different members of the Ellobiidae are present. Ellobiids live near water in estuarine or coastal settings (Kerney et al. 1983), so either these are exceptions to the rule or the taxonomic determination of Kókay (2006) is mistaken.

### 5.2. The Upper Freshwater Molasse (OSM)

Putting the most similar clusters #4, #5 and #6 together, the OSM localities form one all-embracing cluster (Figs. 2-3). There are three well defined groupings that can be seen within it: (1) a group composed of all the OSM localities of Baden-Württemberg and curiously, including Lake Rein (in Austria) (cluster #6); (2) a group composed of the Bavarian localities Riedensheim, Adelschlag-Fasanerie, Sandelzhausen and Undorf (cluster #5), whose close relationship was already alluded to by Salvador et al. (2016); and (3) a unexpected group composed of Steinheim am Albuch and two non-OSM localities, Zwierzyniec and Sansan (cluster #4). Moreover, the absence of the Bavarian OSM locality Gündlkofen is also remarkable; it forms an outlying cluster (#1) of its own, well separated from the rest.

The presence of Lake Rein in cluster #6 is curious, since it does not belong to OSM and it is quite geographically remote from the other localities. Nevertheless, from the 33 land snail species reported from Lake Rein, 18 also occur in coeval OSM deposits, which clearly indicates an affinity between these faunas.

The deposits of Gündlkofen (#1) lie consistently and remarkably outside of the OSM group in all analyses. This may be due to the following reasons: (1) only 9 different species are identified from there, which might bias the analysis; (2) Gündlkofen is the single OSM locality where some species occur, namely: *Serrulastra ptycholarinx*, *Triptychia solida* and *Testacella schuetti*; (3) as suggested by Gall (1980), the deposits of Gündlkofen could be reasonably younger (maybe MN 6) than other Bavarian localities, such as Sandelzhausen and Undorf.

### 5.3. Steinheim am Albuch and the OSM localities

Despite the geographical closeness, Steinheim Basin (part of #4) is separated from most of the OSM localities (#4, #5). Searching for the reason, we compare the Steinheim fauna with that of Mörsingen, which is here used as a representative of the OSM localities.

Steinheim am Albuch counts with 60 land snail species, while Mörsingen counts with 46. They have only 13 species in common: *Aegopinella subnitens*, *Carychium nouleti*, *Cecilioides aciculella*, *Cochlicopa subrimata*, *Discus pleuradrus*, *Gastrocopta acuminata*, *Gastrocopta nouletiana*, *Helicodonta involuta*, *Apula coarctata*, *Leucochroopsis kleini*, *Oxyloma minima*, *Pseudidyla moersingensis* and *Pseudoleacina eburnea.* Taking into account the habit requirements of present-day congeners, most of the species listed above would have inhabited more humid environments. More specifically, *Aegopinella*, *Helicodonta* and *Discus* are typical humid forest dwellers, while *Oxyloma* and *Pseudoleacina* would have lived near the lakeshore.

Despite both localities having counted with wet forest habitats, there is a curious increase in the number of xerophilic species: from 4.6% in the older Mörsingen to 11.8% in the younger Steinheim (Höltke & Rasser, in preparation). This agrees with studies with the mammalian fauna from Steinheim, which is a mixture of semi-aquatic species, woodland species, and species from more open and arid habitats (probably representing a warm-temperate landscape; Tütken et al. 2006). In Steinheim, the sheer abundance and relative diversity of the xerophilic gastropod genus *Granaria* is remarkable, counting with three different species (*G. schuebleri*, *G. pachygastra* and *G. grossecostata*). Only unidentifiable *Granaria* remains were found in Mörsingen. Moreover, there are four species of the genus *Vallonia* in Steinheim (and none in Mörsingen), which is also deemed an inhabitant of dry grasslands (*e.g.*, Welter-Schultes 2012).

The genus *Palaeotachea* is important due to one species, namely *Palaeotachea silvana*, which lends its name to the Silvana-beds of the OSM. A strong change happens during the Middle Miocene, since in the later part of this period the species is “replaced” by the form named *Palaeotachea sylvestrina* (Höltke & Rasser, submitted). A similar case happens in the genus *Pseudochloritis*, where the MN 5 *Pseudochloritis incrassata* seems to have died out at the time of the Ries event and in later sediments is “replaced” by *Pseudochloritis insignis*.

All aspects considered, there is a remarkable change in the species composition from Mörsingen (and, generally, of the other MN 5 OSM localities) to the younger Steinheim. Three factors may affect this separation: (1) Age: Steinheim is younger (MN 7) than the remaining OSM localities (Silvana-beds, MN 5) and some species simply went extinct. (2) Ries impact: The devastating impact may have caused a faunal change between the pre-Ries (MN 5) and post-Ries (MN 7) environments. (3) Ecology: Different environmental conditions (*e.g.*, global or regional climatic changes) led to a different faunal composition. A more informed decision would, however, require further studies.

### 5.4. Steinheim am Albuch, Zwierzyniec and Sansan

These three localities form an unexpected cluster (#4) in our analyses, since they are not exactly coeval and not even geographically close. Steinheim (southern Germany) and Zwierzyniec (Poland) are of MN 7 age, while Sansan is of MN 6 age. All of them are, however, post-Ries localities.

The first two localities are, unsurprisingly given their age, more closely related (with a relatively high similarity index of ca. 0.5), sharing 12 species: *Palaeotachea sylvestrina*, *Discus pleuradrus*, *Gastrocopta acuminata*, *Gastrocopta nouletiana*, *Granaria schuebleri*, *Pupilla iratiana*, *Pupilla steinheimensis*, *Strobilops joosi*, *Vallonia subcyclophorella*, *Vertigo angulifera*, *Vertigo callosa*, *Vitrea procrystallina*. Given the habitat requirements of Recent congeners, these species would have inhabited a very broad array of habitats. As such, not much information can be extracted from them. Zwierzyniec (similar to what was explained above for Steinheim) would have counted with several types of habitats, from more humid woodlands to more open and drier areas (Stworzewicz et al. 2013).

Sansan shares six species with Steinheim and Zwierzyniec: *Carychium nouleti*, *Discus pleuradrus*, *Gastrocopta acuminata*, *Gastrocopta nouletiana*, *Pupilla iratiana* and *Vallonia lepida*. Moreover, some species are only known from Sansan: *Cepaea leymerieana*, *Leucochroopsis asthena*, *Pupilla blainvilleana*, *Milax lartetti*, *Tacheocampylaea ludovici* and *Triptychia lartetti.* According to Fischer (2000), this species assemblage would be preferentially found in humid substrates, either in forests or shrublands. Species that would prefer drier open areas are absent.

### 5.5. Korneuburger Basin

The Korneuburger Basin (cluster #9) lies apart from the others in the NMDS diagrams (Figs. 3–4), as well as in the cluster analysis using the Kulczynski index (Fig.1). Only in the cluster analysis using the Ochiai index (Fig. 2), Korneuburger Basin is close to cluster #10 with the localities Amstetten-Stubersheim and Harthausen auf der Scher. The reason for this may be the fact that the species *Pseudochloritis incrassata* is present in all three localities. The deposits also have nearly the same age (early MN 5 for Korneuburger Basin and MN 4–5 for the others).

## 6. Conclusions

Besides the localities studied here, there are several more Miocene deposits containing land snails in Central Europe. However, only for our 28 localities the state of knowledge and number of species was deemed adequate for a statistical paleobiogeographical study. The restriction of eight species per locality was imposed in order to avoid sampling biases; this number is considered sufficient for our purposes.

Cluster and NMDS analyses, using two different indexes, resulted in comparable similarities between the faunas of the studied localities. Given a similarity index ≥ 0.36, ten clusters were obtained from the cluster analysis. Among them are four clusters with only one locality each. Most of the statistical similarities can be explained by stratigraphic level and/or paleogeographic position. But what actually caused the changes in time? That the observed faunal changes were influenced by climate change at the end of the Miocene Climatic Optimum can be assumed, but the present lack of high-resolution stratigraphy does not allow this conclusion to be reached with certainty. The same is true for the devastating influence of the Ries/Steinheim meteorite impacts, which may have triggered the effect of climate change. Both aspects require further investigation.

Further factors for unexpected differences/similarities should be paleoenvironmental controls that influenced the distribution of land snail taxa. More definitive decisions, however, can only be made when more paleoecological information about each locality is known. Paleogeographic barriers are further factors that can explain the distribution of land snails. One example could be the isolated position of the Bakony Mountains. Again, such interpretations require further paleogegraphic and tectonic studies that were beyond the scope of this paper.

We assume that the present study shows the power of fundamental taxonomic research combined with statistical aspects. Without more detailed information about stratigraphy, paleoecology and paleogeography, however, several interpretations necessarily remain tentative.

## Acknowledgements

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## Appendix

Below is given the list of species reported for each locality, according to the references given on Table 1. The lists only include those species that were confidently identified to the species level by the original authors.

### AUSTRIA

#### Gratkorn Basin

*Discus euglyphoides*
*Gastrocopta sandbergeri*
*Negulopsis gracilis*
*Nesovitrea boettgeriana*
*Punctum propygmaeum parvulum*
*Pupilla iratiana*
*Testacella schuetti*
*Truncatellina lentilii*
*Vallonia lepida*
*Vertigo angulifera angulifera*

#### Korneuburg Basin

*Archaeozonites costatus*
*Gastrocopta nouletiana*
*Negulopsis lineolata*
*Palaeotachea turonensis*
*Pomatias turonicum*
*Pseudochloritis incrassata*
*Serrulastra ptycholarinx*

#### Lake Rein

*Aegopinella subnitens*
*Apula coarctata*
*Archaeozonites costatus*
*Carychium minimum*
*Carychium nouleti*
*Cecilioides aciculella*
*Cochlicopa subrimata*
*Discus pleuradrus*
*Gastrocopta acuminata*
*Gastrocopta sandbergeri*
*Klikia giengensis*
*Leucochroopsis kleinii*
*Opeas minutum*
*Oxychilus procellarius*
*Oxyloma minima*
*Palaeoglandina porrecta*
*Palaeotachea turonensis*
*Pomatias consobrina*
*Pseudochloritis incrassata*
*Vallonia lepida*
*Vertigo angulifera angulifera*
*Vertigo callosa*

#### Pfänder bei Bregenz

*Aegopinella subnitens*
*Agardhia pseudoennea*
*Apula coarctata*
*Archaeozonites costatus*
*Azeca lubricella*
*Canariella disciformis*
*Carychium nouleti*
*Discus euglyphoides*
*Discus pleuradrus*
*Helicodonta involuta scabiosa*
*Janulus supracostatus*
*Klikia giengensis*
*Leucochroopsis kleinii*
*Opeas minutum*
*Palaeoglandina porrecta*
*Palaeotachea silvana*
*Palaeotachea turonensis*
*Praeoestophorella phacodes barreri*
*Pseudidyla moersingensis*
*Pseudochloritis incrassata*
*Pseudoleacina eburnea*
*Strobilops costata costata*
*Testacella zellii*
*Triptychia teutonica*
*Vitrea procrystallina*

### FRANCE

#### Sansan

*Carychium nouleti*
*Discus pleuradrus*
*Gastrocopta acuminata*
*Gastrocopta nouletiana*
*Palaeotachea turonensis*
*Pupilla iratiana*
*Vallonia lepida*
*Vertigo diversidens*

### GERMANY, Baden-Württemberg

#### Altheim bei Ehingen

*Azeca lubricella*
*Cochlicopa subrimata*
*Discus euglyphoides*
*Helicodonta involuta*
*Klikia osculina*
*Leucochroopsis kleinii*
*Nesovitrea subhammonis*
*Palaeotachea silvana*
*Pomatias conicus*
*Pseudidyla moersingensis*
*Pseudochloritis incrassata*

**Amstetten-Stubersheim**
*Archaeozonites praecostatus*
*Hemicycla asperula*
*Palaeoglandina gracilis insignis*
*Palaeotachea renevieri*
*Pseudochloritis incrassata*

**Bechingen**
*Apula coarctata*
*Azeca lubricella*
*Discus pleuradrus*
*Gastrocopta acuminata*
*Janulus supracostatus*
*Klikia giengensis*
*Klikia osculina*
*Leucochroopsis kleinii*
*Opeas minutum*
*Oxyloma minima*
*Palaeoglandina porrecta*
*Palaeotachea silvana*
*Palaeotachea turonensis*
*Pomatias conicus*
*Pseudochloritis incrassata*

**Harthausen auf der Scher**
*Archaeozonites praecostatus*
*Hemicycla asperula*
*Palaeoglandina gracilis insignis*
*Palaeotachea renevieri*
*Pseudochloritis incrassata*

**Hohenmemmingen**
*Aegopinella subnitens*
*Archaeozonites costatus*
*Azeca lubricella*
*Carychium nouleti*
*Cochlicopa subrimata*
*Discus euglyphoides*
*Discus pleuradrus*
*Gastrocopta acuminata*
*Gastrocopta nouletiana*
*Granaria schuebleri*
*Helicodonta involuta*
*Klikia giengensis*
*Leucochroopsis kleinii*
*Opeas minutum*
*Oxyloma minima*
*Palaeoglandina gracilis*
*Palaeotachea silvana*
*Pseudidyla moersingensis*
*Pseudochloritis incrassata*
*Strobilops uniplicata*
*Vertigo callosa*

**Mörsingen**
*Aegopinella subnitens*
*Apula coarctata*
*Archaeozonites costatus*
*Argna oppoliensis*
*Azeca lubricella*
*Carychium nouleti*
*Cecilioides aciculella*
*Cochlicopa subrimata*
*Discus euglyphoides*
*Discus pleuradrus*
*Gastrocopta acuminata*
*Gastrocopta nouletiana*
*Helicodonta involuta*
*Janulus moersingensis*
*Janulus supracostatus*
*Klikia giengensis*
*Klikia osculina*
*Leucochroopsis kleinii*
*Lucilla subteres*
*Opeas minutum*
*Oxyloma minima*
*Palaeoglandina porrecta*
*Palaeotachea silvana*
*Palaeotachea turonensis*
*Poiretia taurinensis*
*Pomatias conicus*
*Pomatias consobrina*
*Pomatias turonicum*
*Pseudidyla moersingensis*
*Pseudochloritis incrassata*
*Pseudoleacina eburnea*
*Testacella zellii*
*Triptychia kleini*
*Triptychia teutonica*

**Oggenhausen**
*Archaeozonites costatus*

*Argna oppoliensis*
*Discus pleuradrus*
*Palaeotachea renevieri*
*Palaeotachea silvana*
*Pomatias conicus*
*Pseudochloritis incrassata*
*Triptychia kleini*
*Urticicola perchtae*

**Randeck Maar**
*Apula coarctata*
*Archaeozonites costatus*
*Cochlicopa loxostoma*
*Discus pleuradrus*
*Gastrocopta sandbergeri*
*Helicodonta involuta*
*Leucochroopsis kleinii*
*Negulopsis lineolata*
*Palaeoglandina gracilis*
*Palaeomastus filocinctus*
*Palaeotachea renevieri*
*Palaeotachea silvana*
*Pomatias conicus*
*Praeoestophorella phacodes*
*Pseudochloritis incrassata*
*Pseudoleacina eburnea*
*Testacella zellii*
*Triptychia kleini*
*Triptychia randeckiana*
*Vitrina suevica*

**Steinheim am Albuch**
*Aegopinella subnitens*
*Apula coarctata*
*Archaeozonites costatus*
*Carychium nouleti*
*Cecilioides aciculella*
*Cochlicopa subrimata*
*Discus pleuradrus*
*Gastrocopta acuminata*
*Gastrocopta nouletiana*
*Gastrocopta sandbergeri*
*Granaria schuebleri*
*Helicodonta involuta*
*Leucochroopsis kleinii*
*Negulopsis gracilis*
*Oxychilus procellarius*
*Oxyloma minima*
*Palaeotachea sylvestrina*
*Pseudidyla moersingensis*
*Pseudoleacina eburnea*
*Punctum propygmaeum parvulum*
*Pupilla iratiana*
*Pupilla steinheimensis*
*Strobilops joosi*
*Vallonia lepida*
*Vallonia subcyclophorella*
*Vertigo angulifera angulifera*
*Vertigo callosa*
*Vertigo protracta suevica*
*Vitrea procrystallina*
*Vitrina suevica*

**Stoffelberg bei Ehingen**
*Aegopinella subnitens*
*Apula coarctata*
*Cochlicopa subrimata*
*Discus pleuradrus*
*Gastrocopta acuminata*
*Gastrocopta nouletiana*
*Helicodonta involuta scabiosa*
*Klikia giengensis*
*Leucochroopsis kleinii*
*Palaeotachea silvana*
*Palaeotachea turonensis*
*Praeoestophorella phacodes barreri*
*Pseudoleacina eburnea*
*Pseudochloritis incrassata*

**GERMANY, Bavaria**

**Adelschlag-Fasanerie**
*Carychium galli*
*Carychium nouleti*
*Discus pleuradrus*
*Gastrocopta acuminata*
*Oxyloma minima*
*Palaeotachea renevieri*
*Palaeotachea silvana*
*Vertigo callosa*

**Gündlkofen**
*Lucilla subteres*
*Planogyra nana*
*Pomatias consobrina*
*Serrulastra ptycholarinx*
*Testacella schuetti*
*Triptychia teutonica*

**Riedensheim**
*Azeca peneckei*
*Carychium eumicrum*
*Carychium galli*
*Discus pleuradrus*

*Gastrocopta acuminata*
*Gastrocopta nouletiana*
*Negulopsis lineolata*
*Oxyloma minima*
*Pseudidyla moersingensis*
*Strobilops costata*
*Strobilops uniplicata*
*Urticicola perchtae*
*Vertigo angulifera*
*Vitrea ammoni*
*Vitrina suevica*

**Sandelzhausen**

*Carychium eumicrum*
*Carychium galli*
*Discus pleuradrus*
*Gastrocopta nouletiana*
*Gastrocopta acuminata*
*Janulus supracostatus*
*Leucochroopsis kleinii*
*Lucilla subteres*
*Oxyloma minima*
*Pseudidyla moersingensis*
*Testacella zellii*
*Urticicola perchtae*
*Vallonia lepida*
*Vertigo callosa*

**Undorf**

*Aegopinella subnitens*
*Agardhia praeambula*
*Agardhia pseudoennea*
*Archaeozonites costatus*
*Carychium eumicrum*
*Carychium nouleti*
*Gastrocopta acuminata*
*Gastrocopta nouletiana*
*Helicodonta involuta*
*Janulus supracostatus*
*Klikia giengensis*
*Leucochroopsis kleinii*
*Lucilla subteres*
*Milax crassus*
*Negulopsis lineolata*
*Opeas minutum*
*Oxyloma minima*
*Palaeoglandina porrecta*
*Palaeotachea silvana*
*Platyla alta*
*Pomatias consobrina*
*Pseudidyla moersingensis*
*Pseudochloritis incrassata*
*Strobilops costata costata*
*Strobilops uniplicata plana*
*Testacella zellii*
*Triptychia kleini*
*Truncatellina lentilii*
*Vallonia lepida*
*Vertigo callosa*
*Vitrina suevica*

**HUNGARY**

**Bakony Mountains, Layer C**

*Apula coarctata*
*Archaeozonites costatus*
*Carychium eumicrum*
*Carychium minimum*
*Carychium nouleti*
*Cochlostoma septemspirale*
*Emneopupa subcylindrella*
*Janulus moersingensis*
*Oxyloma minima*
*Palaeotachea silvana*
*Pseudochloritis incrassata*
*Strobilops subconoidea*

**Bakony Mountains, Layer D**

*Apula coarctata*
*Archaeozonites costatus*
*Canariella bakonyensis*
*Canariella disciformis*
*Carychium nouleti*
*Emneopupa subcylindrella*
*Palaeoglandina porrecta*
*Perforatella (Monachoides) punctigera*
*Platyla alta*
*Pomatias conicus*
*Praeoestophorella phacodes barreri*
*Vitrea procrystallina*

**Bakony Mountains, Layer E**

*Apula coarctata*
*Archaeozonites costatus*
*Argna suemeghyi*
*Canariella bakonyensis*
*Carychium nouleti*
*Carychium sandbergeri*
*Discus pleuradrus*
*Galactochilus silesiacus*
*Gastrocopta acuminata*
*Gastrocopta nouletiana*
*Gastrocopta nouletiana gracilidens*

*Gastrocopta sandbergeri*
*Helicigona wenzi*
*Janulus moersingensis*
*Klikia giengensis*
*Negulopsis lineolata*
*Nesovitrea mendica*
*Nesovitrea subhammonis*
*Opeas minutum*
*Palaeoglandina porrecta*
*Palaeotachea silvana*
*Perforatella (Monachoides) punctigera*
*Platyla polita*
*Poiretia taurinensis*
*Pomatias conicus*
*Pomatias consobrina*
*Pseudochloritis incrassata*
*Semilimax intermedius*
*Strobilops costata costata*
*Strobilops subconoidea*
*Strobilops tiarula*
*Strobilops uniplicata plana*
*Tropidomphalus gigas*
*Vertigo callosa*
*Vertigo diversidens*
*Vertigo kochi*
*Vertigo ovatula trolli*
*Vertigo protracta suevica*
*Vitrea procrystallina*
*Zonitoides suevicus*

**Bakony Mountains, Layer F**

*Agardhia praeambula*
*Agardhia pseudoennea*
*Archaeozonites costatus*
*Argna oppoliensis*
*Argna suemeghyi*
*Azeca lubricella frechi*
*Canariella bakonyensis*
*Carychium eumicrum*
*Carychium nouleti*
*Carychium pachychilus*
*Carychium sandbergeri*
*Cochlicopa subrimata*
*Cochlostoma septemspirale*
*Daudebardia praecursor*
*Discus pleuradrus*
*Emneopupa subcylindrella*
*Gastrocopta acuminata*
*Gastrocopta nouletiana*
*Gastrocopta obstructa ferdinandi*
*Gastrocopta sandbergeri*
*Helicigona wenzi*
*Janulus supracostatus*
*Klikia giengensis*
*Milax crassus*
*Negulopsis gracilis*
*Nesovitrea mendica*
*Oxychilus procellarius*
*Oxyloma minima*
*Palaeoglandina porrecta*
*Palaina martensi*
*Perforatella (Monachoides) punctigera*
*Planogyra nana*
*Platyla polita*
*Poiretia taurinensis*
*Pomatias conicus*
*Pomatias consobrina*
*Praeoestophorella phacodes barreri*
*Pseudochloritis incrassata*
*Pupilla iratiana*
*Semilimax intermedius*
*Strobilops costata costata*
*Strobilops subconoidea*
*Strobilops tiarula*
*Tropidomphalus gigas*
*Vallonia lepida*
*Vertigo callosa*
*Vertigo ovatula trolli*
*Vertigo protracta*
*Vitrea procrystallina*
*Zonitoides suevicus*

**Mátraszőlős**

*Carychium nouleti*
*Cecilioides aciculella*
*Gastrocopta acuminata*
*Gastrocopta nouletiana*
*Gastrocopta nouletiana gracilidens*
*Gastrocopta obstructa ferdinandi*
*Gastrocopta sandbergeri*
*Nesovitrea boettgeriana*
*Palaeoglandina porrecta*
*Tropidomphalus gigas*
*Vertigo angulifera angulifera*
*Vertigo callosa*

**POLAND**

**Belchatów**

*Archaeozonites costatus*

*Carychium eumicrum*
*Carychium pachychilus*
*Gastrocopta acuminata*
*Gastrocopta nouletiana*
*Gastrocopta sandbergeri*
*Gastrocopta turgida*
*Negulopsis lineolata*
*Planogyra nana*
*Pomatias rivulare*
*Renea pretiosa*
*Strobilops boettgeri*
*Strobilops costata costata*
*Strobilops tiarula*
*Strobilops uniplicata*
*Vallonia subcyclophorella*
*Vertigo angulifera angulifera*
*Vertigo callosa*
*Vertigo diversidens*
*Vertigo protracta*

**Opole**
*Apula coarctata*
*Azeca lubricella frechi*
*Carychium minimum*
*Daudebardia praecursor*
*Galactochilus silesiacus*
*Gastrocopta obstructa ferdinandi*
*Gastrocopta turgida*
*Negulopsis lineolata*
*Oxyloma minima*
*Palaina martensi*
*Renea pretiosa*
*Strobilops boettgeri*
*Strobilops costata costata*
*Vertigo callosa*
*Vertigo kochi*
*Vitrea procrystallina*

**Zwierzyniec**
*Archaeozonites costatus*
*Discus pleuradrus*
*Gastrocopta acuminata*
*Gastrocopta nouletiana*
*Granaria schuebleri*
*Klikia giengensis*
*Negulus suturalis*
*Palaeotachea sylvestrina*
*Pomatias rivulare*
*Pseudochloritis incrassata*
*Pupilla iratiana*
*Pupilla steinheimensis*
*Strobilops joossi*
*Vallonia subcyclophorella*
*Vertigo angulifera angulifera*
*Vertigo callosa*
*Vertigo protracta*
*Vitrea procrystallina*

# Gastropod palaeohabitats of lake Randeck Maar and its hinterland (Miocene, SW Germany) using the "Extant Genus Bracket"

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## ABSTRACT

The Randeck Maar lake sediments, SW Germany, were deposited during a climatic phase known as the Mid-Miocene Climatic Optimum and therefore provides a unique window into this last period favorable for thermophilous plants and animals in Central Europe. Previous palaeoecological reconstructions of this environment focused on the flora and vertebrate fauna. Here we present a palaeoecological analysis of the molluscan fauna using an actualistic approach. The molluscan fauna of Randeck Maar counts with 32 species of continental snails, mostly terrestrial pulmonates, and are related to one or more of the following palaeohabitat types: profundal, littoral, supralittoral (marsh and reed belt), crater ring-wall boulder zone, shrublands, forests and open habitats. Both the gastropods and other data (mainly insects and flora) indicate a warm-temperate climate with a dry season, similar to the present-day Mediterranean biome. To use the gastropods as palaeoecological proxies, we are herein introducing the "Extant Genus Bracket" with the following null hypothesis: if all extant species of one genus share the same ecological niche, then there is a high probability that a fossil representative of this genus occurred in an equal niche. This approach, therefore, requires a sound taxonomic framework.

**Key words:** Gastropoda, palaeoenvironment, palaeohabitats, MN 5 European Mammal Neogene zone.

## INTRODUCTION

The Randeck Maar lake sediments in SW Germany were deposited during an event known as the Mid-Miocene Climatic Optimum (Zachos *et al.*, 2001), which was the last time interval favorable for a thermophilous fauna and flora in Europe. A palaeoenvironmental reconstruction based on 363 taxa provided a relatively detailed picture of its habitats (Rasser *et al.*, 2013): (1) deep- and open- water lake habitats with local and short-termed mass occurrences of insect larvae, amphibians, and/or gastropods (fish are extremely scarce and obviously restricted to only one or 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. (3) Crater slopes and surrounding plateaus mainly covered by subhumid, sclerophyllous to mixed-mesophytic forests, depending on exposition to sun and local soil conditions. Horses and other forest-dwellers preferably lived in forested habitats, whereas proboscideans and rhinoceratids occupied more open habitats.

The snail fauna comprises 32 species of continental gastropods, most of which are pulmonate land snails (Salvador *et al*., 2015). They occur in various sediment types and the question arises, to which degree this is linked to ecological parameters. This paper uses the gastropods (on genus level) as palecological proxies, using the concept of the “Extant Genus Bracket”. This approach is widely used in the literature, but it has been only roughly delineated and explained so far. Through this analysis, an environmental reconstruction of the Randeck Maar lake and its surrounding is presented in detail, focusing on the niches inhabited by the gastropods. After the definition of what we call the “Extant Genus Bracket” (EGB), the Randeck Maar continental gastropods are listed together with the ecological requirements of their extant congeners. We then use this information to interpret the palaeoecological niches of the existing gastropods along an idealized ecological profile of the lake and its hinterland. Finally, we discuss the applicability and limitations of the EGB.

## GEOLOGICAL SETTING

The Randeck Maar in SW Germany, located on the northern margin of the Swabian Alb, belongs to a large volcanic area that was active during the Early/Middle Miocene and was 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, *i.e.*, latest Early Miocene to earliest Middle Miocene (Fig. 1; Heizmann 1983; Rasser *et al*. 2013). Due to its volcanogenic origin, a crater with a diameter of ca. 1.8 km was formed, with steep slopes and a crater rim. The resulting 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 are preserved.

Jankowski (1981) separated three consecutive lake stages (Fig. 2). The first one appeared immediately after the maar formation, consisting of an alluvial stage with reworked vulcanites. It is followed by a brackish and lacustrine-eutrophic lake stage, comprising bituminous laminites (dysodil) in the deepest parts, calcareous and marly laminites in the more marginal parts as well as littoral limestones and dolomites. The third lake stage is characterized by massive, fossiliferous freshwater limestones.

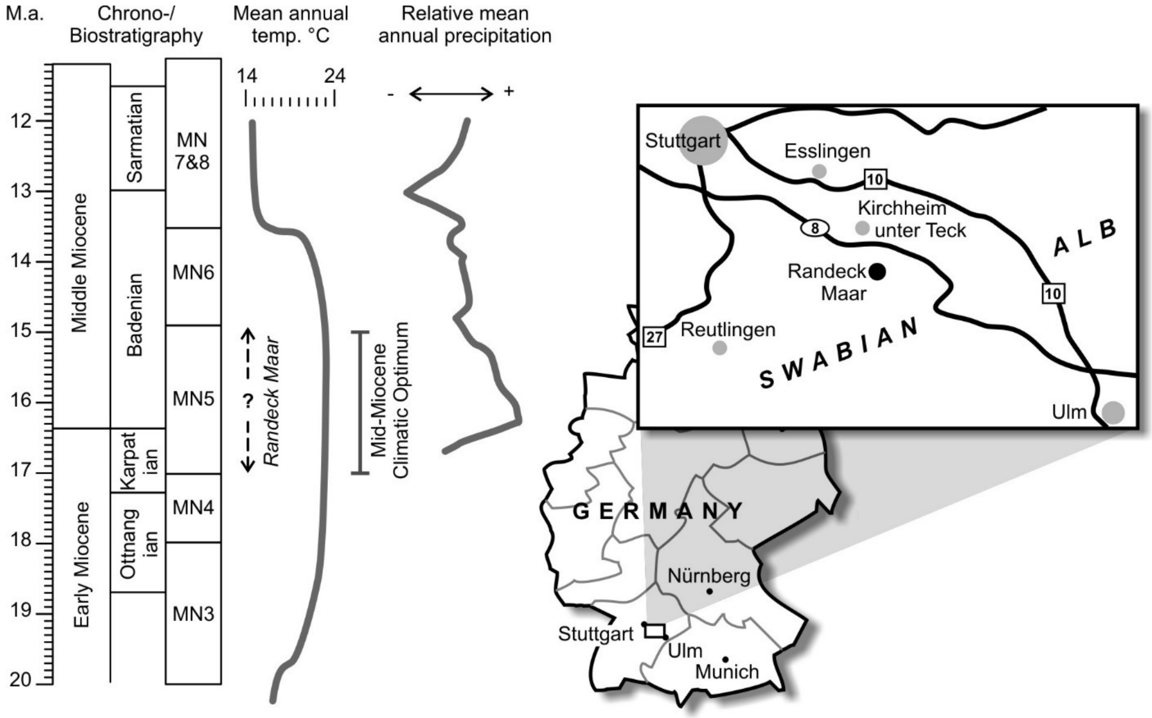

**Figure 1.** Geographical location and stratigraphy of Lake Randeck Maar.

Most of the terrestrial gastropods come from the reworked volcanites, generally referred in the literature as “light” (*i.e.*, yellowish to brownish) and “dark” (*i.e.*, greyish to black) tuffites. 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 subaerially in a more marginal position. The findings of Salvador *et al*. (2015) agrees 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 marl facies and the laminites facies are aquatic sediments (Rasser *et al*. 2013), but, 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). Moreover, a few species are exclusively found in this facies, such as the slugs *Deroceras* sp. and *Milax* sp. as well as the semi-slug *Testacella zellii* Klein, 1853 (Table 1; Salvador *et al*., 2015).

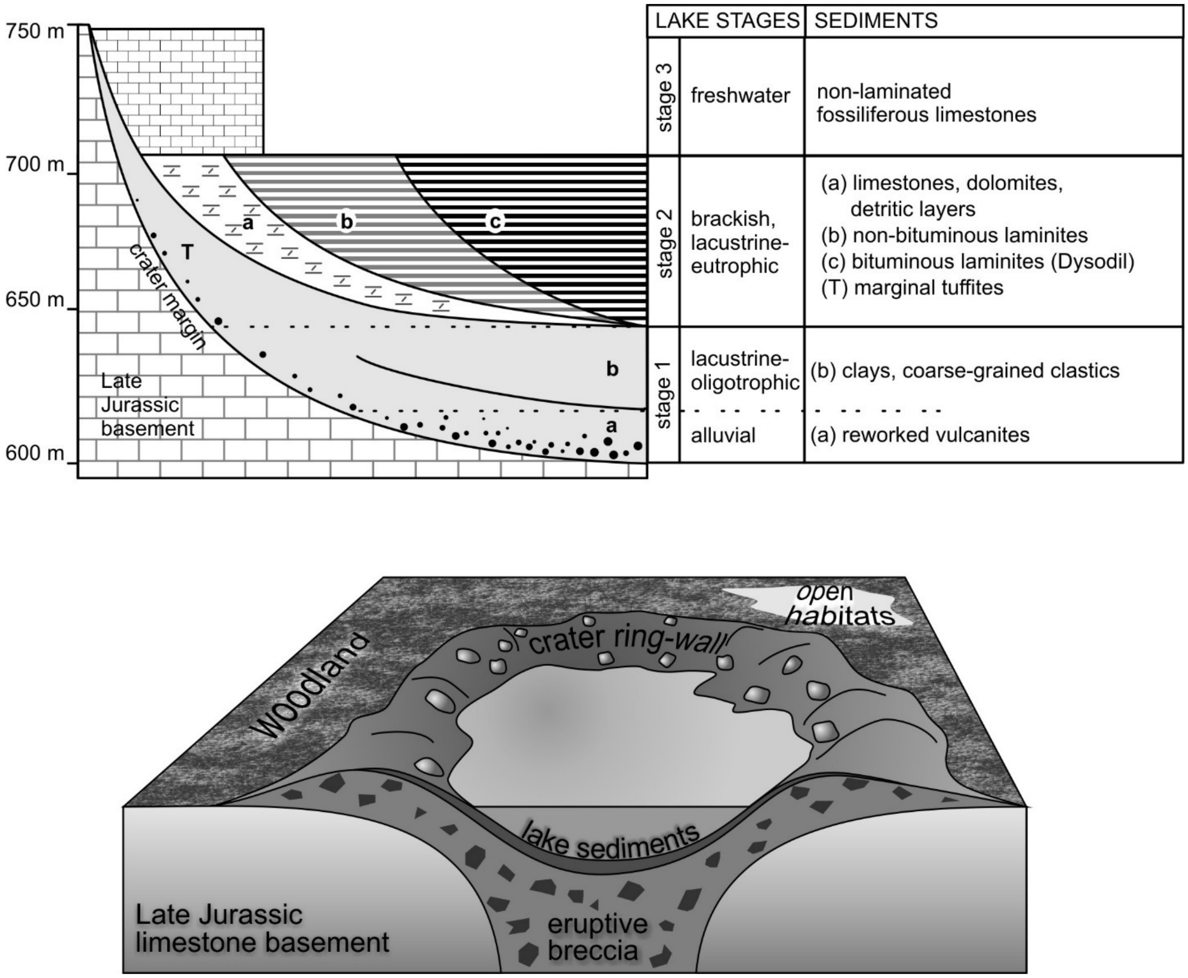

**Figure 2. A.** Schematic cross section through the Randeck Maar sediments after Jankowski (1981). See Table 1 for the distribution of snails in the different facies types. **B.** Reconstruction of the lake system after Rasser *et al.* (2013).

## THE EXTANT GENUS BRACKET

There are continental gastropods adapted to all kinds of ecological conditions but, below the family level and especially within a genus, snails usually tend to be restricted to (or to strongly prefer) a single kind of habitat (Barker, 2001; Cook, 2001; Miller & Tevesz, 2001; Pearce & Örstan, 2006). This is especially well marked in land snails, which makes them excellent ecological indicators. While many species do occur in a broad range of habitats, many will have a clear preference for one specific kind of habitat. Therefore, ecological data (habitat preferences) from extant genera are often used as a guide for palaeoecological inferences of congeneric fossil species.

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

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

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 (*e.g.*, Clarke, 1979; Fordinál, 1996; Albesa *et al.*, 1997; Esu & Ciangherotti, 2004; Moser *et al.*, 2009; Salvador *et al.*, in press), but it was never fully explained or formalized. We aim to do this here, naming this methodoly the “Extant Genus Bracket” (EGB).

## Why genus-level taxa?

Since the generic assignment of both fossil and Recent species is central to the "Extant Genus Bracket" (EGB), it is necessary to explain this choice. In palaeontology, the working concepts of genera are the "phylogenetic" or "cladistic" one and the "phenetic" or "gap" one (*sensu* Allmon, 1994), although the former is much rarer due to the lack of actual phylogenies. Regardless, both are used 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 proved to be an invaluable tool for many kinds of analyses in both palaeo- and neontological studies, especially for macroinvertebrates (*e.g.*, Williams & Gaston, 1994; Sepkosky, 1998; Heino & Soininen, 2007; Mandelik *et al*., 2007).

Fossil gastropod taxonomy might be problematic in many instances, mainly on the species-level, but most genera are integrated into a modern taxonomic framework. Nevertheless, historically there have been authors that preferred not to place fossils in extant genera, leading to a large amount of exclusively-fossil genera (taxonomic inflation) disconnected from their Recent relatives (*e.g.*, 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 EGB, which bases the palaeoecological reconstruction on living congeners of fossil forms. In this case (as seen for some species of Randeck Maar below), an extant genus related to the fossil one should then be found; this should hopefully be a sister-taxon, but actual phylogenies are usually lacking. Luckily, this can be done for many (if not most) cases; when not possible, it is necessary to use family or subfamily levels, which makes the palaeoecological reconstruction much more tentative.

## 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, behavior) as the fossil forms.

As an attempt to solve these problems, Witmer (1995) introduced the Extant Phylogenetic Bracket concept (EPB) for the reconstruction of soft tissues. The EPB uses the position of a taxon within a phylogenetic tree in order 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 (Witmer, 1995; Bryant & Russell, 1992). The EPB is a common method for soft-tissue reconstruction of fossil taxa, but might also be used to infer physiological and behavioral traits (*e.g.*, Benton, 2010). However, this method requires a sound phylogenetic framework, which is not available for most gastropod lineages, especially pulmonates.

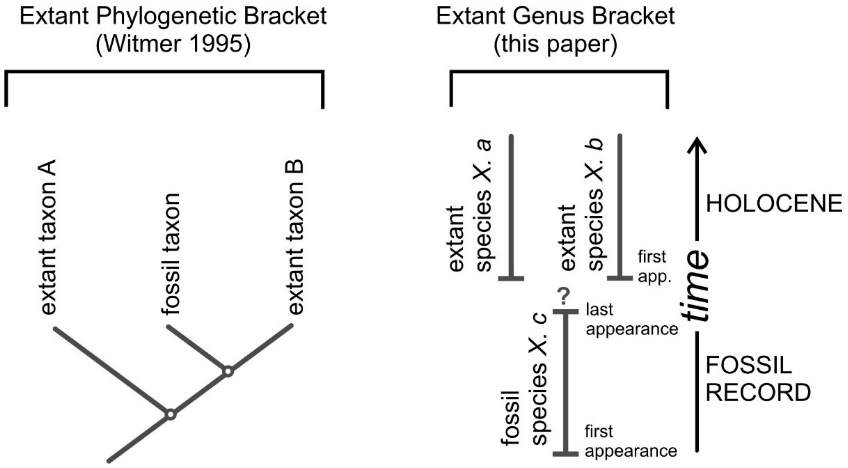

**Figure 3.** Schematics comparing the Extant Phylogenetic Bracket (Witmer 1995) with the Extant Genus Bracket (this paper).

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

## How to apply the Extant Genus Bracket

Our actualistic approach draw on features of both the EPB and the NLR. It uses extant close relatives (congeners) of fossil gastropods to define a range of habitats for the fossil taxa. Here, we take the core ideas of these methods and adapt them to the reality of actualistic palaeoecological analyses for gastropods, formalizing the methodology and naming it “Extant Genus Bracket” (EGB). Figure 3 schematically explains the EGB and compares it with the EPB.

The null hypothesis behind it is as follows: if all extant species of a given genus share a certain basic ecological requirement, then there is a great probability that a fossil congener of this genus share this requirement. It is important to stress out that we can only talk about probabilities of the fossil species sharing the requirements of its living congeners: (1) This probability is highest, if all species of one genus share the same requirements, quasi "high-probability taxa". (2) This probability has varying degrees of likeliness, if one or a few extant species in the genus have disparate requirements from the rest. (3) This probability is very low, if the extant species in the genus have a broad range of requirements, and if a genus is poorly defined or polyphyletic.

Clearly, the EGB starts 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 this data is reasonably easily available for European, North American and Australian molluscan faunas, but it might be more problematic for other continents. Moreover, published data on molluscan ecology might often be too generalized (Yang *et al.*, 2001) and thus not very helpful for the purposes of the EGB.

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 also allows reconstructing the evolution of the environment 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 whole palaeoenvironmental reconstruction.

Finally, beyond the taxonomic aspect of the EGB, there are other sources of data to inform palaeoecological reconstructions. Some clues of habitat preferences might be gained from functional morphology: features of the shell, such as the presence of hair pits or apertural barriers, might give extra palaeoecological information. Glimpses of trophic interactions might also be gained from trace fossils, such as predation marks.

## RESULTS

As explained above for the EGB, in order to extract information out of Randeck Maar gastropods and and use them as palaeoecological proxies, it is necessary to look at their closest living relatives (congeners) and their ecological requirements. This information is summarized below.

For each species, Table 1 gives the number of shells that is stored at the SMNS and UHH collections. These numbers give a rough idea about the abundance of the different species. It is important to note, however, that historical collections were frequently affected by sampling biases. This means that usually only large and attractive shells were collected, so any quantitative discussion must remain tentative. Nevertheless, in absence of proper quantitative data, the numbers on Table 1 do give an estimate about habitat characterization. Figure 4 shows a pie chart with the relative abundance of each species.

### Aquatic snails

Freshwater pulmonates usually have broad distributions on genus level. 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. They live on various substrates, such as fleshy macrohpytes or rocks, where they feed on aufwuchs (*e.g.*, diatoms, microbes, protozoans, invertebrates). The distribution of aufwuchs is a main factor influencing their substrate preferences (Russel-Hunter, 1978; Dillon, 2010).

The pond snails (Lymnaeidae) are among the most common pulmonate freshwater gastropods. The group is represented in Randeck Maar by ***Lymnaea* cf. *dilatata* (Noulet, 1854)**, which is common in Miocene sediments. In Lake Randeck Maar, shells reached 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). Consequently, extant *Lymnaea* spp. populations can sometimes live at depths down to 200 m (Roskowski, 1914). They feed on algae and biofilms, as well as on carrion (Glöer, 2002). The extant species *L. stagnalis* (Linnaeus, 1758) prefers richly vegetated, shallow standing or slow-flowing waters, and is 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, or ramshorn snails, which is represented by three species. ***Ferrissia deperdita* (Desmarest, 1814)** is a limpet that can form mass occurrences together with *Lymnaea* cf. *dilatata*. Extant congeners live in standing or slowly moving waters and are not very sensitive to water quality. They live underneath leaves on partly exposed stems of reeds (Glöer, 2002).

***Gyraulus kleini* (Gottschick & Wenz, 1916)** is the most abundant aquatic snail, but it is usually poorly preserved due to sediment compaction affecting the fragile shell. Therefore, it is 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). *Gyraulus* snails can take up dissolved oxygen from the water, which allows them to live in great 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 cornu*** **(Brongniart, 1810)** is also abundant, but usually poorly preserved as well. Recent species of *Planorbarius* are found in standing or slow moving waters, typically richly vegetated (Welter-Schultes, 2012). Extant *P. corneus* (Linnaeus, 1758) can survive desiccation and thus can live in ephemeral waters as well (Glöer, 2002). Representatives of this genus take up mainly pulmonary oxygen, but their hemoglobin allows them to store large amounts of oxygen for longer dives (Russel-Hunter, 1978).

### Terrestrial snails

***Pomatias conicus*** **(Klein, 1853):** Pomatiidae stem from the caenogastropod lineage of marine periwinkles (Littorinoidea) and are thus operculate land snails. Curiously, *Pomatias conicus*, the only non-pulmonate snail in Randeck Maar, is the most abundant land snail species (Fig. 4). Recent *Pomatias* are found in warmer Mediterranean climates in Europe, living in forests or shrublands with more humid and loose (usually calcareous) soil where they can burrow (Kerney & Cameron, 1979; Welter-Schultes, 2012).

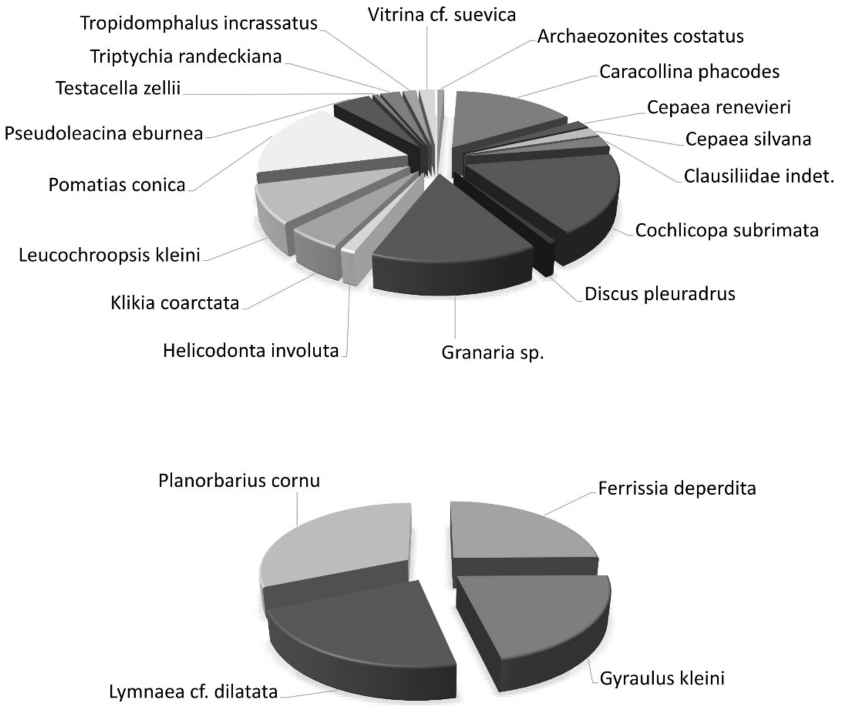

**Figure 4.** Pie charts showing the relative abundance of terrestrial (**A**) and freshwater (**B**) gastropod species.

***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, 2013).

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

***Triptychia kleini* Schnabel, 2006 & *T. randeckiana* (Kranz, 1908):** Being a fossil taxon, not much can be said about the habitats occupied by Filholiids. Nevertheless, it is usually suggested in the literature that they were mostly wood-dwelling animals preferring humid and warm forests (Schnabel, 2007, and references therein), similar to what is proposed for fossil coeval clausiliids (the sister-taxa of Filholiidae; Schnabel, 2006; Nordsieck, 2007).

***Cochlicopa loxostoma* (Reuss, 1852):** This species is the second most abundant land snail in Randeck Maar. The Recent European *Cochlicopa* species show a very broad ecological amplitude, from grasslands to woods and from dry to wet environments (Häßlein, 1966; Welter-Schultes, 2012), thus being of limited use for palaeoecological inferences.

***Palaeomastus filocinctus* (Reuss, 1860):** This fossil genus is related to the Recent genus *Napaeus* Albers, 1850. Present-day *Napaeus* spp. 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, 2009b, 2011a, 2011b), rendering them largely unsuitable for palaeoecological inferences. Nevertheless, Binder (2004) considers *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 woodland dweller.

***Archaeozonites costatus* Sandberger, 1875:** Since this is a fossil genus, any palaeoecological inference must remain tentative. Nevertheless, Lueger (1981) considers that *A. laticostatus* (Sandberger, 1885), also from the Miocene of Central Europe, lived under leaves or between rocks in moist forests.

***Apula coarctata* (Klein, 1853):** The genus became extinct in the Pleistocene (Lueger, 1981), so comparison with living relatives is somewhat tentative. Nevertheless, based on the palaeoenvironments of the fossil sites where *Apula* spp. occurs in the Central European Miocene, Lueger (1981) suggested that species in this genus could thrive in both dry and wet habitats, proposing that they grazed on riparian and/or herbaceous plants. For this reason, *A. coarctata* is not considered for palaeoecological reconstructions herein.

***Pseudochloritis incrassata* (Klein, 1853):** This is also a fossil genus. Binder (2008) considers that the shell of *Pseudochloritis* is an adaptation for ground-dwelling gastropods to reduce water loss in drier environments. Moser *et al.* (2009) suggested that the genus inhabited more open and drier habitats and had a “way of life like strong-shelled Balkanese representatives of Ariantinae”.

***Palaeotachea renevieri* (Maillard, 1892) & *P. silvana* (Klein, 1853):** This fossil genus is likely related to Recent *Cepaea* spp., which have too broad a range of habitats (*e.g.*, Welter-Schultes, 2012) to be useful for a palaeoenvironmental analysis.

***Helicodonta involuta* (Thomä, 1845):** Recent European congeners are typical forest dwellers (mainly in deciduous forests) and can be found in more humid leaf litter and rock rubble, more usually than not on calcareous substrate (Cameron, 1972; Maltz, 2003, 2007; Welter-Schultes, 2012). See also *Leucochroopsis kleinii* (Klein, 1847) below.

***Leucochroopsis kleinii* (Klein, 1847):** *Leucochroopsis kleinii* is considered an inhabitant of relatively damp forests (Lueger, 1981), but it is an entirely fossil genus. Nevertheless, it was once considered a subgenus of the recent *Trochulus* Chemnitz, 1786, which inhabits a broad range of environments, from grasslands to shrublands and forests and from dry to wet habitats (Häßlein, 1966; Tappert, 2002; Welter-Schultes, 2012). The pits on the shell surface of the fossil indicate the presence of hair on the shell of the living animal. The hairs of *Trochulus* snails (and hygromiids in general) were shown to increase the adherence of the snails to plant leaves during foraging, especially in high humidity levels (Pfenninger *et al*., 2005). A similar function would be expected for the hairs of helicodontids, like *Helicodonta involuta*, above.

***Praeoestophorella phacodes* (Thomä, 1845):** This fossil genus is related to the Recent *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 shady habitats, mainly woods (Kerney *et al*., 1983; Welter-Schultes, 2012).

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

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

***Granaria* sp.:** Recent *Granaria* species prefer dry and open (usually calcareous) habitats (Welter-Schultes, 2012; Höltke & Rasser, 2013).

***Gastrocopta* cf. *acuminata* (Klein, 1846) & *Gastrocopta sandbergeri* Stworzewicz & Prisyazhnyuk, 2006:** There are no Recent native *Gastrocopta* species in

Europe; they are found in all other continents, inhabiting a very broad range of habitats and being especially diverse in North America (Zilch, 1959–1960).

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

**?*Truncatellina* sp.:** As the precise 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, 1972)** [identified as *Negulus suturalis* (Sandberger, 1858) in Salvador *et al*. 2015]**:** The new identification is due to a taxonomic mistake by Wenz (1923) that remained in the literature until the present; a full explanation of the taxonomy of this species is presented by Salvador *et al*. (in press). This fossil genus is related to the Recent *Negulus* Boettger, 1889. Very little is known about Recent *Negulus* species, but they seem to live on leaf litter in tropical African forests (Bruggen, 1994).

***Pseudoleacina eburnea* (Klein, 1853):** *Pseudoleacina* Wenz, 1914 is a fossil genus, but likely, as the rest of the family, should have been a malacophagous predator (Barker & Efford, 2004). Moreover, most authors consider *Pseudoleacina* species to be hygrophilic woodland inhabitants (*e.g.*, Lueger, 1981; Harzhauser & Binder, 2004; Harzhauser & Tempfer, 2004), despite some (*e.g.*, Gall, 1980) considering it a calciphilic and xerophilic species. Judging by the rather scarce land snail record of Randeck Maar and the relatively abundant material of *P. eburnea*, it seems this species was rather common around the lake.

***Palaeoglandina gracilis* (Zieten, 1830):** Likely, as the Recent species in the family, *Palaeoglandina* spp. were malacophagous predators (Barker & Efford 2004). Recent European species in the family have varied lifestyles (*e.g.*, Cossignani & Cossignani 1995; Welter-Schultes 2012). However, Moser *et al*. (2009) suggested that *Palaeoglandina* species, based on overall shell morphology, would have displayed the same lifestyle and habitat preference as the recent North American *Euglandina rosea* (Férussac, 1821). The rosy wolfsnail, as it is commonly called, is a voracious predator and was introduced as control agents in some localities, where of course it has become a problem for the native fauna (*e.g.*, Clarke *et al*., 1984; Hadfield, 1986; Hadfield *et al*., 1993). *Euglandina rosea* is even know to prey on freshwater snails, like lymnaeids, and may be found hunting partially immersed in water (Kinzie, 1992).

***Testacella zellii* Klein, 1853:** Recent *Testacella* species are voracious predators, feeding mainly on earthworms, but also on gastropods and centipedes; they live underground (sometimes also under rocks), requiring a moist soil cover (Barker & Efford, 2004; Liberto *et al*., 2011). This burrowing habit should make preservation in the fossil record more difficult.

## DISCUSSION

### Reconstruction of gastropod palaeohabitats in Randeck Maar

As seen above, extant congeners of the Randeck Maar snails exist for most species. Using the Extant Genus Bracket, this chapter uses them as palaeoecological proxies.

Randeck Maar terrestrial snails are surprisingly diverse, but the same does not seem to be the case for the freshwater species: of the 32 gastropod species found, only four are freshwater snails. 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 other 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* (curiously the only non-pulmonate in the fauna), *Cochlicopa loxostoma*, *Granaria* sp. and *Praeoestophorella phacodes* (Table 1; Fig. 4).

As argued above, the palaeohabitat model presented by Rasser *et al*. (2013), focusing mainly on the flora and the vertebrate fauna (Fig. 2 below), 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 (summarized in Fig. 5).

**Profundal:** The profundal realm of lake Randeck Maar is supposed to have been subject 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). Two planorbid snail species (*Gyraulus kleini* and *Planorbarius cornu*) occur in these sediments, but they have most likely been transported into this environment from shallower parts of the littoral rather than naturally inhabiting this zone.

**Littoral:** Littoral sediments consist of laminated carbonates (stage 2b in Fig. 2) and various limestones in the most marginal portions (stage 2a in Fig. 2). This is the most likely place to find the freshwater snails *Lymnaea*, *Gyraulus* and *Planorbarius*. There are mass occurrences of *Gyraulus* on bedding planes, which could point to mass-mortality events.

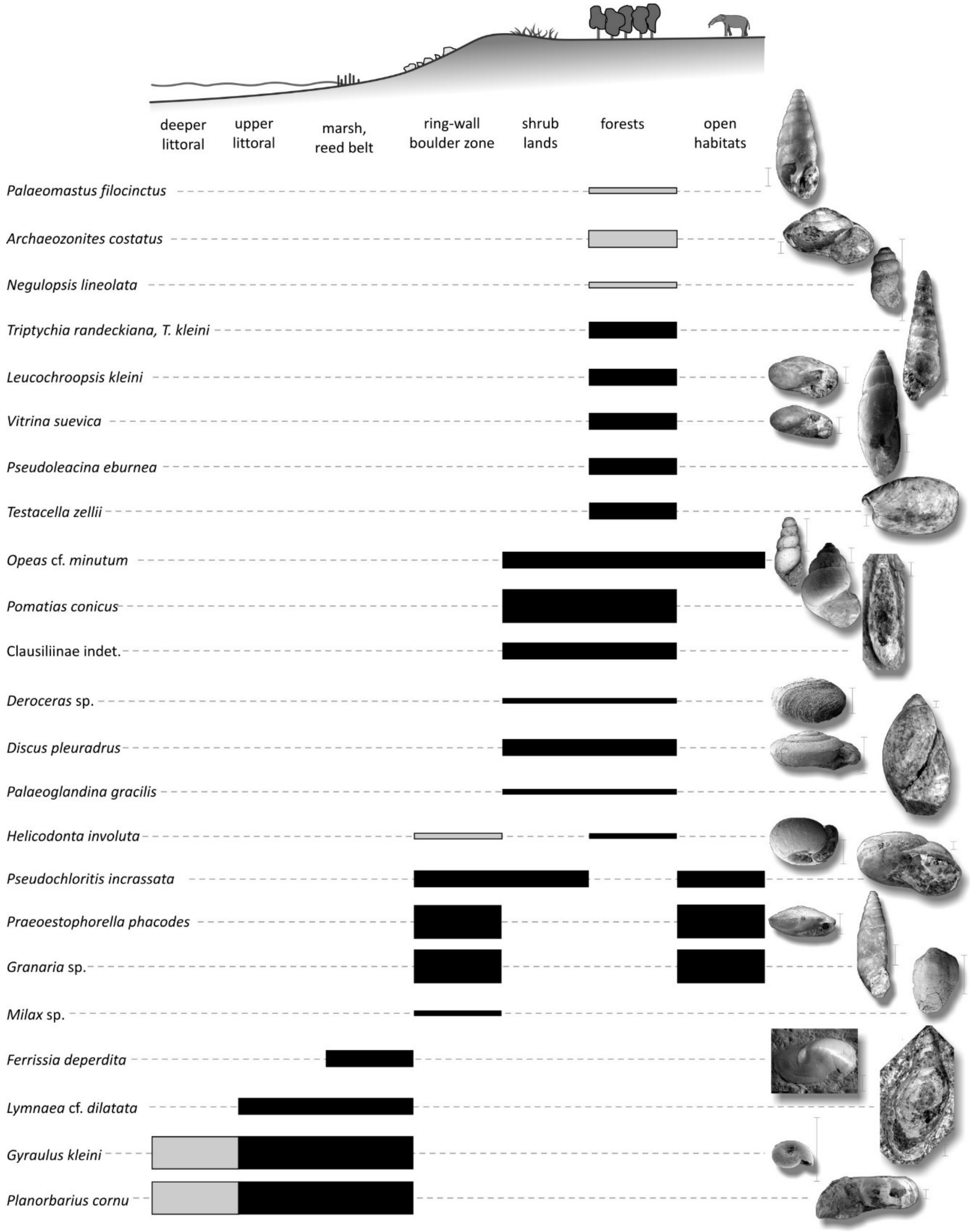

**Figure 5.** Palaeohabitats of the gastropods from Lake Randeck Maar and its hinterland, based on the Extant Genus Bracket. Scale bars = 2mm. Thickness of bar reflects the general abundance of the respective species in the studied material; thin bar: <10 individuals, medium thickness: >10, thick bar: >200. The total number of individuals is shown in Table 1, the relative abundance in Fig. 4.

**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* could 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* on certain bedding planes suggest that these two taxa may have lived in similar habitats and that there have been mass-mortality events, as mentioned for *Gyraulus* above. Furthermore, *Palaeoglandina* may have hunted for other snails in this environment. Surprisingly, other common hygrophilous genera usually found in these habitats in other Miocene localities, such as *Carychium* and *Succinea*/*Oxyloma*, are notably absent.

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

**Shrublands:** There is no single species in Randeck Maar that would be restricted to the shrubland area; all of them likely would also have inhabited other areas (Fig. 5), usually the forests.

**Forests:** Rasser *et al*. (2013) suggested subhumid sclerophyllous to mixed mesophytic forests (which is found in seasonally dry climates, such as present-day Mediterranean and its pre-anthropogenic vegetation), as the most likely vegetation type in Randeck Maar. There seems to be a large number of species that would have been restricted to the forest area in Randeck Maar, as well as many that would also have inhabited the shrublands (Figs. 2, 5). Due to the underground formed by Jurassic carbonate rocks, the substrate might have been calcareous, although the influence of the volcanic ash is unknown. The gastropod taxa are indicative of such calcareous substrate. *Archaeozonites, Helicodonta* and *Praeoestophorella* lived under leaves or between rocks. *Pomatias* was burrowing here in the humid litter and so did *Testacella*, preying on earthworms and gastropods.

**Open habitats:** Most of the species from the ring-wall area would also have been found in these more open grassland areas (Figs. 2, 5). Moreover, other species such as *Opeas minutum* and *Deroceras* sp. might also have inhabited this area.

### Limitations for the EGB

Approximately half of the Randeck Maar gastropods could not be used for palaeoecological considerations. Several species (compare Table 1 and Fig. 5) were excluded from the palaeoecological analysis for the following reasons: (1) The extant species of the genera *Deroceras, Cochlicopa* and *Vallonia* show a too broad range of ecological requirements. (2) *Apula*, *Palaeomastus* and *Palaeotachea* do not have an appropriate extant congener and/or their supposed sister-taxa have too broad a range of ecological requirements. (3) The taxonomic identification is uncertain for *?Truncatellina*.

Although the following genera do not have an extant congener, they were used herein for the following reasons (see remarks on the particular taxa in the Results section above): (1) *Archaeozonites*, *Palaeoglandina, Pseudochloritis* and *Pseudoleacina,* because their palaeoecological distribution is well established in literature. (2) *Leucochroopsis*, *Negulopsis*, and *Praeoestophorella*, because there is a general consensus about their relationship with extant genera. (3) Furthermore, there is additional morphological information for *Leucochroopsis* (hair pits) and *Pseudochloritis* (shell shape).

**Trophic interactions**

No signs of predation were found on the studied shells, which may be due to sampling bias and/or to the poor preservation of the majority of the specimens. 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 incrassata*), 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 interesting to notice that *Pseudoleacina eburnea* is among the most abundant terrestrial snails in Randeck Maar. 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 malacophagous predators, such as crabs and crayfish, are not known, 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 (*e.g.*, Archangelsky & Durand, 1992; Inoda *et al*., 2015). Vertebrates of the Randeck Maar that may have preyed on aquatic gastropods are tooth carps, newts, as well as amphibious and aquatic turtles. Insects were common in the studied sediments and there are many terrestrial insects that prey on snails (Barker, 2004, and references therein), but whether or not some of them have preyed on gastropods in the surrounding of the Randeck Maar, requires further detailed studies. Among the vertebrates, terrestrial turtles may have preyed on the land snails, while smaller adequate carnivores are absent (Rasser *et al*., 2013).

### Climate proxies

Until now, different methods have been used to reconstruct climatic conditions for the Early/Middle Miocene of Central Europe in general and the 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 minutum*, *Negulopsis lineolata* and *Palaeomastus filocinctus*), which would indicate a warmer climate. Similar findings in insect taxa (Rasser *et al*., 2013) also point to a warm-temperate to sub-tropical 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

In palaeobiological studies, genus-level taxa are frequently used as substitutes for species for good reasons. The Extant Genus Bracket (EGB) concept follows this idea and suggests that if all extant species of a genus exhibit the same ecological requirements, then there is a high probability that a fossil species of the same genus would have shown the same preference. It is evident that his concept implies a sound taxonomic framework, which is not always the case.

The Miocene fossil lagerstaette Randeck Maar comprises 32 species of aquatic and terrestrial snails. Among them, the EGB could be directly applied to 16 genera. Seven further genera provide additional palaeoecological information beyond the EGB.

There are three categories for the applicability of fossil genus-level taxa as palaeoecological proxies: (1) In terms of probability, the application of the EGB is most reliable if all extant species of the genus in question share the same ecological requirements. (2) The genera must be used with caution, if one or more species show different requirements. Additionally, fossil genera without extant congeners might be used as palaeoecological proxies with caution, if: (a) the palaeoecological requirements are based on the distribution among other fossil sites; (b) there is a general consensus in literature about its living relatives; or (c) there are additional morphological traits that are ecologically relevant (*e.g.*, shell structures). (3) The EGB fails when one or more species of a given genus show too disparate ecological preferences or too wide a range of preferences, or, naturally, if the taxonomic identification is insufficient.

The EGB obviously 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 EGB much more reliable for this time interval. The methodology can be safely used for many Neogene fossils, as we could show in our study, since most genera still exist. However, the EGB becomes more tentative the further it goes back in time, since not many extant genera lived in older periods.

Despite our focus on continental gastropods, the EGB can also be used for continental bivalves and for marine mollusks in general. It is common for marine genera to be easily identified as either planktonic or benthonic, as epi- or infaunal etc., which can facilitate paleoecological reconstructions The potentials uses of the EGB for other animal phyla should be further investigated, but there is no obvious reason to exclude them.

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# Paleoecological and isotopic analysis of fossil continental mollusks of Sandelzhausen (Early/Middle Miocene, Germany)

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## ABSTRACT

The fossil molluscan fauna of Sandelzhausen (Early/Middle Miocene, SE Germany) comprises a total of 44 continental gastropod species, mostly terrestrial pulmonate snails. Herein we present a paleoecological analysis of this fauna based on an actualistic approach and on data on the stable isotopes of carbon and oxygen and radiogenic isotopes of strontium (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 points 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*. Concomitantly, changes in the strontium isotopic signal reflect a change in the water source of this newly formed lake. The terrestrial habitat would have gone from a more relatively 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 signal of *P. moersingensis*, ranges from 18.5 to 20.5 ℃, but with no significant trend of change throughout the layers.

**Keywords:** Gastropoda, MN 5 European Mammal Neogene zone, paleoenvironment, Pulmonata, stable isotope analysis.

## 1. INTRODUCTION

Lacustrine sediments and their biogenic carbonates are considered important sources of paleoenvironmental information, especially in small lakes, which are more prone to reflect environmental changes (Filippi et al., 1997; Anadón et al., 2007; Deocampo, 2010). Among the carbonate-producing animals, mollusks, especially continental gastropods, are reliable paleoecological and paleoenvironmental indicators (Goodfriend, 1992; Miller & Tevesz, 2001; Yang et al., 2001; Mienis & Ashkenazi, 2011).

There are two main approaches that have been used to reconstruct past climatic and environmental settings: analyses of faunal composition and of the isotope composition of shell carbonate (Goodfriend, 1992). The first one is a qualitative method of species composition in the fossil assemblage and comparison with the ecology of Recent faunas; this procedure may be accompanied by quantitative analysis, such as relative abundance of species and/or ecological groups. Mollusks are adapted to all kinds of ecological conditions, but at genus level they tend to be restricted to certain habitats; this is especially well-marked in land snails, which makes them good paleoecological and paleoenvironmental indicators (Barker, 2001; Cook, 2001; Moine et al., 2002; Pearce & Örstan, 2006). Therefore, ecological data of habitats known from Recent genera can be extrapolated to congeneric fossil species. This actualistic methodology is very informative, being well established and successfully explored in many cases (*e.g.*, Sparks, 1961; Nuttall, 1990; Fordinál, 1996; Albesa et al., 1997; Esu & Ciangherotti, 2004).

The analysis of stable isotopes (oxygen and carbon) of shell carbonate can provide key information for paleoenvironmental and paleoclimatological reconstruction, and have been 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 & Ellis, 2002), extracting data on environmental settings, temperature, rainfall etc. The usefulness and reliability of both $\delta^{18}O$ and $\delta^{13}C$ analysis is well established, although $\delta^{13}C$ values are more difficult to interpret and should be taken more cautiously, especially for land snails (Stuiver, 1970; Fritz & Poplawski, 1974; Miller & Tevesz, 2001; Balakrishnan & Yapp, 2004; McConnaughey & Gillikin, 2008).

As both methods have their own sets of advantages and drawbacks, using more than one climate proxy usually allows a better paleoenvironmental interpretation (Grimes et al., 2003; Latal et al., 2006; de Francesco et al., 2007). Therefore, in the present work we explore both methodologies for the continental molluscan fauna of the Middle Miocene fluvio-lacustrine setting of Sandelzhausen, in SE Germany. We use taxonomic diversity and shell isotope compositions (both of stable and radiogenic isotopes) to reconstruct the paleoenvironmental conditions of this setting, such as hydrology, vegetation cover and temperatures. Finally, we compare our results with proxy data assessed from other fossil groups: mollusks (Moser et al., 2009b), ostracods (Witt, 1998) and vertebrates (Fahlbusch et al., 1972; Böhme, 2010; Tütken & Vennemann, 2009).

## 2. 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 was located near the city of Mainburg, 60 km north of Munich (Fig. 1), and is part of the group known as Upper Freshwater Molasse (Obere Süßwassermolasse, OSM); its fossils belong to a member 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: *ca*. 16.47–16.27 Ma, belonging to the Early/Middle Miocene Burdigalian/Langhian boundary (MN 5 European Mammal Neogene zone; Moser et al., 2009a).

The classification of the facies of the Sandelzhausen deposits was first established by Fahlbusch & Gall (1970), receiving only some posterior refinement (Moser et al., 2009a). From bottom to top (Fig. 1): **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 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 carbonatic nodules; rich in fossils, many in excellent preservation state due to a less intense compaction; **Layer E:** silty clays with microvertebrate fossils; **Layer F:** laminite with alternating light and dark bands, carbonate concretions and desiccation cracks; no fossils. Fossil mollusks can be found from layer A to D. For a more throughout description of the site's lithology, see Moser et al. (2009a). The sediment and fossils are deemed to have been deposited quickly and no time averaging was detected (Tütken & Vennemann, 2009).

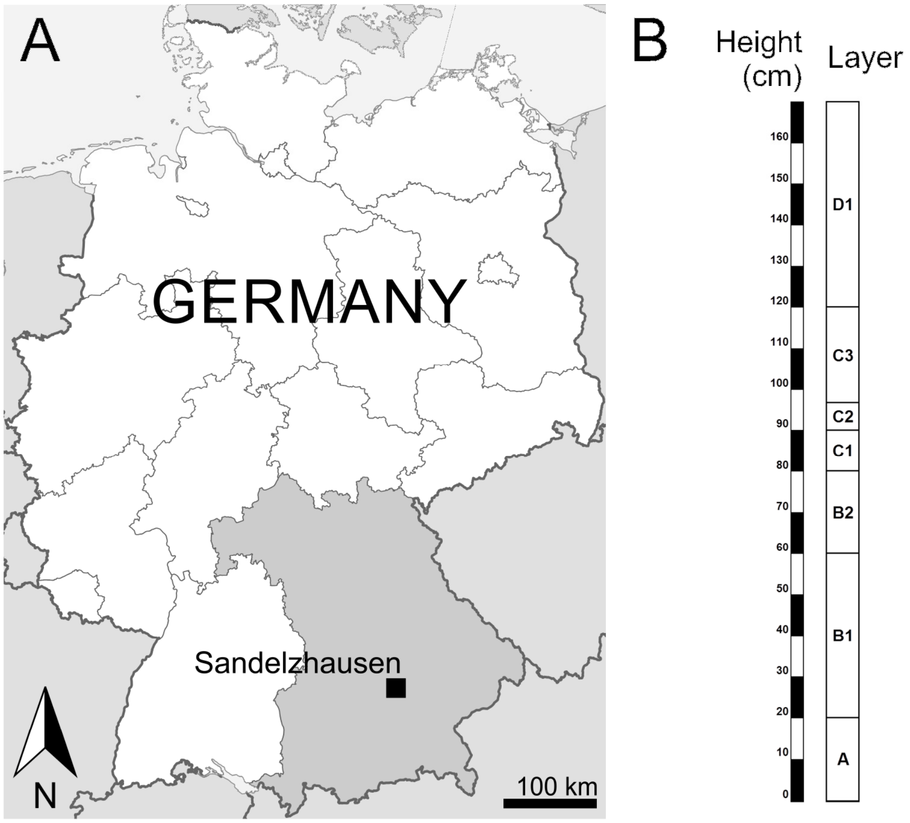

**Figure 1. A.** Map showing the location of Sandelzhausen. **B.** Division in layers of the sedimentary profile of Sandelzhausen, with height of sediment measured in centimeters; figure modified from Moser et al. (2009b).

## 3. MATERIAL & METHODS

### 3.1. 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 in Salvador & Rasser (2014) and Salvador (2015). These species were chosen for the present study for (1) they are extremely abundant, so enough well-preserved specimens could be easily gathered, and (2) they are present throughout all the mollusk-bearing sediment layers.

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 provenience (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 formed in isotopic equilibrium (both oxygen and carbon) with the water and so their isotope contents are still very useful paleoenvironmental indicators (Stuiver, 1970; Fritz & Poplawski, 1974).

All specimens stem from the digging site PQ 10-G of Moser et al. (2009a, 2009b), where the snails were collected in intervals of 5 to 15 cm. Nine of these intervals were chosen (the same for both species), spanning layers B2, C3 and D1, which contain the better preserved specimens. Up to four specimens of each species from each interval were analyzed (depending on availability of specimens and their preservation state). The material is housed in the collection of the Bayerische Staatssammlung für Paläontologie und Geologie (BSPG; Munich, Germany) under the record number BSPG 1959 II. The specimens used here came from the following lots: *Galba dupuyiana*: BSPG 1959 II 17477 (B2, 65–70 cm), 17476 (C3, 95–105 cm), 17478 (C3, 105–110 cm), 17479 (C3, 115–120 cm), 17482 (D1, 135–140 cm), 17483 (D1, 140–145 cm), 17484 (D1, 150–155 cm), 17485 (D1, 155–160 cm), 17486 (D1, 160–165/170 cm); *Pseudidyla moersingensis*: BSPG 1959 II 17282 (B2, 65–70 cm), 17283 (C3, 95–105 cm), 17284 (C3, 105–110 cm), 17285 (C3, 115–120 cm), 17286 (D1, 135–140 cm), 17287 (D1, 140–145 cm), 17288 (D1, 150–155 cm), 17289 (D1, 155–160 cm), 17290 (D1, 160–165/170 cm). The notation in parenthesis following each lot indicates the layer of origin and the height in the sediment in relation to the base (for more details, see Moser et al., 2009a, 2009b).

### 3.2. 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 air-dried, the entire specimen (*i.e.*, the shell) was crushed and ground, and the whole homogenized powder was used in 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 is usually restricted to the warmer seasons) and results in an averaged value for the growing season.

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 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 300 µm beam diameter and a large 2-dimensional detector (µ-XRD$^2$) (Berthold et al., 2009). In all chosen shells aragonite could be identified as the only carbonate phase and none showed hints of recrystallization, such as crystallite coarsening. It is assumed that, if no recrystallization occurred, the original isotopic composition has been preserved (Grossman

& Ku, 1986; Latal et al., 2004, 2006) and thus the shells can be used for paleoenvironmental analyses.

### 3.3. Oxygen and carbon 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 minutes at 70℃ 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 in the water (Leng et al., 1999; Miller & Tevesz, 2001; McConnaughey & Gillikin, 2008); effects of diet in carbon isotope composition is negligible (Fritz & 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 & 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 & 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 & Yapp, 2004). The oxygen isotope composition of this 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 & Ellis, 2002; Balakrishnan & 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 & Ellis, 2002). The carbon isotope composition of the shell is mainly related to diet (dissolved inorganic carbon, or DIC, plays only a minor role), but often with a considerable enrichment of $^{13}C$ (Francey, 1983; Balakrishnan & Yapp, 2004; McConnaughey & Gillikin, 2008).

In all cases, the other factor controlling the isotopic composition of the shell is the ambient temperature (*e.g.*, Latal et al., 2004). Shells from large lacustrine environments, in particular, are more reliable for paleoenvironmental analysis, since the oxygen isotope composition of the lake water remains relatively constant throughout the year, being much less sensitive to seasonal variation (Leng et al., 1999; White et al., 1999 As such, temperature becomes the main controlling factor of shell $\delta^{18}O$ values (White et al., 1999), which can be used to reconstruct paleotemperatures. In this regard, shallow water and terrestrial snail species are better suited than deep water ones (Yang et al., 2001).

### 3.4. Strontium isotope analysis

For the strontium isotope analysis, three specimens of *Galba dupuyiana* were used, coming from the following lots: BSPG 1959 II 17477 (layer B2, 65–70 cm), 17476 (layer C3, 95–105 cm), 17483 (layer D1, 140–145 cm). A single specimen of *P. moersingensis* (BSPG 1959 II 17287; layer D1, 140–145 cm) was also available for analysis.

About 1–2 mg of shell carbonate were dissolved in 3 ml suprapure $HNO_3$. After evaporation the sample was dissolved in 0.3 ml 3N $HNO_3$ and loaded on 0.5 ml mini-columns from Evergreen Scientific filled with 300 µl of Eichrom Sr-Spec (100–150 µm) resin. After eluation of the matrix with 3N $HNO_3$, the Sr fraction was eluated with 1 ml 0.06 N $HNO_3$. From each sample 5 ml solution with 100 ng/g Sr was prepared for Sr isotope measurement. NBS 987 standard solutions in the same Sr concentration as the samples (100 ng/g) were measured after each bloc of three samples. The $^{87}Sr/^{86}Sr$ were measured with the Thermofisher Neptune MC-ICP-MS (with a signal intensity of about ≥ 3V on mass $^{88}Sr$) at the Steinmann-Institute for Geology, Mineralogy and Paleontology of the University of Bonn. Samples were injected into a Scott-type borosilicate glass spray chamber using a 100 µl PFA nebulizer. Mass bias and interference ($^{87}Rb$, $^{83}Kr$) corrected $^{87}Sr/^{86}Sr$ were normalized on a daily basis the NBS 987 standard using the accepted $^{87}Sr/^{86}Sr$ value of 0.71025. The precision of $^{87}Sr/^{86}Sr$ measurements was better than $3*10^{-5}$ (2 RSD).

### 3.5. Actualistic ecological analysis

The actualistic ecological analysis mentioned above, which is often used for the molluscan fauna, is very similar to the “Nearest Living Relative” method (NLR), usually applied in paleoclimatological studies. While the latter often focus on the Coexistence Approach (for a review, see Utescher et al., 2014), we here focus on genus-level, as usual for mollusks. As such, based on the known ecological preferences of extant congeners gathered from the literature, potential paleohabitats of the fossil snails are inferred: if all extant species of a given genus show the same habitat preferences, there is a very high probability that the fossil species shared these preferences (especially if this does not contradict the sedimentary and taphonomical signals); however, if the extant species inhabit a wide range of habitats, they are of very limited use (or no use at all) for paleoecological inferences. Finally, some clues might be gained from functional morphology, since some shell features might give additional paleoecological information.

The continental molluscan fauna of Sandelzhausen is almost exclusively composed of pulmonate snails, being fully described elsewhere (Salvador, 2013a, 2013b, 2015; Salvador

& Rasser, 2014). These works served as the basis for the stratigraphical distribution of the species presented here and the paleoecological analysis.

The work of Moser et al. (2009b) has already dealt with the paleoecology of Sandelzhausen's fossil mollusks, determining by the faunal composition 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, 2013b, 2015; Salvador & Rasser, 2014), which brings about important changes in the paleoecological interpretations.

### 3.6. 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 from 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 below).

## 4. RESULTS

The isotopic values of each sample for can be found on Table 1. Likewise, 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 obtained (Table 1) and the faunal composition (Table 2) throughout the layers. This will be explored in further detail in the Discussion.

### 4.1. Oxygen isotope analysis

The $\delta^{18}O$ 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 ($R^2 = 0.8$):

$$T(°C) = 1.72 * \delta^{18}O_{\text{shell aragonite (VPDB)}} + 15.46$$

Secondly, Zanchetta et al. (2005) did a similar study for the Recent Italian snails, providing the following equation ($R^2 = 0.36$):

$$T\ (°C) = 1.15 * \delta^{18}O_{\text{shell aragonite (VPDB)}} + 15.79$$

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

**Table 1.** Oxygen, carbon and strontium isotope values for all specimens of the two gastropod species, with a column with the standard deviation (SD), when applicable. Note that, for some layers, poor preservation or lack of material precluded achieving the desired number (four) of measurements for Oxygen and Carbon isotopes. Only four samples could be measured for Strontium isotopes.

| Species | Layer | Height in sediment | $\delta^{18}O$ (‰) | | | | SD | $\delta^{13}C$ (‰) | | | | SD | $\delta^{87}Sr$ (‰) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pseudidyla moersingensis*<br>(O. Boettger, 1877) | B2 | ~67.5 cm | -3.50 | -3.95 | -4.66 | - | 0.59 | -5.04 | -6.90 | -6.32 | - | 0.95 | - |
| | C3 | ~100 cm | -4.12 | -3.81 | - | - | 0.22 | -4.99 | -5.72 | - | - | 0.52 | - |
| | C3 | ~107.5 cm | -3.14 | -3.07 | -3.29 | - | 0.11 | -4.11 | -6.81 | -7.54 | - | 1.81 | - |
| | C3 | ~117.5 cm | -3.26 | -3.19 | -2.26 | -2.74 | 0.46 | -7.10 | -5.88 | -6.63 | -7.61 | 0.73 | - |
| | D1 | ~137.5 cm | -2.88 | -3.93 | - | - | 0.75 | -4.78 | -5.31 | - | - | 0.38 | - |
| | D1 | ~142.5 cm | -2.37 | - | - | - | - | -4.89 | - | - | - | - | 0.710833 |
| | D1 | ~152.5 cm | -3.40 | -3.45 | -1.83 | - | 0.92 | -5.18 | -6.58 | -4.23 | - | 1.18 | - |
| | 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*<br>(Noulet, 1854) | B2 | ~67.5 cm | -2.50 | -2.64 | -2.06 | -1.46 | 0.53 | -7.21 | -5.73 | -3.05 | -6.91 | 1.90 | 0.710471 |
| | C3 | ~100 cm | -2.19 | -2.36 | -5.21 | - | 1.70 | -5.59 | -5.21 | -9.79 | - | 2.54 | 0.710645 |
| | C3 | ~107.5 cm | -5.54 | -3.30 | -2.84 | - | 1.44 | -6.52 | -2.95 | -0.18 | - | 3.18 | - |
| | C3 | ~117.5 cm | -1.53 | -4.66 | -4.92 | -3.98 | 1.55 | -8.03 | -6.42 | -8.27 | -4.30 | 1.83 | - |
| | D1 | ~137.5 cm | -0.56 | -2.13 | -3.10 | -2.21 | 1.06 | -9.11 | -9.35 | -8.39 | -9.17 | 0.42 | - |
| | D1 | ~142.5 cm | -2.25 | -2.93 | - | - | 0.48 | -8.80 | -8.13 | - | - | 0.47 | 0.710790 |
| | D1 | ~152.5 cm | -2.81 | -1.85 | -3.52 | -1.95 | 0.79 | -10.05 | -2.89 | -7.90 | -7.47 | 3.01 | - |
| | D1 | ~157.5 cm | -2.86 | -2.14 | -0.52 | -5.91 | 2.26 | -8.25 | -7.69 | -3.00 | -7.24 | 2.40 | - |
| | D1 | ~165 cm | -2.58 | -2.72 | -0.98 | -3.40 | 1.02 | -7.25 | -7.31 | -10.54 | -7.26 | 1.63 | - |

### 4.2. Carbon isotope analysis

The main interest in the carbon isotope values is to known whether they co-vary with the oxygen isotopes or not. This seems to be the case in Sandelzhausen from layer B2 to the beginning of layer C3 (heights 60 to 100 cm; Fig. 3); taking only these lower heights 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).

**Table 2.** Occurrence of mollusk species in the sedimentary layers of Sandelzhausen, from B1 (bottom) to D1 (top). 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, 2009b). Symbols: x = rare species (0–10 specimens), xx = common species (11–100 specimens), xxx = abundant species (>100 specimens), ? = precise layer undefined.

| | **Layers** | | | | | | **Layers** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **B1** | **B2** | **C1** | **C3** | **D1** | **Species** | **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* (Klein, 1846) | | | | | x |
| *Pomatias* sp. | ? | ? | ? | | | *Granaria* cf. *grossecostata* (Gottschick & Wenz, 1919) | | x | | x | |
| NERITIMORPHA | | | | | | *Granaria* sp. | | x | | x | |
| *Theodoxus* sp. | | | | | x | *?Helicodonta* sp. | ? | ? | ? | ? | ? |
| Lower HETEROBRANCHIA | | | | | | *Janulus supracostatus* (Sandberger, 1873) | ? | ? | ? | ? | ? |
| *Valvata* sp. | | | | x | | *Leucochroopsis kleini* (Klein, 1847) | | | ? | ? | x |
| HYGROPHILA | | | | | | *Lucilla subteres* (Clessin, 1877) | ? | ? | ? | | |
| *Ferrissia deperdita* (Desmarest, 1814) | ? | ? | ? | | | *Oxyloma minima* (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* (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* (Klein, 1853) | x | x | x | x | x |
| *Planorbarius mantelli* (Dunker, 1848) | xx | xx | xx | xx | xxx | ?*Pyramidula* sp. | ? | ? | ? | ? | ? |
| *Radix socialis* (von Zieten, 1830) | | | | | xx | *Strobilops* sp. | ? | ? | ? | ? | |
| *Segmentina larteti* (Noulet, 1854) | | | ? | ? | x | *Testacella zellii* Klein, 1853 | ? | ? | ? | | |
| EUPULMONATA | | | | | | *Triptychia* sp. | | x | | x | |
| *Apula* cf. *coarctata* (Klein, 1853) | | | | x | x | *Urticicola perchtae* Salvador, 2013 | | | | 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 | |

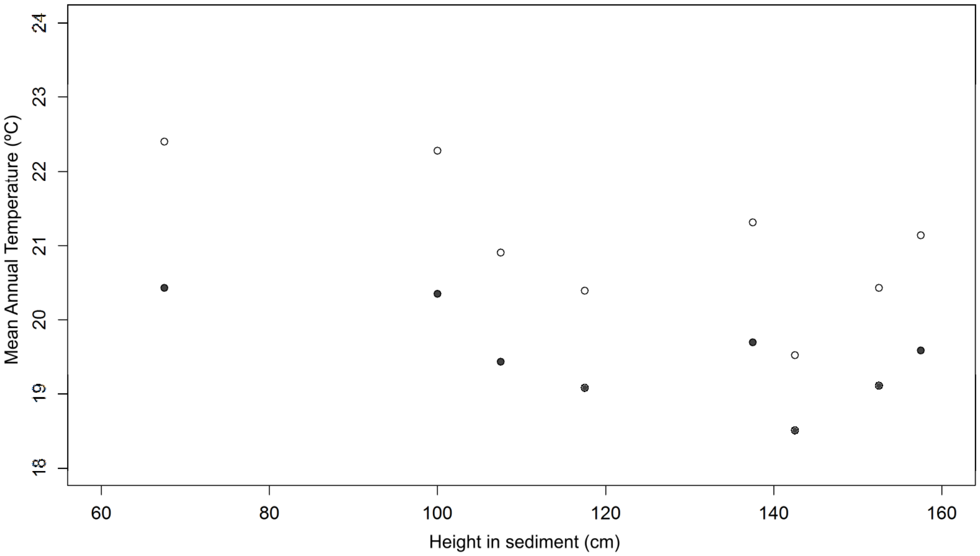

**Figure 2.** MAT, shown by height in the sediment profile (in cm), obtained by imputing the δ18O values of *P. moersingensis* in the equations of Lécolle (1985) [open circles] and Zanchetta et al. (2005) [black circles].

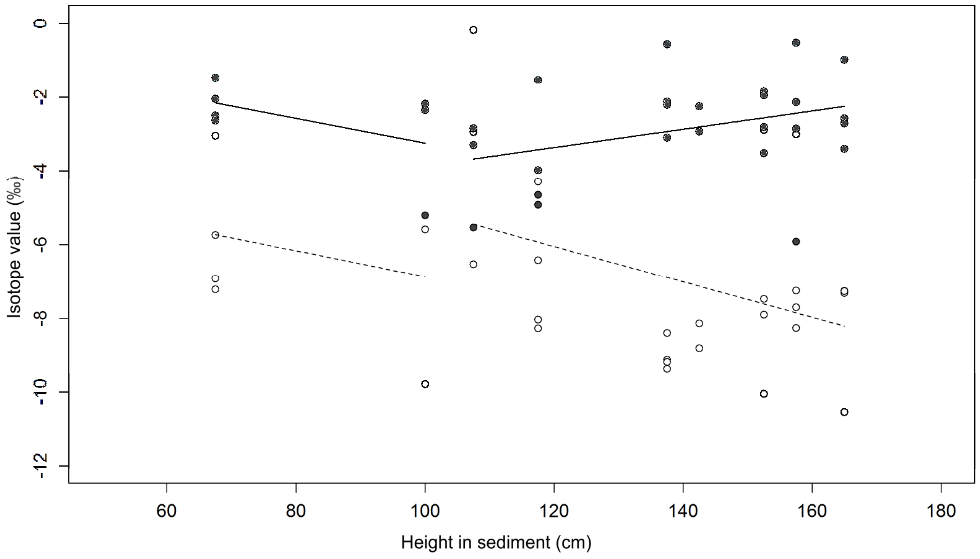

**Figure 3.** Oxygen [black circles] and carbon [open circles] isotope values for each interval of the sediment profile. The curves represent the intervals from layer B2 to the beginning of layer C3 (heights 60 to 100 cm) and from the bottom of layer C3 onwards (heights greater than 100 cm). The slopes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

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, the interaction was significant, meaning that the slopes for each isotope type were significantly different (Table 3).

### 4.3. Strontium isotope analysis

Despite counting with only three measurements, the obtained values (Table 1) display a significant increase throughout the sediment layers (P= 0.03; Fig. 4).

### 4.4. Mollusk assemblage: paleoecology

A list of all the mollusk species found in Sandelzhausen can be seen on Table 2, alongside their presence/absence in each sedimentary layer. For the present actualistic paleoecological analysis we used 32 different species (some identified only to genus level) and ca. 9,000 individuals in total. The remaining 12 species seen on Table 2 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 & Rasser, 2014) and Unionidae indet. (Moser et al., 2009b; Salvador, 2013a).

**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. 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.

| **a) Whole dataset** | | **Estimate** | **SE** | **F-test** | **ndf** | **ddf** | **P-value** |
|---|---|---|---|---|---|---|---|
| Height:Isotope | | | | 3.91 | 1.00 | 30.00 | 0.06 |
| | Oxygen | 0.03 | 0.01 | | | | |
| Isotope | Carbon | -6.87 | 0.35 | 72.04 | 1.00 | 31.00 | **< 0.01 *** |
| | Oxygen | -2.80 | 0.35 | | | | |
| Height | | -0.01 | 0.01 | 2.03 | 1.00 | 30.00 | 0.16 |

| **b) Between heights 60 and 100** | | **Estimate** | **SE** | **F-test** | **ndf** | **ddf** | **P-value** |
|---|---|---|---|---|---|---|---|
| Height:Isotope | | | | 0.00 | 1.00 | 5.00 | 0.97 |
| | Oxygen | 0.00 | 0.04 | | | | |
| Isotope | Carbon | -6.21 | 0.64 | 40.64 | 1.00 | 6.00 | **< 0.01 *** |
| | Oxygen | -2.63 | 0.64 | | | | |
| Height | | -0.03 | 0.04 | 0.89 | 1.00 | 5.00 | 0.39 |

| **b) Heights greater than 100** | | **Estimate** | **SE** | **F-test** | **ndf** | **ddf** | **P-value** |
|---|---|---|---|---|---|---|---|
| Height:Isotope | | | | 7.13 | 1.00 | 23.00 | **0.01 *** |
| | Oxygen | 0.07 | 0.03 | | | | |
| Isotope | Carbon | -0.29 | 2.81 | | | | |
| | Oxygen | -6.33 | 2.81 | | | | |
| Height | | -0.05 | 0.02 | | | | |

## 5. DISCUSSION

### 5.1. Oxygen isotope analysis

The interpretation of isotopic data from fossil snails depends to a good extent of studies with modern analogues (Yanes et al., 2008, 2009; Colonese et al., 2014). Zanchetta et al. (2005) state that these equations 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 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 discussion below) also more closely resembles the Recent Mediterranean one.

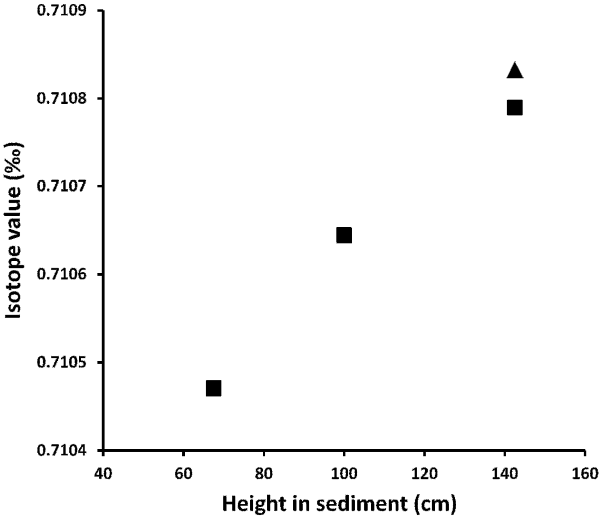

**Figure 4.** Strontium isotope values for selected intervals of the sediment profile. Squares indicate samples of the freshwater *G. dupuyiana*; the tringle indicates the single specimen of *P. moersingensis*.

The MAT values obtained from the equations (Fig. 2; roughly 19.5 to 22.5 ºC from the equation of Lécolle, 1985; roughly 18.5 to 20.5 ºC 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) for the ectothermic vertebrates: 18.0 to 20.8 °C. Böhme (2010) proposed a more semi-arid/sub-humid climate for the basal layers and a more sub-humid/humid one for the upper layers. However, as stated above, no statistically significant overall decrease in MAT could be detected based on snail $\delta^{18}O_{shell}$ values; MAT is not significantly correlated to height in the sediment (Fig. 2), meaning that there is no trend of temperature variation throughout the studied sediment profile.

As a cautionary note, the calculated MAT might be a little overestimated because there usually is no shell growth during the coldest and/or drier months; as such, the MAT values would reflect the warmer and/or wetter months of the snails' growing season (Balakrishnan & Yapp, 2004). However, if there was no clear dry or cold season, the snails could grow throughout the whole year. At least regarding temperature, low seasonal variability in MAT was suggested by Tütken & Vennemann (2009) based on a single intra-tooth $\delta^{18}O$ profile of a *Gomphotherium* tusk.

Finally, methods for deducing (water) temperature from freshwater snails are still not very developed (Tevesz et al., 1997; Miller & Tevesz, 2001) and only some tentative species-specific equations for Recent species have been proposed so far (*e.g.*, Grossman & 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). Some authors even state that temperature calculations for freshwater species can only be done by using species-specific equations (Filippi et al., 1997). As such, we refrain here from using data on freshwater species for temperature reconstruction.

### 5.2. Carbon isotope analysis

Land snail shell carbon isotope composition reflects mainly the isotopic composition of the snail's diet (Goodfriend & Ellis, 2002; Stott, 2002; Metref et al., 2003; McConnaughey & Gillikin, 2008; Zhang et al., 2014). It is often used to infer preference for a particular kind of plant material ($C_3$, $C_4$ or CAM plants; Goodfriend & 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 & Ellis, 2002; McConnaughey & Gillikin, 2008; Colonese et al., 2014). Nevertheless, the scarcity of data on shell carbon isotope composition of Recent snails hamper further analysis. Another proxy for this is the isotopic signals of mammalian teeth: fossil teeth from Sandelzhausen indicate an exclusiveness of $C_3$ plants (Tütken & Vennemann, 2009), which is to be expected since $C_3$ plants are considered to have dominated the Neogene 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 & 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 & Ku, 1997; Deocampo, 2010). This seems to happen in Sandelzhausen from layer B2 to the beginning of layer C3 (60 to 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 two measurements available from these layers, 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 isotopic profiles of oxygen and carbon 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 faunal (see below; see also Moser et al., 2009b).

Finally, the low $\delta^{13}C$ values, especially in the later stages of the Sandelzhausen lake (Fig. 3) indicates 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 & Tevesz, 2001). This would also be in line with the proposed increase in riparian vegetation in the upper layers and slightly eutrophic conditions (Böhme, 2010).

### 5.3. Strontium isotope analysis

The strontium isotope ratio $^{87}Sr/^{86}Sr$ can be used for paleoenvironmental studies, for ambient water is recorded in the shell carbonate and thus information on paleohydrology and water mass provenance of freshwater settings can be recovered (Rosenthal et al., 1989). The strontium content of the aragonitic shells of aquatic snails is virtually the same as the lake water composition and remains constant through geological time, provided little or no recrystallization into calcite has occurred (Krinsley, 1960; Rosenthal & Katz, 1989; Rosenthal et al., 1989; Kaaandorp et al., 2006; Deocampo, 2010). The Sr isotopic composition of the water is the same as that of the rocks being weathered in the catchment area of fluvial or limnic systems (Deocampo, 2010). The $^{87}Sr/^{86}Sr$ rate is only altered if the geology of the drainage area changes significantly and/or if the catchment area changes (Jones & Faure, 1978; Neat et al., 1979; Hart et al., 2004). Hence $^{87}Sr/^{86}Sr$ of carbonate shells from aquatic organisms are a useful indicator for fluctuations in lake level, *i.e.*, inflow of isotopically distinct ground or surface waters (Hart et al., 2004; Tütken et al., 2006).

The freshwater snail *G. dupuyiana* displays an increase of $^{87}Sr/^{86}Sr$ from 0.710471 to 0.710792 throughout the layers B2 to D1, while the single terrestrial snail *P. moersingensis* from layer D1 has an even a slightly higher value of 0.710833 (Fig. 4). This reflects inflow of water with somewhat more radiogenic Sr into the lake of Sandelzhausen, likely caused by changes in the catchment area (and thus water source) of the lake, which started to form in uppermost layer C3. The snail shell $^{87}Sr/^{86}Sr$ values are often a bit higher than those measured in large mammal teeth of equids and proboscids from Sandelzhausen (0.710382±0.000172, n= 4, likely from layer D1; data from Tütken & Vennemann, 2009). The change to a perennial lake was formerly attributed to an increase in precipitation values (Böhme, 2010). Our Sr isotope data indicate that rising ground/lake water levels may have resulted from a change in catchment area and/or new tributaries that started to discharge water with higher $^{87}Sr/^{86}Sr$ in the Sandelzhausen lake region.

## 5.4. Mollusk assemblage: paleoecology

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

### 5.4.1. Freshwater species

Most of the Recent congeners of the freshwater species can be found in many 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). Living representatives of the bivalve *Sphaerium* may be found in almost any kind of water bodies, despite not been resistant to desiccation (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 consolidate water bodies and/or that do not tolerate desiccation (Bandel, 2001; Zettler et al., 2004; Bunje, 2005; Welter-Schultes, 2012): *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* would be an exception to this trend, judging by the Recent *S. nitida*, which is commonly found in temporary water bodies or marshy environments (Clark, 2011; Welter-Schultes, 2012). A possibility is that the fossil *Segmentina larteti* inhabited a more marshy littoral area of the Sandelzhausen lake. Moser et al. (2009b) also proposed that alongside this change in the environments, 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 scenario) and being substituted by the latter in the top layers (*i.e.*, the lake). Nevertheless, with the larger number of samples studied by Salvador & Rasser (2014), the lymnaeid *Galba dupuyiana* remains the most abundant species in the lake throughout all the layers, so no clear substitution is seen. Still, the planorbids do increase in abundance towards the top layers.

### 5.4.2. 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 & 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). As for the entirely fossil genera, some are also supposed to inhabit damp woods, tending towards warmer environments, namely *Pseudidyla*, *Triptychia* and *Leucochroopsis* (Lueger, 1981; Harzhauser & Binder, 2004; Harzhauser & Tempfer, 2004; Nordsieck, 2007; Schnabel, 2007). *Leucochroopsis*, in particular, has pits on the shell surface; this indicate the presence of hairs, which increase adherence of Recent hygromiids to plant leaves during foraging, especially in high humidity levels (Pfenninger et al., 2005). Nevertheless, for other fossil genera the supposed paleoecological preferences should be taken more carefully. For instance, *Archaeozonites* and *Palaeoglandina* are considered by some to inhabit moist forests (*e.g.*, Lueger, 1981), while others consider them inhabitants of drier and more open environments (Moser et al., 2009b). If not considering the last two 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 & Cameron, 1979; Barker & Efford, 2004; Welter-Schultes, 2012; Rowson et al., 2014). The very abundant *Pseudidyla* occurs throughout all layers (Table 2).

The genus *Janulus* is a curious case. *Janulus supracostatus* is known from the German Silvana-beds (“Silvanaschichten”, in German) and the single specimen found in Sandelzhausen does not have proper stratigraphical data, although 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 perhaps also on the Canary Islands (Waldén, 1983; Cameron et al., 2007; Seddon, 2008). This archipelago has 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 & Short, 1994; Capelo, 2004).

Some of the species in Sandelzhausen prefer drier and more open habitats. *Granaria* is a good indicator of these environments, being often found on calcareous rocks (Welter-Schultes, 2012; Höltke & Rasser, 2013). The fossil genus *Apula*, and more specifically *A.*

*coarctata*, is thought to have preferred drier environments (Lueger, 1981). The 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); the species would have, therefore, inhabited more open and dry habitats, similarly to Recent Ariantinae (Moser et al., 2009b). 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 the layers in Sandelzhausen (Tables 2, 4), so it is plausible to image that the lake's hinterland would have always counted with areas that are more open. This 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 are voracious predators, feeding mainly on earthworms (but also on gastropods and centipedes), that live underground, requiring a moist soil cover (Barker & Efford, 2004; Liberto et al., 2011). As the rest of the family, *Palaeoglandina* was very likely a malacophagous predator (Barker & Efford, 2004). Recent European species display varied lifestyles (*e.g.*, Cossignani & Cossignani, 1995; Welter-Schultes, 2012), but Moser et al. (2009b) suggested (based on shell morphology) that *Palaeoglandina* would have had the same lifestyle and habitat as the Recent North American *Euglandina rosea*. This species is a voracious predator, even hunting partially immersed in water, preying on freshwater snails, like the lymnaeids (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 an optimal 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).

## 6. CONCLUSION

The data on the fossil mollusks presented here is in line with previous environmental reconstructions of Sandelzhausen (Fahlbusch et al., 1972; Witt, 1998; Böhme, 2010; Moser et al., 2009b; Tütken & Vennemann, 2009). 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 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 $\delta^{18}O$ and $\delta^{13}C$ values of the freshwater snail *G. dupuyiana*. Increasing shell $^{87}Sr/^{86}Sr$ reflect a change in the hydrology of Sandelzhausen, which would have likely been caused by changes in the catchment area of the newly formed lake (starting in uppermost layer C3), but that could also have been triggered by the increase in precipitation proposed by Böhme (2010).

The terrestrial habitat would have gone from a more relatively open environment (semi-arid/sub-humid scrubland; 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 (*contra* Moser et al. 2009b). Although plant remains are scarce in Sandelzhausen proper, they are well known from nearby coeval deposits (*e.g.*, Jechorek & Kovar-Eder, 2004; Böhme et al., 2007), where evergreen to deciduous subtropical forests are reported; the molluscan fauna of coeval sites is also similar to that from Sandelzshausen (Höltke et al., submitted).

**Table 4.** Occurrence of land snail species in the sedimentary layers of Sandelzhausen, separated by habitat type. Only the species with significance to the paleoecological analysis were included.

| | **Layers** | |
|---|---|---|
| **Habitat type / species** | **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 |

Furthermore, our study argues for the greater strength of paleoecological analyses when based on a thorough taxonomic framework and integrated with complementary isotope analyses. As the paleoecological actualistic depends on data from Recent molluscan species, the fossil isotope analysis would likewise greatly benefit from more systematical studies on extant species. For instance, differences in isotopic composition of the shell of a single species might exist between distinct habitats, or more inclusive taxonomic groups (*e.g.*, at family-level and above) might have their own isotopic signatures.

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## Erklärung nach § 5 Abs. 2 Nr. 7 der Promotionsordnung der Math.-Nat. Fakultät
## -Anteil an gemeinschaftlichen Veröffentlichungen-

## Declaration according to § 5 Abs. 2 No. 7 of the PromO of the Faculty of Science
## -Share in publications done in team work-

**Name:** Rodrigo Brincalepe Salvador

**List of Publications**

1. HÖLTKE, O.; SALVADOR, R.B.; RASSER, M.W. Submitted. Paleobiogeography of Middle Miocene terrestrial gastropods in Central Europe, with special emphasis on the Upper Freshwater Molasse. Palaeogeography, Palaeoclimatology, Palaeoecology.
2. RASSER, M.W.; SALVADOR, R.B.; HÖLTKE, O. Submitted. The gastropod palaeohabitats of lake Randeck Maar and its hinterland (Miocene, SW Germany) using the "Extant Genus Bracket". Palaeogeography, Palaeoclimatology, Palaeoecology.
3. SALVADOR, R.B. & RASSER, M.W. 2014. The fossil pulmonate snails of Sandelzhausen (Early/Middle Miocene, Germany) (Hygrophila, Punctoidea and limacoids). Archiv fur Molluskenkunde, 143: 187–202.
4. SALVADOR, R.B. & RASSER, M.W. 2016. Fossil land and freshwater gastropods from the Middle Miocene of Bechingen and Daugendorf, southwestern Germany. Archiv für Molluskenkunde 145(1): 1–14.
5. SALVADOR, R.B. & RASSER, M.W. 2016. The fossil land and freshwater snails of Oggenhausen (Middle Miocene, Germany). Revista Brasileira de Paleontologia, 9(1): 41–52.
6. SALVADOR, R.B.; PIPPÈRR, M.; REICHENBACHER, B.; RASSER, M.W. 2016a. Early Miocene continental gastropods from new localities of the Molasse Basin in southern Germany. Paläontologische Zeitschrift: published online [DOI 10.1007/s12542-016-0291-y].
7. SALVADOR, R.B.; PRIETO, J.; MAYR, C.; RASSER, M.W. 2016b. New gastropod assemblages from the Early/Middle Miocene of Riedensheim and Adelschlag-Fasanerie, southern Germany. Neues Jahrbuch fur Geologie und Palaontologie, Abhandlungen, 279(2): 127–154.
8. SALVADOR, R.B.; RASSER, M.W.; HÖLTKE, O. 2015a. Fossil gastropods from Miocene Lake Randeck Maar and its hinterland (SW Germany). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 277(3): 251–273.
9. SALVADOR, R.B.; SACH, V.J.; VALENTAS-ROMERA, B.L. 2015b. The fossil continental mollusks in the Upper Freshwater Molasse (Middle Miocene) of the districts of Biberach, Ravensburg and Neu-Ulm, Germany. Revista Brasileira de Paleontologia, 18(2): 201– 216.
10. SALVADOR, R.B.; TÜTKEN, T; TOMOTANI, B.M.; BERTHOLD, C.; RASSER, M.W. Submitted. Paleoecological and isotopic analysis of fossil continental mollusks of Sandelzhausen (Early/Middle Miocene, Germany). Paläontologische Zeitschrift.

| **Nr.** | **Accepted for publication yes/no** | **Number of all authors** | Position of candidate in list of authors | Scientific ideas of candidate (%) | Data generation by candidate (%) | Analysis and Interpretation by candidate (%) | Paper writing by candidate (%) |
|---|---|---|---|---|---|---|---|
| **1** | submitted | 3 | 2nd | 25 | 25 | 25 | 25 |
| **2** | submitted | 3 | 2nd | 25 | 25 | 25 | 25 |
| **3** | published | 2 | 1st | 75 | 75 | 75 | 75 |
| **4** | published | 2 | 1st | 75 | 75 | 75 | 75 |
| **5** | published | 2 | 1st | 75 | 75 | 75 | 75 |
| **6** | published (online) | 4 | 1st | 50 | 50 | 50 | 50 |
| **7** | published | 4 | 1st | 50 | 50 | 50 | 50 |
| **8** | published | 3 | 1st | 50 | 50 | 50 | 50 |
| **9** | published | 3 | 1st | 50 | 50 | 50 | 50 |
| **10** | submitted | 5 | 1st | 50 | 50 | 50 | 50 |

I certify that the above statement is correct.

Date, Signature of the candidate

I/We certify that the above statement is correct.

Date, Signature of the doctoral committee or at least of one of the supervisors