Taxonomy and Palaeobiogeography of the landgastropods of the Miocene *silvana*- and *sylvestrina*-beds in SW Germany.

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1. Abbreviations

A = Arithmetic mean

as = Angle of spire

BM = Brackwassermolasse

BSPG = Bayerische Staatssammlung für Paläontologie und Geologie (Munich, Germany)

di = Distance between the insertions

GPIT = Department of Geosciences, Eberhard Karls Universität Tübingen (Tübingen, Germany; formerly Geologisch-Paläontologisches Institut Tübingen)

GÜNDLK. = Gündlkofen

lwh = Height of the last whorl

mh = Height of the aperture

NAFB = North Alpine Foreland Basin

NHMUK = Natural History Museum (London, UK)

NMDS = Non-metric multidimensional scaling

OGGEN. = Oggenhausen

OMM = Obere Meeresmolasse.

OSM = Obere Süßwassermolasse.

PCA = Principal Component Analysis

PIMUZ = Paläontologisches Institut und Museum, Universität Zürich (Zurich, Switzerland)

RIEDENS. = Riedensheim

SANDELZ: = Sandelzhausen

SD = Standard deviation

sh = Shell height

SMF = Senckenberg Museum Frankfurt am Main

SMNS = Staatliches Museum für Naturkunde Stuttgart

sw = Shell width

UMM = Untere Meeresmolasse

USM = Untere Süßwassermolasse

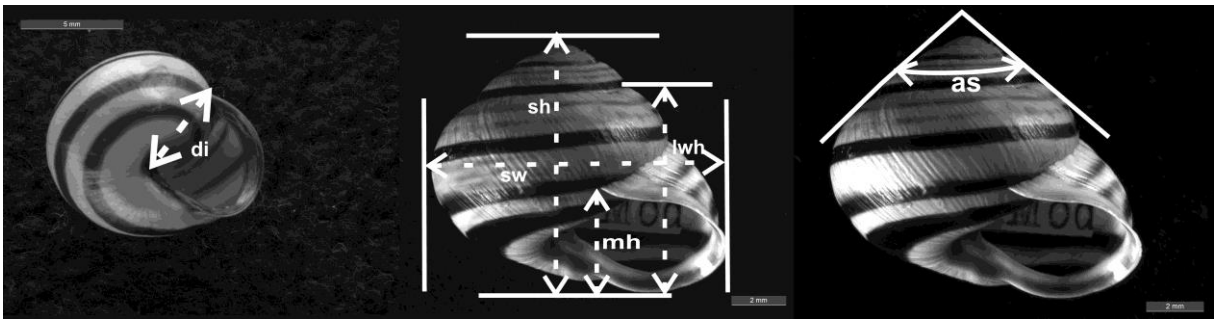

Fig. 1 Morphometrics (modified after Höltke & Rasser 2016)

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3. Zusammenfassung

Diese Arbeit behandelt die miozäne Landschneckenfauna der *silvana*-Schichten, welche vor dem Nördlinger Ries Meteoriten Ereignis abgelagert wurden, und den nach dem Einschlag entstandenen *sylvestrina*-Schichten. Die Arbeit gliedert sich grob in die Teilbereiche Fundstätten, Taxonomie und Morphometrie sowie Paläobiogeographie, welche stark miteinander verzahnt sind und zueinander in enger Beziehung stehen. Mit Hilfe von morphometrischen und statistischen Methoden (Cluster-Analyse, PCA) ließen sich die zwei sehr ähnlichen und als Leitfossilien dienenden Arten *Palaeotachea silvana* und *P. sylvestrina* voneinander unterscheiden. Es konnten zudem noch vier weitere *Palaeotachea*-Spezies in dem genannten Zeitabschnitt nachgewiesen werden. Aus den *silvana*-Schichten konnten 35 Landschneckenarten identifiziert und beschrieben werden wobei die Schwerpunkte auf den Fundorten Mörsingen, Dischingen und Hohenmemmingen lagen. Aus den gleichalten Schichten des Randecker Maares konnten 32 verschiedene nicht-marine Mollusken identifiziert werden. Die jüngeren *sylvestrina*-Schichten des Steinheimer Beckens beinhalten 48 verschiedenen Landschneckenarten. Taxonomische Probleme bei der dort sehr individuenreichen, xerophilen Gattung *Granaria* wurden beseitigt ebenso wie bei der Gattungszuordnung der ebenfalls dort in großen Mengen vorkommenden Spezies *Pseudochloritis insignis*. Letzteres wurde auch mit Hilfe morphomertischer und statistischer Methoden (Cluster-Analyse, PCA) gelöst. Viele der für diese Arbeit untersuchten Gastropoden haben rezente Verwandte und den Hauptanteil nehmen hygrophile Arten ein. Im Vergleich mit den *silvana*-Schichten hatte sich aber der Anteil an xerophilen Arten in den jüngeren *sylvestrina*-Schichten leicht erhöht. Im Zuge der Recherche ließ sich in der Sammlung des SMNS Typusmaterial von ca. 180 känozoischen Land-und Süßwassermollusken feststellen, welche in einem Katalog erfasst wurden. Mit Hilfe von statistischen Methoden (Cluster, NMDS) wurden schließlich sämtliche Mittel-Miozänen Landschneckenvorkommen untersucht, welche mit zwei Ausnahmen mindestens acht verschiedene Arten enthalten. Die Verteilung kann anhand der Paläogeographie oder der Biostratigraphie erklärt werden. Taxonomische Resultate wurden ebenfalls dazu verwendet, einen Fundorte-Katalog für die *silvana*-Schichten am Südrand der Schwäbischen Alb zu erstellen.

4. Abstract

The most common continental stratigraphic units in the SW-German Miocene are the the *silvana*-beds deposited prior to the Ries meteorite impact, as well as the post-Ries deposited *sylvestrina*-beds (MN6-MN9). They contain a lot of different landgastropods, which were studied with respect to taxonomy (including morphometrics), palaeogeography and palaeoecology. The index fossils *Palaeotachea silvana* and *P. sylvestrina* could be clearly separated with morphometrical and statistical methods (Cluster analyses, PCA). Additionally, four other *Palaeotachea* species could be identified in the studied SW German Miocene deposits. At least 35 different species of landgastropods could be identified and illustrated from the *silvana*-beds based on the deposits of Dischingen, Hohenmemmingen and Mörsingen. The contemporaneous sediments of Randeck Maar (MN5) provide insights into the gastropod diversity of an ancient Maar lake. All in all 32 different continental gastropod taxa were identified from this locality. In the younger *sylvestrina*-beds of the Steinheim Basin (MN7), 48 different landsnail species could be described and illustrated. Taxonomic problems concerning the Chondrinidae from the *sylvestrina*-beds were solved as well as the genus membership of *Pseudochlorits insignis*. The majority of the landgastropods were hydrophilic species and a lot of them have Recent relatives. However, the *sylvestrina*-beds contain a higher proportion of xerophilic taxa. According to the ecological preferences of the single taxa, different micro-habitats could be reconstructed. During the research approximately 180 type specimens of continental gastropods could be identified in the collection of the SMNS which were illustrated in a type catalogue. Additional to the taxonomic work, statistical methods (Cluster and NMDS analyses) were used to compare all published Middle Miocene continental deposits in Middle Europe. The resulting clusters reflect the palaeogeographic situation of that time interval. Finally, the taxonomic results were also used for a species catalogue for the *silvana*-beds at the southern margin of the Swabian Alb.

5. List of publications in the thesis

Published papers:

Höltke, O. & Rasser, M.W (2017): Landsnails from the surrounding of the Miocene Steinheim impact crater lake (Baden-Württemberg, South Germany). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen.* **285**(3): 267–302.

Höltke, O. & Rasser, M.W. (2016): The *Palaeotachea* complex (Gastropoda: Pulmonata) in the Miocene of SW Germany: a morphometric approach. *Journal of Conchology*, **42**(4), 239-256.

Höltke, O. & Rasser, M.W. (2015): *Pseudochloritis insignis* - A peculiar large land-snail from the Miocene of SW Germany: Taxonomic status and census of morphologically related forms. *Journal of Conchology*, **42**(1), 21-32.

Höltke, O. & Rasser, M.W. (2013): The chondrinid land snail *Granaria* (Stylommatophora: Chondrinidae) in the Miocene of the Alpine Foreland: State of the art and taxonomic reassessment. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen,* **270**(2): 181-194.

Höltke, O., Salvador, R.B & Rasser, M.W (2018): Miocene continental gastropods from the southern margin of the Swabian Alb (Baden-Württembnerg, SW Germany). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen,* **287** (1): 17-44.

Höltke, O, Salvador, R.B., Rasser, M.W. (2016): Palaeobiogeography of Early/Middle Miocene terrestrial gastropods in Central Europe: a statistical approach using similarity indices. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **461**: 224-236.

Rasser, M.W., Höltke, O. & Salvador, R.B. (2019): Gastropod palaeohabitats of lake Randeck Maar and its hinterland (Miocene, SW Germany) using the “Extant Genus Bracket”. *Lethaia,* https://doi.org/10.1111/let.12353

Salvador, R.B., Höltke, O. & Rasser, M.W. (2018): Miocene continental gastropods from Dischingen, Germany. *Palaeodiversity*, **11**: 11-19.

Salvador, R.B., Höltke, O. & Rasser, M.W. (2017): Fossil land and freshwater gastropods from the Miocene of Hohenmemmingen, Germany. *Palaeodiversity*, **10**(1): 41-48.

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., Rasser, M.W. & Höltke, O. (2015): Fossil gastropods from Miocene Lake Randeck Maar and its hinterland (SW Germany). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen,* **277**(3): 251-273.

Submitted:

Höltke, O., Salvador, R.B. & Rasser, M.W.: The Miocene land- and freshwater gastropods of Mörsingen (Baden-Württemberg, South Germany). *Palaeobiodiversity and Palaeoenvironments.*

6. Introduction

6.1. Landsnails and morphospecies concept

Fossil landsnails are known since the Carboniferous period (see Solem & Yochelson 1979). Prior to the Cenozoic, the fossil record of land gastropods is very rare, and only since the Oligocene they comprise a high biodiversity. Since then, landsnails have inhabited a variety of environments resulting in a great number of different adaptions of the hard part (shell) morphology.

Landsnails belong to the phylum Mollusca, class Gastropoda. Within the Gastropoda, most of the landsnail taxa belong to the informal group Pulmonata, clade Stylommatophora (see Bouchet & Rocroi 2005), while only one family (Carychiidae) is placed in the clade Eupulmonata (Pulmonata). According to Bouchet & Rocroi (2005), the landsnail family Cochlostomatidae is located in the Informal group Architaenioglossa and the Pomatiidae in the clade Hypsogastropoda within the clade Littorinimorpha. However, the taxonomy of terrestrial gastropods based mainly on anatomic features, which points to an important problem in the examination and determination of fossil landsnails: The taxonomy of Recent Pulmonata is often based on the structure of the reproductive organs and on DNA analyses. For the study of fossil landsnail the morphospezies concept is used in which species are discerned by phenotypic differences (Benton & Perason 2001). Morphospecies, however, are by no means restricted to fossils (Allmon 2016). According to the last named author, many modern species in many higher taxa (e.g. mollusks, crustaceans, insects, fishes, snakes, frogs) have been, and continue to be, described solely on the basis of dead, preserved material. In modern echinoderms, for example, studies of recent species confirm the overall usefulness of the skeleton for differentiating species as well as higher taxa (Allmon 2016).

6.2. Geological overview of the study area.

Fossil landsnail shells in terrestrial sediments of the Cenozoic are common nearly worldwide. In Southwest Germany, the North Alpine Foreland Basin (NAFB) and adjacent areas bear a high diversity of Miocene terrestrial mollusks, which are often very well preserved. The development of the NAFB started during the Late Eocene due to the Alpine Orogeny (Geyer & Gwinner 1991; Kuhlemann & Kempf 2002). After

a deep-marine “Flysch phase”, the so called “Molasse phase” began in the Early Oligocene (Bieg et al. 2007). The “Molasse” is divided into five stages: Untere Meeresmolasse (UMM), Untere Süßwassermolasse (USM), Obere Meeresmolasse (OMM), Brackwassermolasse (BM) and Obere Süßwassermolasse (OSM). See fig. 2 for stratigraphic details. A sub-unit the basis of the OSM are the “Helicidenmergel”. However, there a discrepancy, if this unit still belongs to the OMM or if it is already a part of the OSM (see Geyer & Gwinner 1991; Schweigert 1996).

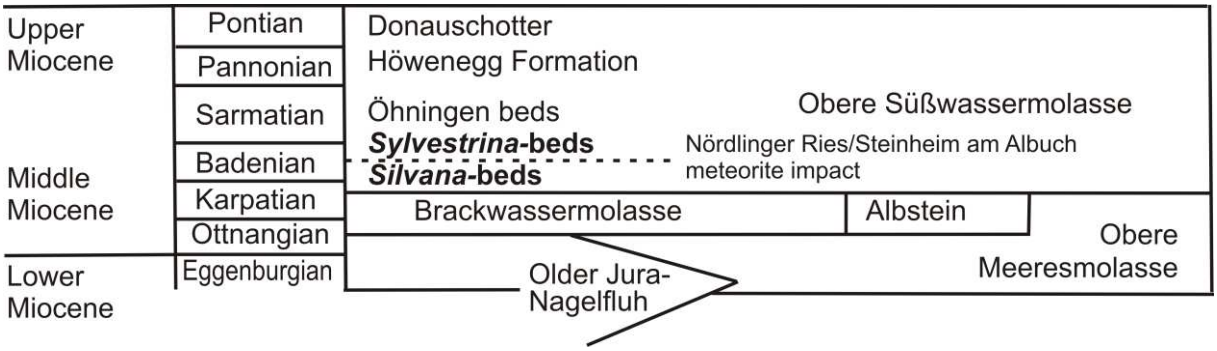

Fig. 2. Stratigraphy modified after Geyer & Gwinner 1984, 1991; Berger et al. 2005 & Höltke et al. 2018).

The OSM was deposited during the Mammal zones (MN) MN 5 to MN 9. The youngest sediments were found in the Hegau region, NW of Lake Constance. The OSM can be divided into different sub-units. The most abundant units are the *silvana*-beds named after the landsnail *Palaeotachea silvana* (Klein, 1853) (Badenian, MN 5, according to Esu 1999). The sediments following above are characterized by the absence of *P. silvana* and the presence of *P. sylvestrina* (Schlotheim, 1820). According to that these sediments were named as *sylvestrina*-beds by some authors (e.g. Wenz 1921). The lithofazies of the OSM consists of limestones and marls as well as sands. Within the time range of the OSM, the Nördlinger Ries/Steinheim am Albuch meteorite event (see Böhme et al. 2001; Buchner et al. 2003) took place with the formation of Palaeolake Steinheim. Its lake sediments bear a rich fossil fauna and flora and it is the type locality for the Mammal Neogene Zone MN 7 (Rössner & Heißig 1999). Prior to that, Lake Randeck Maar was formed by a magmatic explosion and comprises MN 5 sediments (Rasser et al. 2013). These localities were not part of the NAFB, but situated on the Swabian Alb mountain range. Despite that they were included in this study, because the according sediments are contemporaneous with the OSM deposits and contain a rich and often

well-preserved fossil landsnail fauna (especially Steinheim am Albuch). Despite the abundance and distribution of landsnails in Miocene sediments, this topic received only little attention in modern literature.

6.3. Historical overview and state of knowledge

Already in 1832, Zieten described different landsnail species from the Miocene (see Zieten 1832). In the middle of the 19th century, Adolf von Klein published three papers dealing with the fossil land- and freshwater snails of Baden-Württemberg (see Klein 1846; 1852; 1853), and Kurr (1856) described some continental mollusks from the OSM sediments. In the 1870ies, Sandberger published a work describing fossil land- and freshwater molluscs in several volumes (see Sandberger 1870-1875). The famous Swabian geologists Quenstedt (1884), Fraas (1882) and Engel (1883) described the terrestrial Miocene deposits in Baden-Württemberg and gave lists and partly illustrations of the terrestrial mollusks occurring therein. Within the turn of the century, the two malacologists O. Boettger and his nephew C.R. Boettger published their research about the Tertiary landsnails in Europe (see O. Boettger 1909; C.R. Boettger 1909 & 1911). However, according to the relationship between Tertiary and Recent forms, both had contradictive opinions. C.R. Boettger (1909 & 1911) argued that the Recent relatives of the European Tertiary landsnails still live in Europe, while his uncle suggested that their extant relatives can be found in tropical regions (see O. Boettger 1909). The early 20th century was also the peak phase in the research of the terrestrial mollusks in the OSM of SW-Germany and adjacent areas. In 1900, Miller described the land- and freshwater gastropods of the Steinheim Basin (see Miller 1900). In the following years, the authors Wenz, Gottschick and Jooss published articles about land gastropods from these areas (see Höltke et al. 2016 for citations). Apart from papers dealing with specific taxa, also complete malacological overviews were given for four localities (Dischingen by Mengele 1916; Hohenmemmingen by Gottschick & Wenz 1916; the OSM of the Pfänder region in Austria by Jooss 1910; Wenz 1933, 1935; Steinheim Basin by Miller 1900; Gottschick 1911; Gottschick & Wenz 1919; Gottschick 1919-1920). Another monographic work about the gastropod fauna of the Helicidenmergel was published by Jooss in 1923 (see Jooss 1923). During that time, Wenz (1923, 1928) published his “Gastropoda extramarina tertiaria”, an important work of Tertiary

continental mollusks. In 1929, the work of Pfeffer on Tertiary landsnails was published. Concerning the taxonomy and phylogeny of the fossil landsnails, this author had a different opinion in contrast to the other researchers. Pfeffer (1929) erected new fossil taxa that were based, among others, on the microsculpture of shells, and also split Recent genera, for example *Cepaea*. Later authors ignored the results of Pfeffer, and the taxa erected by him were treated as synonyms (For example Zilch & Wenz 1959-1960). It was not until the works of Nordsieck on fossil landsnails (Nordsieck 1986, 2014a & b) that Pfeffers considerations were taken seriously and the taxa designated by him were adopted in the taxonomic literature. One problem with the work of Pfeffer (1929) is that he gave no illustrations for his descriptions of microsculpture and details of shell morphology.

With the publication of Wenz (1935), the peak phase of malacological research in the South German terrestrial Miocene ended. Only a few studies followed in the next decades, such as Groiß (1968), Schlickum (1976) for Zwiefaltendorf and Finger (1998) for the Steinheim Basin.

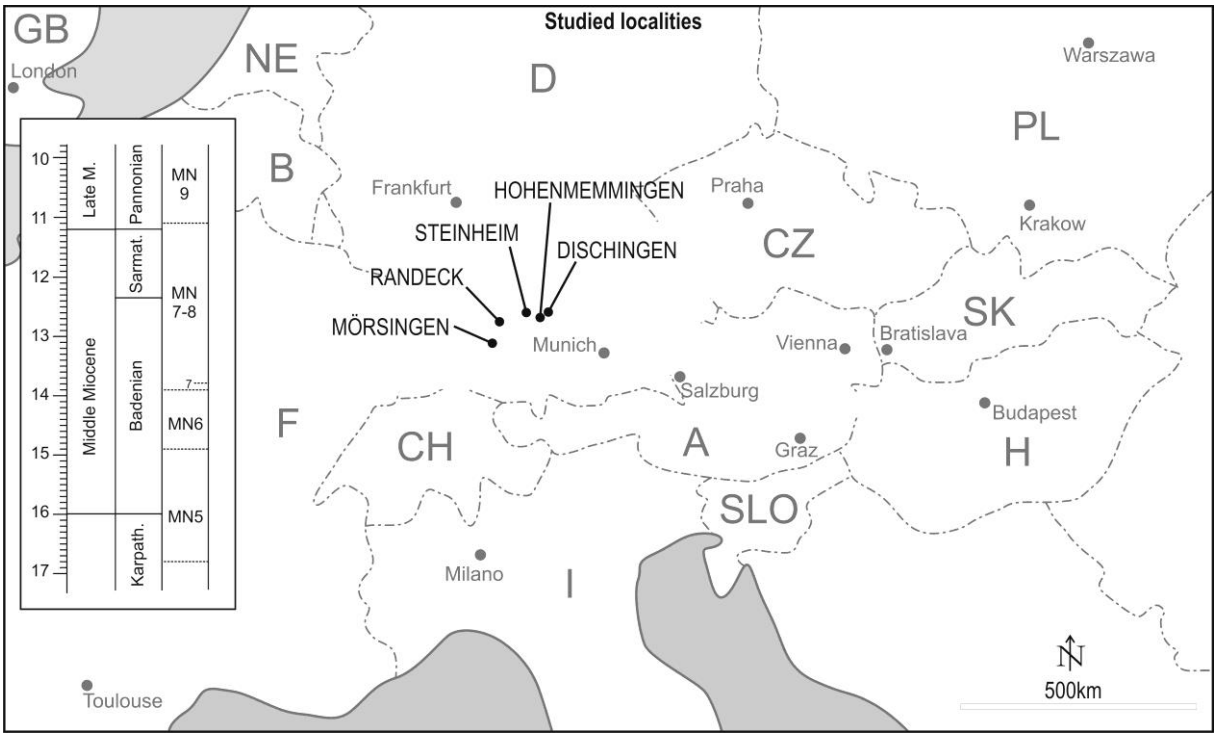

Fig. 3. Studied localities (modified after Höltke et al. 2016).

6.4. Studied localities (see fig. 3)

The best locality for studying the *silvana*-beds are the according freshwater deposits of Mörsingen, a district of Zwiefalten. The deposit lies within the NAFB and the sediments consist of limestone and marl. Large numbers of well preserved continental gastropods were found in outcrops around this village, from the middle of the 19th to the beginning of the 20th century. Most of the continental gastropods from the *silvana*-beds stored in the museums collections are from Mörsingen. Despite of the large amount of fossil continental mollusks coming out in the past, it was only mentioned incidentally in the literature, for example Wenz (1923) or other ones quoted in Höltke et al.(submitted). In this last named paper, all the terrestrial mollusks of Mörsingen were illustrated and described for the first time.

Other deposits of the *silvana*-beds mentioned in the literature are Hohenmemmingen and Dischingen near the eastern margin of the Swabian Alb. The mollusk fauna of Hohenmemmingen was already examined by Gottschick & Wenz (1916) but since that time this theme has never been the subject to subsequent studies. Therefore, material from different collections were added to the compilation of Gottschick & Wenz (1916), offering an updated classification of the species and illustrating several of the Hohenmemmingen fossils for the first time. The freshwater limestones of Dischingen were examined by Mengele (1916). This author presented a list of 27 terrestrial and freshwater gastropod species from this locality, which was compiled by malacologist Carlo G. H. Jooss. Later, Gall (1971) presented a list of 29 gastropod species compiled with newly collected material.

The “Randeck Maar” near Kirchheim/Teck bears sediments which are contemporaneous to the *silvana*-beds. This sediments also contain a rich continental mollusk fauna which has never been studied before in detail. With the knowledge of the gastropod taxa the different palaeo-microhabitats surrounding the “extreme” habitat of an ancient Maar lake can be reconstructed. There are different other Maar lakes (“Maar-Seen”) in SW-Germany (see Seemann 1926) but the Randeck Maar is the only one with such a great amount of well preserved fossils. The lake sediments bear a rich fauna and flora including land- and freshwater gastropods.

The Miocene freshwater lake sediments of the Steinheim Basin are the best and richest locality for studying the landsnail fauna during the post-Ries period of the *sylvestrina*-beds (see Fig. 2). No other locality contains such an amount of well preserved continental gastropods. This basin has a diameter of ca. 3.5 km and is characterized by a peculiar central elevation, the so-called central hill ("Zentralhügel"). Among the invertebrates the Steinheim basin is known for the freshwater snails. Already in the 19th century, Hilgendorf discovered the endemic evolution of the freshwater snail species of the genus *Gyraulus* within the ancient lake. The lake sediments, called the "Steinheimer Seeschichten" were subdivided in different units characterized and named by the different *Gyraulus* species. For details see Rasser (2013). The ancient flora was examined by Schweigert (1993) and the ostracod fauna by Janz (1992). The last work about the whole mollusk fauna was done by Gottschick & Wenz (1919) as well as Gottschick (1919; 1920a-c) in a periodical series. Wilhelm Wenz was a known malacologist and Franz Gottschick was a forester in Steinheim am Albuch. Unfortunately, the original material to works of Gottschick & Wenz named above could not be found. Perhaps it has been in the collection of Wenz which was destroyed in World War II. Since that time, the landsnails of the Steinheim basin hasn`t been the subjects of a detailed study. So for the first time, all the available landsnails from the "Steinheimer Seeschichten" were described and illustrated in detail.

6.5. Taxonomy and Morphometrics

6.5.1. *Palaeotachea*

The most abundant landsnails in the Miocene of SW Germany are the "*Cepaea*" shaped species of the genus *Palaeotachea* Jooss, 1912a. This genus bears the "index fossils" of the *silvana*- and *sylvestrina*-beds (*P. silvana* and *P. sylvestrina*). Originally, the fossil taxa were also place in the genus *Cepaea*, whereas Pfeffer (1929) as well as Nordsieck (1986, 2014) were the opinion, that the fossil forms have nothing to do with the genus *Cepaea*. In addition to that Neiber & Hausdorf (2015) found out that the Recent *Cepaea* complex is a polyphyletic complex. Because *P. silvana* and *P. sylvestrina* are relative abundant, they are very useful for chronostratigraphic questions. The problem is that both species has a distinct variability according to their shell morphology and can also look very similar. Despite

of their importance as index fossils and the widely use of the name *silvana*-beds, no one has ever proved the validity of this species. Features of clearly differentiating these two species are missing in the literature. Another important aspect quoted in the literature (Truc 1971; Schlickum & Strauch 1971) is the possible relationship between *Palaeotachea* and the Pliocene genus *Frechenia* Schlickum & Strauch, 1971 as well as the Recent *Eobania vermiculata*. The assumption of a relationship between the three taxa is based on the similar morphology of the aperture region (see Höltke & Rasser 2016).

6.5.2 *Granaria*

In the *sylvestrina*-beds of the Steinheim Basin, chondrinid snails of the genus *Granaria* are one of the most abundant landsnails, especially the species *Granaria schuebleri* (Klein, 1846). In the literature this species is often named as *Granaria antiqua* (Zieten, 1832), and was also placed in different genera. The extant representatives of *Granaria* are all inhabitants of a more dry, calcareous and open landscape. Due to this fact, the fossil species of *Granaria* are important facies fossils and according to that a precious tool for reconstructing the palaeo-microhabitats. Therefore it is necessary to study the different *Granaria* species in the NAFB and solve the according taxonomic problems.

6.5.3. *Pseudochloritis*

The Steinheim Basin is the type locality of the largest landsnail from the Miocene in SW-Germany, *Pseudochloritis insignis* (Zieten, 1832). Despite of its remarkable size, only little is known about this species according to its systematic position, origin and stratigraphic as well as geographic distribution. Greater knowledge of this unusual large snail (in comparison to other contemporaneous snails) will give valuable tool in reconstructing palaeoenvironment and snail evolution during the period of the *silvana*- and *sylvestrina*-beds. Originally the species was named as *Helix insignis* by Zieten in 1832. Kurr (1856) was the first who discussed the phylogenetic relationships of this species. He related *P. insignis* to the South African genus *Trigonephrus* (Dorcasidae). Sandberger (1872) placed it near the species *Liburnica hoffmanni* (Rossmässler, 1836) (Helicidae: Ariantinae). In contrast to that, O. Boettger saw *P. insignis* as an ancestor of *Monacha homalospira* (Reuss, 1860) and the Madagascan genus *Ampelita* (Acavidae) (see O. Boettger 1909). Gottschick

(1920a) as well as C.R. Boettger & Wenz (1921) compared *P. insignis* with the extant *Dinarica stenomphala* (Menke, 1830) (Helicidae, Ariantinae). Also Schileyko (2006) placed it in *Dinarica*, which he treated as subgenus of *Campylaea*. Already in 1909, C.R. Boettger mentioned that some authors placed *P. insignis* into the relationship of *Chloritis* (Camaenidae). In 1929, Pfeffer erected the new monospecific genus *Joossia* for the species *insignis* within the family Eulotidae (see Pfeffer 1929). Later, Nordsieck (1986) placed it in the family Xanthonychidae. The authors Miller (1900), C.R. Boettger (1909; 1911), Nordsieck (1986) and Binder (2008) saw a strong relationship with the Badenian species *Pseudochloritis incrassata* (Klein, 1853), which is the type species of *Pseudochloritis* (see C.R. Boettger 1911; Binder 2008). According to the different opinions named above, an examination of the species is necessary. Also the remarkable variations in shell morphology and shape make a detailed examination of this species absolutely necessary. Another unsolved question is the stratigraphic and geographic distribution of this species as well as its palaeoecology.

6.5.4. Type catalogue

For the detailed examination and determination of the different fossil landsnails, a comparison with the according type material is often essential. According to this, a catalogue was made containing all the type material as well as biographies of the different collectors and authors (see Salvador et al. 2016).

6.6. Palaeobiogeography

With the taxonomic results of the themes named above as well as with literature data, it is possible to compare the different Middle Miocene landsnail localities in Central Europe with statistical methods. Through the analyses of the different deposits, it is possible to get a more comprehensive picture of the ecologically relationships between the single localities.

Another part is a fossil catalogue with illustrations of the Miocene continental molluscs and their deposits occurring at the southern margin of the Swabian Alb. From this region, much well preserved material came out in the past and is stored in different museums collections. Unfortunately, permanent outcrops are very rare in this region today. The information about that are scattered in the literature as well as in the collections.

6.7. Material and Methods

6.7.1. Localities

For studying the continental mollusks of the localities named above, the collections of the BSPG, GPIT and SMNS were searched for material from these deposits. Also the collection of The Hauff museum in Holzmaden, Baden-Württemberg were searched after snails from the Randeck Maar. All the different mollusk taxa were taken out and then examined under a microscope (Wild Heerburg) as well as under an Automontage-microscope (Leica), which were also used for the illustrations. In addition to that, some photos were made using a SEM-microscope.

6.7.2. Taxonomy and Morphometrics

6.7.2.1. *Palaeotachea*

To solve this problem, the following paramerters were measured on their shells (see fig. 1): Shell height (sh), shell width (sw), height of the aperture (mh), height of the last whorl (lwh), angle of spire (as), distance of insertions (di). The following ratios were calculated from the above parameters: sh/sw; lwh/mh; sh/mh; sh/di; as/mh; as/lwh; as/sh; as/sw; as/di; mh/di; sw/di; lwh/di; sw/mh; as/mh to as/lwh ratio; sh/sw to as/di ratio; as/sh to as/sw ratio; sh/mh to sw/mh ratio; lwh/mh to sh/di ratio; as/mh to as/sh ratio; as/mh to as/sw ratio; as/di to as/mh ratio. The values from all specimens were used to calculate a cluster analysis (euclidean, Ward`s method) using the software “PAST” (Hammer et al. 2001). In a next step, the arithmetic means of each given ratio were calculated and then used for another cluster analysis. In order to test for different growth rates, the size of the first three whorls was measured and compared with the total shell width. These measurements were made using the image analysis software of a Keyence microscope. The studied material comes from the following localities. (1.) Gastropods labelled as *Cepaea silvana* (Klein, 1853): Zwiefalten, Baden-Württemberg, South Germany (type locality of *P. silvana*), MN5: 15 specimens (n=15), Mörsingen, MN 5 (Esu 1999): 138 specimens (n=138). (2.) Gastropods labelled as *Cepaea sylvestrina* (Schlotheim, 1820): Steinheim am Albuch, Baden-Württemberg, South Germany, MN 7 (Höltke & Rasser 2017): 114 specimens (n=114). Reimlingen, at the Sportplatz, Nördlinger Ries, Bavaria, South Germany, according to Bolten (1977) from Post-Ries sediments: 44 specimens (n=44). Apart from the *silvana/sylvestrina* problem named

above, different other species of *Palaeotachea* were described for the SW German Miocene which could possibly also be used as index fossils.

For the examination of a possible relationship of *Palaeotachea turonensis*, *Frechenia* and *Eobania vermiculata,* the following taxa were examined: *Frechenia reichenbachi* (type species) (n=14) from the Plicoene of Frechen near Cologne; *Palaeotachea turonensis* (n=24) from the Miocene of Grund near Vienna; *Eobania vermiculata* (type species) (n=24) from Italy; *Cepaea nemoralis* (type species) (n=24) from France; *Caucasotachea vindobonensis* (n=24) from Austria. The last two species were taken for two reasons: 1. Apart from the distinct palatal margin, *Frechenia* has a "*Cepaea*"-like outer morphology and *C. nemoralis* is the type species of the genus. 2. *Caucasotachea vindobonensis* was included, because like *C. nemoralis*, it bears an outer morphology similar to *Frechenia*. The same measurement as named above for the *silvana/sylvestrina* problem were also used for the shells from the forenamed taxa. With this data, two cluster analyses and two PCA were constructed using the statistic software "PAST" (Hammer et al. 2001).

6.7.2.2. *Granaria*

For the examination of the different *Granaria* species*,* collection material and the according literature were studied. Whenever it was possible, also original material was examined. Especially the teeth and folds within the aperture were studied in detail. The available specimens were examined under a microscope (Wild Heerburg) as well as under an Automontage-microscope (Leica), which were also used for the photos. In addition to that, some photos were made using a SEM-microscope.

6.7.2.3 *Pseudochloritis*

In order to solve the taxonomic problems, the following standard parameters were measured on the shells of the species *insignis* (see fig. 1): shell height (sh), shell width (sw), height of the aperture (mh), height of the last whorl (lwh) as well as the angle of spire (as) and the distance between the insertions (di). This measurements were made with a digital slide gauge and a goniometer. Next to the shells of *P. insignis*, also measurements were done for the species *Pseudochloritis incrassata* as well as *Dinarica pouzolzi*. The last two named species are the type species of their genus. They were chosen, because they represent the morphologically and

palaeogeographically closest forms to *P. insignis.* For further statistic calculations the following ratios were calculated: sh/sw, sh/mh, sh/lwh, sh/di, sh/as, sw/mh, sw/lwh, sw/di, sw/as, lwh/mh, mh/di, mh/as, lwh/di, lwh/as. In addition to that, the arithmetic mean (A) and the standard deviation (SD) were calculated for each ratio. A cluster analyses (Ward`s method, euclidean) was made using the ratios named above as well as one with the arithmetic mean values only. Also a PCA was calculated using the single parameters (sh, sw, etc.). The statistics were done using the statistic software "PAST" (Hammer et al. 2001). After this "modern" statistic methods, a "classic" height/width-diagram was constructed for the three forenamed species. Furthermore, the relationships proposed by the different authors in the introduction were discussed in detail as well as the stratigraphic and geographic distribution of *P. insignis* and its palaeoecology.

6.7.2.3 Type catalogue

For this purpose, the collection of fossil land- and freshwater gastropods in the SMNS were searched for type material.

6.7.3. Palaeobiogeography

For the analysis of the Early/Middle Miocene continental deposits, all localities with at least eight different species were listed in a table. The only exceptions are Amstetten-Stubersheim and Harthausen auf der Scheer, both in SW Germany which bears only five specimens but they are the best representatives of the Helicidenmergel according to the number of species. The data is based on collection material of the SMNS as well as on the according literature (see Höltke et al. 2016). This data was used for three NMDS analysis and three cluster analysis to see the differences or similarities between the different deposits. This statistical analyses were done with the software "PAST" (Hammer et al. 2001).

For the fossil catalogue the collection of the SMNS was searched for according material, supplemented by literature data (see Höltke et al. 2018). Visits in the BSPG as well as in the GPIT, NHMUK and PIMUZ and SMF added some new material to the according data.

7. Objectives and expected output of the doctoral research

Although landsnails are a very common faunal element during the Miocene, only little is known about their biodiversity, palaeobiogeography, and palaeoenvironmental distribution. The rich faunas from fossillagerstätten in SW Germany provide the unique opportunity to learn more about this time of geological (Alpine orogeny) and climate (Mid-Miocene Climate Optimum) changes.

In order to search for differences in biological diversity during the Middle Miocene *silvana-* and *sylvestrina*-beds, it was necessary to solve some crucial taxonomic problems. For this, detailed studies were conducted on *Palaeotachaea*, *Pseudochloritis* and *Granaria*. The examination of the different *Palaeotachea* species, especially *P. silvana* and *P. sylvestrina* will solve the problem of how to differentiate them. With the according data, there are greater possibilities for classifying unknown sediments in the Miocene of SW Germany. The analyses of a possible relationship between *Frechenia* and *Palaeotachea* as well as detailed study of *Pseudochloritis insignis* will give insights into landsnail evolution. In the same way an examination of the different *Granaria* species will not only solve the genus problem but will also be a valuable tool in reconstruction of the palaeoenvironment.

In a next step, the faunas of fossillagerstätten from “hot spot” localities of the *silvana-* and *sylvestrina*-beds will be examined. These are Mörsingen, Hohenmemmingen and Dischingen for the *silvana*-beds and the Steinheim Basin for the *sylvestrina*-beds. The mollusk fauna of the Randeck Maar will give additional information of the mollusk diversity during the time of the *silvana*-beds. The type catalogue will be a valuable tool for the determination of the single species. In order to test for the palaeoecological lessons that can be learned from Miocene terrestrial snails, their different ecological niches were reconstructed. Based on actualistic comparisons, the palaeoenvironments as a whole, and the micro-habitats in particular were analyzed. That gives also the opportunity to get an impression of the ecological changes or similarities between pre-Ries deposited *silvana*-beds and the younger *sylvestrina*-beds. Finally, this thesis aimed to test, whether or not there is palaeobiogeographic signal among the landsnails. With the help of statistical methods the similarities and differences between the Middle Miocene continental deposits will become visible. In the same way the research of the biodiversity from the *silvana*-beds deposits at the

southern margin of the Swabian Alb will reveal important details of the ecology during the time of the *silvana*-beds. All the studies named above have enhanced the knowledge of landsnail evolution and the palaeoenvironment during this time of earth history.

8. Results and discussion

8.1. Localities

8.1.1. Mörsingen

With the help of local people, the exact localities could be found where the fossil material came out from the end of the 19th to the middle of the 20th century. One is an ancient clay pit which is already visible today as a topographic feature. The other place were also a clay pit which is today used as farmland. The latter named place has been also named as “Schneckenacker” or “Schneckengarten” by the local people. A total of 35 different landsnail taxa could be identified and 9 different freshwater ones. Additionally, 10 landsnail and 2 freshwater taxa came from literature data. A new species (*Aegopinella moersingensis* n. sp.) could also been described. From the different taxa verified from Mörsingen, 11 genera are completely extinct (*Apula, Archaeozonites, Klikia, Leucochroopsis, Miodiscula, Palaeotachea, Protodrepanostoma, Pseudidyla, Pseudochloritis, Pseudoleacina, Triptychia)*. The species *Miodiscula disciformis* (Wenz, 1923) was placed in the extant genus *Canariella* Hesse, 1918 by Wenz in 1924 (see Wenz 1924). Nordsieck (2014c), however, put the species in his new erected genus *Miodiscula*. Hesse (1918) has named the genus *Canariella* only upon anatomical features of the soft body. So the decision if a fossil snail belongs to this taxon is not unproblematic (or probably impossible). Five genera (*Janulus, Gastrocopta, Poiretia, Opeas, Hypnophila*) are only extinct in Middle Europe. All the other taxa have Recent relatives in the landsnail fauna of Middle Europe. The ecological preferences range from xerophilc species (*Granaria*) to hygrophilic ones like *Oxyloma* with all intermediary stages. However, there are only few specimens of this xerophilic taxa. Probably, the ancient environment consisted of more shaded and moist habitats like forests. Two taxa (*Discus* and *Protodrepanostoma*) were also mainly forest inhabitants. The freshwater snail fauna contains one taxa (*Tinnyea*) which is extinct. The freshwater genus *Esperiana* is absent from Middle Europe today and lives in the Pontian region. It is

represented in Mörsingen by one species, *Esperiana kleinii* (Kurr, 1856). Originally, this species was placed in the genus *Melanopsis*. Considering the flat whorls and very low sutures, the species *kleinii* fits more to the genus *Esperiana*. The others have Recent relatives in our latitudes. Most of the freshwater species prefer stagnant or only slowly flowing water apart from *Esperiana* which lives in rivers and streams. Other fossils than snails are rare from Mörsingen. There are some *Celtis* (Plantae) and remains of freshwater bivalves as well as some undetermined ostracods. This ostracods were found in a sediment sample taken in 2013.

8.1.2. Hohenmemmingen and Dischingen

In total, 23 gastropod species, all pulmonates, could be documented in the material from Hohenmemmingen (whereas 33 species had been previously reported in the literature). The material includes five freshwater species and 18 terrestrial ones (see Salvador et al. 2017). From an actualistic palaeoecological approach, this palaeoevironment featured a humid and warm forest cover, with a well-vegetated and likely shallow water body.

In the freshwater limestones from Dischingen, 35 gastropod species were found (7 freshwater and 28 terrestrial), mainly belonging to Pulmonata, but also with representatives of Neritimorpha and Caenogastropoda. Seven species are reported here for the first time from Dischingen: *Palaina diezi, Radix socialis, Granaria sp., Serrulina? sp., Discus pleuradrus, Punctum pumilio, and Oxyloma minima* (see Salvador et al. 2018).The palaeoenvironment would be a humid and warm forest, as indicated by the vast majority of terrestrial gastropod genera present, while the freshwater environment would be well-vegetated and slow-moving or stagnant waters.

8.1.3. Randeck Maar

The snail fauna of the Randeck Maar now comprises a total of 32 continental gastropod species, among which only four are freshwater ones: *Lymnaea* cf*. dilatata, Ferrissia deperdita, Gyraulus kleini* and *Planorbarius cornu*. Most of the *Gyraulus* snails are flattened due to sediment compaction and are poorly preserved. Only one specimen with a sufficiently preserved protoconch could be found and identified as *G. kleini*. The terrestrial snail fauna consists 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*. The species *Triptychia randeckiana* described by Kranz (1908) is endemic to this locality. The gastropod *Palaeomastus filocinctus* (Reuss, 1860) was original named by Seemann (1926) as *Ena (Napaeus) schützei* Jooss & Seemann in a footnote without a description or illustration. The footnote simply stated that a more detailed treatment of the species would soon follow in the journal what was not happened. So Ena (*Napaeus) schützei* is a nomen nudum. Nordsieck (2014c) included all Oligocene to Miocene species of the genus *Napaeus* Albers, 1850 in his new erected genus *Palaeomastus* Nordsieck, 2014c. The specimen from the Randeck Maar fits to *Palaeomastus filocinctus* (Reuss, 1860) only known from Tuchořice (Early Miocene, MN 3, Czech Republic; Harzhauser et al., 2014). Thus, the present record greatly expands the stratigraphical and geographical occurrence of this species. 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*. The remains of the Clausiliinae (Clausiliidae) are lacking the taxonomic important aperture region so a more exactly determination is not possible.

An examination of the ecologically preferences of the Recent relatives of the fossil landsnails of the Randeck Maar makes it possible to reconstruct the different ecological niches around the ancient Maar lake (see Rasser et al. 2019).

8.1.4. Steinheim Basin

The examination of the material from the Steinheim Basin (Miocene, MN7) resulted in the verification of 48 Miocene landsnail species belonging to the following genera (number of species in brackets): *Cochlostoma* (2); *Carychium* (1); *Oxyloma* (1); *Pseudoleacina* (1); *Palaeoglandina* (1); *Azeca* (1); *Cochlicopa* (1); *Strobilops* (1); *Truncatellina* (1); *Vertigo* (4); *Gastrocopta* (3); *Negulopsis* (1); *Granaria* (3); *Vallonia* (3); *Gibbulinopsis* (1), *Pupilla* (2); *Triptychia* (1); *Pseudidylla* (1); *Opeas* (1); *Ceciloides* (1); *Punctum* (1); *Discus* (1); *Janulus* (1); *Aegopinella* (2); *Oxychilus* (1); *Vitrea* (1); *Archaeozonites* (2); *Vitrina* (1); *Helicodonta* (1); *Leucochroopsis* (1); *Apula* (1); *Pseudochloritis* (1); *Palaeotachea* (1); *Arion* (1); *Milax* (1) (see Höltke & Rasser 2017). The fauna covers a whole range of different ecological niches from very moist

habitats (*Oxyloma*) to very dry ones (*Granaria*). The last named genus is also the most abundant landsnail taxa in the Steinheim deposits. This implies the presence of open and dry habitats around the ancient Steinheim lake. Three different *Granaria* species could be verified in the Steinheim deposits. The following fifteen species are only known from the Steinheim Basin: *Cochlostoma ebfraasi* (Jooss, 1902); *Cochlostoma excellens* (Jooss, 1912b); *Azeca tridentiformis* Gottschick, 1911; *Cochlicopa procera* Gottschick, 1920b; *Granaria crassiventer* Salvador, Höltke, Rasser & Kadolsky, 2016; *G. grossecostata* (Gottschick & Wenz, 1919) *Strobilops joossi* Gottschick, 1911; *Truncatellina lentilli* (Miller, 1900); *Vertigo milleri* Gottschick & Wenz, 1919; *Pupilla iratiana suevica* Gottschick & Wenz, 1919; *Pupilla steinheimensis* (Miller, 1900); *Gibbulinopsis submuscorum* (Gottschick & Wenz, 1919); *Janulus gottschicki* (Jooss, 1912); *Aegopinella erecta* (Gottschick, 1920a); *Helicodonta involuta angitorta* Jooss, 1912b. If the reason for this restricted distribution is due to the scarcity of MN7- aged outcrops in SW Germany or due to ecological reasons can not be answered at the moment. The Steinheim Basin is also the type locality of *Pseudochloritis insignis* (Zieten, 1832) which is the largest landsnail in the South German Miocene (up to 40 mm in diameter) as well as *Granaria schuebleri* (Klein, 1846).

The genus *Klikia*, which is common in the *silvana*-beds, is absent. Only the morphologically very similar genus *Apula* could be identified with *Apula steinheimensis* (Jooss, 1918). Gottschick & Wenz (1919) erected the species *Pupilla submuscorum* from Steinheim Basin. The species shows a net-like sculpture on the protoconch which is characteristic for *Gibbulinopsis* Germain, 1919 (Zilch & Wenz 1959-1960). According to that the name for the species is *Gibbulinopsis submuscorum* (Höltke & Rasser 2017). The taxon *Aegopinella erecta* (Gottschick 1920a), original named as subspecies of *A. subnitens*, was taken in species rank. Among the 34 genera, 24 are extant. Most of the extant ones (21) are also part of the Recent landsnail fauna in Europe. The remaining three genera occur today in North, South and Middle America (*Strobilops*); USA, Sibiria, Central and East Asia (*Gastrocopta*); Canary Islands and Madeira (*Janulus*). The slugs could only be roughly determined by their vestigial shells. The two genera *Milax* and *Arion* could be identified according to the shape of their rudimentary shells. Unfortunately not all

species described by Gottschick & Wenz (1919); as well as Gottschick (1919, 1920a, b, c) could be find in the collection of the SMNS. The most common landsnails in the Miocene sediments of Steinheim am Albuch are the xerophilic chondronoid snails (Chondrinidae). According to Schweigert (1993) the ancient climate can be interpreted as warm-temperate with marked dry periods. The author also supposed for the surrounding of the crater lake a deciduous dry forest. This environment is consistent with the ecological preferences of the Recent Chondrinidae. For detailed climatic features in the SW German Miocene see Tütken et al. (2006) as well as Böhme et al. (2007).

8.2. Taxonomy and Morphometrics

8.2.1. *Palaeotachea*

All in all 6 different *Palaeotachea* species could be identified in the Miocene of SW Germany (see Höltke & Rasser 2016). These are *Palaeotachea silvana* (Klein, 1853), *P. sylvestrina* (Schlotheim, 1820), *P. dentula* (Quenstedt, 1867), *P. renevieri* (Maillard, 1891), *P. elevata* (Berz & Jooss, 1927), *P. turonensis* (Deshayes, 1831).

The statistics clearly revealed a separation of the two species *Palaeotachea silvana* and *P. sylvestrina*. The two species differ in the following points:

1. *P. sylvestrina* is usually more spherical and higher.

2. P. sylvestrina is usually larger.

3. The protoconch of *P. sylvestrina* is a bit flatter than that of *P. silvana*.

4. *P. silvana* has a flatter spire and is more stretched in width.

5. The outline of the last whorl of *P. silvana* is stronger curved and can be indistinctly subangulate. Also some specimens of *P. sylvestrina* can have a very slight angulation on the last whorl, but it is usually less distinct than in *P. silvana*.

6. *P. sylvestrina* has a deeper suture.

7. The peristome of *P. silvana* is more expanded.

8. In *P. silvana*, the periostome region is generally more thickened.

9. The angle of spire around 117° in *P. silvana* and around 100° in *P. sylvestrina*.

Wenz (1920a & b) named three subspecies of *Palaeotachea sylvestrina: P. sylvestrina sylvestrina (Schlotheim), P. sylvestrina gottschicki* (Wenz) and *P. sylvestrina geniculata* (Sandberger). This subspecies were emended because there are no clear dividing lines, also in the statistical charts, which would justify a division into subspecies. Already Wenz (1920a & b) wrote that they are not clearly distinguishable. Contemporaneous with *P. sylvestrina* lived the smaller sized *Palaeotachea* species *P. elevata* (Berz & Jooss, 1927). Other *Palaeotachea* species occuring in the *silvana*-beds are *Palaeotachea dentula* (Quenstedt, 1867); *P. renevieri* (Maillard, 1891) and *P. turonensis* (Deshayes, 1831) which could be differentiated of *P. silvana* by size and shell morphology.

The *silvana*-beds:
Our taxonomic results in fact confirm the differentiation between *Palaeotachea silvana* and *P. sylvestrina* and accordingly the presence of two different lithostratigraphic units (*silvana*-beds and *sylvestrina*-beds). The *silvana*-beds seem to be deposited before the Ries event whereas the *sylvestrina*-beds represent Post-Ries sediments. According to the missing of permanent outcrops, one has to rely to a large extent on the stratigraphic information of Wenz (1919; 1920a & b; 1921) and Jooss (1923). This authors divided the *silvana*-beds in three parts (Lower, Middle and Upper *silvana*-beds) according to the occurrence of the different *Palaeotachea* species.
Genus *Frechenia:*
The morphometric analysis yielded no results. So the potential relationship between *Palaeotachea turonensis* and the Pliocene genus *Frechenia* as well as the Recent *Eobania vermiculata* mentioned in literature, cannot be solved with morphometric features.
An identification key for the six different *Palaeotachea* species are given by Höltke & Rasser (2016).

8.2.2. *Granaria*

All in all 12 different *Granaria* species were discussed for the NAFB, five are known for the Miocene of SW-Germany (see Höltke & Rasser 2013). Taphonomic features are often a problem in the identification of the different *Granaria* species. Especially, the important aperture teeth/folds of the *Granaria* species were often not preserved.

The most common species in the Miocene of SW Germany is *Granaria schuebleri* (Klein, 1846) which has a shell height of c. 5 mm. All of the fossil Chondrinidae show the typical aperture and size of *Granaria.* Following Zilch & Wenz (1959-1960), the genera names *Pupa* Drapanaud, 1801 and *Torquilla* Studer, 1820 used in older literature, are synonyms. Originally, *Granaria schuebleri* was named as *Pupa antiqua* by Zieten in 1832. Following Klein (1846), this is a junior synonym because the French malacologist Matheron had also named a species as *Pupa antiqua* earlier in 1832 (see Matheron 1832; Höltke & Rasser 2013). According to that Klein (1846) changed the name of *Pupa antiqua* in *Pupa schuebleri*. The original material of Klein (1846) was designated as neotype because the original material of Zieten (1832) is lost. Other occurrences of *G. schuebleri* apart from the Steinheim Basin are near Geisingen/Donau and in the Hegau region. Other verified *Granaria* species which are only known from the Steinheim Basin are *Granaria grossecostata* (Gottschick & Wenz, 1919) and *Granaria crassiventer* Salvador, Höltke, Rasser & Kadolsky, 2016. The latter was formerly named as *Granaria pachygastra* (Fraas in Miller, 1900) by Höltke & Rasser (2013) but this name is preoccupied (see Salvador et al. 2016).

Another taxon often named for the Miocene of SW-Germany is *Pupa noerdlingensis* Klein, 1846 (=*Granaria noerdlingensis* (Klein, 1846). The author erected this species only on the basis of casts (see Klein 1846, pl. 1, fig. 20) which originated from Goldberg near the Nördlinger Ries. The original material of Klein (1846) is lost. According to the lack of information and the incomplete preservation of the figured and lost original specimen of Klein (1846), the status of this species is completely unclear and therefore *Pupa noerdlingens* Klein, 1846 is a nomen nudum. An additional *Granaria* species, *Granaria subfusiformes* (Sandberger, 1872) named in the literature for the *silvana*-beds, could only be verified from Mörsingen in 2016 (see Höltke et al. submitted). According to that, the taxa was already termed as nomen dubium by Höltke & Rasser (2013). From the Helicidenmergel, Jooss (1923) described the species *Granaria helicidarum* (Jooss, 1923). The original material is stored in the SMNS but consists only of three steinkern fragments. Due to the size and morphology of the shell fragments, they are different from the *Granaria* species named before. As type locality Jooss (1923) named Zollhaus-Blumberg, Baden-Württemberg.

An older *Granaria* species is *G. subvariabilis* (Sandberger, 1863), which occurred during the late Oligocene and early Miocene. The author gave an illustration of this species and according to that it is very similar to the neotype designated for *G. schuebleri*. However, the description given by Sandberger (1872) shows morphological differences to *G. schuebleri.* The taxa *G. subavariabilis* is known from Hochheim/Hessen, Tuchořice, Bohemia as well as from the Untere Süßwassermolasse from Thalfingen near Ulm, Baden-Württemberg.

For the Miocene of Austria, three *Granaria* species could be verified according to the recent literature (Lueger 1981; Harzhauser & Binder 2004): *Granaria costata* (LUEGER**,** 1981); *Granaria schlosseri* (Cossmann**,** 1908); *Granaria moedlingensis* Harzhauser & Binder**,** 2004.

From the older literature (Slavik 1869; Gutzwiller 1905; Wenz 1923) two other Tertiary species are known: *Granaria intrusa* (Slavik, 1869) from the Early Miocene of Tuchořice and Lipno/Czech Republik and G. *multicostulata* (Gutzwiller, 1905) from the Eocene of Lausen/Baselland, Switzerland.

Höltke & Rasser (2013) also gave an identification key for the verified species from the Miocene of SW-Germany.

8.2.3. *Pseudochloritis*

The statistics as well as the sh/sw diagram show no signs of the existence of more than one species (see Höltke & Rasser 2015). The species shows a high degree of variability according to the height of the spire. The range is from flat forms to higher, helicoid-shaped ones. The remarkable bulbuos protoconch of *P. insignis* shows a distinct microsculpture. It consits of little pustulae and pits. Also fold-like ribs can be seen. On the teleoconch, little pits, probably hair-pits, can be seen on the first whorls which disappear on the later ones. The original material of Zieten (1832) is lost so a specimen from the Klein collection was designated as neotype. The largest specimen stored in the SMNS has a diamter of 40 mm, the avarage diameter is between 24 and 36 mm. In the sh/sw diagram, the values of *Pseudochloritis insignis* and *P. Incrassata* form a linear function. The values of *Dinarica pouzolzi* form a separate linear function. According to the measured A and SD values of the different ratios named in the introduction, *Pseudochloritis insignis* and *P. incrassata* show the

highest SD in the sw/di division. So this ratio seems to be the most variable one among the shells of this species. The forenamed species has the lowest SD in the sh/lwh ratio. So the relationship of the shell height and the height of the last whorl seems to be relative constant. *Dinarica pouzolzi* hast the highest SD in the lwh/di ratio. The cluster analysis of the A values shows a more distinct affinity between *Pseudochloritis insignis* and *P. incrassata* than between the forenamed one and *Dinarica pouzolzi*. The PCA scatter plots reveal a clear separation of the three species. Most overlaps occur between *Pseudochloritis insignis* and *P. incrassata.*

Palaeogeographic and stratigraphy:
It seems that *P. insignis* had a limited geographical distribution. Most of the specimen stored in the collections are from the Steinheim Basin. The second locality with a higher number of shells is Höwenegg near Engen, Baden-Württemberg (Upper Miocene, MN9, see Munk et al. 2007). However, the specimens from the last named deposit are mostly deformed. Another verified occurrence is Münsingen-Böttingen on the Swabian Alb, Baden-Württemberg (probably Middle Miocene according to Rosendahl et al. 2003).

Palaeoecology:
The size and the presence of hair indicate more moist and humid micro-habitats (see Goodfriend 1986; Pfenninger et al. 2005).

Discussion of the systematic position:
All the proposed genera (*Helix, Trigonephrus, Ampelita, Liburnica*) from the authors named before could be ruled out according to palaeogeographic aspects and/or morphological features, especially the sculpture of the protoconch. The species *Monacha homalospira* (Reuss, 1860), also proposed by O. Boettger (1909) as descendant of *P. insignis*, only occurs in the Early Miocene deposits of Lipno and Tuchořiche/Czech Republic (Sandberger 1872; Harzhauser et al. 2014). According to that fact, *P. insignis* cannot be its ancestor.

A snail-group with *P. insignis*-like species is the genus *Chloritis* Beck, 1837 (Camaenidae). The Camaenidae includes many shell forms and the family was defined only by anatomical features of the soft body. According to that, it is difficult to affiliate a fossil snail to this taxon. Only the fact that this group lives in tropical latitudes can be used as indication against a relationship with *P. insignis*. The most

similar forms concerning morphology and distribution are *Pseudochloritis incrassata* and *Dinarica stenomphala*. As named above, the statistics show a stronger relationship of the species *insignis* with *Pseudochloritis incrassata* as with the type species of *Dinarica*, *D. pouzolzi.* The taxon *insignis* shows also the same growth rate and sculpture on the protoconch like *P. incrassata.* Following this reasons, *insignis* are placed in the genus *Pseudochloritis (*see Höltke *&* Rasser 2015). The morphological features named by Pfeffer (1929) do not justify the establishing of a new genus (see Höltke & Rasser 2015).

Binder (2008) assumed a relationship of *Pseudochloritis* with the Ariantinae, whereas Nordsieck (1986) proposed a membership within the Eloninae (Elonidae sensu Gittenberger 1979). From the discussed geographic distribution, the general shell morphology and the microsculpture of the embryonic whorls, *Pseudochloritis* fits more to the Ariantinae (Helicidae) (see Höltke & Rasser 2015).

8.2.4. Type catalogue

The collection of the SMNS comprises circa 180 type specimens of fossil land and freshwater gastropod from Cenozoic and Pleistocene fossil sites, mainly in the Baden-Württemberg and Bavaria. For 20 taxa lectotypes were designated.

8.3. Palaeobiogeography

8.3.1. Statistical comparison of the Early/Middle Miocene landsnail deposits.

All in all 30 different Early/Middle Miocene deposits (fig.4) of Central Europe (European Mammal Neogene zones MN 4 to MN 8) was compared using statistical methods (cluster and NMDS analyses) (see Höltke et al. 2016). This includes 300 different species that have been identified so far. Most of the analyzed deposits were part of the Miocene Paratethys region and are today located in France, SW Germany (Baden-Württemberg state), SE Germany (Bavaria), Austria, Poland, and Hungary. The NMDS analyses brought no useful results. The Cluster analyses resulted in different clusters including 4 “main clusters”. These are: The Bavarian localities; the Baden-Württemberg localities (including the Austrian OSM localities); The Bakony Mountains and the Helicidenmergel localities. When plotted on a palaeogeographic 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". Perhaps this results from the presence of probably

endemic species and/or on the comparably low dataset. A distinct contrast is between Mörsingen as representative of the Pre-Ries event OSM deposits and the younger, post-Ries event deposit of the Steinheim Basin. They have only 13 species in common, which most of them had preferred more humid environments. In comparison to Mörsingen, there is a distinct increase in the number of xerophilic species in the younger Steinheim deposit. If the differences in the malacofaunal content between the two deposits are due to climatic change or due to the Ries /Steinheim meteorite event can not be said at the moment. Another remarkable point is the comparable high amount of endemic Clausiliidae in the Middle Miocene of Opole, Poland.

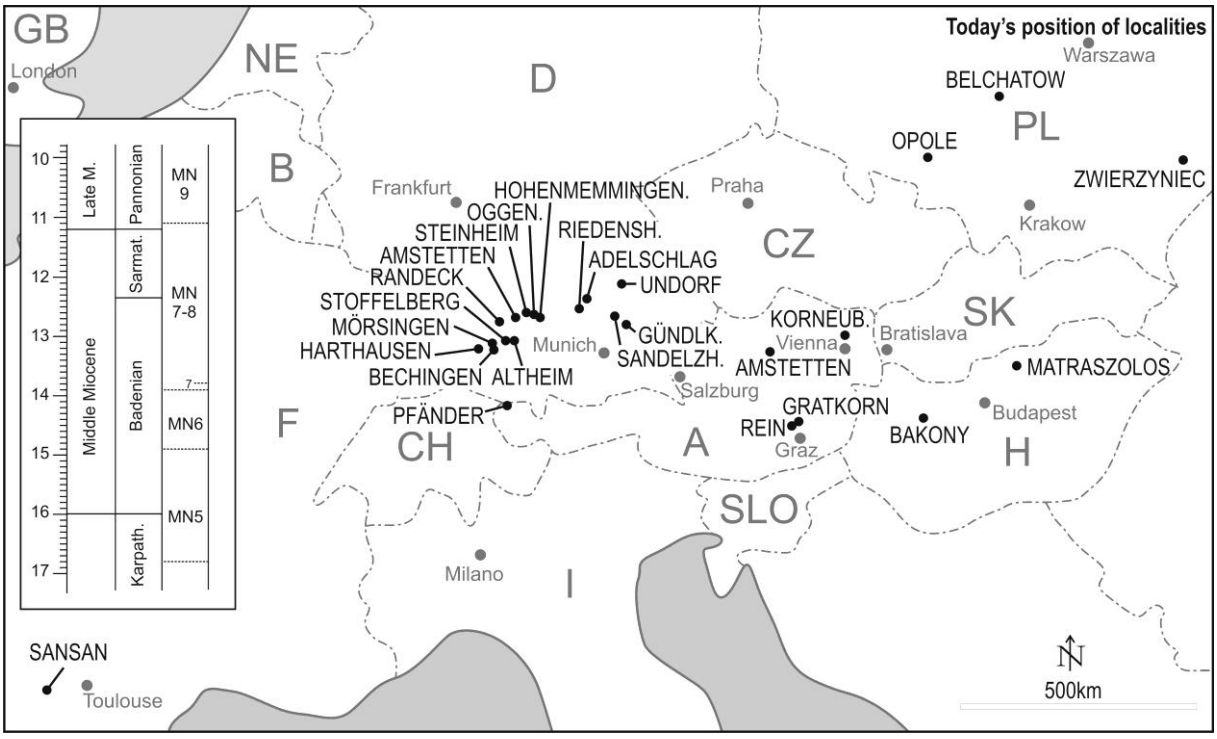

Fig. 4. Studied localities (modified after Höltke et al. 2016).

8.3.2. Miocene continental gastropods from the southern margin of the Swabian Alb, SW Germany.

All in all 14 freshwater and 50 landsnail species could be verified from this region but not all species reported in the literature could be confirmed (see Höltke et al. 2018). The different localities can be seen in fig. 5. A lot of the verified taxa have Recent

relatives. The freshwater snails were mostly inhabitants of stagnant waters. The reported landsnails covered all the different ecological niches from very moist to dry environments. However, only very few localities from this region have already been extensively explored and further collection efforts should take place in all the localities where excavation is still possible. Such efforts will no doubt be rewarded with an extensive amount of new occurrence data (including non-molluscan fossils) and help to get a better overall idea of the region's palaeoenvironment.

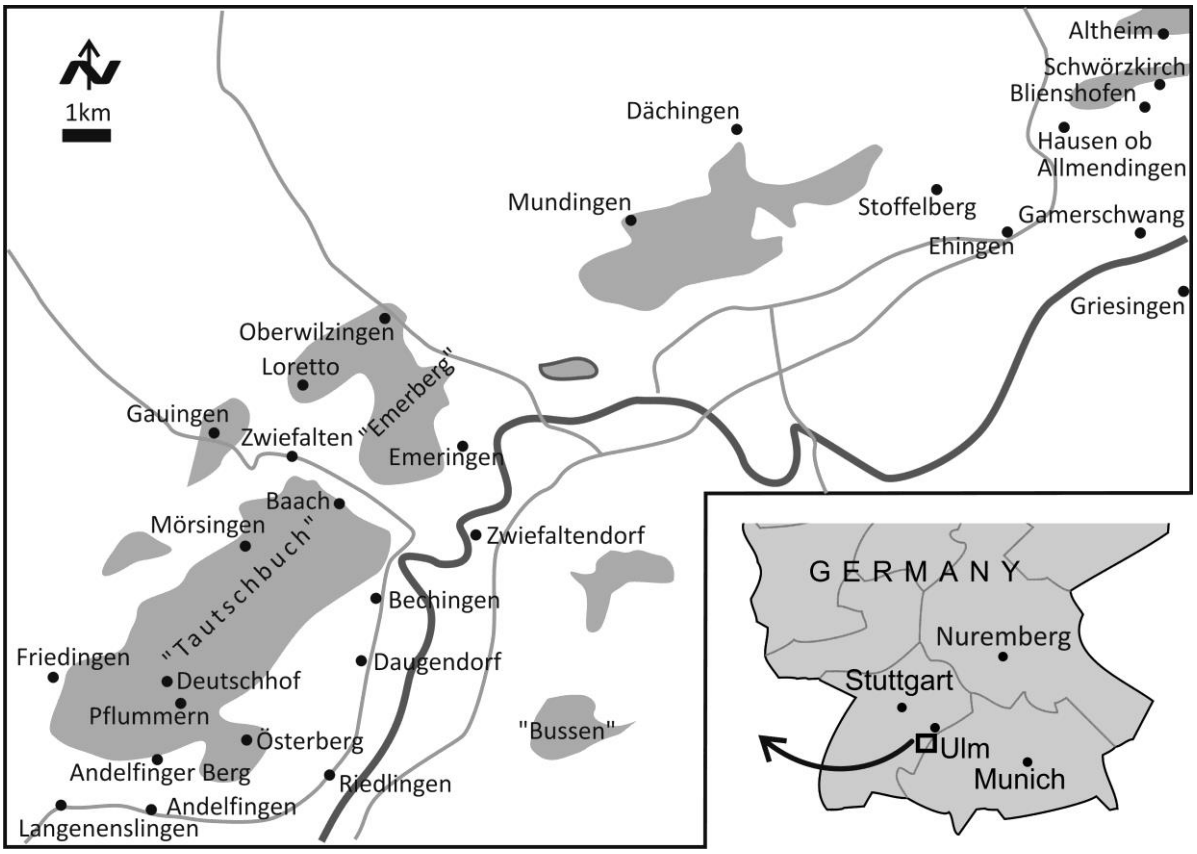

Fig. 5. Localities at the southern margin of the Swabian Alb (modified after Höltke et al. 2018).

9. Conclusion

The *silvana*-beds of Mörsingen contain at least 35 landsnail and 9 freshwater species. The *silvana*-beds of Dischingen bear 7 different freshwater and 35 landsnail species and from Hohenmemmingen 5 freshwater- and 18 landsnail species could be identified. Hygrophilic landsnail species are dominating and most of them have extant relatives. The contemporaneous sediments of the Randeck Maar contain 32 different land- and freshwater gastropod species. The landsnails cover the whole range of different micro-palaeohabiatats (moist to dry) which existed around the ancient maar lake. The two important index fossils, *Palaeotachea silvana* and *P. sylvestrina* could be clearly separated using statistic and morphometric methods. In addition to that four other *Palaeotachea* species could be identified in the Miocene of SW Germany. The *sylvestrina*-beds of the Steinheim Basin contain 48 different landsnail species. In contrast to the landsnail fauna of the *silvana*-beds, the proportion of xerophilic species in the *sylvestrina*-beds was increased. One of the most abundant species in the Steinheim Basin is the xerophilic landsnail *Granaria schuebleri*. Next to this one, four other *Granaria* species could be verified in the SW German Miocene, which can all be used as facies fossils. The largest landsnail in the Miocene of SW-Germany, *Pseudochloritis insignis*, could clearly be asigned to the genus *Pseudochloritis* according to morphometrics and microsculpture. A membership of *Pseudochloritis* within the Ariantinae (Helicidae) is the most likely but this can not finally clarified without knowledge of the soft body. The resulting cluster of the statistical comparison of the Middle Miocene continental deposits could mostly be explained by palaeobiogeographic and biostratigraphic features. The localities within the *silvana*-beds at the southern margin of the Swabian Alb contain landsnail species which cover the whole range of different micro-habitats (moist to dry). The according freshwater snails were mostly inhabitants of stagnant waters. Most of this localities, however, has never been the subject of a scientific excavations. So an intensive field work would certainly expanded the knowledge of the ancient terrestrial mollusk fauna.

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Article

Land snails from the Miocene Steinheim impact crater lake sediments (Baden-Württemberg, South Germany)

Olaf Höltke and Michael W. Rasser

With 5 figures and 2 tables

Abstract: Although the Middle Miocene (Mammal zone MN7) freshwater deposits of the impact crater of Steinheim am Albuch (Steinheim Basin, SW Germany) are famous for their fossil mammal and freshwater gastropod fauna, the rich land snail fauna has not been studied for almost 100 years. A re-study of the available material resulted in the identification of 48 species belonging to the following genera (number of species in brackets): *Cochlostoma* (2); *Carychium* (1); *Oxyloma* (1); *Pseudoleacina* (1); *Palaeoglandina* (1); *Azeca* (1); *Cochlicopa* (1); *Strobilops* (1); *Truncatellina* (1); *Vertigo* (4); *Gastrocopta* (3); *Negulopsis* (1); *Granaria* (3); *Vallonia* (3); *Gibbulinopsis* (1); *Pupilla* (2); *Triptychia* (1); *Pseudidyla* (1); *Opeas* (1); *Cecilioides* (1); *Punctum* (1); *Discus* (1); *Janulus* (1); *Aegopinella* (2); *Oxychilus* (1); *Vitrea* (1); *Archaeozonites* (2); *Vitrina* (1); *Helicodonta* (1); *Leucochroopsis* (1); *Apula* (1); *Pseudochloritis* (1); *Megalotachea* (1); *Arion* (1); *Milax* (1). Steinheim am Albuch is also the type locality of 26 Miocene land snail taxa. The fauna covers a whole range of different terrestrial ecological niches from very wet habitats (*Oxyloma*) to very dry ones (*Granaria*). In contrast to the older *silvana*-beds (MN5), the Steinheim deposits contain three clearly distinguishable species of *Granaria*. This genus is the most abundant land snail in the Steinheim deposits, implying a dryer and warmer climate than during the deposition of the *silvana*-beds. The genus *Klikia*, which is common in the *silvana*-beds, is absent. Among the 34 genera, 24 are extant and most of them (21) are also part of the Recent land snail fauna of Europe. The remaining three genera occur today in North, South and Central America (*Strobilops*); North and South America, Cap Verde Islands, North Africa, Siberia, Central and East Asia, Australia, Pacific Ocean islands (*Gastrocopta*); Canary Islands and Madeira (*Janulus*). The slugs could only be roughly determined by their vestigial shells.

Key words: Steinheim am Albuch, gastropods, Pulmonata, Prosobranchia, Miocene, impact crater.

1. Introduction

Apart from the Nördlinger Ries and Randecker Maar, the Miocene meteorite impact crater of Steinheim am Albuch is one of the best known Tertiary freshwater deposits in South Germany. It is especially famous for the diverse and well preserved mammal fauna (see Rössner & Heissig 1999 for information and literature). Among the invertebrates, the aquatic snails of the genus *Gyraulus* are even more famous, because they reveal a unique intralacustrine evolution that was discovered soon after the publication of Darwin's 'Origin of Species' (1859) (Hilgendorf 1867; for a review see Rasser 2013), and thus provided a tangible example for morphological evolution through time. Further papers on the freshwater snails where published by Gorthner (1992), Nützel & Bandel (1993) and Finger (1998). The fossil vegetation was examined by Schweigert (1993) and the

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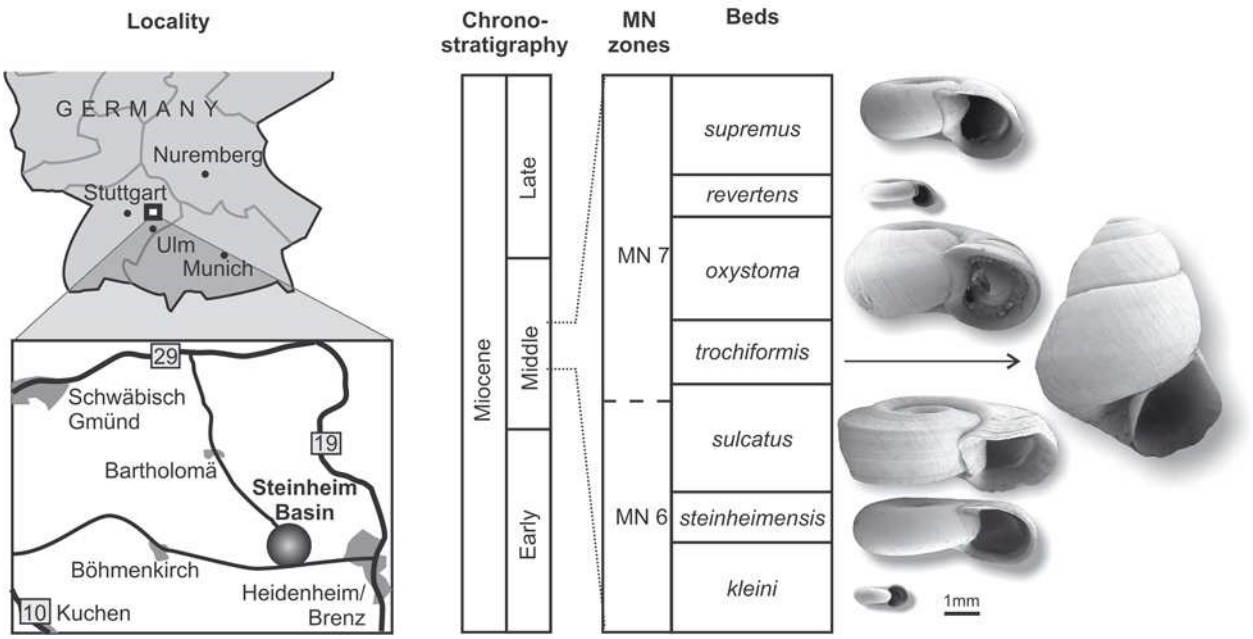

Fig. 1. Locality and stratigraphy of the lake sediments of the Steinheim Basin. The shells are representatives of the genus *Gyraulus* that were used to define the different beds (i.e., *Gyraulus kleini*, etc.). Modified from Rasser (2013).

ostracods by Janz (1992). In contrast to studies of their aquatic counterparts, studies of the land snails have been underrepresented. The first taxonomically important paper with the description of new species was published by Klein (1846), and the first monographic publication of both land and freshwater snails was by Miller (1900). Soon after this, Jooss (1902, 1912, 1918) and Gottschick (1911) described different freshwater and land gastropod taxa.

Later, Gottschick & Wenz (1919) and Gottschick (1919, 1920a-d, 1921) described 63 landsnail taxa, including four slugs. In more recent times, some of the land snails from the basal *kleini* beds were figured by Finger (1998), but a comprehensive modern study is still lacking.

This paper provides the first modern revision and description of the important Middle Miocene land snail fauna from the Steinheim Basin based on the collections of the Staatliches Museum für Naturkunde Stuttgart (SMNS). Altogether 48 land snail taxa, including two slugs, could be identified. The snails examined are from the collections of Franz Gottschick, Carlo Jooss, Adolf v. Klein, Imme Finger, Wilhelm Bechter and Konrad Miller which are all stored in the SMNS (Salvador et al. 2016). All available land snail taxa are described and illustrated. Not all of the taxa described by Gottschick & Wenz (1919) and Gottschick (1919, 1920a-d, 1921) could be found or identified in this study. The missing ones are listed in Table 2.

2. Geological setting

The Steinheim Basin in southwestern Germany (Fig. 1) is situated in the Swabian Alb. The basin has a diameter of c. 3.5 km and is characterised by a peculiar central elevation. After long discussions about the volcanic nature of this basin, comparisons with the nearby Nördlinger Ries revealed that the basin was formed by a meteorite impact c. 14.8 Ma ago (Reiff 1988; Buchner et al. 2003; Buchner & Schmider 2015), whereby the central elevation represents a rebound structure formed as a response to the impact. The basin was filled with lake sediments that can be correlated with the Mammal

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Neogene Zone MN 7, which is Late Badenian (Middle Miocene) in age (summaries in Gorthner 1992; Heizmann & Reiff 2002; Tütken et al. 2006). These lake sediments contain, besides other fossils like plants and vertebrates, the famous freshwater snail fauna (see Rasser 2013 for a review) as well as the landsnails described here. Today, 30-40 m of lake sediments are still preserved. The duration of the lake has long been debated and estimations range from some hundred thousand to more than one million years. This characterises Lake Steinheim as a palaeolake (Gorthner 1992). The endemic *Gyraulus* species flock (Hilgendorf 1867; for latest reviews see Rasser 2013 and Rasser & Covich 2014) allows a subdivision of the lake sediments into seven units based on their evolutionary stages; land snails can occur in all of these units. The units are (from the base to the top, see Fig. 1): *kleini* bed [with *Gyraulus kleini* (Gottschick & Wenz, 1916)], *steinheimensis* bed [with *G. steinheimensis* (Hilgendorf, 1867)], *sulcatus* bed [*G. sulcatus* (Hilgendorf, 1867)], *trochiformis* bed [*G. trochiformis* (Stahl, 1824)], *oxystoma* bed [*G. oxystoma* (Klein, 1846)], *revertens* bed [*G. revertens* (Hilgendorf, 1867)], *supremus* bed (*G. supremus* (Hilgendorf, 1867)]). The next older Miocene deposits in South Germany are the *silvana*-beds (MN5), which were deposited prior to the Ries/Steinheim impact ("pre-Ries"). These sediments occur south of the Steinheim Basin, along the margin of the Swabian Alb, and are characterized by the occurrence of the land snail *Palaeotachea silvana* (Klein, 1853), which is absent in sediments younger than the Ries/Steinheim impact (i.e., "post-Ries"), such as in Steinheim, Nördlinger Ries and Höwenegg. The characteristic "*Cepaea*"-like species of the younger deposits is *Palaeotachea sylvestrina* (Schlotheim, 1820). Wenz (1921) made the proposal to name these sediments *sylvestrina*-beds. This term, however, is no longer in use. During the 19th and the beginning of the 20th century, the Steinheim lake sediments, called the "Steinheimer Seeschichten", were commercially exploited in several sandpits.

3. Material and methods

For the documentation of the Steinheim land snails, we studied the collections of Klein, Gottschick, Jooss and Miller as well as the original material of Finger (1998). We only considered taxa that where available for examination. Franz Gottschick (1865-1927) was a forester in Steinheim am Albuch). The material dealt with in his 1919-1921 papers is, however, are not present. Maybe it was part of the Wenz collection that was destroyed during World War II in Frankfurt. Details about the different collections and collectors mentioned here can be found in Salvador et al. (2016). The shells were examined under a microscope (Wild Heerbrugg) with a magnification of up to ×50 and with an automontage microscope (Leica) with a magnification of up to ×300. Additionally, the protoconch was studied using a scanning electron microscope. The suprafamilial classification follows Bouchet & Rocroi (2005), and the arrangement of families follows Wiese (2014). Table 1 shows the stratigraphic distribution of some of the species described here according to Gottschick & Wenz (1919) and Gottschick (1919, 1920a-d).

4. Systematic palaeontology

Caenogastropoda Cox, 1960
Architaenioglossa Haller, 1892
Cochlostomatidae Kobelt, 1902

Cochlostoma ebfraasi (Jooss, 1902)
Fig. 2.1

1902 *Pomatias Eb.Fraasi* Jooss, p. 305, fig. 2.
1921 *Pomatias fraasi* Jooss. – Gottschick p. 166.
1967 *Cochlostoma fraasi* (Jooss). – Schütt, p. 201.
2016 *Cochlostoma ebfraasi* (Jooss 1902). – Salvador et al., p. 24, pl. 3, fig. 17.

Material: SMNS 106385 (1 specimen, Jooss collection, syntype); SMNS IMDAS If. 45192/2005 (1 specimen, Jooss collection, syntype).

Type locality: Steinheim am Albuch (Salvador et al. 2016).

Type horizon: Steinheimer Seeschichten (Salvador et al. 2016).

Description: Tower-shaped, dextral shell with c. seven whorls. The apex is not preserved. The whorls are rather flat and only slightly convex. The whorls grow slowly but regularly. The aperture has a round to oval shape. The aperture is circular, attaching to the previous whorl at almost a single point. The peristome is strongly reflected with a sharp margin. The teleoconch is covered by more or less regularly arranged prosocline ribs. The specimen is 8 mm high and 3 mm wide.

Discussion: The species name has usually been changed to "*fraasi*". The original spelling was reinstated by Salvador et al. (2016). The species differs from *C. excellens* by its flatter whorls.

Distribution: Wenz (1923) mentioned only Steinheim am Albuch.

Ecology: According to Fechter & Falkner (1989), the family is calciphilic and lives on rocks and boulders.

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Cochlostoma excellens (Jooss, 1912)
Fig. 2.2

1912 *Pomatias excellens* Jooss, pp. 43-44, pl. 2, fig. 9.
1921 *Pomatias excellens* Jooss. – Gottschick, p. 167.
1967 *Cochlostoma excellens* (Jooss). – Schütt, pp. 200-201.
2016 *Cochlostoma excellens* (Jooss 1912). – Salvador et al., p. 25, pl. 4, fig. 6.

Material: SMNS 106390 (1 specimen, Jooss collection, holotype).

Type locality: Steinheim am Albuch (Salvador et al. 2016).

Type horizon: Steinheimer Seeschichten (Salvador et al. 2016).

Description: Tower-shaped shell, of which only the last three whorls are present. The whorls are rounded with rather deep sutures. The aperture is obliquely egg shaped. The peristome is strongly reflected. The parietal callus is continuous with the columellar and palatal callus. Umbilicus narrow. The whorls are covered with prosocline ribs. Between these ribs, there is a variable number of small growth lines. The specimen is 6.5 mm high and 4 mm wide.

Discussion: The species differ from the *C. ebfraasi* by its more convex whorls.

Distribution: Wenz (1923) mentioned only Steinheim am Albuch.

Ecology: See *C. ebfraasi*.

Orthogastropoda Ponder & Lindberg, 1996
Eupulmonata Haszprunar & Huber, 1990
Carychiidae Jeffreys, 1830

Carychium suevicum O. Boettger, 1877
Fig. 2.3

1877 *Carychium suevicum* Boettger, p. 79.
1900 *Carychium suevicum* Böttg. – Miller, p. 401, fig. 24.
1920c *Carychium suevicum* Boettger. – Gottschick, pp. 108-110.
1923 *Carychium nouleti suevicum* Boettger. – Wenz, p. 1198.

Material: SMNS 36702/2005 (1 specimen, material original of Miller 1900); SMNS 63016 (1 specimen, original to Finger 1998, *kleini* bed); 63017 (1 specimen, original of Finger 1998, *kleini* bed); SMNS 12402/2008 (50 specimens).

Type locality: Steinheim am Albuch (O. Boettger 1877).

Type horizon: Steinheimer Seeschichten (O. Boettger 1877).

Description: Very small elongate-oval dextral shell, consisting of 4 moderately rounded whorls. The whorls grow relatively rapidly but regularly. The last whorl makes ups a bit more than half of the total shell height. The suture is deep. The last whorl does not change the direction before reaching the aperture, which has an oblique-oval shape. The peristome is reflected. Three teeth are present within the aperture. One is the end of the parietal fold and another at the end of the columellar fold. The third is a rounded palatal tooth. The palatal tooth and the parietal lamella reach the peristome. The columellar lamella ends a little bit further back in the aperture than the two others. The parietal callus is thick. Umbilicus slit-like. The teleoconch ornamentation consists of regularly arranged and closely spaced, thread-like ribs. The large protoconch consists of c. 1.5 whorls and has a bulbous shape, without visible sculpture (under 50x magnification). The maximum shell height is c. 2 mm.

Discussion: According to Gottschick (1920c), there are some morphological differences between specimens from the "Sandgrube" in Steinheim am Albuch and from the *kleini* bed. Also the extant representantives of *Carychium* show intraspecific variation (see Welter-Schultes 2012a; Wiese 2014). According to Miller (1900), *Carychium suevicum* is similar to *C. antiquum* A. Braun from Wiesbaden. According to him, *C. suevicum* is a bit larger, more barrel-shaped

Fig. 2. 1 – *Cochlostoma ebfraasi* (Jooss, 1902) Syntype. Scale 10 mm. SMNS 106385. **2** – *Cochlostoma excellens* (Jooss, 1912), holotype. Scale 5 mm. SMNS 106390. **3** – *Carychium suevicum* Boettger, 1877. Scale 500 µm. SMNS 10585. **4** – *Oxyloma minima* (Klein, 1853). Scale 5 mm. SMNS 15817-4. **5** – *Pseudoleacina eburnea* (Klein, 1853). Scale 2 mm. SMNS J68.574. **6** – *Palaeoglandina porrecta* (Gobanz, 1854). Scale 5 mm. SMNS 15817-12. **7** – *Azeca tridentiformis* Gottschick, 1911. Scale 1 mm. SMNS 15817-34. **8** – *Cochlicopa procera* Gottschick, 1911. Scale 1 mm. SMNS 63030. **9** – *Strobilops joossi* Gottschick, 1911. Scale 1 mm. SMNS 106403. **10** – *Truncatellina lentilii* (Miller, 1900). Scale 500 µm. SMNS 15817. **11** – *Vertigo angulifera* Boettger, 1884. Scale 500 µm. SMNS 15817. **12** – *Vertigo milleri* Gottschick & Wenz, 1919. Scale 500 µm. SMNS J67.326. **13** – *Vertigo callosa* Reuss, 1849. Scale 500 µm. SMNS J67.49. **14** – *Vertigo protracta suevica* Gottschick & Wenz, 1919. Scale 500 µm. SMNS 15817 (16254/2007). **15** – *Gastrocopta acuminata* (Klein, 1846). Scale 1 mm. SMNS 15817. **16** – *Gastrocopta nouletiana* (Dupuy, 1850). Scale 500 µm. SMNS 15817 (14704/2007). **17** – *Gastrocopta sandbergeri* Stworzewicz & Prisyazhnyuk, 2006 Scale 500 µm. SMNS 15817. **18** – *Negulopsis gracilis* Gottschick & Wenz, 1919 Scale 500 µm. SMNS J68.577.

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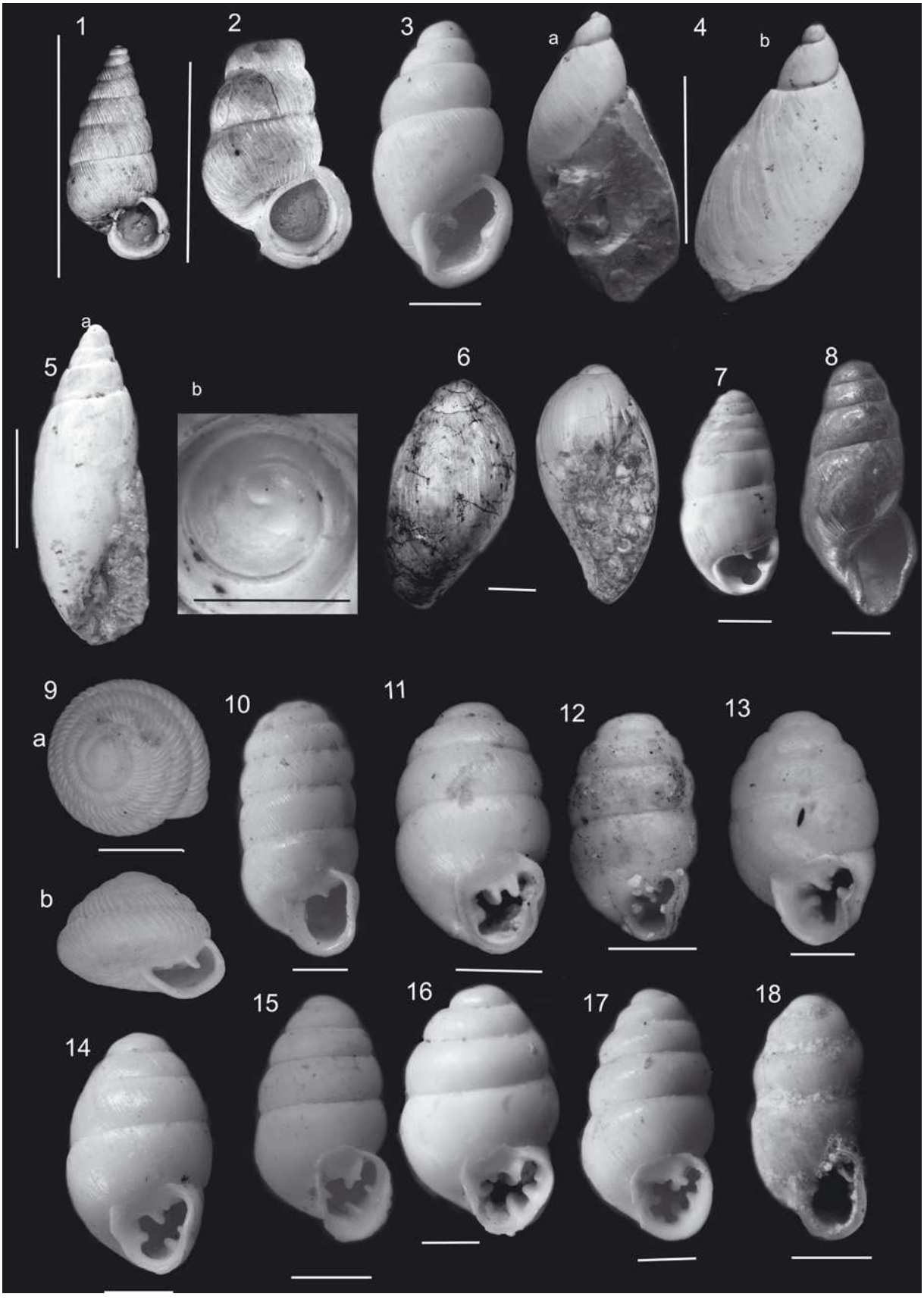

Fig. 2.

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with a smaller peristome, which is comparably more pressed to the last whorl.

Additional distribution: According to Kókay (2006): Nyrirád and Várpolata, Hungary (Sarmatian).

Ecology: The Recent European relatives live mostly in humid habitats. See Welter-Schultes (2012a) for the ecology of the different extant relatives.

Succineidae Beck, 1837
Oxyloma minima (Klein, 1853)
Figs. 2.4, 5.7

1853 *Succinea minima* Klein, p. 205.
1872 *Succinea minima* Klein. – Sandberger, pl. 29, fig. 26; 1875: 601.
1923 *Succinea (Amphibina) minima* Klein. – Wenz, p. 893.
1998 *Succinea minima* von Klein. – Finger, p. 18, pl. 12, fig. H.
2014a *Oxyloma minima* (Klein 1853) n. comb. – Harzhauser et al., p. 27, pl. 9, figs. 1, 2, 6.
2016 *Oxyloma minima* (Klein 1853). – Salvador et al., pp. 30-31, pl. 6, fig. 13.

Material: SMNS 13651/2007 (1 specimen); SMNS 13940/2007 (2 specimens, coll. Gottschick); 63032 (1 specimen, original of Finger 1998, *kleini* bed).

Type locality: Mörsingen, Baden-Württemberg (Salvador et al. 2016).

Type horizon: *Silvana*-beds (Salvador et al. 2016).

Description: Small, dextral gastropod with a pointed, egg-like to spindle-like shape. The convex whorls increase rather rapidly resulting in a very broad last whorl, which comprises c. 88% of the total shell height. The last whorl appears to be a little less convex. The shell consists of 2½ to 2¾ whorls. The sutures are rather deep. The aperture is egg- to pear-shaped. The peristome is simple. Umbilicus absent. The teleoconch is covered with thread-like, irregular prosocline growth lines. The bulbous protoconch consists of c. 1¼ whorls and lacks sculpture. The maximum height is c. 10 mm.

Discussion: One lot was labelled as *Succinea minima* var. *steinheimeinsis* by Gottschick. However, this name has never been published. It shows no significant differences to Klein's material of *S. minima*. Gottschick (1920b) labelled another Steinheim form as *Succinea minima* fa. *pfeifferi* [preoccupied by *Succinea pfeifferi* Rossmässler, 1835]. Unfortunately, the original material is lost. We did not find any other specimen of this variety among the studied material and therefore the validity of this taxon cannot be verified. The specimen illustrated here fits exactly with the syntypes from the Klein collection (see also Salvador et al. 2016).

Additional distribution: Baden-Württemberg, southern Germany, *silvana*-beds (MN5 according to Schweigert 1996; Esu 1999): Zwiefaltendorf (Schlickum 1976), and according to Wenz (1923) also Hohenmemmingen, Emerberg, Mundingen. For localities in Switzerland see Wenz (1923).

Ecology: The extant European relatives live mostly near water but can also be found in drier places (Wiese 2014).

Oleacinidae H. & A. Adams, 1855
Pseudoleacina eburnea (Klein, 1853)
Fig. 2.5

1853 *Poiretia eburnea* Klein, p. 213, pl. 5, fig. 1
1911 *Oleacina hildegardiae* Gottschick, pp. 498-499, pl. 7, fig. 1, 1a.
1919 *Poiretia eburnea hildegardiae* Gottschick. – Gottschick, pp. 120-121.
1981 *Pseudoleacina eburnea* (Klein). – Lueger, pp. 55-56, pl. 7, figs. 15-16.
2004 *Pseudoleacina eburnea* (Klein, 1853). – Harzhauser & Binder, p. 130, pl. 9, fig. 2.
2016 *Pseudoleacina eburnea* (Klein 1853). – Salvador et al., p. 24, pl. 3, fig. 18.

Material: SMNS J685742 (1 specimen, Jooss collection, *trochiformis* bed); 14763/2007 (1 specimen, Gottschick collection).

Type locality: Mörsingen, Baden-Württemberg (Salvador et al. 2016).

Type horizon: *Silvana*-beds (Salvador et al. 2016).

Description: Spindle-like, dextral shell. It consists of approximately five rapidly and regularly growing whorls. The last whorl is very large, c. 79% of the total shell height. The whorls are only slightly convex with shallow sutures. The aperture has a narrow, pear-like shape. The peristome is simple and not reflected. No umbilicus. The teleoconch has very fine growth lines. A spiral sculpture mentioned by Lueger (1981) was not observed; possibly it is not preserved. The protoconch consists of c. 1¾ whorls and has a bulbous shape. It lacks any sculpture. Maximum shell height is 12 mm.

Discussion: According to Lueger (1981) this species shows a variable shell morphology. Gottschick (1911) named the Steinheim species *Oleacina hildegardiae*, but later he placed it as a subspecies of *P. eburnea* (see Gottschick 1919). Following Lueger (1981), *P. hildegardiae* cannot be maintained as a taxon separate from *P. eburnea*. The spindle-shaped shell with the remarkably large last whorl makes this species unique and distinctive within the Steinheim land snail fauna.

Additional distribution: Baden-Württemberg, *silvana*-beds (MN5 according to Schweigert 1996; Esu 1999): Mörsingen, Zwiefaltendorf. Localities in Austria according to Lueger (1981): Leobersdorf (Heilsamer Brunnen, brickyard), Pannon D; Vösendorf, Pannon E; Velm, Pont G/H.

Ecology: Possibly like the extant European representatives of *Poiretia* (open habitats with shrubs and forests; see Welter-Schultes 2012a).

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Palaeoglandina porrecta (Gobanz, 1854)
Fig. 2.6

1854 *Achatina porrecta* m. – Gobanz, p. 196, fig. 5.
1900 *Glandina porrecta* Gobanz (var. zu *inflata* Reuss) Sandb. – Miller, p. 401, fig. 25.
1923 *Poiretia* (*Palaeoglandina*) *gracilis porrecta* (Gobanz). – Wenz, p. 846.

Material: SMNS 15817-12 (1 specimen, Gottschick collection).

Type locality: Rein, Styria, Austria (Gobanz 1854).

Type horizon: Early Middle Miocene (Harzhauser et al. 2014a) freshwater limestone (Gobanz 1854).

Description: Comparably large, spindle-shaped, dextral shell with blunt apex. Shell incompletely preserved. The whorls increase in size rapidly, so that the last whorl is large, comprising c. 79% of the total shell height. Maximum height of the shells is 47 mm, with c. 3¼ whorls. Both the whorls and the suture are shallow. The aperture has an adapically elongated pear shape. The peristome is simple and not reflected. A thin parietal callus seems to be present but is poorly preserved. The shell is imperforate. The teleoconch has thread-like growth lines. Because of the incomplete preservation of the Steinheim specimens, the shape of the protoconch cannot be identified. Specimens from Dischingen, Baden-Württemberg (probably MN5) show a slightly bulbous protoconch consisting of c. 1.5 whorls without visible sculpture.

Discussion: There seems to be variation in the presence of ribs and growth lines and in how pronounced these are. Compared with *Palaeoglandina gracilis* illustrated in Zieten (1832, pl. 39, fig. 3) *P. porrecta* has a more convex last whorl and a generally more bulbous habitus.

Distribution: In Baden-Württemberg, South Germany, *silvana*-beds (MN5 according to Schweigert 1996; Esu 1999) following Wenz (1923): Mörsingen, Hohenmemmingen, Randecker Maar near Kirchheim unter Teck. Other localities in Baden-Württemberg according to this author are: Altheim near Ehingen (Miocene), Dischingen (Miocene). For further localities see Wenz (1923).

Ecology: Possibly like the extant European *Poiretia* species, open habitats with shrubs and forests (see Welter-Schultes 2012a).

Azecidae Kennard & Woodward, 1926
Azeca tridentiformis Gottschick, 1911
Figs. 2.7, 4.13

1911 *Cionella tridentiformis* Gottschick, pp. 507-508, pl. 7, fig. 3, 3a.
1923 *Azeca (Azeca) tridentiformis* (Gottschick). – Wenz, p. 1096.

Material: SMNS 16261/2007 (27 specimens, Gottschick collection); SMNS 14752/2007 SMNS (3 specimens, Gottschick collection); J67239 (4 specimens, Jooss collection); SMNS 63029 (1 specimen, original to Finger 1998, *kleini* bed). The holotype is missing (Salvador et al. 2016).

Type locality: Steinheim am Albuch (Gottschick 1911).

Type horizon: Steinheimer Seeschichten (Gottschick 1911).

Description: Spindle-like, dextral shell with c. seven slowly but regularly growing whorls. Whorls and suture are remarkably shallow. The last whorl comprises more than half of the total shell height. The aperture is obliquely pear-shaped. The peristome is thickened and slightly reflected at the base of the columellar region as well as along the lower half part of the outer margin. On the upper half part of the upper margin, there is a remarkably deep indentation. There is one distinct fold-like parietalis with a small spiralis that lies in the front area of the parietal margin. One pronounced bump-like palatal tooth near the peristome. One small basal tooth lies deep within the aperture. One flat, broad, bump-like columellar tooth near the peristome. Above the latter, there is a distinct, fold-like second columellar tooth deep within the aperture that is not visible in the normal apertural view.

The teleoconch shows no sculpture in the specimens that we examined. However, according to Gottschick (1911), there can be occasionally very fine growth lines visible. The protoconch has a bulbous shape and lacks sculpture. The end of the protoconch where it connects to the teleoconch is not visible and therefore its size and number of whorls cannot be determined. The maximum shell height is 4.7 mm and the maximum width 2 mm (Gottschick 1911).

Discussion: This is the only representantive of the genus Azeca in Steinheim am Albuch.

Distribution: Wenz (1923) mentioned only Steinheim am Albuch.

Ecology: The extant *Azeca goodalli* (Férussac, 1821) lives in deciduous forests with ground vegetation, in humid and moderately open places, in moss and ground litter (Welter-Schultes 2012).

Cochlicopidae Pilsbry, 1900 (1879)
Cochlicopa procera Gottschick, 1920
Fig. 2.8

1920b *Cochlicopa subrimata procera* n. v. – Gottschick, pp. 63-64.
1923 *Cochlicopa subrimata procera* Gottschick. – Wenz, p. 1108.
1998 *Cochlicopa subrimata* (Reuss 1852). – Finger, pp. 18, 25, pl. 5, fig. F.

Material: SMNS 63030 (1 specimen, original material of Finger 1998, *kleini* bed). The holotype is missing (Salvador et al. 2016).

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Type locality: Steinheim am Albuch (Gottschick 1920b).

Type horizon: Steinheimer Seeschichten (Gottschick 1920b).

Description: Incomplete specimen with a damaged aperture. Elongated-oval shell with a blunt apex region. Approximately 5 1/2 convex whorls and a slightly sunkened suture. The whorls grow rather rapidly and regularly. The aperture has an oval shape. The columellar margin is reflected, enclosing a narrow umblilicus. The teleoconch shows no sculpture. The blunt, knob-like protoconch consists of c. $1^{1/4}$ whorls. It lacks any sculpture. The shell is 4 mm high and 2 mm wide.

Discussion: "*Cochlicopa*" *subrimata* (Reuss, 1849) is today considered as a species of the genus *Hypnophila* Bourguignat, 1858 (cf. Harzhauser et al. 2014b), whereas the present form belongs to *Cochlicopa* Férussac, 1821 because of its more rounded whorls.

Distribution: Wenz (1923) mentioned only Steinheim am Albuch.

Ecology: The extant European representatives of Cochlicopa live both in humid and dry habitats (see Wiese 2014 for the different species).

Strobilopsidae Wenz, 1915
Strobilops joossi Gottschick, 1911
Fig. 2.9

1900 *Strobilops costatus* Sandb. – Miller, p. 396, fig. 8.
1911 *Strobilops Joossi* Gottschick, p. 503, pl. 7, fig. 16.
2016 *Strobilops joossii* Gottschick 1911. – Salvador et al., p. 29, pl. 5, fig. 15.

Material: SMNS IMDAS If 45281/2005 (1 specimen, original material of Miller 1900); SMNS 106403 (1 specimen, *laevis* bed, syntype).

Type locality: Steinheim am Albuch (Salvador et al. (2016).

Type horizon: Steinheimer Seeschichten (Salvador et al. (2016).

Description: Small, trochiform and dextral shell with c. five convex whorls and a deep suture. The whorl size increases slowly and regularly. The last whorl does not change the direction before reaching the aperture. The last whorl also shows a very slight keel on its periphery. The aperture has a narrow oblique-oval shape. The peristome is reflected with a slightly thickened margin. A thin parietal callus is present. On this callus, two folds run inwards. The adaxial one is relatively small. The abaxial fold has a remarkable size and ends much closer to the parietal margin than the adaxial one. The deep umbilicus is rather narrow. The teleoconch shows distinct and regularly arranged prosocline ribs that are more or less evenly spaced. These ribs are less distinctive on the umbilical side of the shell and some of them disappear. The flat protoconch shows no sculpture and consists of c. 1.5 whorls. The maximum diameter according to Gottschick (1911) is 2.1 mm.

Discussion: According Gottschick (1911), *Strobilops joossi* differs from *S. costatus* (Sandberger) because: (1) it has a higher spire, (2) five whorls instead of the 4½ in *S. costatus*, (3) a deeper suture, (4) narrower whorls and finer spiral ribs ("Querrippchen"), and (5) a more fragile and not reflected peristome.

Additional distribution: Wenz (1923) mentioned only Steinheim am Albuch.

Ecology: The genus is today restricted to America (Zilch 1959-1960).

Vertiginidae Fitzinger, 1833
Truncatellina lentilii (Miller, 1900)
Fig. 2.10

1900 *Pupa (Isthmia) Lentilii* Miller, p. 406.
1923 *Truncatellina lentilii* (K. Miller). – Wenz, p. 1020 [and further synonyms].

Material: SMNS 63013 (1 specimen, original material of Finger 1998, *kleini* bed); SMNS 16251/2007 (14 specimens, Gottschick collection). The holotype is lost (Salvador et al. 2016).

Type locality: Steinheim am Albuch (Miller 1900).

Type horizon: Steinheimer Seeschichten (Miller 1900).

Description: Small, pupiform, cylindrical and dextral shell, consisting of approximately 5 ½ convex whorls. They grow relatively slowly and regularly. The suture is deep. The aperture has an oval shape. The peristome is reflected, particularly on the abapical part of the palatal margin. Approximately in the middle of the palatal margin, there is a low indentation. Parietal callus very thin. Umbilicus narrow. The aperture has a fold-like parietal tooth and a columellar tooth which lies relatively far back within the aperture. Miller (1900) also described a palatal tooth, which is not present in all specimens. The teleoconch shows regularly arranged, prosocline ribs. These ribs are most pronounced from about the second to the fourth whorl. The flat protoconch consists of c. 1¾ whorls and lacks sculpture. Maximum shell height is 1.6 mm (Miller 1900).

Discussion: The number of teeth/folds within the aperture seems to vary. It is the only *Truncatellina* species known from Steinheim am Albuch and its cylindrical-shaped shell (see Fig. 2.10) makes the identification easy.

Distribution: Wenz (1923) mentioned only Steinheim am Albuch.

Ecology: The Recent European representatives of the genus prefer mostly dry or moderately humid, vegetated habitats (Welter-Schultes 2012a).

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Vertigo angulifera Boettger, 1884
Fig. 2.11

1884 *Vertigo* (*Alaea*) *angulifera* Boettger, p. 271, pl. 4, fig. 10.
1900 *Pupa* (*Alaea*) *aperta* Sandb. – Miller, p. 397, pl. 7, fig. 13 [non Martens 1863, nec Sandberger 1895].
1923 *Vertigo* (*Vertilla*) *angulifera angulifera* Boettger. – Wenz, p. 1006.
1919 *Vertigo angulifera* Boettger. – Gottschick & Wenz, p. 18, pl. 1, figs. 36-37.
1998 *Vertigo angulifera* Boettger. – Finger, p. 18.

Material: SMNS 36706/2005 (1 specimen, original material to Miller 1900); SMNS 63014 (1 specimen, original material to Finger 1998, *kleini* bed); SMNS 15817 (21 specimens, Gottschick collection).

Type locality: Niederrad, near Frankfurt am Main, Hesse, Germany (Boettger 1884).

Type horizon: *Corbicula*-Tone (Boettger 1884).

Description: Small, pupiform dextral shell with a nearly cylindrical shape and c. 4 ½ relatively flat whorls. The whorls increase in size regularly, apart from that there is a comparatively rapid increase in size between the second and the third whorl. The sutures are rather deep. The last whorl comprises c. ½ of the total shell height. The aperture has the shape of a slightly oblique oval with a distinct impression in the middle region of the palatal margin. The peristome is slightly reflected. Four teeth lie within the aperture. Two are distinct parietal teeth/folds, of which the abaxial one nearly reaches the peristome whereas the adaxial one ends further back. The columellar tooth lies relatively deep within the aperture. That is also the case with the palatalis, which is the most inconspicuous tooth/fold and can be missing in some specimens. The umbilicus is a slit. The two insertions are connected by a very thin parietal shield, often hard to see. The teleoconch has prosocline, closely packed growth lines, but these can only be seen on very well preserved specimens. The flat protoconch lacks a sculpture and consists of c. 1.5 whorls. Maximum height c. 1.4 mm (Jooss 1912).

Discussion: Miller (1900) originally named his illustrated specimen *Pupa aperta* Sandberger. Sandberger gave the description of this species in a letter to the "Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, I, page 216" from 1895 but without any illustration. As Gottschick & Wenz (1919) already noticed, the description given by Sandberger (1895) does not fit to the specimens from Steinheim am Albuch. According to them the Steinheim specimens are identical with *Vertigo angulifera* Boettger, 1884. The species differs from *V. callosa* and *V. protracta suevica* by having two distinct parietal teeth and not so rounded a shell shape. For differences to *V. milleri* see below.

Distribution: According to Gottschick & Wenz (1919): Undorf near Regensburg (MN 5 according to Fejfar 1999), Frankfurt am Main (Upper Oligocene/Miocene, see Reichenbacher 2000).

Ecology: The extant European relatives live in a variety of habitats (Kerney et al. 1983; Welter-Schultes 2012a).

Vertigo milleri Gottschick & Wenz, 1919
Fig. 2.12

1912 *Vertigo aperta* Sandberger. – Jooss, pp. 40-41, pl. 2, fig. 7.
1919 *Vertigo angulifera milleri* n. var. – Gottschick & Wenz, p. 21, pl. 1, figs. 38-39.
1919 *Vertigo peraperta* Pilsbry, p. 219.
1923 *Vertigo angulifera milleri* Gottschick & Wenz. – Wenz, pp. 1006-1007.

Material: SMNS J67326 (2 specimens, Jooss collection, *discoides–trochiformis* beds), SMNS IMDAS If. 45501/2005 (1 specimen, original material of Jooss 1912)**.** The holotype is missing (Salvador et al. 2016).

Type locality: Steinheim am Albuch (Gottschick & Wenz 1919).

Type horizon: Steinheimer Seeschichten (Gottschick & Wenz 1919).

Description: Pupiform, dextral shell with c. 4 ½ whorls. These are moderately convex and usually regularly increasing in size. There is also a more rapid increase in size between the second and third whorl. The sutures are deep and the aperture has an oval shape with an impression in the middle region of the palatal margin. The peristome is slightly reflected and the umbilicus is a slit. The two insertions are connected by a parietal shield. The number of teeth is the same as in *V. angulifera*: two parietal teeth, one columellar and one palatalis. All four teeth are fold-like and remarkably pronounced. The abaxial parietal tooth reaches up to the margin of the parietal shield. It seems as if the end of the abaxial parietal tooth is merged with the outer margin of the parietal shield. Neither the teleoconch nor the flat protoconch reveals a sculpture, but this may be due to poor preservation. Gottschick & Wenz (1919) mentioned fine stripes on the shell ("…feiner gestreifte Schale…").

Discussion: Gottschick & Wenz (1919) originally described it as variation of *V. angulifera*. Compared to *V. angulifera* it has a slender shell with more rounded whorls and the two parietal teeth are not as pronounced (see also Gottschick & Wenz 1919). According to this it seems to be justified to take this taxon into species rank. *V. milleri* is slenderer than *V. callosa* and *V. protracta suevica*. In Steinheim am Albuch, this species only occurrs in the *discoides–trochiformis* beds, whereas *V. angulifera* is only present in the *kleini* bed (Gottschick & Wenz 1919).

Distribution: Wenz (1923) mentioned only Steinheim am Albuch.

Ecology: The extant European relatives live in a variety of habitats (Kerney et al. 1983; Welter-Schultes 2012a).

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Vertigo callosa Reuss, 1849
Figs. 2.13, 5.5

1852 *Vertigo callosa* Reuss, p. 30, pl. 3, fig. 7.
1919 *Vertigo callosa* (Reuss). – Gottschick & Wenz, pp. 13-14, pl. 1, figs. 26-34.
1999 *Vertigo callosa* (Reuss 1849). – Stworzewicz, p. 137, figs. 6-7.

Material: SMNS J67570 (1 specimen, Jooss collection); SMNS J67499 (3 specimens, Jooss collection); SMNS J67391 (3 specimens, Jooss collection); SMNS 63012-1, 63012-2, 63012-3, 63012-4, 63012-5, 63012-6 (6 specimens, original material to Finger 1998, *kleini* bed); SMNS 15817-108 (13 specimens, Gottschick collection).

Type locality: Tuchorice, Lipno and Kolosoruk, Bohemia, Czech Republic (Reuss 1849).

Type horizon: Miocene freshwater limestone (Reuss 1849).

Description: Small, dextral pupiform shell, with c. five rounded whorls. It has a typical *Vertigo* shape. The whorls increase in size regularly. The sutures are moderately deep and the umbilicus is a slit. The peristome is reflected. On the palatal side of the peristome there is a distinct indentation. The parietal region is covered by a pronounced parietal callus which connects the columellar margin with the palatal one. The folds in the aperture do not reach the peristome. The specimen illustrated here has one angularis and one parietalis, two palatal folds/teeth and one columellar tooth/fold. The teleoconch has prosocline, more or less regularly arranged growth lines. The flat protoconch consists of c. 1½ whorls and lacks a sculpture. The maximum shell height is c. 2 mm.

Discussion: The number of the teeth varies remarkably (Stworzewicz 1999), as is the case in many extant species (Kerney et al. 1983; Walden 1986; Stworzewicz 1999). Stworzewicz (1999) also wrote that shells of *V. callosa* from Belchatów, Poland are very variable in their size and shape. According to this variability, Gottschick & Wenz (1919) named four variations of *V. callosa* and Wenz (1923) named six subspecies of *V. callosa* from Steinheim Following Stworzewicz (1999) it is necessary to take into account that most of those variations and subspecies were described on the basis of very scanty material, in some cases single specimens only, hence intraspecific variability was not known. The specimens of *V. callosa* examind have a stouter and more rounded shell shape than *V. protracta suevica*. For differences to the other *Vertigo* species from Steinheim am Albuch see their descriptions.

Additional distribution: According to Lueger (1981): Hochheim, Hessen (Upper Oligocene); Tuchorice, Czech Republic (MN 3, Ginsburg 1999); Eichkogel, Austria (Pont) H; Öcs, Varpolata, Tab, Hungary (Pont).

Ecology: The extant European relatives live in a variety of habitats (Kerney et al. 1983; Welter-Schultes 2012a).

Vertigo protracta suevica Gottschick & Wenz, 1919
Fig. 2.14

1919 *Vertigo protracta suevica* n. var. – Gottschick & Wenz, pp. 21-22, pl. 1, figs. 40-41.
1923 *Vertigo protracta suevica* Gottschick & Wenz. – Wenz, p. 1001.
1981 *Vertigo protracta suevica* Gottschick & Wenz. – Lueger, pp. 21-22, pl. 2, figs. 14-15.

Material: SMNS 15817 (60 specimens, Gottschick collection). Type material is missing (Salavdor et al. 2016).

Type locality: Steinheim am Albuch (Gottschick & Wenz 1919).

Type horizon: Steinheimer Seeschichten (Gottschick & Wenz 1919).

Description: Small, dextral pupiform shell with blunt apex. It consists of c. 5 regularly increasing whorls. The whorls are rounded and the sutures moderately deep. The aperture has an oval shape and a simple peristome. Only in the columellar and basal regions is the peristome slightly reflected. The two insertions are connected by a thin callus layer. The umbilicus is a slit. A distinct crest is present. The following dentition is present: a fold-like parietalis, a distinct small angularis, one distinct columellaris and two palatales. The upper palatalis extends further forward than the lower one. None of these five fold-like teeth reaches the peristome. Gottschick & Wenz (1919) and Lueger (1981) also mentioned the occasional occurrence of a very fine basal tooth, which we could not see in the specimens examined. The teleoconch has fine thread-like growth lines that are poorly visible even at a magnification of ×50. The flat protoconch of the specimens examined lacks any sculpture so that its size is difficult to determine.

Discussion: For differences to the other *Vertigo* species from Steinheim am Albuch see their descriptions.

Additional distribution: Wenz (1923) mentioned only Steinheim am Albuch. According to Lueger (1981) it also occurs at Eichkogel, Austria (Pont H).

Ecology: The extant European relatives live in a variety of habitats (Kerney et al. 1983; Welter-Schultes 2012a).

Gastrocopta acuminata (Klein, 1846)
Fig. 2.15

1846 *Pupa acuminata* mihi. – Klein, p. 75, pl. 1, fig. 19a, b.
1923 *Gastrocopta acuminata acuminata* (Klein). – Wenz, p. 916.
1981 *Gastrocopta acuminata acuminata* (Klein). – Lueger, pp. 23-24, pl. 2, fig. 10.
2016 *Gastrocopta (Albinula) acuminata* (Klein, 1846). – Salvador et al., p. 18, pl. 1, figs. 1-2.

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Material: SMNS 106361 (2 specimens, KLEIN collection, syntypes); SMNS 63010 (1 specimen, original material of FINGER 1998, *kleini* bed); SMNS 15817 (70 specimens, GOTTSCHICK collection).

Type locality: KLEIN (1846) named no type locality.

Type horizon: *Silvana*-beds (SALVADOR et al. 2016).

Description: Dextral, pupiform shell, slightly egg-shaped with c. five convex whorls. The whorls increase regularly in size and the sutures are deep. About ½ to ¾ of a revolution behind the aperture, the last whorl distinctively narrows. The aperture has a rounded shape. The peristome is strongly reflected. The parietal region is covered by a pronounced parietal callus. The angular and the parietal teeth are fused and reach the peristome. The palatal side comprises three folds. The palatalis inferior is the most pronounced, followed by the palatalis superior. The infrapalatalis is very small and bump-like. The bulbous basalis is located relatively far back in the aperture. The columellaris is very pronounced and runs in an arc from the peristome into the aperture. Only the columellaris and the fused parietalis/angularis reach the peristome. The teleoconch has regularly arranged, fine prosocline growth lines. The protoconch lacks sculpture.

Discussion: This species is variable in the shell morphology and dentition (MANGANELLI & GIUSTI 2000a). The specimens of *G. acuminata* examined have more slender shells than *G. nouletiana*. *G. acuminata* has flatter whorls than *G. sandbergeri*. In *G. acuminata* the basalis is located far back inside the aperture in comparison to *G. sandbergeri*. In addition, *G. sandbergeri* has a more pronounced palatalis inferior than *G. acuminata*.

Additional distribution: According to LUEGER (1981) the species is present in all location of the *silvana*-beds (MN5 according to SCHWEIGERT 1996; ESU 1999).

Ecology: The genus *Gastrocopta* is extinct in Europe (WEDEL 2008). According ZILCH (1959-1960), the genus occurs in tropical regions as well as in North America and also Siberia. In addition, KOVANDA (2004) mentioned Central and East Asia.

Gastrocopta nouletiana (DUPUY, 1850)
Fig. 2.16

1850 *Pupa nouletiana* DUPUY, pp. 309-310, pl. 15, fig. 6.
1919 *Leucochila nouletiana* (DUPUY). – GOTTSCHICK & WENZ, pp. 12-13, pl. 1, figs. 22-23.
1923 *Gastrocopta nouletiana nouletiana* (DUPUY). – WENZ, p. 930 [and further synonyms].
1981 *Gastrocopta nouletiana* (DUPUY). – LUEGER, pp. 25-26, pl. 2, figs. 16-19, 22.

Material: SMNS 15817 (c. 200 specimens, GOTTSCHICK collection); SMNS 63008/1-3 (3 specimens, original material to FINGER 1998, *kleini* bed).

Type locality: Sansan, France (DUPUY 1850).

Type horizon: Middle Miocene (FISCHER 2000) freshwater limestone (DUPUY 1850).

Description: Dextral, pupiform shell. It consists of c. 4¾ distinctively convex whorls. The penultimate whorl is the most convex one. The sutures are deep and somewhat channel-like. The whorls grow rapidly and regularly. The last whorl comprises c. 50% of the total shell height. The umbilicus is narrow. Close to the aperture, the last whorl has a weakly pronounced bulge. The aperture has an oblique-oval shape with a reflected peristomehaving simple and sharp margins. The two insertions are connected by a very thin parietal callus, which cannot be seen on all specimens. The aperture contains seven teeth. The angularis and parietalis are fused together to form a distinct lobe-like fold which ends shortly before reaching the peristome. The infraparietalis is very small and knob-shaped. There are three palatal teeth. The upper one is small and knob-shaped whereas the others are fold-like. The middle tooth is somewhat broader and shorter than the lowest tooth. The basalis is also knob-shaped. The only columellaris forms a distinct fold. The teleoconch has regularly arranged, prosocline, thread-like growth lines, which are barely visible even at a magnification of ×50. The protoconch lacks sculpture and is therefore hard to deliminate. Maximum shell height is 2.3 mm (LUEGER 1981).

Discussion: According to LUEGER (1981) the species *Pupa gracilidens* SANDBERGER, 1875, later named *Gastrocopta nouletiana gracilidens* by GOTTSCHICK & WENZ (1919), is a junior synonym of *G. nouletiana*. This species differs markedly from the other two *Gastrocopta* species by its more bulbous shell shape.

Additional distribution: According to LUEGER (1981) the species occurs throughout the *sivlana*-beds. He reported it also from Hollabrun, Austria (Sarmatian). Other locations listed by LUEGER are a sandpit in Leobersdorf, Austria (Pannon B/C), the brickyard Leobersdorf, Austria (Pannon D) and Vösendof, Austria (Pannon E). For other localities see WENZ (1923) and LUEGER (1981).

Ecology: See *G. acuminata*.

Gastrocopta sandbergeri STWORZEWICZ & PRISYAZHNYUK, 2006
Figs. 2.17, 5.2

1875 *Pupa* (*Vertigo*) *suevica* sp. nov. – SANDBERGER, p. 654.
1900 *Pupa* (*Leucochilus*) *suevica* SANDBERGER 1875. – MILLER, p. 398, pl. 7, fig. 16.
2006 *Gastrocopta sandbergeri* sp. nov. – STWORZEWICZ & PRISYAZHNYUK, pp. 167-169, fig. 1, 2A-E [and further synonyms].

Material: SMNS 15817 (>20 specimens, GOTTSCHICK collection); SMNS 63009-3; SMNS 63009-2, SMNS 63009-1 (3 specimens, originals of FINGER 1998).

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Type locality: Bełchatów, Poland (Stworzewicz & Prisyazhnyuk 2006).

Type horizon: Bel-B horizon, Miocene, MN5 (Stworzewicz & Prisyazhnyuk 2006).

Description: Small dextral, pupiform, slightly egg shaped shell with c. 5 rounded whorls that increase in size regularly. The last whorl of some specimens can be rather flat. The sutures are rather deep. The umbilicus is a slit. The peristome is reflected. The columellar margin and palalatal margin are connected by a parietal shield resulting in an unbroken continuous peristome. The aperture has a rounded shape. The angularis and parietalis are fused together, with the former abaxially curved. The infraparietalis fold is small. Three palatal teeth are visible, increasing in strength adapically. The upper one is small, whereas the third one forms a distinct fold. The basalis is also small and bump-like. The columellaris is strong and fold-shaped. The teleoconch of some specimens has irregularly arranged thread-like, prosocline growth lines. The protoconch is slightly bulbous and no sculpture was visible on the shells examined. The maximum size seems to be 2 mm.

Discussion: This species was originally introduced by Sandberger (1875) as *Pupa* (*Vertigo*) *suevica*, but without description or illustration. Nevertheless, this name was used in later literature. Stworzewicz & Prisyazhnyuk (2006) designated it is a nomen nudum and re-named the species *G. sandbergeri*. For a detailed discussion see Stworzewicz & Prisyazhnyuk (2006).

Additional distribution: According to Stworzewicz & Prisyazhnyuk (2006) *G. sandbergeri* is a rare species. Apart from Steinheim am Albuch it occurs only in Bełchatów, Poland (MN5 according to Stworzewicz & Prisyazhnyuk 2006).

Ecology: See *G. acuminata*.

Negulopsis gracilis (Gottschick & Wenz, 1919)
Fig. 2.18

1912 *Negulus lineolatus* Al. Braun. – Jooss, pp. 36-37.
1919 *Negulus suturalis gracilis* n. var. – Gottschick & Wenz, pp. 9-10, pl. 1, figs. 12, 13.
2004 *Negulus gracilis* Gottschick & Wenz 1919. – Harzhauser & Binder, p. 126, pl. 6, figs. 9-10.
2014 *Negulopsis gracilis* (Gottschick & Wenz 1919). – Nordsieck, pp. 175-176.

Material: SMNS J68.577 (3 specimens, original material of Jooss 1912; Jooss collection). Type material is missing (Salvador et al. 2016).

Type locality: Steinheim am Albuch (Gottschick & Wenz 1919).

Type horizon: Steinheimer Seeschichten (Gottschick & Wenz 1919).

Description: Very small, dextral shell with a tower-like, cylindrical shape and blunt apex. It consists of approximately four regularly and relatively rapidly growing whorls and therefore the last whorl comprises nearly half of the total shell height. The whorls are slightly rounded whereas the last one is more flat. The sutures seem to be moderately deep. Due to preservation, not all details are visible. The aperture is obliquely egg shaped. The peristome is simple. The umbilicus is a slit. Due to the poor preservation there is no sculpture visible on both teleoconch and protoconch. According to Harzhauser & Binder (2004) the entire teleoconch is ornamented with thin, widely spaced but prominent prosocline axial ribs and much weaker, densely spaced secondary ribs in the interspaces. For the protoconch, these authors mentioned a hammered, regularly wrinkled surface sculpture and a size of 1.25 whorls. Maximum height is 1.95 mm (Lueger 1981).

Discussion: Originally described by Gottschick & Wenz (1919) as subspecies/variation of *Negulopsis suturalis* (Sandberger, 1858), Harzhauser & Binder (2004) designated it as a species. Originally named as *Negulus gracilis*, Nordsieck (2014) placed it in his newly erected genus *Negulopsis*. For the differences between the genera *Negulus* and *Negulopsis* see Nordsieck (2014). According to Lueger (1981), *N. gracilis* is smaller and more slender than *Negulopsis suturalis*

Fig. 3. 1 – *Granaria schuebleri* (Klein, 1846). Scale 1mm. SMNS 100110-1. **2** – *Granaria grossecostata* (Gottschick & Wenz, 1919). Scale 1mm. SMNS 15509. **3** – *Granaria pachygastra* (Fraas in Miller, 1900). Scale 5 mm. SMNS 100111. **4** – *Vallonia subcyclophorella* (Gottschick, 1911), neotype. Scale: a: 1mm; b: 500 µm. SMNS-FGO 15817/1+108. **5** – *Vallonia lepida* (Reuss, 1849). Scale 500 µm. SMNS 15817-54. **6** – *Vallonia major* Gottschick, 1920. Scale 1 mm. Lectotype. SMNS 15817. **7** – *Pupilla iratiana suevica* Gottschick & Wenz, 1919. Scale 1 mm. Inv. Nr. SMNS 15151. **8** – *Pupilla steinheimensis* (Miller, 1900). Scale 500 µm. SMNS J67.537. **9** – *Pupilla submuscorum* Gottschick & Wenz, 1919. Scale 500 µm. SMNS J67.498. **10** – *Triptychia steinheimensis* (Quenstedt, 1884) Scale 10 mm. Original of Fraas (1910). SMNS 107216. **11** – *Pseudidyla* sp. Scale 1mm**.** Inv. Nr. SMNS J66.933. **12** – *Opeas minutum* (Klein, 1853) Scale 2 mm. SMNS J67.040. **13** – *Cecilioides aciculella* (Sandberger, 1872). Scale 1 mm. SMNS J67.230. **14** – *Punctum propygmaeum* Andreae, 1904. Scale 500 µm. SMNS 15817-128. **15** – *Discus pleuradrus* (Bourguignat, 1881). Scale: a, b: 1 mm; c: 500 µm SMNS J65.813. **16** – *Janulus gottschicki* (Jooss, 1912). Scale 1 mm. SMNS 106394. **17** – *Aegopinella subnitens* (Klein, 1853) Scale 2 mm. SMNS 15817-41. **18** – *Aegopinella erecta* (Gottschick, 1920) Scale 2 mm. SMNS J65.683.

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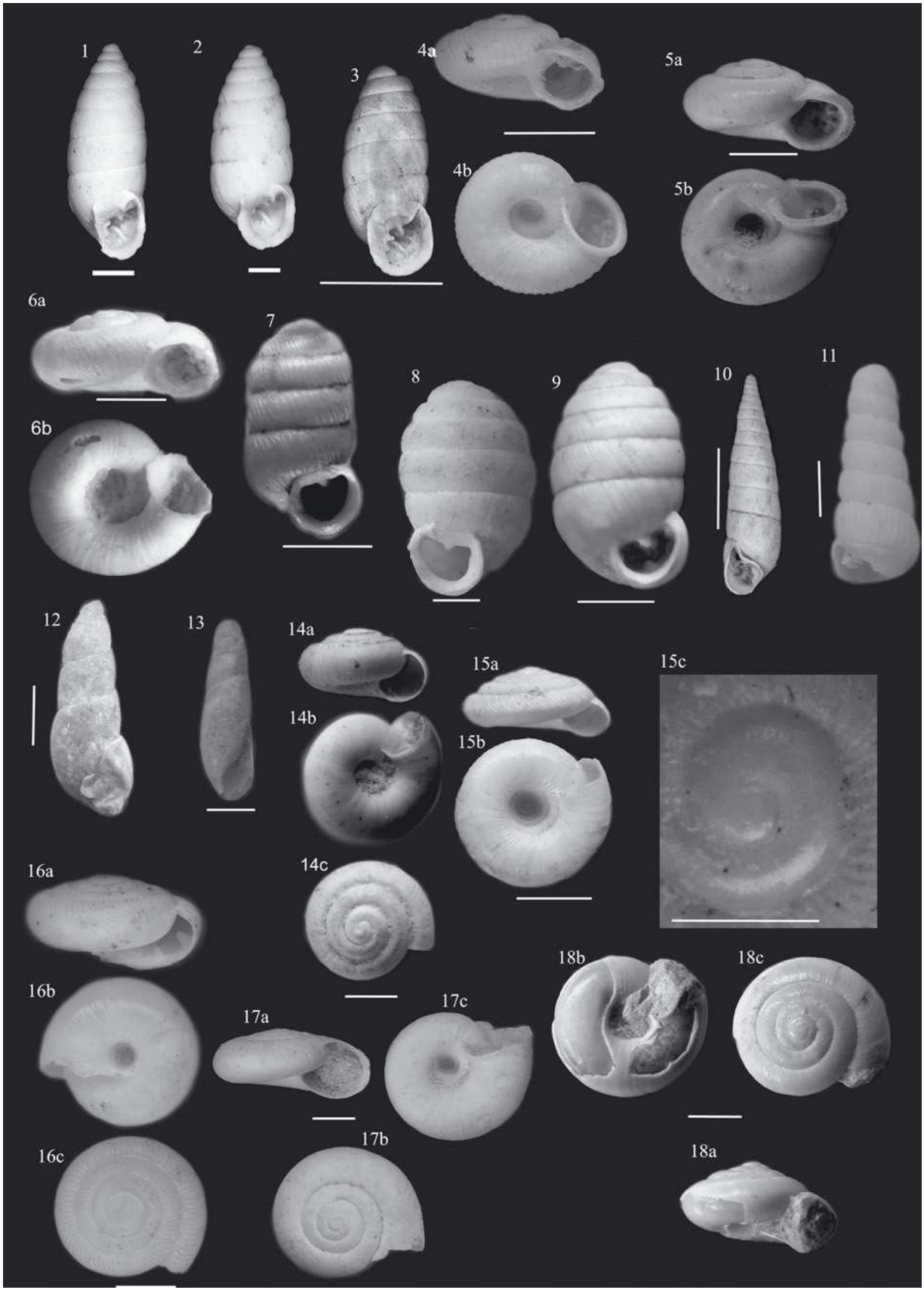

Fig. 3.

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(Sandberger 1858) from the *Hydrobia*-beds of the Mainz Basin. Following this author, the Pliocene *Negulopsis truci* (Schlickum, 1975) could be a descendant of *N. gracilis*.

Additional distribution: According to Harzhauser & Binder (2004) is common throughout the Pannonian of Austria, Slovakia, and Hungary.

Ecology: Unknown.

Chondrinidae Steenberg, 1925
Granaria schuebleri (Klein, 1846)
Fig. 3.1

1832 *Pupa antiqua* Schübler. – Zieten, pl. 19, fig. 7.
1846 *Pupa schuebleri* mihi. – Klein, p. 74, pl. 1, fig. 18.
1900 *Pupa schuebleri* (Klein 1846). – Miller, p. 396, pl. 7, fig. 12
2013 *Granaria schuebleri* (Klein 1847). – Höltke & Rasser, pp. 185-186, fig. 4.1-4.3.
2016 *Granaria schuebleri* (Klein 1846). – Salvador et al., p. 34, pl. 8, fig. 3.

Material: SMNS 100110-1 (neotype, designated by Höltke & Rasser 2013; Klein collection).

Type locality: Steinheim am Albuch (Zieten 1832; Klein 1846).

Type horizon: Steinheimer Seeschichten (Zieten 1832).

Description: The neotype was designated and described by Höltke & Rasser (2013) as follows: The neotype of this species is 5 mm high and 2 mm wide. It has a dextral, pupiform and slightly conical shell. The shell has nine whorls. These are only slightly convex and the suture is moderately deep. The whorl size increases regularly. On the whorls, there are very fine axial lines. They are prosocline and more or less regularly arranged in a close distance. The aperture has an oval shape. The shell has a slit-like umbilicus. The peristome is bent backwards. The palatal margin runs down in a more or less straight line and then forms a very rounded basis. The parietal region is covered by a thin parietal callus, which connects the outer and inner lip. A part of this parietal callus is not preserved in the type specimen. The aperture comprises six lamellae: One prominent angularis, one dominant palatalis inferior and one parietalis. Possibly there was an infraparietalis on the abraded part of the parietal callus. There is also a distinct columellaris and an infracolumellaris, but they are less strong than the p. inferior and the parietalis. Above the palatalis inferior, a short and very indistinct palatalis superior is recognisable. The angularis has a knob-like shape, whereas the others are folds running deep into the mouth. The palatalis inferior and the palatalis superior do not reach the peristome.

Discussion: For a detailed discussion about the two names *Pupa antiqua* Schübler, 1832 and *P. schuebleri* Klein, 1846 see Höltke & Rasser (2013). For differences from the other two *Granaria* species see the according descriptions.

Distribution: Höwenegg (MN 9 according to Heissig 1999); according to Wenz (1923) "Phonolithtuff des Hohentwiel" (Late Miocene to Early Pliocene after Geyer & Gwinner 1991) and Hinterried maar near Geisingen (Miocene).

Ecology: More dry habitats (see Welter-Schultes 2012a; Höltke 6 Rasser 2013).

Granaria grossecostata (Gottschick & Wenz, 1919)
Fig. 3.2

1919 *Torquilla schuebleri grossecostata* n. var. – Gottschick & Wenz, p. 3, pl. 1, fig. 3;
2013 *Granaria grossecostata* (Gottschick & Wenz 1919). – Höltke & Rasser, pp. 186-187, figs. 3.3, 4.4, 4.5.

Material: SMNS 15509 (2 specimens, Gottschick collection, *kleini* bed).

Type locality: Steinheim am Albuch (Gottschick & Wenz 1919).

Type horizon: Steinheimer Seeschichten (Gottschick & Wenz 1919).

Description: The description based on the single specimen by Höltke & Rasser (2013) is as follows: Only one of the two specimens has an aperture free of sediment. This specimen is 6 mm high and c. 2.5 mm wide. It has a dextral, pupiform shell. The eight whorls increase in size regularly. The shell is slightly cylindrical, but becomes narrow towards the apex. The whorls are more convex than in *G. schuebleri*. They have fine and regular, prosocline axial ribs. The distance between them is two times of the ribs' width. Near the aperture, the ribs are more distinct and less regular. The suture is deeper than in *G. schuebleri*. The shell has a slit-like umbilicus. The mouth is more circular than that of *G. schuebleri*. The peristome is bent backwards. Outer and inner lips are connected by a parietal callus. Marked angular fold and parietals, which run into the mouth. A strong palatalis inferior and a weaker palatalis superior, which ends behind the p. inferior. Columerllaris and infracolumellaris are restricted to the columellar region and are equally distinct way. At the inner side of the palatal margin, there is also a little knob. Apart from the Angularis, none of the folds reach the peristome.

Discussion: Type material is missing (Salvador et al. 2016). According to Höltke & Rasser (2013) the species differs from *G. schuebleri* by the following points: (1) More convex whorls; (2) a deeper suture; (3) stronger ribs; (4) a more distinct palatalis superior; (5) a small knob on the inner side of the palatal margin.

Additional distribution: Mentioned only from Steinheim am Albuch (Wenz 1923).

Ecology: See *G. schuebleri*.

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Granaria crassiventer Salvador, Höltke, Rasser & Kadolsky, 2016
Fig. 3.3

1882 *Pupa pachygastra* Fraas, p. 174 (nomen nudum).
1883 *Pupa pachygastra* Fraas. – Engel, p. 287 (nomen nudum).
1900 *Pupa schuebleri* var. *pachygastra* Fraas. – Miller, pp. 396-397, pl. 7, fig.12.
2013 *Granaria pachygastra* (Fraas in Miller 1900). – Höltke & Rasser, p. 187, fig. 4.6.
2016 *Granaria crassiventer* Salvador, Höltke, Rasser & Kadolsky, pp. 23, 31-32, pl. 1, fig. 7.

Material: SMNS 106416 (1 specimen, syntype, original material of Fraas 1882).

Type locality: Steinheim am Albuch (Miller 1900; Höltke & Rasser 2013).

Type hoizon: Steinheimer Seeschichten (Miller 1900).

Description*:* The description based on a single specimen by Höltke & Rasser (2013) is as follows: The specimen is 10 mm high and 4 mm wide. It has a dextral, pupiform, barrel or cylindrical shape. There are seven whorls, which are slightly rounded and increase in size regularly. The protoconch is abraded. The suture is moderately deep. The whorls are covered by regular prosocline ribs. They are stronger than in *Granaria schuebleri*. The distance between the ribs is two times of the respective ribs width. The umbilicus is a slit. The aperture has a rounded, slightly circular shape. The peristome is bent backwards. Outer and inner lips are connected by a parietal callus. At the inner side of the reflected palatal margin there is a little knob. The parietalis and angularis are very prominent. Both are fold-like and run inside the mouth. On the parietal callus there is also one small, knob-like infraparietalis. Beside this, there is a prominent columellaris and an infracolumellaris. The latter is situated far away from the peristome. The basalis, palatalis inferior and p. superior are slender, but marked. The palatalis inferior is more distinct than the palatalis superior. From the last three, the palatalis inferior runs mostly towards the forepart, but does not reach the peristome.

Discussion: Due to the larger size and slightly ton-shaped shell morphology of *G. crassiventer*, this species is remarkable different from both *G. schuebleri* and *G. grossecostata*.

Additional distribution: Only named from Steinheim am Albuch.

Ecology: See *G. schuebleri*.

Valloniidae Morse, 1864
Vallonia subcyclophorella (Gottschick, 1911)
Fig. 3.4

1911 *Helix* (*Vallonia) subcyclophorella* Gottschick, p. 503, pl. 7, fig. 2, 2a, b.
1993 *Vallonia subcyclophorella* (Gottschick 1911). – Gerber, pp. 147-150, figs. 3w, x, 56b-e, 59, 60, 61a-c [and further synonyms].
2016 *Vallonia subcyclophorella* (Gottschick 1911). – Salvador et al., p. 36.

Material: SMNS-FGO 15817/1+108 (1 specimen. Neotype designated by Gerber 1993 and 108 other specimens; Gottschick collection).

Type locality: Steinheim am Albuch.

Type horizon: Steinheimer Seeschichten, *kleini* bed (Salvador et al. 2016).

Description: Small, dextral shell. Discoidal shape with only slightly elevated spire. It consists of c. three rounded whorls. They increase regularly in a moderately pace. The sutures are deep. The last whorl runs obliquely downwards towards the aperture. The aperture has the shape of an egg laid on its side ("quer-eiförmig" according to Gerber 1993). The aperture lies at an oblique angle to the shell axis. The peristome is reflected. The two insertions are remarkably close to each other. They are connected by a callus layer. The umbilicus is relative wide and incorporates according to Gerber (1993) c. $^1/_3$ of the total shell width. The teleoconch comprises thread-like ribs that are clearly visible. The distance between them is a bit irregular. Within the space, there is a varying number of additional smaller growth lines. The protoconch comprises according Gerber (1993) $1^1/_8$ whorls. It lacks a sculpture. Maximum diameter 2.36 mm (Gerber 1993).

Discussion: For differences to the two other species of *Vallonia* from Steinheim am Albuch see the according descriptions.

Distribution: The species has a wide distribution. Gerber (1993) mentioned locations in Austria and in Kazakhstan. From the Molasse Zone, only Steinheim am Albuch and Undorf (Bavaria), MN 5 were mentioned. According to Gerber (1993), it ranges from MN5 to MN10.

Ecology: The extant European relatives live in different habitats (See Wiese 2014).

Vallonia lepida (Reuss, 1849)
Fig. 3.5

1849 *Helix lepida* Reuss, p. 24, pl. 2, fig. 4.
1993 *Vallonia lepida* (Reuss 1849). – Gerber, pp. 88-98, figs. 3d, 29a-g, 30a-d, 31a-f, 32a-c, 33 [and further synonyms].

Material: SMNS 15817-54 (45 specimens, Gottschick collection).

Type locality: Korozluky, NW Bohemia, Czech Republic (Gerber 1993).

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Type horizon: Lower Miocene freshwater limestone (Gerber 1993).

Description: Small, slightly discoidal shell with low spire and blunt apex. Gerber (1993) described the morphology as "stark gedrückt kugelig bis sehr dick scheibenförmig". It has c. 3 ¼ convex whorls and a voluminous last whorl. The whorls grow rapidly and regularly. The sutures are only slightly deepened. The last whorl slowly runs downwards before reaching the aperture. The peristome is strongly reflected and forms a torus ("Ringwulst" according to Gerber 1993). The aperture has an oblique-oval shape. The two insertions are relatively converged and connected by a parietal callus. The deep umbilicus comprises c. 18% of the total shell width and has a relatively steep marginal slope. The teleoconch comprises occasionally unregular growth lines, which are distinctly pronounced. The blunt protoconch consists of c. 1 whorl and comprises no sculpture. As maximum diameter of this species Gerber (1993) mentioned 2.80 mm.

Discussion: According to Gerber (1993), *V. lepida* shows a certain variability in shell morphology. According to the examined material, *V. lepida* differs from *V. major* by a higher spire and from *V. subcyclophorella* by the absence of the thread-like ribs on the teleoconch.

Additional distribution: The known stratigraphic and geographic distribution is very wide, ranging from the Oligocene of Rheinland Pfalz, Germany, to the Pliocene of France (for details see Gerber 1993).

Ecology: The extant European relatives live in various habitats (see Wiese 2014).

Vallonia major Gottschick, 1920
Fig. 3.6

1920b *Vallonia subcyclophorella major.* – Gottschick, p. 54, pl. 2, fig. 4.
1993 *Vallonia major* Gottschick 1920. – Gerber, pp. 150-154, figs. 3Y; 58a, b, 59, 60 [and further synonyms}.

Material: SMNS 15817 (5 specimens including the lectotype and 4 paralectotypes designated by Gerber 1993).

Type horizon: Steinheim am Albuch, sandpit (Gottschick 1920b).

Type horizon: Steinheimer Seeschichten (Gottschick 1920b).

Description: Small, slightly disk-shaped, dextral shell with very low spire and c. three convex whorls. They grow rapidly and regularly. The sutures are deep. The last whorl bends slowly downwards, shortly before reaching the aperture. The peristome is slightly reflected. The aperture has the shape of an egg laid on its side (Gerber 1993 "quer-eiförmig"). The two insertions lie very close to each other. They are connected by a parietal callus. The deep umbilicus is very wide. It comprises c. 40% of the total shell width. The teleoconch has curved, regularly arranged ribs with growth lines between them. Mostly, there are two growth lines between two ribs (Gerber 1993). The protoconch is large and bulbous. It lacks sculpture and comprises according to Gerber (1993) c. $1^{1}/_{8}$ whorls. Maximum diameter c. 2.75 mm (Gerber 1993).

Discussion: Originally this taxon was designated by Gottschick (1920) as a variety of *Vallonia subcylophorella* (Gottschick, 1911), but Gerber (1993) defined it as a species. According to Gerber (1993), the species differs from *V. subcyclophorella* by its larger protoconch and more rapidly growing whorls. *V. major* is more disc-shaped than *V. subcyclophorella* and *V. lepida*.

Additional distribution: Nördlinger Ries, Bavaria, MN 6 (Gerber 1993).

Ecology: The extant European relatives live in different habitats (see Wiese 2014).

Pupilliidae Turton, 1831

Pupilla iratiana suevica Gottschick & Wenz, 1919
Fig. 3.7

1919 *Pupilla iratiana suevica* n. var. – Gottschick & Wenz, pp. 5-6, pl. 1, figs. 4-5.
1923 *Pupilla iratiana suevica* Gottschick et Wenz. – Wenz, p. 960 [and further synonyms].

Material: SMNS 15151 (9 specimens, Gottschick collection, *kleini* bed). Type material is missing (Salvador et al. 2016).

Type locality: Steinheim am Albuch (Gottschick & Wenz 1919).

Type horizon: Steinheimer Seeschichten, *kleini* bed (Salvador et al. 2016).

Description: Small, pupiform, cylindrical and dextral shell with blunt apex and c. 5 ½ convex whorls with comparablly deep sutures. The whorls grow relatively slowly, but regularly. The umbilicus is narrow or a slit. The aperture has an oval shape with a strongly reflected peristome. The two insertions are connected by a pronounced parietal shield. Distinct neck bulge. The aperture contains five teeth: one bump-like angularis, one distinct parietal fold and a fold-like columellaris. On the palatal side, there are two bump-like teeth relatively far inside the aperture. The upper one is small and inconspicuous. Apart from the angularis, none of the other teeth reach the peristome. The teleoconch comprises regularly arranged prosocline ribs that are comparably wide-spaced. The protoconch consists of c. 1¼ whorls and lacks a sculpture. According to Gottschick & Wenz (1919) the maximum size is 2.6 mm in height and 1.4 mm in width.

Discussion: The specimen illustrated by Kókay (2006, pl. 25, fig. 7) named as *P. iratiana suevica* is definitively a dif-

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ferent species. According to Gottschick & Wenz (1919), *P. iratiana suevica* differs *P. iratiana iratiana* (Dupuy, 1850) by stronger ribs and the presence of a remarkable angularis. *P. iratiana suevica* differs from *P. steinheimensis* by its dextral shell.

Additional distribution: Wenz (1923) mentioned only Steinheim am Albuch.

Ecology: The extant European relatives live in different habitats (see Welter-Schultes 2012a).

Pupilla steinheimensis (Miller, 1900)
Figs. 3.8, 5.3

1877 *Pupa (Pupilla) steinheimensis* n. sp. – Boettger, p. 79 [nomen nudum].
1900 *Pupa (Pupilla) steinheimensis* Miller, p. 398, pl. 7, fig. 15.
1923 *Pupilla (Primipupilla) steinheimensis* (Miller). – Wenz, pp. 966-967.

Material: SMNS J67537 (1 specimen, Jooss collection, *trochiformis* bed); SMNS J67535 (1 specimen, Jooss collection, *trochiformis* bed). Type material is missing (Salvador et al. 2016).

Type locality: Steinheim am Albuch (Miller 1900).

Type horizon: Steinheimer Seeschichten (Miller 1900).

Description: Sinistral, pupiform shell with a slightly cylindrical shape consisting of c. 6 ½ convex whorls. The whorls grow rapidly and regularly. The sutures are deep. The aperture has a rounded shape with a reflected peristome. The two insertions are connected by a distinct parietal callus so that the aperture seems to have a continuous circulating peristome. The umbilicus is a slit. Distinct neck furrow ("Nackenfurche"). The aperture contains three teeth: One remarkable, fold-like parietal tooth; one columellar tooth, also fold-like but not as pronounced as the first one; one small and more bump-like basal tooth relatively far inside the mouth. The teleoconch usually lacks a sculpture. Only on some specimens, a few thread-like, prosocline growth lines are visible. The flat protoconch lacks a sculpture as well. Maximum height is 2.4 mm according to Miller (1900).

Discussion: The species was named by O. Boettger (1877) without an illustration nor description. The first description was given by Miller (1900). According to him, the basal tooth mentioned above is not always present.

Additional distribution: Wenz (1923) mentioned only Steinheim am Albuch.

Ecology: The Recent European species of the Pupillidae prefer different habitats but most live in dry and open landscapes (see Welter-Schultes 2012a; Wiese 2014).

Gibbulinopsis submuscorum (Gottschick & Wenz, 1919) nov. comb.
Figs. 3.9, 5.4

1919 *Pupilla submuscorum* n. sp. – Gottschick & Wenz, pp. 6-7, pl. 1, figs. 6-7.
1923 *Pupilla (Pupilla) submuscorum* Gottschick et Wenz. – Wenz, p. 957.

Material: SMNS J67498 (2 specimens, Jooss collection, *kleini* bed). Type material is missing (Salvador et al. 2016).

Type locality: Steinheim am Albuch (Gottschick & Wenz 1919).

Type horizon: Steinheimer Seeschichten, *kleini* bed (Gottschick & Wenz 1919).

Description: Dextral, pupiform, cylindrical shell with c. 6 ½ slightly rounded whorls. The shell comprises a narrow winding and the whorls growth slowly but regularly. The sutures are relative shallow. The aperture half-circular. The peristome is slightly reflected. Behind the aperture, there is a shallow impression, followed by a crest. Umbilicus is a slit. According to Gottschick & Wenz (1919) the two insertions are connected by a thin callus layer (elevation). The specimens examined in this study do, however, not show this feature due to preservation. The aperture comprises three teeth: one fold-like distinct parietalis and one columellaris as well as a palatalis located adapically. The columelaris and palatalis do not reach the peristome, but the parietalis does. It is also the most pronounced tooth. The teleoconch comprises prosocline, closely packed growth lines which are regularly arranged. The protoconch consists of c. 1.5 whorls and has a flat-bulbous shape. It shows a net-like sculpture. Maximum height is 3.5 mm (Gottschick & Wenz (1919).

Discussion: According to Gottschick & Wenz (1919) the following features allow separation from *Pupilla muscorum*: (1) the dentition within the aperture; (2) the keel-like bulge; (3) a broader impression between aperture and torus at *P. submuscorum*. Originally described by the above authors as *Pupilla steinheimensis*. However, according to Zilch (1959) the net-like sculpture on the protoconch (see pl. 4, fig. 4) is characteristic for *Gibbulinopsis* Germain, 1919. Other authors interpreted this taxon as a subgenus of *Pupilla* Fleming, 1928, whereas Schileyko (1998) took it in genus rank. The net-like protoconch sculpture separates it from the other two *Pupilla* species.

Additional distribution: Wenz (1923) mentioned only Steinheim am Albuch.

Ecology: The Recent European species of the Pupillidae prefer different habitats, but prefer mostly dry and open habitats (see Welter-Schultes 2012a; Wiese 2014). The modern member of the genus *Gibbulinopsis* live in E Europe, Cape Verde Islands, Réunion, N and E Asia as well as in Australia (Zilch 1959-1960).

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Filholiidae Wenz, 1923
Triptychia steinheimensis (Quenstedt, 1884)
Fig. 3.10

1872 *Clausilia (Triptychia) suturalis* Sandberger, pl. 28, fig. 11, 11a; 1875: 652.
1884 *Clausilia steinheimensis*. – Quenstedt, p. 94, pl. 187, figs. 136-138.
1908 *Clausilia (Triptychia) suturalis* Sandb. – Engel, p. 566, pl. 6, fig. 25.
1910 *Clausilia suturalis*. – E. Fraas, p. 220, pl. 66, fig. 33.
2006 *Triptychia (Triptychia) steinheimensis* (Quenstedt 1884). – Schnabel, pp. 169-171, pl. 8, figs. 91-93.

Material: SMNS 107216 (1 specimen, original material to E. Fraas 1910); SMNS 15817-8 (1 specimen, Gottschick collection; SMNS IMDAS If. 12422/2008 (1 specimen, Bechter collection).

Type locality: Steinheim am Albuch (Schnabel 2006).

Type horizon: Steinheimer Seeschichten (Schnabel 2006).

Description: Sinistral, spindle-shaped shell. Typical "*Clausilia* shape" with a bulbous apex. The number of whorls ranges from 12.5 to 15 (Schnabel 2006). The whorls grow very slowly and irregularly. The first four whorls indistinct. Only from the fifth to ninth whorl, a remarkable increasing in size is visible. From the ninth to the last whorl, the increase in the width is constant. The sutures are flat but distinct. The aperture has an oblique pear shape. The aperture seems to be detached from the last whorl. The sinulus is remarkably pronounced. The two insertions are connected by a distinct parietal callus and therefore the peristome is continuous. It is slightly reflected and thickened. No umbilicus. The aperture comprises three fold-like teeth: One distinct parietalis, one upper and one lower columellaris. The two latter are very close to each other. The parietalis and upper columellaris terminate distinctly before the peristome. The lower columellaris terminates shortly before reaching the peristome. The teleoconch comprises regularly arranged straight ribs. However, the pronouncement of this ribs is variable within the shell. Up to c. the seventh whorl, the ribs are very distinct. After that, they become less distinct and fading. The protoconch has a bulbous shape and lacks a sculpture. The maximum height is 31.5 mm (Schnabel (2006).

Discussion: This species is often mentioned in older literature as *Triptychia suturalis* (Sandberger, 1872). It was originally described by Sandberger (1872) as *Clausilia (Triptychia) suturalis*. According to Nordsieck (1998) and Schnabel (2006) this taxon is a junior homonym, because in 1861 Küster had already named a species *Clausilia suturalis*. For the differences to other *Triptychia* species see Schnabel (2006). *T. steinheimensis* is the only known *Triptychia* species from Steinheim am Albuch.

Additional distribution: Further Miocene occurrences in Baden-Württemberg according to Wenz (1923) are Limburg and Böttingen. For Switzerland, he mentioned (with a question mark) Vermes bei Delsberg, Kanton Bern.

Ecology: The genus became extinct in the Pliocene (Zilch 1959-1960). The related Recent Clausiliidae mostly live in humid habitats, occasionally in forests on trees (see Nordsieck 2007 or Welter-Schultes 2012a for the climate preferences of the individual species).

Pseudidyla sp.
Fig. 3.11

Material: SMNS J66.933 (1 specimen, Jooss collection, *sulcatus* bed).

Description: One incomplete specimen with c. six whorls. These whorls are slightly convex with deep sutures. The whorls grow rapidly and regularly. At the last two whorls, distinct, straight ribs are visible. The protoconch has no sculpture. It is flat but still a little bulbous. The specimen is 4 mm high.

Discussion: The snail is labeled as *Pseudidyla moersingensis*. According to the missing of taxonomic important features like the dentition of the aperture, a specific identification is not possible.

Ecology: See *Triptychia steinheimensis* above.

Subulinidae Fischer & Crosse, 1877
cf. *Opeas minutum* (Klein, 1853)
Fig. 3.12

1853 *Bulimus minutus* Klein, p. 212, pl. 5, fig. 9.
1872 *Subulina minuta* Klein. – Sandberger, pl. 29, fig. 16; 1875: 596.
1923 *Opeas minutum* (Klein). – Wenz, pp. 872-874.
1976 *Opeas (Opeas) minutum* (Klein). – Schlickum, p. 15, pl. 3, fig. 46.

Material: SMNS 67.040 (1 specimen, Jooss collection). Type material is missing (Salvador et al. 2016).

Type locality: "Württemberg" (Klein 1853 did not mention a specific locality) (Salvador et al. 2016).

Type horizon: "Süßwasserkalkformation" (Klein 1853).

Description: Only one steinkern is known. Tower-shaped shell, 7 mm high, with slowly but regularly growing whorls. The c. 4 1/2 whorls are flat. The aperture is crescent-shaped and relatively low. It comprises only c. 50% of the height of the last whorl.

Discussion: Due to the incomplete preservation, a clear identification is not possible.

Additional distribution: *Opeas minimum* is widely distributed in the *silvana*-beds (MN5 according to Schweigert 1996; Esu 1999).

Ecology: The extant relatives live in tropical America (Welter-Schultes 2012b).

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Ferussaciidae Bourguignat, 1883
Cecilioides aciculella (Sandberger, 1872)
Fig. 3.13

1872 *Caecilianella aciculella* Sandberger, pl. 29, fig. I5, 15a; 1875: 595.
1900 *Caecilianella aciculella* Sandb. – Miller, p. 399, pl. 7, fig. 18.
1920b *Cecilioides aciculella* Sandberger. – Gottschick, pp. 64-65.
1981 *Cecilioides (Cecilioides) aciculella* (Sandberger). – Lueger, p. 49, pl. 7, fig. 1.
2004 *Cecilioides (Cecilioides) aciculella* (Sandberger 1874). – Harzhauser & Binder, p. 129, pl. 9, figs. 8-11.

Material: SMNS J67.230 (2 specimens, Jooss collection, *trochiformis* bed).

Type locality: Birk near Mörsingen, Baden-Württemberg (Sandberger 1875).

Type horizon: *Silvana*-beds.

Description: Slender, a bit spindle-shaped shell. Dextral, with a blunt, bulbous apex. The thin-shelled gastropod comprises c. five relatively flat whorls. The sutures are comparably deep. The first whorls grow slowly and regularly. From the penultimate to the last whorl there is a remarkable increase in size. Therefore, the last whorl is relative large. It comprises a bit more than 50% of the total shell height. The aperture is relatively low and comprises c. half of the height of the last whorl. The aperture is pear-shaped with a simple peristome. The columellar region is truncated near the basis of the shell. The columellar region appears somewhat thickened. It turns into a thin parietal callus. No umbilicus. Neither the teleoconch nor the protoconch comprise sculpture elements. Maximum height according to Lueger (1981) is 4.7 mm.

Discussion: Lueger (1981) described indistinct spiral channels close to the sutures, which are absent on the shells examined herein. The slender and tapered shell differs significantly from other taxa found in Steinheim am Albuch.

Additional distribution: Baden-Württemberg, South Germany, *silvana*-beds (MN5 according to Schweigert 1996; Esu 1999): Mörsingen, Zwiefaltendorf (Schlickum 1976). In Austria (according to Lueger 1981): Hollabrunn (Sarmatian); Eichkogel (Pont H); St. Margarethen and Richardhof (Harzhauser & Binder 2004).

Ecology: The extant European relatives live in subterranean soil habitats (Welter-Schultes 2012a).

Punctidae Morse, 1864
Punctum propygmaeum Andreae, 1904
Fig. 3.14

1904 *Punctum propygmaeum* n. sp. – Andreae, p. 6, fig. 4.
1920a *Punctum propygmaeum parvulum* n. v. – Gottschick, pp. 39-40.
1981 *Punctum (Punctum) pygmaeum propygmaeum* Andreae – Lueger, p. 39, pl. 4, figs. 4a-c; 5a-b.
2004 *Punctum propygmaeum* (Andreae 1904) – Harzhauser & Binder, p. 22.

Material: SMNS 15817-128 (5 specimens, Gottschick collection, *kleini* bed).

Type locality: Opole, Czech Republic (Andreae 1904).

Type horizon: Middle Miocene (MN7 according to Ginsburg 1999) freshwater limestone (Andreae 1904).

Description: Very small, low spired, slightly discoidal to trochiform shell. It consists of c. 3 ¾ whorls (Gottschick 1920a named a specimen with 4 ¼ whorls). The whorls are rounded with relative distinct sutures which are channel-like pronounced. According to that, the top of the single whorls looks a little bulged. The last whorl doesn`t bend down before reaching the aperture. The latter has an oblique-oval shape. The peristome is simple and sharp. The umbilicus is wide and deep and comprises c. 25% of the total shell width. The teleoconch of the examined specimens show thread-like densely packed growth lines on the last whorl, which are visible also on the lower side. Lueger (1981) mentioned a fine spiral sculpture, which cannot be seen on the examined specimens due to preservation. Also the growth lines are only visible on the last whorl. No sculpture is visible on the flat protoconch and therefore its size is unclear. The maximum diameter is c. 1.7 mm according to Lueger (1981).

Discussion: According to Lueger (1981), this could be only a local race or ecological variation ("Standortformen") of the extant *Punctum pygmaeum* (Draparnaud, 1801). The genera differs from similar taxa like *Discus* or *Janulus* by its higher spire and the wider umbilicus. *Punctum propygmaeum* is the only species of this genus in Steinheim am Albuch.

Additional distribution: According to Lueger (1981): Opole, Czech Republic (MN7 after Ginsburg 1999); Krems-Stein, Austria (Upper Miocene), Velm, Austria (Pont G/H), Eichkogel, Austria (Pont H).

Ecology: The Recent European relatives live mostly in litter layers of forests, with a wide ecological amplitude between wet habitats and warm and dry places (Welter-Schultes 2012a).

Patulidae Tyron, 1866
Discus pleuradrus (Bourguignat, 1881)
Fig. 3.15

1881 *Helix pleuradra* Bourguignat, p. 53, pl. 3, figs. 67-72.
1911 *Patula (Charopa) costata* n. sp. – Gottschick, pp. 501-502, pl. 7, fig. 15a-c.
1923 *Gonyodiscus (Gonyodiscus) pleuradra pleuradra*

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(Bourguignat). – Wenz, p. 341 [and further synonyms].
1981 *Discus pleuradrus* (Bourguignat). – Lueger, pl. 4, figs. 6a-c, 7.
2004 *Discus pleuradrus* (Bourguignat 1881). – Harzhauser & Binder, p. 130, pl. 7, figs. 9-11.

Material: SMNS J.65813 (9 specimens, Jooss collection, *kleini* bed).

Type locality: Sansan, France (Bourguignat 1881).

Type horizon: Middle Miocene (Fischer 2000), freshwater limestone (Bourguignat 1881).

Description: Small, dextral, discifom shell with moderately elevated spire. Typical *Discus*-shape. It consists of c. 5 ¾ closely wounded, convex whorls. The whorls are growing regularly and increase in size very slowly. The last whorl builds up a distinct keel on the periphery. It runs straight up to the aperture without turning down. The aperture has an oblique-oval shape. The peristome is simple and sharp. The two insertions are connected by a thin callus layer. The umbilicus is relative wide and perspectival. It comprises c. 25% of the total shell width. The teleoconch comprises remarkable, regularly arranged prosocline ribs with more or less constant space between them. These ribs run across the keel and continue on the lower side of the shell with the more or less same pronouncement. The protoconch has a slightly bulbous shape and consists of c. 1½ whorls. It lacks a sculpture.

Discussion: According to the pronouncement of the mentioned keel, there seems to be a distinctive variability within the species (see Lueger 1981). Following this author, *Patula costata* from Steinheim, described by Gottschick (1911) is a synonym of *D. pleuradrus*. It differs from the similar *Discus euglyphoides* (Sandberger, 1872) by a more convex basis and much weaker ribs on the lower side of the shell.

Additional distribution: Widespread species. In Baden-Württemberg it occurs in the *silvana*-beds (MN5 according Schweigert 1996; Esu 1999) of Mörsingen and Zwiefaltendorf (Schlickum 1976). Wenz (1923) also quoted Öhningen (Miocene). For Bavaria Wenz (1923) listed Undorf near Regensburg (MN 5 according to Scott 1981 quoted in Fejfar 1999), Georgensgmünd (Miocene), Hasenmühle near Eichstätt (Miocene), Fenterbach (Miocene), Wirtachtobel (Miocene). In Austria, the species occurs from the Badenian to the late Pannonian of the Austrian basins (Lueger 1981, quoted in Harzhauser & Binder 2004). For the localities in Hungary see Kókay (2006). For other localities see Wenz (1923).

Ecology: The Recent European relatives live under wood or gravel (Welter-Schultes 2012a; Wiese 2014).

Gastrodontidae Tyron, 1866
Janulus gottschicki (Jooss, 1912)
Fig. 3.16

1912 *Patula gottschicki* n. sp. – Jooss, pp. 32-33, pl. 2, fig. 2.
1920a *Janulus gottschicki* Jooss. – Gottschick, p. 38.
1923 *Janulus gottschicki* (Jooss). – Wenz, p. 302.
2016 *Janulus gottschicki* (Jooss 1912). – Salvador et al., p. 26, pl. 4, fig. 14.

Material: SMNS J65.7382 (1 specimen, Jooss collection; SMNS 106394 (1 specimen, Jooss collection, holotype).

Type locality: Steinheim am Albuch (Salvador et al. 2016).

Type horizon: *Pupa* (*Granaria*) layer of Pharion sandpit; upper *Gyraulus discoideus* bed to *G. trochiformis* bed) (Salvador et al. 2016).

Description: Small, disciformis, dextral shell. It consists of c. four moderately rounded whorls. The whorls are relative narrowly winded and they are regularly increasing in size. The sutures are deep. The aperture as well as the terminate portion of the last whorl is not preserved on the examined shells. According to Zilch (1960) the genus *Janulus* has a crescent aperture. The inside of the palatal region comprises two teeth. One lower tooth near the basis of the shell and one at approximately the middle of the palatal region. The last named tooth is a bit larger and lies a little further in front. Whether the two insertions are connected, cannot be clearly determined, but most probably they are not. The umbilicus has a steep margin. The teleoconch comprises regularly arranged, closely packed prosocline ribs. The space between them seems to be more or less constant all over the shell. At the periphery of the last whorl, these ribs change into fine stripes running towards the lower side of the shell. The flat protoconch comprises c. 1¼ whorls. It lacks a sculpture. Maximum diameter is 2.9 mm (Gottschick 1912).

Discussion: The stratigraphically older relative, *Janulus moersingensis* (Jooss, 1918), differs from *J. gottschicki* by a lower spire and the presence of six whorls.

Additional distribution: Wenz (1923) mentioned only Steinheim am Albuch.

Ecology: The extant relatives live on the Canary Islands and Madeira (Zilch 1959-1960).

Oxychilidae Hesse in Geyer, 1927 (1879)
Aegopinella subnitens (Klein, 1853)
Fig. 3.17

1853 *Helix subnitens* mihi. – Klein, p. 210, pl. 5, fig. 7.
1920a *Hyalina subnitens* Klein fa. *recedens* n. f. – Gottschick, p. 33.
1923 *Oxychilus subnitens subnitens* (Klein). – Wenz, p. 282 [and further synonyms].
1998 *Aegopinella subnitens* (v. Klein 1853). – Finger, p. 18.
2016 *Aegopinella subnitens* (Klein 1853). – Salvador et al., p. 37, pl. 8, fig. 20.

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Material: SMNS 106435-a (1 specimen, Klein collection, lectotype); SMNS 106435-b (2 specimens, Klein collection, paralectotype); SMNS 15817-41 (35 specimens, Gottschick collection, *sulcatus*/*trochiformis* beds).

Type locality: Zwiefalten, Baden-Württemberg (Salvador et al. 2016).

Type horizon: *Silvana*-beds (Salvador et al. 2016).

Description: Dextral, flat and thin shell with a very low spire and c. four convex whorls. The whorls grow regularly and rapidly with a large last whorl. The peristome is simple and sharp. Whether or not the two insertions are connected, cannot be seen on the studied specimens from Steinheim am Albuch. According to shells from Mörsingen (*silvana*-beds, MN5 according to Schweigert 1996; Esu 1999) the insertions are not connected. The umbilicus is remarkably wide with relatively steep marginal slope. It comprises c. 36% of the total shell width. The teleoconch is covered by fine, prosocline growth lines. However, these are unevenly expressed on the shell. Spiral lines as mentioned by Gottschick (1920a) cannot be seen at 50x magnification. The flat protoconch lacks a sculpture and consists of c. 1¼ whorls. According to the present specimens, the maximum diameter is 10 mm.

Discussion: Due to the smaller size, Gottschick (1920a) named the specimens from Steinheim am Albuch *Hyalina subnitens* fa. *recedens*. For the differences to *A. erecta* see there.

Additional distribution: Baden-Württemberg, South Germany, *silvana*-beds (MN5 according to Schweigert 1996; Esu 1999): Emerberg near Zwiefalten, Hohenmemmingen (Wenz 1923), Mörsingen. Other occurences quoted by Wenz (1923) are: Öhningen (Miocene) and Hengen (Middle Miocene). In Bavaria, Undorf near Regensburg (MN 5 according to Scott 1981, as cited in Fejfar 1999). For more localities see Wenz (1923).

Ecology: Probably more wet habitats like most of the extant European species of *Aegopinella* (see Wiese 2014).

Aegopinella erecta (Gottschick, 1920)
Fig. 3.18

1920a *Hyalina subnitens* Klein var. *erecta* n. v. – Gottschick, p. 33.
1923 *Oxychllus subnitens erectum* (Gottschick). – Wenz, p. 284.
1976 *Aegopinella erecta* (Gottschick). – Schlickum, p. 13, pl. 3, fig. 41.

Material: SMNS /65.683 (4 specimens, Jooss collection). Type material is missing (Salvador et al. 2016).

Type locality: Steinheim am Albuch, Grothau (Gottschick 1920a).

Type horizon: Steinheimer Seeschichten (Gottschick 1920a).

Description: Flat, slightly disciform, dextral shell. It has a relative weakly elevated spire. The shell consists of c. 4 ½ rounded whorls that grow regularly. The sutures are moderately deep. The last whorl does not bend down before reaching the aperture. The aperture has an oblique-oval shape and a simple and sharp peristome. Whether the two insertions are connected or not, cannot be seen on the present specimens. The umbilicus comprises c. 25% of the total shell width and has a relatively steep marginal slope. The teleoconch comprises fine, prosocline growth lines which are unevenly pronounced within the shell. Spiral lines are not visible (50x magnification). The slightly bulbous protoconch lacks a sculpture. It consists of c. 1¼ to 1½ whorls. Maximum diameter according to Gottschick (1920a) is 6.5 mm.

Discussion: Originally, Gottschick (1920a) described this species as variation of *A. subnitens*. Because of the following differences to *A. subnitens*, a species rank is justified: (1) the more rounded whorls; (2) the slower growth of the whorls; (3) as the result of (2), a lower last whorl; (4) a higher spire; (5) a more bulbous protoconch; (6) a smaller umbilicus.

Additional distribution: Wenz (1923) mentioned only Steinheim am Albuch.

Ecology: See *A. subnitens*.

Aegopinella? procellaria (Jooss, 1918)
Fig. 4.1

1918 *Hyalina procellaria* Jooss, p. 289.
1923 *Oxychilus procellarius* (Jooss). – Wenz, p. 279 [and further synonyms].
1981 *Oxychilus procellarius* (Jooss). – Lueger, p. 46, pl. 6, fig. 2a-c.
2006 *Oxychilus procellarius* (Jooss) 1918. – Kókay, p. 78.
2016 *Aegopinella? procellaria* (Jooss 1918). – Salvador et al., p. 32, pl. 7, fig. 8.

Material: SMNS 15817 (1 specimen, Gottschick collection, *sulcatus* bed).

Type locality: Mörsingen, Baden-Württemberg (Salvador et al. 2016).

Type horizon: S*ilvana*-beds (Salvador et al. 2016).

Description: Small, dextral and flat shell. Typical "*Oxychilus*- shape". It consists of c. 3 1/2 rounded whorls which increase in size relatively rapidly. Particularly the last one is very convex. The sutures comprise a concave indentation. The last whorl does not turn down before reaching the aperture. The latter has an oblique-oval shape and a simple peristome. The two insertions are connected by a callus layer, which is, however, incompletely preserved. The deep umbilicus comprises c. 14% of the total shell width. The teleoconch

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bears no sculpture. Only some traces of thread-like growth lines are hardly visible. The flat protoconch also comprises no sculpture and consists of c. 1.5 whorls. The maximum diameter according to Lueger (1981) is 7.3 mm.

Discussion: According to the small size, this specimen is probably a juvenile/subadult one. *Aegopinella*? *procellaria* is remarkably flatter than *A. erecta*. *A. subnitens* has a weakly higher spire and a more oblique aperture.

Additional distribution: Mörsingen, Baden-Württemberg, South Germany, *silvana*-beds (MN5 according to Schweigert 1996; Esu 1999). For Austria, Wenz (1923) and Lueger (1981) quoted Leobersdorf, Vienna Basin (Pannon ?D/E). Harzhauser & Binder (2004) also mentioned Eichkogel, Vienna Basin (Pannonian). Hungary: Öcs, (Upper Pannonian, Fordinál 1996), Somlóvásárhely (Lower Miocene), Vápalota (Sarmatian) (Kókay 2006). Slovakya: Orešany (Upper Pannonian; Fordinál 1996).

Ecology: Probably more wet habitats like its extant European relatives (see Welter-Schultes 2012a).

Pristilomatidae Cockerell, 1891

Vitrea procrystallina steinheimensis Gottschick, 1920
Fig. 4.2

1920a *Vitrea procrystallina steinheimensis* n. v. – Gottschick, pp. 37-38.
1923 *Vitrea procrystallina steinheimensis* Gottschick. – Wenz, p. 294.
1981 *Vitrea procrystallina steinheimensis* Gottschick. – Lueger, pp. 42-43, pl. 5, figs. 4, 7.
2004 *Vitrea procrystallina steinheimensis* Gottschick 1920. – Harzhauser & Binder, pp. 132-133, pl. 11, figs. 11-13.

Material: SMNS J 65.703 (6 specimens, Jooss collection, *kleini* beds). Type material is missing (Salvador et al. 2016).

Type locality: Steinheim am Albuch (Gottschick 1920a).

Type horizon: Steinheimer Seeschichten, *kleini* bed (Gottschick 1920a).

Description: Small, flat discifom shell with a low spire. It has c. 4 ¾ whorls which grow moderately rapid and regularly. The whorls are slightly rounded. The sutures are flat. The last whorl develops a faint shoulder. It does not turn down before reaching the aperture. The peristome has a sharp margin and is crescent shaped. The funnel-like umbilicus comprises c. 25% of the total shell width. Shell basis slightly rounded. Maximum width c. 2.5 mm. On the teleoconch, some growth lines are visible, but only at a magnification of 25x. The spiral lines described by Gottschick (1920a) could not be seen. The protoconch is flat and very hard to determine. It consists of c. 1.5 whorls and lacks a sculpture.

Discussion: According to Gottschick (1920a), this subspecies is more domed on the upper side than the nominate species. It is the only *Vitrea* species known from Steinheim am Albuch.

Additional distribution: Germany: Andelfinger Berg, Baden-Württemberg (Miocene) (Gottschick 1920a); Richardhof, Austria (Late Miocene) (Harzhauser & Binder 2004); Leobersdorf, Austria (Miocene) (Wenz 1923).

Ecology: The extant European relatives live in various habitats (Welter-Schultes 2012a).

Zonitidae Mörch, 1864

Archaeozonites subcostatus (Sandberger, 1875)
Fig. 4.3

1875 *Archaeozonites subcostatus* Sandberger, p. 604.
1902 *Archaeozonites subcostatus* Sandberger. – Jooss, p. 304.
1919 *Zonites subcostatus* Sandberger. – Gottschick, p. 126.

Material: SMNS 10588 (1 specimen, original material of Jooss 1902). Type material is missing (Salvador et al. 2016).

Fig. 4. 1 – *Oxychilus procellarius* (Jooss, 1918) Scale 1 mm. SMNS 15817. **2** – *Vitrea procrystallina steinheimensis* Gottschick, 1920 Scale 500 µm. SMNS J65.703. **3** – *Archaeozonites subcostatus* (Sandberger, 1875). Scale 5 mm. SMNS 10588. **4** – *Archaeozonites costatus* (Sandberger, 1875). Scale 5 mm. 15817-38. **5** – *Vitrina suevica* Sandberger, 1872. Scale 2 mm. SMNS 15817-11. **6** – *Helicodonta involuta angitorta* Jooss, 1912, holotype. Scale 2 mm. SMNS 106365. **7** – *Leucochroopsis kleini* (Klein, 1846). Scale 2 mm. SMNS 15817/13. **8** – *Apula steinheimensis* (Jooss, 1918). Scale 10 mm. Syntype. SMNS 106432. **9** – *Pseudochloritis insignis* (Zieten, 1832) Neotype. Scale 10 mm. SMNS 23910b. **10** – *Megalotachea sylvestrina* (Schlotheim, 1820). Scale 10 mm. SMNS 15.817-130. **11** – *Arion* sp. Scale 1 mm. SMNS 15817. **12** – *Milax* sp. Scale 1 mm. SMNS 15817-19. **13** – *Azeca tridentiformis* Gottschick, 1911. Detail of the protoconch. Scale 100 µm. SMNS 15817-34. **14** – *Leucochroopsis kleini* (Klein, 1846). Detail of the protoconch. Scale 100 µm. SMNS 15500.

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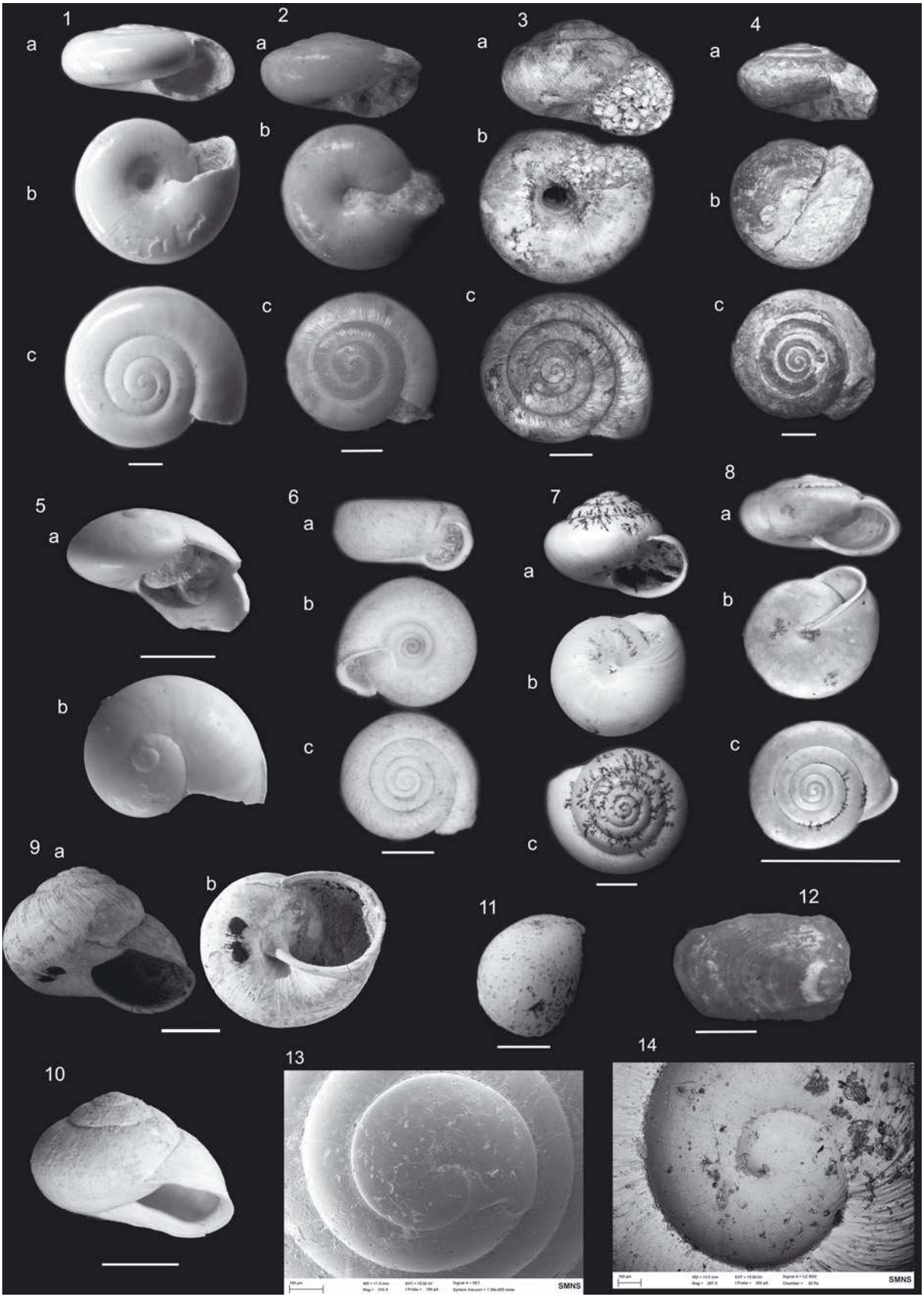

Fig. 4.

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Type locality: Sandberger (1875) did not mention a type locality.

Type horizon: Obere Süßwassermolasse (Miocene) (Sandberger 1875).

Description: Dextral, helicoid shell with blunt apex. It consists of approximately 4 ½ rounded whorls which grow regularly. The sutures are generally deep apart from the first one, which is remarkable flat. The last whorl comprises a slight keel, which disappeared c. ¼ whorl before the aperture. The last whorl does not turn down before reaching the aperture. The latter has an oval shape. The peristome is simple. Whether the two insertions are connected or not, cannot be seen because this region is covered by sediment. The deep umbilicus comprises c. 29% of the total shell width and has a relatively steep marginal slope. The teleoconch comprises regularly arranged, prosocline ribs that can already be seen without microscope. These ribs are continued at the basis of the shell but in a much lesser pronouncement. The protoconch is flat and consists of c. 1 to 1¼ whorls. No sculpture is visible. The specimen has a diameter of 18 mm.

Discussion: This species was described by Sandberger (1875), but without illustration. The description given by the author fits to the examined specimen. Wenz (1923) expected *M. subcostatus* to be a synonym of *Miozonites costatus* (Sandberger, 1875). However, *M. subcostatus* differs from *M. costatus* with respect to the keel and umbilicus width. The latter has an umbilicus width of c. 22% of the total shell width, while at *M. subcostatus* the percentage is c. 29%.

Additional distribution: Sandberger (1875) qouted Häder (Dinkelscherben), Bavaria, Miocene, Öhningen, Baden-Württemberg (MN7 according to Gentry et al. 1999) and Würrenlos, Kanton Aargau, Switzerland, Miocene.

Ecology: Probably more wet habitats like many of the extant European Zonitidae (see Welter-Schultes 2012a).

Archaeozonites costatus (Sandberger, 1875)
Fig. 4.4

1875 *Archaeozonites costatus* Sandberger, p. 604.
1916 *Zonites costatus* (Sandberger). – Gottschick & Wenz, pp. 21-23, pl. 1, fig. 1a-c.
1923 *Zonites costatus* (Sandberger). – Wenz, pp. 254-257.
2002 *Miozonites costatus* (Sandberger 1874). – Binder, pp. 168-169, pl. 1, figs. 14-16; pl. 3, fig. 8; pl. 7, fig. 3; pl. 8, fig. 4.

Material: SMNS 15817-38 (2 specimens, Gottschick collection, *kleini* bad). Type material is missing (Salvador et al. 2016).

Type locality: Sandberger (1875) named no type locality.

Type horizon: Obere Süßwassermolasse (Miocene) (Sandberger 1875).

Description: Flat, dextral helicoid shell. Typical "Zonitidae-shape". It consists of 4 ¼ regularly growing whorls, which are flat apart from the last one. The last whorl forms a distinct keel in the middle, which extends towards the aperture. The upper part of the last whorl runs ramp-like down to this keel. The sutures are flat. The deep umbilicus comprises about 22% of the total shell width. The umbilicus walls run downward relatively steeply. The protoconch is flat. The specimens are not completely preserved. According to that, no sculptures are visible. Also the aperture region is incomplete. The aperture probably had an oblique-oval shape. The specimen has a diameter of 20 mm.

Discussion: The species was described by Sandberger (1875), but without any illustration. Gottschick & Wenz (1916, pl. 1, fig. 1a-c) gave a drawing of the species and wrote, it might be identical with *Miozonites costatus* (Sandberger, 1875) („…dürfte wohl identisch sein mit dem von Sandberger nur flüchtig erwähnten *Archaeozonites costatus*"). The here described specimen fits to the description given by Sandberger (1875). According to Binder (2002) this species shows a distinct disparity in shell morphology.

Additional distribution: Locations quoted by Sandberger (1875) are Mörsingen, Häder (Dinkelscherben), Bavaria, Miocene, and Gutgrieder Graben at the Peissenberg, Bavaria (all are Miocene in age). Gottschick & Wenz (1916) also mentioned Hohenmemmingen (*silvana*-beds, MN5 according to Schweigert 1996; Esu 1999) and Undorf near Regensburg (MN 5 according to Scott 1981, as quoted in Fejfar 1999) and the Pfänder region near Bregenz, Austria (probably MN5/6). For Hungary, Kókay (2006) listed the following locations: Pusztamiske (Upper Badenian), Hegymagos (Lower Badeinan), Herend (Lower Badenian), and Vápalota (Sarmatian). Binder (2002) mentioned the following locations in the Korneuburg Basin (Karpatian) in Austria: Teiritzberg, Obergänserndorf and Großrußbach. For other localities see Wenz (1923).

Ecology: Probably forests (Binder 2002).

Vitrinidae Fitzinger, 1833
Vitrina suevica Sandberger, 1872
Figs. 4.5, 5.6

1872 *Vitrina suevica* Sandberger, pl. 29, figs. 27, 27b; 1875, p. 602.
1919 *Vitrina suevica* Sdbgr. – Gottschick, pp. 122-123.
1923 *Vitrina suevica suevica* Sandberger. – Wenz, pp. 219-220.
2016 *Vitrina suevica* (Sandberger 1872). – Salvador et al., p. 38, pl. 9, fig. 11.

Material: SMNS 106439 (1 specimen, holotype); SMNS 15917-11 (20 specimens, Gottschick collection).

Type locality: Neuselhalder Hof near Steinheim am Albuch (Salvador et al. 2016).

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Type horizon: Marl layers with *Planorbarius cornu* (Brongniart, 1810) (Salvador et al. 2016).

Description: Small, ear-shaped shell with a very low spire. It consists of ca 2 ½ convex whorls which increases in size very rapidly. This results in a wide last whorl. The sutures are flat but also somewhat gutter-like. The peristome is simple. No umbilicus is present. The teleoconch comprises mostly no sculpture. Some specimens show hardly visible punctate depressions. The flat protoconch has c. 1.5 whorls and shows regularly arranged rows of tiny dots. This feature is characteristic for the Vitrinidae (Kerney et al. 1983).

Discussion: Gottschick (1920b) described *Vitrina suevica* fa. *erecta*. Unfortunately, the original material is lost and no other specimen of this variation could be found. The typical ear-shaped shell makes this taxon undistinguishable from all others found in Steinheim am Albuch.

Additional distribution: According to Wenz (1923): Hohenmemmingen, Baden-Württemberg, South Germany (*silvana*-beds, MN5 according to Schweigert 1996; Esu 1999). Undorf near Regensburg, Bavaria (MN5 after Schötz 1981 quoted in Fejfar 1999). Vermes near Delsberg, Switzerland (Miocene) (Wenz 1923). For other localities see Wenz (1923).

Ecology: The Recent European relatives live mostly in cool and humid habitats (Kerney et al. 1983).

Helicodontidae Kobelt, 1904
Helicodonta involuta angitorta Jooss, 1912
Fig. 4.6

1912 *Helicodonta involuta* Thomä var. *angitorta* n. var. – Jooss, p. 34, pl. 2, figs. 3, 3a.
1923 *Helicodonta* (*Helicodonta*) *involuta angitorta* Jooss. – Wenz, p. 452.
2016 *Protodrepanostoma involutum angitortum* (Jooss, 1912). – Salvador et al., p. 19, pl. 7, fig. 1.

Material: SMNS 196365 (1 specimen, holotype).

Type locality: Steinheim am Albuch, Pharion sandpit (Salvador et al. 2016).

Type horizon: *Pupa* (i.e., *Granaria*) layer (upper *Gyraulus discoideus* bed to *G. trochiformis* bed), Steinheimer Seeschichten (Salvador et al. 2016).

Description: Flat, dextral shell with sunken spire. The shell consists of c. 4 ½ rounded whorls. They grow slowly and regularly. The sutures are comparably deep. The last whorl runs ramp-like downward just before reaching the aperture. The aperture has a crescent shape and the peristome is reflected. The two insertions are not connected. The perspectival and deep umbilicus comprises c. 25% of the total shell width. The teleoconch is covered by straight ribs which are more or less regularly arranged. These ribs comprise small and irregularly distributed papillae. This irregularity is possibly due to preservation. The flat protoconch incorporates ca 1¼ whorls. No sculpture is visible. The diameter is 5 mm.

Discussion: We follow Manganelli & Giusti (2000b: 356) who assigned the species *involuta* to *Helicodonta*. Jooss (1912) described the here illustrated specimen as var. *angitorta*. However, there seem to be a certain degree of morphological disparity within this species. This can also be seen among the Recent *Helicodonta obvoluta* (Müller, 1774). Following Welter-Schultes (2012a), specimens of this taxon from Albania and Montenegro show some morphological differences compared to those from other regions. Already Jooss (1912) has mentioned the significant variability of the extant *H. obvoluta*. According to that more material would be necessary to determine the variability of the ancient *Helicodonta involuta* (Thomae, 1845).

Additional distribution: Wenz (1923) mentioned only Steinheim am Albuch.

Ecology: The Recent European relatives live in more humid habitats (see Welter-Schultes 2012a).

Hygromiidae Tyron, 1866
Leucochroopsis kleinii (Klein, 1846)
Fig. 4.7, 4.14

1846 *Helix kleinii* Krauss. – Klein, p. 69, pl. 1. fig. 8.
1846 *Helix mucronata* Klein, p. 72, pl. 1, fig. 15.
1853 *Helix carinulata* Klein, p. 208, pl. 5, fig. 5.
1916 *Hygromia* (*Trichiopsis*) *kleini* (Klein). – Gottschick &Wenz, pp. 30-31.
1920a *Hygromia* (*Trichiopsis*) *kleini* Klein. – Gottschick, pp. 42-43.
?1920a *Hygromia* (*Trichiopsis*) *kleini scalaris* n. f. – Gottschick, pp. 42-43, pl. 1, fig. 2.
1923 *Trichia* (*Leucochroopsis*) *kleini kleini* (Klein). – Wenz, pp. 429-434 [and further synonyms].
1976 *Leucochroopsis kleini* (Klein). – Schlickum, p. 15, pl. 3, fig. 52.
2004 *Leucochroopsis kleini* (Klein 1846). – Harzhauser & Binder, p. 133, pl. 11, figs. 8-10.
2016 *Leucochroopsis kleinii* (Klein 1846). – Salvador et al., pp. 21, 31, pl. 2, fig. 11.

Material: SMNS 15817/37 (4 specimens, *laevis* bed); SMNS 15817/35 (3 specimens, *laevis* bed); SMNS 15817/33 (3 specimens, *laevis* bed); SMNS 15817/31 (15 specimens, *laevis* bed); 15817/29 (8 specimens, *laevis* bed); SMNS 15817/13(1 specimen, *laevis* bed). All the specimens are from the Gottschick collection.

Type locality: Neue Steige near Hohenmemmingen, Baden-Württemberg (Klein 1846).

Type horizon: *Silvana*-beds.

Description: Dextral, helicoid shell with 4 to 5 convex whorls. The height and width of this species appears to be

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very variable. The flatter specimens have shallow sutures, while the high-spired ones have deeper sutures. Some specimens also comprise a more or less distinct keel on the last whorl. Shortly before reaching the aperture, the last whorl turns down very slowly. The peristome is simple and the aperture has a horseshoe-like shape. Only at the umbilicus region, the columellar margin is reflected. The umbilicus ranges from small and slit-like to completely covered. The teleoconch comprises radial growth lines whose intensity is different within the species. The shell comprises little, regularly arranged papillae, which sometimes causes a net-like appearance together with the growth lines. However, the distribution of these papillae can be very variable. According to Gottschick (1920a) also their shape can be extremely variable. The protoconch lacks a sculpture and consists of c. 1¼ to 1½ whorls. According to the examined specimens, the maximum diameter of this species seems to be 10 mm.

Discussion: Similar to the specimens of the *silvana*-beds, the shells from Steinheim am Albuch show an extreme disparity. There are no clearly differences between the Steinheim specimens and those of the *silvana*-beds. The variability includes the height-width ratio, the shape of the papillae as well as their distribution on the shell. Also, the umbilicus ranges from slit-like to completly closed. Already Gottschick (1920a) mentioned a significant variability. The original material to *Helix kleini* Krauss in Klein, 1846 is lost (Salvador et al. 2016). Only the original material to *Helix carinulata* Klein, 1846 and *Helix mucronata* Klein, 1846, which were later synonymized with *Helix kleini*, are present. Gottschick (1920a) separated a form as *Hygromia* (*Trichiopsis*) *kleini scalaris* n. f. Unfortunately, no specimen of that form could be found during our studies. Only a drawing is present in Gottschick (1920a, pl. 1, fig. 2) and therefore it is not possible to verify the status of this taxon.

Additional distribution: Baden-Württemberg, South Germany, *silvana* beds (MN5 according to Schweigert 1996; Esu 1999): Zwiefalten; Randecker Maar near Kirchheim unter Teck, Zwiefaltendorf (Schlickum 1976). According to Wenz (1923): Altheim near Ehingen, Deutschhof near Pflummern, Emeringen (Miocene). For other localities in Germany and Switzerland see Wenz (1923). Austria (after Lueger 1981): Leobersdorf (brickyard) (Pannon D); Vösendorf, Hennersdorf (Pannon E), Götzendorf (Pont F). For other localities in Austria and Hungary see Lueger (1981) and Harzhauser & Binder (2004).

Ecology: More humid habitats like forests (Lueger 1981).

Apula steinheimensis Jooss, 1918
Figs. 4.8, 5.1

1918 *Klikia coarctata* (Klein) *var. steinheimensis* n. var. – Jooss, p. 294.
1923 *Klikia (Apula) coarctata steinheimensis* (Jooss). – Wenz, p. 537.
1981 *Klikia (Apula) coarctata steinheimensis* Jooss. – Lueger, pp. 69-70, pl. 10, fig. 4.
2016 *Apula coarctata* (Klein 1853). – Salvador et al., p. 35, pl. 8, fig. 10.

Material: SMNS 106432 (1 specimen, Jooss collection, ?syntype); SMNS J66.311 (1 specimen, Jooss collection); SMNS J66.309 (1 specimen, Jooss collection); SMNS J66.308 (1 specimen, Jooss collection).

Type locality: Steinheim am Albuch (Salvador et al. 2016).

Type horizon: Steinheimer Seeschichten (Salvador et al. 2016).

Description: Medium-sized, flat shell with hardly recognizable spire. It consists of c. five convex whorls. The last one comprises a slight keel, which already disappeared c. ¼ whorl before reaching the aperture. The pronouncement of this keel seems to be variable within this species. The whorls grow regularly and with a medium growth rate. The sutures are moderately deep. The last whorl runs straight up until c. 2 mm before the aperture. At this point it runs obliquely downwards. The aperture has an oblique-oval to egg-like shape. The peristome is remarkably reflected and the margin is slightly thickened. The shell has rimate umbilicus region. The teleoconch of the syntype comprises no sculpture. However, growth lines are visible on other shells and Lueger (1981) mentioned a thread-like spiral sculpture and a hardly visible papillae sculpture. The protoconch consists of c. 1¼ flat whorls. Indistinct radial ribs are visible on some specimens (pl. 4, fig. 1). Maximum diameter according to Lueger (1981) is 13.2 mm.

Discussion: Jooss (1918) named this species as a variety of *Apula coarctata* (Klein, 1853). The two taxa are very similar according to their morphology. *A. steinheimensis* is flatter and has a different upper part of the palatal margin. Additionally to that *A. coarctata* has a bit more rounded whorls.

Additional distribution: Lueger (1981) mentioned Leobersdorf (brickyard) (Pannon D).

Fig. 5. 1 – *Apula steinheimensis* (Jooss, 1918). Detail of the protoconch. Scale 100 μm. 15524. **2** – *Gastrocopta sandbergeri* Stworzewicz & Prisyazhnyuk, 2006. Detail of the protoconch. Scale 20 μm. 15817. **3** – *Pupilla steinheimensis* (Miller, 1900). Detail of the protoconch. Scale 100 μm. SMNS J67.537. **4** – *Gibbulinopsis submuscorum* (Gottschick & Wenz, 1919). Detail of the protoconch. Scale 100 μm. SMNS J67.498. **5** – *Vertigo callosa* Reuss, 1849. Detail of the protoconch. Scale 30 μm. SMNS 15817- 108. **6** – *Vitrina suevica* Sandberger, 1872. Detail of the protoconch. Scale 30 μm. SMNS 15817-34. **7** – *Oxyloma minima* (Klein, 1853). Detail of the protoconch. Scale 200 μm. SMNS 15817-4. **8** – *Pseudochloritis insignis* (Zieten, 1832). Detail of the protoconch. Scale 200 μm. SMNS 23910b.

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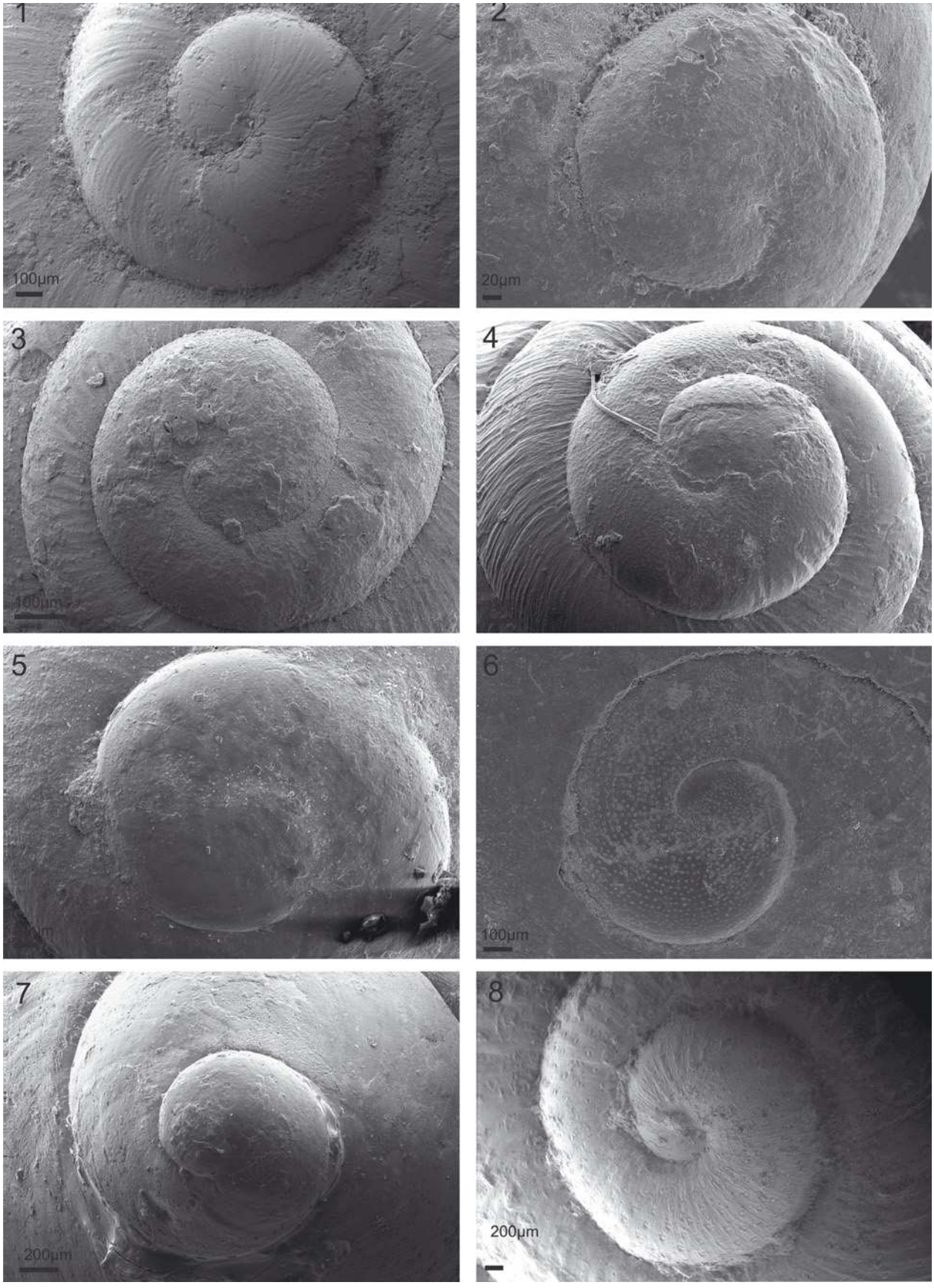

Fig. 5.

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Ecology: Probably drier habitats (Lueger 1981).

Helicidae Rafinesque, 1815
Pseudochloritis insignis (Zieten, 1832)
Figs. 4.9, 5.8

1832 *Helix insignis* Schübler. – Zieten, p. 38, pl. 29, fig. 1.
1846 *Helix insignis* Schübler. – Klein, p. 65, pl. 1, fig. 2.
1846 *Helix Steinheimensis*. – Klein, p. 70, pl. 1, fig. 10.
1900 *Helix (Campylaea) insignis* var. *maior*. – Miller, p. 394, pl. 7, fig. 1.
1920a *Chilostoma (Dinarica) insignis* (Schübler) Zieten. – Gottschick, p. 44.
1929 *Joossia insignis* (Zieten). – Pfeffer, p. 246
2008 *Joossia insignis* (Zieten 1830). – Binder, pp. 176-177, pl. 2, fig. 5a-c, pl. 5, figs. 1, 2, pl. 6, fig. 4.
2015 *Pseudochloritis insignis* (von Zieten 1832) – Höltke & Rasser, figs. 4.1, 4.2, 4.7, 4.8, 5.7, 5.8, 6.1-6.12.
2016 *Tropidomphalus insignis* (fide Höltke & Rasser 2015). – Salvador et al., p. 28, pl. 5, fig. 10.

Material: SMNS 23910b (1 specimen, neotype); SMNS J66.156 (7 specimens, Jooss collection, *trochiformis* bed); SMNS 4779a (1 specimen, holotype of *Helix (Campylaea) insignis* var. *maior* Miller, 1900); SMNS 106431 (1 specimen, holotype of *Helix steinheimensis* Klein, 1846).

Type locality: Steinheim am Albuch (Zieten 1832; Salvador et al. 2016).

Type horizon: Steinheimer Seeschichten (Salvador et al. 2016).

Description: Dextral, helicoid and massive shell with c. 4 1/2 convex whorls, which grow regularly. The sutures are deep. Height and width of this species are extremely variable. It ranges from flat shells to high-spired specimens. The shells of *P. insignis* are normally wider than high. The last whorl runs obliquely downwards towards the aperture. The latter has an oblique egg-like shape. The peristome is deflected. The two insertions are connected by a thin callus layer. The umbilicus is deep and half covered by a parietal/columellar callus. The teleoconch comprises partly regularly arranged axial ribs/growth lines. The intensity of this ribs/growth lines is very different within this species. The secondary ribs on the last whorl, described by Binder (2008), are also variable according strengthens. On some specimens, very weak traces of spiral lines are visible. The microsculpture of the teleoconch consists of little pits on the first whorls and disappear later. The protoconch is built up of c. 1½ whorls which have a remarkable bulbous shape. The protoconch has little pustulae and hair pits (Fig. 5.8), which was already described by Gottschick (1920) and Binder (2008). On some specimens, also some folds can be found on the protoconch. The size ranges from 24 to 40 mm.

Discussion: According to biogeography as well as shell morphology, a membership in the genus *Pseudochloritis* is most reasonable. For a detailed discussion about this species see Binder (2008) as well as Höltke & Rasser (2015). According to the last named authors, *Pseudochloritis insignis* differs from the very similar *P. incrassata* (Klein, 1853) by its larger size, more prominent prosocline radial ribs and a less reflected peristome.

Additional distribution: Höwenegg near Engen, Baden-Württemberg, South Germany (MN9 according to Hünermann 1989, quoted in Heissig 1999); Böttingen, Baden-Württemberg, South Germany, Miocene. Specimens from these localities exist in the SMNS collection and could be verified herein. Wenz (1923) also quoted other occurrences, but the determinations are not verifiable. Large forms of the Badenian species *Pseudochloritis incrassata* (Klein, 1853) often look very similar to *P. insignis*. Therefore, literature data about the distribution are difficult without re-evaluation of the material.

Ecology: Probably warm and humid forests (Binder 2008).

Palaeotachea sylvestrina (Schlotheim, 1820)
Fig. 4.10

1820 *Helicites sylvestrinus* Schlotheim, p. 99.
1920b *Cepaea gottschicki* Wenz. – Gottschick, pp. 49-52.
1923 *Cepaea sylvestrina gottschicki* Wenz – Wenz, pp. 93-695 [for the very large number of synonyms see Wenz 1923].
1929 *Megalotachea sylvestrina* Schlot. – Pfeffer, p. 147.
2016 *Palaeotachea sylvestrina* (Schlotheim 1820). – Höltke & Rasser, pp. 245-248, figs. 5.6-5.9, 6.5.

Material: SMNS 106767 (1 specimen, original to Höltke & Rasser 2016); SMNS 15817-112 (9 specimens, Gottschick collection); SMNS IMDAS IF. 12193/2008 (16 specimens, Bechter collection).

Type locality: Miocene freshwater limestone of the Nördlinger Ries, Bavaria (Wenz 1920a).

Type horizon: Obere Süßwassermolasse, *sylvestrina*-beds (Wenz 1920a).

Description: Dextral, helicoid shell with a typical "*Cepaea*-shape". It consists of c. 4 ½ regularly growing whorls. The sutures are moderately deep. The last whorl runs obliquely downward shortly before reaching the aperture. The aperture has an oblique-oval shape. The peristome is slightly reflected and also slightly thickened. The two insertions are connected by a parietal callus. No umbilicus. The teleoconch comprises fine, irregularly arranged growth lines, which is, however, not visible on all specimens. On some very well preserved specimens, fine spiral lines are visible as well. The protoconch consists of c. 1¾ whorls and lacks a sculpture. The maximum width is c. 27.25 mm. The species is, however, very variable in height and width.

Discussion: The specimens from Steinheim am Albuch

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can be often found in literature as *Palaeotachea gottschicki* Wenz, 1920, or *Palaeotachea sylvestrina gottschicki* Wenz, 1920. For genus discussion see Pfeffer (1929) and Nordsieck (1986, 2014). Wenz (1920a, b) divided *sylvestrina* into three subspecies: *P. sylvestrina sylvestrina* (Schlotheim), *P. sylvestrina gottschicki* Wenz and *P. sylvestrina geniculata* (Sandberger). However, he also mentioned that there are no distinct boundaries between them. We agree with this finding and summarize them into one species, *Palaeotachea sylvestrina* (Schlotheim, 1820) (see Höltke & Rasser 2016 for details).

Additional distribution: Baden-Württemberg, South Germany: Höwenegg (MN9 according Hünermann 1989, quoted in Heissig 1999); Hohenstoffeln (Middle to Upper Miocene according to Geyer & Gwinner 2011). Bavaria, South Germany: Lauchheim (Miocene); Reimlingen at Nördlinger Ries (Miocene); Trendel near Öttingen (Miocene). Switzerland: Nebelbergweg near Nunningen, Kanton Solothurn (MN9 according Kälin & Engesser 2001); Le Locle, Kanton Neuenburg (MN 7 according to Boon-Kristkoiz & Kristkoiz 1999); Ramsen, Kanton Schaffhausen (Miocene).

Ecology: Probably the same mesophile habitat like the extant and morphologically similar genus *Cepaea*.

Slugs

According to their shape, the calcareous plates can be assigned to three different families: Arionidae, Limacidae and Milacidae. Whether or not the morphology of the plates are taxonomically relevant for the determination on genus or species level, is unknown. Taxonomic studies of extant slugs focus only on anatomy and DNA (see for example Rowson et al. 2014).

Arionidae Gray, 1840
Arion sp.
Fig. 4.11

Material: SMNS 15817 (>10 specimens, Gottschick collection). Whitish, rounded calcareous granule, c. 2 mm in length. Without any recognizable sculpture.

Ecology: Varying, but the extant European relatives live generally in more humid habitats (see Welter-Schultes 2012a).

Milacidae Ellis, 1926
Milax sp.
Fig. 4.12

Material: SMNS 15817-19 (>10 specimens, Gottschick collection). The plate-shaped shell rudiments are up to c. 4 mm long and 3 mm wide. The nucleus is situated more or less in the centre, but this can vary. There are concentric growth lines on the surface. The shell rudiment is mostly fairly symmetrical.

Ecology: The extant European relatives live in different habitats (Welter-Schultes 2012a).

5. Palaeoenvironmental aspects

The land snails identified and described here cover the complete range from xerophil to hygrophil habitats, and some forms with unkown ecological preferences. What is striking is the high abundance of specimens from the xerophile genus *Granaria*. This fits with the results of Schweigert (1993), who concluded that the surroundings of the crater lake was a deciduous dry forest rich in species of *Quercus*, accompanied by *Celtis*, *Juglans*, *Pistacia* and Leguminosae. Laurophyllous trees and conifers were nearly totally absent. Schweigert (1993) interpreted the climate as warm-temperate with marked dry periods. Gregor (1983) stated that Steinheim had a dense and uniform mesophytic deciduous forest with a palaeotropical-arctotertiary character. Most of the fossil plants from Steinheim have relatives inhabiting Southeast Asia as well as the southeastern part of the USA (Gregor 1983). The macroflora is currently under revision by J. Kovar-Eder (pers. comm. 2017). Mean annual precipitation in Central & Eastern Europe during the time of Lake Steinheim was between 125 and 375 mm (Böhme et al. 2011). The mean annual temperature was approximately 15 °C (Böhme 2003), which is in accordance with Gregor (1983) and with estimates from other south-west German localities (Eberhard 1989), even though Tütken et al. (2006, and discussion therein) found that lake water temperatures ranged from 16.7 to 21.8 °C.

6. Conclusion and comparison with other Miocene localities

48 different land snail species representing 34 different genera could be identified within the collections of Miller, Jooss and Gottschick as well as in the original material of Finger (1998) from the Steinheim Basin. They indicate a considerable spectrum of different habitats. The inferred ecological preferences of the studied snails range from very humid (*Oxyloma*) to dry (*Granaria*) environments. The most abundant specimens are members of *Granaria*. Most of the genera (24) are extant. Most of them (21) are also common among the modern land gastropod fauna of Central Europe. The

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remaining three taxa are today distributed in other geographic regions: *Gastrocopta* in North and South America, Cap Verde Islands, North Africa, Sibiria, Central and East Asia, Australia, Pacific Ocean islands (Zilch 1959; Kovanda 2004); *Strobilops* in North, South and Central America (Zilch 1959); *Janulus* on the Canary Islands and Madeira (Zilch 1960). 13 species from the Steinheim sediments (MN7) also occur in the older *silvana*-beds (MN5). The landsnail fauna of Steinheim comprises 15 endemic taxa: *Cochlostoma ebfraasi*, *C. excellens*, *Azeca tridentiformis*, *Cochlicopa procera*, *Strobilops joossi*, *Truncatellina lentilii*, *Vertigo milleri*, *Granaria grossecostata*, *Granaria crassiventer*, *Pupilla iratiana suevica*, *P. steinheimensis*, *Gibbulinopsis submuscorum*, *Janulus gottschicki*, *Aegopinella erecta*, and *Helicodonta involuta angitorta*. The abundance of the three species of *Granaria* contrasts with their rarity in the older *silvana*-beds, which could be a response to a warmer and drier climate. The genus *Klikia*, which is very abundant in the *silvana*-beds, was not found in the Steinheim sediments. 15 species from Steinheim are also known from the older *silvana*-beds: *Oxyloma minima*, *Pseudoleacina eburnea*, *Palaeoglandina porrecta*, *Vertigo angulifera*, *Gastrocopta acuminata*, *G. nouletiana*, *Vallonia subcyclophorella*, *Opeas minutum*, *Cecilioides aciculella*, *Discus pleuradrus*, *Aegopinella subnitens*, *Aegopinella? procellaria*, *Archaeozonites costatus*, *Vitrina suevica*, and *Leucochroopsis kleinii*. The Upper Badenian part of the Bakony Mountains in Hungary (Kókay 2006) shares at least two species with the Steinheim sediments (*Gastrocopta nouletiana*, *Discus pleuradrus*). The Sarmatian sediments of the Bakony Mountains comprise additional species similar to those of the Steinheim Basin. Kókay (2006) mentioned nine species from Sarmatian sediments of the Bakony Mountains that are also present in Steinheim: *Carychium suevicum*, *Palaeoglandina porrecta*, *Vertigo callosa*, *Gastrocopta acuminata*, *G. nouletiana*, *Vallonia lepida*, *Discus pleuradrus*, *Oxychilus procellarius*, and *Vitrea procrystallina steinheimensis*. The forenamed author also mentioned *Klikia* for the Sarmatian sediments of the Bakony Mountains, which is absent in Steinheim. The younger Pannonian and Pontian sediments of the Vienna Basin share 13 species with Steinheim: *Pseudoleacina eburnea*, *Vertigo callosa*, *V. protracta suevica*, *Gastrocopta acuminata*, *G. nouletiana*, *Negulopsis gracilis*, *Cecilioides aciculella*, *Punctum propygmaeum*, *Discus pleuradrus*, *Oxychilus procellarius*, *Vitrea procrystallina steinheimensis*, *Leucochroopsis kleini*, and *Apula steinheimensis (*Lueger 1981). The Pannonian D of Leobersdorf, Austria, is the only known occurrence of *Apula steinheimensis* besides the type locality Steinheim am Albuch (Lueger 1981). The genus *Klikia* is also present in the Pannonian and Pontian of the Vienna Basin. Lueger (1981) also described *Granaria schuebleri* from the Vienna Basin, but the accompanying illustration shows the species *Granaria schlosseri* (Cossmann, 1908) (see Höltke & Rasser 2013). The malacofauna of Sansan, France (MN6) shares only two species with the younger Steinheim fauna: *Gastrocopta nouletiana*, *Discus pleuradrus* (Fischer 2000).

Unfortunately, most of the examined material from Steinheim had not been collected stratigraphically within the basin (apart from Finger 1998). Therefore, it is not possible to make assumptions about the vertical distribution of the single taxa within the sediments.

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Appendix

Table 1. Stratigraphic distribution of some of the landsnail species described from the Steinheim Basin according to Gottschick & Wenz (1919) and Gottschick (1919, 1920a-d). (A = abundant; R = rare).

Species	*kleini* beds	*steinheimensis* beds	*sulcatus* beds	*trochiformis* beds	*oxystoma* beds	*revertens* beds	*supremus* beds
Carychium suevicum	*x* (R)						
Oxyloma minima	x (A)						
Pseudoleacina eburnea	x (R)						
Azeca tridentiformis	x (A)						
Cochlicopa procera	x (R)						
Strobilops joossi	x (R)						
Truncatellina lentilli	x (R)		x (R)				
Vertigo angulifera			x (R)	x (R)			
Vertigo milleri			x	x			
Vertigo callosa	x (A)		x (A)				
Vertigo protracta suevica			x (R)				
Gastrocopta nouletiana	x (A)		x (R)				
Granaria schuebleri	x (A)						
Granaria grossecostata	x						
Vallonia subcyclophorella	x (A)						
Pupilla iratiana suevica	x						
Gibbulinopsis submuscorum	x (R)						
Triptychia steinheimensis	x	x	x	x	x	x	x
Cecilioides aciculella	x (R)						
Punctum propygmaeum	x (A)						
Discus pleuradrus	x (A)						
Janulus gottschicki	x						
Aegopinella subnitens	x (A)						
Archaeozonites subcostatus	x (R)						
Archaeozonites costatus	x (R)						
Vitrina suevica	x (A)						
Helicodonta involuta	x (R)						
Apula steinheimensis	x						
Pseudochloritis insignis	x (A)			x			

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Table 2. Missing material.

Missing taxa as named by Gottschick & Wenz	Reference
Succinea minima Klein fa. *pfeifferi* Gottschick 1920	Gottschick (1920b), pp.65-66, pl. 2, fig. 7.
Poiretia (Palaeoglandina gracilis) porrecta Gobanz fa. *steinheimensis* Jooss	Gottschick (1919), pp. 119-120.
Azeca (*Azeca*) *sexdentata* n. sp.	Gottschick (1920b), pp. 62-63, pl. 2, fig. 6.
Cochlicopa subrimata loxostoma Klein	Gottschick (1920b), pp. 63-64.
Strobilops (Strobilops) subconoidea (Jooss)	Gottschick & Wenz (1919), pp. 22-23.
Vertigo (Alaea) callosa divergens Flach	Gottschick & Wenz (1919), p. 14, pl. 1, fig. 29.
Vertigo (Alaea) callosa diversidens Sandberger	Gottschick & Wenz (1919), pp. 14-15, pl. 1, figs. 30-31.
Vertigo (Alaea) callosa steinheimensis n. var.	Gottschick & Wenz (1919), p. 15, pl. 1, figs. 32-33.
Vertigo (Alaea) callosa perarmata n. var.	Gottschick & Wenz (1919), pp. 15-18, pl. 1, figs. 34-35.
Leucochila acuminata procera Gottschick & Wenz	Gottschick & Wenz (1919), p. 11, pl. 1, figs. 18-19.
Leucochila acuminata larteti (Dupuy)	Gottschick & Wenz (1919), pp. 11-12, pl. 1, figs. 20-21.
Torquilla n. sp.?	Gottschick & Wenz (1919), p. 5.
Vallonia subcyclophorella major n. v.	Gottschick (1920b), pp. 54-58, pl. 2, fig. 4.
Vallonia lepida Reuss var. *steinheimensis* n. v.	Gottschick (1920b), pp. 58-61.
Pupilla perlabiata n. sp.	Gottschick & Wenz (1919), pp. 7-8.
Hyalinia (Hyalinia) subnitens Klein *fa. recedens n. f.*	Gottschick (1920a), pp. 33-35
Hyalinia (Gyralina) circumscisa n. sp.	Gottschick (1920a), pp. 35-37, pl. 1, fig. 2
Zonites (Aegopsis) verticilloides Thomae	Gottschick (1919), pp. 123-124.
Zonites (Aegopsis) costatus Sdbgr.	Gottschick (1919), pp. 124-126.
Vitrina (Vitrina) suevica Sdbgr. fa. *erecta* n. f.	Gottschick (1919), pp. 122-123
Hygromia (Trichiopsis) kleini scalaris n. f.	Gottschick (1920a), pp. 42-43.

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THE PALAEOTACHEA COMPLEX (GASTROPODA: PULMONATA) IN THE MIOCENE OF SW GERMANY: A MORPHOMETRIC APPROACH

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Abstract *Gastropods in the Obere Süßwassermolasse ("Upper Freshwater Molasse") of Germany formerly referred to the genus Cepaea include five species:* Palaeotachea dentula *(MN 5),* P. silvana *(MN 5),* P. renevieri *(MN 5) as well as* P. turonensis *(MN 5/6),* P. sylvestrina *(MN 7- MN 9-?) and* P. elevata *(MN7). Their taxonomic status is discussed in this study.* Palaeotachea sylvestrina *and* P. silvana *can be differentiated morphologically using statistical methods. The previously recognized subspecies* Palaeotachea sylvestrina sylvestrina *(Schlotheim, 1820),* P. sylvestrina gottschicki *(Wenz, 1919) and* P. sylvestrina geniculata *(Sandberger, 1872) are no longer maintained in the species* Palaeotachea sylvestrina *(Schlotheim, 1820). Likewise, a subspecies* P. silvana malleolata *(Sandberger, 1875) is no longer recognized in the species* Palaeotachea silvana *(Klein, 1853). The taxon* Palaeotachea renevieri elevata *(Berz & Jooss, 1927) is elevated to species rank. The attempt to solve the proposed relationship of* Palaeotachea turonensis *with the* Pliocene Frechenia *and the Recent* Eobania vermiculata *using morphometric features brought no result.*

Key words Cepaea, Megalotachea, Palaeotachea, *Obere Süßwassermolasse, silvana-beds, morphometrics.*

INTRODUCTION

Traditionally, a wide range of helicid landsnail species have been attributed to the genus *Cepaea*, although already Pfeffer (1929) suggested that the fossil forms cannot be related to the extant forms of this genus. Instead, all fossil species-level taxa of this group should be summarized into *Palaeotachea* Jooss 1912 (see also Nordsieck 2014b & c). Members of *Palaeotachea* are among the most abundant and conspicuous landsnails of the Obere Süßwassermolasse (OSM) ("Upper Freshwater Molasse", Middle to Late Miocene). Despite their abundance and although their taxonomic status is problematic in most cases, they have never been subject of detailed studies. Particularly two common species, Schlotheim's (1820) "*Cepaea*" *sylvestrina* and Klein's (1853) "*C.*" *silvana* are problematic due to their high morphological variability. A further problematic genus of this taxonomic complex is *Frechenia*, because its taxonoic status is under debate as well. This paper aims to answer of the following questions: (1.) How many species of *Palaeotachea* were present in the OSM and what is their taxonomic status? (2.) Can a *Frechenia /Palaeotachea* relationship be demonstrated using morphometic features? (3.) Which are the differences between *Palaeotachea silvana* (Klein, 1853) and *P. sylvestrina* (Schlotheim, 1820), and can they be considered as different species? (4.) What is the palaeogeographic distribution of this species complex in Central Europe? The single species are described in detail together with their distinguishing features. Finally, we provide an identification key for the *Palaeotachea* species of the OSM.

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MATERIAL AND METHODS

In order to test for the separation of the two species *Palaeotachea silvana* and *P. sylvestrina*, more than one hundred specimens were measured and statistically analysed. The material comes from Middle Miocene Obere Süßwassermolasse (OSM; "Upper Freshwater Molasse") locations and time equivalent sites in South Germany, which were chosen because they yield the highest numbers of well-preserved specimens. The OSM is a freshwater episode in the North Alpine Foreland Basin (NAFB), which was formed during the Alpine orogeny. Sediments of the NAFB are dived into four units: Untere Meeresmolasse, Untere Süßwassermolasse, Obere Meeresmolasse and Obere Süßwassermolasse. The lake basins of Randeck Maar and Steinheim Basin are time-equivalent developments of the OSM situated on the Swabian Alb. For a detailed overview of the geological background see Geyer & Gwinner (2011).

An important event in the Middle Miocene was the Nördlinger Ries/Steinheim Basin meteorite impact between 14.6 and 15.0 Ma bp (Buchner *et al.* 2013). The gastropods examined in this study are from sediments deposited both before and after the Ries/Steinheim event. All studied material is stored in the Staatliches Museum für Naturkunde Stuttgart (SMNS) and the Senckenberg Museum in Frankfurt am Main. Important complexes are the collections of Adolf von Klein (1805–1892) and Carlo Jooss (1883-?), because they contain type material. The former include the original material of *Palaeotachea silvana* and *Palaeotachea dentula*. The latter hosts the original material of *Palaeotachea elevata*.

The studied material comes from the following localities. (1.) Gastropods labelled as *Cepaea silvana* (Klein, 1853): Zwiefalten, Baden-Württemberg, South Germany (type locality of *C. silvana*), MN5/6: 15 specimens (n =15), Mörsingen (district of Zwiefalten), MN 5 (Esu 1999): 138 specimens (n=138). (2.) Gastropods labelled as *Cepaea sylvestrina* (Schlotheim, 1820): Steinheim am Albuch, Baden-Württemberg, South Germany, MN 7 (Gentry *et al.* 1999): 114 specimens (n=114). Reimlingen, at the Sportplatz, Nördlinger Ries, Bavaria, South Germany, according Bolten (1977) from Post-Ries sediments 44 specimens (n=44).

For morphometric examination of the Pliocene landgastropod genus *Frechenia* Schlickum & Strauch 1971, the following taxa were examined: *Frechenia reichenbachi* (type species) (n= 14), from Frechen near Cologne; *Palaeotachea turonensis* (n=24) from the Miocene of Grund near Vienna; *Eobania vermiculata* (type species) (n=24), from Italy; *Cepaea nemoralis* (type species) (n=24), from France; *Caucasotachea vindobonensis* (n=24) (formerly *Cepaea vindobonensis*, see Neiber & Hausdorf 2015) from Austria. This two species were taken for two reasons: 1. Apart from the distinct outerlip, *Frechenia* has a "*Cepaea*"-like outer morphology and *C. nemoralis* is the type species of the genus. 2. *Caucasotachea vindobonensis* was included, because like *C. nemoralis*, it bears an outer morphology similar to *Frechenia*.

For statistics, the following parameters were measured (Fig. 1): (1.) Shell height (sh), (2.) shell width (sw), (3.) height of the aperture (ah), (4.) height of the last whorl (lwh), (5.) angle of spire (as), (6.) distance of insertions (di). The measurements were made using the software "Image J" (Burger & Burge 2006) and a digital slide gauge as well as a simple goniometer. The following statistical methods were applied to the *Palaeotachea* specimens: (1.) The above parameters were used for a principal component analysis (PCA) (Matrix Variance-covariance) using "PAST" software (see Hammer *et al.* 2001). (2.) The following ratios were calculated from the above parameters: sh/sw; lwh/ah; sh/ah; sh/di; as/ah; as/lwh; as/sh; as/sw; as/di; ah/di; sw/di; lwh/di; sw/ah; as/ah to as/lwh ratio; sh/sw to as/di ratio; as/sh to as/sw ratio; sh/mh to sw/mh ratio; lwh/mh to sh/di ratio; as/ah to as/sh ratio; as/mh to as/sw ratio; as/di to as/ah ratio. The values from all specimens were used to calculate a cluster analysis (euclidean, Ward's method) using PAST software. The analysis of these measured dimensions alone did not provide any reasonable results and is therefore not shown here. In a next step, the arithmetic means of each given ratio were calculated and then used for another cluster analysis. These results are presented below. (3.) In order to test for different growth rates, the size of the first three whorls was measured and compared with the total shell width. These measurements were made using the image analysis software of a Keyence microscope. In addition to the *silvana/sylvestrina* problem, we aimed to test for the taxonomic status of further species

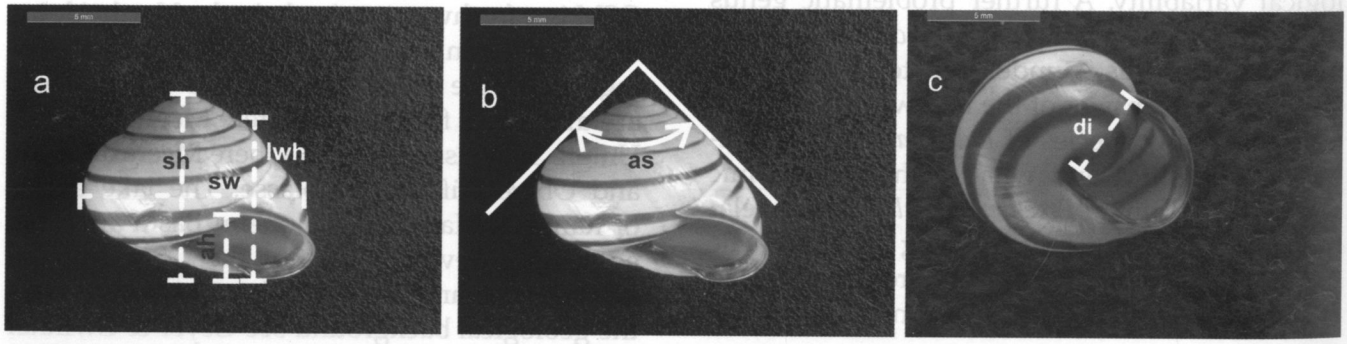


Figure 1 Shell morphometric features mentioned in the text and used for statistics.

that had been attributed to the "*Palaeotachea*"-group. For this purpose we studied all available material of the related species in the Staatlichen Museum für Naturkunde Stuttgart (SMNS) and the Senckenberg Museum in Frankfurt am Main and described it taxonomically. In addition to that, SEM-photos of the protoconches of the different species were made. However, due to incomplete preservation, no distinct features can be identified. According to that, they are not illustrated here. The stratigraphic information for each locality is listed in Table 1. Table 2 lists the localities with verified Mammal zone (MN).

For the examination of *Frechenia* the according ratios were used for two cluster analyses. One with a Paired Group Algorithm and Euclidean Similarity Index, the other with Single Linkage Algorithm and Bray-Curtis Similarity Index. Additionally, two Principal Component Analyses (PCA) were conducted: 1. Correlation matrix, disregard groups, Mean value imputation (PCA1). 2. Variance-covariance Matrix and disregard groups, Mean value imputation (PCA2). Both PCAs have 15 components (PC). The statistics were also calculated using PAST (Hammer *et al.* 2001).

Cepaea and the Palaeotachea complex

Cepaea-type shell morphologies are common among Cenozoic landsnails, but their taxonomic attribution on the genus level is difficult due to a high variability and the discrepancy between taxonomic features used in fossil (morphology), and extant (anatomy, molecular genetics) snails, respectively. According to Zilch (1959–1960), Kerney *et al.* (1983) and Welter-Schultes (2012b), the genus *Cepaea* Held 1837 includes four extant species: *Cepaea nemoralis* (Linnaeus, 1758) (type species) (Fig. 5.4), *C. hortensis* (O.F.Müller, 1774) (Fig. 5.3), *C. silvatica* (Draparnaud, 1801) (Fig. 5.2) and *C. vindobonensis* (Férussac, 1821) (Fig. 5.1). Schileyko (2006) divided the genus into two subgenera: *Cepaea* (*Cepaea*) with the species *hortensis* and *nemoralis* as well as *Cepaea* (*Austrotachea*) with *silvatica* and *vindobonensis*.

Based on nuclear and mitochondrial DNA marker sequences, Cadahia *et al.* (2014) recently suggested that *Cepaea* is a paraphyletic taxon and that *C. nemoralis* and *C. hortensis* are closer related to *Eobania vermiculata* (O.F.Müller, 1774) then to *Cepaea vindobonensis*. In 2015, Neiber & Hausdorf confirmed the polyphyly of *Cepaea*. Following these authors, only *C. nemoralis* and *C. hortensis* remain in *Cepaea*. The species *vindobonensis* is referred to *Caucasotachea*, and *sylvatica* to *Macularia*. In fact, already Pfeffer (1929) has splitted the four extant *Cepaea* species into three different genera according to their different callous columellar plate ("Columellar-Callusplatte") and the shell fine sculpture. He proposed the new genera *Hyalotachea* for *silvatica* and *Austrotachea* for *vindobonensis*, while *nemoralis* and *hortensis* remained in the genus *Cepaea*. The problem with Pfeffer`s work is that he gave no illustrations of his observations and descriptions. As justification for this he wrote that the relevant shell features are not visible in only one view but the shell has to be turned into different directions (Pfeffer, 1929, p. 136). For the extant species, these new genera were not accepted by later authors (Zilch 1959–1960).

The Oligocene and Miocene "*Cepaea*"-like forms are traditionally placed in the genus *Cepaea* (e.g., Wenz, 1920a & b; Schlickum, 1976; Lueger, 1981; Kókay, 2006). Because of the microsculpture and the columellar area, however, Pfeffer (1929) was the opinion that the fossil forms has nothing to do with the extant *Cepaea*. He therefore placed the fossil species in his newly designated genera *Megalotachea and Pachytachea* as well as in the genus *Palaeotachea* Jooss, 1912. The author differentiated the genera according to the microsculpture and the formation of the columellar plate. This was later rejected by Zilch (1959–1960). In 1986, Nordsieck grouped the Oligo-Miocene species of the "*Cepaea*"-group, based on Pfeffer`s observation and stratigraphy, into two genera: *Palaeotachea* Jooss, 1912 and *Megalotachea* Pfeffer 1929 (see Nordsieck 1986). The author saw *Pachytachea* as a synonym of *Megalotachea* and published a comment on the terminology used by Pfeffer (1929) (see Nordsieck 2014a). According to Nordsieck (1986; 2014b; 2014c), the *Palaeotachea* species exhibit radial rib-striae granulated by spiral striae, while the *Megalotachea* species does not. In the *Palaeotachea* species, the end of the columellar plate is mostly in a higher (more umbilical) position than *Megalotachea*. However, Nordsieck (2014c) wrote that the delimitation of both genera proved to be difficult because these differences do not allow a clear separation. For example, *Palaeotachea subcarinata* has a microsculpture like *Palaeotachea* but a columellar plate like *Megalotachea* (Nordsieck 2014c). According

Table. 1 Localities with Miocene land gastropods and their stratigraphic correlation. If exact correlations are known, the appropriate reference is given. Otherwise, the stratigraphic information comes from labels of the SMNS collection.

Locality	Country	Biostratigraphy
Altheim near Ehingen	Baden-Württemberg, Germany	Miocene (collection data)
Aulfingen	Baden-Württemberg, Germany	Miocene, Helicidenmergel (Jooss 1923)
Baach near Zweifalten	Baden-Württemberg, Germany	Miocene (Wenz 1923; collection data)
Bechingen near Riedlingen	Baden-Württemberg, Germany	Miocene (collection data)
Bonladen	Baden-Württemberg, Germany	MN 6 (Sach 1999)
Diepflingen	Switzerland	Miocene (collection data)
Edelbeuren-Mauerkopf	Baden-Württemberg, Germany	MN 5 (Sach 1999)
Edelbeuren-Schlachtberg	Baden-Württemberg, Germany	MN 5/6 (Sach 1999)
Emerberg (a ridge near Zwiefalten)	Baden-Württemberg, Germany	Miocene (collection data)
Faluns de Touraine	France	MN 5 (Ginsburg 2001)
Frechen near Cologne	Nordrhein-Westfalen, Germany	Pliocene (Schlickum & Strauch 1971)
Grund	Vienna, Austria	MN5 (Zorn 2004)
Häder near Dinkelscherben	Baden-Württemberg, Germany	MN 5 (Heizmann 1973, quoted in Ginsburg 1999)
Hard near Densbüren	Switzerland	Miocene (collection data)
Harthausen auf der Scheer	Baden-Württemberg, Germany	Miocene, Helicidenmergel (Jooss 1923)
Herznach	Switzerland	Miocene (collection data)
Heselberg near Ochsenhausen	Baden-Württemberg, Germany	Miocene (Sach 1999)
Heuhof near Oggenhausen	Baden-Württemberg, Germany	MN5 (Böttcher *et al.* 2009)
Hohenhewen	Baden-Württemberg, Germany	Middle to Upper Miocene (Geyer & Gwinner 2011)
Hohenmemmingen	Baden-Württemberg, Germany	Miocene (Gottschick & wenz 1916; collection data)
Hohenstoffeln	Baden-Württemberg, Germany	Middle to Upper Miocene (Geyer & Gwinner 2011)
Höwenegg	Baden-Württemberg, Germany	MN 9 (Hünermann 1989, quoted in Heißig 1999)
Korneuburger Basin	Lower Austria, Austria	MN5 (Harzhauser & Wessely 2003)
Lauchheim	Baden-Württemberg, Germany	Miocene (collection data)
Le Locle, Kanton Neuenburg	Switzerland	MN 7 (Kälin 1993, quoted in Boon-Kristkoiz & Kristkoiz 1999)
Manthelan	Indre-et-Loire, France	MN 5 (Hugueney 1999)
Michalesberg near Dischingen	Baden-Württemberg, Germany	Miocene (collection data)
Mörsingen	Baden-Württemberg, Germany	MN 5 (Esu 1999)
Nebelbergweg near Nunningen, Kanton Solothurn	Switzerland	MN 9 (Kälin & Engesser 2001)
Neuberg	Switzerland	Miocene (collection data)
Nördlinger Ries	Bayern, Germany	Post Ries, probably MN6
Oberwilzingen am Emerberg	Baden-Württemberg, Germany	Miocene (collection data)
Oggenhausen	Baden-Württemberg, Germany	MN5 (Böttcher *et al.* 2009)
Ramsen, Kanton Schaffhausen	Switzerland	Miocene (collection data)
Randecker Maar near Kirchheim Teck	Baden-Württemberg, Germany	MN 5 (Heizmann 1983 quoted in Hellmund & Hellmund 2002; Rasser *et al.* 2013)
Ravensburg	Baden-Württemberg, Germany	MN 5 (van der Made 1999)
Reimlingen at Nördlinger Ries	Bayern, Germany	Post Ries, probably MN6 or later (Bolten 1977)
Riesental near Epfenhofen	Baden-Württemberg, Germany	Miocene, Helicidenmergel (Jooss 1923)
Rognes	Bouches-du-Rhône, France	Miocene (collection data)
Route de la Sagne	Neuchâtel, Switzerland	Miocene (collection data)
Rumpel bei Oltingen	Switzerland	Miocene (collection data)

Locality	Country	Biostratigraphy
Sandelzhausen	Bayern, Germany	MN 5 (Moser *et al.* 2009)
Sansan	Gers, France	MN 6 (Hugueney 1999)
Steinheim am Albuch	Baden-Württemberg, Germany	MN 7 (Gentry *et al.* 1999)
Steubersheim	Baden-Württemberg, Germany	Miocene, Helicidenmergel (Jooss 1923)
Stoffelberg near Ehingen	Baden-Württemberg, Germany	Miocene (collection data)
Tennikerfluh near Tenniken	Switzerland	Miocene (collection data)
Tobel Oelhalde-Nord	Baden-Württemberg, Germany	MN 5/6 (Sach 1999),
Tobel Oelhalde-Süd	Baden-Württemberg, Germany	MN 5 to MN 5/6 (Sach 1999)
Trendel near Öttingen	Bayern, Germany	Post Ries, probably MN6
Undorf near Regensburg	Bayern, Germany	MN 5 (Fejfar (1999)
Wannenwaldtobel	Baden-Württemberg, Germany	MN 5/6 (Sach 1999),
Wirtachtobel at the Pfänder near Bregenz	Vorarlberg, Austria	Miocene (collection data)
Wölflinswil	Switzerland	Miocene (collection data)
Zwiefalten	Baden-Württemberg, Germany	Miocene (collection data)
Zwiefaltendorf	Baden-Württemberg, Germany	Miocene (collection data)

Table 2 List of occurrences of *Palaeotachea* with verified Mammal Neogene Zones (MN).

Locality	Species	Mammal zone (MN)
Mörsingen	*P. silvana*	MN 5 (Esu 1999)
Sandelzhausen	*P. silvana*	MN 5 (Moser *et al.* 2009)
Randecker Maar	*P. silvana*	MN 5 (Rasser *et al.* 2013)
Ravensburg	*P. silvana*	MN 5 (van der Made 1999)
Steinheim am Albuch	*P. sylvestrina*	MN 7 (Gentry *et al.* 1999)
Le Locle, Kanton Neuenburg	*P. sylvestrina*	MN 7 (Kälin 1993, quoted in Boon-Kristkoiz & Kristkoiz 1999)
Höwenegg	*P. sylvestrina*	MN 9 (Hünermann 1989, quoted in Heißig 1999)
Nebelbergweg near Nunningen, Kanton Solothurn	*P. sylvestrina*	MN 9 (Kälin & Engesser 2001)
Faluns de Touraine	*P. turonensis*	MN 5 (Ginsburg 2001)
Korneuburger Becken	*P. turonensis*	MN 5 (Harzhauser & Wessely 2003)
Sansan	*P. turonensis*	MN 6 (Hugueney 1999)
Le Locle, Kanton Neuenburg	*P. elevata*	MN 7 (Kälin 1993, quoted in Boon-Kristkoiz & Kristkoiz 1999)
Oggenhausen	*P. renevieri*	MN 5 (Böttcher *et al.* 2009)
Randecker Maar	*P. renevieri*	MN 5 (Rasser *et al.* 2013)

to this author it is therefore recommendable, to rank both groups only as subgenera of one genus, which means that all Oligo-Miocene "*Cepaea*" group species are classified within the genus *Palaeotachea* (see Nordsieck 2014b & c).

With respect to the generic designation, the current paper follows Nordsieck (2014b & c). However, due to the poor delimitation mentioned above, a separation into subgenera are waived. It is important to note, however, that due to the DNA results from Cadahia *et al.* (2014) and Neiber & Hausdorf (2015) mentioned above, the discussion on "*Cepaea*" relationships is still open.

RESULTS

MORPHOMETRICS AND STATISTICS

The measurements of the relationship between the size of the first three whorls and the total shell width (see Material and methods) provided no differences between the two species *Palaeotachea silvana* and *P. sylvestrina*. However, the cluster analysis (Fig. 2) shows a distinct separation between the specimens from Zwiefalten (type locality of *P. silvana*) and Mörsingen, on the one side, and those of Nördlinger Ries and Steinheim am Albuch (*P. sylvestrina*), on the other. The PCA analysis (Figs 3 & 4) confirms these

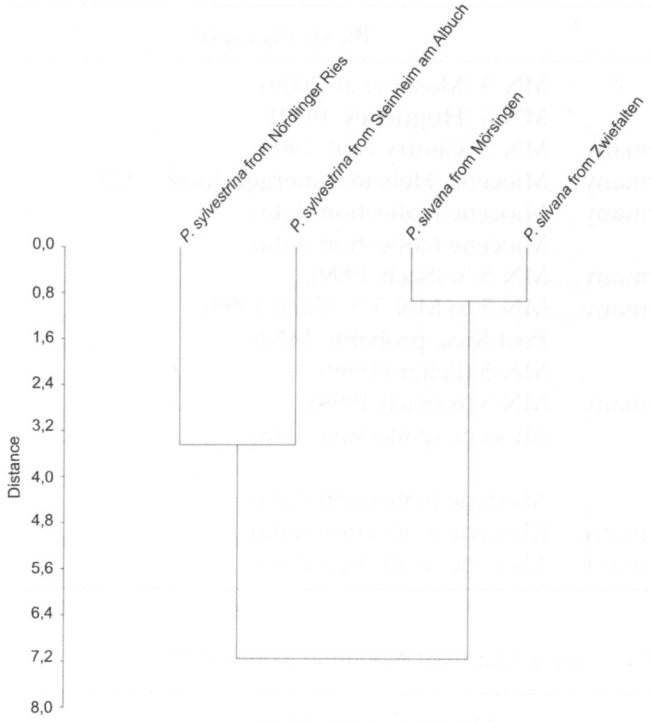


Figure 2 Hierarchical cluster analysis.

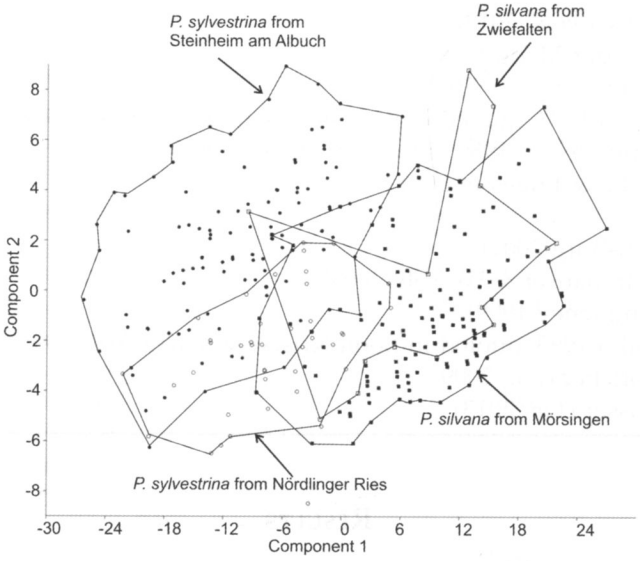


Figure 3 Principal component analysis (PCA). Scatter plot of PC1 and PC2.

results. The first component accounts for a variance of 92.21%, followed by the second one with 7.24% variance. The remaining four components range between 0.21% and 0.06% variance. The scatter plot of PC 1 (Eigenvalue 134.83) and PC2 (Eigenvalue 10.58) (Fig. 3) shows a remarkable differentiation of the specimens from Mörsingen and Zwiefalten (*P. silvana*) on the one side, and from Nördlinger Ries and Steinheim am Albuch

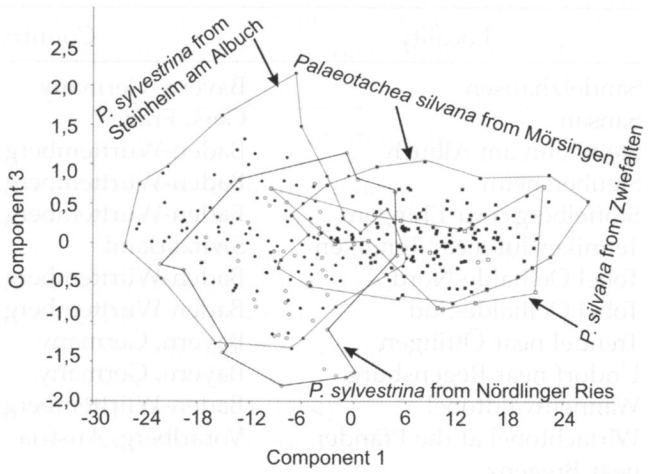


Figure 4 Principal component analysis (PCA). Scatter plot of PC1 and PC3.

(*P. sylvestrina*), on the other. The scatter plot of PC1 and PC3 (Eigenvalue 0.31) (Fig. 4) shows the same separation. In both scatter plots there is a remarkable overlapping zone of the four different localities.

The cluster analyzes as well as the principal component analyzes (PCA) did not reveal any morphological relationships between *Frechenia* and one of the other measured taxa. According to that, an illustration of the diagrams was waived.

TAXONOMY

Palaeotachea silvana (Klein, 1853)
(Figs 5.1–5; Figs 6.3 & 6.4)

Helix silvana Klein, 1853: 205, Pl. V, fig. 2.
Helix sylvana- Sandberger 1872: Pl. XXIX, figs. 13a–d [non Fig. 13b]
Helix (Macularia) sylvana- Sandberger 1875: 592–594 (ref. Pl. XXIX, figs.13a,13c–d)
Helix malleolata Sandberger, 1875: 594.
Cepaea silvana silvana (Klein)-Wenz 1923: P. 667–679. See here for the very large number of synonyms.
Cepaea silvana malleolata (Sandberger)-Wenz 1923 679–680.
Megalotachea silvana KLEIN-Pfeffer 1929: 146–147.
Palaeotachea silvana (Klein)-Nordsieck 2014b: 21

Material examined 100 specimens, including a syntype, see Material and Methods section.

Type locality The locality quoted on the collection label of the syntype is Zwiefalten,

Baden-Württemberg, South Germany. According to Klein's (1853) description, it comes from freshwater limestones south of Zwiefalten, the so-called Tautschbuch. In this forested area north of river Danube, several limestones of the so-called *silvana*-limestones are still outcropping in old quarries.

Description The syntype is 12.3mm high and 17.1mm wide. The height of the aperture is 9.2mm and of the last whorl 10.3mm. The height/width ratio is 0.75. The shell appears to have three colour bands. The height ranges from 10.1 to 16.8mm and the width from 14.7 to 21.0mm. The shell has a typical helicoid, dextral "*Cepaea*"-like form with all transitions between the lower and the higher measures. The 4 ¼ convex whorls are growing regularly. The last whorls often show an indistinct keel. It usually disappears ca. 0.5 whorls prior to the aperture. Shortly before reaching the aperture, the last whorl obliquely turns the abapical direction.

The aperture has an oblique-oval shape and the two intersections are connected by a thin callus. The peristome is turned backwards (see Figs 5.4 & 5.5). At the lower margin, there is a slight callosity folding near the umbilicus region. This can be more or less pronounced in the individual specimens. The umbilicus is covered by a parietal callus. The sutures are moderately deep. The protoconch, which consists of ca. 1.5 whorls is almost entirely smooth and without a sculpture. It has a diameter of ca. 3.6mm. The teleoconch is covered by very fine and regular growth lines or collabral striation (Fig. 6.3). On the outer side of the lower peristome, there are tiny knobs that are difficult to identify even under higher magnification (Fig. 6.4).

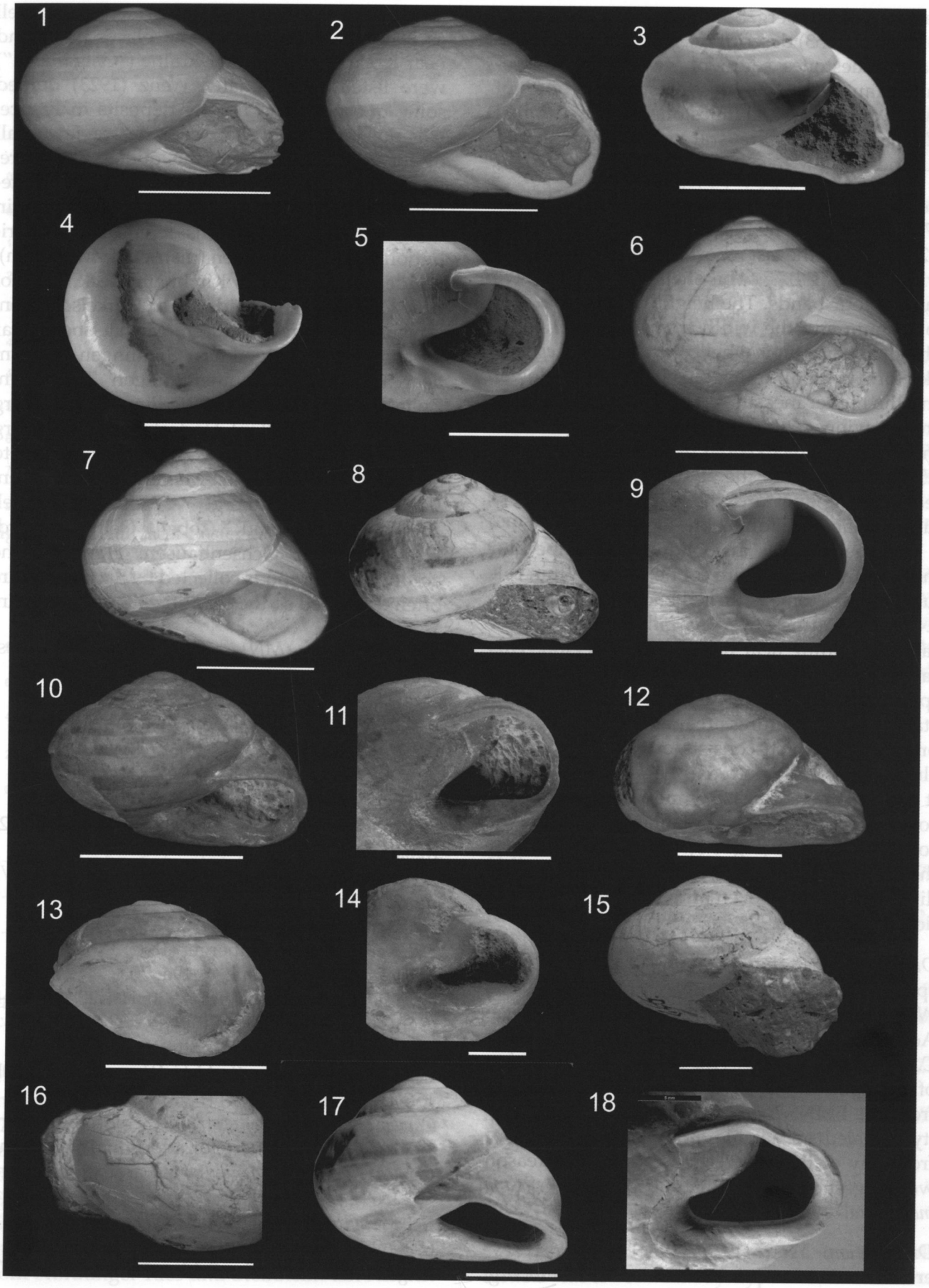
Discussion Sandberger (1874) designated a species from Altheim near Ehingen, Baden-Württemberg, Germany as *Helix malleolata*. According to Wenz (1923), this is a subspecies of *C. silvana*. Sandberger (1874) gave no illustration of his species. An investigation of a specimen from the SMNS-Jooss collection from this locality revealed no notable differences to *C. silvana* from any of the other localities. For this reason we suggest to emend the subspecies *C. silvana malleolata*.

Distribution Wenz (1923 &1924) mentioned several Miocene localities in Baden-Württemberg, Bavaria and Oberhessen (Germany) as well as in Switzerland. Also some places in Poland near Krakow and in the Ukraine ("Ostgalizien") were listed. Additionally, Wenz (1923) quoted some questionable Pliocene deposits in France. It is not very likely that Wenz has reviewed all of the identifications in the quoted literature. For this reason, only examined collection material (SMNS and the Senckenberg Museum in Frankfurt am Main) is considered for the distribution herein. Mörsingen (district of Zwiefalten), Randecker Maar near Kirchheim Teck, Heuhof near Oggenhausen, Häder near Dinkelscherben. Ravensburg, Sandelzhausen, Michaelsberg near Dischingen, Bechingen near Riedlingen, Altheim near Ehingen, Hohenmemmingen Zwiefalten, Zwiefaltendorf (district of Riedlingen), Emerberg (ridge near Zwiefalten). Undorf near Regensburg (Sandberger 1872, pl. XXIX, fig.13c) According to Sach (1999): Edelbeuren-Mauerkopf, Bonladen, Edelbeuren-Schlachtberg, Wannenwaldtobel, Tobel Oelhalde-Süd, Tobel Oelhalde-Nord, Heselberg near Ochsenhausen. However, the according gastropods collected by Sach (1999) are often deformed so the Identification is uncertain.

Mammal zone (MN) range MN5 (Prae-Ries-sediments).

Palaeotachea sylvestrina (Schlotheim, 1820)
(Figs 5.6–9; Fig. 6.5)

Helicites sylvestrinus Schlotheim, 1820: 99.
Helix silvestrina nobis, Zieten 1832: 38, pl. 29 figs.2a–c
Helix geniculata Sandberger, 1872: 629, pl. XXVI, fig. 23–23b
Helix platychelodes Sandberger, 1875: 626.
Helix geniculata -Sandberger, 1875: P. 629,
Cepaea gottschicki Wenz, 1919a: 70.
Cepaea sylvestrina- Wenz 1920: 19–20, fig. 1–2 (Syntype Schlotheim 1820)
Cepaea gottschicki Wenz-Gottschick 1920: 49.
Cepaea sylvestrina gottschicki Wenz-Wenz 1920b: 156, figs. 7–8.
Cepaea sylvestrina sylvestrina (Schlotheim)-Wenz 1923: 690–691. See here for additional synonyms.
Cepaea sylvestrina geniculata (Sandberger)-Wenz 1923: 691–693.
Cepaea sylvestrina gottschicki Wenz-Wenz 1923: P. 693–695.
Megalotachea silvestrina Schlot.-Pfeffer 1929: 147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Material examined > 100 specimens, see Material and Methods section.

Description The dextral shell has helicoid typical *Cepaea*-like form and consists of 4 ½ whorls. It has a maximum width of ca. 27.3mm and a maximum height of ca. 22.5mm. The size is extremely variable. Like in *P. silvana*, both higher and lower forms exist. The average ratio between shell height and height of aperture is ca. 1.6. The regularly growing whorls are convex and the sutures is moderately deep. Before reaching the aperture, the last whorl turns in abapical direction. The degree of inclination can also be different. It ranges from a relatively abrupt down-turning, to a more shallow dip. The aperture is oblique-oval with a slightly turned back periostome (see Fig. 5.9). The first part of the upper margin runs more or less straight and parallel to the lower one. The lower margin of the aperture shows a small callous thickening, the distinctiveness of which is variable between the different shells. The umbilicus is covered by a parietal callus. Also the intersections are connected by a thin callous layer. The teleoconch is covered with a very fine, irregularly radial striation which is not visible on all specimens (Fig. 6.5). Also more or less regularly arranged fine spiral lines can be seen on very well preserved shell. The protoconch, which consists of ca. 1 ¼ whorls, is smooth. The according whorls have a more bulbous shape.

Discussion Originally described by Schlotheim (1820) as *Helicites sylvestrinus*, the author mentioned the following distribution: Buschweiler (today`s name Bouxviller, Alsace) and Ermreuth, Bavaria, as well as the Kanton Basel ("Jurakalk") in Switzerland. Von Zieten (1832) then described this species from Steinheim am Albuch as *Helix sylvestrina* nobis. Already in 1830, Schübler wrote in a letter to the "Journal de Géologie par MM", that the reference of the according Steinheim am Albuch specimens to the species *Helicites sylvestrinus* sensu Schlotheim is doubtful (p. 301, "Correspondance et Variétés"). Also Wenz (1919) suggested that the according gastropods from Steinheim do not fit with the description of Schlotheim and erected for the Steinheim specimens the new species *Cepaea gottschicki* n. nom Wenz, 1919. In the same year he visited the Geological-Palaeontological Institute in Berlin in order to study the original material of Schlotheim (1820), because he had strong doubts about the accuracy of Schlotheim's geographic information. Already Miller (1900) had claimed that Schlotheim (1820) mixed different species together under the name *Helicites sylvestrinus*.

After closer examination, Wenz (1920a) came to the conclusion that this material originated from the Nördlinger Ries, Bavaria, Germany, and that Schlotheim (1820) had made a mistake in the geographic distribution. Following Wenz (1920a), *Helicites sylvestrinus* is also identical with *Helix platychelodes* from the Nördlinger Ries, designated by Sandberger (1875). Wenz (1920a) determined a "Typus" from the Schlotheim collection. In 1920b, he designated his *C. gottschicki*

Figure 5 Shells of *Palaeotachea* species **5.1**. *P. silvana* (Klein, 1853). Middle Miocene, Scale 10mm. Zwiefaltendorf, Baden-Württemberg, Germany. Inv. Nr. SMNS 106768. **5.2.** *P. silvana* (Klein, 1853). Middle Miocene. , Scale 10mm. Zwiefaltendorf, Baden-Württemberg, Germany. Inv. Nr. SMNS 106769. **5.3 & 5.4.** P. *silvana* (Klein, 1853). Middle Miocene. Scale (both figures) 10mm. Zwiefalten, Baden-Württemberg, Germany. Syntype. Inv. Nr. SMNS 22738. **5.5** *P. silvana* (Klein, 1853). Middle Miocene. Scale 10mm. Mörsingen, Baden-Württemberg, Germany. Inv. Nr. SMNS 105.005. **5.6. & 5.7.** *P. sylvestrina* (Schlotheim, 1820). Middle Miocene. Scale (both figures) 10mm. Steinheim am Albuch, Baden-Württemberg, Germany. Inv. Nr. SMNS 106766 (Fig. 6); Inv. Nr. SMNS 106767 (Fig. 7). **5.8.** *P. sylvestrina* (Schlotheim, 1820). Middle Miocene. Scale 10mm. Trendel near Öttingen im Ries, Bavaria, Germany. Original material to Wenz (1920a & b). Inv. Nr. SMNS 105.000. **5.9**. *P. sylvestrina* (Schlotheim, 1820). Middle Miocene. Scale 10mm. Steinheim am Albuch, Baden-Württemberg, Germany. Inv. Nr. SMNS 15.817–129. **5.10 & 5.11.** *P. renevieri* (Maillard, 1891). Middle Miocene. Scale (both figures) 10mm. Harthausen auf der Scheer, Baden-Württemberg, Germany. Original material to Jooss (1923). Inv. Nr. SMNS 105.001. **5.12.** *P. dentula* (Quenstedt, 1867). Middle Miocene. Scale 5mm. Emerberg near Zwiefalten, Baden-Württemberg, Germany. Paratype of *Helix pachyostoma* Klein, 1853. Inv. Nr. 105.004. **5.13 & 5.14**. *P. dentula* (Quenstedt, 1884). Middle Miocene. Scale: Fig. 5.13: 10mm; Fig. 5.14: 5mm. Emerberg near Zwiefalten, Baden-Württemberg, Germany. Holotype of *Helix pachyostoma* Klein, 1853. Inv. Nr. 105.004. **5.15** & **5.16** *P. elevata* Berz & Jooss, 1927. Middle Miocene. Scale (both figures) 5mm. Near Le Locle, Kanton Neuch?tel, Switzerland. Holotype. Inv. Nr. SMNS 105.002. **5.17** &5.**18** *P. turonensis* (Deshayes, 1831). Middle Miocene. Scale Fig. 16: 5mm; fig. 17: 10mm. Manthelan, Dept. Indre-et Loire, France. Original material to Wenz (1920b). Inv. Nr. SMNS 105.003.

as a subspecies of *C. sylvestrina* (see Wenz 1920a and 1920b), and defined three subspecies: *C. sylvestrina sylvestrina* (Schlotheim), *C. sylvestrina gottschicki* (Wenz) and *C. sylvestrina geniculata* (Sandberger). In the same year, Gottschick (1920) put C. gottschicki back into the species rank. The taxa *geniculata* was originally designated by Sandberger (1872) as *Helix geniculata* Sandberger. According Sandberger, it is abundant in the Gypsum and Limestones of the Hohenhewen. This is the only locality named for this taxa by the author.

Distribution Steinheim am Albuch, Höwenegg, Hohenstoffeln, Lauchheim, Reimlingen at Nördlinger Ries, Trendel near Öttingen, Nördlinger Ries. Hohenhewen (Sandberger 1872) Switzerland: Nebelbergweg near Nunningen Le Locle, Ramsen.

Mammal zone (MN) range MN6-MN9-? (Post-Ries-sediments).

Palaeotachea dentula (Quenstedt, 1867)
(Figs 5.12–14; Fig. 6.1)

Helix pachyostoma Klein, 1853: 207, Pl. V, Fig. 4.
Helix dentula Quenstedt 1867: 482, pl. XLV, fig. 6.
Cepaea lepida Wenz, 1919a: 70.
Cepaea dentula (Quenstedt)-Wenz 1919b: 64.
Pachytachea dentula Quenst.-Pfeffer 1929: 146.

Material examined Four specimens (SMNS105004) including the holotype of *Helix pachyostoma* Klein, 1853, figured in Figs 5.13 & 5.14.

Description The dextral helicoid shell has a maximum width of ca.14.2mm and a maximum height of ca. 9.2mm. The height of the aperture is in average 51% of the shell height. Like in other "*Cepaea*"-group species, there are different forms with a high or a very low spire. The species has 3 ¾ regularly growing and moderately deep whorls. The protoconch consists of ca. 1.5 whorls. The first teleoconch whorl is relatively flat. The last one is more bulbous and forms with low spires can be slightly subangulate. Shortly before the aperture, the last whorl strongly descends. The columellar margin is more or less straight. The peristome is slightly thickened (see Figs 5.13 & 5.14). On the columellar margin, there is also a callous thickening. This extends to the point where the columellar margin passes arc-shaped to the convex upper one. The parietal callus is well developed. Also the umbilicus is covered by this parietal callus. The Protoconch is smooth. On the teleoconch, there are barely visible, regularly arranged and slightly S-curved growth lines.

Discussion Discussion: Wenz (1919a) discovered that a senior homonym *Helix pachystoma* Hombron & Jacquinot 1841 existed, and therefore he changed the name of Klein's species into *Cepaea lepida* n. nom. Later, Wenz (1919b) discovered that *Cepaea dentula* (Quenstedt, 1867) is identical with *Helix pachystoma* Klein, 1853. Because of being the next younger synonym, *Palaeotachea. dentula* is the valid name for the species designated by Klein, 1853.

P. dentula is with a maximum width of ca. 14.2mm the smallest *Palaeotachea* species in the OSM. *P. sylvestrina* and *P. turonensis* are significantly larger than *P. dentula*. *P. silvana* has a peristome that is more expanded. The aperture of both species is noticeable different. At *P. dentula* the abapical margin runs more straight. The adapical one goes steeper downward than it is the case at *P. silvana*. *P. dentula* differs from *P. renevieri* by a more or less straight lower periostome margin, an earlier downward flexing of the upper periostome margin, and a less convex last whorl.

Distribution The original material comes from the Miocene of Ober-Wilzingen am Emerberg near Zwiefalten. According to Wenz (1923) it occurs also in the Miocene of Baach near Zwiefalten and of Wirtachtobel at the Pfänder near Bregenz, Austria.

Mammal zone (MN) range MN5 (Prae-Ries-sediments).

Palaeotachea renevieri (Maillard, 1891)
(Figs 5.10 & 5.11)

Helix (Macularia) renevieri, Maillard, 1891: 43, Pl. 3, fig. 18
Cepaea renevieri (Maillard)-Jooss 1923: 198–200, Pl. XI, fig. 18–23
Cepaea renevieri (Maillard)-Wenz 1923: 652–653 (see there for further synonyms)
Cepaea renevieri renevieri (Maillard)-Berz & Jooss 1927: 203
Cepaea renevieri coniuncta Berz & Jooss, 1927: 203
Palaeotachea renevieri Maillard-Pfeffer 1929: 143

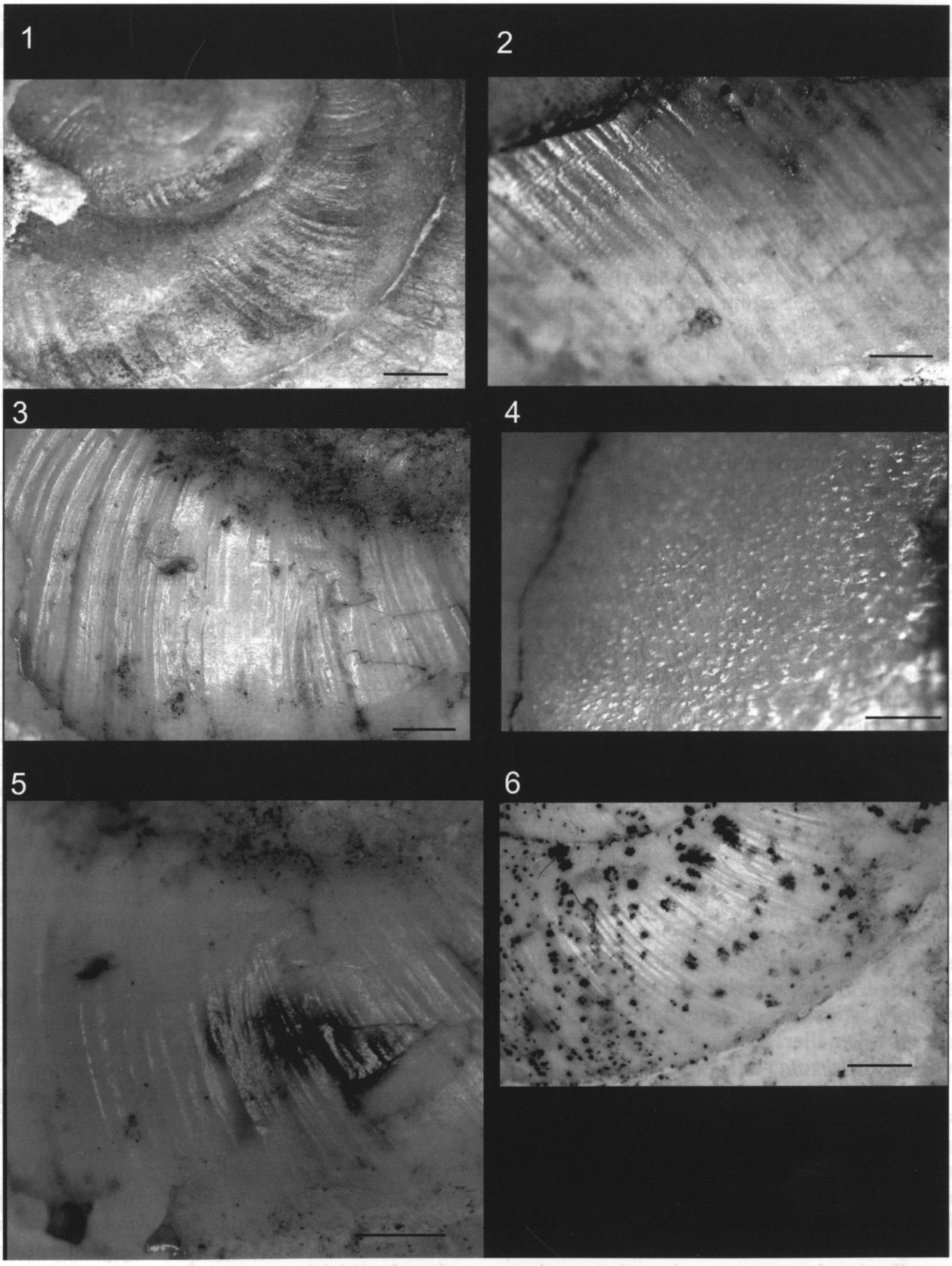

Figure 6 Sculptural details of the shells *Palaeotachea* species **6.1** Detail of Fig. 5.12. Scale 1mm. **6.2** Detail of Figs 5.15 & 5.16. Scale 0.5mm. **6.3 & 6.4** Detail of Figs 5. 3 & 5.4. Scale 0.5mm. **6.5** Detail of Fig. 5.6 Scale 0.5mm. **6.6** *Palaeotachea turonensis* (Deshayes, 1831). Middle Miocene. Mörsingen, Baden-Württemberg, Germany. Scale 1mm. Inv. Nr. SMNS J66.799.

Material examined Ten specimens.

Description Dextral helicoid shell with typical "*Cepaea*"-form. Maximum height ca. 11.4mm, maximum width ca. 14.9mm. Shell-height to height of the aperture relationship is ca. 1.5. It consists of 3 ¾ to 4 ¼ regularly growing whorls and moderately deep sutures. The last whorl is subangulate and becomes rounded ca. ¼ whorls before reaching the aperture. Right before the aperture, the last whorl turns slowly in abapical direction. The aperture has an oval form and the margins are only very slightly thickened and expanded (see Fig. 5.11). The adapical margin runs more or less straight before it goes over a very slight bend in the arched lateral margin. This straightness is a relatively variable feature. On some specimens this adapical margin is slightly curved. The abapical margin is slightly sloping downward. The insertions are connected by a thin callus. This parietal callus completely covers the umbilicus. Neither the teleoconch nor the protoconch sculpture is preserved. The protoconch is hardly recognizable. It consists of ca. 1 ¾ whorls, which are relatively flat. On one specimen (Fig. 5.7) four spiral pigment bands are well visible.

Discussion Berz & Jooss (1927) designated the subspecies *Cepaea renevieri coniuncta* nov. var. The original material is stored in the SMNS (Inv. Nr. SMNS 101369). The differences to *P. renevieri* are insufficient and also Berz & Jooss (1927) wrote that the nominal species and the subspecies are connected by transitions and are often difficult to differentiate. According to this the subspecies *Cepaea renevieri coniuncta* Berz & Jooss, 1927 is emended. *P. renevieri* differs from *Palaeotachea silvana*, *P. sylvestrina* and *P. turonensis* by the remarkably smaller shell size. For *Palaeotachea dentula* and *P. elevata* see there.

Distribution Harthausen auf der Scheer, Oggenhausen. According to Jooss (1923) also Steubersheim, Riesental near Epfenhofen, Aulfingen, Hard near Densbüren, Herznach, Wölflinswil, Rumpel bei Oltingen, Diepflingen, Neuberg and Tennikerfluh near Tenniken. In the Jooss collection there are several specimens where an exact determination is not possible because of the incomplete preservation. Therefore, the above list of Jooss must be treated with caution. For other localities see also Maillard (1891). Two well preserved specimens from the Jooss collection come also from the Zipfelbachschlucht of Randecker Maar.

Mammal zone (MN) range MN5 (Prae-Ries-sediments).

Palaeotachea elevata Berz & Jooss, 1927
(Figs 5.15 & 5.16; Fig. 6.2)

Cepaea renevieri elevata Berz & Jooss, 1927: 204.

Material examined 3 specimens, original material of Berz & Jooss (1927).. SMNS105002. Internal numbers of the Joss collection: 246 (the specimen shown in Figs 5.15 & 5.16), 247, 248.

Description Dextral, helicoid shell with regularly growing whorls, in the outline very similar to *P. renevieri*. It has 4 ¼ rounded whorls with moderately deep sutures. The shell is ca. 14.6mm wide and 12.1mm high. The sh/mh ratio is 1.6. Shortly before the aperture, the last whorl turns slowly downwards. The aperture is of oval shape with a turned-back peristome. The upper aperture margin runs slightly oblique before it passes into the arched lateral margin. The length of this upper one is variable. The lower margin passes obliquely downward. The insertions are connected by a parietal callus which also covers the umbilical region completely. The protoconch is slightly bulbous and without any sculpture. It consists of 1 ¼ whorls. The teleoconch bears more or less regularly arranged growth lines, which are only visible at higher magnifications.

Distribution According to Berz & Jooss (1927) the species occurs in the *sylvestrina*-beds of Le Locle and Route de la Sagne.

Mammal zone (MN) range MN7-? (Post-Ries-sediments).

Diagnostic features *Palaeotachea turonensis*, *P. silvana* and *P. sylvestrina* differ remarkably in size. In the same size range is *Palaeotachea dentula*. *P. elevata* differs in the following points from *P. dentula*: (1.) More rounded last whorl. (2.) More strongly reflected peristome. (3.) At. *P. dentula* the lower aperture margin runs more or less straight. (4.) The aperture of *P. dentula* is more laterally

tapered. (5.) At *P. dentula* the last whorl is going down more strongly and abrupt shortly before the aperture. (6.) Due to 5, the upper aperture edge of *P. dentula* seems to be pulled more forward than that of *P. elevata*.

As mentioned further above, the outline of *Palaeotachea renevieri* is very similar to *P. elevata*. The differences are: (1.) *P. elevata* has a more strongly turned-back peristome (see Fig. 5.16). (2.) The upper aperture margin runs more obliquely in *P. elevata* than in *P. renevieri*. (3.) The last whorl of *P. elevata* is not as "keel-like" rounded as it is the case for *P. renevieri*. (4.) *P. elevata* has a more bulbous protoconch.

Palaeotachea turonensis (Deshayes, 1831)
(Figs 5.17 & 5.18; Fig. 6.6)

?Helix asperula Deshayes 1830 or 1832: 251 (see Welter-Schultes 2012a).
?Helix duvauxi Deshayes 1830 or1832: 252 (see Welter-Schultes 2012a).
Helix turonensis Deshayes 1830 or 1832: 252 (see Welter-Schultes 2012a)
Helix turonensis Deshayes, 1831: 39–40. pl. 1, fig. 1–2
Helix larteti de Boissy, 1840: II, p. 75
Helix eversa Deshayes in Férussac, 1851: I, p. 395, pl. 1, fig. 5–7
Cepaea eversa eversa (Deshayes)-Wenz 1920b: 156, fig. 1–2
Cepaea eversa larteti (Boissy)-Wenz 1920b: 156, fig. 3–6.
Cepaea eversa eversa (Deshayes)-Wenz 1923: 617–619
Cepaea eversa larteti (Boissy)-Wenz 1923: 619–625
? *Cepaea eversa baumbergeri* Jooss, 1923: 200–204, pl. XI, fig. 24–27
Megalotachea turonensis Desh.-Pfeffer 1929: 147, Pl.. II, fig. 30–31
Megalotachea turonensis (Deshayes, 1831)-Truc 1971: 284–293, pl. 15, fig. 1–3. (See here for further synonyms)
Cepaea larteti (Boissy, 1844)-Fischer 2000:147, fig. 25a–c, 26a-c.

Material examined 5 specimens.

Description Relatively large, distinctly massive dextral helicoid shell with typical "*Cepaea*-form". The whole shell looks much more bulbous than that of all the other species. It is up to ca. 24mm wide and ca. 20mm high. The shell height to height of the aperture relationship is 1.7. It consists of 4 ¾ to 5 convex, regularly growing whorls. Sutures are moderately deep. Before reaching the aperture, the last whorl runs obliquely downward. The aperture has an oval shape stretched in width. The first part of the upper margin runs more or less straight and the lower one goes obliquely downward. The peristome are turned backwards and are remarkably thickened on the inner side. The insertions are connected by a relative thick parietal callus. The umbilicus region is completely covered by this callus. The smooth protoconch consists of ca. 1 ¼ relative flat whorls. The teleoconch bears fine regularly arranged growth lines. On some specimens traces of up to three bands are preserved.

Discussion According Kadolsky (pers. comm., 2015) there are taxonomic and nomenclatorial uncertainties considering the taxa *P. turonensis*, *Helix asperula* Deshayes, 1830 or 1832 and *Helix duvauxi*, Deshayes, 1830 or 1832. Also the publication dates are not sure (see Welter-Schultes 2012). For a clear solution of this problem it is indispensable to examine the original material of Deshayes. However, this would go beyond the scope of this paper. Following Truc (1971), *Helix larteti* de Boissy, 1840 and *Helix eversa* Deshayes in Ferussac, 1851 are synonym with *Palaeotachea turonensis* (Deshayes, 1831). Jooss (1923) designated a species *Cepaea eversa baumbergeri* from the Helicidenmergel. It is only a steinkern, but with traces of a remarkable reflected and distinct peristome. However, due to the incomplete preservation, no definitive identification is possible. The shell is also a little stretched in width. The remarkable inner thickened aperture especially the thickened columellar makes *P. turonensis* uniquely identifiable.

Distribution Hohenmemmingen, Stoffelberg near Ehingen, Emerberg, Grund near Vienna. Sandelzhausen (Gall 1972), Korneuburger Basin (Binder 2002), Sansan (Fischer 2000), Manthelan (Wenz 1920b), Faluns de Touraine (Truc 1971), Rognes (Schlickum & Strauch 1971). For other localities see Wenz 1923, p. 619 & 624–625).

Mammal zone (MN) range MN5-MN6.

DISCUSSION

How many genera?

Our morphometric considerations confirmed that *P. silvana, P. sylvestrina, P. dentula, P. renevieri, P. elevata* and *P. turonensis*, formerly attributed to *Cepaea*, are morphologically closely related to each other and can be attributed to *Palaeotachea*. Yet, all of them could be confirmed to represent valid species.

In 1971, Schlickum & Strauch designated the genus *Frechenia* for Pliocene, helicoid land snails with a remarkable reflected and distinct outer lip / palatal margin. The type locality is a coal pit in Frechen near Cologne, Germany. As type species, they defined *Frechenia reichenbachi*. Due to the distinct palatal margin, the authors assumed a possible relationship with the Miocene *Palaeotachea turonensis* (Deshayes, 1830) and the Recent *Eobania vermiculata* (O.F.Müller 1774), which have similar morphological characters. They also wrote, however, that they had not enough appropriate material to resolve this question. Later, Truc (1971) postulated that *Frechenia* is a side branch that has developed from *Megalotachea* (=*Palaeotachea*), which he in turn interprets as the ancestor of the Recent, monospecific genus *Eobania*. According to Nordsieck (2014c), *Frechenia* may be related to *Cepaea*. Our morphometric analysis suggests that *Frechenia* does not show any relationship with the species studied herein.

Differences between P. silvana and P. sylvestrina

It is important to note that a qualitative comparison of the measurements (see Methods and Results sections) does not allow spearation between *P. silvana* and *P. sylvestrina*. This reflects a problem that is frequently addressed in literature. Cluster and PCA analysis do, however, confirm the separation into two species. In summary, the younger *P. sylvestrina* differs in the following morphological aspects from *P. silvana*:

1. *P. sylvestrina* is usually larger.
2. *P. sylvestrina* is usually more spherical and higher.
3. *P. silvana* has a flatter spire and is more stretched in width.
4. The outline of the last whorl of *P. silvana* is stronger curved and can be indistinctly subangulate. Also some specimens of *P. sylvestrina* can have a very slight angulation on the last whorl, but it is usually less distinct than in *P. silvana*.
5. *P. sylvestrina* has a deeper suture.
6. The protoconch of *P. sylvestrina* is a bit flatter than that of *P. silvana*.
7. In *P. silvana*, the periostome region is generally more thickened.
8. The peristome of *P. silvana* is more expanded (see Figs 5. 6, 5.7 & 5.9).
9. The angle of spire around 117°in *P. silvana* and around 100°in *P. sylvestrina*.

Until today, the two species names *gottschicki* and *sylvestrina* were used in different manner in literature. Already Wenz (1920a & 1920b) has mentioned that there are no distinct boundaries between these subspecies and they could only be seen as graphical races ("lokale Rassen"). In fact, there are no clear dividing lines, not even in the statistical charts, which would justify a division into subspecies. The range of morphological disparity is comparable to that of the extant species *Cepaea nemoralis* and *C. hortensis*. For this reason, the subspecies *Palaeotachea sylvestrina sylvestrina, P. sylvestrina gottschicki* and *P. sylvestrina geniculata* are herein emended and summarised into the species *Palaeotachea sylvestrina*.

The silvana and sylvestrina beds

In literature about the geology of Southern Germany, the term "*silvana*-Schichten" is often used. In some publications, such as Miller (1871), the same sediments were named "*sylvestrina*-Schichten". In 1921, Wenz postulated a differentiation between older *silvana* beds and the younger

Table 3 Different angle of spire at *P. silvana* and *P. sylvestrina*.

	Locality	Angle of spire Minimum value	Angle of spire Maximum value	Angle of spire Mean value
P. silvana	Zwiefalten	105°	130°	117,6°
P. silvana	Mörsingen	100°	135°	117,1°
P. sylvestrina	Steinheim am Albuch	84°	116°	99,5°
P. sylvestrina	Reimlingen, Nördlinger Ries	88°	113°	100,9°

Table 4 The *silvana* beds, named after *Palaeotachea silvana*, and their subdivision.

Upper *silvana*-beds	With *Palaeotachea silvana* (formerly *Cepaea silvana malleolata*), known as "Malleolatakalk".
Middle *silvana*-beds	Dominated by *Palaeotachea silvana* and *Palaeotachea turonensis* as well as *Pseudochloritis incrassata*.
Lower *silvana*-beds	*Larteti-Palaeotachea turonensis*) beds "Flammenmergel" with *Palaeotachea dentula* as index fossil.

sylvestrina beds. According to him, only the beds containing *Palaeotachea silvana* should be named *silvana* beds. Following Wenz (1924) the OSM starts with this unit. Our taxonomic results in fact confirm the differentiation between *Palaeotachea silvana* and *P. sylvestrina* and accordingly the presence of two different horizons (*silvana* beds and *sylvestrina* beds). After Wenz (1924), the name-giving species is rare to find in the lower part of the *silvana*-beds. Due to the lack of current outcrops, one has to rely to a large extent on the stratigraphic information of Wenz (1919; 1920; 1921) and Jooss (1923). They presented a subdivision of the *silvana*-bed as shown in Table 4. *Palaeotachea silvana* is often associated with *Pseudochloritis incrassata* (Klein, 1853), *P. sylvestina* often with *Granaria schuebleri* (Klein, 1846) and *Pseudochloritis insignis* (von Zieten, 1832).

Relevant traits and identification key

The traits that are most important for the identification of Miocene *Palaeotachae* species are: (1) shell size, particularly the width; (2) shape of the last whorl; (3) shape of the protoconch (4) margin of periostome, including grade of deflection and thickness; (5) angle of spire; (6) sutures and convexity of whorls.

This key to the identification of *Palaeotoachea* on the species level is based on the morphometric aspects as demonstrated above. Some further considerations that can be helpful are: (1) *P. silvana* and *P. sylvestrina* are the most abundant species in all studied associations. (2) *P. dentula*, *P. renevieri* and *P. elevata* are relative small, while *P. silvana*, *P. sylvestrina* and *P. turonensis* are remarkably larger. (3) The most difficult case is the differentiation between *P. silvana* and *P. sylvestrina*, but measuring the angle of spire can help (see descriptions above and Nr. 3in the key). (4) *P. silvana* can be associated with *P. turonensis*, *P. dentula* as well as *Pseudochloritis incrassata*, while *P. sylvestrina* is associated with *P. elevata*, *P. turonensis*, *P. dentula*, *P. renevieri* as well as *Pseudochloritis insignis*.

1. Shell >15mm wide?
   Yes: go to **2**
   No: go to **4**
2. Peristome remarkably thickened (see Fig. 5.18)?
   Yes: *Palaeotachea turonensis*
   No: go to **3**.
3. Angle of spire on an average 100°
   Yes: *P. sylvestrina*
   No: *P. silvana*
4. Shell ca. 9mm high or less?
   Yes: *P. dentula*
   No: go to **5**
5. Last whorl "keel-like rounded?
   Yes: *P. renevieri*
   No: *P. elevata*

CONCLUSIONS

Several species of the"*Cepaea*-type" genus *Palaeotachea* were described from the Miocene of the North Alpine Foreland Basin and its adjacent smaller basins. This taxonomic complex can now be separated into six species: *Palaeotachea silvana* (Klein, 1853), *P. sylvestrina* (Schlotheim, 1820), *P. dentula* (Quenstedt, 1867), *P. renevieri* (Maillard, 1891), *P. elevata* Berz & Jooss, 1927 and *P. turonensis* (Deshayes, 1831). These species can be separated using morphological features, which could be partly confirmed by the statistical analyses of morphometric indices. The most difficult differentiation is that between *Palaeotachea silvana* and *P. sylvestrina*, but they are clearly two different species from two different stratigraphic levels. As a consequence, the historical differentiation between *silvana* beds and *sylvestrina* beds could be confirmed. In total, only 13 verified locations with defined Mammal Neogene zones (MN) are known. For this reason, the exact biostratigraphic range of the single species is hard to determine with certainty. The potential relation between *Palaeotachea turonensis* and the Pliocene genus *Frechenia* as well as the Recent *Eobania vermiculata*

mentioned in literature, cannot be solved with morphometric features.

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1871; livr. 6–**8**: 161–256, pl. 21–32, 1872; livr. 9–**10**: 257–352, pl. 33–36, 1873; livr. **11**: 353–616, 1875; livr. **12**: 617–1000, 1875. Wiesbaden (Kreidel-Verlag).

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PSEUDOCHLORITIS INSIGNIS – A PECULIAR LARGE LAND-SNAIL FROM THE MIOCENE OF SW GERMANY: TAXONOMIC STATUS AND CENSUS OF MORPHOLOGICALLY RELATED FORMS

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Abstract *The Miocene land gastropod* Pseudochloritis insignis *(von Zieten, 1832) shows a very high variability in size and its systematic designation has been debated for a long time. Statistical analyses reveal no indications for the presence of more than one species. Since the original material is definitely lost, we have defined a neotype. The relationships between P. insignis and the following taxa are discussed: Genus* Ampelita *(Acavidae), genus* Trigonephrus *Pilsbry, 1905 (Dorcasidae), genus* Chloritis *Beck, 1837 (Camaenidae), genus* Liburnica *Kobelt, 1904 (Helicidae: Ariantinae), genus* Dinarica *Kobelt, 1902 (Helicidae: Ariantinae) and* Monacha homalospira *(Reuss, 1860) (Hygromiidae) as well as* Pseudochloritis incrassata *(Klein, 1853) and the family Elonidae Gittenberger, 1979. An assignment to* Ampelita, Trigonephrus, *or* Chloritis *is rejected because of morphologic differences as well as palaeobiogeographic and palaeoclimatic considerations. The species* Monacha homalospira *(Reuss, 1860) is remarkably older than* P. insignis. *Due to teleoconch morphology as well as shape and sculpture of the protoconch, a membership of* insignis *within the fossil genus* Pseudochloritis *C. R. Boettger, 1909 is suggested herein. The stratigraphy of* P. insignis *ranges from late Langhian to early Tortonian (mammal zones MN 7 to MN 9). The suprageneric designation of this genus is, however, problematic. As for the morphological characters, it shows more similarities with the subfamiliy Ariantinae Mörch, 1864 (Helicidae) than with the Elonidae Gittenberger, 1979, but due to the absence of anatomical features this designation remains tentative.*

Key words *Gastropods, Ariantinae, Joossia, Dinarica, Steinheim Basin, microsculpture.*

INTRODUCTION

The Middle to Late Miocene species *Pseudochloritis insignis* (von Zieten, 1832 (Pulmonata, Gastropod) is a large land gastropod from the lacustrine sediments of the Steinheim Basin in SW Germany, a Middle Miocene impact crater lake. It was first described by von Zieten (1832) as *Helix insignis* from Steinheim am Albuch (Baden-Württemberg, SW Germany). Since then, several authors have discussed the phylogenetic relationships of this species. The first was von Kurr (1856), who related *P. insignis* to the South African genus *Trigonephrus* (Dorcasidae), followed by Sandberger (1872), who suggested a relationship with *Liburnica hoffmanni* (Rossmässler, 1836) (Helicidae: Ariantinae). Several authors then made assumptions about the relationship of *P. insignis* and in 1909 O. Boettger saw *P.insignis* as an ancestor of *Monacha homalospira* (Reuss, 1860) and the Madagascan genus *Ampelita* (Acavidae) (see O. Boettger 1909). Gottschick & Wenz (1920) and C.R. Boettger & Wenz (1921) compared it with the extant *Dinarica stenomphala* (Menke, 1830) (Helicidae, Ariantinae) (see also Schileyko 2006). Pfeffer (1929) proposed the new genus *Joossia* for the species *insignis* within the family Eulotidae. Later, Nordsieck (1986) placed it in the family Xanthonychidae. Binder (2008) referred *P. insignis* to the Ariantinae. According to C. R. Boettger (1909), some authors (not mentioned by him) had placed *P. insignis* into the relationship of *Chloritis* (Camaenidae). Miller (1900), C. R. Boettger (1909) and Nordsieck (1986) as well as Binder (2008) saw a strong relationship with the Badenian species *Pseudochloritis incrassata* (Klein, 1853).

This paper presents the first detailed study of *P. insignis* and aims to clarify its taxonomic status with statistical methods and considerations of shell morphology. The geographic distribution as well as stratigraphy and palaeoecology are discussed. After a morphological description with the definition of a neotype, a statistical analysis of shell parameters is presented. Then we compare *P. insignis* with other genera and discuss its attribution to a family.

MATERIAL AND METHODS

The species was first described as *Helix insignis* by von Zieten (1832). The next studies were conducted by Adolph von Klein (1805–1892) in 1846

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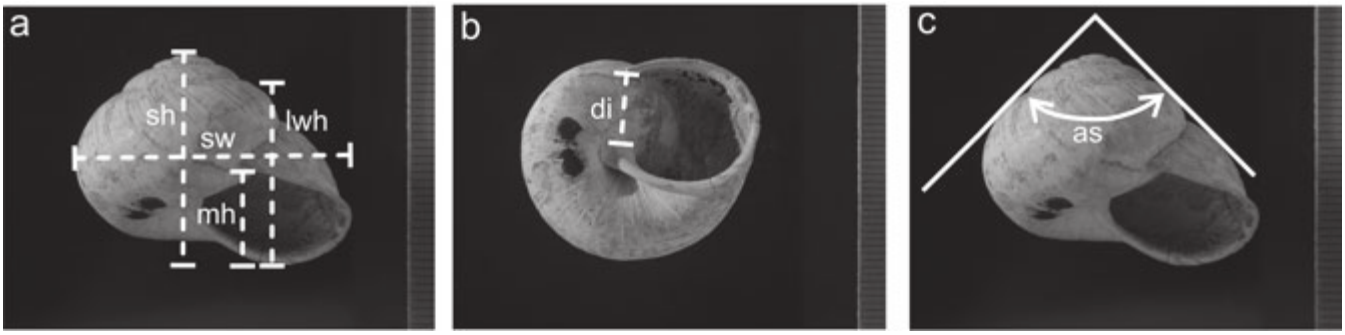


Figure 1 Measurements of the different morphometric features.

and by Miller (1900), the material of whose is present in the collection of Staatliches Museum für Naturkunde Stuttgart (SMNS). A remarkable number of shells also occurs in the collection of Franz Gottschick. He was a forester in Steinheim am Albuch at the beginning of the 20th century and the author of some publications about the fossil snails of Steinheim am Albuch, partly together with the malacologist Wilhelm Wenz. After his death in 1927, his collection came to the SMNS. Another important contemporary collection with a considerable number of unpublished shells of *P. insignis* at the SMNS is that of Carlo H. Jooss (born in 1883).

The collection of the first author Carl Hartwig von Zieten (1785 – 1846) is lost, apart from some Mesozoic material (Cleevely 1983). We searched the SMNS collection intensively and made a survey among other German colleagues and so we can confirm that no relevant material exists. Due to this fact and to delineate it from *Pseudochloritis incrassata* (Klein, 1853) , we are herein defining a neotype in accordance the International Code of Zoological Nomenclature (online version: www.nhm.ac.uk/hosted-sites/iczn/code). The neotype is from the original material of Klein (1846). The front cover of the issue of this journal shows the year 1847, but the pagination within the journal always quotes the year 1846. It is not clear, whether this is because of a typo, but from the beginning (e.g., Klein 1853) this paper was cited as 1846.

In order to analyse the morphological variability of *P. insignis* and to find potential relationships, the following standard parameters were measured (Fig. 1a–c)**:** shell height (**sh**), shell width (**sw**), height of the aperture (**mh**), and height of the last whorl (**lwh**). Additionally, the angle of spire (**as**) and the distance between the insertions (**di**) were measured. This was done for the species *Pseudochloritis insignis* (n=82), *P. incrassata* (n=82) as well as *Dinarica pouzolzi* (n=77). The two last named species are the type species of their genus. They were chosen, because they represent the morphologically and palaeogeographically closest forms to *P. insignis*. Only adult shells were measured. The measurements were made with a digital slide gauge, a goniometer, and the image analyses software Image J (Burger & Burge 2006). All material is stored in the Staatliches Museum für Naturkunde Stuttgart (SMNS): fossil gastropods in the collection of Tertiary and Quaternary Invertebrates, and modern gastropods in the Malacozoology collection. The numbers and localities of the measured specimens are listed in Appendix 1. For further statistical calculations, the following ratios were calculated (compare Fig. 1): sh/sw, sh/mh, sh/lwh, sh/di, sh/as, sw/mh, sw/lwh, sw/di, sw/as, lwh/mh, mh/di, mh/as, lwh/di, lwh/as. Furthermore, arithmetic mean (A) and standard deviation (SD) were calculated for each ratio (Appendix 2). A cluster analyses (Ward`s method, euclidean) was calculated using all measured ratios mentioned above, and another one using arithmetic means only (Fig. 2b; Appendix 2) using the statistics software "PAST" (Hammer *et al*. 2001). Furthermore, a Principal Component Analysis (PCA; variance-covariance Matrix; Fig. 3) was calculated using the measured single parameters (sh, sw, etc.).

All the measured material of *P. insignis* comes from Steinheim am Albuch. The SMNS also has a relatively large number of specimens from the Late Miocene (MN 9) of Höwenegg near Immendingen (Baden-Württemberg, S Germany). These specimens are, however, mostly deformed and therefore not usable for morphometric methods.

RESULTS

SYSTEMATICS

Pseudochloritis insignis (von Zieten, 1832)
(Figs 4.1, 4.2, 4.7, 4.8; Figs 5.7, 5.8; Figs 6.1–12)

Helix insignis Schübler in von Zieten, 1832: P. 38, Tab. XXIX, Fig. 1 (Steinheim am Albuch (Original material lost).
Helix insignis Schübler – Klein, 1846: P. 65, tab. 1, fig. 2
Helix steinheimensis – Klein, 1846: P. 70, tab. 1, fig. 10
Helix steinheimensis Klein- Sandberger 1872: pl. 28 F. 9, 9a
Helix (Campylaea) insignis var. *steinheimensis* Klein- Sandberger, 1872: 650
Helix (Campylaea) *insignis* Schübler – Sandberger, 1872: P. 650.
Chilostoma (Dinarica) insignis (Schübler) Zieten – Gottschick & Wenz, 1920: P. 44.
Campylaea (*Dinarica*) *insignis* (Zieten) – Wenz, 1923: P. 522 (see there for more synonyms)
Joossia insignis (Zieten) – Pfeffer, 1929: P. 246
Joossia insignis (Zieten 1830) – Binder, 2008: P. 177.

Material A most typical specimen of the Klein collection (Figs 4.1, 4.7, 4.8)) is defined as the neotypus of *Pseudochloritis insignis* (von Zieten, 1832). It is stored at Staatliches Museum für Naturkunde Stuttgart (SMNS), inv. no. SMNS 23910b. The *locus typicus* is the Steinheim Basin (coordinates of the basin center: 48°41'11.8"N 10°03'55.8"E), political district Steinheim am Albuch, Baden-Württemberg, SW Germany. The *stratum typicum* are the "Steinheimer Seeschichten", mammal zone MN7, Middle Miocene.

Description The massive shell has a dextral, helicoid shape, ranging from globular to very depressed. It consists of 4.5 regular whorls. The

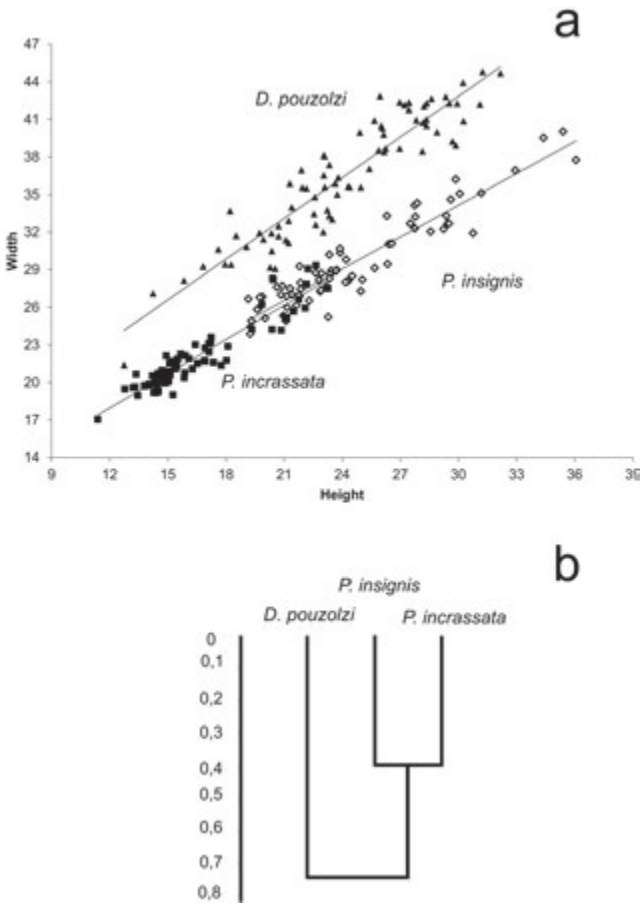


Figure 2a. Diagram with the plotted shell height and shell width. **b.** Cluster analysis with *Pseudochloritis insignis*, *P. incrassata* and *Dinarcia pouzolzi*.

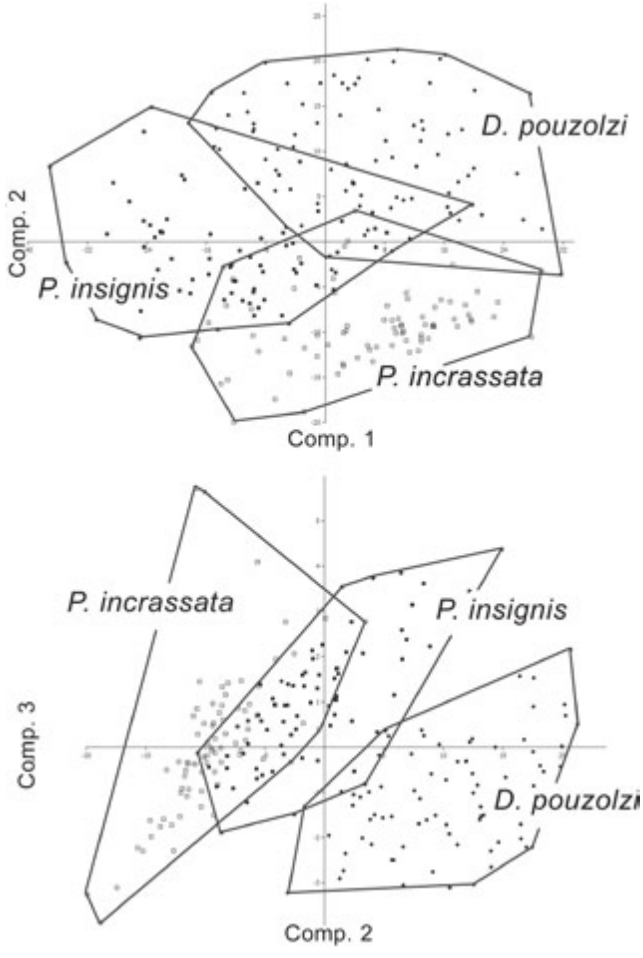


Figure 3 Principal component analysis (PCA) with *Pseudochloritis insignis*, *P. incrassata* and *Dinarcia pouzolzi*.

neotype is 28mm high and 32mm wide. The aperture is 18mm high and the last whorl 24mm. The protoconch of the neotype is ca. 2.5mm in diameter. Height and width measures of the different shells are extremely variable. The average height /width ratio is ca. 0.81, that of the neotype is ca. 0.89. The whorls are convex with moderately deep sutures. Before reaching the periostome, the last whorl runs downwards obliquely. The aperture has an oblique-ovate shape. The peristome is deflected. The insertions are connected by a thin callous layer .The umbilicus is deep and half covered by a columellar callus. There are very distinct and regular prosocline growth lines on the whorls. Their strengths differ between individuals. The microsculpture consists of little hair pits on the first teleoconch whorls (Figs 5.7, 5.8), which disappear on the later whorls. The protoconch consists of ca. 1.5 whorls and has a remarkably bulbous shape. The microsculpture of the protoconch consists of little pustulae and little pits (Fig. 6.10), which was also described by Gottschick & Wenz (1920) and Binder (2008). These are visible on the neotype even at low magnification. Likewise, fold-like ribs can be found on the protoconch. The thickness and strength of these folds are variable. A few specimens bear traces of a brown band near the periphery of the last whorl just like *Pseudochloritis incrassata* (Klein, 1846) (see also C. R. Boettger 1911; Binder 2008). The secondary ribs on the last whorl as described by Binder (2008), are hardly visible in the studied material. In some specimens, also very weak traces of spiral lines can be seen. In the collection of the SMNS, the largest specimen has a width of 40mm. Most of the shells widths range between 24 and 36mm. The maximum diameter according to Miller (1900) is 43mm, but he also wrote that the specimen figured in von Zieten (1832) has 44mm. Quenstedt (1884) mentioned 47mm for the specimen figured by von Zieten. Unfortunately, the original description of von Zieten (1832) contains no size specification and the material is lost.

Statistics The sh/sw diagram (Fig. 2a) for *P. insignis* and *P. incrassata* reveals a linear function between shell height and width. The measured A and SD values are listed in App. 2. *Pseudochloritis insignis* and *P. incrassata* show the highest SD in the sw/di division. This ratio seems to be the most variable one among shells of *P. insignis*. This species has the lowest SD of the sh/lwh ratio with 0.03, which means that the relationship between shell height and height of the last whorl seems to be relatively constant. *D. pouzolzi* has the highest SD of the lwh/di ratio. The cluster analysis of the arithmetic mean values (A) (Fig. 3) shows a closer affinity between *P. insignis* and *P. incrassata* than between the former and *D. pouzolzi*. The first three components of the PCA (Fig. 3) account for 66.73%, 31.69% and 0.94%, respectively. Both a scatter plot of PC1 (Eigenvalue 193.40) and PC 2 (91.85), and one of PC 2 and PC 3 (2.72), respectively, reveal clear separation of the three species. Most overlaps occur between *P. incrassata* and *P. insignis*, on the one hand, and between *P. insignis* and *D. pouzolzi*, on the other.

Palaeogeographic distribution *Pseudochloritis insignis* has a relatively limited geographical distribution in Baden- Württemberg, SW Germany. Most of the specimens in the collections come from Steinheim am Albuch (48°41'16.6"N 10°03'35.6"E). The other locality with a higher number of shells is Höwenegg near Engen (47°54'41.2"N 8°44'30.9"E). Besides that, only one specimen from Böttingen (48°24'44.5"N 9°33'10.0"E) is known. Several other localities are mentioned by Wenz (1923), but none of these findings could be confirmed among the studied collections. Therefore, these records should be treated with caution. A confusion with the species *P. incrassata* is possible.

Palaeoecology Since direct descendants are unknown, the ecological preferences of *P. insignis* are difficult to reconstruct. According to Goodfriend (1986), larger snails are frequently associated with relatively moist conditions. The presence of hairs would also indicate a moist environment (see Pfenninger *et al*. 2005).

Stratigraphy The species is reported from Middle Miocene (mammal zone MN 7, Steinheim am Albuch; summary in Rasser 2013) to Late Miocene (mammal zone MN 9; Höwenegg; summary in Munk *et al*. 2007). The stratigraphy of the locality Böttingen is not supported sufficiently, but assumed to be Middle Miocene (Rosendahl *et al*. 2003). According to Gottschick & Wenz (1920), *P. insignis* occurs in Steinheim am Albuch in the *trochiformis*-beds and in the *kleini*-beds as well as in the layers above them (review

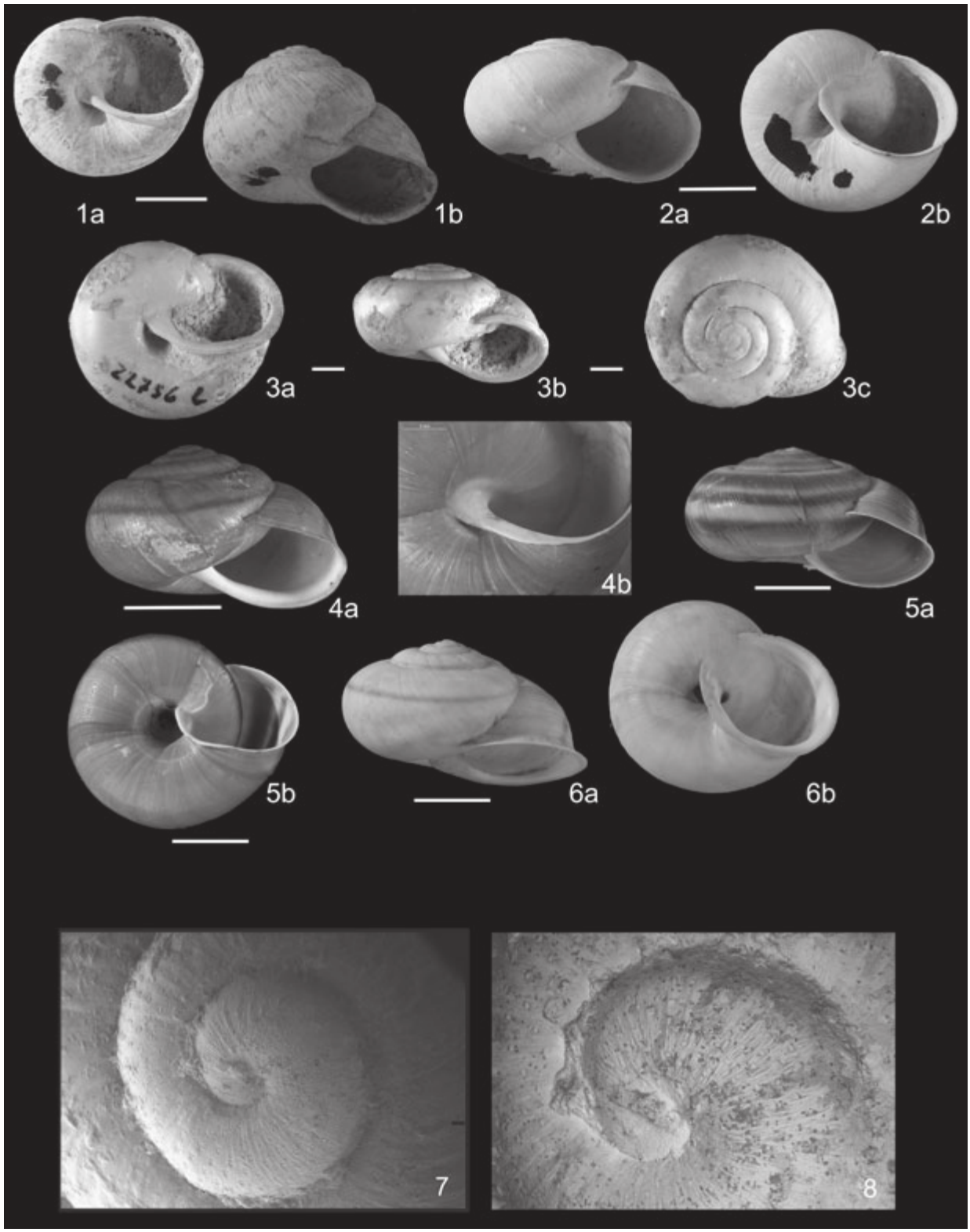


Figure 4.1 *Pseudochloritis insignis* (von Zieten, 1832), Steinheim am Albuch, Miocene, Neotype, Scale 10mm, SMNS 23910b. **4.2** *P insignis*, Steinheim am Albuch, Miocene, Scale 10mm, SMNS 101666. **4.3** *P. incrassata* (Klein, 1853), Zwiefalten, Miocene, One of the original material of *Helix inflexa* Klein, 1846. Scale 10mm. SMNS 101525. **4.4** *Dinarica stenomphala* (Menke, 1830) SMNS-ZI0078280. Welebit, Croatia. Scale: a=5mm, b=2mm. **4.5** *D. pouzolzi* (Deshayes, 1832) SMNS-ZI0078278, Aleksina Medja near Trebinje, Bosnia and Herzegovina, Type species of *Dinarica*. Scale 10mm. **4.6** *Liburnica hoffmanni* (Rossmässler, 1836), SMNS-ZI78279, Dalmatia. Scale 10mm. **4.7** *P. insignis*, Protoconch of Fig. 1, Neotype, Scale 200µm. **4.8** *P. insignis* , Detail of Fig. 7, Neotype, Scale 100µm.

in Rasser 2013). Finger (1998) also mentioned "*Dinarica*-fragments" (probably *P. insignis*) in the basal *kleini* beds. For most specimens, however, detailed stratigraphic information is lacking. Following Binder (2008), the related *P. incrassata* is restricted to the Badenium (Langhian of the International Chronostratigraphy), which incorporates mammal zones MN5 and MN6 (Berger *et al*. 2005; Hilgen *et al*. 2012).

Discussion of the systematic position

The specimens of *P. insignis* show a distinct variability in height and width. They range from very flat forms to relatively high ones. However, morphometric analyses reveal no evidence for the presence of more than one species. Originally, the species *insignis* was placed within the genus *Helix* Linnaeus, 1758, like many of other terrestrial gastropods in the 18th and 19th century. Since this time, different proposals for the systematic position of P. *insignis* were made, which are discussed herein.

Helix Linnaeus, 1758
P. insignis clearly differs from *Helix* (compare Schileyko 2006) by the following points: (1.) height/width ratio, (2.) growth development of the protoconch and (3.) lack of sculpture on the protoconch.

Trigonephrus Pilsbry, 1905 (Dorcasidae)
According to von Kurr (1856), no European species is comparable to *P. insignis*. He assumed that it is related with the South Africanp secies *Trigonephrus rosaceus* (Müller, 1774), because of its funnel-like umbilicus. This genus is known from SW Africa since the Eocene (Wenz & Zilch 1960). Today it is limited to the vicinity of the coastline and rivers in the desert regions of SW Africa (Wenz & Zilch 1960). Following Schileyko (1999), however, the embryonic whorls of *Trigonephrus* are smooth, which is in opposite to *P. insignis*. This fact and the geographic distance between them is an argument against this relationship.

Monacha homalospira (Reuss, 1860) (Hygromiidae)
O. Boettger (1909) suggested that *Pseudochloritis insignis* is a "mixed-type" ("Mischtypus"), being the ancestor of the madagassian genus *Ampelita* (family Acavidae) and of *Helix homalospira* Reuss, 1860 (*Monacha homalospira* according to Wenz 1923). O. Boettger (1909) did, however, not specify his hypothesis. Following Sandberger (1872), the last named species occurs only in Tuchořice and Lipno/Czech Republic. The stratigraphic correlation of these localities is Early Miocene (MN 3b; Harzhauser *et al*. 2014), which is much older than the *stratum typicum* of *P. insignis*. Therefore, *insignis* can hardly be the ancestor of *homalospira*.

Ampelita Beck, 1837 (Acavidae)
O. Boettger (1909) suggested that *P. insignis* is the ancestor of the *Ampelita* Beck, 1837. *Ampelita* contains several species with varying shell morphologies. The genus is known since the Pleistocene (Wenz & Zilch 1960) and is restricted to Madagascar (Schileyko 1999). The type species of the genus is *A. lanx* (Férussac, 1821), which differs significantly from the gastropods discussed herein. The only species within the genus that is morphologically comparable with *P. insignis* is *A. robillardi* (Angas, 1876). Nevertheless, there are two arguments against O. Boettgers hypothesis: (1.) *Ampelita* has smooth embryonic whorls (Schileyko 1999) and (2.) the palaeogeography: when *P. insignis* first appeared in the Miocene, Madagascar was already isolated from the continent.

Chloritis Beck, 1837 (Camaenidae)
Another group with a *P. insignis*- like morphology is the Camaenid genus *Chloritis* Beck, 1837, which includes *Austrochloritis* Pilsbry, 1891 and *Nannochloritis* Iredale, 1938, whose taxonomic rank is under discussion (Schileyko 2003; Dharma 2005; Stanisic *et al*. 2010). The species *Nannochloritis layardi* (Gude, 1906), illustrated in Stanisic *et al*. (2010), has a similarly shaped protoconch and the same pustulated sculpture as *P. insignis*. From the overall outline *Chloritis (Austrochloritis) argillacea* (Férussac, 1821), illustrated in Dharma (2005, Pl. 89), is comparable with *P. insignis*. It has a reflected lip and a half covered umbilicus like *P. insignis*. The Camaenidae are widespread in the tropics (Richardson 1985, cited in Harzhauser *et al*. 2008). It is a very large group with many different shell forms (Dharma 2005 or Abbott 1989). They are, however, a polyphyletic group and need to be revised, because the American forms are closely related to the Helicidae and Helminthoglyptidae, while the Australasian ones are a sister group to the Bradybaenidae (Scott 1996). According to this

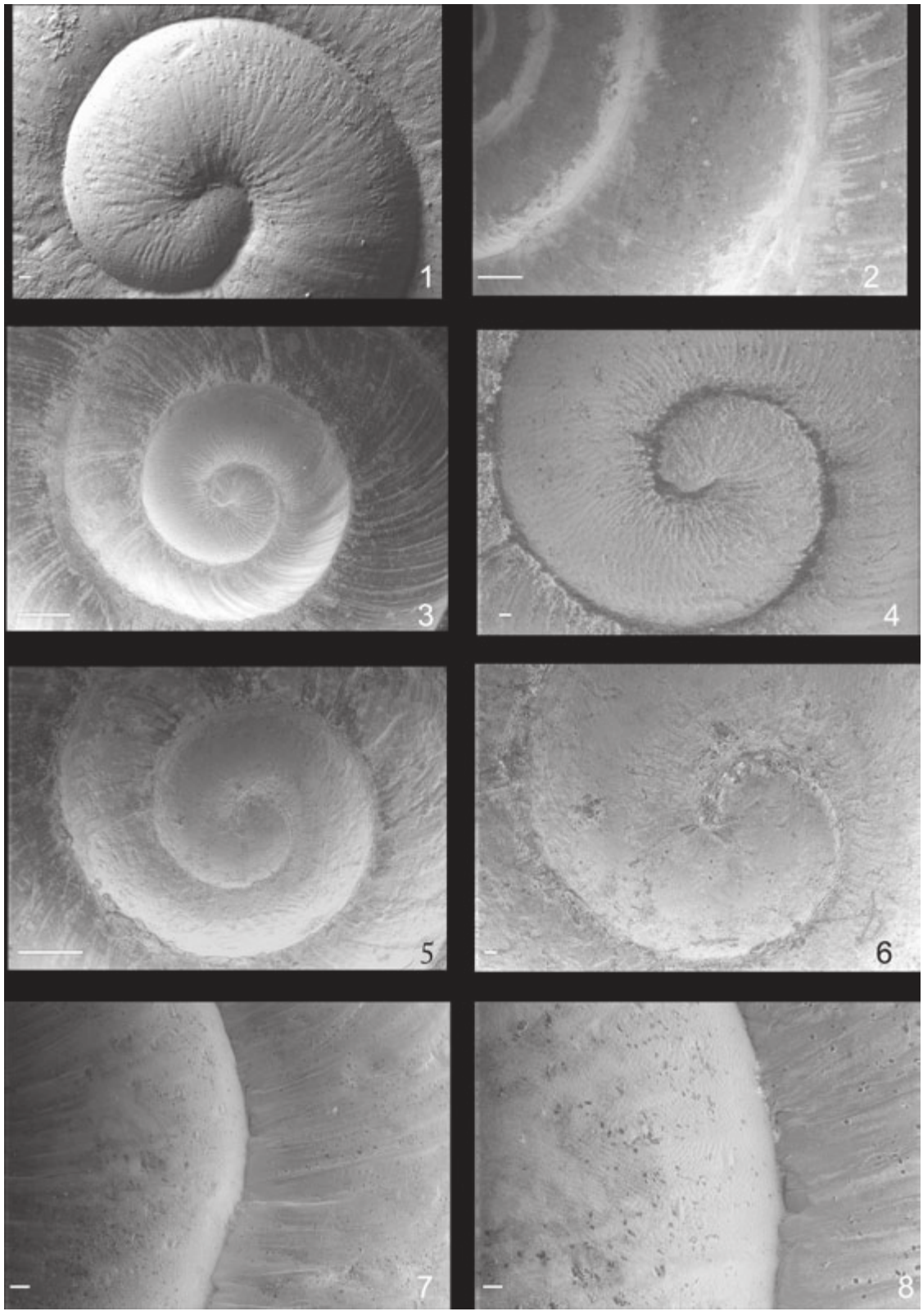


Figure 5.1 *Pseudochloritis incrassata* (Klein, 1846), Protoconch of Fig. 4.3, Scale 100 µm. **5.2** *P. incrassata*, Zwiefalten, Miocene, One of the original material of *Helix inflexa* Klein, 1846, Detail of the teleoconch, Scale 1mm. SMNS 101525. **5.3** *Dinarica pouzolzi* (Deshayes, 1832), Dubrovnik, Croatia. Subadult, Protoconch, Scale 1mm, SMNS-ZI78281. **5.4** *D. pouzolzi* (Deshayes, 1832), Detail of Fig. 3 Scale 100 µm. **5.5** *D. stenomphala* (Menke, 1830), Protoconch of Fig. 4.4. Scale 1mm. **5.6** *D. stenomphala* (Menke, 1830), Detail of fig. 5. Scale 100 µm. **5.7 & 5.8** *P. insignis* (von Zieten, 1832), Steinheim am Albuch, Detail of the teleoconch, Neotype, SMNS 101.524. Scale fig. 7: 200 µm, fig. 8: 100 µm.

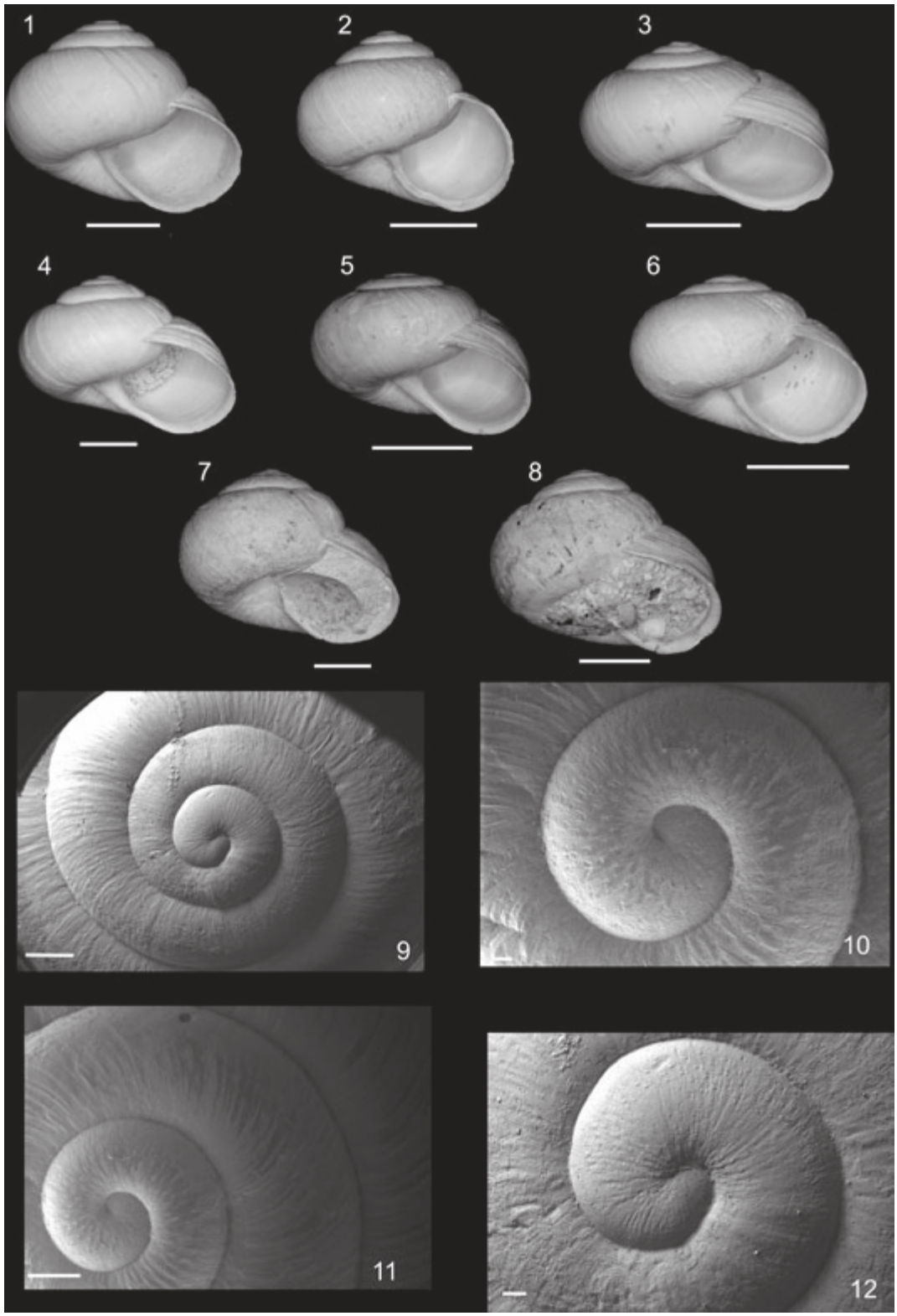
author, the family Camaenidae was defined only by anatomical features (lack of a dart sac and glands). Therefore, an affiliation of a fossil taxon to this family is problematic. Also the "*Chloritis*-group" within the Camaenidae seems to be in need to revision.

Dinarica Kobelt, 1902 (Helicidae, Ariantinae)
Gottschick & Wenz (1920) and C. R. Boettger & Wenz (1921) compared *P. insigins* with the Recent species *Dinarica stenomphala* (Menke, 1830) (Fig. 4.4; Figs 5.5–5.6). The genus *Dinarica* occurs in the Balkan region (Knipper 1939) and the type species is *Dinarica pouzolzi* (Deshayes, 1830) (Fig. 4.5; Figs 5.3–5.4). Following the descriptions of Gottschick & Wenz (1920), however, there are remarkable differences: (1.) Teleoconch: *D. stenomphala* has up to six whorls. The first whorls of *P. insignis* are wider and more massive and the last whorl is more bulbous. The umbilicus in *D. stenomphala* is more covered than that of *P. insignis.* (2.) Embryonic whorls: *D. pouzolzi* and *D. stenomphala* lack the little knobs that occur on the embryonic whorls of *P. insignis*. The growth development of the protoconch is different. The size increases faster in *P. insignis* . (3.) Shells of *Dinarica* are hairless (Subai 2002). (4.) Morphometrics suggest clear separation of the type species *Dinarica pouzolzi* and of *P. insignis* (Figs 2, 3).

Liburnica Kobelt, 1904 (Helicidae, Ariantinae)
Sandberger (1872) placed *P. insignis* close to *Liburnica hoffmanni* (Rossmässler, 1836) (Fig. 4.6; Figs 5.3–5.4), which corresponds particularly with the low-spired forms of *P. insignis*. *L. hoffmanni* has little hair pits on the first whorls (Subai 2002), but the presence of hairs can be different among the single populations and individuals (Knipper 1939). Gottschick & Wenz (1920) have already pointed out the differences between *P. insignis* and *L. hoffmanni*. These are: (1.) The forms of *P. insignis* are lower spired and the peristome is more strongly reflected. (2.) The last whorl is a little more descending and the aperture is not that oblique; *L. hoffmanni* has a thin callus-ledge on the basis of the aperture. (3.) The insertions are remarkably closer to each other in *L. hoffmanni*. (4.) The radial growth lines of *P. insignis* are much stronger. (5.) According to Schileyko (2006), the genus *Liburnica* has mostly smooth embryonic whorls, or they are very finely granulated.

Joossia Pfeffer, 1929 (Eulotidae)
Based on morphology and sculpture, Pfeffer (1929) concluded that *P. insignis* cannot be related to the Ariantinae. Instead, he placed *P. insignis* in his newly designated genus *Joossia* within his also redefined family Eulotidae Möllendorff 1898 (valid name Bradybaenidae Pilsbry 1934 (1898), see Bouchet & Rocroi 2005: 38, 269). This decision was based on a comparison between *P. insignis* and *Dinarica pouzolzi*. However, the differences he described, can even be found between the members within the Ariantinae. Since these arguments are insufficient to place *P. insignis* in the family Bradybaenidae, Wenz & Zilch (1960) and Schileyko (2006) considered *Joossia* a synonym of *Dinarica*.

Pseudochloritis C. R. Boettger, 1909 (Helicidae, Ariantinae)
C. R. Boettger (1909) placed *P. insignis* in his new genus *Pseudochloritis* within the Ariantinae. The most recent work on *Pseudochloritis* was published by Binder (2008). He confirmed the placement within the Ariantinae. Whether *Pseudochloritis* is a subgenus of *Tropidomphalus* or a separate genus, is still debated in literature. We follow Binder (2008) who designated *Pseudochloritis* as a separate genus. Gittenberger (1979) saw *Tropidomphalus*/*Pseudochloritis* as a possible "connection" between the extant *Elona quimperiana* (Férussac, 1821) and *Norelona pyrenaica* (Draparnaud, 1805). Based on anatomical features, he united these two species into the new family Elonidae. Nordsieck (1986) then assumed that *Pseudochloritis* belongs to the Eloninae (= Elonidae *sensu* Gittenberger 1979) as well, but not to the Ariantinae. Later, however, Binder (2008) argued that the similarities between *Pseudochloritis* and *Elona* as well as *Norelona* are only superficial. Binder suggested a relationship with the Ariantinae, which he strongly supported by documenting the similarities in shell microsculpture with the modern species *Helicigona (Campylaea) lefeburiana* (C.Pfeiffer 1828), and we can confirm this with our study. From the discussed geographic distribution, the general shell morphology and the microsculpture of the embryonic whorls, *Pseudochloritis* fits with the Ariantinae. Both *P. insignis* and *P. incrassata* show the same "pattern" of morphological variability as *Arianta arbustorum*, the type species of the Ariantinae (see Fechter & Falkner 1989, p. 227, fig. 3–9).



Figures 6.1–6.3 *Pseudochloritis insignis* (von Zieten, 1832), Miocene, Steinheim am Albuch, *trochiformis*-strata, Collection Jooss. SMNS J66159, Scale 10mm. **6.4** *P. insignis*, Steinheim am Albuch, *trochiformis*- strata, Miocene, Collection Jooss. SMNS J66162, Scale 10mm. **6.5–6.6** *P. insignis*, Steinheim am Albuch, *trochiformis*-strata, Miocene, Collection Jooss. SMNS J66156. Scale 10mm. **6.7–6.8** *P. insignis* , Steinheim am Albuch, *trochiformis*-strata, Miocene, Collection Jooss. SMNS 66161. Scale 10mm. **6.9** *P. insignis* , Protoconch of Fig. 4.2. Inv. No. 101666. Scale 1mm. **6.10** *P. insignis* , Detail of fig. 9. Scale 200µm. **6.11** *P. incrassata*, Protoconch of Fig. 4.3. Scale 1mm. **6.12** *P. incrassata*, Detail of fig. 11. Scale 200µm.

As the type species for his new genus *Pseudochloritis*, C.R. Boettger (1909) chose *Helix inflexa* sensu Klein, 1846, non Zieten 1832, for which the valid name is *Pseudochloritis incrassata* (Klein 1853) according to Binder (2008). The specimens shown in Fig. 4.3; Figs 5.1–5.2; Figs.6.11–6.12 are from the published material of Klein (1846). C.R. Boettger (1911) described *Pseudochloritis* as follows (translated from Latin): "Shell spherical-depressed to conical-depressed, half covered umbilicus, solid to massive, often with one band; low spira, apex in most cases blunt, convex basis; distinct suture. 4.5–5.5 convex whorls, radial ribs and also equipped with pits. The last whorl runs downwards to the tight aperture. Aperture oblique, sickle-shaped, peristome callous thickened, extensively reflected. The columellar region is extended to the outside".

Sandberger (1872) and Miller (1900) pointed to the similarities between *Helix insignis* (i.e., *P. insignis*) and *Helix zelli* Kurr 1856 (i.e., *P. incrassata* according to Binder (2008)). According to our studies, *P. insignis* and *P. incrassata* reveal the following similarities: (1.) The development of the whorls are comparable; because of this, the large forms of *P. incrassata* have often been confused with *P. insignis* (see also Wenz 1923). (2.) Following the sh/sw plot (Fig. 2), the cluster analysis (Fig. 2b), and the PCA (Fig. 3), *P. insignis* is more related to *P. incrassata* than to the type species of *Dinarica*, *D. pouzolzi*. (3.) The growth of the protoconch is similar (see Fig. 5.1 and Figs 6.9–6.12). (4.) The protoconch of both species bears the same pustulae and hair-pits (see Fig. 4.7; Fig. 5.1; Figs 6.10–6.12). For these reasons a membership of the species *insignis* in *Pseudochloritis* C. R. Boettger, 1909 is suggested herein.

The main differences between *P. insignis* and *P. incrassata* are: (1.) *P. insignis* is larger. (2.) *P. incrassata* has a stronger reflected peristome. (3.) *P. insignis* bears more prominent prosocline radial growth lines. (4.) Despite a certain overlap, morphometrics suggest a separation into two different species (Figs 2, 3).

Conclusion

Based on shell characters and morphology, as well as protoconch development and sculpture, *insignis* is placed into the genus *Pseudochloritis*. Regarding shell morphology, variability pattern and protoconch sculpture, *Pseudochlorits* fits more with the subfamily Ariantinae within the Helicidae, than with the Elonidae. Due to the limited amount of differentiating shell characters, and the tendency to convergent morphologies of land snails, however, a final decision may remain tentative for fossil material. The proposal of von Kurr (1856) about a membership within the Dorcasidae with the genus *Trigonephrus* is impossible due to palaeobiogeographic considerations. The same is true for the assumption of O. Boettger (1909) that *P. insignis* is the ancestor of the Madagascan genus *Ampelita*. According to Schileyko (1999), both genera have smooth protoconchs, which is in contrast to the sculptured protoconch of *Pseudochloritis*. The Camaenidae with *Chloritis*, which O. Boettger (1909) brought into discussion, is a problematic group. Some members of the Australian genus/subgenus *Austrochloritis* are similar to *P. insignis*. The Camaenidae are a very large, and according to Scott (1996), obviously a polyphyletic group that needs to be revised. Therefore, an assignment of fossil land-snails to the Camaenidae remains uncertain.

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APPENDIX 1: MEASURED SPECIMENS: THEIR LOCALITIES AND NUMBERS.

Dinarica pouzolzi

Herzigowina, Aleksina Medja bei Trebinje. Original to Pl. 1, fig. 5; Pl. 2, fig. 3 & 4 (**1**): Ragusa (6): location? 24084 (**1**): Ragusa 738 (**1**): Dalmatia (2): Herzigowina, Biléca (**1**): Dalmatia 39830 (**2**): Dalmatia 14943 (**2**): ?Krivorizc 14906 (**2**): Makarska, Dalmatia (**2**): Serbia (**1**): Dubrovnik-Gruz, Dalmatia (**3**): At Sentarisee (3): Dalmatia 2249 (**2**): Cattaro (**1**): Dalmatia 36746 (**2**): Dubrovnik-Gruz, Dalmatia HN 2550 (**2**): Cattaro (**5**): Dalmatia, Dubrovnik-Lapad (**3**): Cetinje (**1**): Bosnia (**2**): Gravosa, Dalmatia (**2**): Dalmatia (**1**): ?Herticea 14934 (**2**): Dubrovnik, Dubrovacko-neretvanska ZI0086291 (**2**): Dubrovnik, Dubrovacko-neretvanska ZI0086292 (**2**): Nasic, Bosnia 39837 (**2**): Ogram (**2**): Bosnia and Herzegowina, Federacija Bosnc i Herzegovine, Hercegovacko-neretvanski, Mostar, Neretva-Valley ZI0086294 (**2**): ?Zvezda, Serbia (**1**): Serbia and Montenegro, Crna Gora Lovcen ZI0086293 (**1**): Jablaniko, Herzegowina, 39832 (**3**): Cattaro (**12**).

Pseudochloritis incrassata

Mörsingen/Germany, Miocene. Coll. JOOSS. SMNS 66.206 (**11**): Mörsingen/Germany, Miocene. Coll. JOOSS. SMNS 68.532 (**3**): Michelsberg near Dischingen/Germany, Miocene. Coll. JOOSS. SMNS 66.214 (**4**): Schauenberg near Hohenmemmingen/Germany, Miocene. Coll. JOOSS. SMNS 66.213 (**4**): Friedingen/Germany. Miocene. Coll. JOOSS. SMNS 66.224 (**2**): Mörsingen/Germany. Miocene. Coll. Bechter 4443/2008. (**16**): Mörsingen/Germany. Miocene. Coll. Bechter 4341/2008 (**4**): Mörsingen/Germany. Miocene. Coll. Bechter 4444/2008 (**18**): Coll. Jooss. 66.221 location ? (**1**): Andelfingen/Germany. ? Miocene. ?Holotype to Helix zelli VON KURR, 1856. IMDAS If. Nr. 38992/2005 (**1**): Mörsingen/Germany, Miocene. Coll. JOOSS. SMNS 66.234 (**1**): Scheuenberg near Hohenmemmingen/Germany. Miocene. Coll. JOOSS. SMNS 66.227 (**1**): Nunningen, Kanton Solothurn, Switzerland. ? Miocene. Coll. Jooss SMNS 66.150 (**1**): Zwiefalten/Germany. ?Holotype of Helix incrassata KLEIN, 1853. IMDAS If. Nr.25251/2005 (**1**): Rein, Steiermark/Austria, Miocene. Coll. JOOSS. SMNS 66.235 (**2**): Zwiefalten/Germany. Miocene. Originals of Helix incrassata KLEIN, 1853. IMDAS Nr. If. 41555/2005 (**1**): Friedingen/Germany, Miocene. Coll. JOOSS. SMNS 66.224 (**2**): Hof, Nebelberg near Munningen Kanton Solothurn/ Switzerland, Miocene. Coll. JOOSS. SMNS 66.164 (**4**): Hof, Nebelberg near Munningen Kanton Solothurn/Switzerland, Miocene. Coll. JOOSS. SMNS 66.165 (**2**): Zwiefalten/ Germany. Miocene. Original material of Helix inflexa Klein, 1853. Inv. No. 101525 (**3**).

Pseudochloritis insignis

Steinheim am Albuch/Germany. Miocene (MN7). Neotype. Original to KLEIN, 1847. Inv. No. 23910b (**1**): Steinheim am Albuch. Original to KLEIN 1847. IMDAS If. Nr. 25138/2005 (**1**): Steinheim am Albuch. Original to MILLER 1900. IMDAS Ifd. Nr. 38305/2005 (**2**): Steinheim am Albuch. Original to Helix steinheimensis Klein, 1847. IMDAS If. 25227/2005 (**1**): Steinheim am Albuch. Coll. JOOSS. SMNS 66.159 (**5**): Steinheim am Albuch. Coll. JOOSS. SMNS 66.158 (**4**): Steinheim am Albuch. Coll. JOOSS. Original material to Pl. 1, fig. 2; Pl. 3, fig. 8; Pl. 4, fig. 5, 6, 9 & 10. SMNS 66.156 (**7**): Steinheim am Albuch. Coll. JOOSS. SMNS 66.161 (**5**): Steinheim am Albuch. Coll. JOOSS. SMNS 66.162 (**1**): Steinheim am Albuch. Coll. Bechter. 12409/2008 (**3**): Steinheim am Albuch. Coll. Bechter. 12410/2008 (**4**): Steinheim am Albuch. Coll. Bechter. 12411/2008 (**5**): Steinheim am Albuch. Coll. Bechter. 12192/2008n (**2**): Steinheim am Albuch. Coll. Bechter. 12414/2008 (**4**): Steinheim am Albuch. Coll. Bechter. 12413/2008 (**4**): Steinheim am Albuch. Syntype. Original to Pl. 1, fig. 2. Inv. No. 101666 (**1**): Steinheim am Albuch. Coll. Degenfeld (5): Steinheim am Albuch. 15873/2007 (**3**): Steinheim am Albuch. Coll. Hermann. 12131/2008 (2): Steinheim am Albuch. 12133/2008 (**5**): Steinheim am Albuch. Leg. KAPITZKE 1986. Original material to Pl. 2, fig. 7 & 8 (**1**).

APPENDIX 2. MEAN VALUES (MV) AND STANDARD DEVIATION (SD) OF THE DIFFERENT RATIOS.

Morphometric ratios	*P.insignis* (mv)	*P. insignis* (sd)	*P. incrassata* (mv)	*P. incrassata* (sd)	*D. pouzolzi* (mv)	*D. pouzolzi* (sd)
sh/sw	0.828	0.052	0.742	0.049	0.658	0.048
sh/mh	1.411	0.086	1.356	0.067	1.387	0.08
sh/lwh	1.526	0.032	1.54	0.032	1.197	0.042
sh/di	2.222	0.221	1.904	0.174	2.023	0.184
sh/as	0.235	0.056	0.138	0.033	0.195	0.046
sw/mh	1.706	0.072	1.831	0.092	2.114	0.115
sw/lwh	1.396	0.076	1.562	0.098	1.826	0.113
sw/di	2.691	0.239	2.56	0.224	3.079	0.237
sw/as	0.281	0.052	0.185	0.034	0.293	0.055
lwh/mh	1.226	0.057	1.175	0.049	1.159	0.046
mh/di	1.583	0.127	1.402	0.115	1.458	0.099
mh/as	0.165	0.033	0.101	0.022	0.14	0.029
hlw/di	1.94	0.175	1.649	0.152	1.69	0.135
hlw/as	0.204	0.047	0.119	0.029	0.162	0.038

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Article

The chondrinid land snail *Granaria* (Stylommatophora: Chondrinidae) in the Miocene of the Alpine Foreland: State of the art and taxonomic reassessment

Olaf Höltke and Michael W. Rasser

With 4 figures and 2 tables

Abstract: Chondrinid snails are common in Middle to Late Miocene freshwater sediments of the North Alpine Foreland Basin (Molasse Zone) and the deposits of adjacent, time-equivalent fossil lakes, but their taxonomic status is unclear in most cases. This paper provides a taxonomic reassessment of this group. *Granaria* is the only genus of chondrinid snails identified in fossil material thus far. A neotype for *Granaria schuebleri* (Klein, 1847) is defined, while *G. antiqua* (Schübler in von Zieten, 1832) is considered a synonym of *G. schuebleri* (Klein, 1847). It is suggested that *G. grossecostata* (Gottschick & Wenz, 1919) be accepted as a separate species instead of a subspecies of *G. schuebleri* (Klein, 1847). The taxonomic status of *G. noerdlingensis* (Klein, 1853) seems very doubtful, because the original description is based on incomplete casts and steinkerns. In Steinheim am Albuch, the type locality of the common species *Granaria schuebleri* (Klein, 1847), two further species could be confirmed, namely *G. grossecostata* (Gottschick & Wenz, 1919) and *G. pachygastra* (Fraas in Miller, 1900). The original specimen of *Pupa* n. sp. (Klein 1853) was located, but a species designation is impossible due to its poor preservation.

Key words: *Abida; Pupa; Granopupa; Solatopupa; Torquilla;* North Alpine Foreland Basin.

1. Introduction

Chondrinidae are pulmonate gastropods known from several fossil localities of Central Europe, particularly from the Alpine Foreland Basin, also known as the Molasse Zone. They are common in the Upper Freshwater Molasse ("Obere Süßwassermolasse") and time-equivalent Miocene deposits (e.g. Sandberger 1870-1875; Gottschick & Wenz 1919), with *Granaria schuebleri* (Klein, 1847) being the most common species. In 19th century publications, such as Schübler (in von Zieten 1830) and Sandberger (1870-1875), this species was traditionally referred to as *Pupa schuebleri*. Since then, this and other species have been attributed to various other genera such as *Abida* or *Torquilla*.

One problem among the identification of fossil snails is that anatomical features used in the taxonomy of extant gastropods, such as the genitals, are not preserved in fossil material. Fossil gastropods are thus identified using morphological features of the preserved calcified shell. This has led, for example, to the fact that all fossil freshwater gastropods with certain aperture features (see below) are today assigned to the genus *Granaria* (see Gittenberger 1973).

This paper provides a reassessment of the taxonomy and palaeoecology of the Middle to Late Miocene Chondrinidae from the freshwater sediments of the North Alpine Foreland Basin and adjacent fossil lakes, and presents a dichotomous identification key. The species are discussed in detail, particularly their generic designation, the associated subspecies, and how they are distinguished from other species. Type specimens and further material were examined for the following species: *Granaria schuebleri*, *G. grossecostata* and *G. pachygastra*. The taxonomic position of

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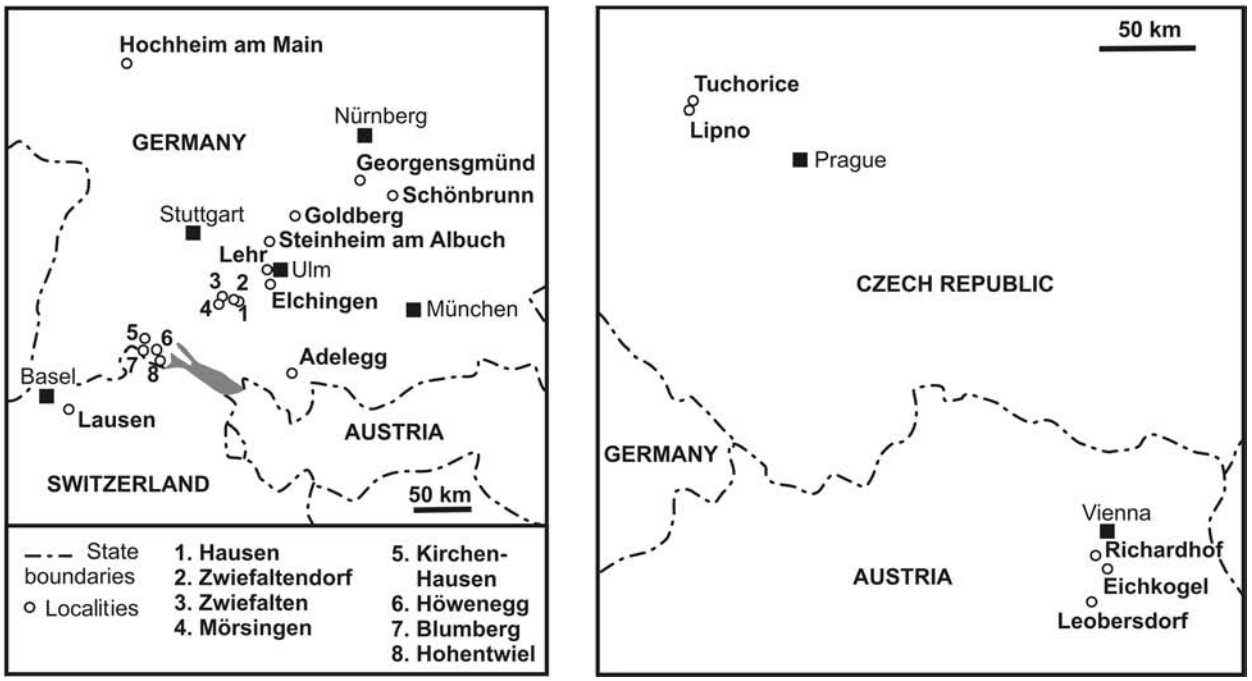

Fig. 1. Occurrences of the single *Granaria* species in Germany, Austria, Switzerland and Czech Republic.

Granaria costata, G. moedlingensis and *G. schlosseri* is clear and they are only mentioned briefly. The validity and status of the following taxa are still unclear or doubtful: *Granaria noerdlingensis, G. subfusiformis, G. subvariabilis, G. helicidarum*?, *G. intrusa* and *G. multicostulata*. Based on comparisons with extant species of this family, the ecology of the genus *Granaria* is also discussed.

2. Material and geological background

The development of the Alpine Foreland Basin started during the Late Eocene due to the Alpine Orogeny (Geyer & Gwinner 1991; Kuhlemann & Kempf 2002). After a deep-marine "Flysch phase", the so called "Molasse phase" began in the Early Oligocene. This phase is divided into two major transgressive-regressive cycles traditionally known as the Lower Marine Molasse/Lower Freshwater Molasse, and the Upper Marine Molasse/Upper Freshwater Molasse (Geyer & Gwinner 1991). Most of the material studied herein originates from the Upper Freshwater Molasse and deposits of adjacent lakes. Three of the species are derived from the Vienna Basin, which was subject to a different geological development (e.g., Rasser & Harzhauser. 2008). The localities and their stratigraphy are listed in Table 1 and Fig. 1. Unfortunately, for some localities, modern stratigraphic data are lacking.

The studied material is derived from the collection of the Staatliches Museum für Naturkunde Stuttgart (SMNS) and partly from the Bayerische Staatssammlung München. Most of the material is present in the in the collection of Klein (1847) which is stored in the SMNS. This collection is, however, incomplete and some specimens are lost. The original material of G. Schübler, published in von Zieten (1832), is completely lost. Further material comes from the collection of F. Gottschick (also in the SMNS).

3. The genus Granaria

The land snail family Chondrinidae (subfamily Chondrininae) are pulmonate land snails characterised by a high and slender shell, which is conical at the apex and becomes more cylindrical towards the last whorl (Kerney et al. 1983). It is not restricted to Europe as it also occurs in Pakistan (pers. comm. E. Gittenberger) According to Moore (1960: Fig. 65F) the shell morphology can be described as pupiform. The genus *Granopupa* was separated from other genera of this family, because the construction of the genitals is different (Gittenberger 1973). In terms of morphology, *Granopupa* can be separated from *Granaria* only by its size, because *Granopupa* reveals a width of less than 2 mm (Kerney et al. 1983). *Chondrina* has more

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Table 1.

Location	Stratigraphy
Baden-Württemberg, Germany	
Blumberg (Jooss 1923)	Ottnangian (Franz & Rohn 2004)
Hausen near Ehingen (Sandberger 1870-75)	Late Miocene (Sandberger 1870-75)
Hinterried at Kirchen-Hausen, Geisingen (Wenz 1923)	Late Miocene (Schalch 1984).
Höwenegg near Immendingen (unpublished data)	Late Miocene, MN 9 (Hünermann 1989, quoted in Heissig 1999)
Lehr near Ulm (Wenz 1918)	The exact locality is unkown, but Werner (1994) mentioned Early Miocene (USM, MN 2) sediments along the street from Ulm to Jungingen, which is a few kilometres from Lehr.
Phonolithtuff of Hohentwiel near Singen (Wenz 1923)	Late Miocene to Early Pliocene (Geyer & Gwinner 1991)
Mörsingen (Sandberger 1874)	Miocene; a paper on this location is in preparation by O. Höltke.
Steinheim am Albuch (Gottschick & Wenz 1919).	Middle Miocene, MN 7 (Gentry et al. 1999)
Thalfingen near Ulm (today part of Elchingen) (Sandberger 1874)	Late Oligocene (Jooss 1911)
Zwiefalten (Klein 1853)	Klein (1853) wrote that the material came from the freshwater sediments in the vicinity of Zwiefalten. Consequently, it might be time-equivalent with Zwiefaltendorf below
Zwiefaltendorf (Schlickum 1976)	Middle Miocene, Sarmatian (Schlickum 1976)
Bavaria, Germany	
Adelegg (Sandberger 1874)	Late Early Miocene (MN 5) to early Late Miocene (MN 8) sediments occur at Adelegg (Eberhard 1986)
Georgensgmünd (Sandberger 1874)	Middle Miocene, MN 6 (Hühnermann 1999)
Goldberg near Nördlingen (Klein 1847)	Middle Miocene, MN 6 (Bolliger 1994, quoted in Rummel 1999)
Schönbrunn near Kipfenberg. (Sandberger 1874). Now a part of Denkendorf	Late Miocene (Sandberger 1874).
Hesse, Germany	
Hochheim am Main (Sandberger 1874)	The sediments there reach from Late Oligocene to Early Miocene (Reichenbacher 2000)
Austria	
Eichkogel (Schlosser 1907; Binder & Harzhauser 2004)	Late Miocene, MN 11 (Binder & Harzhauser 2004)
Leobersdorf (Lueger 1981)	Late Miocene, Pannonian D (Lueger 1981)
Richardhof near Mödling (Binder & Harzhauser 2004)	Late Miocene, MN 9 (Binder & Harzhauser 2004)
Czech Republic	
Lipno (Wenz 1923)	Burdigalian (Wenz 1923)
Tuchořice (Sandberger 1874)	Early Miocene, MN 3 (Kuss 1965, quoted in Ginsburg 1999)
Switzerland	
Lausen, Kanton Basel-Landschaft (Gutzwiller 1905; Wenz 1923)	Early Miocene, Late Lutetian (Middle Eocene) (Wenz 1923)

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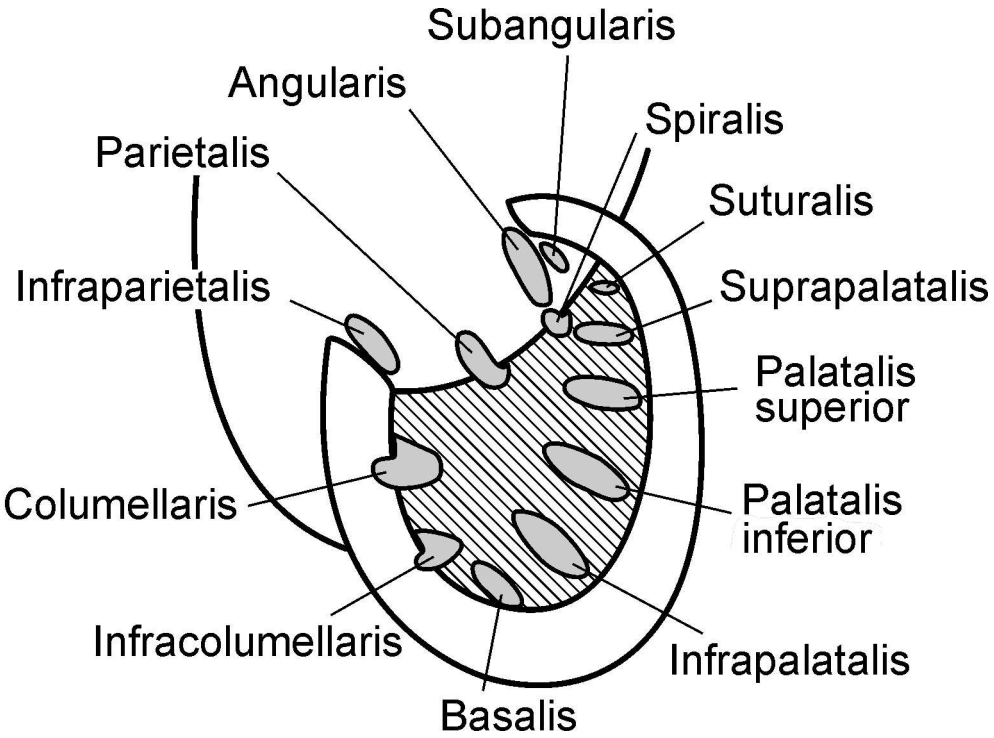

Fig. 2. Terminology of the aperture of *Granaria*.

convex whorls and only short, weak teeth (Fig. 2; Kerney et al. 1983). *Solatopupa* does not have a swollen thickened outer lip (Gittenberger 1973). After Kerney et al. (1983) *Granaria* is more cylindrical than *Abida*, but this property is often difficult to judge.

The arrangement of folds and teeth (Fig. 2) is a crucial diagnostic feature of the genus and species level. Gittenberger (1973) proposed that *Granaria* and *Granopupa* have four palatal folds, while *Abida* has three. Welter-Schultes (2012) also named four palatal folds for *Granaria*. According to this author, in the genus *Abida* the upper and lower palatal teeth are equally strongly developed. According to Kerney et al. (1973), *Granaria variabilis* (Draparnaud, 1801) has three to four palatal folds. *G. stabilei* (E. v. Martens, 1865) has approximately seven teeth and *G. braunii* (Rossmässler, 1842) mostly six (Kerney et al. 1983). Following Welter-Schultes (2012), *G. braunii* has two palatal folds. A certain variation in the number of teeth may occur. Kerney et al. (1983) mentioned that *Abida* has stronger ribs then *Granaria*. Gittenberger (1973) noted, however, that *Abida secale* (Draparnaud, 1801) can have fine to very rough or even smooth ribs.

According to Gittenberger (1973), all of the fossil Chondrinidae show the typical aperture of *Granaria* and *Granopupa*. Since fossil forms are always characterized by a larger size, they are assigned to the genus *Granaria*. Gittenberger (1973) stated that the columellar folds of *Granaria* are restricted to the columellar region. In *Abida,* these folds reach the inner lip ("*Columellarwand*") (Gittenberger 1973). *Abida secale brauniopsis* Altimira, 1963 and *Abida secale cadica* (Westerlund, 1902), however, have a smooth inner lip (Gittenberger 1973). The palatalis inferior is the strongest palatal fold in *Granaria*, while the palatalis inferior and the palatalis superior are like those of *Abida* (Kerney et al. 1983). Also Gittenberger (1973) stated that the palatalis inferior has the strongest palatal fold in *Granaria* with simple palatal folds.

Fossil forms with knob-like palatal folds are not present in the specimens studied herein. Likewise, the palatal folds do not reach the outer lip in species with simple palatal folds. These differences in combination

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with the extent of the columellar folds seem to be the best method to distinguish *Abida* from *Granaria* in fossil material. For more information concerning the phylogeny of the extant species, see KOKSHOORN (2008) and FEHÉR et al. (2010). The genus names *Pupa* DRAPARNAUD, 1801 and *Torquilla* STUDER, 1820 used in the older literature are synonyms according to ZILCH & WENZ (1959-1960).

4. Systematic palaeontology

Granaria schuebleri (KLEIN, 1847)
(Fig. 4.1-4.3)

1832	*Pupa antiqua* SCHÜBLER, 1832. – SCHÜBLER in VON ZIETEN, pl. 19, fig. 7.
1847	*Pupa Schübleri* mihi. – KLEIN, p. 74, pl. 1, fig. 18.
1875	*Pupa antiqua* (SCHÜBLER, 1830). – SANDBERGER, p. 623, pl. 28, fig. 12.
1900	*Pupa schübleri* (KLEIN, 1847). – MILLER, p. 396, pl. 7, fig. 12
1911	*Pupa schübleri* (SCHÜBLER, 1830). – GOTTSCHICK, p. 506.
1919	*Torquilla schübleri* (KLEIN, 1847). – GOTTSCHICK & WENZ, p. 3, pl. 1, figs. 1 & 2.
1923	*Abida antiqua antiqua* (ZIETEN). – WENZ, p. 940 (see there for further synonymies).
non 1981	*Abida schuebleri* (KLEIN). – LUEGER, p. 29, pl. 3, fig. 2a-c, 3 (= *Granaria schlosseri* (COSSMANN, 1908)).
1998	*Granaria schübleri* (v. KLEIN 1846). – FINGER, pl. 8, figs. H-I.

Material: The original material figured IN ZIETEN (1832; Fig. 3) is lost. Therefore, a neotype from the collection of KLEIN (Figs. 4.1, 4.2); SMNS 100110-1 is defined.

Description: The neotype (Fig. 4.1, 4.2) of this species is 5 mm high and 2 mm wide. It has a dextral, pupiform and slightly conical shell. The shell has nine whorls. These are only slightly convex and the suture is moderately deep. The whorl size increases regularly. There are very fine axial lines on the whorls,. They are prosocline and more or less regularly arranged at a close distance. The aperture has an oval shape. The shell has a slit-like umbilicus. The peristome is turned backwards. The palatal margin runs down in a more or less straight line and then forms a very rounded basis. The parietal region is covered by a thin parietal callus which connects the outer and inner lip. A part of this parietal callus is not preserved in the type specimen. The aperture comprises six lamellae, a prominent angularis, a dominant palatalis inferior and a parietalis. Possibly, there was an infraparietalis on the abraded part of the parietal callus (Fig. 4.1) which is no longer preserved. There is also a distinct columellaris and an infracolumellaris, but they are less strong than the parietal inferior and the parietalis. Above the palatalis inferior, a short and very indistinct palatalis superior is recognisable. The angularis has a knob-like shape, whereas the others are folds run deep into the mouth. The palatalis inferior and the palatalis superior do not reach the periostome.

Discussion: In older literature (Fig. 3; e.g., KLEIN 1847; GOTTSCHICK & WENZ 1919) this species was referred to the genera *Pupa* or *Torquilla* and later to *Abida* (e.g., LUEGER 1981). Due to the shell morphology and the folds and teeth, the species clearly belongs to the family Chondrinidae. The morphology is similar to some Orculidae, but the latter lack an angularis (KERNEY et al. 1983). The genera of the Chondrinidae are morphologically very difficult to distinguish. Due to the following arguments, however, the species *schuebleri* is referred to the genus *Granaria*:
1. Width >2 mm
2. Whorls only weakly rounded
3. Very fine axial lines
4. Dominant palatalis inferior

According to KERNEY et al. (1983), *Granopupa* is less than 2 mm wide and *Chondrina* has more rounded whorls as well as less distinct teeth. The shells of *Abida* are characterized by equally strongly developed palatalis inferior and palatalis superior (KERNEY et al. 1983).

SCHÜBLER (in *von* ZIETEN 1832) first described this species as *Pupa antiqua* (Fig. 3.1). In the same year, MATHERON (1832) named another form *Pupa antiqua* in the September/ October edition of "Annales des Sciences et de l`Industrie du Midi de la France". So possibly, the edition of MATHERON (1832) was published in early September 1832. For the publication of VON ZIETEN ("Heft Nr. V"), the only information is that it was published in the second half of the year 1832. This information comes from a typewritten notice on the beginning of the complete works of VON ZIETEN stored in the library of the Staatliches Museum für Naturkunde Stuttgart. On this notice, the years of appearance of all the single publications ("Hefte") by this author are listed. The time interval between the two publications has to have been only a month or even weeks. It is thus not possible to determine which author should be given priority. According to KLEIN (1847), MATHERON was the earlier author and therefore he changed the name of SCHÜBLER's *Pupa antiqua* into *Pupa schuebleri* (KLEIN, 1847) (Fig. 3.2). The holotype of *Pupa antiqua* SCHÜBLER in VON ZIETEN (1832) and possibly existing syntypes are missing. Apart from some Mesozoic material, the collection of CARL HARTWIG VON ZIETEN (Feb. 1st, 1785-June 20th 1846) is lost (see CLEEVELY 1983 for details). According to SHERBORN (1940), the collection was sold while VON ZIETEN was still alive. It is not known how many specimens of *Pupa antiqua* VON ZIETEN had available for study. Also, there is no further information about the holotype in the literature. The abovementioned specimen from the KLEIN collection is thus hereby defined as the neotype for *Granaria schuebleri* (KLEIN, 1847). This is the only complete shell of *Granaria schuebleri* in the KLEIN collection. Indeed, KLEIN (1847) wrote that he had only one specimen with the last four inferior whorls preserved, while the early whorls are absent (orginal quote: "*Die Schale, welche ich besitze, hat nur die vier unteren Umgänge, die Größe und Anzahl der Umgänge ist nach der Abbildung angegeben...*"). The single specimen in the SMNS box (Fig. 4.3) could thus correspond to that of KLEIN (1847). Except

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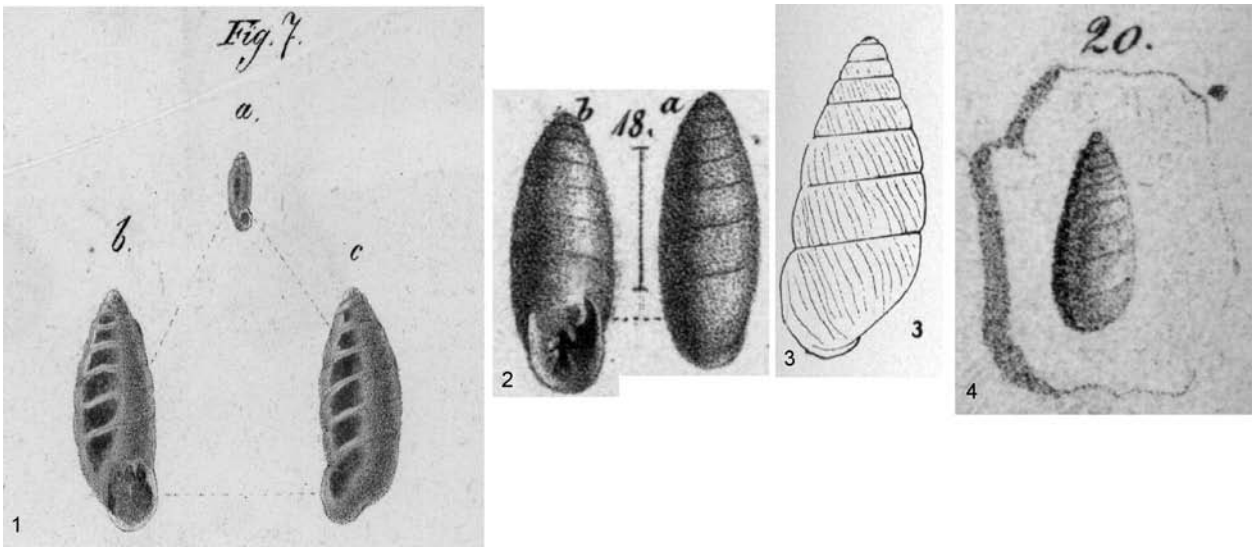

Fig. 3. Drawings from the original literature. (1) *Pupa antiqua* in VON ZIETEN (1832). (2) *Pupa schübleri* in KLEIN (1847). (3) *Torquilla schübleri grossecostata* n. var. in GOTTSCHICK & WENZ (1919). (4) *Pupa nördlingensis* in KLEIN (1847).

for one aspect, KLEIN`s description fits with the morphology of the presented neotype specimen. KLEIN (1847) noted the presence of only a single palatal fold, while the neotype comprises two palatal folds. In the broken specimen mentioned above, traces of a second palatal fold are visible only at strong magnification. This could be the specimen that KLEIN (1847) used for his description of the aperture. It is, however, not known which specific specimen KLEIN used as the basis for his drawing.

The number of palatal folds varies between authors. MILLER (1900) mentioned two folds and in the SMNS material he even found two shells with four folds, but the two upper and the lowest folds were only weakly developed. Unfortunately, it is not known which specimen he examined. Also BÖTTGER (quoted in MILLER 1900) described four palatal folds for *Granaria schuebleri* and seldom two or three. MAILLARD (1891) named equally three palatal folds and GOTTSCHICK (1911) even a very weak fifth palatal fold on some specimens. MILLER (1900) suggested a great variability among *Granaria schuebleri*. It cannot be excluded, however, that the recognisable number of folds is biased by taphonomic processes (see discussion below).

Occurrence: The type locality for the designated lectotype and holotype is Steinheim am Albuch and the type horizon is the "Steinheim Lake Beds" ("*Steinheimer Seeschichten*") (MN 7 according to GENTRY et al. 1999). Further occurrences are Höwenegg (HÖLTKE, unpublished data), Late Miocene, MN 9 (HÜNERMANN 1989, quoted in HEISSIG 1999) and according to WENZ (1923) "Phonolithtuff des Hohentwiel", Late Miocene to Early Pliocene (GEYER & GWINNER 1991) and Hinterried near Geisingen, Late Miocene (SCHALCH 1984).

Granaria grossecostata (GOTTSCHICK & WENZ, 1919) (Figs. 4.4, 4.5; Fig. 3.3)

1919 *Torquilla schübleri grossecostata* n. var. – GOTTSCHICK & WENZ, p. 3, pl. 1, fig. 3.

Material: The collection of GOTTSCHICK contains a box with two shells determined by him as *Torquilla schübleri grossecostata* (SMNS 15509). The collection label is dated 1926, but the meaning of the date is unknown. Since a reference to the GOTTSCHICK (1911) publication is absent, it is unclear whether or not GOTTSCHICK & WENZ (1919) used this material for their description.

Description: Only one of the two specimens has an aperture free of sediment. This specimen is 6 mm high and ca. 2.5 mm wide. It has a dextral, pupiform shell. The eight whorls regularly increase in size. The shell is slightly cylindrical, but narrows towards the apex. The whorls are more convex than in *G. schuebleri*. They have fine and regular, prosocline axial ribs. The distance between the ribs is two times that of the rib width. Near the aperture, the ribs are more distinct and less regular. The suture is deeper than in *G. schuebleri*. The shell has a slit-like umbilicus. The mouth is more circular than that of *G. schuebleri*. The periostome is turned backwards. Outer and inner lips are connected by a parietal callus. Marked angular folds and parietals are present which run into the mouth. A strong palatalis inferior is present along with a weaker palatalis superior, which ends behind the palatalis inferior. Columellaris and infracolumellaris are restricted to the columellar region and are equally distinct. There is also a small knob at the inner side of the palatal margin. Apart from the angularis, none of the folds reach the periostome.

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Discussion: Gottschick & Wenz (1919) separated one variety of *G. schuebleri* as *G. schuebleri* var. *grossecostata* (Fig. 3.3). They noted regular, straight to slightly bent ribs in the diagnosis. They, however, also mentioned that all types of ribs occur, from fine-striped to coarsely ribbed. The following aspects are judged to separate *G. grossecostata* (Gottschick & Wenz, 1919) from *G. schuebleri* (Klein, 1847):
1. More convex whorls
2. A deeper suture
3. Stronger ribs
4. A more distinct palatalis superior
5. A small knob on the inner side of the palatal margin

The species presented here belongs to *Granaria* because the palatalis inferior is the strongest palatal fold and the columellar folds do not reach the inner lip. The small knob on the inner side of the palatal margin is only known from *Granaria pachygastra* (Fraas in Miller, 1900) and according to Sandberger (1870-1875) from *Granaria subfusiformis* (Sandberger, 1874). *G. pachygastra* Fraas, 1882 has a larger size and a more cylindrical shape. *Granaria subfusiformis* (Sandberger, 1870-1875) is unfortunately not figured and cannot be compared with this subspecies. *Granaria moedlingensis* (Harzhauser & Binder, 2004) has more convex whorls and *Granaria costata* (Lueger, 1981) is different in shape.

Due to the above listed morphological features, the attribution to the genus *Granaria* is justified. Owing to the clear separation from other species, *Granaria grossecostata* is designated as a species independent from *G. schuebleri*.

Granaria pachygastra (Fraas in Miller, 1900) (Fig. 4.6)

1882 *Pupa pachygastra* Fraas. – Fraas, p. 174 (nomen nudum).
1883 *Pupa pachygastra* Fraas. – Engel, p. 287 (nomen nudum).
1900 *Pupa schuebleri* var. *pachygastra* Fraas. – Miller, p. 396-397, pl. 7, fig.12.
1923 *Abida antiqua antiqua* (Zieten). – Wenz, p. 941.

Material: One specimen occurs in the SMNS collection; SMNS 100111. Fraas (1882) did not supply an image or description for this species. A specimen is present in the collection that that is labelled as the Fraas original for this species (Fig. 4.6). It is not known whether or not Miller (1900) used the same specimen for his drawing.

Description: The specimen is 10 mm in height and 4 mm in width. It has a dextral, pupiform, barrel or cylindrical shape. There are seven whorls, which are slightly rounded and regularly increase in size. The protoconch is abraded. The suture is moderately deep. The whorls are covered by regular prosocline ribs. They are stronger than in *Granaria schuebleri*. The distance between the ribs is two times of the respective rib width. Shell is slit-umbilicated. The aperture has a rounded, slightly circular shape. The peristome is turned backwards. The outer and inner lips are connected by a parietal callus. There is a small knob at the inner side of the turned-back palatal margin. The parietalis and angularis are very prominent; both are fold-like and run inside the mouth. There is also one small, knob-like infraparietalis on the parietal callus. Beside this, there is also a prominent columellaris and an infracolumellaris. The latter is situated far away from the periostome. The basalis, palatalis inferior and palatalis superior are slender, but prominent. The palatalis inferior is more distinct than the palatalis superior. From the basalis, palatalis inferior and palatalis superior, the palatalis inferior runs mostly towards the forepart, but does not reach the periostome.

Discussion: Fraas (1882) defined this species in his publication without a description or image, which makes it a "nomen nudum". Also Engel (1883) named it only in a species list. Miller (1900) was the first who published a drawing and size description of this species. It is not known which specimen Miller used for this figure. Miller (1900) designated *G. pachygastra* as a variety of *G. schuebleri*. There are several features, however, that justify the separation of *pachygastra* as a distinct species.
1. The large size of 10 mm shell height and 4 mm width
2. A more convex shell, which becomes slightly narrower towards the apex
3. A distinct palatalis superior
4. The angularis is more fold-like
5. The presence of a basalis
6. The aperture is more circle-like, while that of *G. schuebleri* is more egg-like
7. The knob at the inner side of the palatal margin.
8. Stronger ribs

The last feature is problematic, because *G. schuebleri* can be finely-triped to coarsely ribbed (Gottschick & Wenz 1919). Among extant representatives, the knob on the inner side of the palatal margin is only present in *Granaria brauni* (Rossmässler, 1842), but this shell differs in other characteristics from *G. pachygastra*.

Occurrence: Steinheim am Albuch.

Granaria costata (Lueger, 1981)

1981 *Abida costata* Lueger, 1981. – Lueger, p. 30, pl. 3, fig. 1.

Material: The holotype is in the Papp collection of the Institute for Palaeontology, University of Vienna, Austria (Lueger 1981).

Discussion: After Lueger (1981) this species differs from all others by particularly strong ribs. Harzhauser & Binder (2004) attributed this species to *Granaria costata* (Klein, 1981).

Occurrence: The type stratum and locality is Pannonian D of Leobersdorf, Austria ("Ziegelei", Freshwater limestone); unknown from other localities.

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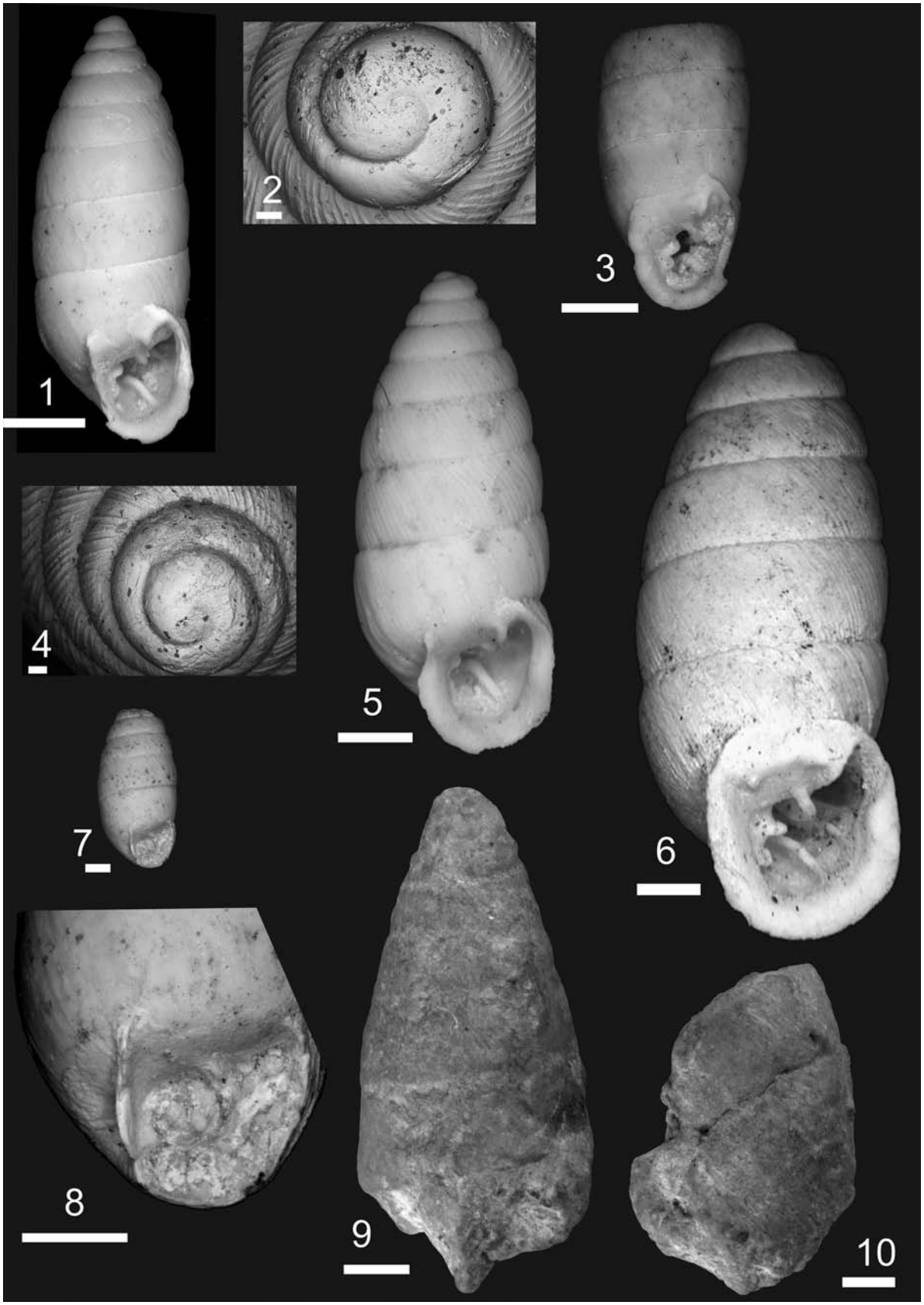

Fig. 4.

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Granaria schlosseri (Cossmann, 1908)

1907 *Pupa oviformis* Schlosser, 1907. – Schlosser, p. 98, pl. 17, fig. 5.
1908 *Pupa schlosseri* Cossmann, 1908. – Cossmann, p. 257.
1923 *Abida schlosseri* (Cossmann, 1908). – Wenz, p. 946.
2004 *Granaria schlosseri* (Cossmann, 1908). – Harzhauser & Binder, p. 125.

Material: According to Schlosser (1907), the holotype is stored in the Bayerische Staatssammlung für Geologie und Paläontologie in Munich, which could, however, not be verified by the authors.

Discussion: Schlosser (1907) named this species *Pupa oviformis*. This name turned out to be pre-occupied and thus Cossmann (1908) proposed *Pupa schlosseri* as the new name (Harzhauser & Binder 2004). It is a relatively large species. The height is 10.5 mm and the width 3.2 mm (Schlosser 1907). The shell has a distinct umbilicus and strong, sloping ribs (Schlosser 1907). After Harzhauser & Binder (2004) the specimen figured in Lueger (1981) as *Abida schuebleri* (Klein, 1847) is actually *Granaria schlosseri* (Cossmann, 1908). In their description of *G. schlosseri*, Harzhauser & Binder (2004) noted that *G. schuebleri* develops flat whorls and bears a prominent angularis.

Occurrence: Pannonian of Eichkogel and Reipersbach, Austria. (Schlosser 1907; Harzhauser & Binder 2004).

Granaria moedlingensis Harzhauser & Binder, 2004

2004 *Granaria moedlingensis* Harzhauser & Binder. – Harzhauser & Binder, p. 125, pl. 9, figs. 3-4.

Material: The holotype is stored in the Naturhistorisches Museum Wien, inv. no. 2003z0005/0073 (Harzhauser & Binder 2004).

Description and Discussion: This species has seven strongly convex whorls. It is 6 mm high, 3.4 mm wide, and has three palatal folds (Harzhauser & Binder 2004). Only one specimen was available for the first description. Locus typicus and stratum typicum are Richardhof close to Mödling in Lower Austria (Vienna Basin) from marls deposited in a Pannonian (Late Miocene) swampy lake adjacent to Lake Pannon which are dated to mammal zone MN 9. After Harzhauser & Binder (2004) this species is reminiscent of the Pliocene to Recent *Granaria frumentum* (Draparnaud, 1801) as far as shape and sculptures are concerned. A difference, however, is the fourth palatal fold of the extant representative (Harzhauser & Binder 2004).

Occurrence: Richhardhof near Mödling, Lower Austria (Harzhauser & Binder 2004).

Granaria noerdlingensis (Klein, 1847) nomen dubium
(Fig. 3.4)

1847 *Pupa Nördlingensis* mihi. – Klein, p. 75, pl. 1, fig. 20.
1875 *Pupa (Alloglossa) nördlingensis* Klein. – Sandberger, p. 627, pl. XXV, fig. 23, 23a.
1923 *Abida antiqua nördlingensis* (Klein). – Wenz, p. 942 (see here for more synonyms).
1977 *Granaria antiqua nördlingensis* (Klein). – Bolten, p. 144.

Material: The original material is unknown.

Description: Klein (1847) described casts that show nine striped whorls with a very shallow suture and an elongate egg-like shape (Fig. 3.4). The periostome and the folds are not visible (Klein 1847). Sandberger (1875) wrote that the last whorl reaches 1/4 of the complete height and ends in a perpendicular positioned ("*senkrecht gestellte*"), broad, egg-shaped mouth. The margins of the mouth seemed to be shortly expanded ("*deren Ränder kurz ausgebreitet erscheinen*") (Sandberger (1875). According to Sandberger (1875) the aperture is not completely known, but it bears four palatal folds ("*Gaumenfalten*"), which increase in size from the top towards the base.

Fig 4. 1-3 – *Granaria schuebleri* (Klein, 1847). (1) Neotype. Steinheim am Albuch, Baden-Württemberg (SMNS 100110-1). Scale 1 mm. (2) Protoconch of Fig. 1; scale bar: 100 μm. (3) Perhaps the original from the description of Klein (1847). Steinheim am Albuch, Baden-Württemberg (SMNS 100110-2). Scale = 1 mm. **4-5** – *Granaria grossecostata* (Gottschick & Wenz, 1919). (4) Protoconch of the shell in Fig. 5. (5) Steinheim am Albuch, Baden-Württemberg. (SMNS 15509). Scale = 1 mm. **6** – *Granaria pachygastra* (Fraas, 1882) (SMNS 100111). Steinheim am Albuch, Baden-Württemberg. Scale = 1 mm. **7-8** – *Granaria subfusiformis*? (Sandberger, 1870-1875). (7) Specimen of *Pupa* spec. nov. Klein (1853). Zwiefalten, Baden-Württemberg (SMNS 100112). Scale = 1 mm. (8) Close-up of the mouth of Fig. 7. Scale 1 mm. **9-10** – *Granaria helicidarum* (Jooss, 1923). (9) Part of the teleconch. Blumberg, Baden-Württemberg. Scale 1 mm; SMNS 100113-1. (10) Dorsal side of the last two whorls. Blumberg, Baden-Württemberg. Scale = 1 mm; SMNS 100113-2.

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Table 2.

Species	Habitat
G. frumentum (Draparnaud, 1801)	Open, chalky habitats: Grasses, rubble-fields, on walls, on the bases of rocks
G. illyrica (Rossmässler, 1837)	Dry, open localities on chalky underground
G. variabilis (Draparnaud, 1801)	Dry, warm and exposed localities: Chalky grasses, rubble-fields and rocks
G. stabilei (G. v. Martens, 1865)	Dry, exposed localities between rocks and rubble
G. brauni (Rossmässler, 1842)	Exposed localities between rocks and rubble; montane

Discussion: It is not clear from which source Sandberger (1875) received the information concerning the folds mentioned above. They are not preserved on the specimen figured by Klein (1847). All of the authors prior to Sandberger (1875), as quoted in Wenz (1923), only list this species without further descriptions. On the basis of Sandberger's description, Bolten (1977) determined specimens from the Nördlinger Ries as *Granaria antiqua noerdlingensis* (Klein). According to Bolten (1977), *G. antiqua antiqua* (Zieten) (= *Granaria schuebleri*) has weaker growth-ribs and a more bulged upper part of the spire. He denotes that *G. antiqua grossecostata* (Gottschick) (= *Granaria grossecostata*) has stronger ribs then *G. antiqua nördlingensis* (Klein). Bolton's material was investigated in this study, but this material does not show diagnostic features that allow any species identification. Due to the lack of information and the incomplete preservation of the figured and lost original specimen of Klein, the status of this species is completely unclear.

Occurrence: Klein (1847) described casts and steinkerns of this species from Goldberg near Nördlingen, Bavaria (MN 6 according to Bolliger 1994, quoted in Rummel 1999). For other localities see Sandberger (1875) and Bolten (1977).

Granaria subfusiformis (Sandberger, 1874) nomen dubium
(Figs. 4.7, 4.8)

1853 *Pupa* nov. spec.? – Klein, p. 216.
1874 *Pupa subfusiformis* Sandberger. – Sandberger, p. 598.
1976 *Granaria subfusiformis* (Sandberger). – Schlickum, p. 9.

Material: Only one specimen occurs in the Klein collection, which can therefore be the original specimen of *Pupa* nov. spec.? Klein, 1853; SMNS 100112. The original material of Sandberger's *P. subfusiformis* is unknown.

Description of the original material of *Pupa* nov. spec.: This specimen is 4 mm high and 2 mm wide, but only the last four whorls are preserved. The fifth whorl is fragmentary. The shell has a pupiform, dextral shape. The suture is moderately deep and the whorls are only slightly rounded. On the third whorl, there are very fine, prosocline and more or less regular axial ribs. The shell is slightly umbillicated. The periostome is not completely preserved with possible presence of a parietal callus. No angularis is visible and only a fragment of the parietalis is present. The mouth is filled with sediment and teeth are therefore not visible (Fig. 4.8).

Description of Sandberger: The translated description of Sandberger (1874: 598) reads as follows: A slender, slightly cylindrical shell with blunt upper end and a narrow, but deep umbilicus. It has eight almost flat whorls with a slender suture. There are oblique axial ribs on the whorls. The width of the grooves between the ribs is two-times of the ribs' width. The last whorl is slightly narrowed in the forepart and a slightly angular on the backside ("*am Nacken schwach kantig*"). This whorl reaches 2/5 of the total height. The aperture is egg-shape, and the outer and inner lips are connected. On the right lip, there is a knob ("*schwielige Verdickung*") at the inner side. An obtuse tooth (= angularis) lies in the vicinity of the corner, which is formed by the right outer lip and the parietal margin ("*Mündungswand*"). A larger and lesser bended tooth (= parietalis) is situated at the lower part of the parietal margin ("*Mündungswand*"). These teeth continue to the inner side of the mouth. There are also two little, obtuse folds on the columellar region (columellaris). The presence of palatal folds is not clear, because this region is not exposed.

Discussion: For *Pupa* nov. sp.? Klein, 1853, Klein (1853) described eight whorls, but the shell was broken when he removed it from the matrix. The specimen stored in the SMNS fits with this description of Klein (1853). After Sandberger (1874) this specimen is identical with his *Granaria subfusiformis* (Sandberger, 1874). After Miller (1900) and Gottschick & Wenz (1919), the latter species is identical with *Pupa noerdlingensis* Klein, 1847. Maillard (1891) designated *Pupa subfusiformis* and *Pupa* nov. sp.? Klein, 1853 as synonyms of *Granaria schuebleri* (Klein, 1847). Lueger (1981) also assumed that *Granaria subfusiformis* (Sandberger, 1874) is identical with *Granaria schuebleri* (Klein, 1853) because they show the same shape. Unfortunately, Sandberger (1874) did not published a figure of his *Pupa subfusiformis*. In his description, he named a small knob at the inner side of the palatal margin, which is absent in *Granaria schuebleri* (Klein, 1853). Consequently, they should represent two different species. Sandberger (1874) mentioned one angularis, one parietalis and two columellar folds for *G. subfusiformis* (Sandberger, 1874). The palatal folds could not be seen in the specimens examined by Sandberger (1874). He also did not mention if the colu-

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mellar folds reach the inner lip or not. Since the supposed original specimen of *Pupa* nov. sp.? Klein (1853) is poorly preserved, a species designation is impossible. It perhaps represents *Granaria schuebleri* (Klein, 1847).

Occurrences: The specimen of *Pupa* nov. spec.? originates from Zwiefalten (Miocene). Other occurrences of *Granaria subfusiformis* (Sandberger, 1874) are, according to Sandberger (1874): Mörsingen, Middle Miocene, MN 5 (Esu 1999); Hausen, Late Miocene (Sandberger 1874); Georgensgemünd, Middle Miocene, MN 6 (Hühnermann 1999); Schönbrunn (today part of Denkendorf, Bavaria), Late Miocene (Sandberger 1874); Adelegg, where late Early Miocene (MN 5) to early Late Miocene (MN 8) sediments occur (Eberhard 1986). Another locality is Zwiefaltendorf, Middle Miocene (Sarmatian) (Schlickum 1976).

Granaria subvariabilis (Sandberger, 1863)

1863 *Pupa subvariabilis* Sandberger. – Sandberger, pl. 5, fig. 6.
1874 *Pupa subvariabilis* Sandberger. – Sandberger, p. 393.
1923 *Abida subvariabilis* (Sandberger). – Wenz, p. 948 (see here for more synonyms).

Material: The original material of Sandberger is unknown.

Description and Discussion: According to the drawing in Sandberger (1874) the height is 8.5 mm. Sandberger (1874) wrote that either the palatalis inferior or the palatalis superior can be the most prominent fold ("*und auch im Schlunde sind noch drei lange sichtbar, von welchen bald die unterste bald die mittlere stärker entwickelt erscheint*"). The shape of the image in Sandberger (1874) looks similar to the shape of the neotype of *G. schuebleri* (Klein, 1847) described further above. Following the description of Sandberger (1874), however, *G. subvariabilis* (Sandberger, 1863) must have a much more distinct palatalis superior. According to Sandberger (1874), the species has two tooth-like columellar folds and three long ones in the inner mouth ("*im Schlunde sind noch drei lange sichtbar*"). Moreover, it has an angularis and a parietalis ("*Am Zusammenstosse des rechten Randes und der Mündungswand liegt eine stark vortretende stumpfe, weiter nach links eine schmale, tief ins Innere fortsetzende Lamelle*").

Occurrence: According to Sandberger (1874) the sediments of Hochheim, Hesse range from the Late Oligocene to Early Miocene (Reichenbacher 2000); Tuchořice (Bohemia), Early Miocene, MN 3 (Kuss 1965, quoted in Ginsburg 1999); Thalfingen near Ulm (today part of Elchingen), Late Oligocene (Jooss 1911)

Remarks: Wenz (1918) established the "mutation" *Granaria subvariabilis* mut. *ulmensis* n. mut., which differs from other forms of *G. subvariabilis* (Sandberger, 1863) in having larger and stronger shells, more flattened whorls, coarser, stronger and more irregular growth lines. It is restricted to the localities Lehr and Thalfingen. The shell is similar to *Granaria intrusa* (Slavik, 1869) but has a more cylindrical morphology and lacks a basal carina ("*Basalkiel*") (Wenz 1918).

Granaria helicidarum (Jooss, 1923) (Figs. 4.9, 4.10)

1923 *Abida helicidarum* n. sp. – Jooss, p. 205.

Material: Jooss (1923) founded his description on three fragments of the teleconch and one of the aperture. This fits to the content of a glass vial from the Jooss collection of the SMNS, which is labelled as the original of the description of Jooss (1923). The presence of mouth fragments, however, leads to some confusion (see discussion below); SMNS 100113-1 and 100113-2.

Description and Discussion: The three fragments are steinkerns, which are partly filled and covered with calcite. The type locality is Blumberg (Zollhaus), Baden-Württemberg, Germany. Jooss (1923) mentioned "Helicidenmergel" as the lithostratigraphic horizon, and "middle Vindobon" as the biostratigraphic level. According to Franz & Rohn (2004) the "Helicidenmergel is Ottnangian (Early Miocene) in age. Jooss (1923) gave the following description: "The largest fragment consists of eight whorls which are almost flat and separated by shallow sutures. From the second one, the whorls are covered with densely arranged, oblique and slightly bended growth lines." The largest shell fragment in the glass vial fits with the description above. Jooss (1923) wrote about the aperture: "In the mouth, two parietal, four palatal and three columellar folds are visible." The inner side of the shell found in the vial is, however, partly filled with crystalline calcite, so it is impossible to identify the presence of any folds. Therefore it is unclear, which material was used for the description of the aperture folds.

After Jooss (1923), *G. helicidarum* is larger than *G. schuebleri* (Klein, 1847) and differs with respect to the teeth and folds. The above named teleconch fragment is a maximum of 7 mm high and 4 mm wide. So, in fact, this gastropod had a distinctly larger size than *G. schuebleri* (Klein, 1847), but due to the poor preservation, an exact determination is not possible.

Granaria intrusa (Slavik, 1869)

1869 *Pupa intrusa*. – Slavik, p. 267, pl. IV, figs. 12-13.
1923 *Abida intrusa* (Slavik). – Wenz, p. 944 (see here for further synonymies).

Material: Holotype unknown.

Description and Discussion: Slavik (1869) described this species from the chalk of Tuchořice, Czech Republic. It is 9.5 mm high and 3.5 mm wide. Unfortunately, the mouth aperture is not exposed (Slavik 1869). According to

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Sandberger (1874) this species is identical with his *G. subvaraibilis* (Sandberger, 1863).

Occurrence: Tuchořice, Czech Republic, Lipno, Czech Republic (Slavik 1869; Wenz 1923)

Granaria multicostulata (Gutzwiller, 1905)

1905 *Pupa multicostulata*. – Gutzwiller, p. 28, pl. 4, fig. 30.
1923 *Abida multicostulata* (Gutzwiller). – Wenz, p. 945.

Material: Holotype unknown.

Discussion: Gutzwiller (1905) defined this species as *Pupa multicostulata* from an Eocene freshwater chalk in Lausen, Baselland, Switzerland. He mentioned three specimens, but only one of them is complete and figured. Unfortunately, the inner part of the mouth could not be exposed (Gutzwiller 1905).

Occurrence: Lausen, Baselland, Switzerland (Gutzwiller 1905, Wenz 1923).

5. Identification key to *Granaria* in the North Alpine Foreland Basin

An identification key is summarised from the above descriptions. The species *G. noerdlingensis*?, *G. subfusiformis*?, *G. multicostulata* and *G. intrusa* are excluded, because important features are missing.

1. barrel or cylindrical shape
- Yes … 2
- No … 3
2. Very convex whorls
- Yes … *Granaria moedlingensis*
- No … *Granaria pachygastra*
3. Conical shape; very strong and distinct ribs
- Yes … *Granaria costata*
- No or indistinct ribs … 4
4. A prominent angularis
- Yes … 5
- No … *Granaria schlosseri*
5. A small knob on the inner side of the palatal margin
- Yes … *Granaria grossecostata*
- No ... 6
6. Two parietalis
- Yes … *Granaria helicidarum*
- No ... 7
7. One parietalis ... 8
8. More distinct palatalis superior
- Yes … *Granaria subvariabilis*
- No … *Granaria schuebleri*

6. Taphonomic remarks

A general taphonomic problem that is common among all gastropods is the aragonitic shell mineralogy, since aragonite is metastable and diagenetic processes transfer it into calcite. This is accompanied by a loss of the primary shell structure and/or the formation of steinkerns, such as the one in Fig. 4.9. Furthermore, the shell interior represents primary pore space that can be filled with calcite cement, which may overprint important features, such as in *Granaria helicidarum*? (see above).

A crucial diagnostic feature is the parietal region with folds, teeth and knobs (Fig. 2) placed on a parietal callus. This callus, however, flakes off very easily. This problem is visible when comparing Fig. 4.1, which shows a flaked-off callus, with Fig. 4.6, which shows a well-preserved parietal region with all the essential features. This seems to be a particular problem among *Granaria*. Furthermore, the aperture is frequently filled with sediment, as shown in Fig. 4.8, which is often difficult to remove. This sediment covers important taxonomic features in the mouth. A removal of the sediment easily leads to a fragmentation of the teeth and flaking of the parietal region.

7. Palaeoecological remarks

These remarks pertain to the ecological requirements of extant representatives of *Granaria* in order to use fossil species as palaeoecological proxies. Like most of pulmonate gastropods, Chondrinidae, to which *Granaria* belongs, are herbivorous. Following Lueger (1981) the Chondrinidae are xerophilous and inhabited open landscapes such as grassland, savannas and steppe environments. Kerney et al. (1983) lists five species of *Granaria* from northern and central Europe. Only one of them, *G. frumentum* (Draparnaud, 1801) occurs in Germany (southern to central Germany). All of these species live in open and exposed habitats (Kerney et al. 1983). According to Hagen (1952), *G. frumentum* is a thermophilic species that mainly lives on chalk or loess and rarely on „Nagelfluh"-conglomerates or serpentinites. After Ehrmann (quoted in Hagen 1952), *G. frumentum* (Draparnaud, 1801) is locally found on mica slates and phyllites in warm regions and avoids pine-woods (Hagen 1952). Using an actualistic comparison, the occurrence of *Granaria* in fossil material is mainly indicative for open exposed, dry, rocky and chalky environments.

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Article

Miocene continental gastropods from the southern margin of the Swabian Alb (Baden-Württemberg, SW Germany)

Olaf Höltke, Rodrigo B. Salvador, and Michael W. Rasser

With 6 figures

Abstract: The Middle Miocene *silvana*-beds outcropping at the southern margin of the Swabian Alb bear a wide array of terrestrial and freshwater gastropods. Especially in the surroundings of the Emerberg and Tautschbuch hills, there are records of several collection sites. In the present work, we investigated material from the historical localities from these two regions, housed in museum collections, in order to provide an updated check list, synthesizing the knowledge of the region in the hopes to spur renewed interest. In total, we report 14 freshwater and 50 land snail species from the area, but not all species reported in the literature could be confirmed.

Key words: Baden-Württemberg, European Land Mammal Zone MN 5, Langhian, *silvana*- beds, Upper Freshwater Molasse.

1. Introduction

The southern margin of the Swabian Alb, especially the Emerberg and Tautschbuch hills, bears a considerable number of continental Miocene deposits (Fig. 1). These are built up by the *silvana*-beds, a lithostratigraphic unit of the Miocene Upper Freshwater Molasse ("Obere Süßwassermolasse" or OSM), which is a unit of the North Alpine Foreland Basin. The *silvana*-beds are famous for the occurrence of large quantities of fossil gastropods, both terrestrial and freshwater. In the works of the famous pioneer geologists of the 19th century, like Quenstedt and Fraas, localities from this area (e.g., Zwiefalten-Mörsingen) were always featured in the section on the Tertiary of SW Germany.

Despite the rich occurrence of often well-preserved fossil shells, there has never been a systematical palaeontological excavation in this region. The finds listed in the literature, as well as the material stored in museum collections, are all "accidental finds" and, for many localities, the most recent publication is the work of Wenz (1923-1930). Therefore, in the absence of more driven excavations for the moment, here we investigated material from several historical localities from these two regions, housed in museum collections. Our goal is to provide an updated check list of species and localities, thus synthesizing the knowledge of the region in the hopes to spur renewed interest and collection efforts.

2. Geological background

The southern margin of the Swabian Alb region is located within the North Alpine Foreland Basin (also named "Molasse Basin"), which was formed during the uplift of the Alps. For a detailed overview of the North Alpine Foreland Basin and its evolution, see Rasser & Harzhauser (2008) as well as Geyer & Gwinner (2011) and the references therein.

The outcrops in the regions studied in this paper are located within the OSM and, more specifically, belong to the unit known as *silvana*-beds, named after the

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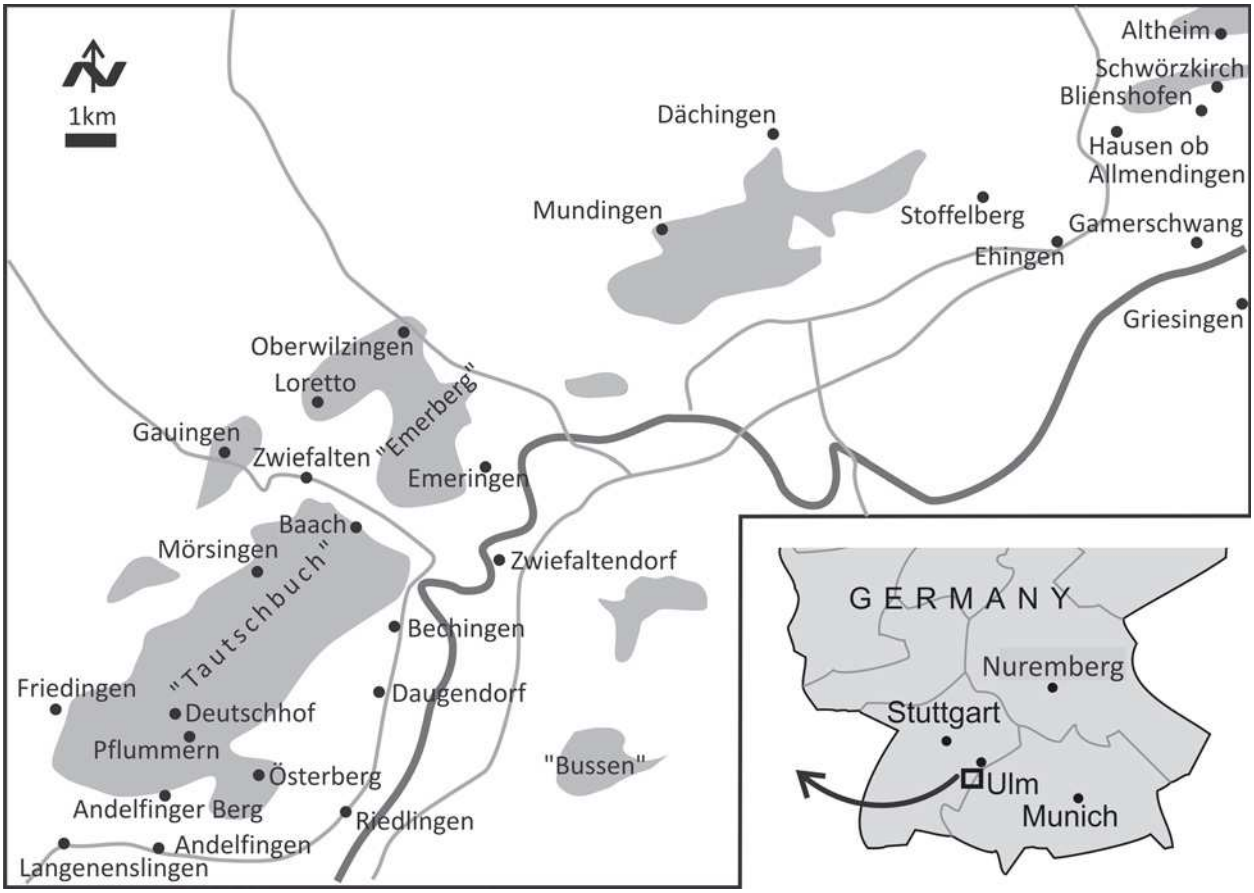

Fig. 1. Map showing the localities treated in this work.

most commonly found fossil land snail: *Palaeotachea silvana* (Klein, 1853). For a stratigraphic overview see Fig. 2. The underlying strata of the *silvana*-beds in the region discussed herein are older Tertiary sediments see (Fig. 2) or the *silvana*-beds were deposit directly on Upper Jurassic limestones (Schwarz 1913). According to Esu (1999), the *silvana*-beds are dated from the European Land Mammal Zone MN 5, which ranges from ca. 15.8 to 13.8 myr (Berger et al. 2005).

Unfortunately, outcrops in the Emerberg and Tautschbuch hills are rare today, hence information about their lithology come either from the literature or are based on observation of the few exposed outcrops (in this decade, Zwiefalten-Gauingen, Zwiefalten-Zwiefalten-Mörsingen and Riedlingen) and loose rocks. Different lithofacies have been observed, ranging from hard and splintery freshwater limestone, to marls with different proportions of chalk and clay, to softer clays in which the continental molluscs are often well preserved. Haag (1960) also mentioned marls and clays with a more or less distinct proportion of sand.

Schwarz (1913) divided the *silvana*-beds from the Tautschbuch/Emerberg region in three different parts, mainly based on the lithology. The lowest part consists of a brown plant and pisolithic limestone ("Pflanzen- und pisolithische Kalke"); the middle part is a light coloured limestone and a multicoloured marl; and the upper part a light coloured hard limestone (for more details, see Schwarz 1913). Apart from molluscs, there are hardly any other fossils known from the *silvana*-beds of this region; there are records only of a few plant remains (*Celtis* sp.) and ostracods from Zwiefalten-Mörsingen (as stated above, Schwarz 1913 named the lowest stratum as "plant limestone", but gave no further details on plant fossils). The situation concerning non-mollusc fossils, however, might only be so because the sediments have never been thoroughly examined. Likewise, more specific details on these regions' geology is

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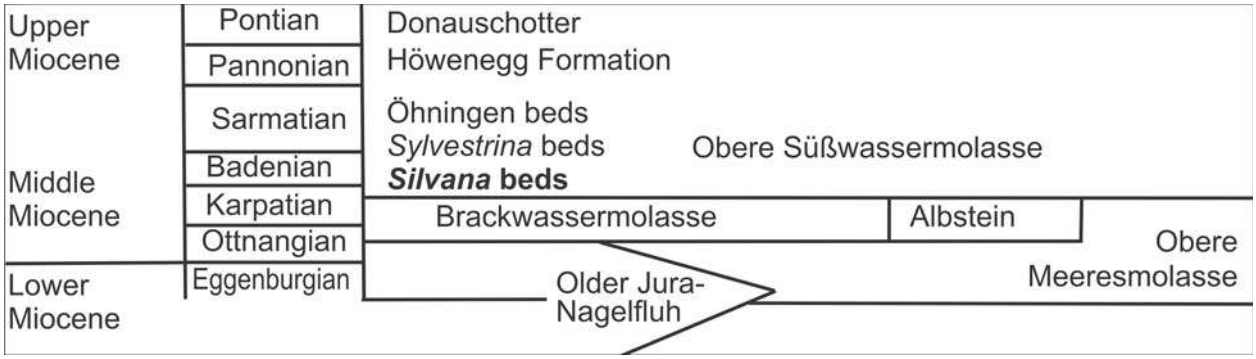

Fig. 2. Stratigraphic overview of the study area (modified after Schweigert 1996 and Geyer & Gwinner 2011).

scarce. Only three localities from this region have been studied in more depth so far: Zwiefaltendorf (Schlickum 1976) and Riedlingen-Bechingen and Riedlingen-Daugendorf (Salvador & Rasser 2016a), with a paper on Zwiefalten-Mörsingen being in preparation (Höltke & Rasser, in prep.).

3. Material and methods

In search of OSM fossil continental molluscs from the Emerberg and Tautschbuch regions, most major museum collections in Germany, Switzerland, Austria and the United Kingdom were contacted, as well as several local collections in Baden-Württemberg state. However, only a few of them housed specimens from the studied region, namely: the following collections were examined: Bayerische Staatssammlung für Paläontologie und Geologie (BSPG; Munich, Germany); Department of Geosciences, Eberhard Karls Universität Tübingen (formerly Geologisch-Paläontologisches Institut Tübingen, GPIT; Tübingen, Germany); Natural History Museum (NHMUK; London, UK); Paläontologisches Institut und Museum der Universität Zürich (PIMUZ; Zurich, Switzerland); Staatliches Museum für Naturkunde Stuttgart (SMNS; Stuttgart, Germany). In addition, the record of two species from the Gauingen locality stem from the private collection of Dietrich Kadolsky (Sanderstead, UK).

The gastropod species recorded are listed below (bivalves are represented only by undeterminable valve fragments), with information on their occurrence in the Emerberg and Tautschbuch regions that could be confirmed with fossil material. When the type locality of some species is located in the region discussed herein this is marked after the locality name. The material examined (with inventory numbers) is fully listed in the Appendix. Additional occurrence data gathered from the literature are presented separately. Please note that the "Verified distribution" and "Further literature data" topics in the check list below refer only to the Emerberg and Tautschbuch regions, which are the focus here; several species are known from other areas. The classification used here follows mainly Bouchet & Rocroi (2005) and Nordsieck (2014).

4. Checklist of taxa

Neritimorpha
Family Neritidae
Theodoxus crenulatus (Klein, 1853)
Fig. 3.1

Illustrated in: Klein (1853, pl. 5, fig. 18); Sandberger (1875, pl. 28, fig. 13); Harzhauser et al. (2012, fig. 2); Salvador et al. (2016a, pl. 3, figs. 6-7).

Verified distribution: Altheim near Ehingen (Donau), Zwiefalten (type locality), Zwiefaltendorf.

Further literature data: Riedlingen-Pflummern (Wenz 1928: 2945).

Caenogastropoda
Family Melanopsidae
Melanopsis kleinii (Kurr, 1856)
Fig. 3.2

Illustrated in: Schlickum (1976, pl. 5, fig. 65); Esu (1980, fig. 8).

Verified distribution: Altheim near Ehingen (Donau), Hausen ob Allmendingen, Zwiefalten-Mörsingen, Zwiefalten, Zwiefaltendorf.

Further literature data: Deutschhof near Riedlingen-Pflummern (Wenz, 1923: 2766).

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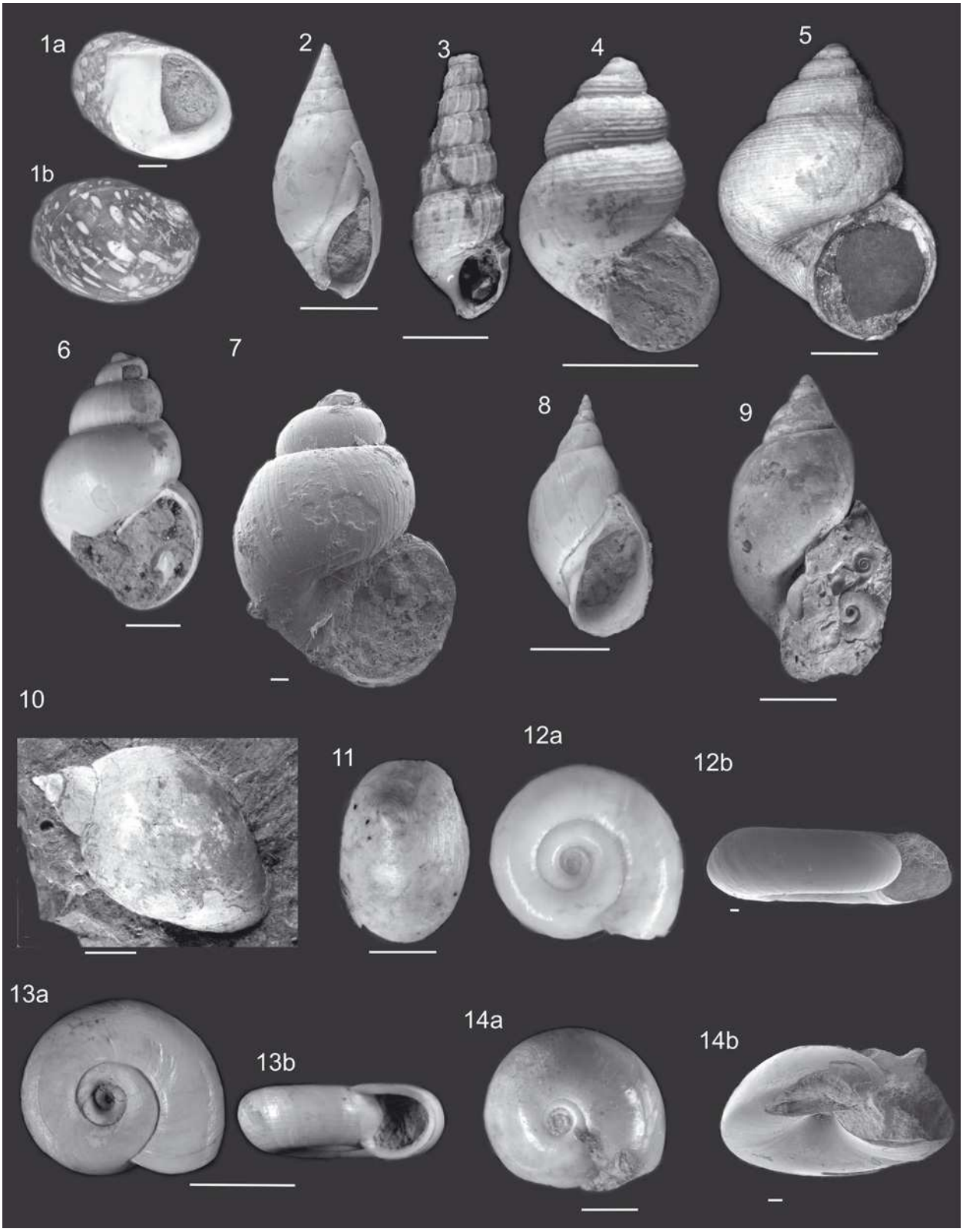

Fig. 3.

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Family Pachychilidae
Tinnyea lauraea (Mathéron, 1842)
Fig. 3.3

Illustrated in: Mathéron (1842, pl. 36, figs. 23, 24); Papp (1953, pl. 3, fig. 29); Schlickum (1976, pl. 1, fig. 9); Mikuž & Pavšič (2000, pl. 1, figs. 1-8); Salvador et al. (2015b, fig. 2A, B); Salvador & Rasser (2016a, fig. 2); Salvador & Rasser (2016b, fig. 2A, B); Salvador et al. (2016a, pl. 4, fig. 19, pl. 9, fig. 17); Salvador et al. (2016b, fig. 4c-d).

Verified distribution: Langenenslingen-Andelfingen, Riedlingen-Bechingen (cf.), Ehingen (Donau)-Dächingen (cf.), Ehingen (Donau), Zwiefalten-Mörsingen, Zwiefalten, Zwiefaltendorf.

Further literature data: Emerberg near Zwiefalten (Wenz 1928: 2601).

Remarks: The species is usually found in the literature as *T. escheri* (Brongniart, 1823), but, as pointed out by Kadolsky (1995), the latter taxon is a *nomen nudum*.

Family Pomatiidae
Pomatias conicus (Klein, 1853)
Fig. 3.4

Illustrated in: Klein (1853, pl. 5, fig. 14); Sandberger (1875, pl. 29, fig. 34); Papp & Thenius (1953, pl. 3, fig. 7); Schlickum (1976, pl. 1, figs. 2, 3); Lueger (1981, pl. 1, figs. 11, 12, pl. 6, fig. 3); Harzhauser & Kowalke (2002, pl. 10, figs. 6-8); Harzhauser & Binder (2004, pl.1, figs. 7-11); Kókay (2006, pl. 4, fig. 4); Rasser et al. (2013, pl. 4, fig. 11); Salvador et al. (2015a, fig. 3A); Salvador & Rasser (2016a: fig. 3); Salvador & Rasser (2016b, fig. 2C).

Verified distribution: Altheim near Ehingen (Donau), Zwiefalten-Baach, Riedlingen-Bechingen (cf.), Ehingen (Donau)-Dächingen, Hausen ob Allmendingen, Zwiefalten-Mörsingen, Zwiefalten, Zwiefaltendorf.

Further literature data: Emerberg near Zwiefalten, Deutschhof, Langenenslingen-Friedingen (Wenz 1923: 1821).

Pomatias consobrinus (Sandberger, 1875)
Fig. 3.5

Illustrated in: Sandberger (1875, pl. 29, fig. 33A); Fraas (1910, pl. 67, fig. 5); Schlickum (1976, pl. 1, fig. 1); Kókay (2006, pl. 4, fig. 3); Salvador (2014, figs. 1, 2).

Verified distribution: Ehingen (Donau), Zwiefalten-Mörsingen, Zwiefaltendorf.

Further literature data: Emerberg near Zwiefalten, Hausen ob Allmendingen, Langenenslingen-Friedingen, Österberg near Riedlingen (Wenz 1923: 1807).

Family Bithyniidae
Bithynia glabra (Zieten, 1832)
Fig. 3.6

Illustrated in: Zieten (1832, pl. 31, fig. 9); Sandberger (1872, pl. 28, fig. 16); Schlickum, (1966, pl. 12, figs. 19-22); Schlickum (1976, pl. 1, fig. 8); Reichenbacher (1989, pl. 1, figs. 6, 7); Kowalke & Reichenbacher (2005, figs. 8.1, 8.2); Salvador & Rasser (2016a: fig. 4); Salvador et al. (2016a: pl. 4, fig. 16); Salvador et al. (2016b: fig. 4e-i).

Verified distribution: Riedlingen-Bechingen, Hausen ob Allmendingen, Zwiefalten-Mörsingen, Zwiefaltendorf.

Further literature data: Mundingen (Wenz 1928: 2243).

Family Hydrobiidae
Pseudamnicola suevicus (Gottschick, 1928)
Fig. 3.7

Fig. 3. 1 – *Theodoxus crenulatus* (Klein, 1853). Altheim near Ehingen (Donau). SMNS 106379. Scale 2 mm. **2** – *Melanopsis kleinii* (Kurr, 1856). Zwiefalten-Mörsingen. SMNS 107217. Scale 5 mm. **3** – *Tinnyea lauraea* (Mathéron, 1842). Zwiefalten-Mörsingen. SMNS 107218. Scale 10 mm. **4** – *Pomatias conicus* (Klein, 1853). Zwiefalten-Mörsingen. SMNS 107220. Scale 5 mm. **5** – *Pomatias consobrinus* (Sandberger, 1872). Zwiefalten-Mörsingen. Original material of Fraas (1910). SMNS 107219. Scale 1 mm. **6** – *Bithynia glabra* (Zieten, 1832). Zwiefalten-Mörsingen. SMNS J68.154. Scale 1 mm. **7** – *Pseudamnicola suevicus* (Gottschick, 1928). Zwiefalten (Zwiefalten-Mörsingen). SMNS 15817. Scale 100 μm. **8** – *Lymnaea turrita* Klein, 1853. Zwiefalten-Mörsingen. SMNS 106408. Scale 10 mm. **9** – *Lymnaea dilatata* (Noulet, 1854). Zwiefalten-Mörsingen. SMNS J67.684. Scale 10 mm. **10** – *Radix socialis* (Zieten, 1832). Riedlingen-Bechingen. SMNS 106794. Scale 5 mm. **11** – *Ferrissia deperdita* (Desmarest, 1814). Zwiefalten-Mörsingen. SMNS J67.925. Scale: 1 mm. **12** – *Gyraulus applanatus* (Thomä, 1845). Zwiefalten-Mörsingen. SMNS J67.780. Scale: a: 1 mm; b: 100 μm. **13** – *Planorbarius mantelli* (Dunker, 1848). Zwiefalten-Mörsingen. SMNS 107221. Scale 10 mm. **14** – *Segmentina lartetii* (Noulet, 1854). Zwiefalten-Mörsingen. SMNS J67.909. Scale: a: 1mm; b: 200 μm.

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Illustrated in: Gottschick (1928, pl. 2, fig. 7); Schlickum (1976, pl. 1, fig. 6); Salvador et al. (2016a, pl. 9, fig. 12); Salvador et al. (2016c, fig. 2D).

Verified distribution: Zwiefalten (type locality).

Hygrophila
Family Lymnaeidae
Galba dupuyiana (Noulet, 1854)

Illustrated in: Sandberger (1872, pl. 28, fig. 27, 27b); Fischer (2000, fig. 4); Kókay (2006, pl. 16, figs. 14-16); Böttcher et al. (2009, figs. 2.1, 2.2); Salvador & Rasser (2014, figs. 1-7); Salvador & Rasser (2016b, figs. 2D-2E); Salvador et al. (2016c, fig. 2E).

Verified distribution: Zwiefalten, Zwiefaltendorf.

Lymnaea dilatata (Noulet, 1854)
Fig. 3.9

Illustrated in: Schlickum (1976, pl. 1, fig. 6); Fischer (2000, figs. 1, 2); Binder (2002, pl. 1, fig. 7a); Binder (2004, pl. 1, fig. 7); Kowalke & Reichenbacher (2005, figs. 9.4, 9.5); Kókay (2006, pl. 17, fig. 14); Böttcher et al. (2009, fig. 2.3); Salvador & Rasser (2014, figs. 8, 9); Salvador et al. (2015b, figs. 2F, 2G); Salvador & Rasser (2016a, fig. 5); Salvador et al. (2016b, fig. 5d); Salvador et al. (2016c, fig. 2G); Salvador et al. (2017, fig. 2.1).

Verified distribution: Langenenslingen-Andelfingen, Riedlingen-Bechingen, Ehingen (Donau)-Dächingen, Riedlingen-Daugendorf, Hausen ob Allmendingen, Zwiefalten-Mörsingen, Zwiefalten, Zwiefaltendorf.

Further literature data: Emerberg near Zwiefalten, Stoffelberg near Ehingen (Donau) (Wenz 1923: 1289).

Lymnaea turrita Klein, 1853
Fig. 3.8

Illustrated in: Klein (1853, pl. 5, fig. 17); Jooss (1913, figs. 5, 6); Schlickum (1976, pl. 1, fig. 5); Kókay (2006, pl. 17, fig. 16); Salvador et al. (2016a, pl. 9, fig. 16).

Verified distribution: Zwiefalten-Mörsingen, Zwiefalten, Zwiefaltendorf.

Radix socialis (Zieten, 1832)
Fig. 3.10

Illustrated in: Zieten (1832, pl. 30, fig. 4); Klein (1846, pl. 2, figs. 8-10); Jooss (1913, figs. 5, 6); Kókay (2006, pl. 17, figs. 11-13); Salvador & Rasser (2014, fig. 10); Salvador & Rasser (2016a, fig. 6); Salvador et al. (2016a, pl. 5, fig. 11, pl. 6, fig. 10, pl. 8, fig. 11); Salvador et al. (2017, fig. 2.2).

Verified distribution: Riedlingen-Bechingen, Ehingen (Donau)-Dächingen, Ehingen (Donau), Emerberg near Zwiefalten, Zwiefalten, Zwiefaltendorf.

Stagnicola armaniacensis (Noulet, 1857)

Illustrated in: Schlickum (1964, pl. 2, fig. 31); Schlickum (1976, pl. 1, fig. 12); Reichenbacher (1989, pl. 2, fig. 7); Kowalke & Reichenbacher (2005, figs. 9.6, 9.7); Harzhauser et al. (2014, pl. 2, figs. 4-11); Salvador et al. (2016b, fig. 5b).

Verified distribution: Riedlingen-Bechingen, Zwiefaltendorf.

Further literature data: Mundingen (Wenz 1923: 1352).

Family Planorbidae
Ferrissia deperdita (Desmarest, 1814)
Fig. 3.11

Fig. 4. 1 – *Oxyloma minima* (Klein, 1853). Zwiefalten-Mörsingen. SMNS 15817. Scale 500 µm. **2** – *Azeca lubricella* O. Boettger, 1870. Zwiefalten-Mörsingen. SMNS J67.234. Scale 2 mm. **3** – *Hypnophila* loxostoma (Klein, 1853). Zwiefalten-Mörsingen. SMNS J67.255. Scale 500 µm. **4** – *Granaria subfusiformis* (Sandberger, 1872). Zwiefalten-Mörsingen. SMNS 16635. Scale 2 mm. **5** – *Gastrocopta acuminata* (Klein, 1846). Zwiefalten-Mörsingen. SMNS J67.427. Scale 1 mm. **6** – *Gastrocopta quadriplicata* (Braun, 1851). Zwiefalten-Mörsingen. SMNS J67.383. Scale 1 mm. **7** – *Pseudydila moersingensis* (O. Boettger, 1877). Zwiefalten-Mörsingen. SMNS 107224. Scale 2 mm. **8** – *Triptychia kleini* Schnabel, 2006. Zwiefalten-Mörsingen. SMNS 107222. Scale 2 mm. **9** – *Cecilioides aciculella* (Sandberger, 1872). Zwiefalten-Mörsingen. SMNS 107225. Scale 500 µm. **10** – *Opeas minutum* (Klein, 1853). Zwiefalten-Mörsingen. SMNS J67.042. Scale 2 mm. **11** – *Palaeoglandina gracilis* (Zieten, 1832). Riedlingen-Bechingen. SMNS 106805. Scale 10 mm. **12** – *Pseudoleacina eburnea* (Klein, 1853). Zwiefalten-Mörsingen. SMNS 107226. Scale 2 mm. **13** – *Pseudoleacina kleiniana* (Pilsbry, 1909). Zwiefalten-Mörsingen. SMNS J 67.037. Scale 2 mm. **14** – *Poiretia taurinensis* (Sacco, 1886). Zwiefalten-Mörsingen. SMNS 16635. Scale 5 mm.

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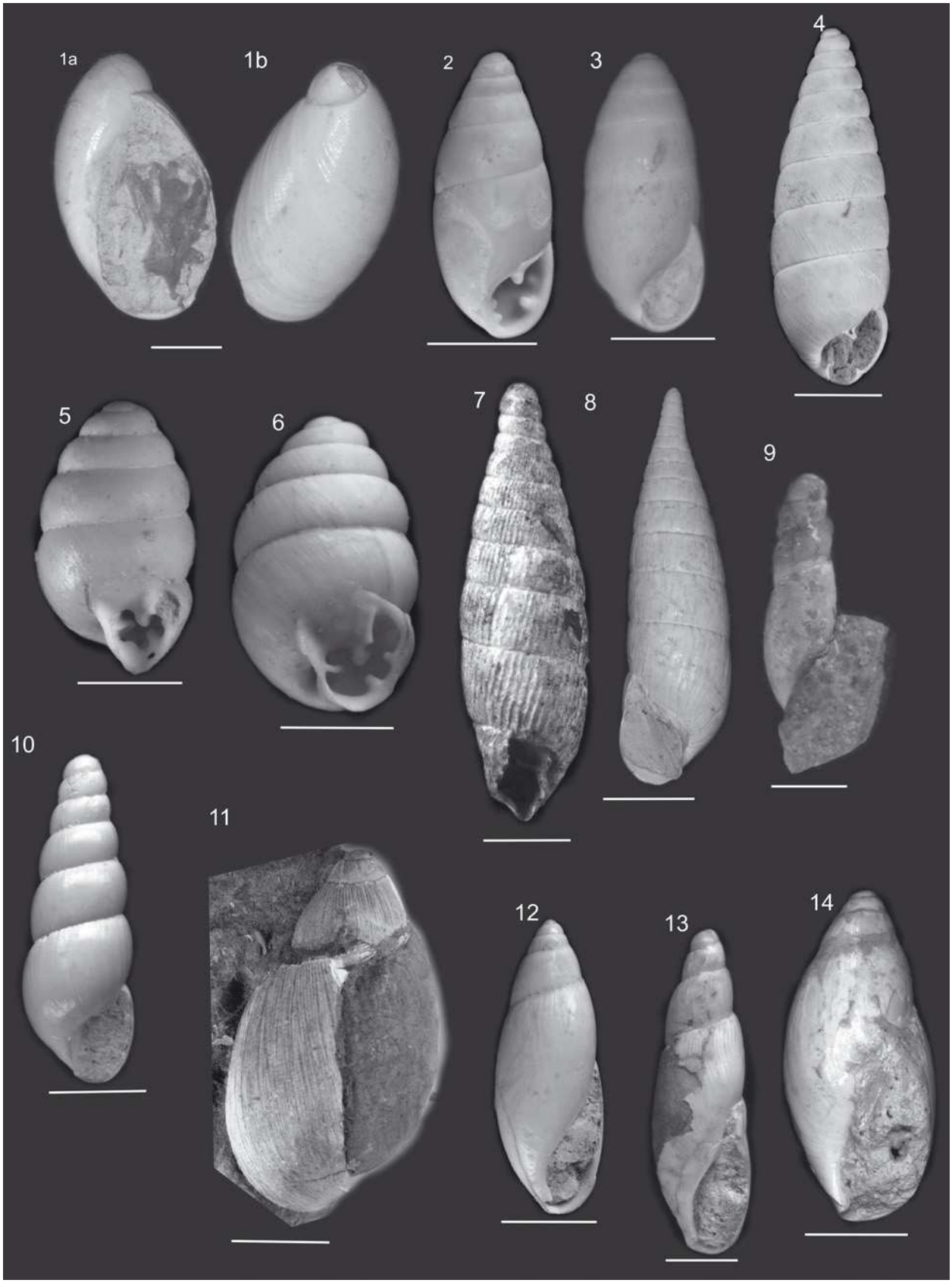

Fig. 4.

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Illustrated in: Desmarest (1814, pl. 1, fig. 14); Schlickum (1976, pl. 1, fig. 20); Kókay (2006, pl. 20, fig. 15, pl. 21, fig. 1); Harzhauser et al. (2014a, pl. 5, figs. 1, 2, 5, 12); Salvador & Rasser (2014, fig. 11); Salvador et al. (2015a, fig. 3C); Salvador & Rasser (2016a, fig. 7); Salvador et al. (2016c, fig. 2H); Neubauer et al. (2017, figs. 3J, K, Q).

Verified distribution: Riedlingen-Bechingen, Ehingen (Donau)-Mundingen, Zwiefalten-Mörsingen, Zwiefaltendorf.

Further literature data: Ehingen (Donau)-Dächingen (Wenz 1923: 1695).

Gyraulus applanatus (Thomä, 1845)
Fig. 3.12

Illustrated in: Gottschick & Wenz (1916, figs. 1, 2); Schlikkum (1964, pl. 2, fig. 35); Schlickum (1970, pl. 10, fig. 6); Steininger et al. (1973, pl. 9, fig. 11); Reichenbacher (1989, pl. 1, fig. 11); Kadolsky (1995, fig. 47); Binder (2004, pl. 2, fig. 1); Kowalke & Reichenbacher (2005, fig. 9.1-9.3); Kókay (2006, pl. 19, figs. 13, 14); Böttcher et al. (2009, figs. 2.7-2.9); Salvador & Rasser (2014, figs. 12-23); Salvador et al. (2015b, figs. 2H, 2I); Salvador & Rasser (2016a, fig. 8); Salvador & Rasser (2016b, figs. 2G, 2H); Salvador et al. (2016b, figs. 5h, 5i); Salvador et al. (2016c, figs. 2K-2M); Salvador et al. (2017, fig. 2.3).

Verified distribution: Riedlingen-Bechingen, Ehingen (Donau)-Dächingen, Riedlingen-Daugendorf, Zwiefalten-Mörsingen, Zwiefalten, Zwiefaltendorf.

Further literature data: Berg near Ehingen (Donau), Ehingen (Donau), Gamerschwang, Griesingen (Wenz 1923: 1587).

Remarks: *Gyraulus dealbatus* (Braun, 1851) is a synonym of this species (Kowalke & Reichenbacher, 2005), but is sometimes listed as a separate species in older literature.

Planorbarius mantelli (Dunker, 1848)
Fig. 3.13

Illustrated in: Dunker (1848, pl. 31, figs. 27-29); Schlikkum (1966, pl. 13, fig. 27); Schlickum (1970, pl. 10, fig. 7); Schlickum (1976, pl. 1, fig. 19); Reichenbacher (1989, pl. 1, fig. 10); Binder (2004, pl. 2, figs. 2, 3); Harzhauer & Binder (2004, pl. 5, figs. 1-4); Kókay (2006, pl. 20, fig. 6); Böttcher et al. (2009, figs. 2.4-2.6); Harzhauser et al. (2014a, pl. 3, figs. 5, 7-13, 15, 16); Salvador & Rasser (2014, figs. 26-28); Salvador et al. (2015a, figs. 3G, 3H); Salvador et al. (2015b, fig. 2J); Salvador & Rasser (2016a, figs. 9-11); Salvador & Rasser (2016b, figs. 2I, 2J); Salvador et al. (2016a, pl. 7, fig. 5); Salvador et al. (2016b, fig. 5j); Salvador et al. (2016c, figs. 2P, 2Q); Neubauer et al. (2017, figs. 3G, H, P); Salvador et al. (2017, fig. 2.5).

Verified distribution: Langenenslingen-Andelfingen, Riedlingen-Bechingen, Ehingen (Donau)-Dächingen, Riedlingen-Daugendorf, Ehingen (Donau), Zwiefalten-Gauingen, Zwiefalten-Mörsingen, Mundingen, Riedlingen-Pflummern, Zwiefalten, Zwiefaltendorf.

Further literature data: Ehingen (Donau)-Mundingen (lost SMNS material), Emerberg near Zwiefalten (Wenz 1923: 1468).

Remarks: Commonly referred to as *P. cornu* (Brongniart, 1810) in the literature (for a discussion, see Harzhauser & Binder 2004 and Harzhauser et al. 2014a).

Segmentina lartetii (Noulet, 1854)
Fig. 3.14

Illustrated in: Schlickum (1976, pl. 1, fig. 18); Harzhauser et al. (2014, pl. 2, figs. 12-16); Salvador & Rasser (2014, figs. 29-31).

Verified distribution: Ehingen (Donau)-Mundingen, Zwiefalten-Mörsingen.

Further literature data: Zwiefaltendorf (Wenz 1923: 1666).

Eupulmonata
Family Ellobiidae
Carychium nouleti Bourguignat, 1857

Illustrated in: Bourguignat (1857, figs. 9, 10); Schlickum (1976, figs. 10, 11); Strauch (1977, pl. 15, figs. 24-27, pl. 18, fig. 61, pl. 20, fig. 83); Stworzewicz(1999a, figs. 19-22); Salvador et al. (2016c, fig. 2U).

Verified distribution: Zwiefaltendorf.

Stylommatophora
Family Succineidae
Oxyloma minima (Klein, 1853)
Fig. 4.1

Illustrated in: Schlickum (1976, pl. 2, fig. 34); Kókay (2006, pl. 27, fig. 13); Harzhauser et al. (2014b, pl. 9, figs. 1, 2, 6); Salvador & Rasser (2016a, figs. 32, 33); Salvador et al. (2016a, pl. 6, fig. 13); Salvador et al. (2016c, figs. 4C, 4D).

Verified distribution: Riedlingen-Bechingen, Ehingen (Donau)-Mundingen, Zwiefalten-Mörsingen (type locality), Zwiefalten, Zwiefaltendorf.

Further literature data: Emerberg (Wenz 1923: 894).

Family Azecidae
Azeca lubricella O. Boettger, 1870
Fig. 4.2

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Illustrated in: Schlickum (1976, pl. 1, fig. 21; neotype); Salvador et al. (2017, fig. 3.3).

Verified distribution: Riedlingen-Bechingen, Zwiefalten-Mörsingen, Zwiefaltendorf.

Further literature data: Altheim near Ehingen (Donau), Hausen ob Allmendingen (Wenz 1923: 1093).

Hypnophila loxostoma (Klein, 1853)
Fig. 4.3

Illustrated in: Klein (1853, pl. 5, fig. 12); Gottschick & Wenz (1916, pl. 1, fig. 14); Papp & Thenius (1953, pl. 4, fig. 7); Schlickum (1976, pl. 1, fig. 22); Lueger (1981, pl. 1, fig. 4); Kókay (2006, pl. 21, fig. 10); Rasser et al. (2013, pl. 4, fig. 6); Salvador et al. (2015a, fig. 3o); Salvador & Rasser (2016a, fig. 13).

Verified distribution: Altheim near Ehingen (Donau), Riedlingen-Bechingen, Emeringen, Hausen ob Allmendingen, Zwiefalten-Mörsingen, Zwiefalten, Zwiefaltendorf.

Further literature data: Emerberg near Zwiefalten (Schlickum 1976: 9).

Family Chondrinidae
Granaria subfusiformis (Sandberger, 1872)
Fig. 4.4

Illustrated in: Schlickum (1976, pl. 2, fig. 25); Höltke & Rasser (2013, figs. 4.7, 4.8).

Verified distribution: Zwiefalten-Baach (cf.), Hausen ob Allmendingen, Zwiefalten-Mörsingen, Zwiefaltendorf.

Family Valloniidae
Pupisoma distans Falkner, 1974

Illustrated in: Falkner (1974, pl. 10, fig. 3, pl. 11, figs. 7, 8).

Verified distribution: Zwiefaltendorf (type locality).

Spermodea candida Falkner, 1974

Illustrated in: Falkner (1974, pl. 10, figs. 1, 2, pl. 11, figs. 5, 6); Stworzewicz (1999b, figs. 30, 31); Kókay (2006, pl. 26, fig. 2); Neubauer et al. (2017, figs. 7E, F, H, I, K).

Verified distribution: Zwiefaltendorf.

Further literature data: Zwiefalten-Mörsingen (Neubauer et al. 2017: 750).

Family Vertiginidae
Vertigo callosa (Reuss, 1849)

Illustrated in: Reuss (1849, pl. 3, fig. 7); Schlickum (1976, pl. 2, fig. 24); Lueger (1981, pl. 2, figs. 3-5); Stworzewicz (1999b, figs. 6, 7); Salvador (2015, figs. 17, 18); Salvador et al. (2016c, fig. 4B).

Verified distribution: Zwiefaltendorf.

Family Gastrocoptidae
Gastrocopta acuminata (Klein, 1846)
Fig. 4.5

Illustrated in: Klein (1846, pl. 1, fig. 19); Gottschick & Wenz (1916, pl. 1, fig. 4); Stworzewicz (1999b, figs. 56-58); Manganelli & Giusti (2000a, pl. 1, figs. 1-6, pl. 2, figs. 1-7); Kókay (2006, pl. 24, fig. 7); Salvador (2015, fig. 7); Salvador & Rasser (2016a, fig. 31); Salvador & Rasser (2016b, fig. 2W); Salvador et al. (2016a, pl. 1, figs. 1, 2, pl. 7, fig. 15); Salvador et al. (2016c, fig. 3P); Salvador et al. (2017, fig. 3.5).

Verified distribution: Altheim near Ehingen (Donau) (cf.), Riedlingen-Bechingen (cf), Riedlingen-Daugendorf (cf.), Emeringen (cf.), Zwiefalten-Mörsingen, Zwiefalten (cf.), Zwiefaltendorf.

Further literature data: Ehingen (Donau)-Mundingen, Hausen ob Allmendingen (Wenz 1923: 918).

Gastrocopta quadriplicata (Braun, 1851)
Fig. 4.6

Illustrated in: Manganelli & Giusti (2000a, pl. 8, figs. 1-4).

Verified distribution: Zwiefalten-Mörsingen.

Family Clausiliidae
Pseudidyla moersingensis (O. Boettger, 1877)
Fig. 4.7

Illustrated in: Boettger (1877, pl. 2, fig. 32); Schlickum (1976, pl. 3, fig. 48); Salvador (2015, figs. 19-22); Salvador et al. (2016a, fig. 2.1); Salvador et al. (2016c, figs. 2V, 2W); Salvador et al. (2017, fig. 3.2).

Verified distribution: Zwiefalten-Mörsingen, Zwiefaltendorf.

Further literature data: Altheim near Ehingen (Donau) (Wenz 1923: 792).

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Family Filholiidae
Triptychia kleini Schnabel, 2006
Fig. 4.8

Illustrated in: Klein (1846, pl. 1, fig. 16); Boettger (1877, pl. 2, fig. 32); Schlickum (1976, pl. 3, fig. 47); Schnabel (2006, pl. 3, figs. 32-34); Salvador et al. (2015a, fig. 3L); Salvador et al. (2016a, pl. 5, figs. 17, 18).

Verified distribution: Zwiefalten-Mörsingen, Zwiefalten (type locality), Zwiefaltendorf.

Further literature data: Ehingen/Donau-Mundingen, Emerberg (Wenz 192: 811; Schnabel 2006: 147-148).

Remarks: Commonly found in the literature by the invalid name *Clausilia grandis* Klein (1846); renamed by Schnabel (2006).

Triptychia teutonica Schnabel, 2006

Illustrated in: Schnabel (2006, pl. 8, figs. 97, 98).

Verified distribution: None.

Further literature data: Zwiefalten-Mörsingen (Schnabel 2006: 172).

Family Ferussaciidae
Cecilioides aciculella (Sandberger, 1872)
Fig. 4.9

Illustrated in: Sandberger (1875, pl. 29, fig. 15); Miller (1900, pl. 7, fig. 18); Schlickum (1976, pl. 5, fig. 68); Lueger (1981, pl. 7, fig. 1); Finger (1998, pl. 12, fig. 1); Harzhauser & Binder (2004, pl. 9, figs. 8-11); Hír & Kókay (2004, fig. 9.3); Harzhauser et al. (2014a, pl. 9, figs. 14, 15); Neubauer et al. (2017, figs. 12A-12D).

Verified distribution: Zwiefalten-Mörsingen, Zwiefaltendorf.

Family Subulinidae
Opeas minutum (Klein, 1853)
Fig. 4.10

Illustrated in: Klein (1853, pl. 5, fig. 9); Sandberger (1875, pl. 19, fig. 16); Schlickum (1976, pl. 3, fig. 46); Kókay (2006, pl. 30, fig. 16); Harzhauser et al. (2014, pl. 9, figs. 3, 5-7); Salvador et al. (2015b, fig. 2K); Salvador & Rasser (2016a, fig. 12).

Verified distribution: Altheim near Ehingen (Donau), Langenenslingen-Andelfingen, Riedlingen-Bechingen, Riedlingen-Daugendorf, Hausen ob Allmendingen, Zwiefalten-Mörsingen Zwiefalten, Zwiefaltendorf.

Further literature data: Emerberg near Zwiefalten (Wenz 1923: 874), Emeringen (Sandberger 1875: 596).

Family Oleacinidae
Palaeoglandina gracilis (Zieten, 1832)
Fig. 4.11

Illustrated in: Zieten (1832, pl. 30, fig. 3); Zilch (1959-1960, fig. 1627); Salvador et al. (2015a, fig. 5E); Salvador & Rasser (2016a: fig. 34).

Verified distribution: Riedlingen-Bechingen, Ehingen (Donau), Zwiefalten-Gauingen.

Palaeoglandina porrecta (Gobanz, 1854)

Illustrated in: Gobanz (1854, pl. 3, fig. 5); Sandberger (1875, pl.29, fig. 32); Schlickum (1976, pl. 5, fig. 69).

Verified distribution: Zwiefaltendorf.

Further literature data: Altheim near Ehingen (Donau), Zwiefalten-Mörsingen (Wenz 1923: 848).

Fig. 5. 1 – *Lucilla subteres* (Clessin, 1885). Zwiefalten-Mörsingen. SMNS 15817. Scale 1 mm. **2** – *Discus euglyphoides* (Sandberger, 1872). Zwiefalten-Mörsingen. SMNS J65.809. Scale 500 μm. **3** – *Discus pleuradrus* (Bourguignat, 1881). Zwiefalten-Mörsingen. SMNS J65.787. Scale 500 μm. **4** – *Discus wenzi* (Jooss, 1918). Zwiefalten-Mörsingen. Syntype. SMNS 106447. Scale 500 μm. **5** – *Aegopinella subnitens* (Klein, 1853). Zwiefalten-Mörsingen. SMNS 107227. **6** – *Aegopinella*? *procellaria* (Jooss, 1918). Scale 5 mm. Zwiefalten (Zwiefalten-Mörsingen). Syntype. SMNS 106419. Scale 10 mm. **7** – *Nesovitrea subhammonis* (Gottschick, 1928). Altheim near Ehingen. Holotype. SMNS 15817. Scale 200 μm. **8** – *Janulus moersingensis* Jooss, 1918. Zwiefalten-Mörsingen. Holotype. SMNS 106411. Scale 2 mm. **9** – *Janulus supracostatus* (Sandberger, 1872). Riedlingen-Bechingen. SMNS 107391. Scale 2 mm. **10** – *Archaeozonites costatus* (Sandberger, 1872). Zwiefalten-Mörsingen. SMNS 17455. Scale 1 mm. **11** – *Praeoestophorella phacodes* (Thomä, 1845). Riedlingen-Daugendorf. SMNS 107208. Scale 2 mm.

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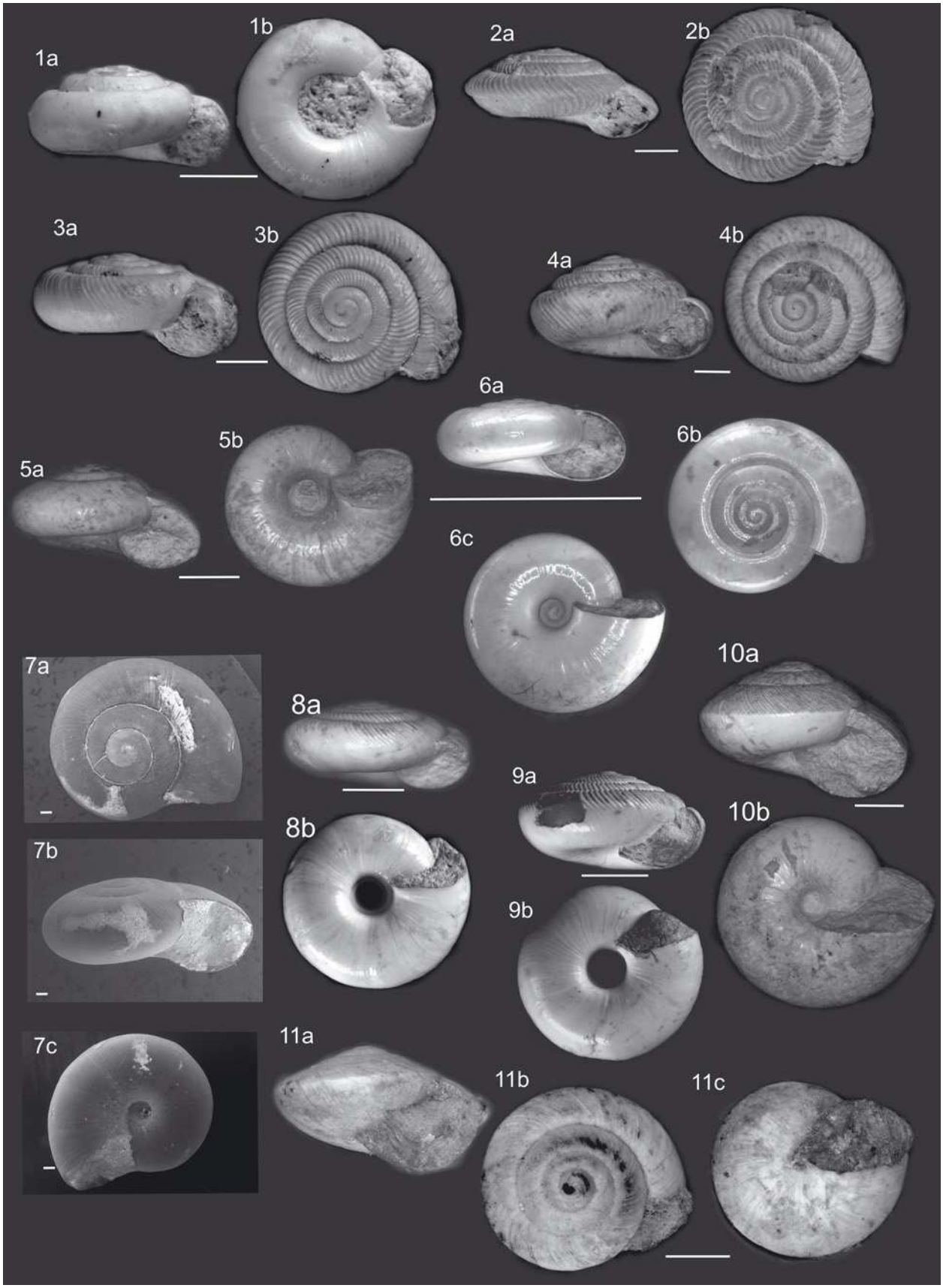

Fig. 5.

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Pseudoleacina eburnea (Klein, 1853)
Fig. 4.12

Illustrated in: Klein (1853, pl. 5, fig. 10); Schlickum (1976, pl. 3, fig. 49); Lueger (1981, pl. 7, figs. 15, 16); Harzhauser & Binder (2004, pl. 9, fig. 2); Salvador et al. (2015a, fig. 5D); Salvador et al. (2016a, pl. 3, fig. 18).

Verified distribution: "Hopfenacker" near Hausen ob Allmendingen, Zwiefalten-Mörsingen (type locality), Zwiefalten, Zwiefaltendorf.

Further literature data: Andelfinger Berg near Riedlingen, Riedlingen-Bechingen (Wenz 1923: 858).

Pseudoleacina kleiniana (Pilsbry, 1909)
Fig. 4.13

Illustrated in: Klein (1853, pl. 5, fig. 11; as *Achatina elegans*), Schlickum (1964, pl.2, fig. 42), Schlickum (1976, pl. 3, fig. 50).

Verified distribution: Zwiefalten-Mörsingen, Zwiefaltendorf.

Poiretia taurinensis (Sacco, 1886)
Fig. 4.14

Illustrated in: Sacco (1886, pl. 2, fig. 3); Kókay (2006, pl. 32, fig. 10).

Verified distribution: Zwiefalten-Mörsingen.

Family Testacellidae
Testacella zellii Klein, 1853

Illustrated in: Klein (1853, pl. 5, fig. 1); Schlickum (1976, pl. 5, fig. 51); Salvador (2013, fig. 5); Salvador et al. (2015a, figs. 5F-G); Salvador et al. (2016a, fig. 5).

Verified distribution: Langenenslingen-Andelfingen, Zwiefaltendorf.

Family Helicodiscidae
Lucilla subteres (Clessin, 1885)
Fig. 5.1

Illustrated in: Clessin (1885, pl. 7, fig. 6); Schlickum (1976, pl. 2, fig. 35); Schlickum (1979, fig. 2); Kókay (2006, pl. 27, figs. 14-16); Salvador (2014, fig. 24); Salvador & Rasser (2014, figs. 34, 35); Neubauer et al. (2017, figs. 9C, F, H, I).

Verified distribution: Zwiefalten-Mörsingen, Zwiefaltendorf.

Family Discidae
Discus euglyphoides (Sandberger, 1872)
Fig. 5.2

Illustrated in: Sandberger (1875, pl. 31, fig. 1); Maillard (1892, pl. 1, fig. 19); Schlickum (1976, pl. 2, fig. 36).

Verified distribution: Altheim near Ehingen (Donau), Hausen ob Allmendingen, Zwiefalten-Mörsingen, Zwiefalten, Zwiefaltendorf.

Further literature data: Emerberg near Zwiefalten, Emeringen (Wenz 1923: 331).

Discus pleuradrus (Bourguignat, 1881)
Fig. 5.3

Illustrated in: Bourguignat (1881, pl. 3, figs. 67-72); Schütt (1967, fig. 16); Schlickum (1976, pl. 2, fig. 37); Lueger (1981, pl. 4, figs. 6, 7); Fischer (2000, fig. 21); Harzhauser & Binder (2004, pl. 7, figs. 9-11); Kókay (2006, pl. 28, figs. 3, 4); Böttcher et al. (2009, figs. 2.10, 2.11); Harzhauser et al. (2014b, pl. 9, figs. 8-13); Salvador & Rasser (2014, figs. 32, 33); Salvador et al. (2015a, figs. 4U, 4W); Salvador & Rasser (2016a, fig. 30); Salvador & Rasser (2016b, fig. 2U); Salvador et al. (2016c, figs. 3M, 3N).

Verified distribution: Riedlingen-Bechingen, Riedlingen-Daugendorf, Zwiefalten-Mörsingen, Zwiefaltendorf.

Discus wenzi (Jooss, 1918)
Fig. 5.4

Illustrated in: Salvador et al. (2016a, fig. 2.4).

Verified distribution: Zwiefalten-Mörsingen (type locality), Zwiefalten.

Family Oxychilidae
Aegopinella erecta (Gottschick, 1920)

Illustrated in: Schlickum (1976, pl. 3, fig. 41).

Verified distribution: Zwiefaltendorf.

Further literature data: Zwiefalten-Mörsingen (Schlickum 1976: 13).

Aegopinella subnitens (Klein, 1853)
Fig. 5.5

Illustrated in: Klein (1853, pl. 5, fig. 7); Schlickum (1976, pl. 3, figs. 39, 40); Lueger (1981, pl. 6, figs. 4-6); Salvador et al. (2016a, pl. 8, fig. 20).

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Verified distribution: Langenenslingen-Andelfingen, Hausen ob Allmendingen, Zwiefalten-Mörsingen, Zwiefalten (type locality), Zwiefaltendorf.

Further literature data: Emerberg near Zwiefalten (Wenz 1923: 284).

Aegopinella? *procellaria* (Jooss, 1918)
Fig. 5.6

Illustrated in: Lueger (1981, pl. 6, fig. 2); Salvador et al. (2016a, pl. 7, fig. 8).

Verified distribution: Zwiefalten-Mörsingen, Zwiefalten (type locality).

Nesovitrea subhammonis (Gottschick, 1928)
Fig. 5.7

Illustrated in: Gottschick (1928, fig. 6); Salvador et al. (2016a, pl. 8, fig. 19).

Verified distribution: Altheim near Ehingen (Donau) (type locality).

Remarks: The species was listed as *Perpolita subhammonis* by Salvador et al. (2016a); hoever, *Perpolita* has been recently listed as a synoymym of *Nesovitrea* (Deutsche Malakozoologische Gesellschaft 2017)

Family Gastrodontidae
Janulus moersingensis Jooss, 1918
Fig. 5.8

Illustrated in: Schlickum (1976, pl. 3, fig. 44); Salvador et al. (2016a, pl. 6, fig. 15).

Verified distribution: Zwiefalten-Mörsingen (type locality), Zwiefalten Zwiefaltendorf.

Janulus supracostatus (Sandberger, 1872)
Fig. 5.9

Illustrated in: Sandberger (1875, pl. 29, fig. 2); Schlickum (1976, pl. 3, fig. 43); Salvador & Rasser (2014, figs. 36, 37).

Verified distribution: Riedlingen-Bechingen, Ehingen (Donau)-Mundingen, Zwiefaltendorf.

Further literature data: Zwiefalten-Mörsingen (Wenz 1923: 305).

Zonitoides suevicus (Jooss, 1918)

Illustrated in: Schlickum (1976, pl. 5, fig. 67); Salvador et al. (2016a, pl. 9 fig. 7).

Verified distribution: Zwiefalten-Mörsingen.

Family Zonitidae
Archaeozonites costatus Sandberger, 1875
Fig. 5.10

Illustrated in: Gottschick & Wenz (1916, pl. 1, fig.1); Schlickum (1976, pl. 5, fig. 66); Binder (2002, pl. 1, figs. 14-16, pl. 3, fig. 8, pl. 7, fig. 3, pl. 8, fig. 4); Kókay (2006, pl. 29, figs. 11, 12); Harzhauser et al. (2014b, pl. 10, figs. 13-19); Salvador et al. (2015a, figs. 3Q, 3R); Salvador et al. (2015b, figs. 2O, 2P); Salvador & Rasser (2016b, fig. 2Z).

Verified distribution: Langenenslingen-Andelfingen, Zwiefalten-Mörsingen, Riedlingen, Zwiefaltendorf.

Further literature data: Gammertingen, Langenenslingen-Friedingen (Wenz 1923: 256).

Remarks: Sandberger (1875) also described the species *A. subcostatus* from the *silvana*-beds, however, without illustration. The taxonomic status of the latter is unknown.

Family Trissexodontidae
Praeoestophorella phacodes (Thomä, 1845)
Fig. 5.11

Illustrated in: Thomä (1845, pl. 2, fig. 8); Schlickum (1976, pl. 4, fig. 55); Rasser et al. (2013, pl. 4, fig. 5); Salvador et al. (2015a, figs. 4N-4P); Salvador & Rasser (2016a, figs. 27-29).

Verified distribution: Riedlingen-Daugendorf, Hausen ob Allmendingen, Zwiefaltendorf.

Further literature data: Zwiefalten-Mörsingen (Wenz 1923: 466).

Family Helicodontidae
Protodrepanostoma involutum (Thomä, 1845)
Fig. 6.1

Illustrated in: Thomä (1845, pl. 2, fig. 8); Sandberger (1875, pl. 22, fig. 17); Jooss (1912, pl. 2, fig. 3); Schlickum (1976, pl. 3, fig. 53); Falkner (1986, pl. 17, figs. 9, 10); Nordsieck (1986, fig. 8); Nordsieck (2014, fig. 29); Salvador et al. (2015a, figs. 4H-4J).

Verified distribution: Hausen ob Allmendingen, Zwiefalten-Mörsingen, Zwiefalten, Zwiefaltendorf.

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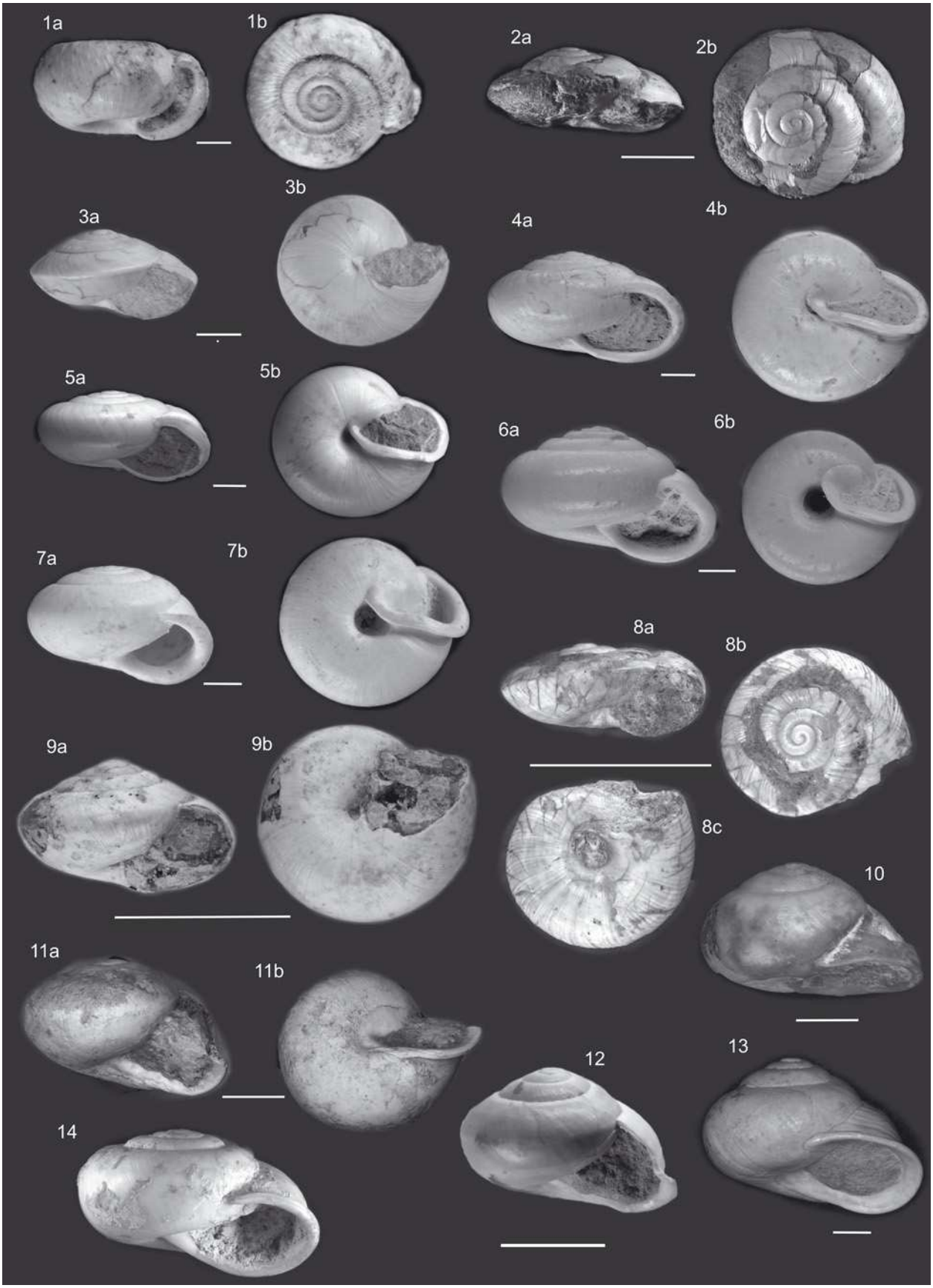

Fig. 6.

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Further literature data: Altheim near Ehingen (Donau) (Wenz 1923: 454).

Remarks: Zilch (1959-1960) listed *Protodrepanostoma* as a synonym of *Trissexodon*, while Manganelli & Giusti (2000b) considered it a synonym of *Drepanostoma*, but, regardless, placed the species *involutum* in the genus *Helicodonta*. The present classification follows Nordsieck (2014).

Miodiscula disciformis (Wenz, 1919)
Fig. 6.2

Illustrated in: Wenz (1924, pl. 2, figs. 1-3); Schlickum (1976, pl. 3, fig. 54); Nordsieck (2014, fig. 28).

Verified distribution: Altheim/Donau, Zwiefalten-Mörsingen, Zwiefaltendorf.

Further literature data: Emerberg near Zwiefalten (Wenz 1923: 461).

Remarks: Family allocation uncertain (Nordsieck 2014).

Miodiscula miocaenica (Gottschick & Wenz, 1927)
Fig. 6.3

Illustrated in: Gottschick & Wenz (1927, pl. 8, fig. 3); Salvador et al. (2016a, pl. 6, fig. 14).

Verified distribution: Zwiefalten-Mörsingen (type locality).

Further literature data: None.

Remarks: Family allocation uncertain (Nordsieck 2014).

Family Elonidae
Apula coarctata (Klein, 1853)
Fig. 6.4

Illustrated in: Klein (1853, pl. 5, fig. 3); Wenz (1911, pl. 4, figs. 16-20, 29, 30); Schlickum (1976, pl. 4, fig. 60); Rasser et al. (2013, pl. 4, fig. 9); Harzhauser et al. (2014b, pl. 11, figs. 5-8, 21); Salvador et al. (2015a, figs. 3S-3U); Salvador & Rasser (2016a: figs. 14-16); Salvador et al. (2017, fig. 3.4).

Verified distribution: Riedlingen-Bechingen, Riedlingen-Daugendorf, Ehingen (Donau)-Mundingen, Emerberg near Zwiefalten, Emeringen, Hausen ob Allmendingen, Zwiefalten-Mörsingen, Zwiefaltendorf.

Further literature data: Deutschhof near Riedlingen-Pflummern (Wenz 1923: 534).

Klikia catantostoma (Sandberger, 1875)
Fig. 6.5

Illustrated in: Sandberger (1875, pl. 29, fig. 6); Schlickum (1976, pl. 4, fig. 61).

Verified distribution: Zwiefalten-Baach, Hausen ob Allmendingen, Zwiefalten-Mörsingen, Zwiefaltendorf.

Further literature data: Emerberg (Wenz 1923: 534).

Klikia giengensis (Klein, 1846)
Fig. 6.6

Illustrated in: Klein (1846, pl. 1, fig. 9); Wenz (1911, pl. 4, figs. 6-10); Schlickum (1976, pl. 4, fig. 58); Binder (2004, pl. 6, fig. 3); Kókay (2006, pl. 35, fig. 9); Harzhauser et al. (2014b, pl. 11, figs. 9-11, 22); Salvador & Rasser (2016a, figs. 17-19).

Verified distribution: Altheim near Ehingen (Donau), Riedlingen-Bechingen, Emerberg near Zwiefalten, Zwiefalten-Mörsingen, Zwiefalten, Zwiefaltendorf.

Further literature data: Deutschhof near Riedlingen-Pflummern, Hausen ob Allmendingen, Österberg near Riedlingen, Stoffelberg near Ehingen (Donau) (Wenz 1923: 543).

Fig. 6. 1 – *Protodrepanostoma involutum* (Thomä, 1845) Zwiefalten-Mörsingen. SMNS 15817. Scale 500 μm. **2** – *Miodiscula disciformis* (Wenz, 1919). Zwiefalten-Mörsingen. SMNS J66.244. Scale 5 mm. **3** – *Miodiscula miocaenica* (Gottschick & Wenz, 1927). Zwiefalten-Mörsingen. SMNS J68.551. Scale 1 mm. **4** – *Apula coarctata* (Klein, 1853). Riedlingen-Bechingen. SMNS J66.290. Scale 2 mm. **5** – *Klikia catanostoma* (Sandberger, 1872). Zwiefalten-Mörsingen. SMNS J66.304. Scale 2 mm. **6** – *Klikia giengensis* (Klein, 1846). Riedlingen-Bechingen. SMNS J66.275. Scale 2 mm. **7** – *Klikia osculina* (Sandberger, 1872). Zwiefalten-Mörsingen. SMNS J66.251. Scale 2 mm. **8** – *Helicopsis suevica* Gottschick & Wenz, 1927. Zwiefaltendorf. Syntype. SMNS 22828. Scale 5 mm. **9** – *Leucochroopsis kleinii* (Klein, 1846). Zwiefalten. Syntype of *Helix carinulata* Klein, 1853. SMNS 106372. Scale 10 mm. **10** – *Palaeotachea dentula* (Quenstedt, 1867). Emerberg. Syntype of *Helix pachystoma* Klein, 1853 and *Cepaea lepida* Wenz, 1919. SMNS 105004. Scale 1mm. **11** – *Palaeotachea renevieri* (Maillard, 1891). Ehingen (Donau)-Dächingen. SMNS 106840. Scale 5 mm. **12** – *Palaeotachea silvana* (Klein, 1853). Zwiefalten. Syntype. SMNS 22738. Scale 10 mm. **13** – *Palaeotachea turonensis* (Deshayes, 1831). Zwiefalten-Mörsingen. SMNS J66.818. Scale 4 mm. **14** – *Pseudochloritis incrassata* (Klein, 1853). Zwiefalten-Mörsingen. SMNS 107230. Scale 2 mm.

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Klikia osculina (Sandberger, 1875)
Fig. 6.7

Illustrated in: Wenz (1919, pl. 4, figs. 21-25); Schlickum (1976, pl. 4, fig. 59).

Verified distribution: Altheim near Ehingen (Donau), Zwiefalten-Baach, Riedlingen-Bechingen, Zwiefalten-Mörsingen.

Further literature data: Emerberg (Wenz 1923: 547).

Family Hygromiidae
Helicopsis suevica Gottschick & Wenz, 1927
Fig. 6.8

Illustrated in: Gottschick & Wenz (1927, pl. 8, fig. 2); Schlickum (1976, pl. 5, fig. 67); Salvador et al. (2016a, pl. 9, fig. 6).

Verified distribution: Zwiefaltendorf (type locality).

Leucochroopsis kleinii (Klein, 1846)
Fig. 6.9

Illustrated in: Klein (1846, pl. 1, figs. 8, 15); Schlickum (1976, pl. 3, fig. 52); Harzhauser & Binder (2004, pl. 11, figs. 8-10); Harzhauser et al. (2014b, pl. 11, figs. 12-14); Salvador et al. (2015a, figs. 4K-4M); Salvador & Rasser (2016a, fig. 26); Salvador et al. (2016a, pl. 2 fig. 11, pl. 6, fig. 17); Salvador et al. (2017, fig. 3.7).

Verified distribution: Altheim near Ehingen (Donau), Langenenslingen-Andelfingen, Riedlingen-Bechingen, Ehingen (Donau)-Dächingen, Riedlingen-Daugendorf, Emeringen, Hausen ob Allmendingen, Zwiefalten-Mörsingen, Stoffelberg near Ehingen (Donau), Zwiefalten, Zwiefaltendorf.

Further literature data: Deutschhof near Riedlingen-Pflummern, Emerberg near Zwiefalten (Wenz 1923: 434).

Family Helicidae
Palaeotachea dentula (Quenstedt, 1867)
Fig. 6.10

Illustrated in: Klein (1853, pl. 5, fig. 4); Quenstedt (1867, pl. 45, fig. 6); Höltke & Rasser (2016, pl. 1, figs. 12-14, pl. 2, fig. 1); Salvador et al. (2016a, pl. 6, fig. 4).

Verified distribution: Emerberg near Zwiefalten, Hayingen-Oberwilzingen.

Further literature data: Zwiefalten-Baach (Wenz 1923: 616).

Palaeotachea renevieri (Maillard, 1891)
Fig. 6.11

Illustrated in: Maillard (1891, pl. 3, fig. 18); Jooss (1923, pl. 11, figs. 18-23); Berz & Jooss (1927, fig. 1); Salvador et al. (2015a, figs. 4A, 4B); Salvador et al. (2015b, figs. 2R-2T); Salvador & Rasser (2016b, figs. 2N-2P); Salvador et al. (2016c, figs. 3D-3F).

Verified distribution: Ehingen (Donau)-Dächingen.

Palaeotachea silvana (Klein, 1853)
Fig. 6.12

Illustrated in: Klein (1853, pl. 5, fig. 2); Schlickum (1976, pl. 4, figs. 62, 63); Reichenbacher (1989, pl. 2, figs. 17-19); Kókay (2006, pl. 36, figs. 2, 3); Böttcher et al. (2009, fig. 2.15); Salvador et al. (2015a, figs. 4C, 4D); Salvador et al. (2015b, figs. 2U-2W); Höltke & Rasser (2016, figs. 5.1-5.5, 6.3, 6.4); Salvador & Rasser (2016a, figs. 20-22); Salvador & Rasser (2016b, figs. 2K-2M); Salvador et al. (2016a, pl. 5, fig. 2, pl. 9, fig. 5; Salvador et al. (2016c, figs. 3A-3C.

Verified distribution: Altheim near Ehingen (Donau), Langenenslingen-Andelfingen, Zwiefalten-Baach, Riedlingen-Bechingen, Ehingen (Donau)-Dächingen, Riedlingen-Daugendorf, Ehingen (Donau), Ehingen (Donau)-Mundingen, Emerberg near Zwiefalten, Zwiefalten-Gauingen, Hausen ob Allmendingen, Zwiefalten-Mörsingen, Riedlingen**,** Zwiefalten (type locality), Zwiefaltendorf.

Further literature data: Allmendingen-Pfraunstetten, Deutschhof near Riedlingen-Pflummern, Bussen hill near Riedlingen, Österberg near Riedlingen (Wenz 1923: 678).

Remarks: This species is the index fossil of the *silvana*-beds.

Palaeotachea turonensis (Deshayes, 1831)
Fig. 6.13

Illustrated in: Wenz (1920, figs. 1-6); Truc (1971, pl. 15, fig. 1); Fischer (2000, figs. 25, 26); Salvador et al. (2017, fig. 3.8).

Verified distribution: Riedlingen-Bechingen, Zwiefalten-Mörsingen, Zwiefaltendorf.

Further literature data: Emerberg near Zwiefalten, Stoffelberg near Ehingen (Donau) (Wenz 1923: 625).

Pseudochloritis incrassata (Klein, 1853)
Fig. 6.14

Illustrated in: Klein (1846, pl. 1, fig. 12); Klein (1853, pl. 5, fig. 6); Schlickum (1976, pl. 4, fig. 56); Kókay (2006, pl.

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34, figs. 12-14); Binder (2008, pl. 3, figs. 2-4, pl. 6, fig. 2); Rasser et al. (2013, pl. 4, fig. 12); Harzhauser et al. (2014b, pl. 12, figs. 9-16, 19-24); Höltke & Rasser (2015, figs. 4.3, 5.1, 5.2, 6.11, 6.12); Salvador et al. (2015a, figs. 4E-4G); Salvador et al. (2015b, figs. 3A-3C); Salvador & Rasser (2016a, figs. 23-25); Salvador & Rasser (2016b, figs. 2Q-2S); Salvador et al. (2016a, pl. 5, fig. 8).

Verified distribution: Altheim near Ehingen (Donau), Langenenslingen-Andelfingen, Riedlingen-Bechingen, Ehingen (Donau)-Dächingen, Riedlingen-Daugendorf, Ehingen (Donau)-Mundingen, Hausen ob Allmendingen, Zwiefalten-Mörsingen, Zwiefalten, Zwiefaltendorf (possible type locality).

Further literature data: Blienshofen in Ehingen (Donau)-Heufelden, Deutschhof near Riedlingen-Pflummern, Emerberg near Zwiefalten (Wenz 1923: 515), Loretto near Zwiefalten (Binder 2008: 173).

5. Concluding remarks

In total, 14 freshwater and 50 terrestrial gastropods could be verified from the Emerberg and Tautschbuch hills region, but not all species reported in the literature could be confirmed. As it can be seen, the molluscan fauna from the southern margin of the Swabian Alb is overall very diverse and can be very abundant in some outcrops, such as Zwiefalten-Mörsingen and Zwiefalten (see also the Appendix). However, only very few localities from this region have already been extensively explored and further collection efforts should take place in all other localities where excavation is still possible. Such efforts will no doubt be rewarded with an extensive amount of new occurrence data (including non-molluscan fossils) and help to get a better overall idea of the region's palaeoenvironment. We can only hope that the present work will spur renewed interest and collection efforts in this area.

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Appendix: material analyzed

Below is listed the material analyzed for the present compilation. For easiness of use, the species are presented here in alphabetical order. An asterisk (*) after the lot's number indicates that it is a rock sample with several incrusted specimens. Most major museum collections in Germany, Switzerland, Austria and the United Kingdom were contacted, as well as several local collections in Baden-Württemberg state. However, only a few of them housed specimens from the studied region; these collections (and their acronyms) are: BSPG = Bayerische Staatssammlung für Paläontologie und Geologie (Munich, Germany); GPIT = Department of Geosciences, Eberhard Karls Universität Tübingen (Tübingen, Germany; formerly Geologisch-Paläontologisches Institut Tübingen); NHMUK = Natural History Museum (London, UK); PIMUZ = Paläontologisches Institut und Museum, Universität Zürich (Zurich, Switzerland); SMNS = Staatliches Museum für Naturkunde Stuttgart (Stuttgart, Germany). In addition, the record of two species from the Gauingen locality stem from the private collection of Dietrich Kadolsky (Sanderstead, UK). The material from the BSPG is arranged with a single inventory number for an entire collection effort, so, as to not repeat the same number over and over, lots from this collection only appear listed below when they represent the single known record for a given species in a given locality.

Altheim near Ehingen (Donau)

Gastrocopta acuminata (Klein, 1846): SMNS 67242 (1 spec.).
Gyraulus applanatus (Thomä, 1845): GPIT/GA/3979 (1 spec.).
Hypnophila loxostoma (Klein, 1853): GPIT/GA/3924 (1 spec.), SMNS 67254 (7 spec.).
Klikia giengensis (Klein, 1846): GPIT/GA/1037 (2 spec.), SMNS 66277 (5 spec.).
Klikia osculina (Sandberger, 1875): SMNS 66316 (31 spec.; not found); SMNS 66317 (3 spec.).
Leucochroopsis kleini (Klein, 1846): GPIT/GA/2688 (18 spec.).
Lymnaea dilatata Noulet, 1854: GPIT/GA/4058 (2 spec.).
Melanopsis kleinii (Kurr, 1856): GPIT/GA/1037 (~20 spec.), GPIT/GA/2676 (5 spec.), GPIT/GA/3964 (1 spec.), GPIT/GA/4063 (10 spec.), GPIT/GA no nr. (2 spec.), NHMUK IP G1380 (10 spec.), SMNS 68414 (10 spec.).
Opeas minutum (Klein, 1853): SMNS 106853 (1 spec.).
Palaeotachea silvana (Klein, 1853): GPIT/GA/2709 (1 spec.), GPIT/GA/3944 (3 spec.), SMNS 66639 (3 spec.), SMNS 66837 (10 spec.).
Nesovitrea subhammonis (Gottschick, 1928): SMNS 15817 (holotype).
Planorbarius mantelli (Dunker, 1848): GPIT/GA/1037 (1 spec.), GPIT/GA/2689 (1 spec.), GPIT/GA/2709 (1 spec.), GPIT/GA/3931 (1 spec.).
Pomatias conicus (Klein, 1853): GPIT/GA/2685 (5 spec.), GPIT/GA/3920 (17 spec.), GPIT/GA/3990 (5 spec.), SMNS 68034 (9 spec.).
Protodrepanostoma involutum (Thomä, 1845): GPIT/GA/4046 (1 spec.).
Pseudidyla sp.: GPIT/GA/4047 (1 spec.).
Pseudochloritis incrassata (Klein, 1853): GPIT/GA/1037 (1 spec.), GPIT/GA/2689 (1 spec.), GPIT/GA/2696 (1 spec.), SMNS 106852 (1 spec.).
Theodoxus crenulatus (Klein, 1853): SMNS 68324 (1 spec.).

Langenenslingen-Andelfingen

Aegopinella subnitens (Klein, 1853): SMNS 12171/2008 (5 spec.).
Archaeozonites costatus Sandberger, 1872: SMNS 47522/2007 (3 spec.).
Leucochroopsis kleinii (Klein, 1846): SMNS 12170/2008 (5 spec.).
Lymnaea dilatata (Noulet, 1854): SMNS 47376/2007 (1 spec.).
Opeas minutum (Klein, 1853): GPIT/GA/4048 (1 spec.).
Palaeotachea silvana (Klein, 1853): SMNS 12143/2008 (1 spec.).
Planorbarius mantelli (Dunker, 1848): SMNS 12134/2008 (9 spec.).
Pseudochloritis incrassata (Klein, 1853): SMNS 38992/2005 (1 spec.), SMNS 12167/2008*.
Testacella zellii Klein, 1853: SMNS 106448 (1 spec.).
Tinnyea lauraea (Mathéron, 1843): SMNS 12169/2008 (1 spec.).

Zwiefalten-Baach

Granaria cf. *subfusiformis* (Sandberger, 1875): GPIT/GA/4077 (2 spec.).
Klikia catanostoma (Sandberger, 1872): SMNS 47385/2007 (1 spec.).
Klikia osculina (Sandberger, 1874): SMNS 66313 (1 spec.).
Palaeotachea silvana (Klein, 1853): GPIT/GA/2735 (3 spec.), GPIT/GA/4066 (1 s).
Pomatias conicus (Klein, 1853): GPIT/GA/4042 (1 spec.).

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Riedlingen-Bechingen

Apula coarctata (Klein, 1853): SMNS 66290 (1 spec.), SMNS 66315 (4 spec.), SMNS 106789 (7 spec.).
Bithynia glabra (Zieten, 1832): SMNS 68142 (3 spec.), SMNS 106810 (1 spec.).
Discus pleuradrus (Bourguignat, 1881): SMNS 65789 (1 spec.).
Ferrissia deperdita (Desmarest, 1814): SMNS 67926 (1 spec.).
Gastrocopta cf. *acuminata* (Klein, 1846): SMNS 67425 (2 spec.), SMNS 106785 (6 spec.).
Gyraulus applanatus (Thomä, 1845): SMNS 23314*, SMNS 67784 (1 spec.), SMNS 106794 (1 spec.), SMNS 106809*, SMNS 106810*, SMNS 106796*, SMNS 106803*, SMNS 106807*.
Hypnophila loxostoma (Klein, 1853): SMNS 106786 (5 spec.).
Klikia giengensis (Klein, 1846): SMNS 66275 (3 spec.).
Leucochroopsis kleini (Klein, 1846): SMNS 65952 (6 spec.), SMNS 106787 (8 spec.), 106800 (1 spec.).
Lymnaea dilatata Noulet, 1854: SMNS 23314*, SMNS 67606 (1 spec.), SMNS 67655 (1 spec.), SMNS 106806 (3 spec.), SMNS 106809*, SMNS 106810*, SMNS 106796*, SMNS 106803 (1 spec.), SMNS 106807*.
Opeas minutum (Klein, 1853): SMNS 67039 (1 spec.).
Oxyloma minima (Klein, 1853): SMNS 67065 (1 spec.), SMNS 106788 (5 spec.).
Palaeoglandina gracilis (Zieten, 1830): SMNS 106805 (3 spec.).
Palaeotachea silvana (Klein, 1853): SMNS 23314*, SMNS 66635 (2 spec.), SMNS 66652 (2 spec.), SMNS 66665 (1 spec.), SMNS 66842 (2 spec.), SMNS 106781 (1 spec.), SMNS 106782 (2 spec.), SMNS 106792 (7 spec.), SMNS 106802 (3 spec.), SMNS 106816 (1 spec.), SMNS 106829 (1 spec.), SMNS 106795*, SMNS 106803 (3 spec.).
Planorbarius mantelli (Dunker, 1848): SMNS 23314*, SMNS 67841 (10 spec.), SMNS 67856 (7 spec.), SMNS 106790 (16 spec.), SMNS 106791 (14 spec.), SMNS 106797 (7 spec.), SMNS 106798 (36 spec.), SMNS 106799 (8 spec.), SMNS 106801 (3 spec.), SMNS 106809*, SMNS 106810*, SMNS 106817 (1 spec.), SMNS 106826 (7 spec.), SMNS 106827 (1 spec.), SMNS 106828 (1 spec.), SMNS 106795*, SMNS 106796*, SMNS 106803 (1 spec.), SMNS 106807*, SMNS 106808*.
Pomatias cf. *conicus* (Klein, 1853): SMNS 106784 (4 spec.), SMNS 106817 (2 spec.), SMNS 106818 (1 spec.), SMNS 106807.
Pseudochloritis incrassata (Klein, 1853): SMNS 23314*, SMNS 66208 (1 spec.), SMNS 106804 (2 spec.), SMNS 106815 (4 spec.), SMNS 106827 (1 spec.), SMNS 106808 (2 spec.).
Radix socialis (Zieten, 1832): SMNS 106794 (1 spec.), SMNS 106803 (1 spec.).
Tinnyea cf. *lauraea* (Mathéron, 1843): SMNS 67854 (1 spec.), SMNS 106783 (1 spec.).

Ehingen-Dächingen

Archaeozonites costatus Sandberger, 1872: GPIT/GA/3974 (1 spec.).
Gyraulus applanatus: NHMUK IP OR62811 (>50 spec.), NHMUK IP OR70081 (~15 spec.), SMNS 106833 (2 spec.).
Leucochroopsis Kleinii (Klein, 1846): SMNS 106830 (1 spec.).
Lymnaea dilatata (Noulet, 1854): SMNS 106839 (1 spec.).
Palaeotachea renevieri (Maillard, 1891): SMNS 106840 (2 spec.).
Palaeotachea silvana (Klein, 1853): SMNS 106825 (18 spec.), SMNS 106831 (2 spec.), SMNS 106834 (3 spec.), SMNS 106837 (31 spec.).
Planorbarius mantelli (Dunker, 1848): SMNS 106830 (2 spec.), SMNS 106832 (7 spec.), SMNS 106833 (15 spec.), SMNS 106835 (16 spec.), SMNS 106841 (3 spec.).
Pomatias conicus (Klein, 1853): SMNS 106842 (1 spec.).
Pseudochloritis incrassata (Klein, 1853): SMNS 106824 (6 spec.), SMNS 106831 (2 spec.), SMNS 106838 (2 spec.).
Radix socialis (Zieten, 1832): SMNS 106823 (1 spec.).
Tinnyea cf. *lauraea* (Mathéron, 1843): SMNS 106836 (5 spec.).

Riedlingen-Daugendorf

Apula coarctata (Klein, 1853): SMNS 106812 (2 spec.).
Discus pleuradrus (Bourguignat, 1881): SMNS 107211 (1 spec.).
Gastrocopta cf. *acuminata* (Klein, 1846): SMNS 106811 (7 spec.)
Gyraulus applanatus (Thomä, 1845): SMNS 106813 (2 spec.), SMNS 107207 (14 spec.).
Leucochroopsis kleini (Klein, 1846): SMNS 106814 (1 spec.), SMNS 107210 (5 spec.).
*Lymnaea dilatata (*Noulet, 1854): SMNS 107212 (1 spec.).
Opeas minutum (Klein, 1853): SMNS 107206 (1 spec.), SMNS 107209 (1 spec.).
Palaeotachea silvana (Klein, 1853): SMNS 66647 (2 spec.), SMNS 106822 (3 spec.), PIMUZ 011663 (29 spec.).
Planorbarius mantelli (Dunker, 1848): SMNS 106793 (3 spec.), SMNS 106821 (10 spec.), PIMUZ 011610*.
Praeoestophorella phacodes (Thomä, 1845): SMNS 107208 (3 spec.).
Pseudochloritis incrassata (Klein, 1853): SMNS 106820 (1 spec.), PIMUZ 011663 (1 spec.).

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Ehingen (Donau)

Bithynia glabra (Zieten, 1832): SMNS 46760/2007 (7 spec.).
Leucochroopsis kleini (Klein, 1846): GPIT/GA/2698 (12 spec.).
Lymnaea dilatata (Noulet, 1854): GPIT/GA/1042*, SMNS 67691 (3 spec.), SMNS 67689 (1 spec.).
Klikia giengensis (Klein, 1846): SMNS 46757/2007 (30 spec.).
Palaeoglandina gracilis (Zieten, 1830): SMNS 67001 (2 spec.), SMNS 67002 (2 spec.).
Palaeotachea silvana (Klein, 1853): NHMUK IP G21490 (1 spec.), SMNS 66640 (4 spec.), SMNS 66645 (1 spec.), SMNS 66870 (3 spec.).
Planorbarius mantelli (Dunker, 1848): GPIT/GA/1042*, GPIT/GA/2695 (1 spec.), NHMUK IP G21507 (1 spec.), SMNS 67816 (6 spec.).
Pomatias consobrinus (Sandberger, 1872): SMNS 46758/2007 (50 spec.).
Pseudochloritis incrassata (Klein, 1853): SMNS 46693/2007 (8 spec.).
Triptychia sp.: SMNS 66970 (1 spec.).
Tinnyea lauraea (Mathéron, 1843): SMNS 106444 (2 spec.; syntypes of *Melania turrita* Klein, 1846).

Ehingen (Donau)-Mundingen

Aegopinella subnitens (Klein, 1853): NHMUK IP G1377 (1 spec.).
Apula coarctata (Klein, 1853): SMNS 66306 (1 spec.).
Discus pleuradrus (Bourguignat, 1881): NHMUK IP OR45263 (3 spec.), NHMUK IP OR47081 (3 spec.).
Ferrissia deperdita (Desmarest, 1814): GPIT/GA/3883 (1 spec.), NHMUK IP G1402 (2 spec.), NHMUK IP OR45249 (1 spec.), NHMUK IP OR45252 (3 spec.), NHMUK IP OR47060 (2 spec.), SMNS 67929 (1 spec.).
Gastrocopta acuminata (Klein, 1846): NHMUK IP G1425 (1 spec.), NHMUK IP OR47050 (1 spec.), NHMUK IP OR47051 (1 spec.).
Gyraulus applanatus (Thomä, 1845): GPIT/GA/4059 (1 spec.), NHMUK IP G1377 (4 spec.), NHMUK IP OR45249 (10 spec.), NHMUK IP OR45250 (5 spec.), NHMUK IP OR47060a (1 spec.), NHMUK IP OR47060b (>40 spec.), NHMUK IP OR47093 (1 spec.), SMNS 67782 (2 spec.).
Hypnophila loxostoma (Klein, 1853): NHMUK IP OR47054 (1 spec.).
Janulus supracostatus (Sandberger, 1873): SMNS 106858 (1 spec.).
Leucochroopsis Kleinii (Klein, 1846): NHMUK IP OR45250 (1 spec.).
Lymnaea dilatata (Noulet, 1854): GPIT/GA/3976 (1 spec.), NHMUK IP OR47060 (5 spec.).
Oxyloma minima (Klein, 1853): NHMUK IP OR47063 (2 spec.), SMNS 67066 (1 spec.), SMNS 47378/2007 (3 spec.).
Palaeotachea silvana (Klein, 1853): NHMUK IP G1358 (1 spec.), NHMUK IP G3237 (2 spec.), SMNS 66644 (4 spec.), SMNS 66648 (2 spec.), SMNS 66805 (1 spec.).
Planorbarius mantelli (Dunker, 1848): GPIT/GA no nr. (5 spec.), NHMUK IP G1373 (2 spec.), NHMUK IP G1377 (3 spec.), NHMUK IP G3237 (3 spec.), NHMUK IP OR45249 (3 spec.), NHMUK IP OR45249a (4 spec.), NHMUK IP OR45250a (2 spec.), NHMUK IP OR45250b (1 spec.), NHMUK IP OR47060 (3 spec.), NHMUK IP OR47084 (7 spec.), NHMUK IP OR47085 (2 spec.), SMNS 67835 (1 spec.; not found), 67842 (3 spec.; not found).
Pomatias consobrinus (Sandberger, 1872): GPIT/GA/4045 (2 spec. + 2 opercula).
Pseudochloritis incrassata (Klein, 1853): SMNS 66225 (1 spec.).
Radix socialis (Zieten, 1832): NHMUK IP G1386 (5 spec.).
Segmentina lartetii (Noulet, 1854): SMNS 67904 (2 spec.).

Emerberg near Zwiefalten

Apula coarctata (Klein, 1853): SMNS 106862 (5 spec.).
Klikia giengensis (Klein, 1846): SMNS 106863 (2 spec.).
Palaeotachea dentula (Quenstedt, 1867): NHMUK IP OR47070 (3 spec.).
Palaeotachea silvana (Klein, 1853): SMNS 106860 (3 spec.), SMNS 106861 (3 spec.), SMNS 106864 (5 spec.).

Emeringen

Apula coarctata (Klein, 1853): SMNS 107205 (16 spec.).
Gastrocopta cf. *acuminata* (Klein, 1846): SMNS 107203 (1 spec.).
Hypnophila loxostoma (Klein, 1853): SMNS 107204 (13 spec.).
Leucochroopsis kleinii (Klein, 1846): SMNS 107203 (1 spec.).

Zwiefalten-Gauingen

Palaeoglandina gracilis (Zieten, 1832): Coll. Kadolsky.
Palaeotachea silvana (Klein, 1853): GPIT/GA/2736 (3 spec.), SMNS 101721 (2 spec.).
Planorbarius mantelli (Dunker, 1848): Coll. Kadolsky.

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Hausen ob Allmendingen

Aegopinella subnitens (Klein, 1853): SMNS 65674 (1 spec.).
Bithynia glabra (Zieten, 1832): SMNS 68157 (4 spec.)
Granaria cf. *subfusiformis* (Sandberger, 1875): SMNS 44648/2007 (2 spec.).
Hypnophila loxostoma (Klein, 1853): SMNS 67253 (3 spec.), SMNS 106855 (9 spec.).
Klikia catanostoma (Sandberger, 1872): SMNS 66300 (1 spec.).
Leucochroopsis kleinii (Klein, 1846): SMNS 65951 (1 spec.), SMNS 65941 (2 spec.).
Lymnaea dilatata (Noulet, 1854): SMNS 44520/2007 (1 spec.).
Melanopsis kleinii (Kurr, 1856): SMNS 106856 (2 spec.).
Opeas minutum (Klein, 1853): SMNS 67041 (1 spec.).
Palaeotachea silvana (Klein, 1853): SMNS 66667 (2 spec.), SMNS 66654 (2 spec.), SMNS 66638 (1 spec.).
Pomatias conicus (Klein, 1853): SMNS 68033 (5 spec.), SMNS 106854 (13 spec.).
Praeoestophorella phacodes (Thomä, 1845): SMNS 106857 (2 spec.), SMNS 44919/2005 (2 spec.).
Protodrepanostoma involutum (Thomä, 1845): SMNS 66008 (1 spec.).
Pseudochloritis incrassata (Klein, 1853): SMNS 66210 (2 spec.).
Theodoxus crenulatus (Klein, 1853): GPIT/GA/4074 (1 spec.).

Zwiefalten-Mörsingen

Aegopinella elatior Höltke, 2015: SMNS 107228 (1 spec.).
Aegopinella? *procellaria* (Jooss, 1918): SMNS 106419 (2 spec.; syntypes).
Aegopinella subnitens (Klein, 1853): GPIT/GA/2659 (2 spec.), NHMUK IP G47076 (2 spec.), SMNS 65690 (6 spec.), SMNS 65679 (5 spec.), SMNS 2013/2008 (80 spec.), SMNS 2029/2008 (8 spec.), SMNS 1959/2008 (15 spec.), SMNS 1975/2008 (8 spec.), SMNS 827/2008 (8 spec.).
Apula coarctata (Klein, 1853): GPIT/GA/4069 (9 spec.), NHMUK IP OR45248 (1 spec.), SMNS 66296 (9 spec.), SMNS 66294 (2 spec.), SMNS 1961/2008 (5 spec.), SMNS 823/2008 (15 spec.).
Archaeozonites costatus Sandberger, 1872: GPIT/GA/2672 (1 spec.), GPIT/GA/3949 (3 spec.), SMNS 44916/2005 (1 spec.), SMNS 2010/2008 (5 spec.), SMNS 2016/2008 (1 spec.).
Azeca lubricella O. Boettger, 1870: SMNS 67234 (7 spec.).
Bithynia glabra (Zieten, 1832): NHMUK IP OR47052d (3 spec.), SMNS 68154 (3 spec.), SMNS 1970/2008 (1 spec.).
Cecilioides aciculella (Sandberger, 1872): SMNS 107225 (1 spec.).
Discus wenzi (Jooss, 1918): SMNS 106447 (syntype).
Discus euglyphoides (Sandberger, 1872): GPIT/GA/4062 (3 spec.), SMNS 65809 (1 spec.), SMNS 65806 (1 spec.).
Discus pleuradrus (Bourguignat, 1881): SMNS 65787 (4 spec.).
Ferrissia deperdita (Desmarest, 1814): GPIT/GA no nr.*, NHMUK IP OR45252 (3 spec.), SMNS 67925 (1 spec.).
Gastrocopta acuminata (Klein, 1846): GPIT/GA/3943 (1 spec.), SMNS 67429 (3 spec.), SMNS 67427 (3 spec.).
Gastrocopta quadriplicata (Braun, 1851): SMNS 67383 (2 spec.).
Granaria cf. *subfusiformis* (Sandberger, 1875): SMNS 67462 (2 spec.), SMNS 16635 (1 spec.).
Gyraulus applanatus (Thomä, 1845): GPIT/GA no nr.*, GPIT/GA/3986 (2 spec.), GPIT/GA/4056 (10 spec.), NHMUK IP G1418 (5 spec.), NHMUK IP OR47052a (5 spec.), NHMUK IP OR47052b (3 spec.), SMNS 67780 (9 spec.).
Helicodiscus subteres (Clessin, 1885): SMNS 15817 (2 spec.).
Hippeutis subfontanus (Clessin, 1887): GPIT/GA/4050 (1 spec.).
Hypnophila loxostoma (Klein, 1853): GPIT/GA/3970 (1 spec.), GPIT/GA/3987 (8 spec.), SMNS 67255 (3 spec.), SMNS 2002/2008 (18 spec.), SMNS 2005/2008 (20 spec.), SMNS 1920/2008 (20 spec.).
Janulus moersingensis Jooss, 1918: SMNS 106411 (holotype), SMNS 15031/2006 (1 spec.).
Janulus supracostatus (Sandberger, 1872): NHMUK IP G1419 (1 spec.), SMNS 45285/2005 (1 spec.).
Klikia catanostoma (Sandberger, 1872): SMNS 66304 (2 spec.), SMNS 66302 (2 spec.), SMNS 66299 (1 spec.).
Klikia giengensis (Klein, 1846): NHMUK IP G1339 (7 spec.), SMNS 21692 (1 spec.), SMNS 66283 (/ spec.), SMNS 66281 (1 spec.), SMNS 66276 (22 spec.), SMNS 2003/2008 (18 spec.), SMNS 2215/2008 (27 spec.), SMNS 1979/2008 (6 spec.).
Klikia osculina (Sandberger, 1874): GPIT/GA/2652 (3 spec.), GPIT/GA/3933 (6 spec.), SMNS 66314 (1 spec.).
Leucochroopsis kleini (Klein, 1846): GPIT/GA/2657 (3 spec.), GPIT/GA/2662 (3 spec.), GPIT/GA/2737 (1 spec.), GPIT/GA/4075 (>20 spec.), NHMUK IP OR45242 (3 spec.), SMNS 106372 (6 spec.; syntypes of *Helix carinulata* Klein, 1853), SMNS 65949 (6 spec.), SMNS 65944 (12 spec.), SMNS 825/2008 (25 spec.).
Lymnaea dilatata (Noulet, 1854): GPIT/GA no nr.*, GPIT/GA/2676 (1 spec.), SMNS 21681 (1 spec.), SMNS 1987/2008 (1 spec.).
Lymnaea turrita Klein, 1853: GPIT/GA/4053 (1 spec.), SMNS 106409 (1 spec.), SMNS 67653 (2 spec.), SMNS 20916/2006 (2 spec.).
Melanopsis kleinii (Kurr, 1856): GPIT/GA/4044 (1 spec.), GPIT/GA/3969 (4 spec.), SMNS 68411 (12 spec.).
Miodiscula disciformis (Wenz, 1919): SMNS 66244 (2 spec.).
Miodiscula miocaenica (Gottschick & Wenz, 1927): SMNS 15817-131 (syntype); SMNS 68551 (1 spec.).
Opeas minutum (Klein, 1853): SMNS 67042 (3 spec.), SMNS 2012/2008 (1 spec.), SMNS 2015/2008 (2 spec.).

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Oxyloma minima (Klein, 1853): GPIT/GA/4052 (3 spec.), NHMUK IP G1424 (1 spec.), NHMUK IP OR41063 (1 spec.), SMNS 67064 (3 spec.), SMNS 1953/2008 (4 spec.), SMNS 1973/2008 (3 spec.).
Palaeoglandina gracilis (Zieten, 1832): GPIT/GA/2669 (2 spec.), GPIT/GA/3939 (1 spec.), SMNS 67011 (3 spec.).
Palaeotachea silvana (Klein, 1853): GPIT/GA no nr.*, GPIT/GA/2642 (4 spec.), GPIT/GA/2651 (1 spec.), GPIT/GA/2662 (2 spec.), GPIT/GA/2666 (4 spec.), GPIT/GA/2673 (1 spec.), GPIT/GA/2674 (8 spec.), GPIT/GA/2676 (>20 spec.), GPIT/GA/2677 (1 spec.), GPIT/GA/2678 (1 spec.), GPIT/GA/2732 (1 spec.), GPIT/GA/2737 (5 spec.), NHMUK IP OR45226 (3 spec.), SMNS 105005 (1 spec.), SMNS 21690 (1 spec.), GPIT/GA/3959 (12 spec.), NHMUK IP G1345 (10 spec.), NHMUK IP G21491 (1 spec.), NHMUK IP no nr. (1 spec.), NHMUK IP no nr. (2 spec.), NHMUK IP OR42225 (3 spec.), NHMUK IP OR45234 (7 spec.), NHMUK IP OR45240 (1 spec.), SMNS 66858 (19 spec.), SMNS 66852 (5 spec.), SMNS 66843 (3 spec.), SMNS 66666 (2 spec.), SMNS 66653 (3 spec.), SMNS 66649 (1 spec.), SMNS 66646 (8 spec.), SMNS 66643 (3 spec.), SMNS 66636 (7 spec.), SMNS 4340/2008 (10 spec.), SMNS 4314/2008 (13 spec.), SMNS 4318/2008 (26 spec.), SMNS 107231 (26 spec.), SMNS 4327/2008 (28 spec.), SMNS 4329/2008 (10 spec.), SMNS 4439/2008 (2 spec.), SMNS 4441/2008 (27 spec.), SMNS 4445/2008 (20 spec.), SMNS 826/2008 (4 spec.), SMNS 867/2008 (24 spec.), SMNS 878/2008 (25 spec.), SMNS 880/2008 (26 spec.), SMNS 486/2008 (1 spec.), SMNS 549/2008 (2 spec.), SMNS 555/2008 (13 spec.), SMNS 556/2008 (17 spec.), SMNS 562/2008 (50 spec.), SMNS 567/2008 (1 spec.).
Palaeotachea turonensis (Deshayes, 1831): SMNS 66818 (3 spec.), SMNS 66808 (2 spec.), SMNS 66799 (2 spec.), SMNS 1986/2008 (2 spec.).
Planorbarius mantelli (Dunker, 1848): GPIT/GA/2644 (4 spec.), GPIT/GA/2650 (4 spec.), GPIT/GA/2655 (1 spec.), GPIT/GA/2659 (6 spec.), GPIT/GA/2661 (1 spec.), GPIT/GA/2665 (5 spec.), GPIT/GA/2670 (11 spec.), GPIT/GA/2674 (1 spec.), GPIT/GA/2732 (1 spec.), GPIT/GA/2737 (7 spec.), GPIT/GA/3941 (3 spec.), GPIT/GA/3973 (2 spec.), NHMUK IP G1372 (10 spec.), NHMUK IP OR47086 (1 spec.), SMNS 21693 (1 spec.), SMNS 2019/2008 (21 spec.), SMNS 4283/2008 (11 spec.), SMNS 4437/2008 (4 spec.), SMNS 4438/2008 (1 spec.), SMNS 47381/2007 (2 spec.).
Poiretia taurinensis (Sacco, 1886): SMNS 16635 (1 spec.).
Pomatias conicus (Klein, 1853): GPIT/GA/2643 (2 spec.), GPIT/GA/3925 (15 spec.), NHMUK IP G1420 (5 spec.), NHMUK IP OR47096 (6 spec.), SMNS 68040 (100 spec.), SMNS 68032 (23 spec.), 2004/2008 (28 spec.), SMNS 2018/2008 (9 spec.), SMNS 1966/2008 (3 spec.), SMNS 4332/2008 (50 spec.).
Pomatias consobrinus (Sandberger, 1872): GPIT/GA/2648 (6 spec.), GPIT/GA/2654 (2 spec.), GPIT/GA/2671 (1 spec.), GPIT/GA/2674 (1 spec.), GPIT/GA/3934 (~20 spec.), GPIT/GA/3946 (7 spec.), GPIT/GA/3937 (4 spec.), NHMUK IP G1469 (9 spec.), NHMUK IP OR45251b (11 spec.), NHMUK IP OR45251a (2 spec.), NHMUK IP OR47097 (1 spec.), SMNS 8457/2005 (9 spec.), SMNS 4343/2008 (26 spec.), SMNS 4448/2008 (1 spec.).
Protodrepanostoma involutum (Thomä, 1845): SMNS 1996/2008 (1 spec.), SMNS 15817 (8 spec.).
Pseudidyla moersingensis (O. Boettger, 1877): GPIT/GA/3948 (1 spec.), SMNS 22830 (1 spec.; holotype of *Clausilia (Pseudidyla) mörsingensis undatistria* O. Boettger, 1877), SMNS 66934 (1 spec.), SMNS 107224 (1 spec.).
Pseudochloritis incrassata (Klein, 1853): GPIT/GA/2644 (2 spec.), GPIT/GA/2667 (6 spec.), GPIT/GA/2673 (7 spec.), GPIT/GA/2674 (7 spec.), GPIT/GA/2676 (1 spec.), GPIT/GA/2737 (1 spec.), GPIT/GA/3942 (1 spec.), GPIT/GA/3945 (1 spec.), GPIT/GA/3961 (6 spec.), NHMUK IP G1360 (4 spec.), NHMUK IP OR45228 (2 spec.), NHMUK IP OR45244 (4 spec.), NHMUK IP OR47082 (1 spec.), SMNS 21698 (1 spec.), SMNS 8462/2005 (8 spec.), SMNS 66234 (1 spec.), SMNS 66226 (2 spec.), SMNS 66206 (8 spec.), SMNS 4341/2008 (9 spec.), SMNS 4443/2008 (16 spec.), SMNS 107230 (16 spec.), SMNS 225/2008 (3 spec.), SMNS 882/2008 (50 spec.), SMNS 551/2008 (3 spec.).
Pseudoleacina eburnea (Klein, 1853): GPIT/GA/2660 (1 spec.), NHMUK IP OR47053 (1 spec.), SMNS 67032 (4 spec.), SMNS 67031 (1 spec.), SMNS 106386a (lectotype), SMNS 106386b (3 spec.; paralectotypes), SMNS 107226 (4 spec.).
Pseudoleacina kleiniana (Pilsbry, 1909): SMNS 67037 (1 spec.).
Radix socialis (Zieten, 1832): GPIT/GA/2645 (4 spec.).
Segmentina lartetii (Noulet, 1854): SMNS 67909 (4 spec.).
Tinnyea lauraea (Mathéron, 1843): GPIT/GA/2675 (1 spec.), GPIT/GA/3966 (9 spec.), SMNS 68392 (2 spec.), SMNS 68387 (10 spec.).
Triptychia kleini Schnabel, 2006: GPIT/GA/2658 (1 spec.), NHMUK IP G1401 (6 spec.), NHMUK IP OR47101 (3 spec.), SMNS 68576 (1 spec.), SMNS 68575 (1 spec.), SMNS 68554 (1 spec.), SMNS 66961 (2 spec.), SMNS 66956 (2 spec.), SMNS 1994/2008 (2 spec.), SMNS 2017/2008 (7 spec.), SMNS 2231/2008 (7 spec.), SMNS 1977/2008 (1 spec.), SMNS 107222/2008 (3 spec.), SMNS 557/2008 (1 spec.), SMNS 560/2008 (8 spec.).

Hayingen-Oberwilzingen

Palaeotachea dentula (Quenstedt, 1867): SMNS 105004 (4 spec.).

Riedlingen

Archaeozonites costatus Sandberger, 1872: SMNS 47135/2007 (1 spec.).
Palaeotachea silvana (Klein, 1853): GPIT/GA/2704 (1 spec.), SMNS 106859 (1 spec.).

Stoffelberg near Ehingen (Donau)

Leucochroopsis kleinii (Klein, 1846): SMNS 106413 (holotype of *Helix mucronata* Klein, 1846).

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Zwiefalten

Aegopinella subnitens (Klein, 1853): SMNS 106435a (lectotype); SMNS 106435b (2 spec.; paralectotypes), SMNS 47416/2007 (3 spec.).
Bithynia sp.: GPIT/GA/3927 (3 opercula).
Discus euglyphoides (Sandberger, 1872): SMNS 65805 (1 spec.), SMNS 46818/2007 (6 spec.).
*Gastrocopta acuminata (*Klein, 1846): SMNS 106421 (3 spec.; syntypes of *Pupa quadridentata* Klein, 1853).
Granaria subfusiformis (Sandberger, 1875): SMNS 100112 (syntype).
Gyraulus applanatus (Thomä, 1845): SMNS 46812/2007 (11 spec.), SMNS 106865 (5 spec.).
Hypnophila loxostoma (Klein, 1853): SMNS 25276/2005 (13 spec.).
Klikia giengensis (Klein, 1846): GPIT/GA/4054 (1 spec.), SMNS 46822/2007 (7 spec.).
Leucochroopsis kleinii (Klein, 1846): GPIT/GA/3928 (2 spec.), SMNS 46793/2007 (1 spec.).
Lymnaea socialis (Zieten, 1832): SMNS 47375/2007 (2 spec.).
Lymnaea turrita Klein, 1853: GPIT/GA/3923 (10 spec.), GPIT/GA/3926 (4 spec.), SMNS 106443a+b (3 spec.), SMNS 46807/2007 (7 spec.), SMNS 46807/2007 (7 spec.).
Melanopsis kleinii (Kurr, 1856): SMNS 47382/2007 (17 spec.).
Opeas minutum (Klein, 1853): SMNS 25269/2005 (1 spec.), SMNS 47517/2007 (2 spec.).
Oxyloma minima (Klein, 1853): GPIT/GA/4057 (1 spec.), SMNS 106410 (2 spec.; syntypes), SMNS 107201 (2 spec.).
Palaeotachea dentula (Quenstedt, 1867): SMNS 105004 (4 spec.; syntypes of *Helix pachystoma* Klein, 1853 and *Cepaea lepida* Wenz, 1919), SMNS 46816/2007 (11 spec.).
Palaeotachea silvana (Klein, 1853): SMNS 10920 (1 spec.; possible syntype of *Helix leymeriana* Sandberger, 1872 and *Helix (Macularia) subvermiculata* Sandberger, 1875), SMNS 22738 (1 spec.; syntype), SMNS 194/2008 (11 spec.), SMNS 195/2008 (3 spec.), SMNS 45500/2005 (3 spec.), SMNS 46790/2007 (4 spec.), SMNS 50325/2007 (4 spec.), SMNS 50326/2007 (4 spec.).
Planorbarius mantelli (Dunker, 1848): GPIT/GA no nr. (1 spec.), SMNS 199/2008 (3 spec.), SMNS 25211/2005 (3 spec.; syntypes of *Planorbis platystoma* Klein, 1853), SMNS 50327/2007 (1 spec.).
Pomatias conicus (Klein, 1853): SMNS 47371/2007 (9 spec.), SMNS 8455/2005 (6 spec.), SMNS 47371/2007 (9 spec.).
Pomatias consobrinus (Sandberger, 1872): NHMUK IP OR45255 (5 spec.), NHMUK IP OR48211 (2 spec.).
*Protodrepanostoma involutum (*Thomä, 1845): SMNS 25264/2005 (1 spec.).
Pseudamnicola suevicus (Gottschick, 1928): SMNS 15817 (11 spec.; syntypes).
Pseudochloritis incrassata (Klein, 1853): GPIT/GA/3951 (1 spec.), NHMUK IP OR45230 (2 spec.), SMNS 22736b (1 spec.), SMNS 22736c (1 spec.), SMNS 22737-1 (1 spec.), SMNS 22737b (1 spec.), SMNS 50323/2007 (1 spec.), SMNS 47516/2007 (1 spec.).
Pseudoleacina eburnea (Klein, 1853): SMNS 107202 (3 spec.).
Radix socialis (Zieten, 1832): SMNS 106408 (syntype of *Limnaea turrita milleri* Jooss, 1913), SMNS 106409 (syntype of *Limnaea turrita milleri* Jooss, 1913).
Theodoxus crenulatus (Klein, 1853): SMNS 106379 (7 spec.; syntypes).
Tinnyea lauraea (Mathéron, 1843): SMNS 25250/2005 (5 spec.), SMNS 25282/2005 (5 spec.), SMNS 47375/2007 (2 spec.).
Triptychia kleini Schnabel, 2006: SMNS 106404a (lectotype of *Clausilia grandis* Klein, 1846 and *Triptychia (Triptychia) kleini kleini* Schnabel, 2006), SMNS 106404b (5 spec.; paralectotypes of *Clausilia grandis* Klein, 1846 and *Triptychia (Triptychia) kleini kleini* Schnabel, 2006).

Zwiefaltendorf

Apula coarctata (Klein, 1853): BSPG 1970 VII.
Bithynia glabra (Zieten, 1832): BSPG 1970 VII.
Carychium nouleti Bourguignat, 1857: BSPG 1964 XXVII.
Discus euglyphoides (Sandberger, 1872): BSPG 1964 XXVII.
Ferrissia deperdita (Desmarest, 1814): SMNS 67924 (1 spec.).
Gastrocopta acuminata (Klein, 1846): BSPG 1964 XXVII.
Gyraulus applanatus (Thomä, 1845): BSPG 1970 VII.
Helicodiscus subteres (Clessin, 1885): BSPG 1964 XXVII.
Helicopsis suevica Gottschick & Wenz, 1927: SMNS 22828 (syntype).
Hypnophila loxostoma (Klein, 1853): BSPG 1970 VII.
Klikia catanostoma (Sandberger, 1872): SMNS 66305 (2 spec.).
Klikia giengensis (Klein, 1846): BSPG 1970 VII.
Leucochroopsis kleinii (Klein, 1846): SMNS 47411/2007 (2 spec.), SMNS 47411/2007 (2 spec.).
Lymnaea dilatata (Noulet, 1854): SMNS 67688 (1 spec.), SMNS 196/2008 (10 spec.).
Opeas minutum (Klein, 1853): BSPG 1964 XXVIII.
Oxyloma minima (Klein, 1853): BSPG 1964 XXVII, BSPG 1970 VII.
Palaeotachea silvana (Klein, 1853): SMNS 66853 (2 spec.), SMNS 197/2008 (4 spec.), SMNS 200/2008 (9 spec.).
Palaeotachea turonensis (Deshayes, 1831): SMNS 46820/2007 (2 spec.).

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Planorbarius mantelli (Dunker, 1848): NHMUK IP no nr. (1 spec.), SMNS 47406/2007 (3 spec.), SMNS 46855/2007 (1 spec.), SMNS 46858/2007 (1 spec.), SMNS 201/2008 (12 spec.), SMNS 47406/2007 (3 spec.).

Pomatias conicus (Klein, 1853): BSPG 1964 XXVII, BSPG 1970 VII.

Pomatias consobrinus (Sandberger, 1872): SMNS 208/2008 (3 spec.).

Pseudidyla moersingensis (O. Boettger, 1877): GPIT/GA/3985 (1 spec.).

Pseudochloritis incrassata (Klein, 1853): SMNS 22736 (3 spec.; syntypes of *Pseudochloritis inflexa* C. Boettger, 1909), SMNS 22737 (2 spec.; possible syntypes).

Radix socialis (Zieten, 1832): BSPG 1964 XXVIII, BSPG 1970 VII.

Stagnicola armaniacensis (Noulet, 1857): SMNS 47418/2007 (3 spec.), SMNS 47418/2007 (3 spec.).

Further species listed by Schlickum (1976), not found in the present material (species names are here updated based on current taxonomy): *Acanthinula trochulus*; *Acicula callosiuscula*; *Aegopinella erecta*; *Aegopinella*? *procellaria*; *Aegopinella subnitens*; *Archaeozonites costatus*; *Argna oppoliensis*; *Azeca lubricella*; *Bythiospeum*? *steinheimensis*; *Cecilioides aciculella*; *Discus pleuradrus*; *Gastrocopta nouletiana*; *Granaria subfusiformis*; *Hippeutis subfontaneus subfontaneus*; *Janulus moersingensis*; *Janulus supracostatus*; *Klikia osculina*; *Lymnaea turrita*; *Melanopsis kleinii*; *Miodiscula disciformis*; *Negulopsis lineolata*; *Palaeoglandina gracilis*; *Praeoestophorella phacodes*; *Protodrepanostoma involutum*; *Pseudoamnicola suevicus*; *Pseudoleacina eburnea*; *Pseudoleacina kleiniana*; *Pupisoma distans*; *Segmentina lartetii*; *Spermodea candida*; *Stagnicola praebouilleti*; *Strobilops uniplicata*; *Testacella zellii*; *Theodoxus crenulatus*; *Tinnyea lauraea*; *Triptychia kleini*; *Truncatellina* sp.; *Vallonia subpulchella*; *Vertigo callosa*; *Vitrea procrystallina*.

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Paleobiogeography of Early/Middle Miocene terrestrial gastropods in Central Europe: An approach using similarity indices

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ABSTRACT

Terrestrial gastropods are a common faunal element in continental 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 incomplete. The land snail faunas of 30 different Early and Middle Miocene deposits of Central Europe (European Mammal Neogene zones MN 4 to MN 8) were compared using statistical methods (cluster and NMDS analyses, using the Ochiai, Simpson and Kulczynski indices). This includes 300 different taxa identified so far. Most of the analyzed 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 different clusters, the majority of which can be explained by their geographic situation and/or by their distribution in time (e.g., the consistently recovered Baden-Württemberg and Bavaria clusters and the Bakony Mountains cluster). The remaining clusters cannot be fully explained so far, but some possibilities are explored here. Our results reveal the power of a solid taxonomic framework as a basis for palaeobiogeographic studies. As such, more "basic" palaeontological studies are required to strengthen future analyses.

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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) broadly 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 and 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 thirty 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 eventually the authors' ongoing works). After an overall statistical analysis clustering these localities in groups, we offer more detailed explanations of the localities and the relationship between them.

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.

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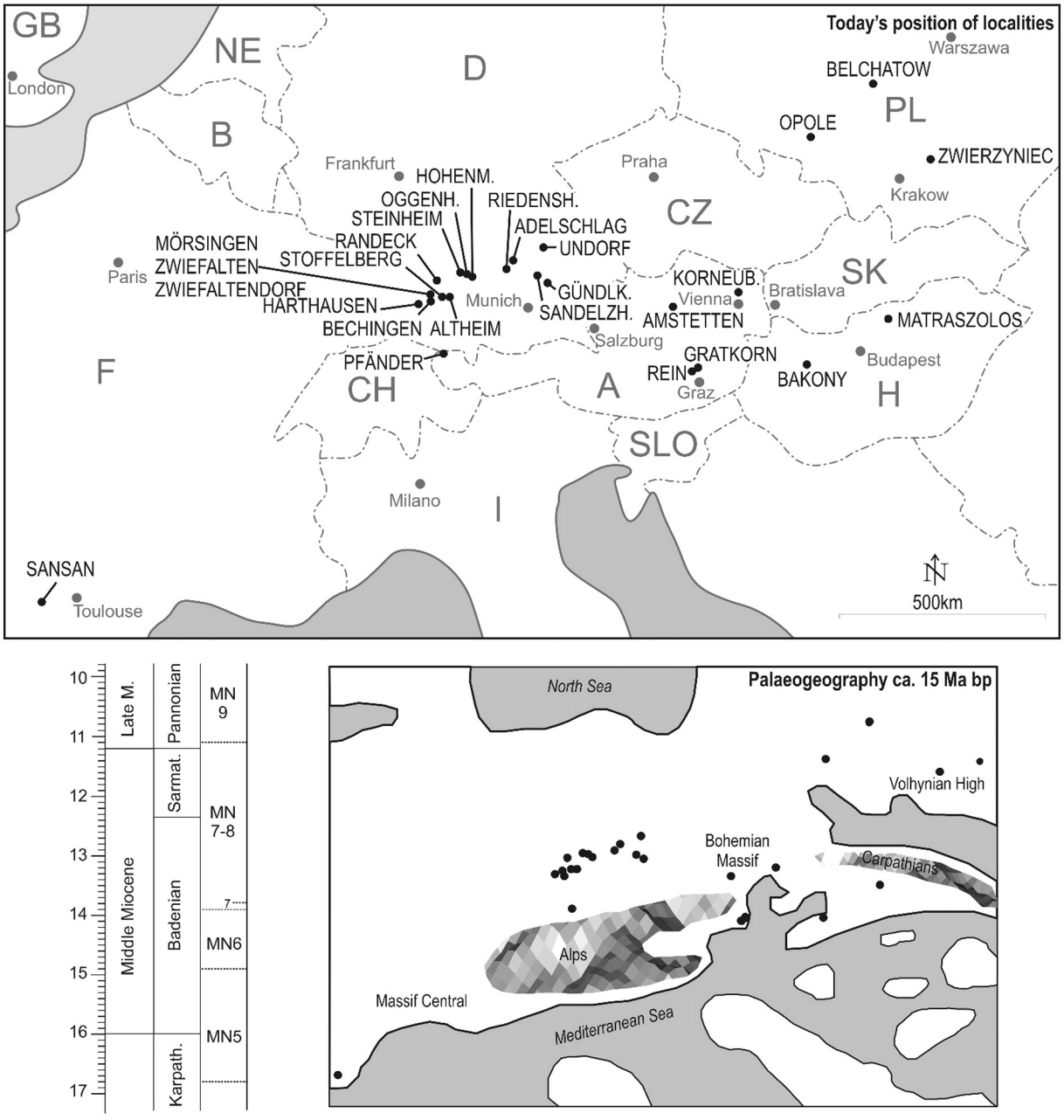

Fig. 1. Stratigraphy and localities. Mammal Neogene (MN) zones after Kälin and Kempf (2009). Map modified after Rasser and Harzhauser (2008).

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).

2.1. Taxonomy

The systematic classification used here follows the most recent works for each locality (as listed on Table 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, so distinct generic placements do not interfere.

2.2. Stratigraphy

Data on stratigraphy and age of the Middle Miocene localities used here were also acquired from the literature (Table 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 and Schmieder, 2013).

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Table 1
List of all localities used for the present analyses, with data on their stratigraphy and age, total number of land snail species, and references for the species list. The full species list of each locality can be found in the Appendix A.

Locality	Country	Stratigraphy/age	Nr. species	References
Adelschlag-Fasanierie	Germany	OSM/MN 5	8	Salvador et al. (2016)
Altheim (near Ehingen)	Germany	OSM (Silvana Beds)/MN 5	11	Wenz (1923), Gottschick (1928), Esu, 1999
Amstetten-Stubersheim	Germany	Helicidenmegel/MN 4–5	5	Jooss (1923), Schweigert (1996), Berger et al. (2005)
Bakony Mts C	Hungary	Lower Badenian	18	Kókay (2006)
Bakony Mts D	Hungary	Middle Badenian	13	Kókay (2006)
Bakony Mts E	Hungary	Upper Badenian	49	Kókay (2006)
Bakony Mts F	Hungary	Sarmatian	79	Kókay (2006)
Bechingen	Germany	OSM (Silvana Beds)/MN 5	15	Salvador and Rasser (2016a)
Bełchatów	Poland	MN 5–6	31	Stworzewicz (1995, 1999a, 1999b), Stworzewicz and Soltys (1996), Stworzewicz and Prisyazhnyuk (2006)
Gratkorn Basin	Austria	MN 7–8	13	Harzhauser et al. (2008)
Gündlkofen	Germany	OSM/MN 5–6	8	Gall (1980), Salvador (2014)
Harthausen auf der Scheer	Germany	Helicidenmegel/MN 4–5	5	Jooss (1923), Schweigert (1996), Berger et al. (2005)
Oggenhausen	Germany	OSM (Silvana Beds)/MN 5	9	Berz and Jooss (1927), Böttcher et al. (2009), Salvador and Rasser (2016b)
Hohenmemmingen	Germany	OSM (Silvana Beds)/MN 5	22	Gottschick and Wenz, 1916; Esu, 1999; SMNS collection material
Korneuburg Basin	Austria	MN 5	20	Daxner-Höck (2001), Binder (2002, 2003)
Lake Rein	Austria	MN 5	30	Harzhauser et al. (2014)
Mátraszőlős	Hungary	MN 7	15	Hír and Kókay (2004)
Mörsingen	Germany	OSM (Silvana Beds)/MN 5	37	Gottschick and Wenz (1916), Wenz (1923), Esu (1999), Höltke and Rasser (in preparation)
Opole	Poland	MN 7	48	Andreae (1902, 1904), Wenz (1923), Nordsieck (1981), Ginsburg (1999)
Pfänder	Austria	OSM (Silvana Beds)/MN 5	25	Jooss (1910), Wenz (1933, 1935), Esu (1999)
Randeck Maar	Germany	OSM (Silvana Beds)/MN 5	20	Salvador et al. (2015)
Riedensheim	Germany	OSM/MN 5	16	Salvador et al. (2016)
Sandelzhausen	Germany	OSM/MN 5	14	Salvador (2013a, 2013b, 2015), Salvador and Rasser (2014)
Sansan	France	MN 6	23	Wenz (1923), Fischer (2000)
Steinheim	Germany	MN 7	52	Gottschick and Wenz (1919), Gottschick (1919, 1920a, 1920b, 1920c, 1921), Wenz (1922, 1923), Finger (1998), Ginsburg (1999), Höltke and Rasser (submitted)
Stoffelberg (near Ehingen)	Germany	OSM (Silvana Beds)/MN 5	16	Wenz (1923), Esu (1999)
Undorf	Germany	OSM (Silvana Beds)/MN 5	33	Clessin (1910-1911), Fejfar (1999)
Zwiefalten	Germany	OSM (Silvana Beds)/MN 5	10	SMNS collection material
Zwiefaltendorf	Germany	OSM (Silvana Beds)/MN 5	47	Schlickum (1976)
Zwierzyniec	Poland	MN 7–8	31	Stworzewicz et al. (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 and Gwinner, 2011).

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, three distinct similarity indices, Kulczynski (1927); Simpson (1949) 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 indeces (not shown) all yielded very similar results. All analyses were conducted using 10,000 bootstrap replicates, in order to test for the robustness of each group (robustness estimates range from 1% to 100% and are shown at each node of the resulting dendograms). The analyses were carried out in PAST 2.17c (Hammer et al., 2001).

3. Results

In total, 30 localities were selected according to the criteria outlined above (Table 1; Fig. 1), containing 300 different species. The full list of species present in each locality is given in the Appendix A. The locality Bakony Mountains, in special, represents a long time span, so it was divided into 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.

The localities with the highest number of species are: Bakony Mountains F (79), Opole (52) and Steinheim am Albuch (52). Apart from Amstetten-Stubersheim and Harthausen auf der Scher, explained above, the locality with the smallest number of species is Adelschlag-Fasanerie (8).

Similar grouping patterns were recovered for the three indices in the cluster analyses (Figs. 2–4). The results of the NMDS-analyses are redundant and thus are not shown here. In order to obtain reasonable groupings, those localities with a similarity of ca. 0.35 were summarized into clusters (a slightly lower value, ca. 0.24, was chosen for some groupings of the Ochiai index in order to allow further discussion). This resulted in 11 clusters for the Ochiai index (Fig. 2), 11 for the Simpson index (Fig. 3) and 12 for the Kulczynski (Fig. 4) index. The main differences in clusters between indices are as follows.

By the Ochiai index (Fig. 2), the following localities are alone in their own clusters: Korneuburg Basin, Sansan, Opole, Gündlkofen and Gratkorn Basin. The larger clusters are: (1) the four levels of the Bakony Mountains; (2) the two Helicidenmergel deposits, namely Harthausen auf der Scher and Arnstetten-Stubersheim (with the highest similarity index, of ca. 0.94); (3) the Baden-Württemberg localities (including the Austrian localities Pfänder and Lake Rein); (4) the Bavarian localities (Adelschlag-Fasanerie, Riedensheim, Sandelzhausen and Undorf); (5) Bełchatów and Mátraszőlős; (6) Steinheim am Albuch and Zwierzyniec.

According to the Simpson index (Fig. 3), the following localities are alone in their own clusters: Korneuburg Basin, Sansan, Bełchatów, Zwierzyniec, Opole, Gündlkofen and Gratkorn Basin. The larger clusters are: (1) the four levels of the Bakony Mountains; (2) the two Helicidenmergel deposits (with similarity index of ca. 1.0); (3) the Baden-Württemberg localities (including the Austrian localities);

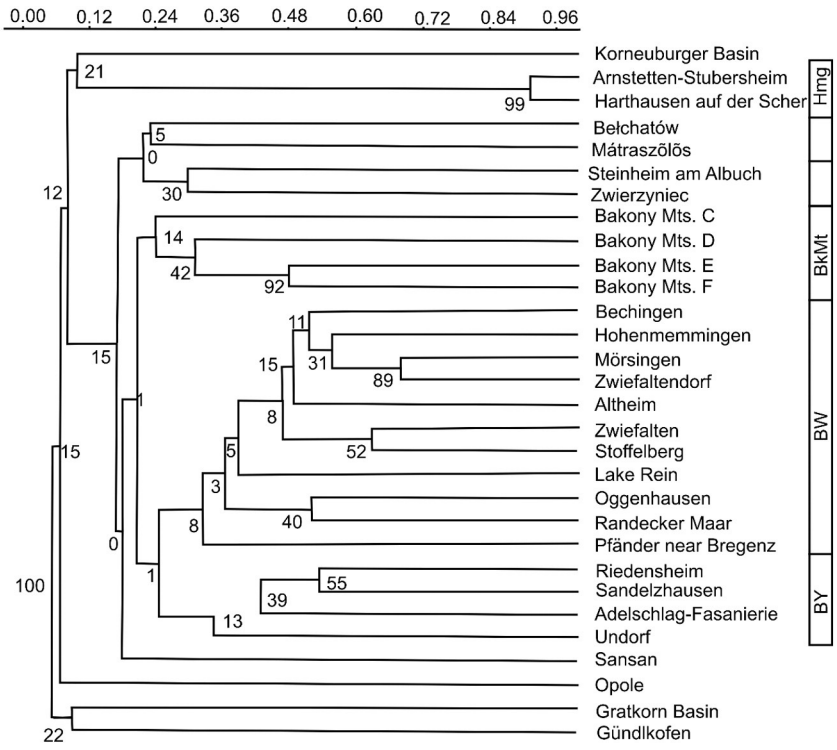

Fig. 2. Result of the cluster analysis using the Ochiai index, indicating the most relevant locality clusters. The top bar indicates overall similarity; numbers on the base of each cluster are robustness estimates resulting from bootstrapping. Abbreviations: **BkMt**, Bakony Mountains cluster; **BW**, Baden-Württemberg cluster (including Austrian localities); **BY**, Bavaria cluster; **Hmg**, Helicidenmergel cluster.

(4) the Bavarian ones (which include, albeit with a clear separation, the localities Mátraszőlős and Steinheim am Albuch). Two other pairs reach a similarity index of ca. 1.0: (1) Altheim near Ehingen and Mörsingen, and (2) Zwiefalten and Zwiefaltendorf.

By the Kulczynski index (Fig. 4), the following localities are alone in their own clusters: Korneuburg Basin, Sansan, Opole, Bełchatów, Gündlkofen, Gratkorn Basin, Mátraszőlős and the level C from the Bakony Mountains. The larger clusters are: (1) the remaining three

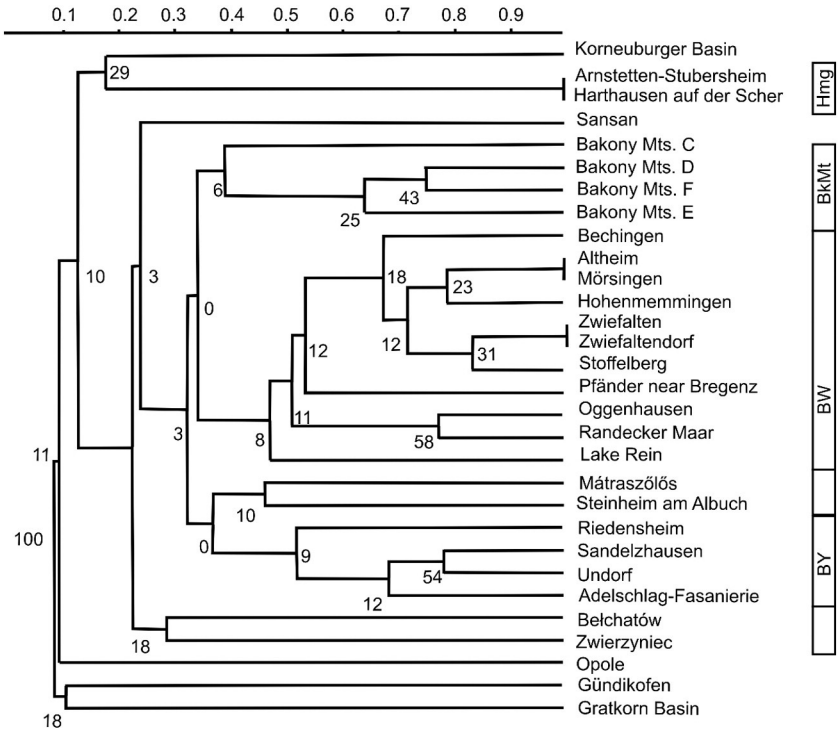

Fig. 3. Result of the cluster analysis using the Simpson index. Abbreviations follow Fig. 2.

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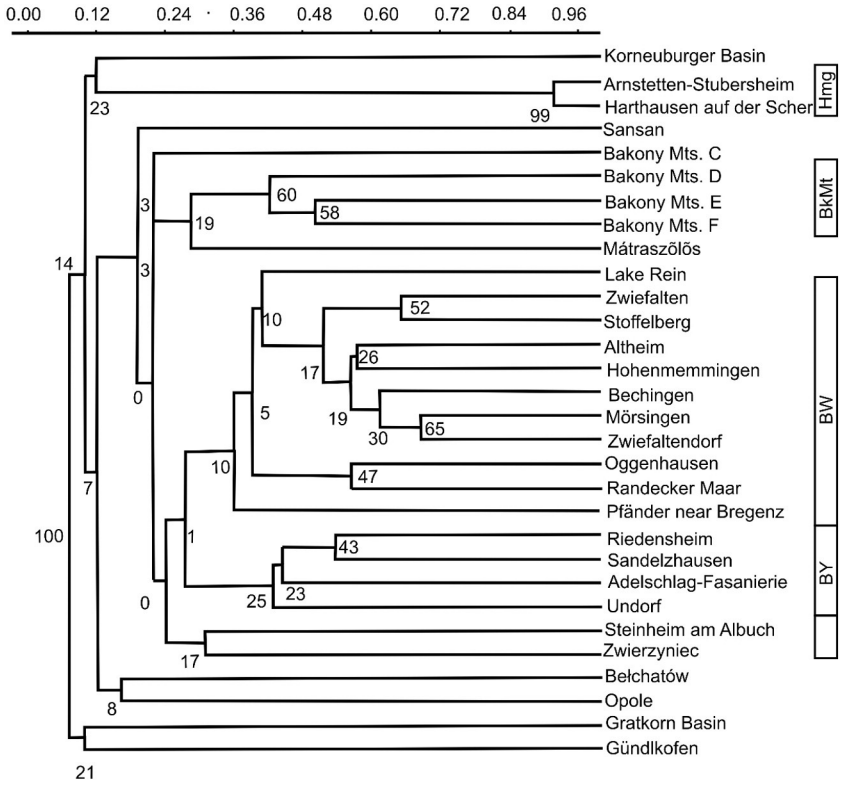

Fig. 4. Result of the cluster analysis using the Kulczynski index. Abbreviations follow Fig. 2.

levels of the Bakony Mountains; (2) the two Helicidenmergel deposits (with the highest similarity index, of ca. 0.94); (3) the Baden-Württemberg localities (including the Austrian localities); (4) the Bavarian localities; (5) Steinheim am Albuch and Zwierzyniec (albeit with a similarity index of only ca. 0.3).

4. Discussion

All the three cluster analyses reached largely the same groupings. Considering the stratigraphic and age relationship (Table 1) and the palaeogeographic situation (Figs. 1, 5) similarities, some of these groupings were reasonably expected, like: (1) the four levels of the Bakony Mountains, despite some differences according to the Kulczynski index; (2) Amstetten-Stubersheim and Harthausen auf der Scher forming a solid group with high similarity indices, since both outcrops are coeval and the only representatives of the Helicidenmergel among the studied localities; (3) the Baden-Württemberg localities (including the Austrian localities); (4) the Bavarian localities (except for Gündlkofen); (5) all the remaining localities being largely isolated. In order to better understand the potential factors behind these clusters, some of them (including the unexpected groupings) are discussed below in more detail.

4.1. Bakony Mountains

The separate stratigraphic levels of the Bakony Mountains form a single cluster on its own according to the Ochiai and the Simpson indeces. An explanation for this might be the palaeogeographic position, because Bakony was part of the Transdanubian Range, which was a separate geodynamic unit. The cluster is most similar to the OSM clusters from Baden-Württemberg and Bavaria, which agrees with the suggestion of Kókay (2006) of a paleobiogeographic relationship between these areas.

The Kulczynski index, however, gives Layer C of Bakony Mountains as a separated unity from the other layers. This could be due to its older age. These remaining layers (D to F) are instead grouped with Mátraszőlős, which is a Hungarian locality of roughly the same age, sharing nine species with them (*Carychium nouleti*, *Gastrocopta acuminata*, *G. nouletiana nouletiana*, *G. n. gracilidens*, *G. sandbergeri*, *G. obstructa ferdinandi*, *Palaeoglandina porrecta*, *Tropidomphalus gigas*, *Vertigo callosa*).

Kókay (2006) reports only one noticeable change in the composition of the land snail fauna 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. In any case, this difference may be the reason why Layer C is a separate unity by the Kulczynski index.

4.2. The Upper Freshwater Molasse (OSM)

The OSM localities form one all-embracing cluster according to the Ochiai and Kulczynski indices (Figs. 2, 4); the Simpson index also include the Bakony Mountains and a small cluster formed by Mátraszőlős and Steinheim am Albuch in this group. Regardless, this large group is divided into two well-defined clusters: (1) a group composed of all the OSM localities of Baden-Württemberg and curiously, including the coeval (MN 5) Austrian localities Lake Rein and Pfänder; and (2) a group composed of the Bavarian localities Riedensheim, Adelschlag-Fasanerie, Sandelzhausen and Undorf, whose close relationship was already alluded to by Salvador et al. (2016). The absence of the Bavarian OSM locality Gündlkofen from this latter cluster is remarkable; it forms an outlying cluster of its own, well separated from the rest. This will be discussed further below.

The presence of the Austrian localities in the Baden-Württemberg OSM cluster is curious, since they are quite geographically removed. While the outcrops of Pfänder are considered to belong to the Silvana Beds, the deposits from Lake Rein do not belong to OSM. Nevertheless, from the 33 land snail species reported from Lake Rein, 18 also occur

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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.

4.3. Steinheim am Albuch and the OSM localities

Despite the geographical closeness, Steinheim Basin is separated from most of the German OSM localities. To get a clearer picture of why this might be, we compare the land snail fauna from Steinheim with that of Mörsingen, which is here used as a representative of the Baden-Württemberg 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 and Rasser, submitted). 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* fragments 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 *Palaeotachea sylvestrina* (Höltke & Rasser, 2016). 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) The 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.

4.4. Steinheim am Albuch, Zwierzyniec and Mátraszőlős

According to the Ochiai and Kulczynski indices, Steinheim am Albuch is clustered together with Zwierzyniec. These two coeval (MN 7) localities are share 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).

By the Simpson index, however, Steinheim am Albuch is grouped together with Mátraszőlős, which is also coeval. These two localities share seven species: *Carychium nouleti*, *Cecilioides aciculella*, *Gastrocopta acuminata*, *Gastrocopta nouletiana*, *Gastrocopta sandbergeri*, *Vertigo angulifera angulifera*, *Vertigo callosa*. The most curious species here is *Ceciolides*, whose Recent congeners live buried in the soil, especially between leaf litter and roots, and also inside rock crevices (Welter-Schultes, 2012; Wiese, 2014).

4.5. Sansan

Sansan is clearly separated in all three indices, forming its own cluster that appears vaguely related to the broader OSM + Bakony Mountains supercluster. Despite sharing some species with the localities in the supercluster, these are mainly freshwater (not studied here, since the drives behind freshwater snails biogeography are distinct from the terrestrial ones). As such, the reason for this isolated palaeogeographic position in our analyses could be the high number of endemic species in Sansan (12 in total): *Cepaea leymerieana*, ?*Helicigona philoscia*, *Leucochroopsis asthena*, *Milax lartetti*, *Pupilla blainvilleana*, *Sansania lartetti*, *Tacheocampylaea ludovici*, *Testacella lartetti*, *Triptychia lartetti*, ?*Tropidomphalus dicroceri*, *Vertigo sandbergeri* and *Zonitoides apneus*. According to Fischer (2000), this species assemblage would be preferentially found in humid habitats, either in forests or shrublands. Species that would prefer drier open areas are absent.

4.6. Korneuburger Basin

The Korneuburger Basin lies apart from the others by all three indices. The reason for this may be the presence of 11 endemic species: *Auriculastra biplicata*, *Helicigona planata*, *Holcotachea beaumonti*, *Klikia orbiculata*, *Leucochroopsis phaseolina papillata*, *Melampus pilula*, *Melampus turonensis*, *Ovatella pisolina*, *Pseudidyla polyptyx*, *Triptychia obliqueplicata austriaca* and *Triptychia suturalis gracilis*. Binder (2002) defined five different faunas of continental mollusks (two freshwater and three terrestrial) for the Korneuburger Basin according to their ecological preferences: (1) the *turonensis*-fauna (after *Megalotachea turonensis*) from open and sunny habitats; (2) the *extinctus*-fauna (after *Tropidomphalus extinctus*) from bushy sparse forests or plant-rich river banks; and (3) the *orbiculatua*-fauna (after *Klikia orbiculata*) from full forests.

4.7. Opole

Opole is separated from all other localities in all three cluster analyses. The deposits of Opole are remarkable because of its comparable high amount of endemic Clausiliidae: *Cochlodina oppoliensis*, *Pseudidyla boettgeri*, *Regiclausilia patula*, *Serrulastra falkneri Serrulastra laevissima Serrulella andreaei*, *Trolliella silesiaca*. This high endemicity may well be the reason for this isolation. According to Nordsieck (1981), fossil clausiliids were forest inhabitants, which could indicate large densely forested areas in Opole during the Miocene.

When these clausiliids are excluded from the analysis (not shown here), Opole consistently group together with Bełchatów. The latter has older outcrops (Table 1), but is also located in Poland. Their similarities, when taken together with their difference from all other Central

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European outcrops, might be the reason why they form a distinct cluster. When including the clausiliids, Opole is grouped with Bełchatów only by the Kulczynski index, but with a low similarity (ca. 0.15).

4.8. Gratkorn Basin

The Gratkorn Basin in Austria forms its own cluster according to all three indices, although this locality has only three endemic species (*Platyla callosiuscula*, *Pleurodonte michalkovaci*, *Pseudidyla martingrossi*). Nevertheless, it is much younger than the other Austrian localities, which could help to explain its isolation in the analyses. According to Harzhauser et al. (2008), the palaeoenvironment of Gratkorn Basin consisted of woodlands with moist soil (offering habitats for the more hygrophilic snail species) and nearby limestone-rich and sun-exposed open areas (habitats for the more xerophilic taxa).

4.9. Bełchatów, Mátraszőlős and Zwierzyniec

By the Simpson index, the Polish localities Bełchatów and Zwierzyniec are grouped together (although with a similarity of only ca. 0.28) despite being of different ages. Both localities share eight species: *Archaeozonites costatus*, *Gastrocopta acuminata*, *Gastrocopta nouletiana*, *Negulopsis suturalis*, *Pomatias rivulare*, *Vallonia subcyclophorella*, *Vertigo angulifera angulifera* and *Vertigo callosa*.

The Ochiai index, however, grouped Bełchatów with Mátraszőlős, although with a similarity index of only ca. 0.24. This is surprising, since these localities not only are of different ages but also remarkably geographically separated. These deposits share only four species: *Gastrocopta nouletiana*, *Gastrocopta sandbergeri*, *Vertigo angulifera angulifera* and *Vertigo callosa*.

5. Conclusion

Besides the localities studied here, there are several more Miocene deposits containing land snails in Central Europe. However, only for our 30 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 three different indices, resulted in comparable similarities between the faunas of the studied localities. Given a similarity index ≥0.35, meaningful clusters were identified. Among them are several standalone localities, but several larger clusters consistently appeared in the results of all three indices. Most of the similarities can be explained by stratigraphic level (and thus age) and/or palaeogeographic position, but insights about what actually caused the changes in time remain elusive. 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 more 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 palaeoenvironmental controls that influenced the distribution of land snail taxa. More definitive decisions, however, can only be made when more palaeoecological information about each locality is known. Palaeogeographic barriers are further factors that can explain the distribution of land snails and one such example would be the isolated position of the Bakony Mountains. Again, such interpretations require further palaeogegraphic 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, palaeoecology and palaeogeography, however, several interpretations necessarily remain tentative.

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We are very grateful to Thomas A. Neubauer (NHMW, Vienna) for the help with the statistical analyses. This work was partly supported by a doctorate grant from CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brazil) to R.B.S. (process #245575/2012-0).

Appendix A

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*
  - *Platyla callosiuscula*
  - *Pleurodonte michalkovaci*
  - *Pseudidyla martingrossi*
  - *Punctum propygmaeum parvulum*
  - *Pupilla iratiana*
  - *Testacella schuetti*
  - *Truncatellina lentilii*
  - *Vallonia lepida*
  - *Vertigo angulifera angulifera*
- Korneuburg Basin
  - *Archaeozonites costatus*
  - *Auriculastra biplicata*
  - *Gastrocopta nouletiana*
  - *Helicigona planata*
  - *Holcotachea beaumonti*
  - *Klikia orbiculata*
  - *Leucochroopsis phaseolina papillata*
  - *Melampus pilula*
  - *Melampus turonense striata*
  - *Negulopsis suturalis*
  - *Ovatella pisolina*
  - *Palaeoglandina taurinensis*
  - *Palaeotachea turonensis*
  - *Pomatias turonicum*
  - *Pseudidyla polyptyx*
  - *Pseudochloritis incrassata*
  - *Serrulastra ptycholarinx*
  - *Triptychia obliqueplicata austriaca*
  - *Triptychia suturalis gracilis*
- Lake Rein
  - *Aegopinella subnitens*
  - *Apula coarctata*
  - *Archaeozonites costatus*
  - *Carychium minimum*
  - *Carychium nouleti*
  - *Cecilioides aciculella*
  - *Cochlicopa subrimata*
  - *Discus pleuradrus*
  - *Discus schneideri*
  - *Euconulus styriacus*
  - *Gastrocopta acuminata*
  - *Gastrocopta sandbergeri*
  - *Klikia giengensis*
  - *Leucochroopsis kleinii*
  - *Opeas minutum*
  - *Oxychilus procellarius*
  - *Oxyloma minima*
  - *Palaeoglandina porrecta*
  - *Palaeotachea reinensis*
  - *Palaeotachea turonensis*
  - *Pomatias consobrina*
  - *Pseudidyla standfesti*

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Appendix A (*continued*)

- *Pseudochloritis incrassata*
- *Strobilops planus*
- *Triptychia peneckei*
- *Triptychia reinensis*
- *Truncatellina pantherae*
- *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*
- *Palaeotachea leymerieana*
- *Discus pleuradrus*
- *Gastrocopta acuminata*
- *Gastrocopta nouletiana*
- *?Helicigona philoscia*
- *Klikia giengensis*
- *Leucochroopsis asthena*
- *Leucochroopsis kleini*
- *Milax larteti*
- *Palaeotachea turonensis*
- *Praeoestophorella phacodes barreri*
- *Pupilla blainvilleana*
- *Pupilla iratiana*
- *Sansania lartetti*
- *Tacheocampylaea ludovici*
- *Testacella larteti*
- *Triptychia larteti*
- *?Tropidomphalus dicroceri*
- *Vallonia lepida*
- *Vertigo diversidens*
- *Vertigo sandbergeri*
- *Zonitoides apneus*

Germany, Baden-Württemberg

Altheim near Ehingen
- *Azeca lubricella*
- *Cochlicopa subrimata*
- *Discus euglyphoides*
- *Helicodonta involuta*
- *Klikia osculina*
- *Leucochroopsis kleinii*
- *Palaeoglandina gracilis*
- *Palaeotachea silvana*
- *Pomatias conicus*
- *Pseudidyla moersingensis*
- *Pseudochloritis incrassata*

Amstetten-Stubersheim
- *Archaeozonites praecostatus*
- *Hemicycla asperula*
- *Palaeoglandina gracilis insignis*
- *Palaeotachea renevieri*
- *Pseudochloritis incrassata*

Appendix A (*continued*)

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
- *Acanthinula trochulus*
- *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
- *Acanthinula trochulus*
- *Aegopinella elatior*
- *Aegopinella subnitens*
- *Apula coarctata*
- *Archaeozonites costatus*
- *Archaeozonites subcostatus*
- *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*

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Appendix A (*continued*)

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
Randecker 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 erecta
Aegopinella subnitens
Amalia larteti
Apula coarctata
Archaeozonites costatus
Archaeozonites subcostatus
Azeca tridentiformis
Carychium nouleti
Carychium suevicum
Cecilioides aciculella
Cochlicopa subrimata
Cochlostoma excellens
Cochlostoma fraasi
Discus pleuradrus
Gastrocopta acuminata
Gastrocopta nouletiana
Gastrocopta sandbergeri
Granaria crassiventer
Granaria grossecostata
Granaria schuebleri
Helicodonta involuta
Hyalinia circumscisa
Isthmia lentilii
Janulus gottschicki
Lauria gottschicki
Leucochila suevica
Leucochroopsis kleinii
Limax crassissimus
Negulopsis gracilis
Oxychilus procellarius
Oxyloma minima
Palaeotachea sylvestrina
Pseudidyla moersingensis
Pseudoleacina eburnea
Punctum propygmaeum parvulum
Pupilla iratiana
Pupilla perlabiata
Pupilla steinheimensis
Pupilla submuscorum
Strobilops joosi
Triptychia steinheimensis

Appendix A (*continued*)

Vallonia lepida
Vallonia major
Vallonia steinheimensis
Vallonia subcyclophorella
Vertigo angulifera angulifera
Vertigo callosa
Vertigo milleri
Vertigo protracta suevica
Vitrea procrystallina
Vitrina suevica
Zonites verticiloides
Stoffelberg bei Ehingen
Aegopinella subnitens
Apula coarctata
Cochlicopa subrimata
Discus pleuradrus
Gastrocopta acuminata
Gastrocopta nouletiana
Granaria subfusiformis
Helicodonta involuta
Scabiosa
Klikia giengensis
Leucochroopsis kleinii
Palaeotachea silvana
Palaeotachea turonensis
Pomatias bisculatum
Praeoestophorella phacodes barreri
Pseudoleacina eburnea
Pseudochloritis incrassata
Zwiefalten
Apula coarctata
Cochlicopa subrimata
Gastrocopta acuminata
Helicodonta involuta
Klikia giengensis
Leucochroopsis kleini
Palaeotachea silvana
Pseudochloritis incrassata
Pseudoleacina eburnea
Triptychia kleini
Zwiefaltendorf
Acanthinula trochulus
Acicula callosiuscula
Aegopinella erecta
Aegopinella subnitens
Agardhia oppoliensis
Apula coarctata
Archaeozonites costatus
Azeca lubricella
Canariella disciformis
Carychium nouleti gibbum
Cecilioides aciculella
Cochlicopa subrimata
Discus euglyphoides
Discus pleuradrus
Gastrocopta acuminate
Gastrocopta nouletiana
Granaria subfusiformis
Helicodiscus subteres
Helicodonta involuta
Janulus moersingensis
Janulus supracostatus
Klikia catanostoma
Klikia giengensis
Klikia osculina
Leucochroopsis kleini
Negulus suturalis
Opeas minutum
Oxychilus procellarius
Oxyloma minima
Palaeoglandina porrecta
Palaeotachea silvana
Pomatias conica
Pomatias consobrina
Praeoestophorella phacodes barreri
Pseudidyla moersingensis
Pseudochloritis incrasssata

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Appendix A (*continued*)

- *Pseudoleacina eburnea*
- *Pseudoleacina kleiniana*
- *Pupisoma distans*
- *Spermodea candida*
- *Strobilops uniplicata plana*
- *Testacella zellii*
- *Triptychia kleini*
- *Vallonia subpulchella*
- *Vertigo callosa*
- *Vitrea procrystallina*
- *Zonitoides suevicus*

Germany, Bavaria

Adelschlag-Fasanerie

- *Carychium galli*
- *Carychium nouleti*
- *Discus pleuradrus*
- *Gastrocopta nouletiana*
- *Oxyloma minima*
- *Palaeotachea renevieri*
- *Palaeotachea silvana*
- *Vertigo callosa*

Gündlkofen

- *Lucilla subteres*
- *Pomatias consobrina*
- *Pseudidyla moersingensis*
- *Serrulastra ptycholarinx*
- *Serrulastra ptycholarinx galli*
- *Testacella schuetti*
- *Triptychia solida*
- *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*
- *Truncatellina pantherae*
- *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

- *Acanthinula trochulus*
- *Acicula isselii*
- *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*

Appendix A (*continued*)

- *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*
- *Melampus turonense striata*
- *Oxyloma minima*
- *Palaeotachea silvana*
- *Pedipes myotis pisolina*
- *Pseudochloritis incrassataq*
- *Stolidoma dolioliformis*
- *Stolidoma gracilis*
- *Stolidoma mayeri*
- *Stolidoma tuornoueri*
- *Strobilops subconoidea*

Bakony Mountains, Layer D

- *Apula coarctata*
- *Archaeozonites costatus*
- *Canariella bakonyensis*
- *Canariella disciformis*
- *Carychium nouleti*
- *Emneopupa subcylindrella*
- *Palaeoglandina porrecta*
- *Perforatella punctigera*
- *Platyla alta*
- *Pomatias conicus*
- *Praeoestophorella phacodes barreri*
- *Vitrea procrystallina*

Bakony Mountains, Layer E

- *Acanthinula trochulus*
- *Apula coarctata*
- *Archaeozonites costatus*
- *Argna suemeghyi*
- *Auriculastra badaniensis*
- *Canariella bakonyensis*
- *Carychium nouleti*
- *Carychium sandbergeri*
- *Discus pleuradrus*
- *Galactochilus silesiacus*
- *Gastrocopta acuminata*
- *Gastrocopta nouletiana*
- *Gastrocopta nouletiana gracilidens*
- *Gastrocopta nouletiana tapeina*
- *Gastrocopta sandbergeri*
- *Helicigona wenzi*
- *Helicodiscus subteres*
- *Janulus moersingensis*
- *Klikia giengensis*
- *Limax crassus*
- *Negulopsis gracilis*
- *Nesovitrea mendica*
- *Nesovitrea subhammonis*
- *Opeas minutum*
- *Palaeoglandina porrecta*
- *Palaeotachea silvana*

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Appendix A (*continued*)

Perforatella punctigera
Platyla falkneri
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 callosa cardiostoma
Vertigo callosa convergens
Vertigo diversidens
Vertigo kochi
Vertigo ovatula miliiformis
Vertigo ovatula trolli
Vertigo protracta suevica
Vitrea procrystallina
Zonitoides suevicus

Bakony Mountains, Layer F
Acanthinula trochulus
Agardhia praeambula
Agardhia pseudoennea
Archaeozonites costatus
Argna oppoliensis
Argna reperta
Argna sublamellata
Argna suemeghyi
Azeca lubricella frechi
Canariella bakonyensis
Carychium eumicrum
Carychium nouleti
Carychium pachychilus
Carychium sandbergeri
Cochlicopa subrimata
Cochlodina varpalotensis
Cochlostoma septemspirale
Daudebardia praecursor
Discus pleuradrus
Emneopupa subcylindrella
Fortuna tertia
Fortuna varpalotensis
Galactochilus leobersdorfensis
Galactochilus sarmaticum
Gastrocopta acuminata
Gastrocopta infrapontica
Gastrocopta nouletiana
Gastrocopta obstructa ferdinandi
Gastrocopta sandbergeri
Helicigona wenzi
Janulus supracostatus
Klikia giengensis
Klikia goniostoma
Klikia kaeufeli
Leiostyla gottschicki
Mactrogastra voesendorfensis
Mastus pupa sarmatica
Milax loerentheyi
Negulopsis gracilis
Nesovitrea mendica
Nordsieckia pontica
Oxychilus procellarius
Oxyloma minima
Palaeoglandina porrecta
Palaeotachea etelkae
Palaina martensi
Perforatella punctigera
Planogyra nana
Platyla polita
Poiretia taurinensis
Pomatias conicus
Pomatias consobrina
Praeoestophorella phacodes barreri
Pseudidyla boettgeri

Appendix A (*continued*)

Pseudidyla tricarinata
Pseudochloritis incrassata
Pseudoleacina rakosdensis
Pupilla iratiana
Retinella applanata
Semilimax intermedius
Spermodea candida
Strobilops costata costata
Strobilops pappi
Strobilops sandbergeri
Strobilops subconoidea
Strobilops tiarula
Triptychia leobersdorfensis sarmatica
Triptychia suturalis
Tropidomphalus gigas
Vallonia lepida
Vertigo bakonyensis
Vertigo callosa
Vertigo oecsensis
Vertigo ovatula trolli
Vertigo protracta
Vertigo pusilia sarmatica
Vitrea procrystallina
Zonitoides schaireri
Zonitoides suevicus

Mátraszőlős
Aegopinella orbicularis
Carychium nouleti
Cecilioides aciculella
Gastrocopta acuminata
Gastrocopta nouletiana
Gastrocopta nouletiana gracilidens
Gastrocopta obstructa ferdinandi
Gastrocopta sandbergeri
Limax crassus
Nesovitrea boettgeriana
Palaeoglandina porrecta
Punctum pumilio
Tropidomphalus gigas
Vertigo angulifera angulifera
Vertigo callosa

Poland
Belchatów
Acanthinula trochulus
Acicula crassistoma
Acicula schlickumi
Archaeozonites costatus
Carychiopsis prisyazhnyuki
Carychium antiquum
Carychium eumicrum
Carychium pachychilus
Carychium rhenanum
Carychium surai
Caspicyclotus belchatoviensis
Gastrocopta acuminata
Gastrocopta edlaueri
Gastrocopta nouletiana
Gastrocopta sandbergeri
Gastrocopta turgida
Negulopsis suturalis
Nesopupa minor
Planogyra nana
Pomatias rivulare
Renea pretiosa
Strobilops boettgeri
Strobilops costata costata
Strobilops fischeri
Strobilops tiarula
Strobilops uniplicata
Vallonia subcyclophorella
Vertigo angulifera angulifera
Vertigo callosa
Vertigo diversidens
Vertigo protracta

Opole
Acanthinula nana
Acanthinula tuchoricensis

(*continued on next page*)

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Appendix A (*continued*)

Acicula callosiuscula
Acicula limbata
Agardhia oppoliensis
Archaeozonites conicus
Azeca lubricella frechi
Bolania leptopomoides
Carychium crossei
Carychium minimum
Cochlodina oppoliensis
Daudebardia praecursor
Galactochilus brauni ehingense
Galactochilus silesiacus
Gastrocopta obstructa ferdinandi
Gastrocopta turgida
Janulus gyrorbis
Klikia coarctata
Limacus crassitesta
Limax excavatus
Mllax oppollensis
Monacha neudorfensis
Negulus raricosta
Negulus suturalis
Oxychilus (Gyralina) roemeri
Oxyloma minima
Palaina martensi
Pleurodiscus mamillatus
Pomatias schrammeni
Pseudidyla boettgeri
Pseudoleacina fossilis
Pseudotruncatella microceras
Punctum propygmaeum
Regiclausilia patula
Renea pretiosa
Serrulastra falkneri
Serrulastra laevissima
Serrulella andreaei
Serrulella multiplicata
Strobilops boettgeri
Strobilops costata costata
Triptychia margaretae
Trolliella silesiaca
Vertigo callosa
Vertigo kochi
Vitrea procrystallina
Vitrina intermedia
Zonitoides mendicus

Zwierzyniec
Archaeozonites costatus
Carychium schlickumi schlickumi
Carychium starobogatovi
Discus pleuradrus
Gastrocopta acuminata
Gastrocopta didymodus
Gastrocopta fissidens
Gastrocopta nouletiana
Gastrocopta serotina
Granaria schuebleri
Hawaiia antiqua
Helicodiscus roemeri
Klikia giengensis
Microstele buryaki
Microstele caucasica
Microstele ikvae
Negulopsis suturalis
Palaeotachea sylvestrina
Phenacolimax suevica
Pomatias rivulare
Pseudochloritis incrassata
Pupilla iratiana
Pupilla steinheimensis
Serrulastra trolli
Strobilops joossi
Triloba magurkai
Vallonia subcyclophorella
Vertigo angulifera angulifera
Vertigo callosa
Vertigo protracta
Vitrea procrystallina

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

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

LETHAIA

Rasser, M. W., Höltke, O., Salvador, R. B. 2019:Gastropod palaeohabitats of Miocene Lake Randeck Maar and its hinterland defined by an actualistic genus-level approach. *Lethaia*, https://doi.org/10.1111/let.12353.

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

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

The snail fauna of Randeck Maar comprises 32 species of continental gastropods, almost exclusively pulmonate snails, which occur in various beds (Salvador *et al.* 2015). This paper uses the gastropods as palaeoecological proxies in an actualistic genus-level approach, which is based in habitat preferences of extant congeners of the fossils. This approach is widely applied in the palaeomalacological literature (Ložek 1964; Clarke 1979; Fordinál 1996; Albesa *et al.* 1997; Esu & Ciangherotti 2004; Moser *et al.* 2009; Salvador *et al.* 2016), but is mostly used in an informal manner, being only roughly delineated and explained so far. Therefore, we thoroughly delineate it, exploring its applicability, potential and shortcomings. We then use the Randeck Maar molluscan fauna to exemplify this approach, presenting a detailed environmental reconstruction of the setting and comparing this approach with previous work on the site's flora and vertebrates (Rasser *et al.* 2013).

Geological setting

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

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

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

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

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

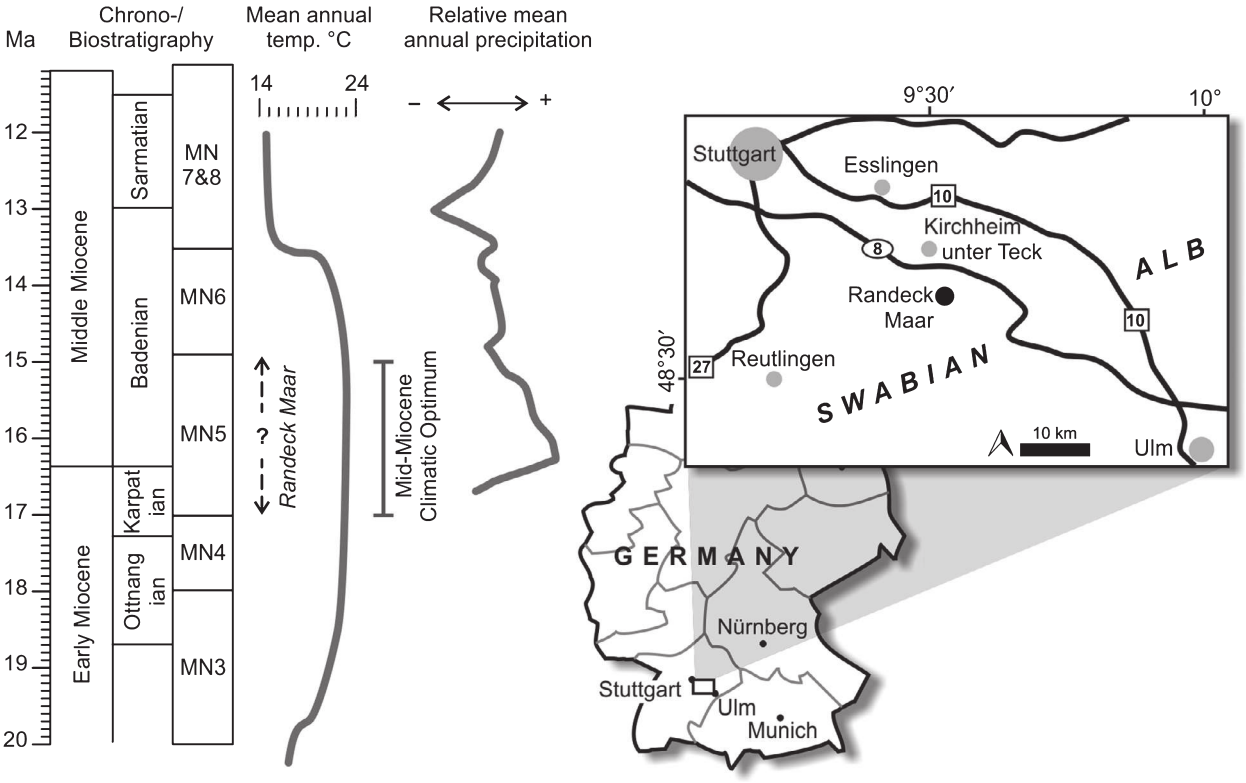

Fig. 1. Geographical location and stratigraphy of Randeck Maar Lake. Redrawn from Rasser *et al.* (2013).

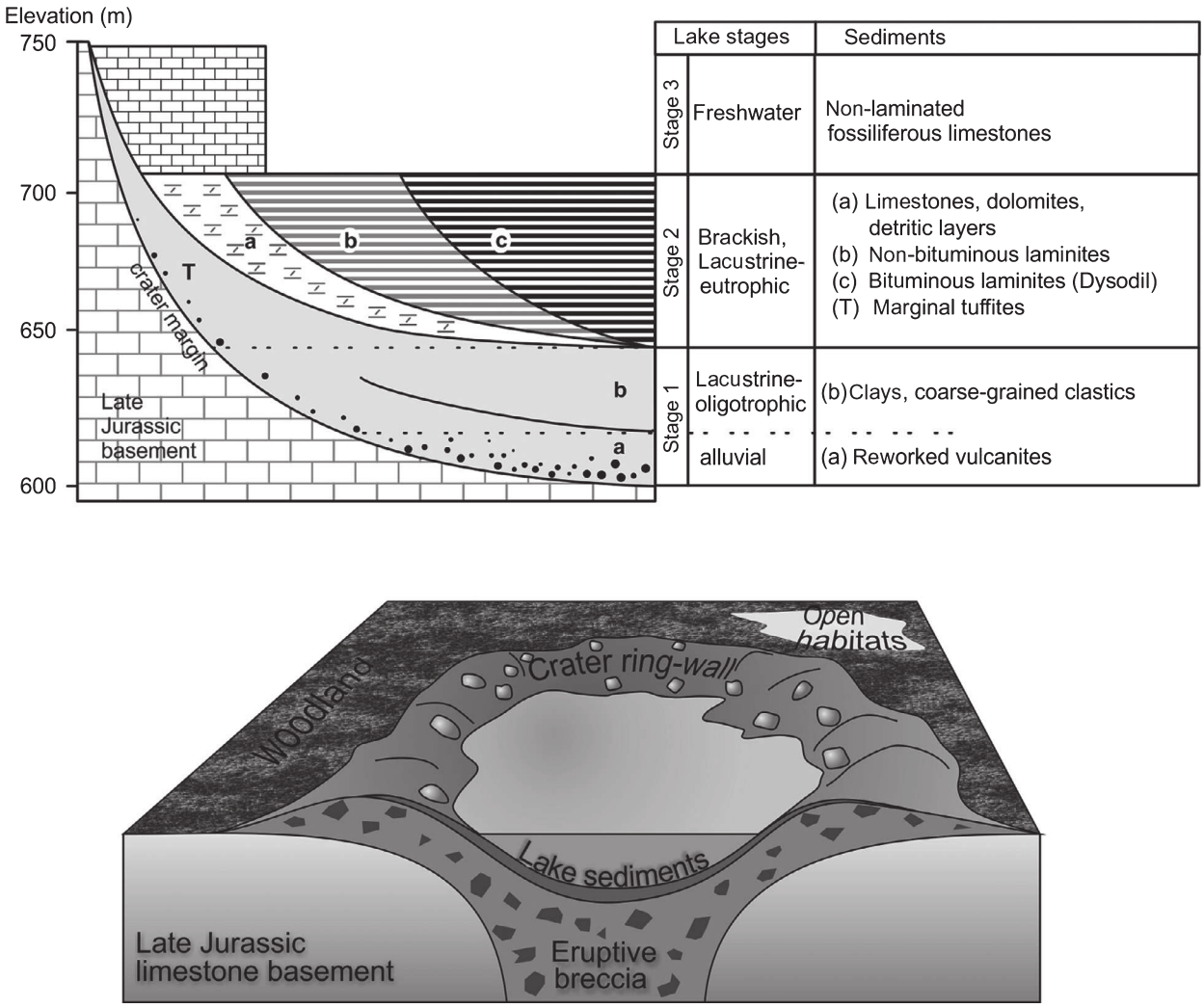

Fig. 2. Top: schematic cross-section through the Randeck Maar sediments after Jankowski (1981). See Table 1 for the distribution of snails in the different facies types. Bottom: reconstruction of the lake habitats after Rasser *et al.* (2013).

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

Material and methods

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

The actualistic genus-level approach

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

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

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

Species	Stage 1	Stage 2				Stage 3
	DT	LT	ML	CL	Dys	FL
Apula coarctata		65	7			
Archaeozonites costatus		1	11			
Clausiliinae indet.			33			
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	
Hypnophila loxostoma	1	254	5			
Leucochroopsis kleinii	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 mantelli	8		47	40	1	2
Pomatias conicus	2	167	76			15
Praeoestophorella phacodes		219	1		1	
Protodrepanostoma involuta		18	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				

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

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

Choice of genus-level taxa

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

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

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

Similar methodologies

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

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

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

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

Applying the actualistic genus-level approach

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

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

The fossil species are then sorted into ecological/habitat/ niche groupings. The handful of resulting groups will define the palaeoenvironmental reconstruction. Quantitative data on species abundance, if available, should also be taken into account. Changes in these groups along the sedimentary profile allow reconstructing the evolution of the palaeoenvironment through time. While it is usually better to have as many species as possible for this kind of analysis, it is not unusual for a single species to have such a narrow range of ecological requirements that it will guide the reconstruction (this is commonly observed in the NLR method).

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

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

Palaeoecological proxies

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

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

Aquatic snails

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

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

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

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

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

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

Terrestrial snails

Pomatias conicus (Klein 1853). The only non-pulmonate snail in Randeck Maar is the most abundant land snail species (Table 1). Recent *Pomatias* are found in Mediterranean climates in Europe, in forests or shrublands with humid and loose (usually calcareous) soil where they can burrow (Kerney & Cameron 1979; Welter-Schultes 2012).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Gastrocopta cf. *acuminata* (Klein 1846) and *G. sandbergeri* Stworzewicz & Prisyazhnyuk 2006. There are no native *Gastrocopta* spp. in Europe today. They can be found worldwide, inhabiting a very broad range of habitats and being especially diverse in North America (Zilch 1959–1960).

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

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

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

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

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

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

Results and discussion

Reconstruction of gastropod palaeohabitats in Randeck Maar

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

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

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

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

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

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

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

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

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

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

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

Limitations of the actualistic approach

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

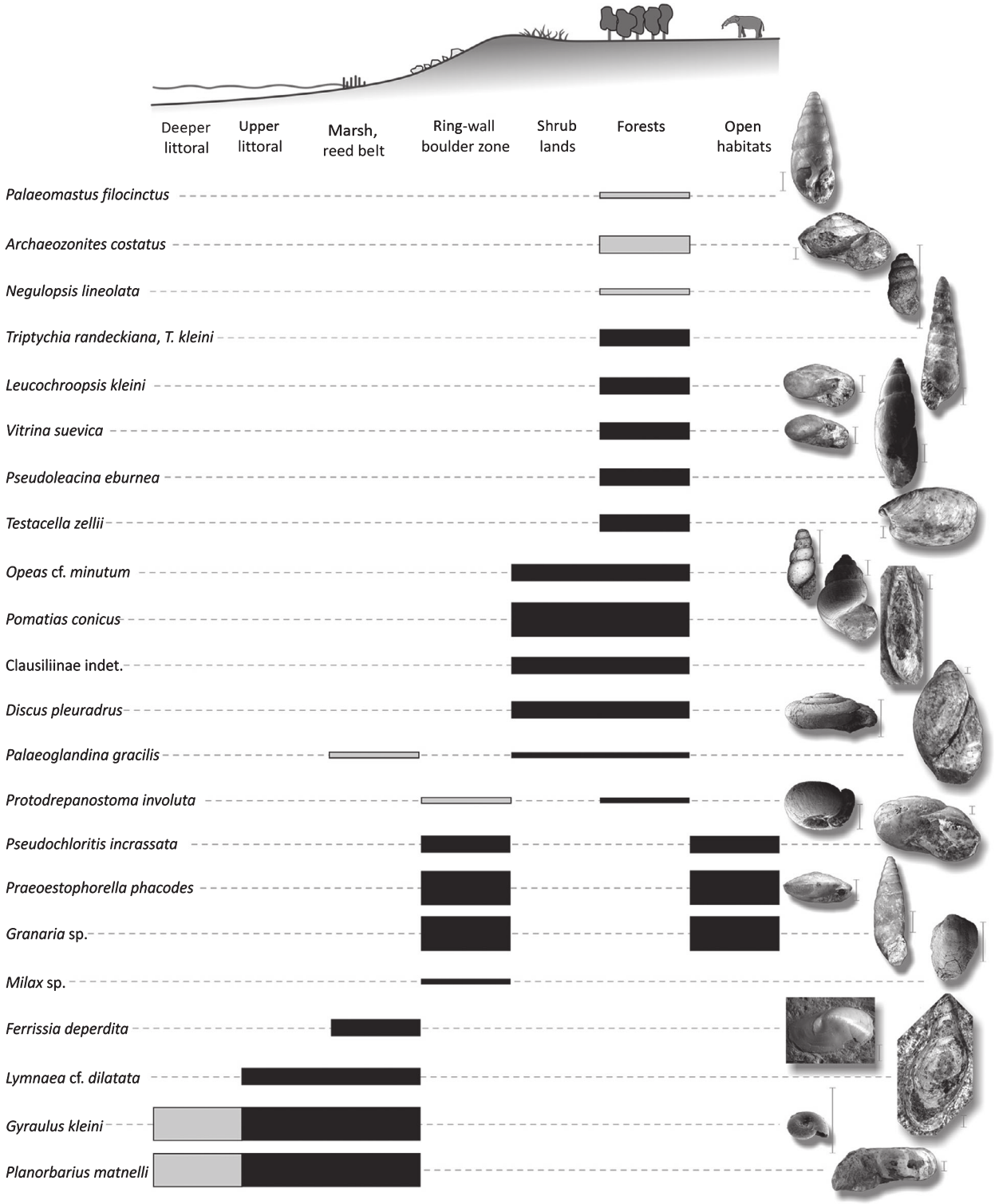

Fig. 3. Palaeohabitats of the gastropods from Lake Randeck Maar and its hinterland, based on the actualistic genus-level approach. Scale bars = 2 mm. Thickness of bar reflects the general abundance of the respective species in the studied material (see also Table 1); thin bar: <10 individuals; medium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

Table 1 and Fig. 3) were excluded from the palaeoecological analysis for the following reasons: (1) the extant species of the genera show a too broad range of ecological requirements (e.g. *Gastrocopta*); (2) some species do not have a clear extant congener and/or their supposed sister taxa have too broad a

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

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

Sampling biases

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

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

Trophic interactions

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

With such diversity and abundance of snails in Randeck Maar, it is no surprise to attest the presence of three malacophagous species: *Pseudoleacina eburnea*, *Palaeoglandina gracilis* and *Testacella zellii*. While *Pseudoleacina eburnea* is rather small, *Palaeoglandina gracilis* is the largest species found in Randeck Maar (together with *Pseudochloritis 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 worthwhile to notice that *Pseudoleacina eburnea* is among the most abundant terrestrial snails in Randeck Maar, a remarkable fact given its predatory trophic level. While *Pseudoleacina eburnea* and *Testacella zellii* would be more restricted to the humid forests and shrublands around the lake, *Palaeoglandina gracilis* (when considering its living relatives, as explained above) would have also hunted in the reed belt and perhaps also ventured in the shallower littoral area.

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

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

Gastropods as climate proxies

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

Conclusions

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

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

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Miocene continental gastropods from Dischingen, Germany

Rodrigo B. Salvador, Olaf Höltke & Michael W. Rasser

Abstract

Here is given an account, based on museum collections, of the fossil land and freshwater gastropods from Dischingen (Baden-Württemberg state, SW Germany). The fossiliferous outcrops belong to the Silvana Beds unit of the Upper Freshwater Molasse group, of late Early to early Middle Miocene age (Neogene European Land Mammal Zone MN 5). In total, 35 gastropod species were found (seven freshwater and 28 terrestrial), mainly belonging to Pulmonata, but also with representatives of Neritimorpha and Caenogastropoda. Seven species are reported here for the first time from Dischingen: *Palaina diezi*, *Radix socialis*, *Granaria* sp., *Serrulina*? sp., *Discus pleuradrus*, *Punctum pumilio*, and *Oxyloma minima*.

Keywords: Caenogastropoda, Pulmonata, Neritimorpha, Silvana Beds, Upper Freshwater Molasse.

1. Introduction

Dischingen is the easternmost community of Baden-Württemberg state (part of Heidenheim district; Fig. 1), SW Germany, and its name is often mentioned in the paleontological literature due to the several fossiliferous deposits outcropping in the region (*e.g.*, Wenz 1923–1930). Dischingen lies at the northern margin of the Molasse Basin. Miocene marine invertebrates and continental mollusks from the different beds of this locality can be found in several museum collections. According to the labels found in these collections, the locality "Michaelsberg/Michelsberg, Dischingen" is seen in the vast majority of cases; this hill is located in the SW part of Dischingen. However, like many other Miocene localities in Baden-Württemberg, there is scarce literature dealing specifically with Dischingen – the outcrops lack detailed documentation and description.

Fraas (1869) was the first researcher to describe the Miocene marine sediments in this region, providing a list of the invertebrates from the sandpits at Michelsberg. He also noted a younger stratum of freshwater limestone with continental mollusks, mentioning that it was similar to the limestone strata known from Zwiefalten and the Tautschbuch region, also in Baden-Württemberg. Afterwards, Quenstedt (1884) listed three land snail species from Dischingen on a broader work about gastropods. Besides this, there is brief mention of the Miocene sediments from Dischingen by Fraas (1882) and Engel (1908) on their works about the geology of Baden-Württemberg.

The gastropod-bearing freshwater limestone of Dischingen was first specifically studied by Mengele (1916). This author presented a list of 27 terrestrial and freshwater gastropod species from this locality, which was compiled by malacologist Carlo G. H. Jooss (Table 1). These fossils were later included on the compilation work of Wenz (1923–1930). Much later, Gall (1971) presented a list of 29 gastropod species compiled with newly collected material (Table 1).

Herein, we examine the original material from the works of Mengele (1916) and Gall (1971), as well as additional specimens from museum collections in Germany. We present an updated classification of the species, including seven new records, and figure the fossil gastropods from Dischingen for the first time.

Abbreviations

Institutions: BSPG = Bayerische Staatssammlung für Paläontologie und Geologie (Munich, Germany); GPIT = Department of Geosciences, Eberhard Karls Universität Tübingen (Tübingen, Germany; formerly Geologisch-Paläontologisches Institut Tübingen); SMNS = Staatliches Museum für Naturkunde Stuttgart (Stuttgart, Germany).

Shell measurements: H = shell height (parallel to coiling axis); D = greatest shell width (perpendicular to H).

2. Geological setting

Dischingen is located at the northern margin of the Molasse Basin in southern Germany (Fig. 1). The Miocene deposits from Dischingen belong to the units known as Upper Marine Molasse ("*Obere Meeresmolasse*", abbreviated OMM) and Upper Freshwater Molasse ("*Obere Süßwassermolasse*", abbreviated OSM). The sediments of the latter can be more especifically assigned to the Silvana Beds, a unit within the OSM characterized by the presence of the land snail *Palaeotachea silvana*. Nevertheless, several other gastropod taxa are also typical of these beds, incuding some of those listed further below (Table 1), such as *Gyraulus applanatus*, *Hypnophila loxostoma*, and *Leucochroopsis kleini* (Esu 1999; Höltke et al. 2018). This supports a late Early to early Middle Miocene age for the Dischingen fossils (Neogene European Land Mammal Zone MN 5).

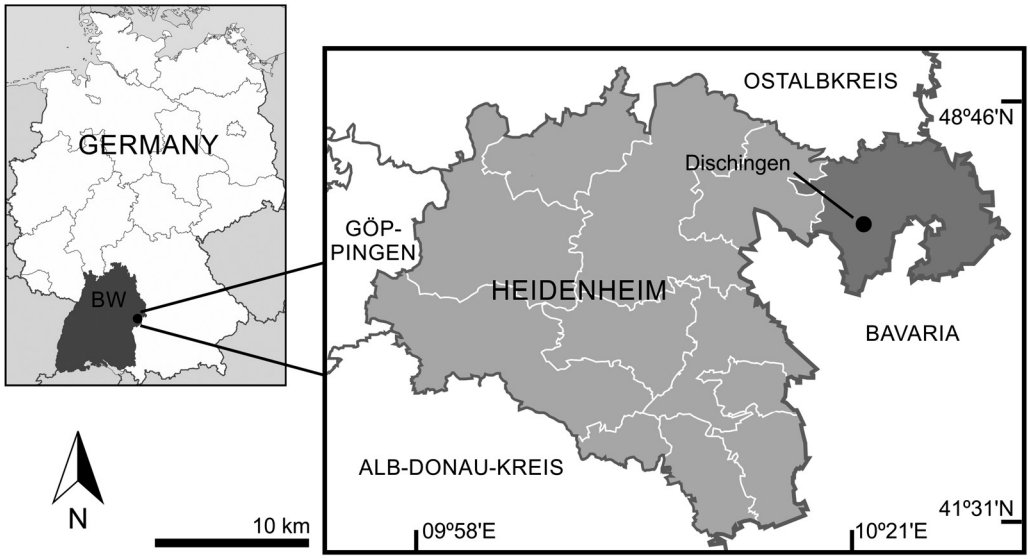


Fig. 1. Map showing the locality of Dischingen, Heidenheim district, Baden-Württemberg state (BW), Germany.

Regrettably, there are no recent outcrops exposed in the region and so only literature data is available for the OSM sediments in Dischingen. Fraas (1869) first referred to these sediments as "freshwater limestones" ("*Süßwasserkalke*", in the original), also mentioning detritus from the Nördlinger Ries and Steinheim meteorite events overlying the OSM layers. The Ries event is currently dated as 14.808 ± 0.021 Ma (Schmieder et al. 2018), thus constraining the minimum age of the Dischingen sediments.

Gall (1971) described two strata from Dischingen, starting on the bottom with typically red colored marly clays, the so-called "flame marls" ("*Flammenmergel*"; Wenz 1924). According to Wenz (1924), the *Flammenmergel* belongs to the lower part of Silvana Beds (for the subdivision of the Silvana Beds, see Höltke & Rasser 2016). The second stratum of Gall (1971), overlying the *Flammenmergel*, becomes more calcareous, passing into lighter colored marls bearing limestone nodules. On the top of the profile are the freshwater limestones representing the middle Silvana Beds.

3. Material and methods

The material analyzed for compiling the present account consisted exclusively of specimens from historical museum collections (see the Appendix for a full list of analyzed lots). This includes the voucher material of Jooss *in* Mengele (1916) and Gall (1971), which were respectively deposited in the SMNS and the BSPG. Unfortunately, not all of Jooss' specimens were preserved to this day, since a part of the SMNS collection was lost (Salvador et al. 2016a).

The best preserved gastropod specimens are illustrated herein (Figs. 2–38), with images obtained either with a Leica auto-montage apparatus or with a scanning electron microscope (SEM) at the SMNS. Shell measurements were obtained with a digital caliper (for larger specimens) or with the software ImageJ (Rasband 2012).

4. Discussion

In total, 35 gastropod species, belonging to the Neritimorpha, Caenogastropoda and Pulmonata, were found in museum collections with material from Dischingen (Table 1). The overall gastropod classification follows Bouchet & Rocroi (2005), with more specific data on the European fossil snails being gathered from Nordsieck (2014) and Salvador et al. (2016a). All these species are commonly found in coeval sediments from the Silvana Beds in southern Germany. Consequently, they have been extensively described and explored elsewhere (*e.g.*, Harzhauser et al. 2014; Salvador et al. 2015, 2016b; Salvador & Rasser 2016) and we will thus refrain from giving a full description of the material here. The best preserved gastropod specimens from Dischingen are shown in Figs. 2 to 38.

Seven species are reported from Dischingen for the first time: *Palaina diezi*, *Radix socialis*, *Granaria* sp., *Serrulina*? sp., *Discus pleuradrus*, *Punctum pumilio*, and *Oxyloma minima*. From the species listed by Jooss *in* Mengele (1916), the following three could not be confirmed by the presently available material (Table 1): *Gastrocopta nouletiana*, *Janulus gyrorbis* (considered dubious by Manganelli et al. 2011), and *Pleurodiscoides orbicularis*.

The composition of the gastropod fauna from Dischingen is very similar to other OSM localities (*e.g.*, Salvador et al. 2017; Höltke et al. 2018). The continental

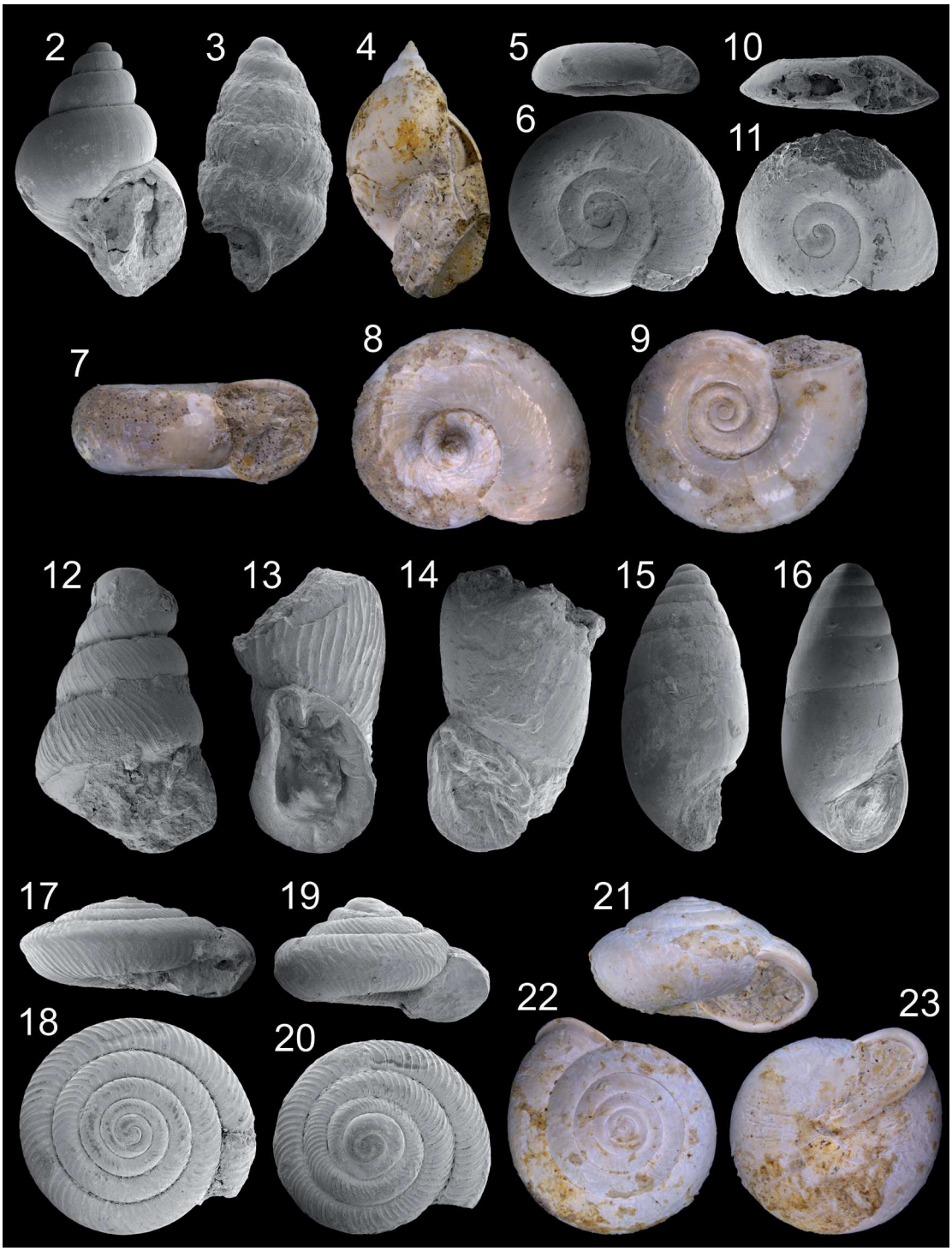
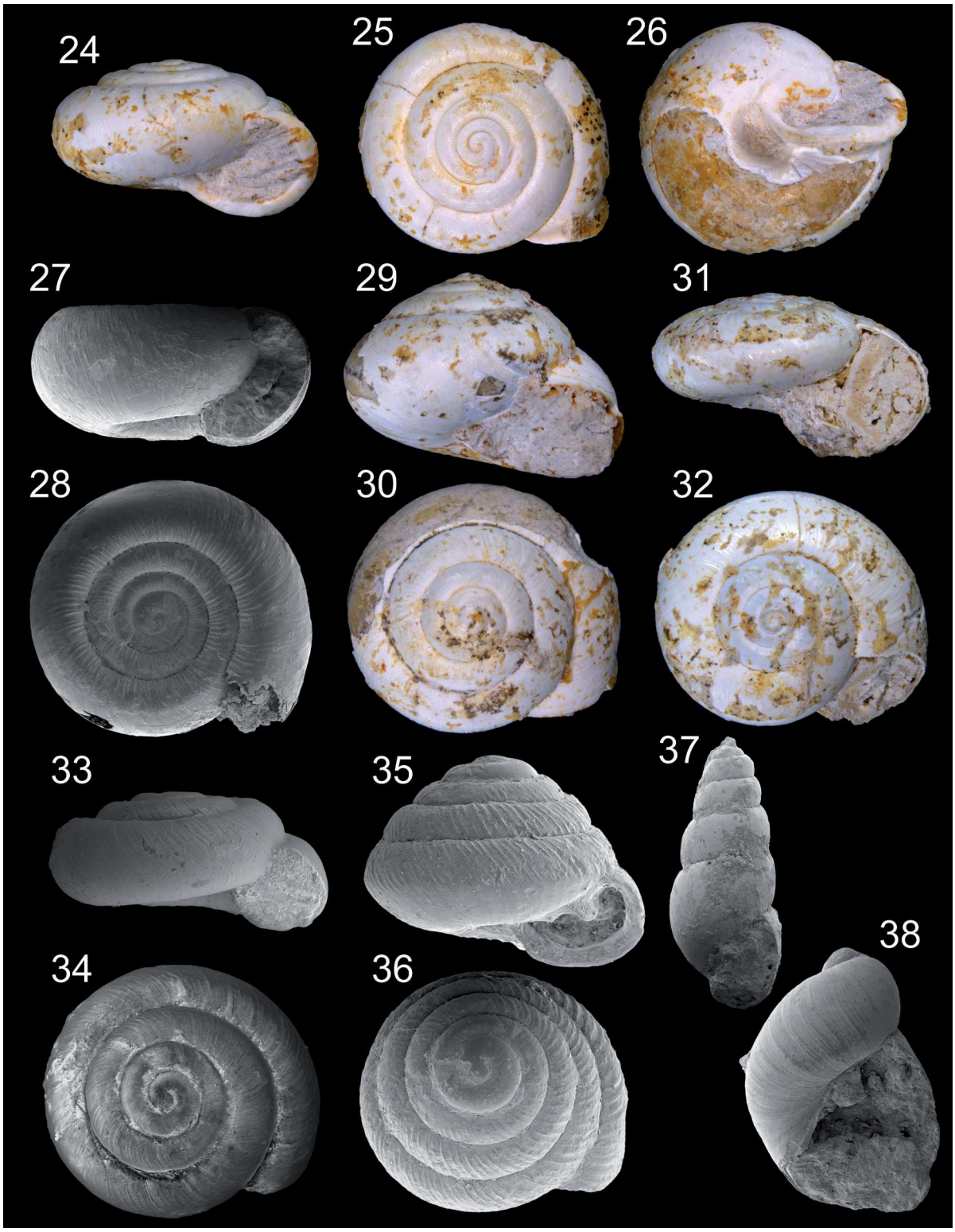


Fig. 2. *Bithynia glabra*, BSPG 1968 II 97 (H = 5.1 mm, D = 3.4 mm). **Fig. 3.** *Palaina dietzi*, SMNS 68553 (H = 2.3 mm, D = 1.3 mm). **Fig. 4.** *Lymnaea dilatata*, SMNS 67687 (H = 19.8 mm, D = 11.0 mm). **Fig. 5.** *Gyraulus applanatus*, SMNS 67783 specimen #1 (H = 1.0 mm, D = 3.0 mm). **Fig. 6.** *Gyraulus applanatus*, SMNS 67783 specimen #2 (D = 4.0 mm). **Figs. 7–9.** *Planorbarius mantelli* SMNS 67843 (H = 7.1 mm, D = 16.1 mm). **Figs. 10, 11.** *Segmentina lartetii*, BSPG 1968 II 92 (H = 0.5 mm, D = 1.7 mm). **Fig. 12.** *Granaria* sp., SMNS 67467 (H = 2.7 mm). **Fig. 13.** *Pseudidyla moersingensis*, SMNS 66936 (H = 3.9 mm). **Fig. 14.** *Serrulina*? sp., SMNS 66923 (H = 5.3 mm). **Fig. 15.** *Azeca lubricella*, BSPG 1968 II 84 (H = 4.6 mm, D = 2.0 mm). **Fig. 16.** *Hypnophila loxostoma*, SMNS 67252 (H = 5.1 mm, D = 2.2 mm). **Figs. 17, 18.** *Discus euglyphoides*, SMNS-65807 (H = 1.7 mm, D = 4.3 mm). **Figs. 19, 20.** *Discus pleuradrus*, SMNS 65830 (H = 2.1 mm, D = 3.8 mm). **Figs. 21–23.** *Apula coarctata*, SMNS 66293 (H = 6.9 mm, D = 11.5 mm).



Figs. 24–26. *Klikia giengensis*, SMNS 66279 (H = 5.4 mm, D = 9.0 mm). **Figs. 27, 28.** *Protodrepanostoma involutum*, SMNS 66009 (H = 2.6 mm, D = 5.0 mm). **Figs. 29, 30.** *Leucochroopsis kleinii*, SMNS 65950 (H = 6.1 mm, D = 9.0 mm). **Figs. 31, 32.** *Aegopinella subnitens*, SMNS 65691 (H = 7.3 mm, D = 12.8 mm). **Figs. 33, 34.** *Punctum pumilio*, syntype SMNS 106420 (H = 1.1 mm, D = 2.0 mm). **Figs. 35, 36.** *Strobilops costatus*, SMNS 68544 (H = 1.6 mm, D = 2.2 mm). **Fig. 37.** *Opeas minutum*, SMNS 67038 (H = 5.1 mm, D = 2.1 mm). **Fig. 38.** *Oxyloma minima*, SMNS 67067 (H = 2.6 mm, D = 1.9 mm).

gastropods have been constantly used as proxies for the paleonvironment from an actualistic standpoint, i.e., using the knowledge of living congeners (see SALVADOR et al. 2015, 2016b, for a full analysis of OSM localities from Baden-Württemberg). As such, it can be surmised that the palaeoenvironment at Dischingen during the deposition of these sediments was likewise similar, consisting of humid forests and a well-vegetated low-energy water body (SALVADOR et al. 2015, 2016b, and references therein).

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Appendix – Material analyzed

Below is listed the material analyzed for producing the present compilation. The species are presented in the same order as in Table 1. An asterisk (*) after the lot's number indicates that it is a rock sample with several incrusted specimens.

Theodoxus crenulatus (Klein, 1853): BSPG 1968 II 98 (1 spec.).
Bithynia glabra (v. Zieten, 1832): BSPG 1968 II 97 (10 spec.).
Palaina dietzi (Flach, 1890): SMNS 68553 (1 spec.).
Pomatias conicus (Klein, 1853): BSPG 1968 II 94 (6 spec.), BSPG 1968 II 96 (~15 spec.), BSPG 1968 II 102 (1 spec.), GPIT/GA/3920 (6 spec.).
Pomatias consobrinus (Sandberger, 1872): GPIT/GA/3917 (17 spec.).
Pomatias sp. (operculum): BSPG 1968 II 95 (1 spec.).
Carychium sp.: SMNS 67175 (1 spec.).
Lymnaea dilatata Noulet, 1854: BSPG 1968 II 88 (3 spec.), BSPG 1968 II 89 (>10 spec.), BSPG 1968 II 90 (8 spec.), SMNS 67687 (1 spec.), SMNS 107260 (1 spec.).
Radix socialis (v. Zieten, 1832): BSPG 1968 II 89 (>10 spec.).
Ferrissia deperdita (Desmarest, 1814): BSPG 1968 II 93 (1 spec.).
Gyraulus applanatus (Thomä, 1845): SMNS 67783 (2 spec.).
Planorbarius mantelli (Dunker, 1848): BSPG 1968 II 91 (>50 spec.), GPIT/GA/2705 (2 spec.), GPIT/GA/2885*, SMNS 67843 (3 spec.).
Segmentina lartetii (Noulet, 1854): BSPG 1968 II 92 (1 spec.).
Granaria sp.: SMNS 67467 (1 spec.).
Pseudidyla moersingensis (O. Boettger, 1877): SMNS 66936 (1 spec.).
Serrulina? sp.: SMNS 66923 (1 spec.).
Azeca lubricella O. Boettger, 1870: BSPG 1968 II 84 (2 spec.).
Hypnophila loxostoma (Klein, 1853): SMNS 67252 (3 spec.).
Discus euglyphoides (Sandberger, 1872): BSPG 1968 II 74 (1 spec.), BSPG 1968 II 75 (3 spec.), SMNS 65087 (1 spec.).
Discus pleuradrus (Bourguignat, 1881): SMNS 65830 (1 spec.).
Apula coarctata (Klein, 1853): BSPG 1968 II 81 (>20 spec.), SMNS 66293 (2 spec.).
Klikia giengensis (Klein, 1846): BSPG 1968 II 80 (2 spec.), BSPG 1968 II 81 (>20 spec.), SMNS 66279 (16 spec.).
Triptychia kleini Schnabel, 2006: BSPG 1968 II 84 (2 spec.).
Gastrocopta acuminata (Klein, 1846): BSPG 1968 II 86 (2 spec.), SMNS 67426 (5 spec.).
Palaeotachea silvana (Klein, 1853): BSPG 1968 II 68 (5 spec.), BSPG 1968 II 69 (1 spec.), BSPG 1968 II 82 (1 spec.), BSPG 1968 II 83 (>40 spec.), SMNS 66656 (4 spec.), SMNS 66857 (2 spec.), SMNS 66875 (2 spec.).
Palaeotachea turonensis (Deshayes, 1831): SMNS 66813 (3 spec.).
Pseudochloritis incrassata (Klein, 1853): BSPG 1968 II 78 (>30 spec.), BSPG 1968 II 79 (1 spec.), SMNS 66150 (3 spec.), SMNS 66214 (4 spec.).
Protodrepanostoma involutum (Thomä, 1845): BSPG 1968 II 77 (1 spec.), SMNS 66009 (2 spec.).
Leucochroopsis kleinii (Klein, 1846): BSPG 1968 II 61 (1 spec.), BSPG 1968 II 76 (~20 spec.), SMNS 65942 (1 spec.), SMNS 65950 (7 spec.).
Palaeoglandina gracilis (v. Zieten, 1832): BSPG 1968 II (1 spec.), BSPG 1968 II 85 (3 spec.).
Aegopinella subnitens (Klein, 1853): BSPG 1968 II 73 (4 spec.), SMNS 65676 (5 spec.), SMNS 65691 (1 spec.).
Punctum pumilio Jooss, 1918: SMNS 106420 (2 spec., syntypes).
Strobilops costatus (Clessin, 1877): SMNS 68544 (1 spec.).
Opeas minutum (Klein, 1853): SMNS 67083 (1 spec.).
Oxyloma minima (Klein, 1853): SMNS 67067 (1 spec.).
Archaeozonites costatus Sandberger, 1872: BSPG 1968 II 67 (1 spec.), BSPG 1968 II 72 (9 spec.), GPIT/GA/4055 (1 spec.).

Table 1. Continental gastropods from Dischingen found in the present material, alongside the identifications by Jooss *in* Mengele (1916) and Gall (1971) as they appear in the original works (authorship was corrected when pertinent). Discrepancies in identification represent either our revision of their original material (partially housed in the SMNS and BSPG, respectively) or simple nomenclatural changes (*e.g.*, new generic allocations, name corrections, *nomina nova*) that have been published since then. Some species listed by Jooss could not be confirmed by the presently available material.

Present work	Jooss *in* Mengele (1916)	Gall (1971)
NERITIMORPHA		
NERITIDAE		
Theodoxus crenulatus (Klein, 1853)	—	*Theodoxus* (*Calvertia*) *crenulatus crenulatus* (Klein, 1853)
CAENOGASTROPODA		
BITHYNIIDAE		
Bithynia glabra (v. Zieten, 1832)	*Bythinia gracilis* Sandberger, 1872	*Bulimus glabrus glabrus* (v. Zieten, 1832)
DIPLOMMATINIDAE		
Palaina diezi (Flach, 1890)	—	—
POMATIIDAE		
Pomatias conicus (Klein, 1853)	*Tudora conica* (Klein, 1853)	*Tudorella conica conica* (Klein, 1853)
Pomatias consobrinus (Sandberger, 1872)	*Cyclostoma consobrium* [sic] (Sandberger, 1872)	*Pomatias consobrium* [sic] (Sandberger, 1872)
PULMONATA: ELLOBIOIDEA		
ELOBIIDAE		
Carychium sp.	—	—
PULMONATA: HYGROPHYLA		
LYMNAEIDAE		
Lymnaea dilatata Noulet, 1854	*Lymnaeus dilatatus* Noulet, 1854; *Limnaeus turritus* Klein, 1853	*Radix* (*Radix*) *socialis dilatata* (Noulet, 1854); *Radix* (*Radix*) *socialis praelongata* (Gottschick & Wenz, 1916); *Limnaea turrita turrita* Klein, 1853
Radix socialis (v. Zieten, 1832)	—	—
PLANORBIDAE		
Ferrissia deperdita (Desmarest, 1814)	—	*Ancylus deperditus deperditus* (Desmarest, 1814)
Gyraulus applanatus (Thomä, 1845)	*Planorbis* (*Gyrorbis*) *declivis* Braun, 1851	—
Planorbarius mantelli (Dunker, 1848)	*Planorbarius cornu mantelli* (Dunker, 1848)	*Planorbarius cornu mantelli* (Dunker, 1848)
Segmentina lartetii (Noulet, 1854)	*Planorbis* (*Segmentina*) *lartetii* Noulet, 1854	*Segmentina* (*Segmentina*) *lartetii* (Noulet, 1854)
PULMONATA: STYLOMMATOPHORA		
CHONDRINIDAE		
Granaria sp.	—	—
CLAUSILIIDAE		
Pseudidyla moersingensis (O. Boettger, 1877)	*Pseudidyla moersingensis* (O. Boettger, 1877)	—
Serrulina? sp.	—	—

Present work	Jooss *in* Mengele (1916)	Gall (1971)
COCHLICOPIDAE		
Azeca lubricella O. Boettger, 1870	*Cochlicopa lubricella* (O. Boettger, 1870)	*Azeca* (*Azeca*) *lubricella lubricella* O. Boettger, 1870
Hypnophila loxostoma (Klein, 1853)	*Azeca loxostoma* (Klein, 1853)	*Cochlicopa subrimata loxostoma* (Klein, 1853)
DISCIDAE		
Discus euglyphoides (Sandberger, 1872)	*Patula* (*Charopa*) *euglyphoides* Sandberger, 1972; *Janulus supracostatus* (Sandberger, 1872)	*Discus euglyphoides euglyphoides* (Sandberger, 1872); *Janulus supracostatus* (Sandberger, 1872)
Discus pleuradrus (Bourguignat, 1881)	—	—
ELONIDAE		
Apula coarctata (Klein, 1853)	*Klikia coarctata* (Klein, 1853)	*Klikia* (*Apula*) cf. *coarctata* (Klein, 1853)
Klikia giengensis (Klein, 1846)	*Klikia osculum giengensis* (Klein, 1846)	*Klikia* (*Klikia*) *giengensis giengensis* (Klein, 1846)
FILHOLIIDAE		
Triptychia kleini Schnabel, 2006	*Triptychia* (*Clausilia*) *grandis* (Klein, 1846)	*Triptychia* (*Triptychia*) *grandis* (Klein, 1846)
GASTROCOPTIDAE		
Gastrocopta acuminata (Klein, 1846)	*Pupa* (*Leucochilus*) *quadriplicatum quadridentatum* Klein, 1853	*Gastrocopta* (*Albinula*) *acuminata acuminata* (Klein, 1846)
—	*Pupa* (*Leucochilus*) *neuletianum* [sic] *gracilidens* Sandberger, 1875	—
GASTRODONTIDAE		
—	*Patula* (*Janulus*) *gyrorbis* (Klein, 1846)	—
HELICIDAE		
Palaeotachea silvana (Klein, 1853)	*Otala sylvana* (Klein, 1853)	*Cepaea silvana silvana* (Klein, 1853); *Cepaea eversa larteti* (Boissy, 1839)
Palaeotachea turonensis (Deshayes, 1831)	—	*Cepaea* cf. *dentula* (Quenstedt, 1867)
Pseudochloritis incrassata (Klein, 1853)	*Pseudochloritis inflexa* C. Boettger, 1909	*Tropidomphalus* (*Pseudochloritis*) *incrassatus incrassatus* (Klein, 1853); *Tropidomphalus* (*Pseudochloritis*) cf. *zelli* (Kurr, 1856)
HELICODONTIDAE		
Protodrepanostoma involutum (Thomä, 1845)	*Helicodonta scabiosa* (Sandberger, 1875)	*Helicodonta* (*Helicodonta*) *involuta scabiosa* (Sandberger, 1875)
HYGROMIIDAE		
Leucochroopsis kleinii (Klein, 1846)	*Trichiopsis carinulata* (Klein, 1853)	*Leucochroopsis kleini kleini* [sic] (Klein, 1846)
OLEACINIDAE		
Palaeoglandina gracilis (v. Zieten, 1832)	—	*Palaeoglandina gracilis porrecta* (Gobanz, 1852)
OXYCHILIDAE		
Aegopinella subnitens (Klein, 1853)	—	*Oxychilus subnitens subnitens* (Klein, 1853); *Vitrina* cf. *suevicus* (Sandberger, 1875)

Present work	Jooss *in* Mengele (1916)	Gall (1971)
PLEURODISCIDAE		
—	*Hyalina orbicularis* (Klein, 1846)	—
PUNCTIDAE		
Punctum pumilio Jooss, 1918	—	—
STROBILOPSIDAE		
Strobilops costatus (Clessin, 1877)	*Strobilus costatus* Clessin, 1877	—
SUBULINIDAE		
Opeas minutum (Klein, 1853)	*Subulina minuta* (Klein, 1853)	—
SUCCINEIDAE		
Oxyloma minima (Klein, 1853)	—	—
ZONITIDAE		
Archaeozonites costatus Sandberger, 1872	*Archaeozonites costatus* Sandberger, 1872	*Archaeozonites costatus* Sandberger, 1872

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Fossil land and freshwater gastropods from the Miocene of Hohenmemmingen, Germany

Rodrigo B. Salvador, Olaf Höltke & Michael W. Rasser

Abstract

Herein we present an account of the fossil terrestrial and freshwater gastropods from the locality of Hohenmemmingen (Baden-Württemberg state, SW Germany) based on museum collections. The fossil outcrops belong to the Silvana Beds of the Upper Freshwater Molasse, being of Early/Middle Miocene age. In total, 23 gastropod species, all pulmonates, are documented in the material (whereas 33 species had been previously reported in the literature): five freshwater species and 18 terrestrial. From an actualistic palaeoecological approach, this palaeoevironment featured a humid and warm forest cover, with a well-vegetated and likely shallow water body.

K e y w o r d s : Pulmonata, Silvana Beds, Upper Freshwater Molasse.

1. Introduction

The Silvana Beds ("Silvanaschichten" in German) are a unit of the Upper Freshwater Molasse ("Obere Süßwassermolasse" in German; abbreviated OSM) that outcrop at several localities in southern Germany (e.g., Sandberger 1870–1875; Wenz 1923–1930; Neubauer et al. 2015; Höltke et al., 2016). These beds are particularly notable for their abundant molluscan fossils (e.g., Salvador et al. 2015; Salvador & Rasser 2016), but many of the localities with outcrops are known only from the older literature. One of them is Hohenmemmingen, in the municipality of Giengen an der Brenz (Heidenheim district, Baden-Württemberg state, SW Germany; Fig. 1)

Fossil mollusks from Hohenmemmingen were mentioned by some authors (Klein 1846; Sandberger 1858–1863, 1870–1875), but a comprehensive faunal list was only provided much later, by Gottschick & Wenz (1916). These authors reported 32 gastropod species and one poorly preserved bivalve; later, Wenz (1923–1930), in his compilation work, repeated this information with a few revisions in taxonomic attribution and a new record of one species. After these accounts, the material has been scarcely mentioned again in the literature until Höltke et al. (2016) compiled a list of species from this locality for a biogeographic analysis using museum specimens. Herein, we add material from other collections, offering an updated classification of the species and illustrating several of the

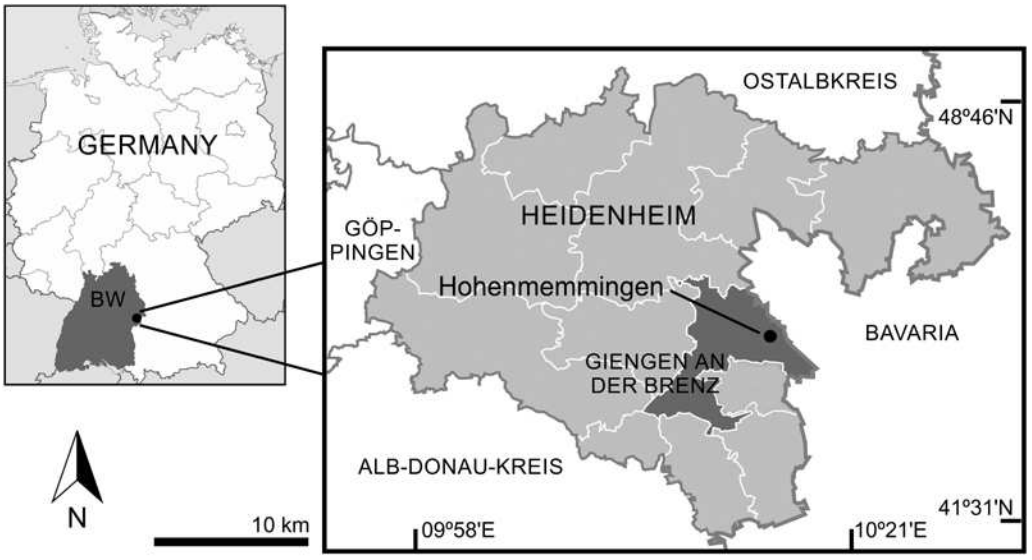

Fig. 1. Map showing the locality of Hohenmemmingen, part of the municipality of Giengen an der Brenz, Heidenheim district, Baden-Württemberg state (BW), Germany.

Table 1. List of all molluscan species reported from the Silvana Beds of Hohenmemmingen. The species whose records have been confirmed in the present work are accompanied by the collection number(s) of the studied material. Species whose record is only known from the literature are indicated accordingly.

Species	Figure(s)	Material studied / References
CAENOGASTROPODA		
PACHYCHILIDAE		
Tinnyea lauraea (Mathéron, 1843)		Wenz (1923)
BITHYNIIDAE		
Bithynia glabra (Zieten, 1832)	—	Gottschick & Wenz (1916), as synonym *B. gracilis* Sandberger, 1872; see Salvador et al. (2016b)
PULMONATA: ELLOBIOIDEA		
ELOBIIDAE		
Carychium nouleti Bourguignat, 1857	—	Gottschick & Wenz (1916), as synonym *C. gibbum* Sandberger, 1875; see Strauch (1977)
PULMONATA: HYGROPHYLA		
LYMNAEIDAE		
Lymnaea dilatata Noulet, 1854	Fig. 2.1	GPIT/GA/3929 (3 spec.), GPIT/GA/3964 (3 spec.), GPIT/GA/3999 (1 spec.), GPIT/GA/4049 (5 spec.), GPIT/GA/4068 (2 spec.), SMNS 107257 (7 spec.)
Radix socialis (Zieten, 1832)	Fig. 2.2	SMNS 107235 (3 spec.), SMNS 107328 (>20 spec.)
PLANORBIDAE		
Ferrissia deperdita (Desmarest, 1814)	—	Gottschick & Wenz (1916)
Gyraulus albertanus (Clessin, 1877)	—	Gottschick & Wenz (1916)
Gyraulus applanatus (Thomä, 1845)	Fig. 2.3	GPIT/GA/3935 (5 spec.), GPIT/GA/3981 (5 spec.), GPIT/GA/3986 (>20 spec.), GPIT/GA/3993 (4 spec.), GPIT/GA/4043 (>20 spec.), GPIT/GA/4061 (>20 spec.), SMNS 107329 (5 spec.), SMNS 107330 (8 spec.)
Hippeutis subfontanus (Clessin, 1887)	Fig. 2.4	GPIT/GA/3984 (1 spec.), SMNS 107331 (7 spec.)
Planorbarius mantelli (Dunker, 1848)	Fig. 2.5	GPIT/GA/3971 (>20 spec.), GPIT/GA/04078 (>30 spec.), SMNS 107335 (18 spec.), SMNS 107336 (>20 spec.), SMNS 107339 (2 spec.), SMNS 107346 (>20 spec.)
Segmentina larteti (Noulet, 1854)	—	Gottschick & Wenz (1916)
PULMONATA: STYLOMMATOPHORA		
SUCCINEIDAE		
Oxyloma minima (Klein, 1853)	—	GPIT/GA/4070 (2 spec.)
COCHLICOPIDAE		
Azeca lubricella O. Boettger, 1870	Fig. 3.3	SMNS 107333 (2 spec.)
Hypnophila loxostoma (Klein, 1853)	—	GPIT/GA/4060 (1 spec.)
CHONDRINIDAE		
Granaria noerdlingensis (Klein, 1846) vel *G. subfusiformis* (Sandberger, 1875)	—	Gottschick & Wenz (1916) and Wenz (1923), respectively; *G. noerdlingensis* is a *nomen dubium* according to Höltke & Rasser (2013)
GASTROCOPTIDAE		
Gastrocopta acuminata (Klein, 1846)	Fig. 3.5	SMNS 67428 (2 spec.), SMNS 67431 (1 spec.)
Gastrocopta nouletiana (Dupuy, 1850)	Fig. 3.6	SMNS 67404 (1 spec.), SMNS 107347 (12 spec.)
STROBILOPSIDAE		
Strobilops uniplicata (Braun *in* Walchner, 1851)	—	Gottschick & Wenz (1916)
VALLONIIDAE		
Acanthinula trochulus (Sandberger, 1872)	—	Gottschick & Wenz (1916)

Species	Figure(s)	Material studied / References
VERTIGINIDAE		
Vertigo callosa (Reuss, 1849)	—	Gottschick & Wenz (1916)
CLAUSILIIDAE		
Pseudidyla moersingensis (O. Boettger, 1877)	Fig. 3.2	SMNS 66932 (1 spec.), SMNS 66937 (1 spec.), GPIT/GA/04015 (4 spec.)
SUBULINIDAE		
Opeas minutum (Klein, 1853)	—	BSPG 1966 XXVI (1 spec.), GPIT/GA/4071 (5 spec.)
OLEACINIDAE		
Palaeoglandina gracilis (Zieten, 1832)	—	BSPG no nr. (1 spec.), GPIT/GA/3965 (4 spec.), SMNS 67013 (1 spec.), SMNS 107337 (1 spec.), SMNS 107343 (1 spec.)
DISCIDAE		
Discus pleuradrus suevicus Gottschick & Wenz, 1916	—	Gottschick & Wenz (1916); Wenz (1923)
Discus euglyphoides (Sandberger, 1872)	—	GPIT/GA/04014 (>20 spec.)
OXYCHILIDAE		
Aegopinella subnitens (Klein, 1853)	—	Gottschick & Wenz (1916)
ZONITIDAE		
Archaeozonites costatus Sandberger, 1872	—	GPIT/GA/03998 (1 spec.), SMNS 65268 (1 spec.), SMNS 65632 (1 spec.), SMNS 107340 (2 spec.)
AGRIOLIMACIDAE		
Deroceras sp.	Fig. 3.1	SMNS 107332 (1 spec.)
VITRINIDAE		
Vitrina suevica Sandberger, 1872	—	Gottschick & Wenz (1916)
ELONIDAE		
Apula coarctata (Klein, 1853)	Fig. 3.4	SMNS 66292 (1 spec.)
Klikia giengensis (Klein, 1846)	—	GPIT/GA/4072 (6 spec.), SMNS 66278 (1 spec.)
HELICIDAE		
Palaeotachea silvana (Klein, 1853)	—	BSPG 11955 IV 71 (1 spec.), GPIT/GA/3935 (1 spec.), GPIT/GA/3947 (10 spec.), GPIT/GA/3951 (8 spec.), GPIT/GA/3954 (5 spec.), GPIT/GA/3967 (1 spec.), GPIT/GA4001 (5 spec.), GPIT/GA4009 (3 spec.), GPIT/GA/4010 (7 spec.), SMNS 66655 (3 spec.), SMNS 66841 (1 spec.), SMNS 107338 (2 spec.), SMNS 107341 (>20 spec.), SMNS 107343 (2 spec.), SMNS 107344 (5 spec.), SMNS 107245 (3 spec.), SMNS 107346 (1 spec.)
Palaeotachea turonensis (Deshayes, 1831)	Fig. 3.8	SMNS 66797 (2 spec.), SMNS 66804 (2 spec.)
Pseudochloritis incrassata (Klein, 1853)	—	GPIT/GA/3953 (5 spec.), GPIT/GA/3968 (3 spec.), GPIT/GA/04080 (12 spec.), SMNS 66148 (2 spec.), SMNS 66227 (1 spec.)
HELICODONTIDAE		
Protodrepanostoma involutum (Thomä, 1845)	—	GPIT/GA/3988 (1 spec.)
HYGROMIIDAE		
Leucochroopsis kleinii (Klein, 1846)	Fig. 3.7	GPIT/GA/3947 (2 spec.), SMNS 65947 (2 spec.), SMNS 107334 (>20 spec.)
BIVALVIA		
SPHAERIIDAE		
Sphaerium? sp	—	Gottschick & Wenz (1916)

Hohenmemmingen fossils for the first time. This work is part of our research group's goal of "rescuing" information on all Silvana Beds outcrops, bringing them back to light in a modern context and, more importantly, making this information available to the entire scientific community.

Abbreviations: Institutions: BSPG = Bayerische Staatssammlung für Paläontologie und Geologie (Munich, Germany); GPIT = Department of Geosciences, Eberhard Karls Universität Tübingen (Tübingen, Germany; formerly Geologisch-Paläontologisches Institut Tübingen); SMNS = Staatliches Museum für Naturkunde Stuttgart (Stuttgart, Germany). Shell measurements: H = shell height (parallel to coiling axis); D = greatest shell width (perpendicular to H).

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2. Geological setting

Hohenmemmingen lies at the northern margin of the Molasse Basin in southern Germany, which is a part of the North Alpine Foreland Basin. As mentioned above, the mollusk-bearing sediments around Hohenmemmingen belong to the unit known as OSM, which lies over the OBM unit (Upper Brackish Molasse). The transition between these two units is indistinct and the faunal composition indicates that the brackish environment of the OBM went through a gradual "freshening" (Pippèrr & Reichenbacher 2017). The OSM unit, as the name implies, is characterized by freshwater sediments, dated as late Early to Middle Miocene (Reichenbacher et al. 2013; Sant et al. 2017).

The sediments at Hohenmemmingen belong, more specifically, to a sub-unit of the OSM known as Silvana Beds (Gottschick & Wenz 1916). These beds are characterized by (and receive their name from) the presence of the helicid *Palaeotachea silvana* (Klein, 1853), but several other gastropod taxa are also typical of these strata (e.g., Esu 1999). The molluscan fauna of Hohenmemmingen is typical of the Silvana Beds and thus supports a late Early to early Middle Miocene age for the sediments (European mammal Neogene zone MN 5, although no mammalian remains are known). Unfortunately, there are no current outcrops known, so only literature data is presently available for this locality. According to Fraas (1869) and Gottschick & Wenz (1916), the Silvana Beds in Hohenmemmingen consist of limestone that was seldom banked and occurred mostly as strongly weathered and irregular nodules (termed as "Knauer" in Gottschick & Wenz 1916).

3. Material and methods

The material studied for the present account consists exclusively of specimens from historical museum collections (see Table 1 for a full list of studied lots). This includes some of the voucher material of Gottschick & Wenz (1916), which was deposited in the SMNS, Germany. Unfortunately, not all of their material has been preserved to this day. A good portion of Gottschick's voucher material was housed in the SMNS, and Wenz's private collection was in Frankfurt a. M.; together, these collections must have contained all the originals of Gottschick & Wenz (1916), but a good portion of the SMNS and Wenz's collection were lost during World War II (Zilch 1960; Salvador et al. 2016a).

The best preserved gastropod species found are illustrated herein; images were obtained either with a Leica auto-montage apparatus or with a scanning electron microscope (SEM) at the SMNS. The main shell measurements were taken either with a digital caliper (for the larger specimens) or with the software ImageJ (Rasband 2012) and Leica Application Suite (LAS, v.3.8.0).

4. Results and discussion

In total, 23 gastropod species, all belonging to the Pulmonata, were found in the material from Hohenmemmingen available in museum collections. Five of these are freshwater species, while the remaining are terrestrial; a full species list can be found in Table 1 (classification follows Bouchet & Rocroi 2005 and Nordsieck 2014). These species are all common finds in coeval sediments from several other outcrops of the Silvana Beds. Therefore, we will refrain from giving a full description of the material here, since these species have been extensively explored and illustrated elsewhere (e.g., Harzhauser et al. 2014; Salvador et al. 2015, 2016c; Salvador & Rasser 2016). Examples of the best preserved specimens found in the present material are displayed in Figs. 2 and 3.

From the species listed by Gottschick & Wenz (1916), twelve could not be confirmed with the material available (Table 1). One special case that deserves further notice concerns the *Gyraulus* species reported by Gottschick & Wenz (1916): *G. applanatus* (Thomä, 1845), *G. dealbatus* (A. Braun, 1851) and *G. kleini* Gottschick & Wenz, 1916. Gottschick & Wenz (1916) reported that these species are linked by a series of intermediate forms, which was also observed in the present material. The specimens of these

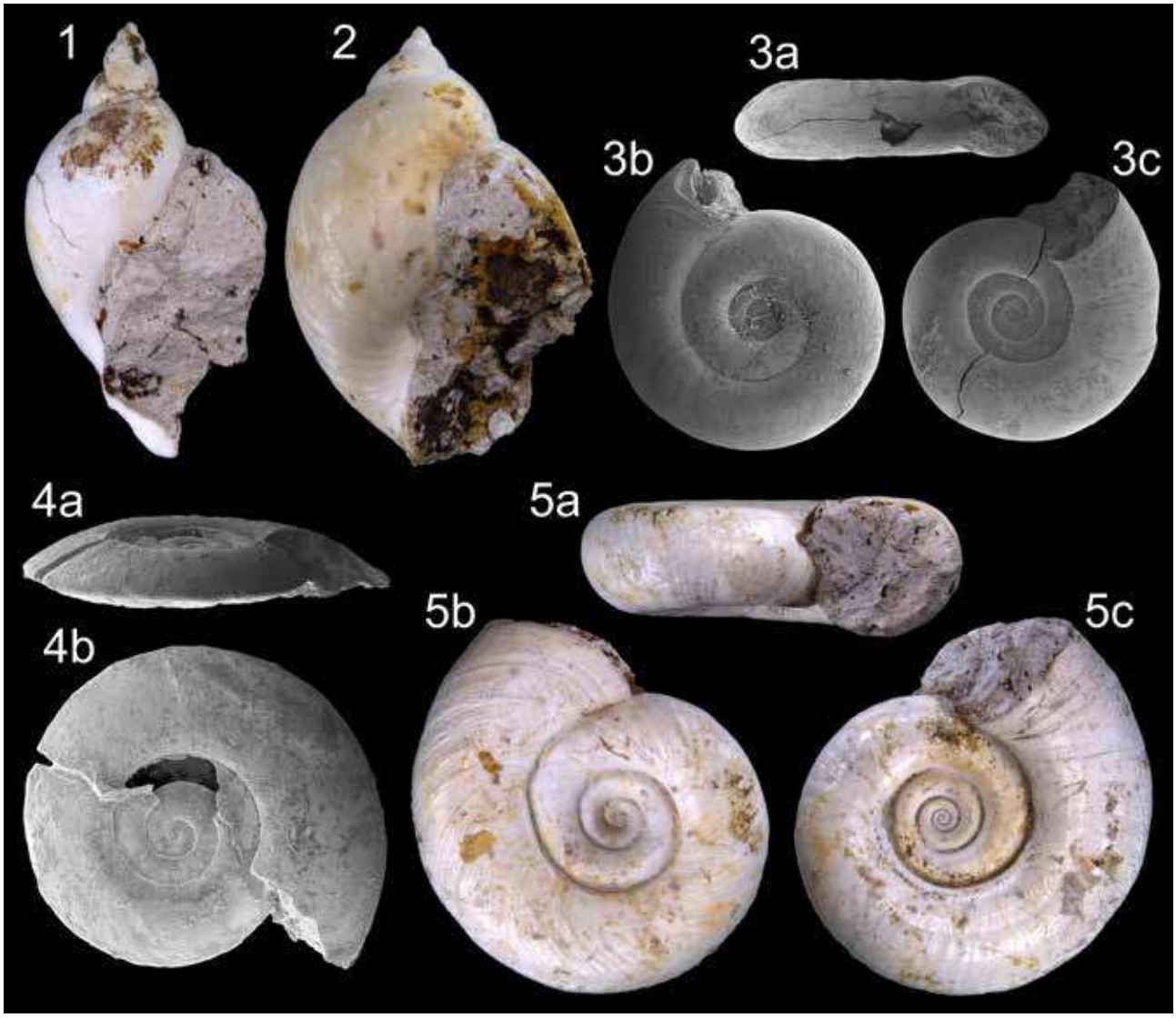

Fig. 2. Fossil freshwater gastropods from Hohenmemmingen. **1.** *Lymnaea dilatata*, SMNS 107257 (H = 12.7 mm, D = 6.5 mm). **2.** *Radix socialis*, SMNS 107235 (H = 19.1 mm, D = 13.0 mm). **3a.** *Gyraulus applanatus*, SMNS 107330/1 (H = 1.1 mm, D = 4.3 mm). **3b.** *Gyraulus applanatus*, SMNS 107330/2 (D = 4.1 mm). **3c.** *Gyraulus applanatus*, SMNS 107330/3 (D = 3.9 mm). **4a.** *Hippeutis subfontanus*, SMNS 107331/1 (H = 0.7 mm, D = 3.4 mm). **4b.** *Hippeutis subfontanus*, SMNS 107331/2 (D = 2.6 mm). **5a–c.** *Planorbarius mantelli*, SMNS 107335 (H = 8.1 mm, D = 22.6 mm).

Gyraulus species display a large amount of morphological variation, with the extremes described as distinct species, but with numerous intermediate forms; this phenomenon has also been observed in conspecifics from other OBM and OSM localities (e.g., Kowalke & Reichenbarcher 2005; Salvador & Rasser 2014; Salvador et al. 2016b). As a result, *Gyraulus dealbatus* is considered a synonym of *G. applanatus* (Kowalke & Reichenbarcher 2005; Salvador et al. 2016b); the status of *G. kleini* still remains uncertain, but it agrees with intermediate forms in the spectrum of morphological variation seem in *G. applanatus*.

From an actualistic palaeoecological approach, it can be surmised that the Miocene Hohenmemmingen environment featured a humid and warm forest cover, as indicated by most terrestrial gastropod genera. In special, *Discus*, *Leucochroopsis* and *Opeas* are considered very good indicators of this type of environment. No species with particular affinity for drier and more open habitats were recorded in the present material (but the literature cites *Granaria*; Table 1), although *Apula* is considered a potential representative of this environment in the literature; absence of other commonly xerophile genera, like

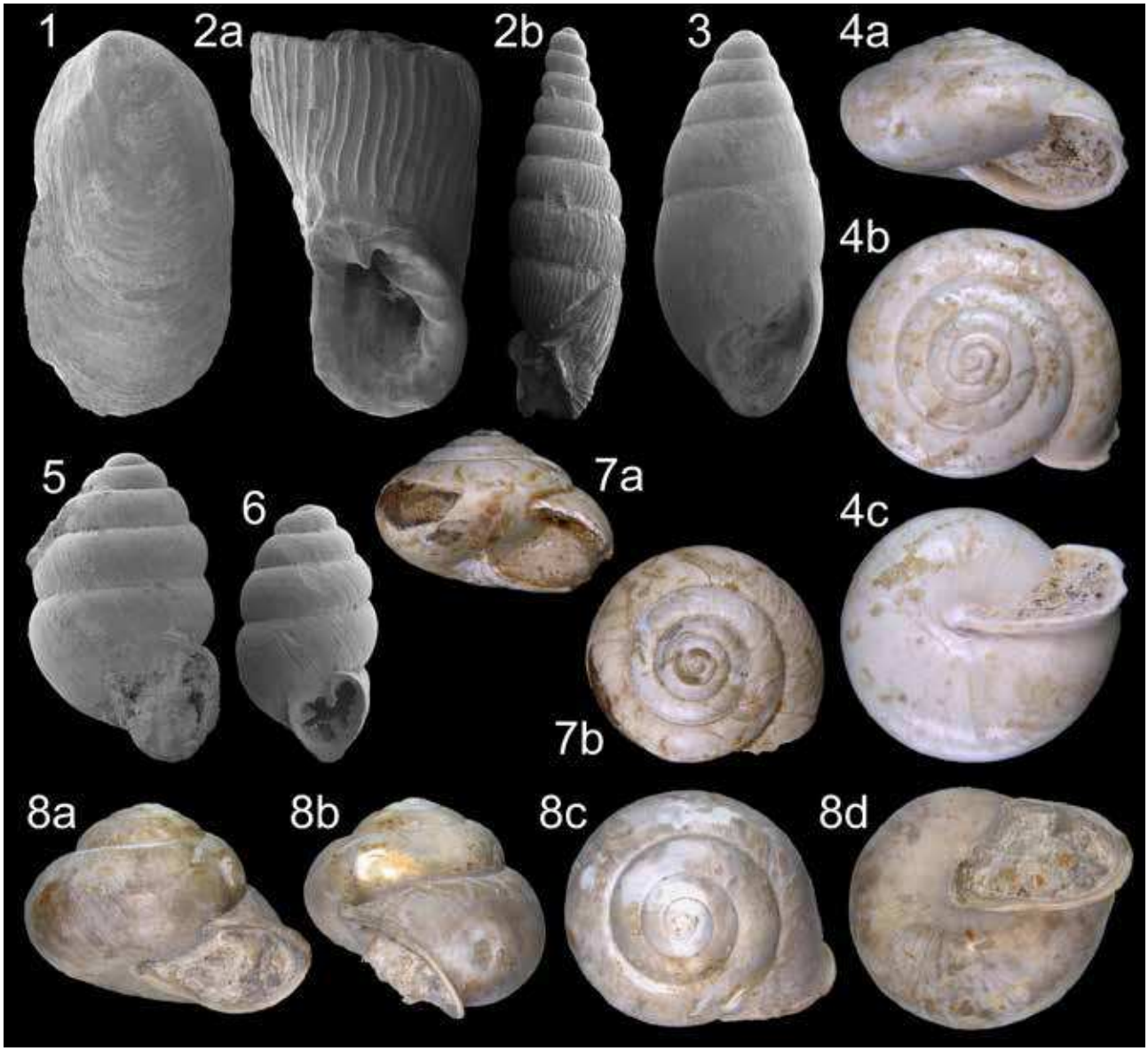

Fig. 3. Fossil terrestrial gastropods from Hohenmemmingen. **1.** *Deroceras* sp., SMNS 107332 (H = 6.0 mm). **2a.** *Pseudidyla moersingensis*, SMNS 66932 (H = 4.2 mm). **2b.** *Pseudidyla moersingensis*, SMNS 66937 (H = 8.7 mm, D = 2.6 mm). **3.** *Azeca lubricella*, SMNS 107333 (H = 4.6 mm, D = 2.1 mm). **4a–c.** *Apula coarctata*, SMNS 66292 (H = 7.9 mm, D = 11.9 mm). **5.** *Gastrocopta acuminata*, SMNS 67428 (H = 2.7 mm, D = 1.6 mm). **6.** *Gastrocopta nouletiana*, SMNS 107347/1 (H = 2.2 mm, D = 1.2 mm), shown in scale with *G. acuminata*. **7a, b.** *Leucochroopsis kleinii*, SMNS 65947 (H = 6.0 mm, D = 8.9 mm). **8a–d.** *Palaeotachea turonensis*, SMNS 66797 (H = 24.2 mm, D = 31.8 mm).

Vallonia and *Pupilla*, is also meaningful. The freshwater species all indicate a slow-moving or stagnant water body and the presence of *Hippeutis* in particular is a good indication of well-vegetated and likely shallow waters. Moreover, representatives of the terrestrial hygrophilic *Oxyloma* are usually found on the vegetation belt surrounding the water. A full discussion of the ecological affinities of these fossil genera can be found in Salvador & Rasser (2014) and Salvador et al. (2015, 2016c), based on the habitat requirements of Recent congeners (e.g., Kerney et al. 1983; Welter-Schultes 2012).

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Annotated type catalogue of the continental fossil gastropods in the Staatliches Museum für Naturkunde Stuttgart, Germany

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Abstract

The type specimens of fossil land and freshwater gastropods deposited in the Staatliches Museum für Naturkunde Stuttgart (SMNS), Germany, are listed and illustrated herein, comprising circa 180 nominal species-group taxa from Cenozoic fossil sites, mainly in the Baden-Württemberg and Bayern states in southern Germany. The list is arranged in alphabetical order of the specific epithets, with information on the original description, taxonomical status, type locality, record number in the collection and comments. A systematically arranged list of the taxa is also given, as well as a list arranged by authorship of the species-group names. At least one type specimen (holotype, lectotype, syntype or neotype) of each nominal species/subspecies is figured here, and further specimens were figured when they added information. In some cases lectotypes are designated herein.

Keywords: Cenozoic, Gastropoda, lectotype designation, non-marine snails, type specimens.

1. Introduction

The collection of fossil invertebrates in the Staatliches Museum für Naturkunde Stuttgart (SMNS; Stuttgart, Germany) comprises more than 200,000 fossil invertebrate lots, mostly of gastropods. Despite having specimens from diverse localities worldwide, the vast majority of the collection stems from Cenozoic fossil sites in the Baden-Württemberg and Bayern states in southern Germany. The collection includes the original material, particularly the name-bearing types, of 19th century and early 20th century paleontologists.

There is a current international consensus that all museums should publish inventories of their type specimens to make them more readily available for the scientific community at large. This is especially true for European fossil gastropods. Many species have a convoluted taxonomic history, often inadequate descriptions and illustrations (or no illustration at all), and little modern taxonomic analysis. Thus, future work would benefit greatly from examination of actual type specimens.

Therefore, we present here an annotated catalogue of the fossil non-marine gastropod types housed in the SMNS collection, arranged alphabetically according to the specific epithets. Furthermore, in order to facilitate locating information, the list of types is presented in two additional ways (Appendixes 1 and 2): a systematically arranged list of the taxa and a list arranged by authorship of the nominal species.

Abbreviations

Biozones: MN = European mammal Neogene zone; MP = European mammal Paleogene zone.

Institutions: GSL = Geological Society of London; MUWIE = Naturwissenschaftliche Sammlung des Museums Wiesbaden (Wiesbaden, Germany); NHMUK = Natural History Museum, London; SMF = Senckenberg Forschungsinstitut und Naturmuseum (Frankfurt am Main, Germany); SMNS = Staatliches Museum für Naturkunde Stuttgart (Stuttgart, Germany).

Shell measurements: H = shell height; D = shell, maximum width (diameter); h = height of operculum. The specimens were measured either with a digital caliper or with the aid of computer software.

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2. Material and methods

2.1. Collections

The SMNS has acquired collections of mollusks from many 19th and early 20th century authors. The fossil continental gastropods are stored in the collection of Cenozoic Invertebrates in the SMNS. This collection is separated into two parts: one sorted geographically, the other systematically. The former focuses on the fossil Lagerstätten of Württemberg (part of Baden-Württemberg), such as Steinheim am Albuch and Randeck Maar. The latter derives from various well-known collectors and can be further divided into two major parts: the Jooss collection and the Geyer collection.

The Jooss collection is the most important collection of gastropods in the SMNS, containing ca. 1,400 species and subspecies and totaling ca. 17,000 specimens. The gastropods are mainly from Germany and neighboring countries, from Oligocene to Pliocene (but focusing on the Miocene). Jooss has intensively exchanged material with colleagues and specimens from his their publications are present as well. A good portion of Clessin's original material was incorporated into the Jooss collection in 1913, whereby Jooss unfortunately replaced Clessin's labels by his own. The Geyer collection contains Geyer's fossil specimens (his Recent mollusks are housed in the Malacozoological collection of the SMNS). This part of the collection contains ca. 250 species and subspecies (ca. 70,000 specimens), mainly of Plio-Pleistocene age.

In addition to Jooss' and Geyer's, collections (or part of them) of other authors were acquired by the SMNS, such as Klein, Gottschick, Miller, Clessin, Kranz and Schütze. Moreover, several other authors contributed types to the SMNS collection, such as Sandberger, O. Boettger and Wenz. The original handwritten labels of most of these authors could be found (Fig. 1), even those of Wenz, whose collection in Frankfurt am Main was destroyed during World War II. Below we give brief information about those malacologists whose material in the SMNS collection are important for historical and/or scientific reasons (biographic notes can be found in Lambrecht et al. 1938 and Mayer 1976).

Stefan Clessin (*1833 in Würzburg, †24.12.1911) was a full-time military officer who later worked for the Bavarian state railway (Quenstedt 1957). He was especially interested in malacology (both Recent and fossil) and described many new nominal species.

David Geyer (*06.11.1855 in Köngen, †06.11.1932 in Stuttgart) was a schoolteacher in Stuttgart and a malacologist (Wenz 1933), famous for his book on Germany's molluscan fauna (Geyer 1927) and his remarkable collection of extant and Quaternary gastropods.

Franz Gottschick (*14.08.1865 in Zang, †18.09.1927 in Tübingen) was a forester in Steinheim am Albuch and Tübingen and was particularly known for his studies of the fossil snails from the Steinheim Basin (Heizmann & Reiff 2002).

Carlo G. H. Jooss (*27.10.1883 in Stuttgart, †unknown [after 1936]) was a private collector in Stuttgart. According to Staesche (1958), Jooss started his study at the University of Tübingen, but never graduated. He had extensive contacts with contemporary malacologists and paleontologists. According to the SMNS documentation, Jooss left Germany on July 1st 1929

Fig. 1. Examples of the original labels of each author. Note that on Sandberger's label, the locality and collection number were added later.

after selling his collection to the SMNS for 2,500 Reichsmark. Today's purchasing value of this price would be ca. € 10,000, which shows the importance of Jooss' collection at that time. It is not known where Jooss emigrated to, but there is a last trace of his whereabouts: a short note in the annual report of the American Museum of Natural History (New York) from 1936 states that the museum purchased 183 fossil invertebrates from Jamaica, Trinidad and British Guyana from "Dr. Carlo H. Jooss of Georgetown, British Guyana".

Adolf von Klein (*30.09.1805 in Stuttgart, †03.04.1892 in Stuttgart) was a military medic and zoologist. He authored three seminal papers about the Miocene and Pleistocene freshwater mollusks of Württemberg, in which he defined many new taxa.

Ferdinand Krauss (*09.07.1812 in Stuttgart, †14.09.1890 in Stuttgart) was the director of the "Naturalienkabinett", the predecessor of the SMNS. He was a zoologist, but also worked with fossils, publishing the first account of the brackish mollusk fauna of the Kirchberg Formation.

Konrad Miller (*21.11.1844 in Oppeltshofen, †25.07.1933) was a theologian and teacher who carried out archaeological and geological research; the latter especially about the Upper Marine and Upper Freshwater Molasses in Württemberg (Hablitzel 1994).

Fridolin C. W. Sandberger (*22.11.1826 in Dillenburg, †11.06.1898 in Würzburg) was head of the "Naturhistorischen Museum" in Wiesbaden (1849–1855), professor of Geology and Mineralogy at the "Polytechnikum" in Karlsruhe (1855–1863), and finally professor of Mineralogy and Geology in Würzburg (Beckenkamp 1899). Besides his geological studies, he also carried out research on fossil continental mollusks. While the largest part of his material is in the Wiesbaden Museum, some originals can be found in Stuttgart.

2.2. Missing material

As the fossil collections of Klein, Jooss, Gottschick, Miller, Clessin, Kranz, Schütze and Geyer had been acquired by the SMNS, it had been expected that the majority of their types of species-group taxa would be present here, but this does not seem to be the case. Some specimens were lost during World War II (Tomlin 1947; Lueger 1981), but others might have been lost during loans or due to neglect. Appendix 3 lists all nominal species-group taxa of these authors of which no type material could be identified in the SMNS collection.

2.3. Type Catalogue

We present this catalogue in the following manner. The species epithets are arranged in alphabetical order. In each entry, the first line gives the species epithet, followed by the author and year, and the original genus-group name. The spelling of the specific epithets is corrected according to the ICZN (1999), article 32.5 (i.e., capitalization, correct gender ending, removal of diacritical marks and conversion of umlauts). The spelling of the genus name is changed to the correct original spelling, as a species-group name published in combination with an emendation or incorrect spelling is deemed to have been published in combination with the correct original spelling (article 11.9.3.2 ICZN). For example, the name originally published as *Limnaeus conicus* Miller, 1907 is deemed to have been published as *Lymnaea conica* Miller, 1907 and, thus, it is cited here in the first line in this form. If a name is nomenclaturally invalid because it is a junior homonym, and if a replacement name exists, the invalid name is listed in its proper alphabetical place with a reference to its replacement name, where all relevant information is given for both names.

The second line gives the species-group name in its original (i.e., uncorrected) form, with bibliographic reference, and in some cases additional bibliographic references to the type material. The following lines give the type status, inventory number(s), type locality, type stratum and age. In order to facilitate the use of the relevant literature, and to emphasize the status of locality and lithostratigraphic terms as proper names (although the latter are usually historical and informal), these have not been translated into English, but translations are given for the information of the reader unfamiliar with the German language. The entry "Taxonomic status" provides a reference or references to the most up-to-date taxonomic treatment of the name in question. It is not intended to present in this paper a taxonomic revision of the taxa involved. In a few cases, hitherto unpublished views of the authors are cited as such, as well as divergent opinions.

At least one type specimen (holotype, lectotype, syntype or neotype) of each nominal species/subspecies is figured here, and further original specimens were figured when they added information. Many nominal species/subspecies are figured here for the first time. Moreover, as authors often did not designate holotypes from their material, some lectotypes are designated herein.

The identification of the type series of nominal species proposed by Sandberger (1870–1875) requires a brief discussion here. Sandberger made many names available by publishing illustrations on plates with captions, thereby publishing new species names up to three years earlier than the pertinent text. It could therefore be argued that only the figured specimen(s) constitute the type series, but we argue that the entire material included in the published text should be regarded as the type series because it is inconceivable that Sandberger would not have this material at his disposal when he decided that a particular form is a new species. This assumption is in accordance with Article 72.4.1.1 ICZN: "For a nominal species or subspecies established before 2000, any evidence, published or unpublished, may be taken into account to determine what specimens constitute the type series." Sandberger's later text is deemed to be such evidence. Obviously the

possibility exists that he may have acquired some material after the publication of the figures, but this can neither be proven nor disproven. To exclude the possibility that such (hypothetical) material be included in the type series, a lectotype from the proven original material would need to be selected. Such proof will in most cases only be the identification of the figured specimen(s). In this paper we refrain from such lectotype fixations, because they should be done only when the Sandberger collection in the MUWIE (and possible other institutions) have been checked.

We accepted all infraspecific names as of subspecies rank and therefore as available (article 45.6 ICZN), even where authors, notably Jooss (1912) and Gottschick (1911–1922), differentiated two or even three categories of infraspecific taxa. It proved impossible to determine consistently whether those names were intended as of subspecific or infrasubspecific rank. None of the authors gave an explanation for the meaning of the terms "var." [varietas] and "f." [forma]; the way these terms were applied, it seemed in some cases that "forma" denoted variants of lower rank than "varieta"', but in others no consistent or convincing difference of taxonomic status could be inferred. Moreover, the ICZN (articles 10.2 and 45.6.4.1) accepts even infrasubspecific names published before 1961 as available if they had been so accepted by subsequent authors, which may have happened in some cases.

The authorship of names had to be reviewed in accordance with article 50.1 ICZN. It had been general practice in the 19th century and even later to accord authorship to the person who coined a name, regardless whether he published it in a way that satisfied the criteria of availability or not, or if he even did not publish it at all, as in the case of names in manuscripts, written communications or collection labels. Finally, the evidence for the actual dates of many publications were checked. Details are given in the reference list.

Several of the nominal species-group taxa were in this paper identified as junior primary or secondary homonyms. Although articles 57.2 and 60.1 ICZN require the junior homonyms to be replaced, we have refrained from so doing except in one case, because (1) of a high probability that article 23.9.5 may be applicable in many cases, i.e., if the primary homonyms were no longer treated as congeneric after 1899, and/or (2) the possibility of a subjective synonym being available as a replacement name could not be categorically ruled out without a taxonomic revision of nominal species similar to the junior homonym (such revision, however, is beyond the scope of this paper). According to article 23.9.5, these cases need to be referred to the ICZN for a ruling.

The classification used here follows Bouchet et al. (2005), complemented by Nordsieck's review (2014); taxa not covered by these works follow Zilch (1959–1960). Where available, other taxonomic revisions were taken into consideration, but all too often the fallback option was to quote Wenz's (1923–1930) synonymies and genus allocations. In many cases the taxonomic status of the nominal species-group taxa is uncertain and in need of revision. Likewise, the stratigraphical and age data presented here are the currently accepted ones whenever possible. However, several of the fossil outcrops remained unstudied after the late 19th and early 20th centuries' works and thus the age given (found on these papers) might be misleading.

3. List of types

acuminata* (Klein, 1846), *Pupa (Plate 1, Figs. 1–2)
Pupa acuminata Klein, 1846: 75, pl. 1, fig. 19a, b.

Syntypes: SMNS 106361 (2 specimens, from Hohenmemmingen).

Type localities: Germany: Baden-Württemberg: Dächingen, Öpfingen and Hohenmemmingen, Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: Valid, as *Gastrocopta (Albinula) acuminata* (Klein, 1846) (revised by Manganelli & Giusti 2000). Family Gastrocoptidae.

Remarks: Klein based the species on incompletely preserved specimens, and figured one with a visible columellar lamella; nevertheless, this feature cannot be seen in the two present specimens.

alsaticus* Jooss, 1918a**, ***Zonites (Grandipatula) (Plate 1, Fig. 3a, b)
Zonites (Grandipatula) alsaticus Jooss, 1918a: 166, figs. 1–3.

Holotype: SMNS 65581.

Type locality: France: Alsace: Bouxwiller ("Buchsweiler"), Bastberg, Süßwasserkalk [freshwater limestone] of the Bouxwiller Formation.

Age: Middle Eocene (Lutetian; MP 13).

Taxonomic status: Valid, as *Grandipatula alsatica* (Jooss, 1918a). Family Grandipatulidae.

alveum* Jooss, 1918b, *Galactochilus (Plate 1, Fig. 4a–c)
See *alveus* Sandberger, 1875, *Helix*.

alveus* Sandberger, 1875, *Helix (Plate 1, Fig. 4a–c)
Helix alveus Sandberger, 1875: 459 (Markbronn, "Nur ein fast vollständiges Stück in der Sammlung des Herrn Caplan Dr. Miller (…)") [non *Helix alveus* C.B. Adams, 1850 (5): 80].
Galactochilus alveum Jooss, 1918b: 293.

? Syntype: SMNS 106362.

Type locality: Germany: Baden-Württemberg: Blaustein (Markbronn), upper "Rugulosa-Thalfinger-Schichten".

Age: Early Miocene (Aquitanian; MN 2).

Taxonomic status: Potentially valid, as *Pseudochloritis*? *alveus* (Sandberger, 1875). Family Elonidae (Eloninae) or Helicidae (Ariantinae).

Remarks: (1) The species epithet is a noun in apposition (alveus, Lat.: a beehive) and therefore immutable. The name

alveum Jooss is the same word with a variant gender ending, and hence an unjustified emendation. The intentional spelling change is evident by Jooss citing *Helix alveus* Sandberger correctly. Names published as unjustified emendations are available and can be utilized to substitute junior primary homonyms (Art. 33.2.3 ICZN). For the reasons given in the preceding chapter, we refrain from substituting the name *alveus* Sandberger for the time being. (2) Sandberger (1875) mentioned one nearly complete specimen in the collection of Miller, and damaged specimens from Gamerschwang and Öpfingen. The present specimen is the former, as it bears original labels from Sandberger and Miller. Jooss' label also indicates it as Sandberger's original material. (3) Jooss (1918b), believing erroneously that Sandberger had published a nomen nudum, treated "*alveum*" as a new species and provided a redescription (using the same type as Sandberger). As Jooss' intention was to redescribe *Helix alveus* Sandberger, which is cited as a synonym, *Galactochilus alveum* "Jooss" is not a new nominal species. (4) Sandberger compared this species with *Cyrtochilus expansilabris* (Sandberger), which is a significantly smaller species. *Galactochilus* species are larger than *alveus*, but similar in habitus: e.g., *Galactochilus ehingensis* as illustrated by Sandberger (1875: 457, pl. 29, fig. 10, from Eggingen near Ulm) measures 26–36 mm, while *alveus* measures 20–24 mm. *Pseudochloritis* species are of similar size, but usually with a more depressed spire and at least partially open umbilicus (Binder 2008).

amerbachensis* Jooss, 1912a, *Limnophysa (Plate 1, Fig. 5)
Limnophysa amerbachensis Jooss, 1912a: 90; Jooss, 1912b: 168, pl. 4, fig. 8, 8a.

Syntypes: SMNS 23918 (2 specimens).

Type locality: Germany: Bavaria: Dobelbuck ("Hobelsbuck") near Amerbach (Wemding), *Pomatias*-Süßwasserkalk des Rieses [*Pomatias* freshwater limestone of the Ries area].

Age: Early Oligocene (Rupelian).

Taxonomic status: Junior synonym of *Stagnicola fabulum* (Brongniart, 1810) (fide Kadolsky 2014). Family Lymnaeidae (Lymnaeinae).

ammoni* Clessin, 1894, *Hyalinia (Vitrea) (Plate 1, Fig. 6a, b)
Hyalina (Vitrea) Ammoni Clessin, 1894: 29.

Syntypes: SMNS 106363 (3 specimens) and 106364 (1 specimen).

Type locality: Germany: Bavaria: Nittendorf (Undorf), mittlere Silvanaschichten [middle Silvana-beds].

Age: Late Early/early Middle Miocene (Karpatian–Badenian; MN 5).

Taxonomic status: Valid as *Vitrea ammoni* (Clessin, 1894) (fide Wenz 1923). Family Pristilomatidae.

Remarks: The syntypes seem to belong to several species (and genera?), as remarked by Clessin (1894) himself. We figure here the specimen which was alone in the lot (SMNS 106364), which possibly is the one to which the description refers to. In the original description, Clessin lists seven specimens; the extra three specimens may be lost, as one lot of this material (SMNS 45257/2005) was not found in the collection.

angitorta* Jooss, 1912c, *Helicodonta (Helicodonta* s. str.*) involuta (Plate 1, Fig. 7a–c)
Helicodonta (Helicodonta s. str.*) involuta* var. *angitorta* Jooss, 1912c: 34, pl. 2, fig. 3, 3a.

Holotype: SMNS 106365.

Type locality: Germany: Baden-Württemberg: Steinheim am Albuch, sand pit Pharion, *Pupa* (i.e., *Granaria*) layer (upper *Gyraulus discoideus* zone to *G. trochiformis* zone), Steinheimer Seeschichten.

Age: Middle Miocene (MN 7).

Taxonomic status: Valid, as *Protodrepanostoma involutum angitortum* (Jooss, 1912) (fide Kadolsky herein). Family Helicodontidae.

angulosus* Miller, 1907, *Archaeozonites (Plate 1, Fig. 8a, b)
Archaeozonites angulosus Miller, 1907: 443, pl. 8, fig. 13a–c.

Syntype: SMNS 27620.

Type locality: Germany: Baden-Württemberg: Blaustein (Arnegg), karst fissure limestone.

Age: Early Oligocene (Rupelian).

Taxonomic status: Valid. Family Archaeozonitidae.

Remarks: Miller (1907) mentioned several specimens.

antiqua* Zieten, 1832, *Pupa
See *schuebleri* Klein, 1846, *Pupa*.

antiqua* Klein, 1852, *Glandina (Achatina) (Plate 1, Fig. 9)
Glandina (Achatina) antiqua Klein, 1852: 162, pl. 3, fig. 9.

Syntypes: SMNS 23908 (3 specimens, from Ulm).

Type localities: Germany: Baden-Württemberg: near Ehingen, Michaelsberg near Ulm, near Hohenmemmingen.

Age: Early Miocene (Aquitanian; MN 2).

Taxonomic status: Junior synonym of *Palaeoglandina gracilis* (Zieten, 1832). Family Oleacinidae.

Remarks: The specimens' label indicates only Ulm. The specimen figured by Klein (1852) is the one indicated as SMNS 23908a in the collection.

antiqua* Miller, 1907, *Patula (Plate 1, Fig. 10a–c)
Patula antiqua Miller, 1907: 454, pl. 9, fig. 13a–c.

Syntype: SMNS 27641.

Type locality: Germany: Bavaria: Bachhagel, karst fissure limestone.

Age: Eocene.

Taxonomic status: Valid, as *Discus antiquus* (Miller, 1907) comb. nov. Family Discidae.

Remarks: Miller (1907) reported this species as frequent.

antiquior* Miller, 1907, *Clausilia (Plate 1, Fig. 11)
Clausilia antiquior Miller, 1907: 455, pl. 9, fig. 16.

Syntype: SMNS 27644.

Type locality: Germany: Bavaria: Bachhagel, karst fissure limestone.

Age: Eocene.

Taxonomic status: Valid, as *Triptychia antiquior* (Miller, 1907) (fide Schnabel 2007: 27, pl. 1, fig.1). Family Filholiidae.

Remarks: Miller (1907) reported two fragmentary specimens, of which Schnabel (2007) designated one invalidly as holotype.

arneggensis* Wenz, 1923, ?*Pomatias (Plate 1, Fig. 12)
Cyclotus scalaris Miller, 1907: 439, pl. 7, fig. 2 a–e [non *Cyclostoma scalare* Pfeiffer, 1851a (: 250), placed in genus *Cyclotus* by Pfeiffer 1851b (: 135, no. 34) and Reeve 1863 (: pl. 9, fig. 51)].
?*Pomatias arneggense* [sic] Wenz, 1923: 1802.

Lectotype (herein): SMNS 27614-a.

Paralectotype: SMNS 27614-b (1 operculum).

Type locality: Germany: Baden-Württemberg: Blaustein (Arnegg), karst fissure limestone.

Age: Early Oligocene (Rupelian).

Taxonomic status: Valid, as *Pomatias (Neobembridgia) arneggensis* Wenz, 1923 (fide Kadolsky 1989). Family Pomatiidae (Pomatiinae).

Remarks: The operculum is too small to belong to the shell and thus must come from a different individual. We select here the shell as the lectotype.

arneggensis* Miller, 1907, *Trochomorpha (Plate 1, Fig. 13a, b)
Trochomorpha arneggensis Miller, 1907: 443, pl. 8, fig. 14a–c.

Syntypes: SMNS 27621 (3 specimens).

Type locality: Germany: Baden-Württemberg: Blaustein (Arnegg), karst fissure limestone.

Age: Early Oligocene (Rupelian).

Taxonomic status: Valid, as *Archaeozonites*? *arneggensis* (Miller 1907). Family Archaeozonitidae.

Remarks: Wenz (1923: 251) lists this taxon as a possible synonym of *Archaeozonites angulosus* Miller, 1907. This is incorrect, as *arneggensis* is almost half the size at a similar number of whorls. It is therefore rather small for the genus *Archaeozonites* and may in fact not belong to it, but a more definite genus attribution requires further study.

arneggensis* Miller, 1907, *Laminifera (Plate 1, Fig. 14a–c)
Clausilia (Laminifera) n. sp. O. Boettger, 1877: 106.
Laminifera arneggensis Miller, 1907: 446, textfig. 23, pl. 8, fig. 23a.

Syntypes: SMNS 27629 (3 specimens).

Type locality: Germany: Baden-Württemberg: Blaustein (Arnegg), karst fissure limestone.

Age: Early Oligocene (Rupelian).

Taxonomic status: Valid (fide Nordsieck 2000, 2007). Family Clausiliidae (Laminiferinae).

Remarks: The only specimen with part of the body whorl preserved does not agree well with the figures provided by Miller (1907), because it does not show the detachment of the body whorl, which is a typical character of *Laminifera* and is strongly developed in *L. arneggensis*, according to Miller's figures and text. Probably the detached part of the last whorl shown by Miller (1907) has broken off and would thus be lost.

arneggensis* Miller, 1907, *Bulimus (Petraeus) (Plate 1, Fig. 15)
Bulimus (Petraeus) arneggensis Miller, 1907: 446, pl. 8, fig. 21a–c.

Syntypes: SMNS 36777 (4 specimens).

Type locality: Germany: Baden-Württemberg: Blaustein (Arnegg), karst fissure limestone.

Age: Early Oligocene (Rupelian).

Taxonomic status: Valid, as *Palaeomastus arneggensis* (Miller, 1907) comb. nov. Family Enidae. The shell shows the conical spire considered as diagnostic for the genus *Palaeomastus* H. Nordsieck, 2014.

badensis* Jooss, 1924, *Zonites (Aegopis) algiroides (Plate 1, Fig. 16a, b)
Zonites (Aegopis) algiroides badensis Jooss, 1924: 193, pl. 11, figs. 5–7.

Holotype: SMNS 65634.

Type locality: Germany: Baden-Württemberg: Blumberg (Zollhaus), Helicidenmergel [helicid marls].

Age: Early Miocene (Ottnangian; MN 3–4).

Taxonomic status: Unknown, possibly a synonym of *Miozonites algiroides* (Reuss, 1849). Family Archaeozonitidae.

baumbergeri* Jooss, 1924, *Cepaea eversa (Plate 1, Fig. 17a, b)
Cepaea eversa baumbergeri Jooss, 1924: 200, pl. 11, figs. 24–27.

Syntypes: SMNS 106366 (Germany: Baden-Württemberg: Stubersheim–Geislingen), 106367 and 106368 (Switzerland: Kt. Aargau: Wölflinswil).

Type locality: Numerous unspecified localities, Helicidenmergel [helicid marls]. Jooss (1924) figured specimens from more than one locality.

Age: Miocene ("Mittelvindobon").

Taxonomic status: Unknown, probably a synonym of *Megalotachea eversa* (Deshayes, 1851). Family Helicidae (Helicinae).

bilamellatus* Clessin, 1885, *Strobilus (Plate 2, Fig. 1)
Strobilus bilamellatus Clessin, 1885: 79.

Holotype: SMNS 106369.

Type locality: Germany: Bavaria: Nittendorf (Undorf), mittlere Silvanaschichten [middle Silvana-beds].

Age: Late Early/early Middle Miocene (Karpatian–Badenian; MN 5).

Taxonomic status: Synonym of *Strobilops costata* (Clessin, 1877). Family Strobilopsidae.

blaviana* Miller, 1907, *Helix (Gonostoma) (Plate 2, Fig. 2a, b)
Helix (Gonostoma) blaviana Miller, 1907: 445, pl. 8, fig. 19a, b.

Syntypes: SMNS 27626 (3 specimens).

Type locality: Germany: Baden-Württemberg: Blaustein (Arnegg), karst fissure limestone.

Age: Early Oligocene (Rupelian).

Taxonomic status: Subjective synonym of *Klikia? praeosculina* (Miller, 1907) (fide Wenz 1923). Family Elonidae (Klikiinae) or Helicidae (Ariantinae).

boettgeriana* Clessin, 1877, *Hyalinia (Plate 2, Fig. 3a, b)
Hyalina Böttgeriana Clessin, 1877: 35.
Hyalina Boettgeri Clessin, 1885: 75 [unjustified emendation or spelling error].

Holotype: SMNS 106370.

Type locality: Germany: Bavaria: Nittendorf (Undorf), mittlere Silvanaschichten [middle Silvana-beds].

Age: Late Early/early Middle Miocene (Karpatian–Badenian; MN 5).

Taxonomic status: Valid, as *Perpolita boettgeriana* (Clessin, 1877) (fide Kadolsky herein). Family Oxychili-

dae (Godwiniinae). WENZ (1923), however, placed the species in *Zonitoides* (family Gastrodontidae).

brancai* SCHÜTZE *in* BRANCA & FRAAS, 1908, *Lymnaea (Plate 2, Fig. 4)
Limnaeus Brancaï SCHÜTZE *in* BRANCA & FRAAS, 1908: 19, figs. 9–10.

Lectotype (herein): SMNS 11897-a.

Paralectotype: SMNS 11897-b (1 specimen).

Type locality: Germany: Bavaria: Monheim (Weilheim im Ries), grey freshwater limestone block in Bunter Breccie [varicoloured breccia, Ries ejecta].

Age: Early Oligocene.

Taxonomic status: Potentially valid, as *Lymnaea* (s.l.) *brancai* SCHÜTZE *in* BRANCA & FRAAS, 1908. Family Lymnaeidae (Lymnaeinae).

Remarks: We designate here as lectotype the largest and best preserved specimen (SCHÜTZE in BRANCA & FRAAS 1908: fig. 9).

bulimoides* KLEIN, 1846, *Melania (Plate 2, Figs. 5–6)
Melania bulimoides KLEIN, 1846: 81, pl. 2, fig. 1a, b [non *Melania bulimoides* EUDES-DESLONGCHAMPS, 1842 (: 229, pl. 12, fig. 15)].

Syntypes: SMNS 106371 (2 specimens and the external mold of one of them).

Type locality: Germany: Baden-Württemberg: Grimmelfingen near Ulm, Grimmelfinger Schichten [Grimmelfingen Beds].

Age: Late Early Miocene (Burdigalian/Ottnangian, MN 4a).

Taxonomic status: Uncertain; WENZ (1923) lists this species as *Galba bulimoides*, but this allocation seems mistaken. Family uncertain.

Remarks: (1) KLEIN (1846) figures a complete specimen, which is either lost or a reconstruction attempt, possibly based on the two preserved syntypes and the external mold. (2) Substitution of the junior primary homonym is not mandatory if the conditions of Article 23.9.5 ICZN are met; a request for a ruling of the Commission under its plenary powers to validate the junior homonymous name is intended.

bythiniformis* MILLER, 1907, *Pupa (Plate 2, Fig. 7)
Pupa bythiniformis MILLER, 1907: 455, pl. 9, fig. 17.

Holotype: SMNS 27645.

Type locality: Germany: Bavaria: Bachhagel, karst fissure limestone.

Age: Eocene.

Taxonomic status: Uncertain, listed as *Abida*? *bythiniformis* (MILLER, 1907) by WENZ (1923). Family Chondrinidae.

capellinii* SANDBERGER, 1873, *Strophostoma anomphalus (Plate 2, Fig. 8a–c)
Strophostoma Capellini FRAAS, 1869: 11 [nomen nudum].
Strophostoma anomphalus var. SANDBERGER, 1871: pl. 21, fig. 19, 19b.
Strophostoma anomphalus var. *Capellinii* SANDBERGER, 1873: 328; SANDBERGER, 1875: 354.

Syntypes: SMNS 22180 (2 specimens).

Type locality: Germany: Baden-Württemberg: Blaustein (Arnegg), karst fissure limestone.

Age: Early Oligocene (Rupelian).

Taxonomic status: Possibly valid, as *Ferussina capellinii* (SANDBERGER, 1873) or *F. anomphalus capellinii*. Family Ferussinidae.

Remarks: SANDBERGER (1873) stated that his "*Strophostoma anomphalus*" came from the "Meeressand" (now Alzey Formation) of Waldböckelheim and Weinheim in the Mainz Basin (Rheinland-Pfalz), and that he figured the only intact specimen from the Paleontological Collection in Munich. According to SANDBERGER, the specimens from Arnegg differ morphologically from those of the Mainz Basin and were named var. *capellinii* by him.

carinatus* MILLER, 1907, *Archaeozonites (Plate 2, Fig. 9a, b)
Archaeozonites carinatus MILLER, 1907: 454, pl. 9, fig. 11.

Lectotype (herein): SMNS 27639-a.

Paralectotypes: SMNS 27639-b, c, d (3 specimens).

Type locality: Germany: Bavaria: Bachhagel, karst fissure limestone.

Age: Eocene.

Taxonomic status: Valid. Family Archaeozonitidae.

Remarks: The best preserved specimen is designated here as the lectotype. The illustration presented by MILLER (1907) in the original description is a reconstruction based on this specimen.

carinatus* JOOSS, 1912a, *Zonites (Archaeozonites) risgoviensis (Plate 2, Fig. 10a, b)
Zonites (Archaeozonites) risgoviensis var. *carinata* JOOSS, 1912a: 89; JOOSS 1912b: 162, pl. 4, fig. 3c [non *Archaeozonites carinatus* MILLER, 1907 (: 454, pl. 9, fig. 11)].

Holotype: SMNS 23921.

Type locality: Germany: Bavaria: Dobelbuck ("Hobelsbuck") near Amerbach (Wemding), *Pomatias*-Süßwasserkalk des Riesgebietes [*Pomatias* freshwater limestone of the Ries area].

Age: Early Oligocene (Rupelian).

Taxonomic status: Junior synonym of *Omphalosagda pyramidalis* (JOOSS, 1912) (fide KADOLSKY, unpublished). Family Archaeozonitidae.

carinulata* KLEIN, 1853, *Helix (Plate 2, Fig. 11a–c)
Helix carinulata KLEIN, 1853: 208, pl. 5, fig. 5.

Syntypes: SMNS 106372 (6 specimens).

Type locality: Germany: Baden-Württemberg: Zwiefalten (near Mörsingen), Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: Junior synonym of *Leucochroopsis kleinii* (KLEIN, 1846) (fide WENZ 1923). Family Hygromiidae (Hygromiinae).

***conica* MILLER, 1907, *Lymnaea*(?)** (Plate 2, Fig. 12)
Limnaeus(?) *conicus* MILLER, 1907: 452, pl. 9, fig. 6 [non *Lymnaea palustris conica* JEFFREYS, 1862 (: 114)].

Holotype: SMNS 27635.

Type locality: Germany: Bavaria: Bachhagel, karst fissure limestone.

Age: Eocene.

Taxonomic status: Potentially valid, but insufficiently known. Questionably placed by WENZ (1923) in *Galba*. Family Lymnaeidae (Lymnaeinae).

Remarks: Substitution of the junior primary homonym is not mandatory if the conditions of Article 23.9.5 ICZN are met; a request for a ruling of the Commission under its plenary powers to validate the junior homonymous name is intended.

coniuncta* Berz & Jooss, 1927, *Cepaea renevieri (Plate 2, Fig. 13a, b)
Cepaea renevieri var. *coniuncta* Berz & Jooss, 1927: 203, fig. 1.

Syntypes: SMNS 101369 (figured by Berz & Jooss 1927), 101370 (3 specimens), 101372 (2 specimens).

Type localities: Germany: Baden-Württemberg: Oggenhausen, several outcrops (Oggenhausen 1 sensu Böttcher et al. 2009), Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (MN 5).

Taxonomic status: Synonym of *Palaeotachea renevieri* (Maillard, 1892). Family Helicidae (Helicinae).

conoidea* Krauss, 1852, *Paludina (Plate 2, Fig. 14)
Paludina conoidea Krauss, 1852: 141, pl. 3, fig. 1 [non *Paludina conoidea* de Reynies, 1844 (: 4); Küster, 1852 (: 43, pl. 9, figs. 3–7)].

Syntypes: SMNS 106373 (5 specimens, from same locality and stratum) and 25500/2005 (lost material).

Type locality: Germany: Baden-Württemberg: Unterkirchberg (now Illerkirchberg), bläulichgrauer weicher Thon des Fischlagers [bluish-gray soft clay of the fish beds] of the Kirchberg Formation.

Age: Late Early Miocene (Burdigalian/ Ottnangian; MN 4b).

Taxonomic status: Valid, as *Ctyrokya conoidea* (Krauss, 1852) (fide Schlickum 1965). Family Hydrobiidae (Hydrobiinae).

Remarks: Substitution of the junior primary homonym is not mandatory if the conditions of Article 23.9.5 ICZN are met; a request for a ruling of the Commission under its plenary powers to validate the junior homonymous name is intended.

constrictelabiata* Miller, 1907, *Helix (Plate 2, Fig. 15a, b)
Helix constrictelabiata Miller, 1907: 455, pl. 9, fig. 15.

Holotype: SMNS 27643.

Type locality: Germany: Bavaria: Bachhagel, karst fissure limestone.

Age: Eocene.

Taxonomic status: Valid, as *Loganiopharynx constrictelabiatus* (Miller, 1907) (fide Nordsieck 2014). Family Hygromiidae.

convexitesta* Jooss, 1912b, *Cepaea (Palaeotachea) (Plate 2, Fig. 16a, b)
Cepaea (Palaeotachea) convexitesta Jooss, 1912b: 164, pl. 4, fig. 5a–c.

Syntypes: SMNS 23914 (2 specimens).

Type locality: Germany: Bavaria: Dobelbuck ("Hobelsbuck") near Amerbach (Wemding), *Pomatias*-Süßwasserkalk des Riesgebietes [*Pomatias* freshwater limestone of the Ries area].

Age: Early Oligocene (Rupelian).

Taxonomic status: Valid as *Palaeotachea convexitesta* (Jooss, 1912b) (fide Kadolsky herein). Family Helicidae (Helicinae).

costataeformis* Jooss, 1912c, *Vallonia (Plate 2, Fig. 17a, b)
Vallonia costataeformis Jooss, 1912c: 35, pl. 2, fig. 5, 5a.

Holotype: SMNS 106375.

Type locality: Germany: Baden-Württemberg: Steinheim am Albuch (according to Gerber [1996] a recent contamination of the Steinheimer Seeschichten [Steinheim Lake beds]).

Age: originally assumed to be Middle Miocene (MN 7), but now interpreted as recent.

Taxonomic status: Synonym of *Vallonia costata* (O. F. Müller, 1774) (fide Gerber 1996). Family Valloniidae.

costata* Gottschick, 1911, *Patula (Charopa) (Plate 3, Fig. 1a–c)
Patula (Charopa) costata Gottschick, 1911: 501, pl. 7, fig. 15.

Syntype: SMNS 106376.

Type locality: Germany: Baden-Württemberg: Steinheim am Albuch, *laevis*-zone of the Steinheimer Seeschichten [Steinheim Lake beds].

Age: Middle Miocene (MN 7).

Taxonomic status: Valid, as *Discus costatus* (Gottschick, 1911) comb. nov. Family Discidae.

Remarks: Gottschick (1911) mentioned two localities in the Steinheim Basin; thus he must have had more than one specimen at his disposal.

costatus* Klein, 1846, *Planorbis (Plate 3, Figs. 2a, b)
Planorbis costatus Klein, 1846: 78, pl. 1, fig. 24a–c.

Lectotype (herein): SMNS 23907-1.

Paralectotypes: SMNS 23907-2 (9 specimens, from same locality and stratum).

Type locality: Germany: Baden-Württemberg: Steinheim am Albuch, Steinheimer Seeschichten [Steinheim Lake beds].

Age: Middle Miocene (MN 7).

Taxonomic status: Valid, as *Gyraulus costatus* (Klein, 1846). Family Planorbidae (Planorbinae).

Remarks: The best preserved specimen in Klein's original material, which fits the original description (Klein 1846) and figure very well, is here designated as lectotype.

costatus* Clessin, 1877, *Strobilus (Plate 3, Fig. 3)
Strobilus costatus (Sandberger MS) Clessin, 1877: 37.

Syntype?: SMNS 106374.

Type locality: Germany: Bavaria: Nittendorf (Undorf), Silvanaschichten [middle Silvana-beds].

Age: Late Early/early Middle Miocene (Karpatian–Badenian; MN 5).

Taxonomic status: Valid, as *Strobilops costata* (Clessin, 1877). Family Strobilopsidae.

Remarks: The specimen's label states that it is the material used by Clessin (1885), not 1877. Clessin (1877) reported the species as very rare, without stating the number of specimens, but his measurements correspond very closely to the present specimen. A second lot is recorded as "on loan" in the collection (SMNS 45172/2005), but could not be traced.

crassa* Clessin, 1894, *Amalia (Plate 3, Fig. 4)
Amalia crassa Clessin, 1894: 27, pl. 1, fig. 10.

Syntype?: SMNS 106378.

Type locality: Germany: Bavaria: Nittendorf (Undorf), Silvanaschichten [middle Silvana-beds].

Age: Late Early/early Middle Miocene (Karpatian–Badenian; MN 5).

Taxonomic status: Valid, as *Milax crassus* (Clessin, 1894). Family Milacidae.

Remarks: In the original description, Clessin (1894) lists "numerous" specimens, housed in the private collection of Diez. The single specimen in his own collection is most likely one of these, which Clessin retained himself.

crassissimus* Jooss, 1902, *Limax (Plate 3, Fig. 5)
Limax crassissimus Jooss, 1902: 303, fig. 1.

Holotype: SMNS 106377.

Type locality: Germany: Baden-Württemberg: Steinheim am Albuch, the Steinheimer Seeschichten [Steinheim Lake beds].

Age: Middle Miocene (MN 7).

Taxonomic status: Potentially valid. Family Limacidae.

Remarks: Falkner (in litt., 15.8.2015) suggested that the specimen could be the shell of a Recent *Limax* species.

crassiventer* nom. nov., *Granaria (Plate 7, Fig. 1)
See *pachygastra* Miller, 1900, *Pupa (Torquilla) schuebleri*.

crenulata* Klein, 1853, *Neritina (Plate 3, Figs. 6–7)
Neritina crenulata Klein, 1853: 221, pl. 5, fig. 18.

Syntypes: SMNS 106379 (7 specimens).

Type locality: Germany: Baden-Württemberg: Deutscher Hof near Zwiefalten, Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: Valid, as *Theodoxus crenulatus* (Klein, 1853). Family Neritidae (Neritininae).

Remarks: Klein's original specimens are poorly preserved; all fit the original description well, but it is impossible to identify the figured specimen.

crepidostoma* Sandberger, 1872, *Helix (Plate 3, Fig. 8a–c)
Helix crepidostoma Sandberger, 1872: pl. 21, fig. 10, 10a.
Helix (Coryda) crepidostoma: Sandberger, 1875: 456 (ref. pl. 21, fig. 10, 10a).

Syntypes?: SMNS 23209 (2 specimens, from Thalfingen).

Type localities: Germany: Bayern: Thalfingen, Thalfinger Schichten [Thalfingen beds]; Eckingen, Unterelchingen, Buckenrain, Kuhberg, Allewind, Göttingen near Ulm, Pappelau, Arnegg (road to Ermingen): oberste kreideartige Kalke, Rugulosa-Schichten [uppermost chalky limestones, Rugulosa Beds].

Age: Early Miocene (Aquitanian; MN 1–2).

Taxonomic status: Junior synonym of *Palaeotachea subsulcosa* (Thomä, 1845). Family Helicidae (Helicinae).

Remarks: One of the present specimens (SMNS 23209-b) compares reasonably well with the one figured by Sandberger (1874), but it is not a perfect match, as its apex is broken and slightly bent to the side. Sandberger's illustration could, of course, be a reconstruction of this fossil (with the axial sculpture being more marked to emphasize its presence), but it is more prudent to leave the status of these specimens as types tentative. A large lot of syntypes (from Eckingen) is present in the MUWIE.

cyrtocelis* Krauss, 1852, *Neritina (Plate 3, Fig. 9a, b)
Neritina cyrtocelis Krauss, 1852: 145.

Syntypes: SMNS 106380 (17 specimens).

Type locality: Germany: Baden-Württemberg: Kirchberg an der Iller, Kirchberg Formation.

Age: Late Early Miocene (Burdigalian/Ottnangian, MN4b).

Taxonomic status: Valid, as *Theodoxus cyrtocelis* (Krauss, 1852) (fide Wenz 1929; Salvador et al. submitted). Family Neritidae (Neritininae).

deplanatus* Miller, 1907, *Archaeozonites (Plate 3, Fig. 10a, b)
Archaeozonites deplanatus Miller, 1907: 442, pl. 8, fig. 12.

Lectotype (herein): SMNS 27619.

Paralectotype: SMNS 106381 (1 specimen).

Type locality: Germany: Baden-Württemberg: Blaustein (Arnegg), karst fissure limestone.

Age: Early Oligocene.

Taxonomic status: Valid, as *Archaeozonites deplanatus* Miller, 1907. Family Archaeozonitidae.

Remarks: We select as lectotype the best preserved specimen; the illustration in the original description (Miller 1907) is a reconstruction of it.

deplanata* Jooss, 1911b, *Helicodonta (Helicodonta) involuta (Plate 3, Fig. 11a–c)
Helicodonta (Helicodonta s. str.*) involuta* var. *deplanata* Jooss, 1911b: 57.

Syntypes: SMNS 106382 (8 specimens).

Type locality: Germany: Hesse: Mosbach-Biebrich, "obere Hydrobienschichten" [upper Hydrobia Beds, now Wiesbaden Formation].

Age: Early Miocene (MN 2a/b).

Taxonomic status: Valid, as *Protodrepanostoma involutum deplanatum* (Jooss, 1911b) (fide Kadolsky herein). Family Helicodontidae.

depressa* Jooss, 1912b, *Cepaea (Palaeotachea) convexitesta (Plate 3, Fig. 12a, b)
Cepaea (Palaeotachea) convexitesta forma *depressa* Jooss, 1912b: 164, fig. 5d–e.

Holotype: SMNS 23914-c.

Type locality: Germany: Bavaria: Dobelbuck ("Hobelsbuck") near Amerbach (Wemding), *Pomatias*-Süßwasserkalk des Riesgebietes [*Pomatias* freshwater limestone of the Ries area].

Age: Early Oligocene.

Taxonomic status: Junior synonym of *Palaeotachea convexitesta* (Jooss, 1912b). Family Helicidae (Helicinae).

dietleni* Miller, 1907, *Megalomastoma (Plate 3, Fig. 13)
Megalomastoma Dietleni Miller, 1907: 440, pl. 7, fig. 5a, b.

Syntypes: SMNS 11886 (2 specimens).

Type locality: Germany: Baden-Württemberg: Ulm (Eselsberg), karst fissure limestone.

Age: Early Oligocene.

Taxonomic status: Unknown. Family Megalomastomatidae(?).

diezi* Clessin, 1894, *Amalia (Plate 3, Fig. 14)
Amalia diezi Clessin, 1894: 27, pl. 1, fig. 9.

Syntype: SMNS 106383.

Type locality: Germany: Bavaria: Nittendorf (Undorf), mittlere Silvanaschichten [middle Silvana-beds].

Age: Late Early/early Middle Miocene (MN 5).

Taxonomic status: Valid, as *Milax diezi* (Clessin, 1894). Family Milacidae.

Remarks: In the original description, Clessin (1894) lists "numerous" specimens in Diez's collection; see remarks under *crass*a Clessin, 1894.

dilatatus* Jooss, 1918b, *Tropidomphalus (Plate 3, Fig. 15a–c)
Tropidomphalus dilatatum Jooss, 1918b: 293; Jooss 1924: 195, pl. 11, fig.11.

Syntype: SMNS 106384.

Type locality: Germany: Baden-Württemberg: Stubersheim–Geislingen, rote Helicidenmergeln [red helicid marls].

Age: Late Middle Miocene ("Vindobonian" = Langhian?).

Taxonomic status: Junior subjective synonym of *Pseudochloritis incrassata* (Klein, 1853), fide Binder (2008). Family Elonidae (Eloninae) or Helicidae (Ariantinae).

Remarks: Jooss (1918b) implied multiple localities, which he listed subsequently (1924).

dubius* Miller, 1907, *Pomatias (Plate 3, Fig. 16)
Pomatias dubius Miller, 1907: 451, pl. 9, fig. 3.

Holotype: SMNS 27632.

Type locality: Germany: Bavaria: Bachhagel, karst fissure limestone.

Age: Eocene.

Taxonomic status: Potentially valid, as *Cochlostoma dubium* (Miller, 1907) (fide Wenz 1923). Family Diplommatinidae (Cochlostomatinae).

ebfraasii* Jooss 1902, *Pomatias (Plate 3, Fig. 17)
Pomatias Eb. Fraasii Jooss, 1902: 306, fig. 2.
Pomatias Fraasii Gottschick, 1911: 533 [unjustified emendation].

Syntypes: SMNS 106385 (1 specimen) and 45192/2005 (1 specimen).

Type locality: Germany: Baden-Württemberg: Steinheim am Albuch, Steinheimer Seeschichten [Steinheim Lake beds].

Age: Middle Miocene (MN 7).

Taxonomic status: Valid, as *Cochlostoma ebfraasii* (Jooss, 1902). Family Diplommatinidae (Cochlostomatinae).

Remarks: The species epithet has usually been changed to "*fraasi*" or "*fraasii*", but according to article 32.5.2.4.4 ICZN the original spelling has to be maintained in an amended form.

eburnea* Klein, 1853, *Glandina (Achatina) (Plate 3, Fig. 18)
Glandina (Achatina) eburnea Klein, 1853: 213, pl. 5, fig. 10.

Lectotype (herein): SMNS 106386-a.

Paralectotypes: SMNS 106386-b (3 specimens).

Type locality: Germany: Baden-Württemberg: near Mörsingen), Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: Valid, as *Pseudoleacina eburnea* (Klein, 1853). Family Oleacinidae.

Remarks: Amongst Klein's original specimens, there is one that clearly is the figured specimen in the species' original description; this specimen is designated here as lectotype.

elegans* Miller, 1907, *Craspedopoma (Plate 3, Fig. 19)
Craspedopoma elegans Miller, 1907: 451, pl. 9, fig. 1.

Syntype: SMNS 27631.

Type locality: Germany: Bavaria: Bachhagel, karst fissure limestone.

Age: Eocene.

Taxonomic status: Valid. Family Craspedopomatidae.

Remarks: Miller (1907) mentioned two specimens.

elevata* Berz & Jooss, 1927, *Cepaea renevieri (Plate 3, Fig. 20a, b)
Cepaea renevieri var. *elevata* Berz & Jooss, 1927: 204.

Syntypes: SMNS 105002 (3 specimens, from Combe Girard), 106387 (1 specimen, from the road to La Sagne), 106388 (1 specimen, from Frankfurt am Main).

Type localities: Germany: Hesse: Frankfurt am Main [Eschenbacher Landstr.-Knoblauchfeld], Landschneckenmergel [land snail marl]. Switzerland: Canton Bern: Le Locle [Combe Girard and road to La Sagne], Sylvestrina-Schichten [Sylvestrina beds].

Age: Late Early/early Middle Miocene (MN 5).

Taxonomic status: Valid, as *Megalotachea elevata* (Berz & Jooss, 1927) (fide Höltke & Rasser submitted). Family Helicidae (Helicinae).

elongata* Klein, 1846, *Lymnaea socialis (Plate 3, Fig. 21)
Limnaeus socialis var. *elongata* Klein, 1846: 85, pl. 2, fig. 8a, b [non *Limneus elongatus* Draparnaud 1805 (: 53, pl. 3 figs. 3–4); nec de Serres 1844 (: 179, pl. 12, fig. 7)].

Syntypes: SMNS 23911 (5 specimens).

Type locality: Germany: Baden-Württemberg: Steinheim am Albuch, Steinheimer Seeschichten [Steinheim Lake beds].

Age: Middle Miocene (MN 7).

Taxonomic status: Synonym of *Radix socialis* (Zieten, 1832). Family Lymnaeidae (Lymnaeinae).

elongata* Miller, 1907, *Glandina (Plate 4, Fig. 1)
Glandina elongata Miller, 1907: 453, pl. 9, fig. 7.

Lectotype (herein): SMNS 27636-a.

Paralectotype: SMNS 27636-b.

Type locality: Germany: Bavaria: Bachhagel, karst fissure limestone.

Age: Eocene.

Taxonomic status: Valid, as *Pseudolecina elongata* (Miller, 1907). Family Oleacinidae.

Remarks: Miller (1907) figured both specimens. Here we define as lectotype the best preserved one.

eocaenica* Miller, 1907, *Bithynia (Plate 4, Fig. 2)
Bythinia [sic] *eocaenica* Miller, 1907: 456, pl. 9, fig. 18.

Holotype: SMNS 8328.

Type locality: Germany: Bavaria: Bachhagel, karst fissure limestone.

Age: Eocene.

Taxonomic status: Unknown. Family Bithyniidae or Hydrobiidae.

eocaenica* Miller, 1907, *Lymnaea (Plate 4, Fig. 3)
Limnaeus eocaenicus Miller, 1907: 452, pl. 9, fig. 5.

Syntypes: SMNS 27634 (2 specimens).

Type locality: Germany: Bavaria: Bachhagel, karst fissure limestone.

Age: Eocene.

Taxonomic status: Potentially valid, but insufficiently known; questionably placed in *Galba* by Wenz (1923: 1366). Family Lymnaeidae (Lymnaeinae).

eocaenicus* Miller, 1907, *Archaeozonites (Plate 4, Fig. 4a, b)
Archaeozonites eocaenicus Miller, 1907: 453, pl. 9, fig. 10.

Lectotype (herein): SMNS 27673-b.

Paralectotypes: SMNS 27673-a and 27673-c (2 specimens).

Type locality: Germany: Bavaria: Bachhagel, karst fissure limestone.

Age: Eocene.

Taxonomic status: Valid. Family Archaeozonitidae.

Remarks: The most complete and best preserved specimen is here designated as the lectotype; the figure provided by Miller (1907) is a reconstruction based on this specimen.

escheri* Sandberger, 1875, *Clausilia (Plate 4, Fig. 5)
Clausilia Escheri (Mayer MS.) Sandberger, 1875: 461.

Lectotype: SMNS 106389-a (designated by Schnabel 2007).

Paralectotype: SMNS 106389-b.

Type locality: Germany: Baden-Württemberg: Berg near Ehingen (Donau), Ehinger Ramondi-Schichten [Ramondi beds of Ehingen].

Age: Late Oligocene (Chattian).

Taxonomic status: Valid, as *Triptychia escheri* (Sandberger, 1875) (revised by Schnabel 2007). Family Filholiidae.

excellens* Jooss, 1912c, *Pomatias (Rhabdotakra) (Plate 4, Fig. 6)
Pomatias (Rhabdotakra) excellens Jooss, 1912c: 43, pl. 2, fig. 9.

Holotype: SMNS 106390.

Type locality: Germany: Baden-Württemberg: Steinheim am Albuch, Steinheimer Seeschichten [Steinheim Lake beds].

Age: Middle Miocene (MN 7).

Taxonomic status: Valid, as *Cochlostoma excellens* (Jooss, 1912c). Family Diplommatinidae (Cochlostomatinae).

Remarks: Jooss (1912c) based the species on one incomplete shell.

excellens* Jooss, 1927, *Laminifera (Laminifera) (Plate 4, Fig. 7)
Laminifera (Laminifera) excellens Jooss, 1927: 146, fig. 1a, b.

Holotype: SMNS 27650.

Type locality: Germany: Hesse: Falkenberg, between the cities of Flörsheim and Hochheim am Main, Landschneckenkalk [land snail limestone, now Hochheim Formation or lower Oppenheim Formation].

Age: Late Oligocene (Chattian).

Taxonomic status: Valid (fide Nordsieck 1981, 2000). Family Clausiliidae (Laminiferinae).

exigua* Miller, 1907, *Cionella
See *milleri* Wenz, 1919, *Cochlicopa*.

flachi* Clessin, 1911, *Acme (Plate 4, Fig. 8)
Acme Flachi Clessin, 1911: 9.
Acme Flachi Clessin, 1913: 110 [described again as new species].

Lectotype (herein): SMNS 106391-a.

Paralectotype: SMNS 106391-b. The paralectotype actually belongs to *Acicula diezi* (Flach 1889); it is a relatively broader specimen, which fits well with this species, likewise described from Undorf.

Type locality: Germany: Bavaria: Nittendorf (Undorf), mittlere Silvanaschichten [middle Silvana-beds].

Age: Late Early/early Middle Miocene (Karpatian–Badenian; MN 5).

Taxonomic status: Valid, as *Acicula flachi* (Clessin, 1911). Family Aciculidae.

Remarks: Kadolsky (2008a) doubted that these specimens were syntypes of *Acme flachi* Clessin, 1911, because the measurements given by Clessin do not agree with these specimens. It is now assumed that these measurements were incorrect, and that the two preserved specimens represent two of the three syntypes mentioned by Clessin (1911), for the following reasons: (1) Many of Clessin's measurements of small specimens were incorrect. (2) The specimens are dark grey, which is close to Clessin's statement that they were black; this coloration is less common for mollusks from Undorf, which are mostly white. (3) The incised collabral lines mentioned by Clessin are well developed. (4) It is implausible that Clessin or Jooss (who incorporated Clessin's collection in his own and who replaced any earlier label with his own) should have labelled the wrong specimens as Clessin's syntypes, and that the supposed real syntypes (which would agree with Clessin's dimensions) were absent.

fraasi* Jooss, 1912a, *Plebecula (Plate 4, Fig. 9a–c)
Plebecula fraasi Jooss, 1912a: 90; Jooss, 1912b: 166, pl. 4, fig. 6–c.

Syntypes: SMNS 23922 (2 specimens) and 106392 (1 specimen).

Type locality: Germany: Bavaria: Dobelbuck ("Hobelsbuck") near Amerbach (Wemding), *Pomatias*-Süßwasserkalk des Riesgebietes [*Pomatias* freshwater limestone of the Ries area].

Age: Early Oligocene (Rupelian).

Taxonomic status: Valid, as *Wenzia fraasi* (Jooss, 1912a) (fide Kadolsky herein). Family Sphincterochilidae.

fraasii* "Jooss, 1902", *Pomatias
See *ebfraasii* Jooss, 1902, *Pomatias*.

geniculata* Sandberger, 1872, *Helix (Plate 4, Fig. 10a–c)
Helix geniculata Sandberger, 1872: pl. 26, fig. 23, 23b; Sandberger, 1875: 629.

Syntypes: SMNS 22179 (3 specimens).

Type locality: Germany: Baden-Württemberg: Engen im Hegau (Hohenhöwen), "gypsum and limestone".

Age: Miocene.

Taxonomic status: Synonym of *Megalotachea sylvestrina* (Schlotheim, 1820). Family Helicidae (Helicinae).

giraudi* Dollfus, 1908, *Valvata (Cincinna) (Plate 4, Fig. 11)
Valvata (Cincinna) Giraudi Dollfus, 1908: 20, text-fig. 2.

Syntypes?: SMNS 106393 (18 specimens, from type locality and stratum; leg. Dollfus, Jooss collection).

Type locality: France: Dép. Allier: Montaigut-le-Blin.

Age: Lower Miocene (Aquitanian).

Taxonomic status: Valid as *Pseudamnicola? giraudi* (Dollfus, 1908) (fide Kadolsky herein), Family Hydrobiidae (Pseudamnicolinae?).

Remarks: It is unclear whether the date "April 1911" on Jooss' label is the date of collection or the date of his acquisition of the material. Only in the latter case the specimens could possibly be syntypes of Dollfus' species.

globosa* Miller, 1907, *Hyalinia (Plate 4, Fig. 12a, b)
Hyalinia globosa Miller, 1907: 454, pl. 9, fig. 12.

Syntypes: SMNS 27640 (3 specimens).

Type locality: Germany: Bavaria: Bachhagel, karst fissure limestone.

Age: Eocene.

Taxonomic status: Potentially valid; questionably placed in *Oxychilus* by Wenz (1923). Family Oxychilidae.

globosa* Miller, 1907, *Patula (Plate 4, Fig. 13a, b)
Patula globosa Miller, 1907: 444, pl. 8, fig. 15.

Syntypes: SMNS 17088 (1 specimen, from Eselsberg) and 27622 (4 specimens, from Örlinger Tal).

Type localities: Germany: Baden-Württemberg: Ulm [Eselsberg and Örlinger Tal], karst fissure limestones.

Age: Early Oligocene (Rupelian).

Taxonomic status: Valid, as *Discus globosus* (Miller, 1907) comb. nov. Family Discidae.

Remarks: A further original lot from Miller (1907) is recorded as SMNS 11904, but is likely lost.

gottschicki* Jooss, 1912c, *Patula (Plate 4, Fig. 14a, b)
Patula gottschicki Jooss, 1912c: 32, pl. 2, fig. 2.

Holotype: SMNS 106394.

Type locality: Germany: Baden-Württemberg: Steinheim am Albuch, *Pupa* (*Granaria*) layer of sand pit Pharion, upper *Gyraulus discoideus* zone to *G. trochiformis* zone).

Age: Middle Miocene (MN 7).

Taxonomic status: Valid, as *Janulus gottschicki* (Jooss, 1912c). Family Gastrodontidae.

gracilior* Sandberger, 1875, *Amalia (Plate 4, Fig. 15)
Amalia gracilior Sandberger, 1875: 603.

Syntype: SMNS 22757 (Probst coll.).

Type locality: Germany: Baden-Württemberg: Maselheim (Heggbach), middle Silvana-beds ("Silvanaschichten").

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: Valid, as *Milax gracilior* (Sandberger, 1875). Family Milacidae.

Remarks: Sandberger (1875) gives the type locality as Biberach (from Probst coll.), but the label gives the more precise locality of Heggbach, which is part of the Biberach district.

gracilis* Sandberger, 1872, *Bithynia (Plate 4, Fig. 16)
Paludina tentaculata: Krauss, 1852: 140-141 (Thon der untersten Fischschicht von Unterkirchberg) [non *Helix tentaculata* Linnaeus, 1758 (: 774, no. 616)].
Bythinia gracilis Sandberger, 1872: pl. 28, fig. 16, 16a; Sandberger, 1875: 561, 575.

Paratypes?: SMNS 106395 (numerous opercula), SMNS 106396 (rock fragment with numerous shells and molds) and 106750 (3 specimens), all Krauss coll., from: Germany: Baden-Württemberg: Kirchberg an der Iller, Kirchberg Formation.

Type localities: Germany: Bavaria: Leipheim near Günzburg, and Kirchberg an der Iller; both Kirchberg Formation.

Age: Late Early Miocene (Burdigalian/Ottnangian, MN4b).

Taxonomic status: Junior synonym of *Bithynia glabra* (Zieten, 1832). Family Bithyniidae.

Remarks: Sandberger (1872) introduced this nominal species with the illustration of a named specimen (1872: pl. 28, fig. 16–16a), which was later said to be from Leipheim (1875: 561). In the later published text (1875: 561, 575) he cites material from numerous additional localities, including that reported by Krauss (1852), which are preserved in SMNS. Since it is most likely that Sandberger had all this material at his disposal when he had the illustration of his *Bythinia gracilis* prepared, Krauss's material has thus the status of syntypes (see articles 72.4.1 and 72.4.1.1 ICZN).

gracilis* Jooss, 1912a, *Limnophysa amerbachensis (Plate 4, Figs. 17–18)
Limnophysa amerbachensis var. *gracilis* Jooss, 1912a: 90; Jooss, 1912b: 168, pl. 4, fig. 8b, c.

Syntypes: SMNS 23924 (2 specimens, from same locality and stratum).

Type locality: Germany: Bavaria: Dobelbuck ("Hobelsbuck") near Amerbach (Wemding), *Pomatias*-Süßwasserkalk des Riesgebietes [*Pomatias* freshwater limestone of the Ries area].

Age: Early Oligocene.

Taxonomic status: Valid as *Lymnaea gracilis* (Jooss, 1912) (fide Kadolsky 2014). Family Lymnaeidae (Lymnaeinae).

grandis* Klein, 1846, *Clausilia
See *kleini* Schnabel, 2006, *Triptychia (Triptychia).*

grossecostata* Klein, 1852, *Melania (Plate 4, Fig. 19)
Melania grossecostata Klein, 1852: 158, pl. 3, fig. 11.

Syntype: SMNS 23909 (1 specimen).

Type locality: Michelsberg near Ulm.

Age: Early Miocene.

Taxonomic status: Junior subjective synonym of *Tinnyea lauraea* (Mathéron, 1843) (syn. *Melania escheri* Merian, 1849; fide Kadolsky 1995). Family Pachychilidae.

Remark: The only available specimen is the original of KLEIN's fig. 11. It appears to be lost, but a photograph taken in ca. 1980 still exists (Plate 4, Fig. 19).

helicidarum* JOOSS, 1924, *Abida (Plate 4, Fig. 20)
Abida helicidarum JOOSS, 1924: 205.

Syntypes: SMNS 100113 (4 specimens).

Type locality: Germany: Baden-Württemberg: Blumberg (Zollhaus), Helicidenmergel [helicid marls].

Age: Early Miocene (Ottnangian; MN 3–4).

Taxonomic status: *Granaria helicidarum* (JOOSS, 1924), but species validity questioned due to incomplete preservation (HÖLTKE & RASSER 2013). Family Chondrinidae.

Remarks: According to HÖLTKE & RASSER (2013), the specimen among the original ones used by JOOSS (1924) that best fits the original description is the largest spire apex.

helicidarum* JOOSS, 1918b, *Hygromia (Trichiopsis) (Plate 4, Fig. 21a, b)
Hygromia (Trichiopsis) helicidarum JOOSS, 1918b: 292.
Fruticicola (Leucochroopsis) helicidarum: JOOSS, 1924: 194, pl. 11, figs. 8–10.

Syntypes: SMNS 106397 (3 specimens).

Type locality: Germany: Baden-Württemberg: Winterlingen (Harthausen auf der Scher), rote Helicidenmergel [red helicid marls].

Age: Middle Miocene (MN 4–5).

Taxonomic status: Possibly valid, as *Leucochroopsis helicidarum* (JOOSS, 1918b). Family Hygromiidae (Hygromiinae).

Remarks: Type material is very poorly preserved and *L. helicidarum* could be a synonym of an earlier named *Leucochroopsis* species.

hesslerana* JOOSS, 1911a, *Acanthinula (Plate 4, Fig. 22)
Acanthinula hesslerana JOOSS, 1911a: 705; JOOSS 1911b: 66, fig. 3.

Syntype: SMNS 67545.

Type locality: Germany: Hesse: Mosbach-Biebrich, obere Hydrobienschichten [upper Hydrobia beds, now Wiesbaden Formation].

Age: Early Miocene (Aquitanian).

Taxonomic status: Valid. Family Valloniidae.

Remarks: JOOSS (1911b: 67) mentioned three specimens. A lot in SMF (no. 151291) is labelled as syntypes from JOOSS' collection, but contains 6 specimens.

hoppla* GERBER, 1996, *Vallonia (Plate 5, Figs. 1–3)
Vallonia hoppla hoppla GERBER, 1996: 201, figs. 2q, 3ai, 81a–c, 82a.

Paratypes: SMNS 106398 (23 specimens).

Type locality: Germany: Hesse: Flörsheim-Hochheim am Main, Landschneckenkalk [land snail limestone, now Hochheim Formation].

Age: Late Oligocene (Chattian).

Taxonomic status: Valid. Family Valloniidae.

hydrobiarum* JOOSS, 1911a, *Omphalosagda (Plate 5, Fig. 4a–c)
Omphalosagda hydrobiarum JOOSS, 1911a: 705; JOOSS 1911b: 54, figs. 1–2.

Lectotype (herein): SMNS 106399.

Type locality: Germany: Hesse: Mosbach-Biebrich, Obere Hydrobienschichten [upper *Hydrobia* beds, now Wiesbaden Formation].

Age: Early Miocene (Aquitanian).

Taxonomic status: Valid. Family Archaeozonitidae.

Remarks: JOOSS (1911b: 55) mentioned "several" specimens in the SMF and the "original" in his collection. The latter is here designated as lectotype.

imperforata* MILLER, 1907, *Hyalinia (Conulus) (Plate 5, Figs. 5a, b)
Hyalinia (Conulus) imperforata MILLER, 1907: 442, pl. 7, fig. 11, 11b.

Holotype: SMNS 27618.

Type locality: Germany: Baden-Württemberg: Ulm (Eselsberg), karst fissure limestone.

Age: Early Oligocene (Rupelian).

Taxonomic status: Uncertain, possibly *Acanthinula* (s. lat.) *imperforata* (MILLER, 1907) (fide WENZ 1923). Family Valloniidae(?).

impressa* KRAUSS, 1852, *Melanopsis (Plate 5, Fig. 6)
Melanopsis impressa KRAUSS, 1852: 143, pl. 3, fig. 3.

Syntypes: SMNS 106400 (11 specimens).

Type locality: Germany: Baden-Württemberg: Kirchberg an der Iller, gelblicher Sand [yellowish sand layer].

Age: Late Early Miocene (Burdigalian/Ottnangian, MN4b).

Taxonomic status: Valid. Family Melanopsidae.

incrassata* KLEIN, 1853, *Helix (Plate 5, Fig. 7a–c)
Helix incrassata KLEIN, 1853: 208, pl. 5, fig. 6 [non *Helix incrassata* REEVE, 1853 (: pl. 150, species 972)].

Syntypes (?): SMNS 22737 (2 specimens).

Type locality: Germany: Baden-Württemberg: Zwiefaltendorf "bei der Birk" (KLEIN 1853: 203), Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: Valid, as *Pseudochloritis incrassata* (KLEIN, 1853) (fide BINDER 2008). Family Elonidae (Eloninae) or Helicidae (Ariantinae).

Remarks: (1) Two specimens in the SMNS collection (no. 22737) were hitherto believed to be KLEIN's originals of his *Helix incrassata*, but the earliest available label gives the date as the year 1854, with the forrester VON ZELL as the collector or donor, and the locality as Zwiefalten. There is no label from KLEIN's hand, unlike the case of *Helix inflexa* (q.v.). As KLEIN received the material for his 1853 paper from ZELL, the year 1854 can only mean that ZELL collected or passed the specimens on in 1854, be it to KLEIN or to the SMNS. The later display labels state that the material is KLEIN's originals of *Helix incrassata*, and give the locality as Zwiefalten. The discrepancies between the original and the subsequent labels could possibly be explained by a more or less arbitrary reinterpretation of the specimens' status and locality, or by a mix-up of different labels. In the latter case the "1854" label may not belong to the two specimens, which could then indeed be syntypes of *Helix incrassata* KLEIN. Neither possibility can be proved or disproved, but it should be noted that the specimens are in shape and size close to KLEIN's figures, although these show an

intact specimen unlike the actual ones; it was, however, common practice to idealize and reconstruct figures. The best preserved of the two specimens is here figured as a questionable syntype (Plate 5, Fig. 7a–c). (2) Reeve's description of *Helix incrassata* is dated February 1853; Klein's paper is listed in "*Neues Jahrbuch für Mineralogie* etc." 1853(6): 689, which printed letters to the editors dated up to 15.9.1853, i.e., it was received by the editors within a similar time. Thus, Klein's paper was published clearly later than February 1853 and consequently *Helix incrassata* Klein is a junior primary homonym. Its substitution is not mandatory if the conditions of Article 23.9.5 ICZN are met; a request for a ruling of the Commission under its plenary powers to validate the junior homonymous name is intended.

inflexa* C. Boettger, 1909, *Pseudochloritis (Plate 5, Fig. 8a–c)
Helix inflexa "Zieten" Klein, 1846: 71, pl. 1, fig. 12a, b [non Zieten, 1832].
Helix inflexa "von Martens": Sandberger, 1872: pl. 29, fig. 8, 8b.
Helix (Campylaea) inflexa "Klein": Sandberger, 1875: 589 (ref. pl. 29, fig. 8, 8b) (author: "Klein non v. Martens sp. Zieten").
Pseudochloritis inflexa "Klein": C. Boettger, 1909: 15.

Syntypes: SMNS 22736 (3 specimens).

Type localities: Zwiefaltendorf (Klein 1846), but Mörsingen on original label, Silvanaschichten; 5 other localities mentioned by Klein (1846).

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: A junior subjective synonym of *Pseudochloritis incrassata* (Klein, 1853) (fide Binder 2008; Nordsieck 2014). Family Elonidae (Eloninae) or Helicidae (Ariantinae).

Remarks: (1) In the introduction of the genus-group name *Pseudochloritis*, C. Boettger cited the type species merely as "*inflexa* Klein", meaning *Helix inflexa* sensu Klein 1846, which is a misidentification of *Helix inflexa* Zieten, 1832 (Die Versteinerungen Württembergs: 41, pl. 31, figs. 1a–c). This is a deliberate application of a misidentification, whereby C. Boettger created a new species-group name (article 11.10 ICZN). This name is unnecessary, as the subjective synonym *Helix incrassata* Klein, 1853 (q.v.) and others exist for the species in question. (2) While Klein (1846) believed to be describing Zieten's "*Helix*" *inflexa*, Sandberger (1875) suggested that Zieten's name actually refered to a large specimen of *Megalotachea silvana* (Klein); but as Zieten's originals were lost, his species could no longer be identified with any certainty and hence the name *inflexa* Zieten could not be used. Sandberger argued that it was therefore acceptable to use the name *inflexa* in the sense of Klein, and with Klein as its author. His action could be construed as the introduction of a new nominal species available from Sandberger (1875), albeit knowingly introduced as a junior primary homonym. In this interpretation Klein's material would also be part of the type series. We suggest, however, that Sandberger's action is simply the continuation of a misidentification initiated by Klein (1846).

insignis* Jooss, 1918b, *Poiretia (Palaeoglandina) gracilis (Plate 5, Fig. 9)
Poiretia (Palaeoglandina) gracilis var. *insignis* Jooss, 1918b: 288; Jooss 1924: 189, pl. 11, figs. 1–2.

Syntype: SMNS 106401.

Type localities: Germany: Baden-Württemberg: Stubersheim–Geislingen area, rote Helicidenmergel [red helicid marls] (figured specimen), and others.

Age: Late Middle Miocene ("Vindobonian" = Langhian?).

Taxonomic status: Possibly a junior synonym of *Palaeoglandina gracilis* (Zieten, 1832). Family Oleacinidae.

Remarks: (1) The type material is very poorly preserved. (2) Jooss (1918b) implied that his material came from numerous localities, which he listed subsequently (1924).

insignis* Zieten, 1832, *Helix (Plate 5, Fig. 10a–c)
Helix insignis (Schübler MS) Zieten, 1832: 38, pl. 29, fig. 1.

Neotype: SMNS 23910-a (designated by Höltke & Rasser 2015).

Neotype locality: Germany: Baden-Württemberg: Steinheim am Albuch, Steinheimer Seeschichten [Steinheim Lake beds].

Age: Middle Miocene (MN 7).

Taxonomic status: Valid, either as *Joossia insignis* (fide Binder 2008; Nordsieck 2014) or as *Tropidomphalus insignis* (fide Höltke & Rasser 2015). Family Elonidae (Eloninae) or Helicidae (Ariantinae).

intermedia* Klein, 1846, *Lymnaea socialis (Plate 5, Fig. 11)
Limnaeus socialis var. *intermedia* Klein, 1846: 85, pl. 2, fig. 9a, b [non *Lymnaea intermedia* (Férussac) Lamarck 1822 (: 162)].

Syntypes: SMNS 23905 (3 specimens).

Type locality: Germany: Baden-Württemberg: Steinheim am Albuch, Steinheimer Seeschichten [Steinheim Lake beds].

Age: Middle Miocene (MN 7).

Taxonomic status: Synonym of *Radix socialis* (Zieten, 1832). Family Lymnaeidae (Lymnaeinae).

involutus* Jooss, 1912a, *Planorbis crassus (Plate 5, Fig. 12a–c)
Planorbis crassus var. *involuta* Jooss, 1912a: 90; Jooss 1912b: 169, pl. 4 fig. 9, 9a [non *Planorbis multiformis steinheimensis* β *involutus* Hilgendorf, 1866 (: 485) (made available according to article 45.6.4.1 ICZN by Hyatt 1880 (: 78, pl. 1, figs. d18, e17–e19; as *Planorbis discoideu*s var. *involutus*)].

Syntypes: SMNS 23926 (6 specimens, from same locality and stratum).

Type locality: Germany: Bavaria: Dobelbuck ("Hobelsbuck") near Amerbach (Wemding), *Pomatias*-Süßwasserkalk des Riesgebietes [*Pomatias* freshwater limestone of the Ries area].

Age: Early Oligocene (Rupelian).

Taxonomic status: Probably a junior synonym of *Planorbarius cornu* (Brongniart, 1810). Family Planorbidae (Coretinae).

joossi* Pfeffer, 1930, *Trachytachea (Plate 5, Fig. 13a–c)
Trachytachea joossi Pfeffer, 1930: 334, pl. 16, fig. 28, pl. 17, fig. 20 [= p. 184, pl. 2, fig. 29, pl. 3 fig. 20].

Holotype: SMNS 106402.

Type locality: Austria: Grund near Vienna, "Vindobon" Helvetien-Meeressand [Vindobonian Austrian marine sand].

Age: Miocene ("Vindobonian" = Langhian?).

Taxonomic status: Potentially valid in the genus *Megalotachea* (fide Nordsieck 1986: 114). Family Helicidae (Helicinae).

joossii* Miller, 1907, *Helix (Plate 5, Fig. 14a, b)
Helix joossii Miller, 1907: 455, pl. 9, fig. 14.

Syntype: SMNS 27642.

Type locality: Germany: Bavaria: Bachhagel, karst fissure limestone.

Age: Eocene.

Taxonomic status: Possibly valid, but genus attribution uncertain; Wenz (1923) placed the species questionably in *Klikia*, but commented that it might be conspecific with *Loganiopharynx constrictelabiatus* (Miller, 1907). Family Elonidae(?) or Hygromiidae (Hygromiinae)(?).

joossii* Gottschick, 1911, *Strobilus (Plate 5, Fig. 15)
Strobilus Joossii Gottschick, 1911: 502, pl. 7, fig. 16, 16c.

Syntype: SMNS 106403.

Type locality: Germany: Baden-Württemberg: Steinheim am Albuch, *laevis*-zone of Steinheimer Seeschichten [Steinheim Lake beds].

Age: Middle Miocene (MN 7).

Taxonomic status: Valid, as *Strobilops joossii* (Gottschick, 1911). Family Strobilopsidae.

Remarks: Gottschick (1911) mentioned two localities in the Steinheim Basin; thus he must have had more than one specimen at his disposal.

kleini* Gottschick & Wenz, 1916, *Gyraulus multiformis (Plate 5, Fig. 16a–c)
Planorbis laevis Klein, 1846: 79, pl. 1, fig. 26a–c [non Alder, 1838 (: 137)].
Gyraulus multiformis kleini Gottschick & Wenz, 1916: 101, fig. 3.

Syntypes: SMNS 25263/2005 (2 specimens).

Type locality: Germany: Baden-Württemberg: Dächingen and Hohenmemmingen (Klein 1846); the original label gives Hohenmemmingen, but the subsequent one "Däschingen"; Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: Valid, as *Gyraulus kleini* Gottschick & Wenz, 1916. Family Planorbidae (Planorbinae).

kleini* Schnabel, 2006, *Triptychia (Triptychia) (Plate 5, Figs. 17–18)
Clausilia grandis Klein, 1846: 73, pl. 1, figs. 16a, b [non *Clausilia similis* var. *grandis* Rossmässler, 1838 (: 17, pl. 34, fig. 469)].
Triptychia (Triptychia) kleini kleini Schnabel, 2006: 147, pl. 3, figs. 32–34.

Lectotype (herein): SMNS 106404-a.

Paralectotypes: SMNS 106404-b (5 specimens).

Type locality: Germany: Baden-Württemberg: Zwiefalten, Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: Valid, as *Triptychia kleini* Schnabel, 2006. Family Filholiidae.

Remarks: The species was revised by Schnabel (2006), who also coined a new name, since the epithet "*grandis*" was preoccupied. Schnabel (2006), believing the types were lost, designated a neotype from the SMF collection. However, the type series is actually present in Klein's original material in the SMNS collection. Article 75.8 of the ICZN (1999) states: "If, after the designation of a neotype, the name-bearing type (holotype, syntypes, lectotype or previous neotype) of the nominal species-group taxon that was (were) presumed lost is (are) found still to exist, on publication of that discovery the rediscovered material again becomes the name-bearing type and the neotype is set aside (…)". The material in the SMNS collection thus constitutes syntypes. In the species' original description (Klein 1846), the figured specimen is clearly a composite drawn from all the available specimens. Therefore, here we designate as lectotype the aperture fragment, which bears the most important characters for clausilioid taxonomy.

kraussii* Klein, 1846, *Planorbis (Plate 5, Fig. 19a, b)
Planorbis Kraussii Klein, 1846: 80, pl. 1, fig. 28a–c.

Syntypes: SMNS 106405 (5 specimens).

Type locality: Germany: Baden-Württemberg: Steinheim am Albuch, Steinheimer Seeschichten [Steinheim Lake beds].

Age: Middle Miocene (MN 7).

Taxonomic status: Valid, as *Gyraulus kraussii* (Klein, 1846). Family Planorbidae (Planorbinae).

laevis* Klein, 1846, *Planorbis
See *kleini* Gottschick & Wenz, 1916, *Gyraulus multiformis*.

laxa* Gerber, 1996, *Vallonia (Plate 6, Figs. 1–3)
Vallonia laxa Gerber, 1996: 206, figs. 2s, 3a–l, 81f, 82c.

Paratypes: SMNS 106406 (4 specimens) and 106407 (5 specimens), all from type locality and stratum.

Type locality: Germany: Hesse: Frankfurt am Main (Palmengarten); Landschneckenmergel [land snail marl, now Niederrad Formation].

Age: Early Miocene (Burdigalian; MN 3).

Taxonomic status: Valid. Family Valloniidae.

lepida* Wenz, 1919a, *Cepaea (Plate 6, Fig. 4a–c)
Helix pachystoma Klein, 1853: 207, pl. 5, fig. 4 [non Hombron & Jacquinot, 1841 (: 62; as *Helyx Pachystoma* [sic])].
Cepaea lepida Wenz, 1919a: 70.

Syntypes: SMNS 105004 (4 specimens).

Type locality: Germany: Baden-Württemberg: Emerberg near Zwiefalten, in a gully running towards Ober-Wilzingen; Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Karpatian/Badenian; MN 5).

Taxonomic status: Subjective synonym of *Palaeotachea dentula* (Quenstedt, 1867). Family Helicidae (Helicinae).

Remarks: (1) Wenz (1919a) substituted the preoccupied name *Helix pachystoma* Klein, but withdrew this name later (1919b: 64), when he recognized that the earlier name *Helix dentula* Quenstedt referred to the same species. (2) Wenz (1919a: 70) designated as "Typus" of *Cepaea dentula* a specimen from Emerberg near Oberwilzingen in his collection. This is incorrect, because as a substitution name, *Cepaea lepida* has the same name-bearing type as the replaced name, *Helix pachystoma* Klein.

leubii* Miller, 1907, *Helix (Gonostoma) (Plate 6, Fig. 5a–c)
Helix (Gonostoma) Leubii Miller, 1907: 445, pl. 8, fig. 18a–d.

Syntypes: SMNS 36777 (4 specimens).

Type locality: Germany: Baden-Württemberg: Blaustein (Arnegg), karst fissure limestone.

Age: Early Oligocene (Rupelian).

Taxonomic status: Subjective synonym of *Klikia*? *praeosculina* (Miller, 1907) (fide Wenz 1923). Family Elonidae (Klikiinae) or Helicidae (Ariantinae).

lincki* Schütze in Branca & Fraas, 1908, *Planorbis (Coretus) (Plate 6, Fig. 6a–c)
Planorbis (Coretus) Lincki Schütze in Branca & Fraas, 1908: 22, figs. 17–18.

Lectotype (herein): SMNS 11902-a.

Paralectotypes: SMNS 11897-b (2 specimens).

Type locality: Germany: Bavaria: Monheim (Weilheim im Ries), grey freshwater limestone block in Bunter Breccie [varicoloured breccia, Ries ejecta].

Age: Early Oligocene.

Taxonomic status: Potentially valid, as *Planorbarius lincki* (Schütze in Branca & Fraas, 1908). Family Planorbidae (Coretinae).

Remarks: We designate here as lectotype the largest and best preserved specimen (Schütze in Branca & Fraas 1908: fig. 18).

lingulatus* Sandberger, 1875, *Limax (Plate 6, Fig. 7)
Limax lingulatus Sandberger, 1875: 603.

Syntype: SMNS 22756.

Type locality: Germany: Baden-Württemberg: Biberach a. d. Riss, mittlere Silvanaschichten [middle Silvana-beds].

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; zones MN 5/6).

Taxonomic status: Potentially valid. Family Limacidae.

maior* Miller, 1900, *Helix (Campylaea) insignis (Plate 6, Fig. 8a–c)
Helix (Campylaea) insignis var. *maior* Miller, 1900: 394, pl. 7, fig. 1 [non *Helix major* Binney 1837 (: 473, pl. 12), and others before 1900].

Holotype: SMNS 4779-a.

Type locality: Germany: Baden-Württemberg: Steinheim am Albuch, Steinheimer Seeschichten [Steinheim Lake beds].

Age: Middle Miocene (MN 7).

Taxonomic status: Synonym of *Joossia insignis* (Zieten, 1832) (fide Binder 2008; Nordsieck 2014) or *Tropidomphalus insignis* (fide Höltke & Rasser 2015). Family Elonidae (Eloninae) or Helicidae (Ariantinae).

milleri* Fulton, 1915, *Helicina (Plate 6, Fig. 9a, b)
Helicina(?) *trochiformis* Miller, 1907: 452, pl. 9, fig. 4 [non G.B. Sowerby II, 1842 (: 7)].
Helicina milleri Fulton, 1915: 241.

Syntypes: SMNS 27633 (4 specimens).

Type locality: Germany: Bayern: Bachhagel, karst fissure limestone.

Age: Eocene.

Taxonomic status: Valid, as *Proserpina*? *milleri* (Fulton, 1915); tentative generic allocation by Kadolsky (2008a). Family Proserpinidae.

milleri* Jooss, 1913, *Lymnaea turrita (Plate 6, Fig. 10)
Limnaea turrita var. *milleri* Jooss, 1913: 61, figs. 5–6.

Syntypes: SMNS 106408 (1 specimen) and 106409 (1 specimen).

Type locality: Germany: Baden-Württemberg: Zwiefalten (Mörsingen), Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: Subjective synonym of *Radix socialis* (Zieten, 1832). Family Lymnaeidae (Lymnaeinae).

milleri* Wenz, 1919, *Cochlicopa (Plate 6, Fig. 11)
Cionella exigua Miller, 1907: 446, pl. 8, fig. 22a, b [non *Bulimus (Cochlicopa) subcylindricus* var. *exigua* Moquin-Tandon, 1856 (: 304)]
Cochlicopa milleri Wenz, 1919: 71.

Syntype: SMNS 27628.

Type locality: Germany: Baden-Württemberg: Blaustein (Arnegg), karst fissure limestone.

Age: Early Oligocene (Rupelian).

Taxonomic status: Valid, as *Cochlicopa milleri* Wenz, 1919. Family Cochlicopidae.

Remarks: (1) Wenz (1919) substituted the name *Cionella exigua* Miller as a putative junior homonym of *Achatina exigua* Menke, 1830 (: 29), which is, however, a nomen nudum. Moquin-Tandon (1856) eventually provided a diagnosis for the name *exigua* "Menke" and made it thus an available name for a modern form of *Cochlicopa*. (2) Miller mentioned several specimens from Arnegg and one from Eselsberg, which were kept in the Munich museum.

milleri* Pilsbry, 1909, *Poiretia (Plate 6, Fig. 12)
Glandina ovata (Sandberger MS.) Miller, 1907: 441, pl. 7, fig. 9a, b [non *Glandina truncata* var. *ovata* Dall, 1890 (: 19)].
Poiretia milleri Pilsbry, 1909: 113.

Lectotype (herein): SMNS 27617-b.

Paralectotype: SMNS 27617-a (1 specimen).

Type locality: Germany: Baden-Württemberg: Blaustein (Arnegg), karst fissure limestone.

Age: Early Oligocene (Rupelian).

Taxonomic status: Valid, as *Palaeoglandina milleri* (Pilsbry, 1909). Family Oleacinidae.

Remarks: Here we designate the best preserved specimen (and likely the base for the original illustration) as lectotype.

minima* Klein, 1853, *Succinea (Plate 6, Fig. 13)
Succinea minima Klein, 1853: 205.

Syntypes: SMNS 106410 (2 specimens).

Type locality: Germany: Baden-Württemberg: near Mörsingen, Silvanaschichten [Silvana-Beds].

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: Valid, as *Oxyloma minima* (Klein, 1853) (fide Harzhauser et al. 2014). Family Succineidae (Succineinae).

Remarks: Both specimens of Klein's original material fit the original description well and none was figured.

miocaenica* Gottschick & Wenz, 1927, *Trochoidea (Plate 6, Fig. 14a, b)
Trochoidea miocaenica Gottschick & Wenz, 1927: 149, pl. 8, fig. 3a–c.

Syntype: SMNS 15817-131.

Type locality: Germany: Baden-Württemberg: Mörsingen near Riedlingen, Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: Valid, as *Miodiscula miocaenica* (Gottschick & Wenz, 1927) (fide Nordsieck 2014). Family Helicodontidae?.

Remarks: Gottschick & Wenz (1927) mention four specimens.

moersingensis* Jooss, 1918b, *Janulus (Plate 6, Fig. 15a–c)
Janulus mörsingensis Jooss, 1918b: 289.

Holotype: SMNS 106411.

Type locality: Germany: Baden-Württemberg: Zwiefalten (Mörsingen), Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: Valid. Family Gastrodontidae.

moguntiaca* Wenz, 1915, *Vallonia (Plate 6, Fig. 16a, b)
Vallonia moguntiaca Wenz, 1915: 41.

Neotype: SMNS 106412 (designated by Gerber 1996).

Type locality: Germany: Rheinland-Pfalz: Budenheim, Hydrobienschichten [*Hydrobia* Beds, now Wiesbaden Formation].

Age: Early Miocene (Aquitanian; MN 2a/b).

Taxonomic status: Synonym of *Vallonia lepida* (Reuss, 1849) (fide Gerber 1996). Family Valloniidae.

mucronata* Klein, 1846, *Helix (Plate 6, Fig. 17)
Helix mucronata Klein, 1846: 72, pl. 1, fig. 15).

Holotype: SMNS 106413.

Type locality: Germany: Baden-Württemberg: Ehingen (Staffelsberg), Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Burdigalian/Langhian, MN 5).

Taxonomic status: Synonym of *Leucochroopsis kleinii* (Klein, 1846) (fide Wenz 1923). Family Hygromiidae (Hygromiinae).

obtusangula* Krauss, 1852, *Neritina (Plate 6, Fig. 18a, b)
Neritina obtusangula Krauss, 1852: 145.

Holotype: SMNS 106414.

Type locality: Germany: Baden-Württemberg: Kirchberg an der Iller, Kirchberg Formation.

Age: Late Early Miocene (Burdigalian/Ottnangian, MN 4b).

Taxonomic status: Valid, as *Theodoxus obtusangula* (Krauss, 1852) (fide Salvador et al. submitted). Family Neritidae (Neritininae).

Remarks: The species epithet is derived from Lat. *angulus* (an angle); as such, "angula" is still a substantive with a variant gender ending and therefore not declensable.

oligocaenica* Miller, 1907, *Clausilia (Plate 6, Fig. 19)
Clausilia oligocaenica Miller, 1907: 449, fig. 29.

Holotype: SMNS 27647.

Type locality: Germany: Baden-Württemberg: Blaustein (Arnegg), karst fissure limestone.

Age: Early Oligocene (Rupelian).

Taxonomic status: Valid, as *Triptychia oligocaenica* (Miller, 1907) (fide Schnabel 2007). Family Filholiidae.

orbicularis* Klein, 1846, *Helix (Plate 6, Fig. 20a, b)
Helix orbicularis Klein, 1846: 71, pl. 1, fig. 13a, b.

Syntype: SMNS 106415.

Type locality: Germany: Baden-Württemberg: Ulm (Michelsberg), Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: Valid, as *Pleurodiscoides* (*Pleurodiscoides*) *orbicularis* (Klein, 1846) (fide Nordsieck 2014). Family Pleurodiscidae.

Remarks: Klein (1846) reported the species as rare, which does not exclude that he had more than one specimen at his disposal.

ovata* Miller ,1907, *Glandina
See *milleri* Pilsbry, 1909, *Poiretia*.

ovulina* Miller, 1907, *Oleacina (Plate 6, Fig. 21)
Oleacina ovulina Miller, 1907: 453, pl. 9, fig. 9.

Syntype: SMNS 27637.

Type locality: Germany: Bavaria: Bachhagel, karst fissure limestone.

Age: Eocene.

Taxonomic status: Synonym of *Pseudoleacina elongata* (Miller, 1907). Family Oleacinidae.

Remarks: Miller (1907) mentioned 3 specimens.

pachygastra* Miller, 1900, *Pupa (Torquilla) schuebleri (Plate 7, Fig. 1)
Pupa pachygastra Fraas, 1882: 174 [nomen nudum].
Pupa (Torquilla) Schübleri var. *pachygastra* (Fraas MS.) Miller, 1900: 397, pl. 7, fig. 12 [non *Pupa pachygastra* Rossmässler, 1837 (: 11, pl. 23, fig. 314, *P. oblongata* on plate)].

Syntype: SMNS 106416.

Type locality: Germany: Baden-Württemberg: Steinheim am Albuch, Steinheimer Seeschichten [Steinheim Lake beds].

Age: Middle Miocene (MN 7).

Taxonomic status: Valid, as *Granaria crassiventrosa* nom. nov. (revised by Höltke & Rasser 2013, as *Granaria pachygastra*). Family Chondrinidae.

Remarks: (1) The single specimen in the SMNS collection is the original of Fraas (1882). Höltke & Rasser (2013)

argued that its type status is uncertain because it cannot be established that Miller (1900) based his diagnosis of the "variety" *pachygastra* on this specimen. But Miller gave a bibliographic reference to Fraas' publication, whereby it is included in the type series. It is unknown whether Miller had additional specimens at his disposal. (2) As the name *pachygastra* is preoccupied, herein we substitute it by *Granaria crassiventer* nom. nov. The epithet, *crassiventer*, is the Latin translation of the Greek *pachygastra*, meaning "fat belly". It is a noun in apposition, i.e., it is unchangeable. Article 23.9.5 ICZN is not applicable in this case, because both homonyms are still placed in the genus *Granaria*; *pachygastra* Rossmässler, 1837 was used as a valid name by Pilsbry (1918: 302, pl. 42 fig. 7, 10, 11; as *Abida frumentum pachygastra*) and is listed as a subjective synonym of *Granaria frumentum illyrica* (Rossmässler, 1835) by Féher et al. (2010: 203, figs. 3K–L).

pachystoma* Klein, 1853, *Helix
See *lepida* Wenz, 1919, *Cepaea*.

palustris* Clessin, 1877, *Ancylus (Plate 7, Fig. 2)
Ancylus palustris Clessin, 1877: 41.

Holotype: SMNS 106417.

Type locality: Germany: Bavaria: Nittendorf (Undorf), mittlere Silvanaschichten [middle Silvana-beds].

Age: Late Early/early Middle Miocene (Karpatian–Badenian; MN 5).

Taxonomic status: Synonym of *Ferrissia deperdita* (Desmarest, 1814). Family Planorbidae (Ancylinae).

physoides* Miller, 1907, *Clausilia (Plate 7, Fig. 3)
Clausilia physoides (Balea?) Miller, 1907: 449, fig. 30.

Holotype: SMNS 27648.

Type locality: Germany: Baden-Württemberg: Blaustein (Arnegg), karst fissure limestone.

Age: Early Oligocene (Rupelian).

Taxonomic status: Valid, as *Neniopsis physoides* (Miller, 1907) (fide Nordsieck 2000, 2007). Family Clausiliidae (Eualopiinae).

planus* Clessin, 1885, *Strobilus (Plate 7, Fig. 4a, b)
Strobilus planus Clessin, 1885: 80, pl. 7, fig. 8.

Holotype: SMNS 106418.

Type locality: Germany: Bavaria: Nittendorf (Undorf), Silvanaschichten [middle Silvana-beds].

Age: Late Early/early Middle Miocene (Karpatian/Badenian; MN 5).

Taxonomic status: Subspecies of *Strobilops uniplicata* (Braun in Walchner, 1851). Family Strobilopsidae.

platystoma* Klein, 1853, *Planorbis (Plate 7, Fig. 5a–c)
Planorbis platystoma Klein, 1853: 219, pl. 5, fig. 16 [non Edwards, 1852 (: 103, pl. 15, fig. 2a–d)].

Syntypes: SMNS 25211/2005 (3 specimens).

Type locality: Germany: Baden-Württemberg: Zwiefalten (Mörsingen), Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: Junior synonym of *Planorbarius cornu* (Brongniart, 1810). Family Planorbidae (Coretinae).

praecostatus* Jooss, 1918b, *Zonites (Aegopis) (Plate 7, Fig. 6a, b)
Zonites (Aegopis) praecostatus Jooss, 1918b: 288; Jooss 1924: 191, pl. 11, figs. 3–4.

Syntype: SMNS 65614.

Type localities: Germany: Baden-Württemberg: Stubersheim–Geislingen, rote Helicidenmergel [red helicid marls] (figured specimen) and other localities.

Age: Late Middle Miocene ("Vindobonian" = Langhian?).

Taxonomic status: Possibly valid, but see below. Family Archaeozonitidae.

Remarks: (1) Type material is very poorly preserved and *A. praecostatus* could be a synonym of a previously described *Archaeozonites* species. (2) Jooss (1918b) implied that he included material from several localities in his species; these are listed subsequently (Jooss 1924).

praeosculina* Miller, 1907, *Helix (Gonostoma) (Plate 7, Fig. 7a, b)
Helix (Gonostoma) praeosculina Miller, 1907: 445, pl. 8, fig. 17a–c.

Syntypes: SMNS 27624 (3 specimens).

Type locality: Germany: Baden-Württemberg: Blaustein (Arnegg), karst fissure limestone.

Age: Early Oligocene (Rupelian).

Taxonomic status: Valid, as *Klikia*? *praeosculina* (Miller, 1907). Family Elonidae (Klikiinae) or Helicidae (Ariantinae).

procellaria* Jooss, 1918b, *Hyalinia (Hyalinia) (Plate 7, Figs 8a–c)
Hyalinia (Hyalinia) procellaria Jooss, 1918b: 289.

Syntypes: SMNS 106419 (2 specimens).

Type locality: Germany: Baden-Württemberg: Zwiefalten (Mörsingen), Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: Valid, as *Aegopinella*? *procellaria* (Jooss, 1918b) (fide Nordsieck 2014). Family Oxychilidae (Godwiniinae).

protocrescens* Nützel & Bandel, 1993, *Gyraulus (Plate 7, Figs. 9–11)
Gyraulus protocrescens Nützel & Bandel, 1993: 332, pl. 1, figs. 3–4, pl. 3, figs. 2–3.

Holotype: SMNS 25669.

Paratypes: SMNS 25668 (1 specimen) and 25711 (1 specimen).

Type locality: Germany: Baden-Württemberg: Steinheim am Albuch, Steinheimer Seeschichten [Steinheim Lake beds], transition of *Gyraulus steinheimensis* zone to *G. tenuis* zone.

Age: Middle Miocene (MN 7).

Taxonomic status: Valid. Family Planorbidae (Planorbinae).

pumilio* Jooss, 1918b, *Punctum (Plate 7, Figs. 12–13b)
Punctum pumilio Jooss, 1918b: 292.

Syntypes: SMNS 106420 (2 specimens, from same locality and stratum).

Type locality: Germany: Baden-Württemberg: Dischingen, mittlere Silvanaschichten [middle Silvana-beds].

Age: Early Late Miocene (Tortonian).

Taxonomic status: Valid. Family Punctidae.

pyramidalis* Jooss, 1912a, *Zonites (Archaeozonites?) (Plate 7, Fig. 14a–c)
Zonites (Archaeozonites?) pyramidalis Jooss, 1912a: 89; Jooss 1912b: 163, pl. 4, fig. 4, 4a.

Holotype: SMNS 23917.

Type locality: Germany: Bavaria: Dobelbuck ("Hobelsbuck") near Amerbach (Wemding), *Pomatias*-Süßwasserkalk des Riesgebietes [*Pomatias* freshwater limestone of the Ries area].

Age: Early Oligocene (Rupelian.)

Taxonomic status: Valid, as *Omphalosagda pyramidalis* (Jooss, 1912a) (fide Kadolsky herein). Family Archaeozonitidae.

quadridentata* Klein, 1853, *Pupa (Plate 7, Fig. 15)
Pupa quadridentata Klein, 1853: 216, pl. 5, fig. 13.

Syntypes: SMNS 106421 (12 specimens, from Zwiefalten).

Type localities: Germany: Baden-Württemberg: Zwiefalten (Mörsingen), Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: Junior synonym of *Gastrocopta acuminata* (Klein, 1846) (fide Manganelli & Giusti 2000). Family Gastrocoptidae.

randeckiana* Kranz, 1908, *Clausilia (Plate 7, Figs. 16–17)
Clausilia randeckiana Kranz, 1908: 590, fig. 2.

Lectotype: SMNS 101212 (designated by Salvador et al. 2015).

Paralectotypes: SMNS 101213 (2 specimens).

Type locality: Germany: Baden-Württemberg: Randeck Maar, gelber Tuff [light/yellow tuffite].

Age: Late Early/early Middle Miocene (Karpatian–Badenian; MN 5).

Taxonomic status: Valid, as *Triptychia randeckiana* (Kranz, 1908) (fide Schnabel 2006). Family Filholiidae.

risgoviensis* Jooss, 1912a, *Zonites (Archaeozonites) (Plate 7, Figs. 18a, b)
Zonites (Archaeozonites) risgoviensis Jooss, 1912a: 89; Jooss, 1912b: 162, pl. 4, fig. 3, 3b.

Syntypes: SMNS 23915 (1 specimen) and 23916 (2 specimens).

Type locality: Germany: Bavaria: Dobelbuck ("Hobelsbuck") near Amerbach (Wemding), *Pomatias*-Süßwasserkalk des Riesgebietes [*Pomatias* freshwater limestone of the Ries area].

Age: Early Oligocene (Rupelian).

Taxonomic status: Subjective synonym of *Omphalosagda pyramidalis* (Jooss, 1912) (fide Kadolsky herein). Family Archaeozonitidae.

rotundostomus* Nützel & Bandel, 1993, *Gyraulus (Plate 7, Figs. 19–21)
Gyraulus rotundostomus Nützel & Bandel, 1993: 348, pl. 8, figs. 5–7.

Holotype: SMNS 25705.

Paratypes: SMNS 25703 (1 specimen) and 25710 (5 specimens).

Type locality: Germany: Baden-Württemberg: Steinheim am Albuch, Steinheimer Seeschichten [Steinheim Lake beds], *Gyraulus oxystoma* zone.

Age: Middle Miocene (MN 7).

Taxonomic status: Valid. Family Planorbidae (Planorbinae).

salomoni* Geyer, 1914, *Pomatias (Plate 7, Fig. 22)
Pomatias salomoni Geyer, 1914: 136, pl. 2, figs. 5, 6, 8, 13.

Lectotype (herein): SMNS 13519-a.

Paralectotype: SMNS 13519-b (1 specimen and numerous fragments)

Type locality: Germany: Bayern: Buch bei Illertissen, diluviale Nagelfluh [diluvial (i.e., Pleistocene) gravel].

Age: Pleistocene.

Taxonomic status: Possibly valid, as *Cochlostoma salomoni* (Geyer, 1914). Family Diplommatinidae (Cochlostomatinae).

Remarks: We designate here as lectotype the only completely preserved specimen (Geyer 1914: fig. 13).

sandbergeri* Clessin, 1885, *Amalia (Plate 7, Fig. 23)
Amalia sandbergeri Clessin, 1885: 72.

Syntypes: SMNS 22754 (2 specimens).

Type locality: Germany: Bavaria: Nittendorf (Undorf), mittlere Silvanaschichten [middle Silvana-beds].

Age: Late Early/early Middle Miocene (Karpatian/Badenian; MN 5).

Taxonomic status: Valid, as *Milax sandbergeri* (Clessin, 1885). Family Milacidae.

saueri* Geyer, 1914, *Pomatias scalarinus (Plate 7, Fig. 24)
Pomatias scalarinus saueri Geyer, 1914: 129, pl. 2, figs. 1–2.

Lectotype (herein): SMNS 106422-a.

Paralectotype: SMNS 106422-b (1 specimen) and 106423 (6 specimens).

Type locality: Germany: Baden-Württemberg: Bietigheim-Bissingen, Enzschotter [River Enz gravel].

Age: Pleistocene.

Taxonomic status: Possibly valid, as *Cochlostoma scalarinum saueri* (Geyer, 1914). Family Diplommatinidae (Cochlostomatinae).

Remarks: We designate here as lectotype the only completely preserved specimen (Geyer 1914: fig. 1).

scalaris* Miller, 1907, *Cyclotus
See *arneggensis* Wenz, 1923, ?*Pomatias*.

scalaris* Miller, 1900, *Planorbis (Dilatata) kraussii (Plate 7, Fig. 25)
Planorbis (Dilatata) Kraussii var. *scalaris* Miller, 1900: 405.

Holotype: SMNS 106424.

Type locality: Germany: Baden-Württemberg: Steinheim am Albuch, Steinheimer Seeschichten [Steinheim Lake beds].

Age: Middle Miocene (MN 7).

Taxonomic status: Unidentifiable teratological specimen of *Gyraulus* sp.; attribution to *Gyraulus kraussii* (Klein, 1846), fide Miller (1900). Family Planorbidae (Planorbinae).

schaefferiana* O. Boettger, 1877, *Clausilia (Emarginaria) (Plate 7, Fig. 26)
Clausilia (Emarginaria) Schaefferiana O. Boettger, 1877: 79, pl. 3, figs. 28a–f, 29.

Lectotype (herein): SMNS 106425-a.

Paralectotypes: SMNS 106425-b (1 specimen) and 106426 (1 specimen).

Type locality: Germany: Bavaria: Nittendorf (Undorf), Braunkohlenthon [lignitic clay], mittlere Silvanaschichten [middle Silvana-beds].

Age: Late Early/early Middle Miocene (Karpatian/Badenian; MN 5).

Taxonomic status: Valid, as *Emarginaria schaefferiana* (O. Boettger, 1877) (fide Nordsieck 1981, 2000). Family Clausiliidae (Clausiliinae).

Remarks: O. Boettger (1877) figured all three specimens. Here we designate as lectotype the aperture fragment, which bears the most important characters for clausilioid taxonomy.

schneideri* Jooss, 1924, *Cepaea (Plate 8, Fig. 1a, b)
Cepaea schneideri Jooss, 1924: 204, pl. 11, figs. 28–31.

Syntypes: SMNS 106427 (2 specimens).

Type locality: Germany: Baden-Württemberg: Winterlingen (Harthausen auf der Scher), rote Helicidenmergel [red helicid marls].

Age: Late Early Miocene (Late Burdigalian; MN 4).

Taxonomic status: Unknown. Family Helicidae (Helicinae).

schneidi* Jooss, 1912b, *Ericia (Plate 8, Fig. 2)
Cyclostoma (Ericia) schneidti Jooss, 1912a: 90 [nomen nudum].
Ericia schneidi Jooss, 1912b: 172, 174, pl.4 fig. 13, 13b.

Syntypes: SMNS 23925 (25 specimens).

Type locality: Germany: Bavaria: Dobelbuck ("Hobelsbuck") near Amerbach (Wemding), *Pomatias*-Süßwasserkalk des Riesgebietes [*Pomatias* freshwater limestone of the Ries area].

Age: Early Oligocene (Rupelian).

Taxonomic status: Valid, as *Pomatias (Neobembridgia) antiquus schneidi* (Jooss, 1912b) (fide Kadolsky 2014). Family Pomatiidae (Pomatiinae).

Remarks: Jooss (1912a) introdued the taxon with the words "*Ericia schneidti* is a smaller *Cyclostoma* from the group of *C. (Ericia) bisulcatum* Zieten" [translated from German], which is deemed insufficient as a diagnosis. Jooss dedicated the taxon to Theodor Schneid, whose name he consistently misspelt. Only in the follow-up publication (1912b) did Jooss provide a diagnosis, figure and the correct spelling of the name of the person to be honoured. Even if the original words (1912a) would satisfy the requirement of a diagnosis or definition (article 12.1 ICZN), *schneidti* is to be treated as an incorrect original spelling and to be corrected to *schneidi* (see article 32.5.1 ICZN, in particular the example).

schuebleri* Klein, 1846, *Pupa (Plate 8, Fig. 3)
Pupa antiqua (Schübler MS) Zieten, 1832: 39, pl. 29, fig. 7 [non Mathéron, 1832 (: 56, pl. 1, figs. 4–5)]
Pupa Schübleri Klein, 1846: 74, pl. 1, fig. 18.

Neotype: SMNS 100110-1.

Type locality: Germany: Baden-Württemberg: Steinheim am Albuch, Steinheimer Seeschichten [Steinheim Lake beds].

Age: Middle Miocene (MN 7).

Taxonomic status: Valid, as *Granaria schuebleri* (Klein, 1846) (fide Höltke & Rasser 2013). Family Chondrinidae.

Remarks: (1) The neotype defined by Höltke & Rasser (2013) is also the neotype for *Pupa antiqua* Zieten, as Klein proposed the name *schuebleri* as a substitute name for *Pupa antiqua* (article 72.7 ICZN). (2) The name *Pupa antiqua* has been published nearly simultaneously by Mathéron and Zieten late in 1832. Höltke & Rasser (2013) discussed the question of precedence, which is here briefly restated, updated and formally resolved in accordance with the IZCN. Mathéron's work appeared in the September/October issue of volume 3 of the Annales des Sciences et de l'Industrie du Midi de la France, i.e., most likely in or after October 1832. Heft 5–6 of Zieten's work is reported in Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde 1833, issue 1. This issue contains letters to the editors dated till 22.11.1832; for Heft 5-6 of Zieten's work to be reported in that issue, it must have been received by the editors at a similar time. The previous issue of this journal (1832[4]) contains letters dated till 10.8.1832, i.e., Zieten's Heft 5-6 had not been received by that date by the editors. The SMNS copy of Zieten's work states only "second half of 1832". The date can now be narrowed down to "after 10.8.1832" and "before 22.11.1832". (3) As the precedence between Mathéron's and Zieten's works cannot be established with any certainty, we determine hereby as First Revisers (article 24.2.1 ICZN) that Mathéron's work shall be accorded precedence over Zieten's Heft 5-6. This is in accordance with the actions of Klein (1846) and Höltke & Rasser (2013). Thus, *Pupa antiqua* Mathéron, 1832 will have precedence over *Pupa antiqua* Zieten, 1832, for which the substitute *Pupa schuebleri* Klein, 1846 becomes the valid name. *Pupa subantiqua* A. d'Orbigny, 1850 (: 208) thus becomes an unnecessary replacement name for *Pupa antiqua* Mathéron, 1832.

semiconvexa* Sandberger, 1875, *Hydrobia (Plate 8, Figs. 4–5)
Litorinella acuta: Krauss, 1852: 142 [non *Cyclostoma acutum* Draparnaud, 1805].
Hydrobia semiconvexa Sandberger, 1875: 561.

Paralectotypes: SMNS 2864 (6 specimens), 106428 (9 specimens; Figs. 4–5) and 106429 (7 specimens); leg. Gatekunst 1851.

Type locality: Germany: Baden-Württemberg: Leipheim, Kirchberg Formation. The paralectotypes in SMNS are from Kirchberg an der Iller (now Illerkirchberg), "bläulichgrauen weichen Thon" [bluish-gray soft clay layer] of the Kirchberg Formation.

Age: Late Early Miocene (Burdigalian/ Ottnangian, MN 4b).

Taxonomic status: The type series is a mixture of four different species. The lectotype, designated by Kadolsky (this volume), and the remaining 8 specimens from the lot in Sandberger's collection in the MUWI are for the time being

classified as *"Hydrobia" semiconvexa* Sandberger, 1875 (family Hydrobiidae), but may belong to *Heleobia* (family Cochliopidae). Lot SMNS 106428 consists of 9 specimens of *Nematurella zilchi* Schlickum, 1960; lot SMNS 2864 consists of 2 *Nematurella* sp. (white fosssils) and 7 *Ctyrokya conoidea* (Krauss, 1852) (blackish fossils); lot SMNS 106429 consists of two rock fragments with many shells of *Nematurella* sp., *Ctyrokya conoidea* and *Bithynia glabra* (Zieten, 1832).

Remarks: (1) Sandberger's own type material is preserved in MUWI and is the species so identified by Schlickum (1960) and subsequent authors in the genus *Hydrobia*. Because Sandberger also included "*Litorinella acuta* Braun" sensu Krauss (1852) in his *Hydrobia semiconvexa*, Krauss' material is part of the type series. Krauss received his material from Fr. Gatekunst of Ulm, whom he mentions [1852: 136] as a punctual collector providing fossils to the Königliche Naturaliencabinet. This material, however, is a mixture of several species (see above). Although *Ctyrokya conoidea*, *Bithynia glabra* and all shells which are not white do not agree with the data published by Krauss for his "*Litorinella acuta*", lots SMNS 2864 and SMNS 106429 were labelled *Hydrobia semiconvexa* by Sandberger. (2) Krauss, as well as other contemporaneous authors, cite A. Braun 1851 as the author of "*Litorinella acuta*". But this species is based on *Cyclostoma acutum* Draparnaud 1805, as Braun's reference to modern occurrences in the Mediterranean lagoons of France make obvious. *Cyclostoma acutum* Draparnaud 1805 is the type species of *Hydrobia* Hartmann 1821 and of *Litorinella* A. Braun 1843.

serratiliniformis* Geyer, 1914, *Neritina (Plate 8, Figs. 6a, b)
Neritina serratiliniformis Geyer, 1914: 131, pl. 2, figs. 7, 9–12.

Lectotype (herein): SMNS 13514-a.

Paralectotype: SMNS 13514-b (39 specimens).

Type locality: Germany: Baden-Württemberg: Bietigheim-Bissingen, Enzschotter [gravels of the river Enz].

Age: Pleistocene.

Taxonomic status: Valid, as *Theodoxus serratiliniformis* (Geyer, 1914) (fide Glöer 2002). Family Neritidae (Neritininae).

Remarks: We designate here as lectotype the best preserved specimen, also figured in the original description (Geyer 1914: fig. 12).

silvana* Klein, 1853, *Helix (Plate 8, Fig. 7a–c)
Helix silvana Klein, 1853: 205, pl. 5, fig. 2.

Syntype: SMNS 22738.

Type locality: Germany: Baden-Württemberg: Zwiefalten (near Mörsingen), Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: Valid, as *Megalotachea silvana* (Klein, 1853) (revised by Höltke in preparation). Family Helicidae (Helicinae).

Remarks: Klein (1853) reported the species as fairly rare ("seltener"), which does not exclude that he had more than one specimen at his disposal.

sparsa* Krauss, 1852, *Neritina (Plate 8, Fig. 8)
Neritina sparsa Krauss, 1852: 145.

Syntypes: SMNS 106430 (7 specimens).

Type locality: Germany: Baden-Württemberg: Kirchberg an der Iller, Kirchberg Formation.

Age: Late Early Miocene (Burdigalian/Ottnangian, MN 4b).

Taxonomic status: Synonym of *Theodoxus cyrtocelis* (Krauss, 1852) (Salvador et al. submitted). Family Neritidae (Neritininae).

steinheimensis* Klein, 1846, *Helix (Plate 8, Fig. 9a–c)
Helix Steinheimensis Klein, 1846: 70, pl. 1, fig. 10a, b.

Holotype: SMNS 106431.

Type locality: Germany: Baden-Württemberg: Steinheim am Albuch, Steinheimer Seeschichten [Steinheim Lake Formation].

Age: Middle Miocene (MN 7).

Taxonomic status: Synonym of *Joossia insignis* (Zieten, 1832) (Binder 2008; Nordsieck 2014) or *Pseudochloritis insignis* (fide Höltke & Rasser 2015). Family Elonidae (Eloninae) or Helicidae (Ariantinae).

steinheimensis* Jooss, 1918b, *Klikia (Klikia) coarctata (Plate 8, Fig. 10a–c)
Klikia (Klikia) coarctata var. *steinheimensis* Jooss, 1918b: 294.

Syntype?: SMNS 106432.

Type locality: Germany: Baden-Württemberg: Steinheim am Albuch, Steinheimer Seeschichten [Steinheim Lake beds].

Age: Middle Miocene (MN 7).

Taxonomic status: Synonym of *Apula coarctata* (Klein, 1853). Family Elonidae (Klikiinae) or Helicidae (Ariantinae).

Remarks: There is no indication in the specimen's original label that it is a type (all the other material from Jooss' collection have such indication). Nevertheless, there is a second label signed by W. R. Schlickum stating that it is a lectotype. The original description is not accompanied by a figure to verify this claim and a lectotype designation has, to our knowledge, never been published. Therefore, the status of the present specimen remains unknown.

striata* Klein, 1846, *Lymnaea socialis (Plate 8, Fig. 11)
Limnaeus socialis var. *striata* Klein, 1846: 85, pl. 2, fig. 10a, b [?non *Limnaeus striatus* Zieten, 1832 (: pl. 30, fig. 5)].

Syntypes: SMNS 23904 (2 specimens).

Type locality: Germany: Baden-Württemberg: Steinheim am Albuch, Steinheimer Seeschichten [Steinheim Lake beds].

Age: Middle Miocene (MN 7).

Taxonomic status: Synonym of *Radix socialis* (Zieten, 1832). Family Lymnaeidae (Lymnaeinae).

Remarks: Klein stated that this variety was "probably" *Limnaeus striatus* Zieten, 1832, i.e., he introduced knowingly a nominal taxon which under the current Code is a junior primary homonym, but in Klein's time "varieties" were not considered to compete for homonymy with species names.

subapicalis* Sandberger, 1872, *Helix (Plate 8, Fig. 12a–c)
Helix subapicalis Sandberger, 1872: pl. 21, fig. 8, 8b.
Helix (Fruticicola) leptoloma var. *subapicalis* Sandberger 1875: 380, pl. 21, fig. 8, 8b.

Syntypes: SMNS 14917 (2 specimens, from Donaurieden).

Type localities: Germany: Baden-Württemberg: Thalfingen, Eckingen, Göttingen (near Ulm), Erbach (Donaurieden), obere Rugulosa-Schichten [upper Rugulosa-beds].

Age: Early Miocene (Aquitanian; MN 2).

Taxonomic status: Synonym of *Leucochroopsis apicalis* (Reuss, 1860). Family Hygromiidae (Hygromiinae).

subcostata* Clessin, 1913, *Helix (Vallonia) (Plate 8, Figs. 13–15)
Helix (Vallonia) subcostata Clessin, 1913: 109 [non *Vallonia lepida* var. *subcostata* O. Boettger, 1903a (: 74); nec *Helix reboudiana subcostata* Bourguignat, 1863 (: 213, pl. 21, fig. 23)].

Lectotype: SMNS 106433 (designated by Gerber 1996).

Paralectotypes: SMNS 45162/2005 (9 specimens).

Type locality: Germany: Bavaria: Nittendorf (Undorf), mittlere Silvanaschichten [middle Silvana-beds].

Age: Late Early/early Middle Miocene (Karpatian–Badenian; MN 5).

Taxonomic status: Synonym of *Vallonia subcyclophorella* (Gottschick, 1911) (fide Gerber 1996). Family Valloniidae.

Remarks: (1) The lectotype and paralectotypes were designated by Gerber (1996). This material, as well as all or most of Clessin's other fossils, were on 2.5.1913 acquired by Jooss, who replaced all original labels with his own and discarded the originals. Jooss' label indicates that Clessin collected the specimens in 1910, but does not provide the name which Clessin gave them. Jooss determined them as *Vallonia subcyclophorella undorfensis* Jooss, which remains an unpublished und unavailable name. Conceivably Clessin 's publication of the name *subcostata* escaped Jooss and was, moreover, not noted down by Clessin, who died 1911 and therefore might not have been able to update his label. (2) O. Boettger (1903) introduced the name *subcostata* independently for a different *Vallonia* form, which is considered to be conspecific with *V. lepida* (Reuss, 1849) (fide Gerber 1996).

subcyclophorella* Gottschick, 1911, *Helix (Vallonia)
Helix (Vallonia) subcyclophorella Gottschick, 1911: 503, pl. 7, fig. 2.

Neotype: SMNS 15817 (designated by Gerber 1996).

Type locality: Germany: Baden-Württemberg: Steinheim am Albuch, Steinheimer Seeschichten [Steinheim lake beds], "*laevis*-Zone" [= *Gyraulus kleini* zone].

Age: Middle-Late Miocene (MN 7).

Taxonomic status: Valid, as *Vallonia subcyclophorella* (Gottschick, 1911) (fide Gerber 1996). Family Valloniidae.

Remarks: Although having been rather recently designated, this type could not be presently found in the collection.

subdiaphana* Clessin, 1885, *Hyalinia (Plate 8, Fig. 16a–c)
Hyalina subdiaphana Clessin, 1885: 75.

Holotype: SMNS 22755.

Type locality: Germany: Baden-Württemberg: Berg near Ehingen (Donau), Ehinger Ramondi-Schichten [Ramondi beds of Ehingen].

Age: Late Oligocene (Chattian).

Taxonomic status: Valid, as *Vitrea subdiaphana* (Clessin, 1885). Family Pristilomatidae.

subfontanus* Clessin, 1877, *Planorbis (Hippeutis) (Plate 8, Fig. 17a–c)
Planorbis (*Hippeutis*) *subfontanus* Clessin, 1877: 39; Clessin 1885: 91, pl. 7, fig. 4a–c.

Syntypes: SMNS 106434 (2 juvenile specimens, from Undorf; actual syntypes are mixed with othe specimens).

Type localities: Undorf and Mörsingen-Birk.

Age: Middle Miocene.

Taxonomic status: Valid, as *Hippeutis subfontanus* (Clessin, 1877). Family Planorbidae (Segmentininae).

Remarks: (1) Clessin (1877) described the species from two "unfinished" (i.e., juvenile) specimens. In 1885, he provided an illustration of the only fully grown specimen which he had subsequently acquired. The present lot consists of 4 juvenile and 2 adult specimens. It is impossible to identify the two juvenile syntypes or the figured adult (1885) in this lot, although they are almost certainly amongst the specimens. Apparently, non-type specimens had been added to the type series after 1877. (2) The figure from 1885 shows the proportions of the shell very different from those of the actual specimens, which is tentatively interpreted as a draftman's error. **(3)** Clessin (1877) included in his species specimens from Mörsingen-Birk from O. Boettger's collection, which is in the Senckenberg Museum, Frankfurt a. Main. This material is thus part of the type series.

subfusiformis* Sandberger, 1875, *Pupa (Torquilla) (Plate 8, Fig. 18)
Pupa nov. spec.? Klein, 1853: 216.
Pupa (Torquilla) subfusiformis Sandberger, 1875: 598.
Granaria subfusiformis: Höltke & Rasser, 2013: 190, fig. 4.7–4.8.

Syntype: SMNS 100112 (from Zwiefalten).

Type localities: Zwiefalten, Mörsingen, Hausen near Ehingen, Georgsgemünd, Schönbrunn near Kipfenberg, Adelegg in Oberschwaben.

Age: M. Miocene, Silvanaschichten [Silvana-beds].

Taxonomic status: *Granaria* sp., indeterminable due to its incomplete preservation (fide Höltke & Rasser 2013). Family Chondrinidae.

Remarks: (1) As Sandberger (1875) included Klein's "*Pupa* n. sp." in *subfusiform*is; it is a syntype. (2) Any redescription of this nominal species should be based on specimens from Schönbrunn near Kipfenberg, because of Sandberger's statement that he based his description on the best preserved specimens, which were from this locality.

subhammonis* Gottschick, 1928, *Zonitoides (Plate 8, Fig. 19a–c)
Zonitoides subhammonis Gottschick, 1928: 146, pl. 2, fig. 6.

Holotype: SMNS 15817.

Type locality: Germany: Baden-Württemberg: Altheim, near Ehingen, Malleolatakalk [Malleolata limestone].

Age: Late Miocene.

Taxonomic status: Potentially valid, as *Perpolita subhammonis* (Gottschick, 1928). Family Oxychilidae (Godwiniinae).

subnitens* Klein, 1853, *Helix (Plate 8, Fig. 20a–c)
Helix subnitens Klein, 1853: 210, pl. 5, fig. 7.

Lectotype (herein): SMNS 106435-a.

Paralectotypes: SMNS 106435-b (2 specimens).

Type locality: Germany: Baden-Württemberg: Zwiefalten (near Mörsingen), Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Karpatian–Badenian; MN 5).

Taxonomic status: Valid, as *Aegopinella subnitens* (Klein, 1853) (fide Schlickum 1976, Nordsieck 2014). Family Oxychilidae (Godwiniinae).

Remarks: Type series with three specimens, we designate here the lectotype as the most complete specimen, which is also the one that best fits the original description and figures.

subteres* Clessin, 1877, *Helix (Patula) (Plate 9, Fig. 1)
Helix (Patula) subteres (Sandberger MS.) Clessin, 1877: 35.

Syntype: SMNS 68501.

Type locality: Germany: Bavaria: Nittendorf (Undorf), mittlere Silvanaschichten [middle Silvana-beds].

Age: Late Early/early Middle Miocene (Karpatian–Badenian; MN 5).

Taxonomic status: Valid, as *Lucilla subteres* (Clessin, 1877) (fide Schlickum 1979a, as *Helicodiscus (Hebetodiscus)*; and Salvador & Rasser 2014). Family Helicodiscidae.

Remarks: A later-added note by G. Falkner on the specimen's label states that it is the material used by Clessin (1877) and, thus, the holotype. As the original number of specimens was not stated (Clessin 1877), it is more prudent to treat the specimen as a syntype.

subtilisticta* Sandberger, 1875, *Helix (Plate 9, Fig. 2a–c)
Helix subtilisticta Sandberger, 1875: 459.

Syntypes: SMNS 14913 (3 specimens).

Type locality: Germany: Baden-Württemberg: Ehingen (Donau), Ehinger Ramondi-Schichten or Rugulosa-Schichten [Ramondi/Rugulosa-beds of Ehingen].

Age: Late Oligocene (Chattian).

Taxonomic status: Valid, as *Pseudochloritis subtilisticta* (Sandberger, 1875) (fide Binder 2008). Family Elonidae (Eloninae) or Helicidae (Ariantinae).

subtruncatula* Clessin, 1885, *Lymnaea (Plate 9, Fig. 3)
Limnaea subtruncatula Clessin, 1885: 89.
Limnaea subtruncata Clessin, 1894: 35 [error or unjustified emendation].

Holotype: SMNS 106436.

Type locality: Germany: Bavaria: Nittendorf (Undorf), originally assumed to be from the mittlere Silvanaschichten [middle Silvana-beds].

Age: Late Early/early Middle Miocene (Karpatian–Badenian; MN 5) or recent contamination.

Taxonomic status: The specimen is certainly a *Galba* s. str.; judging from its shape and state of preservation, it appears to be a recent specimen of *Galba truncatula* (O.F. Müller, 1774). Family Lymnaeidae (Lymnaeinae).

subventrosa* Gottschick, 1921, *Hydrobia (Plate 9, Fig. 4)
Hydrobia subventrosa Gottschick, 1921: 172.

Syntypes: SMNS 15523 (4 specimens) and 15817 (7 specimens).

Type locality: Germany: Baden-Württemberg: Steinheim am Albuch, "Kaltwasserschichten" (=*Gyraulus kleini*-Zone, Steinheimer Seeschichten) ["cold water beds", *Gyraulus kleini* zone, Steinheim Lake Formation].

Age: Middle Miocene (MN 7).

Taxonomic status: Closely related to, or synonym of *Heleobia trochulus* (Sandberger, 1875) (cf. Kadolsky 2008b). Family Cochliopidae.

subvermiculata* Sandberger, 1875, *Helix (Macularia) (Plate 9, Fig. 5a–c)
Helix Leymeriana Sandberger, 1872: pl. 29, fig.11 [non Noulet, 1854 (: 73)].
Helix (Macularia) subvermiculata Sandberger, 1875: 591 (ref. pl. 29, fig. 11).

Syntype?: SMNS 10920, from Mörsingen.

Type locality: Germany: Baden-Württemberg: Mörsingen, Silvanaschichten [Silvana-beds] and seven other localities in Baden-Württemberg, Bavaria and Switzerland.

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: Junior synonym of *Megalotachea silvana* (Klein, 1853). Family Helicidae (Helicinae).

Remarks: The present specimen compares well in shape with the one figured by Sandberger (1872), from Mörsingen. Nevertheless, it does not show the dark spiral bands depicted in the figure, even under UV light. As such, this specimen status as a type remain questionable. The labels state there was a second specimen in the lot, but it could not be located. There are presently three further syntypes in the MUWIE collection.

suevica* Gottschick & Wenz, 1927, *Helicopsis (Plate 9, Fig. 6a–c)
Helicopsis suevica Gottschick & Wenz, 1927: 148, pl. 8, fig. 2a, b.

Syntype: SMNS 22828.

Type locality: Germany: Baden-Württemberg: Zwiefaltendorf, sand pit, reworked block from the Silvanaschichten [Silvana-beds] in Pleistocene sands.

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: Unknown. Family Hygromiidae.

Remarks: Gottschick & Wenz (1927) mentioned two specimens.

***suevica* Jooss, 1918b, *Hyalinia* (*Polita*)** (Plate 9, Fig. 7a–c)
Hyalinia (Polita) suevica Jooss, 1918b: 289.

Holotype: SMNS 106441.

Type locality: Germany: Baden-Württemberg: Dischingen, Silvana-beds ("Silvanaschichten").

Age: Late Miocene (Tortonian).

Taxonomic status: Valid, as *Zonitoides suevicus* (Jooss, 1918b) (fide Wenz 1923). Family Gastrodontidae.

suevica* Miller, 1907, *Melania (Plate 9, Fig. 8)
Melania suevica Miller, 1907: 456, pl. 9, fig. 20.

Syntypes: SMNS 27646 (5 specimens).

Type locality: Germany: Bavaria: Bachhagel, karst fissure limestone.

Age: Eocene.

Taxonomic status: Uncertain; Wenz (1923) lists this species as *Palaeostoa suevica*. Family Palaeostoidae.

suevica* Sandberger, 1875, *Clausilia (Plate 9, Fig. 9)
Clausilia grandis Sandberger, 1872: pl. 29, fig. 18a [non Klein, 1846, nec fig. 18]
Clausilia suevica Sandberger, 1875: 461 (ref. pl. 29, fig. 18a).

Syntypes: SMNS 106438 (2 specimens).

Type locality: Germany: Baden-Württemberg: Berg near Ehingen (Donau), Ehinger-Ramondi-Schichten [Ramondi-beds of Ehingen].

Age: Late Oligocene (Chattian).

Taxonomic status: Valid, as *Triptychia suevica* (Sandberger, 1875) (revised by Schnabel 2007). Family Filholiidae.

Remarks: Schnabel (2007) cites as "holotype" a specimen in Sandberger's collection in the MUWIE, although Sandberger stated that he studied, from Ehingen, one specimen from each of the following: his personal collection, the Stuttgart collection and Probst's collection. Schnabel's "holotype" declaration is invalid (article 73.1 ICZN), and a name-bearing type specimen is to date not validly selected. Sandberger's specimen in the SMNS is a syntype and not just "further material" as mentioned by Schnabel. Moreover, the collection in Stuttgart counts with two specimens as Sandberger's original material, not just a single one.

suevica* Sandberger, 1875, *Helix (Plate 9, Fig. 10a–c)
Helix suevica Sandberger, 1875: 459 (Probst coll.).
Galactochilus brauni var. *suevica* Jooss, 1918b: 292.

Syntypes: SMNS 14914 (4 specimens), 106440 (3 specimens), ex Probst coll.

Type locality: Germany: Baden-Württemberg: Berg near Ehingen (Donau), Ehinger Ramondi-Schichten [Ramondi-beds of Ehingen].

Age: Late Oligocene (Chattian).

Taxonomic status: Uncertain, possibly a synonym of *Galactochilus braunii ehingensis* (Klein, 1846) (fide Wenz 1923). Family Elonidae (Eloninae) or Helicidae (Ariantinae).

Remarks: Jooss (1918b) stated that *Helix suevica* Sandberger, 1875 was a juvenile specimen of his *Galactochilus brauni* var. *suevica*. Although Jooss designated the name *suevica* as new ("n. var."), his citation of *Helix suevica* Sandberger indicates that he meant to redescribe the latter. Analogous to the case of *Helix alveus* Sandberger (q.v.), Jooss believed apparently that *Helix suevica* Sandberger was a nomen nudum. This is incorrect, as Sandberger provided a short diagnosis. Sandberger's original material thus constitutes the type series. Jooss' label indicates that it is Sandberger's original material.

suevica* Sandberger, 1872, *Vitrina (Plate 9, Fig. 11a, b)
Vitrina suevica Sandberger, 1872: pl. 29, figs. 27a–b; Sandberger, 1875: 602.

Holotype: SMNS 106439.

Type locality: Germany: Baden-Württemberg: Neuselhalder Hof near Steinheim am Albuch, marl layers with *Planorbarius cornu* (Brongniart, 1810).

Age: Middle Miocene (MN 7).

Taxonomic status: Valid. Family Vitrinidae.

suevicus* Gottschick, 1928, *Amnicola (Plate 9, Fig. 12)
Amnicola suevica Gottschick, 1928: 148, pl. 2, fig. 7a–c.

Syntypes: SMNS 15817 (11 specimens).

Type locality: Germany: Baden-Württemberg: Zwiefalten (Mörsingen), Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Karpatian–Badenian; MN 5).

Taxonomic status: Uncertain, possibly a subspecies of *Pseudamnicola convexus* (Sandberger, 1875). Family Hydrobiidae (Pseudamnicolinae).

Remarks: The material is labelled "*Amnicola subpseudoglobulus* Gottschick & Wenz". This name was never published, and it is likely that it had been changed because of its clumsiness, but due to his death in 1928, Gottschick was unable to change the label. Gottschick (1928) lists 15 specimens, but the present material consists only of eleven; the remaining four are thus deemed lost. The two syntypes of the "subspecies" *Amnicola suevicus major* Gottschick, 1928 could not be found; this nominal taxon dos not appear to be conspecific.

suevicus* Wenz, 1919, *Viviparus (Plate 9, Fig. 13)
Paludina varicosa Krauss, 1852: 139, pl. 3, fig. 2 [non C. d'Orbigny, 1837 (: 1, pl. 79, figs. 1–3)].
Viviparus suevicus Wenz, 1919a: 76.

Syntype: SMNS 106437.

Type locality: Germany: Baden-Württemberg: Kirchberg an der Iller, lower "greenish-yellow sand" layer ("grünlich gelber Sand") of the Kirchberg Formation.

Age: Late Early Miocene (Burdigalian/Ottnangian, MN 4b).

Taxonomic status: Valid as *Viviparus suevicus* Wenz, 1919. Family Viviparidae (Viviparinae).

Remarks: When Wenz (1919) defined the new name for the species, he also designated a "Typus" from his personal collection. This action is not valid as per ICZN Article 75.8; the replacement name has the same name-bearing type as Krauss' original name.

***trochiformis* Miller, 1907, *Helicina*(?)**
See *milleri* Fulton, 1915, *Helicina*.

trolli* Schlickum, 1979b, *Hydrocena (Hydrocena) (Plate 9, Fig. 14)
Pseudamnicola helicella Andreae, 1902: 24 [partim, non A. Braun, 1851 (: 1126, no. 169)].
Amnicola (*Amnicola*) cf. *helicella* Wenz 1926: 2064 [non A. Braun, 1851].
Amnicola (*Amnicola*) *gobanzi* Wenz, 1930: 3042 [non Frauenfeld, 1864 (: 604)].
Hydrocena (*Hydrocena*) *trolli* Schlickum, 1979b: 71, figs. 3–4.

Paratypes: SMNS 106442 (2 specimens, Andreae leg. III. 2003).

Type locality: Poland: Silesia: Opole (= Königlich Neudorf near Oppeln).

Age: Middle Miocene (MN 6–7).

Taxonomic status: Valid. Family Hydrocenidae.

Remarks: Schlickum (1979) included the material reported by Andreae (1902) and Wenz (1926, 1930) in his new species. This material is therefore part of the type series (article 72.4.2 ICZN).

truncatuliformis* Schütze in Branca & Fraas, 1908, *Lymnaea (Plate 9, Fig. 15)
Limnaeus truncatuliformis Schütze in Branca & Fraas, 1908: 20, fig. 11.

Lectotype (herein): SMNS 11898-a.

Paralectotype: SMNS 11898-b (1 specimen).

Type locality: Germany: Bavaria: Monheim (Weilheim im Ries), grey freshwater limestone block in Bunter Breccie [varicoloured breccia, Ries ejecta].

Age: Early Oligocene.

Taxonomic status: Potentially valid, as *Stagnicola*? *truncatuliformis* (Schütze *in* Branca & Fraas, 1908). Family Lymnaeidae (Lymnaeinae).

Remarks: We designate here as lectotype the specimen figured in the original description (Schütze *in* Branca & Fraas 1908: fig. 9).

turrita* Klein, 1853, *Lymnaea (Plate 9, Fig. 16)
Lymnaeus turritus Klein, 1853: 220, pl. 5, fig. 17.

Lectotype (herein): SMNS 106443-a.

Paralectotypes: SMNS 106443-b (2 specimens).

Type locality: Germany: Baden-Württemberg: Andelfinger Berg near the village of Andelfingen, Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: Valid, as *Lymnaea* (s. lat.) *turrita* Klein, 1853. Family Lymnaeidae (Lymnaeinae).

Remarks: We designate here the lectotype as the most complete specimen, which is also the one figured in the original description (Klein 1853).

turrita* Klein, 1846, *Melania (Plate 9, Fig. 17a, b)
Melania turrita Klein, 1846: 81, pl. 2, fig. 2.

Syntypes: SMNS 106444 (2 specimens).

Type locality: Germany: Baden-Württemberg: Ehingen, Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: Junior synonym of *Tinnyea lauraea* (Mathéron, 1843) (fide Kadolsky 1995). Family Pachychilidae.

ulmensis* Jooss, 1918b, *Discus diezi (Plate 9, Fig. 18a–c)
Pyramidula (Gonyodiscus) diezi var. *ulmensis* Jooss, 1918b: 291.

Syntype: SMNS 106445.

Type locality: Germany: Baden-Württemberg: Ulm (Thalfingen), Thalfinger Schichten [Thalfingen beds].

Age: Early Miocene (Aquitanian, MN2a).

Taxonomic status: Potentially valid in the genus *Discus*, but requiring further study. Family Discidae.

Remarks: Jooss (1918b) reports the species as "rather rare". As this does not exclude the possibility of the type series consisting of more than one specimen, it is prudent to treat the only preserved specimen in the Jooss collection as syntype.

ulmensis* Sandberger, 1875, *Clausilia (Plate 9, Fig. 19)
Clausilia grandis Sandberger, 1872: pl. 29, fig. 18 [non 18a] [non *Clausilia grandis* Klein, 1846].
Clausilia ulmensis Sandberger, 1875: 461, 598 (ref. pl. 29, fig. 18).

Lectotype: SMNS 22181-a (designated by Schnabel 2006).

Paralectotype: SMNS 22181-b.

Type locality: Germany: Baden-Württemberg: Ulm (Michelsberg), Ulmer Subrugulosa-Schichten [Subrugulosa-beds of Ulm].

Age: Early Miocene (Aquitanian; MN 2).

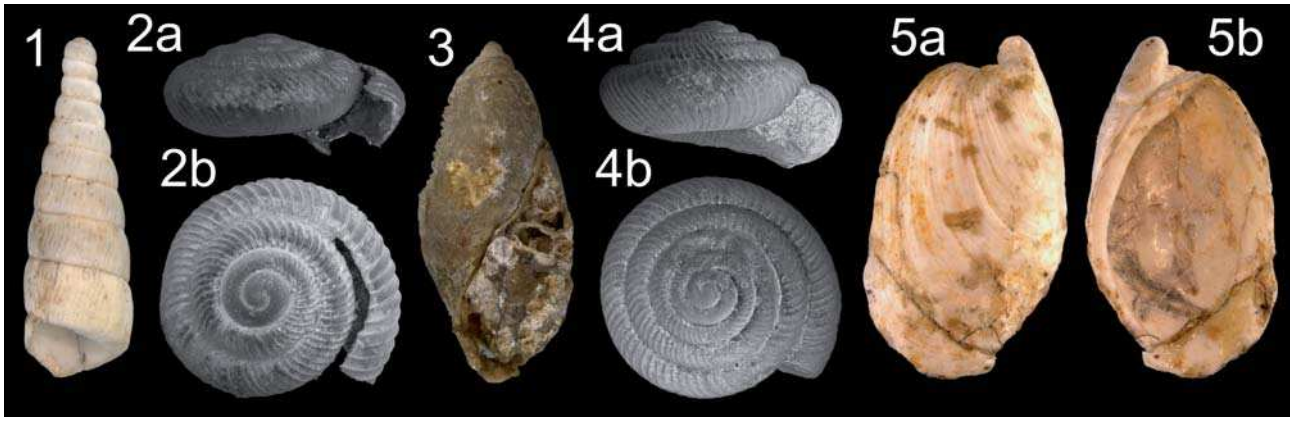

Fig. 2. 1. *Pseudidyla*? *undatistria* (O. Boettger, 1877), holotype (SMNS 22830; H = 8.7 mm). **2a, b.** *Discus euglyphoides undorfensis* (Clessin, 1894), syntype? (SMNS 106446; H = 2.5 mm, D = 2.6 mm). **3.** *Palaeoglandina wagneri* (Miller, 1907), holotype (SMNS 27638; H = 24.9 mm). **4a, b.** *Discus wenzi* (Jooss, 1918), syntype (SMNS 106447; H = 2.5 mm, D = 3.8 mm). **5a, b.** *Testacella zellii* Klein, 1853, holotype (SMNS 106448; H = 11.7 mm, D = 6.3 mm).

Taxonomic status: Valid, as *Triptychia ulmensis* (Sandberger, 1875) (fide Schnabel 2006). Family Filholiidae.

undatistria* O. Boettger, 1877, *Clausilia (Pseudidyla) moersingensis (Fig. 2.1)
Clausilia (Pseudidyla) mörsingensis var. undatistria O. Boettger, 1877: 92, pl. 4, fig. 40.

Holotype: SMNS 22830.

Type locality: Germany: Baden-Württemberg: Zwiefalten (Mörsingen), Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: Unidentified species (fide Nordsieck 1981, 2007). Family Clausiliidae (inc. sed.).

undorfensis* Clessin, 1894, *Patula (Fig. 2.2a, b)
Patula undorfensis Clessin, 1894: 5, pl. 1, fig. 11.

Syntype?: SMNS 106446.

Type locality: Germany: Bavaria: Nittendorf (Undorf), middle Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Karpatian–Badenian; MN 5).

Taxonomic status: Synonym or subspecies of *Discus euglyphoides* (Sandberger, 1872) (fide Wenz 1923). Family Discidae.

Remarks: In the original description, Clessin (1894) lists four specimens, housed in the private collection of Diez. The single specimen in the Clessin collection of the SMNS is probably one of them, retained by Clessin.

varicosa* Krauss, 1852, *Paludina
See *suevicus* Wenz, 1919, *Viviparus*.

wagneri* Miller, 1907, *Glandina (Fig. 2.3)
Glandina Wagneri Miller, 1907: 453, pl. 9, fig. 8.

Holotype: SMNS 27638.

Type locality: Germany: Bavaria: Bachhagel, karst fissure limestone.

Age: Eocene.

Taxonomic status: Valid, as *Palaeoglandina wagneri* (Miller, 1907). Family Oleacinidae.

wenzi* Jooss, 1918b, *Pyramidula (Gonyodiscus) (Figs. 2.4a, b)
Pyramidula (Gonyodiscus) wenzi Jooss, 1918b: 291.

Syntype: SMNS 106447.

Type locality: Germany: Baden-Württemberg: Zwiefalten (Mörsingen), Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: Valid, as *Discus wenzi* (Jooss, 1918b). Family Discidae.

zellii* Klein, 1853, *Testacella (Fig. 2.5a, b)
Testacella Zellii Klein, 1853: 204, pl. 5, fig. 1.

Holotype: SMNS 106448.

Type locality: Germany: Baden-Württemberg: Andelfinger Berg, near the village of Andelfingen, Silvanaschichten [Silvana-beds].

Age: Late Early/early Middle Miocene (Burdigalian/Langhian; MN 5).

Taxonomic status: Valid. Family Testacellidae.

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Plate 1

Fig. 1. *Gastrocopta (Albinula) acuminata* (Klein, 1846), syntype #1 (SMNS 106361; H = 2.5 mm).
Fig. 2. *Gastrocopta (Albinula) acuminata* (Klein, 1846), syntype #2 (SMNS 106361; H = 2.4 mm).
Fig. 3a, b. *Grandipatula alsatica* (Jooss, 1918), holotype (SMNS 65581; H = 16.3 mm, D = 22.4 mm).
Fig. 4a–c. *Pseudochloritis*? *alveus* (Sandberger, 1875), syntype? (SMNS 106362; H = 20.0 mm, D = 24.0 mm).
Fig. 5. *Stagnicola fabulum* (Brongniart, 1810), syntype of *Limnophysa amerbachensis* Jooss, 1912 (SMNS 23918-a; H = 26.6 mm).
Fig. 6a, b. *Vitrea ammoni* (Clessin, 1894), syntype (SMNS 106364; H = 1.7 mm, D = 2.8 mm).
Fig. 7a–c. *Protodrepanostoma involutum angitortum* (Jooss, 1912), holotype (SMNS 106365; H = 2.6 mm, D = 5.0 mm).
Fig. 8a, b. *Archaeozonites angulosus* Miller, 1907, syntype (SMNS 27620; H = 10.1 mm, D = 16.5 mm).
Fig. 9. *Palaeoglandina gracilis* (Zieten, 1832), syntype of *Glandina (Achatina) antiqua* Klein, 1852 (SMNS 23908-a; H = 42.9 mm).
Fig. 10a–c. *Discus antiquus* (Miller, 1907), syntype (SMNS 27641; H = 2.9 mm, D = 5.6 mm).
Fig. 11. *Triptychia antiquior* (Miller, 1907), syntype (SMNS 27644; H = 8.8 mm).
Fig. 12. *Pomatias (Neobembridgia) arneggensis* Wenz, 1923, lectotype of *Cyclotus scalaris* Miller, 1907 and *Pomatias arneggensis* (SMNS 27614-a; H = 14.8 mm).
Fig. 13a, b. *Archaeozonites? arneggensis* (Miller, 1907), syntype (SMNS 27621; H = 5.3 mm, D = 9.4 mm).
Fig. 14a–c. *Laminifera arneggensis* (Miller, 1907), syntype (SMNS 27629; H = 6.1 mm).
Fig. 15. *Palaeomastus arneggensis* (Miller, 1907) comb. nov., syntype (SMNS 36777; H = 9.9 mm).
Fig. 16a, b. *Miozonites algiroides badensis* (Jooss, 1924), holotype (SMNS 65634; H = 16.1 mm, D = 26.9 mm).
Fig. 17a, b. *Megalotachea eversa baumbergeri* Jooss 1924, syntype (SMNS, 106366; H = 15.7 mm, D = 19.4 mm).

1
2
3a
3b
4a
6a
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7c
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10a
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10c
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14b
14c
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12
13b
16a
16b
17a
17b

Plate 2

Fig. 1. *Strobilops costata* (Clessin, 1877), holotype of *Strobilus bilamellatus* Clessin, 1885 (SMNS 106369; H = 1.5 mm, D = 1.6 mm).
Fig. 2a, b. *Klikia praeosculina* (Miller, 1907), syntype of *Helix (Gonostoma) blaviana* Miller, 1907 (SMNS 27626; H = 8.5 mm, D = 13.0 mm).
Fig. 3a, b. *Perpolita boettgeriana* (Clessin, 1877), holotype (SMNS 106370; H = 1.4 mm, D = 3.1 mm).
Fig. 4. *Lymnaea* (s.l.) *brancai* Schütze *in* Branca & Fraas, 1908, lectotype (SMNS 11897-a; H = 15.4 mm)
Fig. 5. "*Melania" bulimoides* Klein, 1846, syntype #1 (SMNS 106371; H = 13.6 mm).
Fig. 6. "*Melania" bulimoides* Klein, 1846, syntype #2 (SMNS 106371; H = 12.1 mm).
Fig. 7. "*Abida" bythiniformis* (Miller, 1907), holotype (SMNS 27645; H = 3.6 mm).
Fig. 8a–c. *Ferussina anomphalus capellinii* (Sandberger, 1873), syntype (SMNS 22180; H = 14.7 mm, D = 26.8 mm).
Fig. 9a, b. *Archaeozonites carinatus* Miller, 1907, lectotype (SMNS 27639-a; H = 11.3 mm, D = 17.5 mm).
Fig. 10a, b. *Omphalosagda pyramidalis* (Jooss, 1912), holotype of *Zonites (Archaeozonites) risgoviensis carinatus* Jooss, 1912, (SMNS 23921; H = 11.1 mm, D = 16.4 mm).
Fig. 11a–c. *Leucochroopsis kleinii* (Klein, 1846), syntype of *Helix carinulata* Klein, 1853, (SMNS 106372; H = 4.7 mm, D = 7.2 mm).
Fig. 12. *"Lymnaea" conica* Miller, 1907, holotype (SMNS 27635; H = 8.2 mm).
Fig. 13a, b. *Palaeotachea renevieri* (Maillard, 1892), syntype of *Cepaea renevieri coniuncta* Berz & Jooss, 1927 (SMNS 101369; H = 10.8 mm, D = 16.1 mm).
Fig. 14. *Ctyrokya conoidea* (Krauss, 1852), syntype (SMNS 106373; H = 5.2 mm).
Fig. 15a, b. *Loganiopharynx constrictelabiatus* (Miller, 1907), holotype (SMNS 27643; H = 6.2 mm, D = 9.2 mm).
Fig. 16a, b. *Palaeotachea convexitesta* (Jooss, 1912), syntype (SMNS 23914-b; H = 8.2 mm, D = 13.0 mm).
Fig. 17a, b. *Vallonia costata* (O.F. Müller, 1774), holotype of *Vallonia costataeformis* Jooss, 1912 (SMNS 106375; H = 1.2 mm, D = 2.4 mm).

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Plate 3

Fig. 1a–c. *Discus costatus* (Gottschick, 1911), syntype (SMNS 106376; H = 2.2 mm, D = 3.8 mm).
Fig. 2a, b. *Gyraulus costatus* (Klein, 1846), lectotype (SMSN 23907-1; H = 1.0 mm, D = 2.0 mm).
Fig. 3. *Strobilops costata* (Clessin, 1877), syntype? (SMNS 106374; H = 1.5 mm, D = 2.1 mm).
Fig. 4. *Milax crassus* (Clessin, 1894), syntype? (SMNS 106378; H = 4.1 mm, D = 2.8 mm).
Fig. 5. *Limax crassissimus* Jooss, 1902, holotype (SMNS 106377; H = 11.1 mm, D = 6.3 mm).
Fig. 6. *Theodoxus crenulatus* (Klein, 1853), syntype #1 (SMNS 106379; H = 8.1 mm, D = 9.1 mm).
Fig. 7. *Theodoxus crenulatus* (Klein, 1853), syntype #2 (SMNS 106379; H = 8.9 mm, D = 7.8 mm).
Fig. 8a–c. *Palaeotachea subsulcosa* (Thomä, 1845), syntype? of *Helix crepidostoma* Sandberger, 1872 (SMNS 23209-b; H = 14.5 mm, D = 19.7 mm).
Fig. 9a, b. *Theodoxus cyrtocelis* (Krauss, 1852), syntype (SMNS 106380; D = 7.5 mm).
Fig. 10a, b. *Archaeozonites deplanatus* Miller, 1907, lectotype (SMNS 27619; H = 17.1 mm, D = 32.7 mm).
Fig. 11a–c. *Protodrepanostoma involutum deplanatum* (Jooss, 1911), syntype (SMNS 106382; H = 3.2 mm, D = 6.3 mm).
Fig. 12a, b. *Palaeotachea convexitesta* (Jooss, 1912), holotype of *Cepaea convexitesta depressa* Jooss, 1912 (SMNS 23914-c; H = 8.1 mm, D = 12.5 mm).
Fig. 13. *"Megalomastoma" dietleni* Miller, 1907, syntype (SMNS 11886; H = 13.3 mm).
Fig. 14. *Milax diezi* (Clessin, 1894), syntype (SMNS 106383; H = 6.9 mm, D = 4.1 mm).
Fig. 15a, b. *Pseudochloritis incrassata* (Klein, 1853), syntype of *Tropidomphalus dilatatus* Jooss, 1918, (SMNS 106384; H = 19.4 mm, D = 27.4 mm).
Fig. 16. *Cochlostoma dubium* (Miller, 1907), holotype (SMNS 27632; H = 1.7 mm).
Fig. 17. *Cochlostoma ebfraasii* (Jooss, 1902), syntype (SMNS 106385; H = 8.5 mm).
Fig. 18. *Pseudoleacina eburnea* (Klein, 1853), lectotype (SMNS 106386-a; H = 11.3 mm).
Fig. 19. *Craspedopoma elegans* Miller ,1907, syntype (SMNS 27631; H = 6.2 mm).
Fig. 20a, b. *Megalotachea elevata* (Berz & Jooss, 1927), syntype (SMNS 105002; H = 10.9 mm, D = 16.0 mm).
Fig. 21. *Radix socialis* (Zieten, 1832), syntype of *Lymnaea socialis elongata* Klein, 1846 (SMNS 23911; H = 15.4 mm).

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Plate 4

Fig. 1. *Pseudoleacina elongata* (Miller, 1907), lectotype (SMNS 27636-a; H = 17.8 mm).
Fig. 2. *"Bithynia" eocaenica* Miller, 1907, holotype (SMNS 8328; H = 5.5 mm).
Fig. 3. *"Lymnaea" eocaenica* Miller, 1907, syntype (SMNS 27634; H = 15.8 mm).
Fig. 4a, b. *Archaeozonites eocaenicus* Miller, 1907, lectotype (SMNS 27673; H = 13.8 mm, D = 21.7 mm).
Fig. 5. *Triptychia escheri* (Sandberger, 1875), lectotype (SMNS 106389-a; H = 27.4 mm).
Fig. 6. *Cochlostoma excellens* Jooss, 1912, holotype (SMNS 106390; H = 7.9 mm).
Fig. 7. *Laminifera excellens* Jooss, 1927, holotype (SMNS 27650; H = 19.6 mm).
Fig. 8. *Acicula flachi* (Clessin, 1911), lectotype (SMNS 106391-a; H = 1.9 mm).
Fig. 9a–c. *Wenzia fraasi* (Jooss, 1912), syntype (SMNS 106392; H = 13.4 mm, D = 16.4 mm).
Fig. 10a–c. *Megalotachea sylvestrina* (Schlotheim, 1820), syntype of *Helix geniculata* (Sandberger, 1872) (SMNS 22179; H = 14.6 mm, D = 21.6 mm).
Fig. 11. *Pseudamnicola? giraudi* Dollfus, 1908, syntype? (SMNS 106393; H = 2.8 mm).
Fig. 12a, b. *Oxychilus*? *globosus* (Miller, 1907), syntype (SMNS 27640; H = 5.0 mm, D = 7.2 mm).
Fig. 13a, b. *Discus globosus* (Miller, 1907), syntype (SMNS 27622; H = 2.3 mm, D = 4.6 mm).
Fig. 14a, b. *Janulus gottschicki* (Jooss, 1912), holotype (SMNS 106394; H = 1.4 mm, D = 2.9 mm).
Fig. 15. *Milax gracilior* (Sandberger, 1875), holotype (SMNS 22757; H = 10.5 mm, D = 3.3 mm).
Fig. 16. *Bithynia glabra* (Zieten, 1832), syntype of *Bithynia gracilis* Sandberger, 1872 (SMNS 106750; h = 7.8 mm).
Fig. 17. *Lymnaea gracilis* (Jooss, 1912), syntype #1 (SMNS 23924; H = 25.2 mm).
Fig. 18. *Lymnaea gracilis* (Jooss, 1912), syntype #2 (SMNS 23924; H = 16.4 mm).
Fig. 19. *Tinnyea lauraea* (Mathéron, 1843), syntype of *Melania grossecostata* Klein, 1852 (SMNS 23909; photograph from ca. 1980, material is missing).
Fig. 20. *Granaria helicidarum* (Jooss, 1924), syntype (SMNS 100113; H = 8.1 mm).
Fig. 21a, b. *Leucochroopsis helicidarum* Jooss, 1918, syntype (SMNS 106397; H = 3.4 mm; D = 5.5 mm).
Fig. 22. *Acanthinula hesslerana* Jooss, 1911, syntype (SMNS 67545; H = 2.6 mm, D = 2.0 mm).

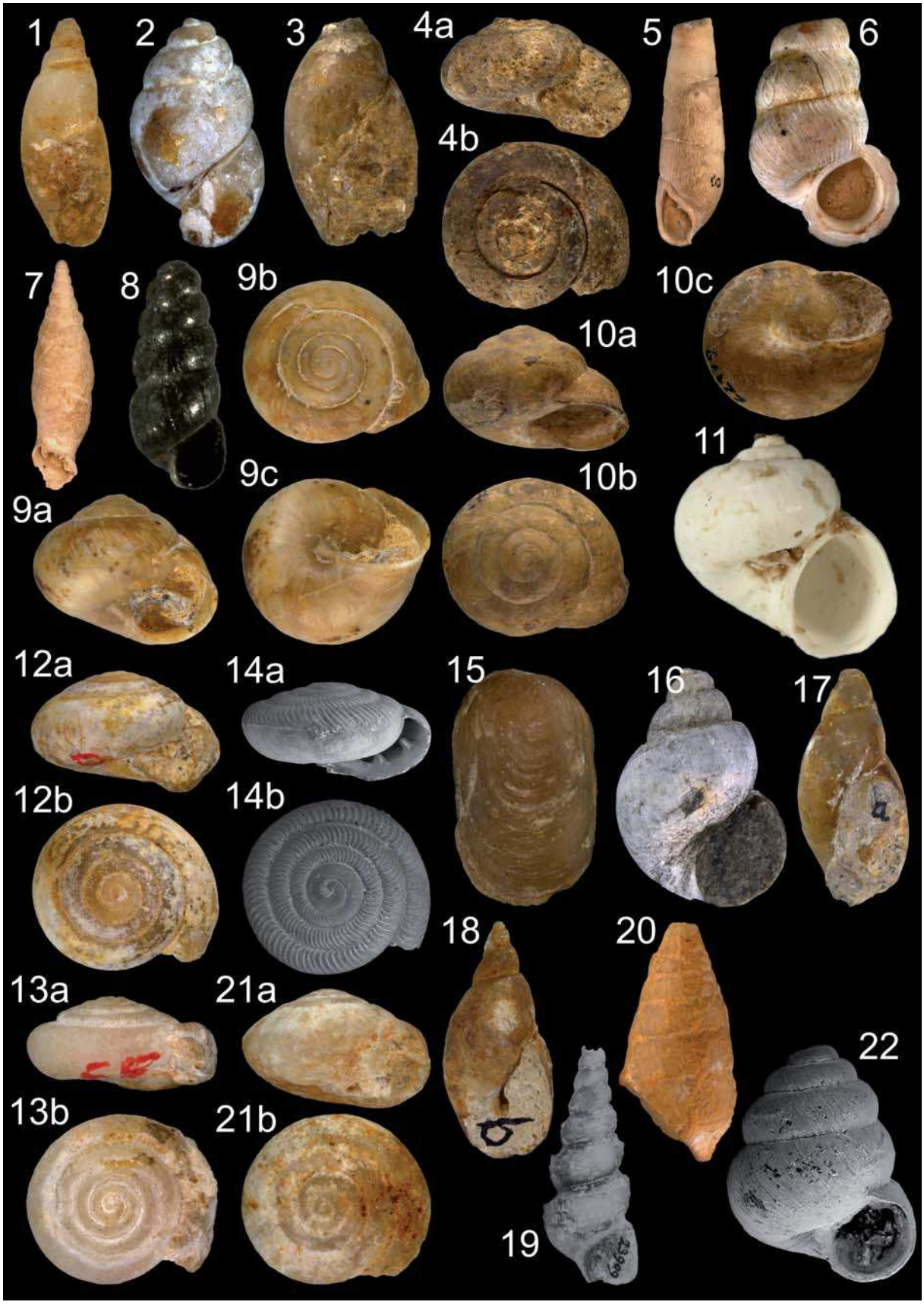
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Plate 5

Fig. 1. *Vallonia hoppla hoppla* Gerber, 1996, paratype #1 (SMNS 106398; H = 1.1 mm, D = 2.3 mm).
Fig. 2. *Vallonia hoppla hoppla* Gerber, 1996, paratype #2 (SMNS 106398; D = 2.5 mm).
Fig. 3. *Vallonia hoppla hoppla* Gerber, 1996, paratype #3 (SMNS 106398; D = 2.4 mm).
Fig. 4a–c. *Omphalosagda hydrobiarum* Jooss, 1911, lectotype (SMNS 106399; H = 15.8 mm; D = 10.3 mm).
Fig. 5a, b. "*Acanthinula" imperforata* (Miller, 1907), holotype (SMNS 27618; H = 3.2 mm; D = 4.1 mm).
Fig. 6. *Melanopsis impressa* Krauss, 1852, syntype (SMNS 106400; H = 15.9 mm).
Fig. 7a–c. *Pseudochloritis incrassata* (Klein, 1853), syntype(?) (SMNS 22737-1; H = 12.4 mm, D = 20.6 mm).
Fig. 8a–c. *Pseudochloritis incrassata* (Klein, 1853), syntype of *Pseudochloritis inflexa* C.R. Boettger, 1909 (SMNS 22736; H = 16.8 mm, D = 24.7 mm).
Fig. 9. *Palaeoglandina gracilis insignis* (Jooss, 1918b), holotype (SMNS 106401; H = 29.3 mm).
Fig. 10a–c. *Tropidomphalus insignis* (Zieten, 1832), neotype (SMNS 23910-a; H = 27.1 mm, D = 34.2 mm).
Fig. 11. *Radix socialis* (Zieten, 1832), syntype of *Radix socialis intermedia* (Klein, 1846) (SMNS 23905; H = 18.3 mm).
Fig. 12a–c. *Planorbarius cornu* (Brongniart, 1810), syntype of *Planorbis crassus involutus* Jooss, 1912 (SMNS 23926; H = 7.4 mm, D = 16.4 mm).
Fig. 13a–c. *Megalotachea joossi* (Pfeffer, 1930), holotype (SMNS 106402; H = 18.9 mm, D = 25.8 mm).
Fig. 14a, b. *"Helix" joossii* Miller, 1907, syntype (SMNS 27642; H = 4.5 mm, D = 7.4 mm).
Fig. 15. *Strobilops joossii* (Gottschick, 1911), syntype (SMNS 106403; H = 1.5 mm, D = 1.9 mm).
Fig. 16a–c. *Gyraulus kleini* Gottschick & Wenz, 1916, syntype of *Planorbis laevis* Klein, 1846 and *Gyraulus kleini* (SMNS 25263/2005; H = 1.0 mm, D = 3.6 mm).
Fig. 17. *Triptychia kleini* Schnabel, 2006, lectotype of *Clausilia grandis* Klein, 1846 and *Triptychia kleini* (SMNS 106404-a; H = 14.2 mm).
Fig. 18. *Triptychia kleini* Schnabel, 2006, paralectotype of *Clausilia grandis* Klein, 1846 and *Triptychia kleini* (SMNS 106404-b; H = 19.0 mm).
Fig. 19a, b. *Gyraulus kraussii* (Klein, 1846), syntype (SMNS 106405; H = 0.8 mm, D = 2.5 mm).

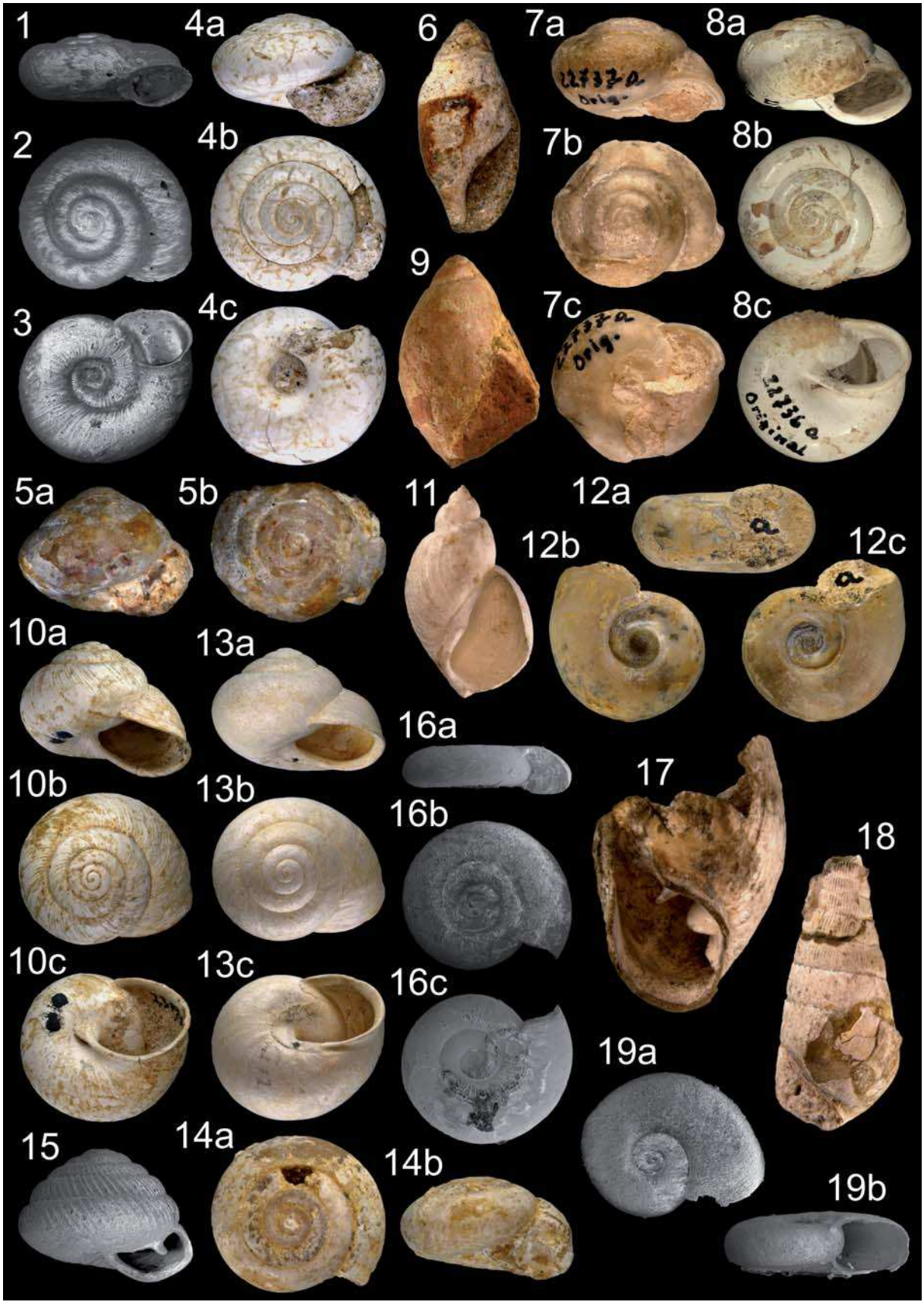
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Plate 6

Fig. 1. *Vallonia laxa* Gerber, 1996, paratype #1 (SMNS 106406; H = 1.1 mm, D = 2.4 mm).
Fig. 2. *Vallonia laxa* Gerber, 1996, paratype #2 (SMNS 106406; D = 2.1 mm).
Fig. 3. *Vallonia laxa* Gerber, 1996, paratype #3 (SMNS 106406; D = 2.6 mm).
Fig. 4a–c. *Palaeotachea dentula* (Quenstedt, 1867), syntype of *Helix pachystoma* Klein, 1853 and *Cepaea lepida* Wenz, 1919 (SMNS 105004; H = 8.9 mm, D = 14.2 mm).
Fig. 5a–c. *Klikia*? *praeosculina* (Miller, 1907) , syntype of *Helix leubii* Miller, 1907 (SMNS 36777; H = 7.4 mm; D = 11.1 mm).
Fig. 6a–c. *Planorbarius lincki* (Schütze *in* Branca & Fraas, 1908), lectotype (SMNS 11902-a; H = 2.7 mm, D = 5.2 mm).
Fig. 7. *Limax lingulatus* Sandberger, 1875, syntype (SMNS 22756; H = 5.3 mm; D = 3.8 mm).
Fig. 8a–c. *Joossia insignis* (Zieten, 1832), holotype of *Helix (Campylaea) insignis maior* Miller, 1900 (SMNS 4779-a; H = 35.1 mm, D = 38.1 mm).
Fig. 9a, b. *Proserpina*? *milleri* (Fulton, 1915), syntype of *Helicina(?) trochiformis* Miller, 1907 and *Helicina milleri* (SMNS 27633; D = 4.52 mm).
Fig. 10. *Radix socialis* (Zieten, 1832), syntype of *Lymnaea turrita milleri* Jooss, 1913 (SMNS 27633; H = 29.2 mm).
Fig. 11. *Cochlicopa milleri* Wenz, 1919, syntype of *Cionella exigua* Miller, 1907 and *Cochlicopa milleri* (SMNS 27628; H = 5.0 mm).
Fig. 12. *Palaeoglandina milleri* (Pilsbry, 1909), lectotype of *Glandina ovata* Miller, 1907 and *Poiretia milleri* (SMNS 27617-b; H = 42.4 mm).
Fig. 13. *Oxyloma minima* (Klein, 1853), syntype (SMNS 106410; H = 6.1 mm).
Fig. 14a, 4b. *Miodiscula miocaenica* (Gottschick & Wenz, 1927), syntype (SMNS 15817-131; H = 1.8 mm, D = 3.2 mm).
Fig. 15a–c. *Janulus moersingensis* Jooss, 1918, holotype (SMNS 106411; H = 3.1 mm, D = 5.8 mm).
Fig. 16a, b. *Vallonia lepida* (Reuss, 1849), neotype of *Vallonia moguntiaca* Wenz, 1915 (SMNS 106412; H = 2.4 mm, D = 2.3 mm).
Fig. 17. *Leucochroopsis kleinii* (Klein, 1846), holotype of *Helix mucronata* Klein, 1846 (SMNS 106413; D = 4.7 mm).
Fig. 18a, b. *Theodoxus obtusangula* (Krauss, 1852), holotype (SMNS 106414; H = 8.1 mm).
Fig. 19. *Triptychia oligocaenica* (Miller, 1907), holotype (SMNS 27647; H = 26.5 mm).
Fig. 20a, b. *Pleurodiscoides* (*Pleurodiscoides*) *orbicularis* (Klein, 1846), syntype (SMNS 106415; H = 8.7 mm, D = 16.5 mm).
Fig. 21. *Pseudoleacina elongata* (Miller, 1907), syntype of *Oleacina ovulina* Miller, 1907 (SMNS 27637; H = 7.0 mm).

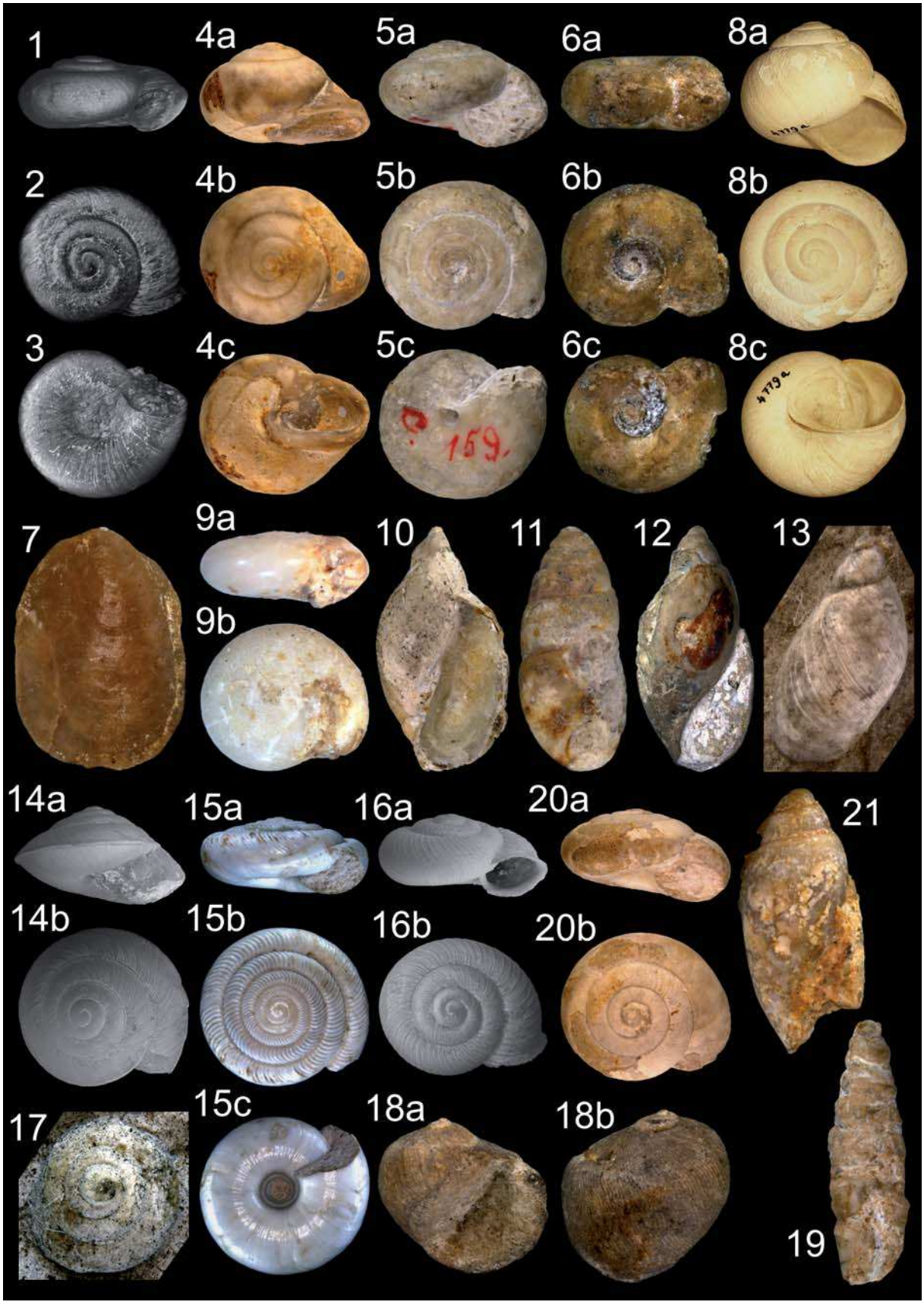
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Plate 7

Fig. 1. *Granaria crassiventer* nom. nov. for *Pupa (Torquilla) schuebleri pachygastra* (Miller, 1900), syntype (SMNS 106416; H = 9.9 mm).
Fig. 2. *Ferrissia deperdita* (Desmarest, 1814), holotype of *Ancylus palustris* Clessin, 1877 (106417; H = 1.2 mm, D = 2.7 mm).
Fig. 3. *Neniopsis physoides* (Miller, 1907), holotype (SMNS 27648; H = 10.9 mm).
Fig. 4a, b. *Strobilops uniplicata plana* (Clessin, 1885), holotype (SMNS 106418; H = 1.0 mm, D = 2.1 mm).
Fig. 5a–c. *Planorbarius cornu* (Brongniart, 1810), syntype of *Planorbis platystoma* Klein, 1853 (SMNS 25211/2005; H = 4.5 mm, D = 7.7 mm).
Fig. 6a, b. *Archaeozonites*? *praecostatus* (Jooss, 1918), syntype (SMNS 65614; H = 16.1 mm; D = 24.9 mm).
Fig. 7a, b. *Klikia*? *praeosculina* (Miller, 1907), syntype (SMNS 27624; H = 5.8 mm; D = 9.2 mm).
Fig. 8a–c. *Aegopinella*? *procellaria* (Jooss, 1918), syntype (SMNS 106419; H = 3.7 mm; D = 7.7 mm).
Fig. 9. *Gyraulus protocrescens* Nützel & Bandel, 1993, holotype (SMNS 25669; H = 0.5 mm, D = 1.4 mm).
Fig. 10. *Gyraulus protocrescens* Nützel & Bandel, 1993, paratype #1 (SMNS 25668; D = 1.3 mm).
Fig. 11. *Gyraulus protocrescens* Nützel & Bandel, 1993, paratype #2 (SMNS 25711; D = 1.4 mm).
Fig. 12. *Punctum pumilio* Jooss, 1918, syntype #1 (SMNS 106420; H = 1.1 mm, D = 2.0 mm).
Fig. 13a, b. *Punctum pumilio* Jooss, 1918, syntype #2 (SMNS 106420; D = 2.1 mm).
Fig. 14a–c. *Omphalosagda pyramidalis* (Jooss, 1912), holotype (SMNS 23917; H = 11.72 mm; D = 14.8 mm).
Fig. 15. *Gastrocopta (Albinula) acuminata* (Klein, 1846), syntype of *Pupa quadridentata* Klein, 1853 (SMNS 106421; H = 2.1 mm).
Fig. 16. *Triptychia randeckiana* (Kranz, 1908), lectotype (SMNS 101212; H = 16.3 mm).
Fig. 17. *Triptychia randeckiana* (Kranz, 1908), paralectotype (SMNS 101213; H = 17.2 mm).
Fig. 18a, b. *Omphalosagda pyramidalis* (Jooss, 1912), syntype of *Zonites (Archaeozonites) risgoviensis* Jooss, 1912 (SMNS 23916-a; H = 11.8 mm, D = 17.1 mm).
Fig. 19. *Gyraulus rotundostomus* Nützel & Bandel, 1993, holotype (SMNS 25705; H = 1.5 mm, D = 2.3 mm).
Fig. 20. *Gyraulus rotundostomus* Nützel & Bandel, 1993, paratype #1 (SMNS 25710; D = 2.0 mm).
Fig. 21. *Gyraulus rotundostomus* Nützel & Bandel, 1993, paratype #2 (SMNS 25710; D = 1.7 mm).
Fig. 22. *Cochlostoma salomoni* (Geyer, 1914), lectotype (SMNS 13519-a; H = 7.8 mm).
Fig. 23. *Milax sandbergeri* (Clessin, 1877), syntype (SMNS 22754; H = 5.4 mm, D = 3.8 mm).
Fig. 24. *Cochlostoma scalarinum saueri* (Geyer, 1914), lectotype (SMNS 106422-a; H = 6.2 mm).
Fig. 25. *Gyraulus kraussii* (Klein, 1846), holotype of *Planorbis (Dilatata) kraussii scalaris* Miller, 1900 (SMNS 106424; H = 6.5 mm).
Fig. 26. *Emarginaria schaefferiana* (Boettger, 1877), lectotype (SMNS 106425-a; H = 5.9 mm, D = 4.4 mm).

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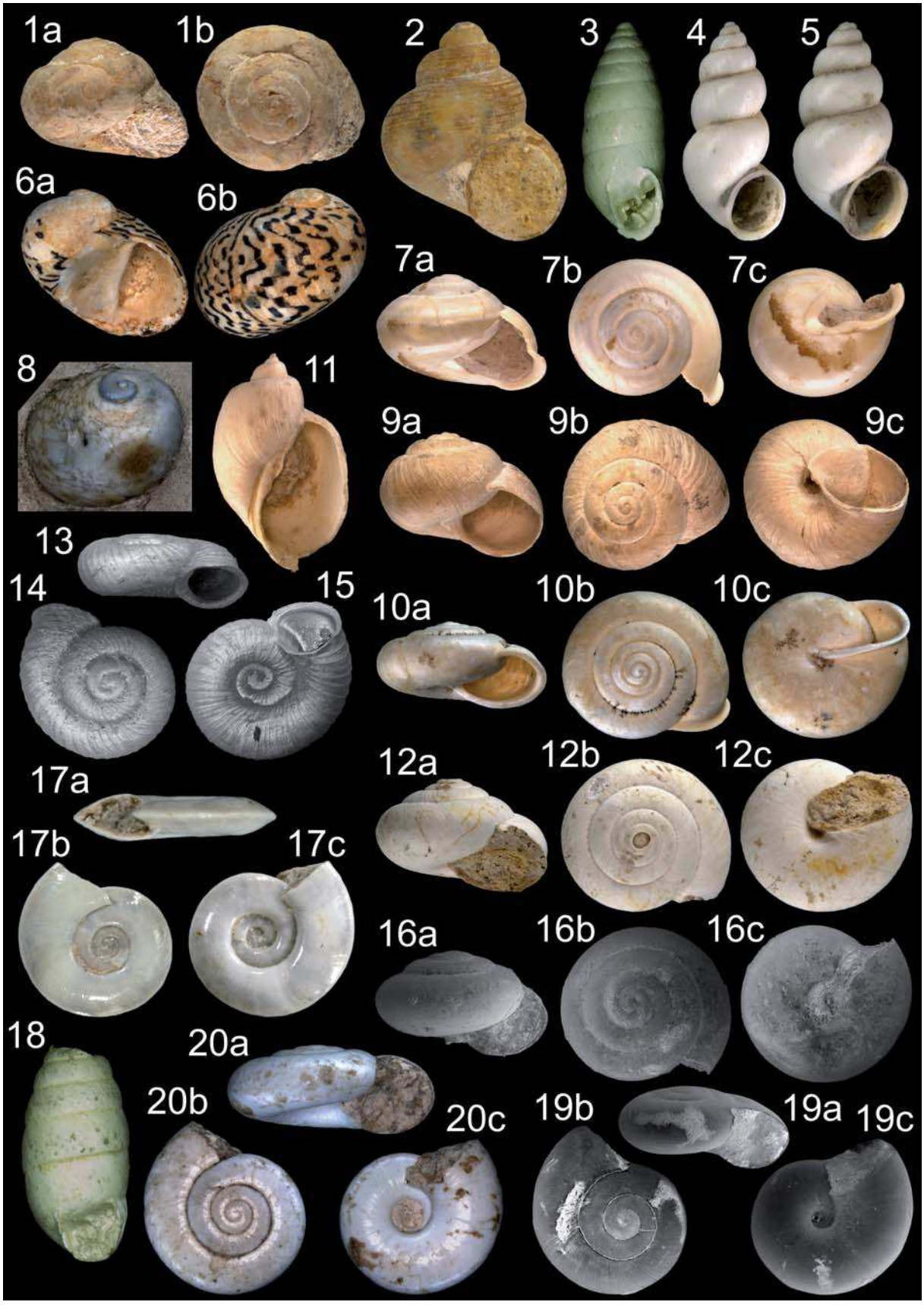
Plate 8

Fig. 1a, b. *"Cepaea" schneideri* Jooss, 1924, syntype (SMNS 44967/2005; H = 20.8 mm, D = 28.5 mm).
Fig. 2. *Pomatias (Neobembridgia) schneidi* (Jooss, 1912), syntype (SMNS 23925; H = 9.4 mm).
Fig. 3. *Granaria schuebleri* (Klein, 1846), neotype (SMNS 100110-1; H = 8.3 mm).
Fig. 4. *Nematurella zilchi* Schlickum, 1960 (= syntype #1 of *Hydrobia semiconvexa* Sandberger, 1875) (SMNS 106428; H = 5.5 mm).
Fig. 5. *Nematurella zilchi* Schlickum, 1960 (= syntype #1 of *Hydrobia semiconvexa* Sandberger, 1875) (SMNS 106428; H = 4.3 mm).
Fig. 6a, b. *Theodoxus serratiliniformis* (Geyer, 1914), lectotype (SMNS 13514-a; H = 8.9 mm, D = 9.6 mm).
Fig. 7a, b. *Megalotachea silvana* (Klein, 1853) (SMNS 22738; H = 18.9 mm, D = 12.6 mm).
Fig. 8. *Theodoxus cyrtocelis* (Krauss, 1852), syntype of *Neritina sparsa* Krauss, 1852 (SMNS 106430; D = 5.7 mm).
Fig. 9a–c. *Pseudochloritis insignis* (Zieten, 1832), holotype of *Helix steinheimensis* Klein, 1846 (SMNS 106431; H = 20.3 mm, D = 25.5 mm).
Fig. 10a–c. *Apula coarctata* (Klein, 1853); syntype? of *Klikia (Klikia) coarctata steinheimensis* Jooss, 1918 (SMNS 106432; H = 5.8 mm, D = 10.5 mm).
Fig. 11. *Radix socialis* (Zieten, 1832), syntype of *Lymnaea socialis striata* Klein, 1846 (SMNS 23904; H = 16.0 mm).
Fig. 12a–c. *Leucochroopsis apicalis* (Reuss, 1860), syntype of *Helix subapicalis* Sandberger, 1872 (SMNS 14917; H = 6.9 mm; D = 10.1 mm).
Fig. 13. *Vallonia subcyclophorella* (Gottschick, 1911), lectotype? of *Helix* (*Vallonia) subcostata* Clessin, 1913 (SMNS 106433; H = 1.0 mm, D = 2.0 mm).
Fig. 14. *Vallonia subcyclophorella* (Gottschick, 1911), paralectotype? #1 of *Helix* (*Vallonia) subcostata* Clessin, 1913 (SMNS 45162/2005; D = 2.0 mm).
Fig. 15. *Vallonia subcyclophorella* (Gottschick, 1911), paralectotype? #2 of *Helix* (*Vallonia) subcostata* Clessin, 1913 (SMNS 45162/2005; D = 2.1 mm).
Fig. 16a–c. *Vitrea subdiaphana* (Clessin, 1885), holotype (SMNS 22755; H = 1.4 mm, D = 2.3 mm).
Fig. 17a–c. Possible syntypes (see text) of *Hippeutis subfontanus* (Clessin, 1877) (SMNS 106434; H = 0.6 mm, D = 2.3 mm).
Fig. 18. *Granaria* sp., syntype of *Pupa (Torquilla) subfusiformis* Sandberger, 1875 (SMNS 100112; H = 5.8 mm).
Fig. 19a–c. *Perpolita subhammonis* (Gottschick, 1928), holotype (SMNS 15817; H = 1.9 mm, D = 3.7 mm).
Fig. 20a–c. *Aegopinella subnitens* (Klein, 1853), lectotype (SMNS 106435-a; H = 2.6 mm, D = 5.6 mm).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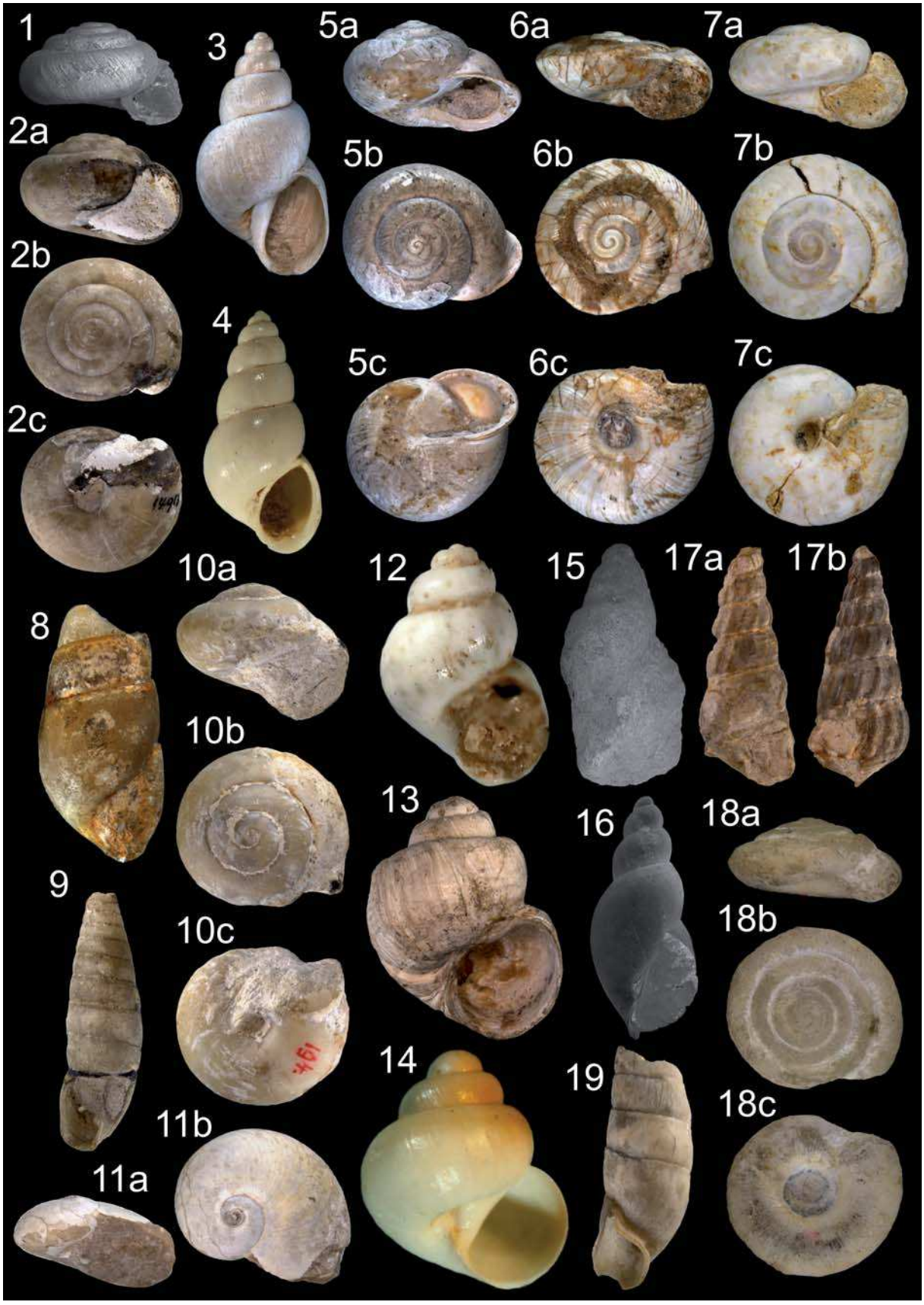
13
14
15
10a
10b
10c
17a
12a
12b
12c
17b
17c
16a
16b
16c
18
20a
20b
20c
19b
19a
19c

Plate 9

Fig. 1. *Lucilla subteres* (Clessin, 1877), syntype (SMNS 68501; H = 1.4 mm, D = 2.2 mm).
Fig. 2a–c. *Pseudochloritis subtilisticta* (Sandberger, 1875), syntype (SMNS 14913; H = 17.5 mm, D = 24.8 mm).
Fig. 3. *Galba truncatula* (O.F. Müller, 1774), holotype of *Lymnaea subtruncatula* Clessin, 1885 (SMNS 106436; H = 6.8 mm).
Fig. 4. *Heleobia subventrosa* (Gottschick, 1921), syntype (SMNS 15817; H = 4.5 mm).
Fig. 5a–c. *Megalotachea silvana* (Klein, 1853), syntype of *Helix (Macularia) subvermiculata* Sandberger, 1875 (SMNS 10920; H = 15.7 mm, D = 23.9 mm).
Fig. 6a, b. *"Helicopsis" suevica* Gottschick & Wenz, 1927, syntype (SMNS 22828; H = 3.1 mm, D = 6.1 mm).
Fig. 7a–c. *Zonitoides suevicus* (Jooss, 1918), holotype (SMNS 106441; H = 3.1 mm, D = 5.0 mm).
Fig. 8. *"Palaeostoa" suevica* (Miller, 1907), syntype (SMNS 27646; H = 13.1 mm).
Fig. 9. *Triptychia suevica* (Sandberger, 1875), syntype (SMNS 106438; H = 28.8 mm).
Fig. 10a–c. *Galactochilus* sp., syntype of *Helix suevica* Sandberger, 1875 (SMNS 14914; H = 16.0 mm, D = 20.2 mm).
Fig. 11a, b. *Vitrina suevica* Sandberger, 1872, holotype (SMNS 106439; H = 4.4 mm, D = 8.1 mm).
Fig. 12. *Pseudamnicola suevicus* (Gottschick, 1928), syntype (SMNS 15817; H = 1.7 mm).
Fig. 13. *Viviparus suevicus* Wenz, 1919, syntype (SMNS 106437; H = 39.4 mm).
Fig. 14. *Hydrocena trolli* Schlickum, 1979b, paratype (SMNS 106442; H = 2.1 mm).
Fig. 15. *Stagnicola*? *truncatuliformis* (Schütze, 1908), lectotype (SMNS 11898-a; H = 4.4 mm).
Fig. 16. *Lymnaea* (s.l.) *turrita* Klein, 1853, lectotype (SMNS 106443-a; H = 5.5 mm).
Fig. 17a, b. *Tinnyea lauraea* (Mathéron, 1843), syntype of *Melania turrita* Klein, 1846 (SMNS 106444; H = 24.2 mm).
Fig. 18a–c. *Discus diezi ulmensis* (Jooss, 1918), syntype (SMNS 106445; H = 2.0 mm, D = 4.0 mm).
Fig. 19. *Triptychia ulmensis* (Sandberger, 1875), lectotype (SMNS 22181-a; H = 31.3 mm).


1
3
5a
6a
7a
2a
5b
6b
7b
2b
4
5c
6c
7c
2c
10a
12
15
17a
17b
8
10b
13
16
18a
9
10c
18b
14
19
18c
11b
11a

Appendix 1: Systematic list of taxa

Here is presented a list of the species/subspecies whose types can be found in the SMNS collection. The classification follows Bouchet et al. (2005), with modifications by Nordsieck (2014). Superfamilies in each greater group are listed in alphabetical order for ease of use. Subfamilies are omitted in cases, where a taxon could not be attributed to one.

GASTROPODA INCERTAE SEDIS
Melania bulimoides Klein, 1846

NERITIMORPHA
CYCLONERITIMORPHA
Superfamily Helicinoidea Férussac, 1822
Family Proserpinidae Gray, 1847
Proserpina milleri (Fulton, 1915) [= *trochiformis* Miller, 1907]

Superfamily Hydrocenoidea Troschel, 1857
Family Hydrocenidae Troschel, 1857
Hydrocena trolli Schlickum, 1979b

Superfamily Neritoidea Rafinesque, 1815
Family Neritidae Rafinesque, 1815
Subfamily Neritininae Poey, 1852
Theodoxus crenulatus (Klein, 1853)
Theodoxus cyrtocelis (Krauss, 1852) [with syn. *sparsa* Krauss, 1852)
Theodoxus obtusangula (Krauss, 1852)
Theodoxus serratiliniformis (Geyer, 1914)

CAENOGASTROPODA
ARCHITAENIOGLOSSA
Superfamily Cyclophoroidea Gray, 1847
Family Aciculidae Gray, 1850
Acicula flachi (Clessin, 1911)
Family Craspedopomatidae Kobelt & Möllendorff, 1898
Craspedopoma elegans (Miller, 1907)
Family Diplommatinidae L. Pfeiffer, 1857
Subfamily Cochlostomatinae Kobelt, 1902
Cochlostoma dubium (Miller, 1907)
Cochlostoma excellens (Jooss, 1912c)
Cochlostoma ebfraasii (Jooss, 1902) [syn. *fraasi* auct.]
Cochlostoma salomoni (Geyer, 1914)
Cochlostoma scalarinum saueri (Geyer, 1914)
Family Ferussinidae Wenz, 1923 (1915)
Ferussina [*anomphalus* ssp.?] *capellinii* (Sandberger, 1873)
Family Megalomastomatidae Blanford, 1864
Megalomastoma? dietleni Miller, 1907

Superfamily Viviparoidea Gray, 1847 (1833)
Family Viviparidae Gray, 1847 (1833)
Subfamily Viviparinae Gray, 1847 (1833)
Viviparus suevicus Wenz, 1919 [= *varicos*a Krauss, 1852]

SORBEOCONCHA
Superfamily Cerithioidea Fleming, 1822
Family Melanopsidae H. Adams & A. Adams, 1854
Melanopsis impressa Krauss, 1852
Family Pachychilidae P. Fischer & Crosse, 1892
Tinnyea lauraea (Mathéron, 1843) [syn. *turrita* Klein, 1846, *grossecostata* Klein, 1852]

LITTORINIMORPHA
Superfamily Littorinoidea Children, 1834
Family Pomatiidae Newton, 1891 (1828)
Subfamily Pomatiinae Newton, 1891 (1828)
Pomatias (Neobembridgia) arneggensis Wenz, 1923 [= *scalaris* Miller, 1907]
Pomatias (Neobembridgia) antiquus schneidi (Jooss, 1912b) [= *schneidti* Jooss, 1912a, nom. nud.]

Superfamily Truncatelloidea Gray, 1840
Family Bithyniidae Gray, 1857
Bithynia glabra (Zieten, 1832) [syn. *gracilis* Sandberger, 1872]
Bithynia? eocaenica (Miller, 1907)
Family Cochliopidae Tryon, 1866
Heleobia?subventrosa (Gottschick, 1921)
Heleobia? semiconvexa (Sandberger, 1875)
Family Hydrobiidae Stimpson, 1865
?Subfamily Hydrobiinae Stimpson, 1865
Nematurella zilchi Schlickum, 1960
Ctyrokya conoidea (Krauss, 1852)
Subfamily Pseudamnicolinae Radoman, 1977
Pseudamnicola suevicus (Gottschick, 1928)
*Pseudamnicola? giraudi (*Dollfus, 1908)

HYGROPHILA
Superfamily Lymnaeoidea Rafinesque, 1815
Family Lymnaeidae Rafinesque, 1815
Subfamily Lymnaeinae Rafinesque, 1815
Stagnicola fabulum (Brongniart, 1810) [syn. *amerbachensis* Jooss, 1912a]
Lymnaea gracilis (Jooss, 1912)
Galba? *conica* (Miller, 1907)
Galba? *eocaenica* (Miller, 1907)
Galba subtruncatula (Clessin, 1885) [?= *truncatula* (O.F. Müller, 1774)]
Galba truncatuliformis (Schütze *in* Branca & Fraas, 1907)
Lymnaea brancai (Schütze *in* Branca & Fraas, 1907)
Lymnaea turrita Klein, 1853
Lymnaea turrita milleri Jooss, 1913
Radix socialis (Zieten, 1832) [syn. *elongata* Klein, 1846, *intermedia* Klein, 1846, *striata* Klein, 1846]

Superfamily Planorboidea Rafinesque, 1815
Family Planorbidae Rafinesque, 1815
Subfamily Coretinae Gray, 1847
Planorbarius cornu (Brongniart, 1810) [syn. *involutus* Jooss, 1912a, *platystoma* Klein, 1853]
Planorbarius lincki (Schütze *in* Branca & Fraas, 1908)
Subfamily Planorbinae Rafinesque, 1815
Gyraulus costatus (Klein, 1846)
Gyraulus kraussii (Klein, 1846) [with ? syn. *scalaris* Miller, 1900]
Gyraulus kleini Gottschick & Wenz, 1916 [= *laevis* Klein, 1846]
Gyraulus protocrescens Nützel & Bandel, 1993
Gyraulus rotundostomus Nützel & Bandel, 1993
Subfamily Ancylinae Rafinesque, 1815
Ferrissia dewperdita (Desmarest, 1814) [syn. *palustris* Clessin, 1877]

Subfamily Segmentininae F.C.Baker 1945
Hippeutis subfontanus (Clessin, 1877)

STYLOMMATOPHORA
ELASMOGNATHA
Superfamily Succineoidea Beck, 1837
Family Succineidae Beck, 1837
Subfamily Succineinae Beck, 1837
Oxyloma minima (Klein, 1853)

ORTHURETHRA
Superfamily Cochlicopoidea Pilsbry, 1900 (1879)
Family Cochlicopidae Pilsbry, 1900 (1879)
Cochlicopa milleri Wenz, 1919 [= *exigua* Miller, 1907]

Superfamily Pupilloidea Turton, 1831
Family Chondrinidae Steenberg, 1925
Granaria? bythiniformis (Miller, 1907)
Granaria helicidarum (Jooss, 1923)
Granaria crassiventer nom. nov. [= *pachygastra* Miller, 1900]
Granaria schuebleri (Klein, 1846) [= *antiqua* Zieten, 1832]
Family Gastrocoptidae Pilsbry, 1918
Gastrocopta acuminata (Klein, 1846) [with syn. *quadridentata* Klein, 1853]
Family Pleurodiscidae Wenz, 1923
Pleurodiscoides (*Pleurodiscoides*) *orbicularis* (Klein, 1846)
Family Strobilopsidae Wenz, 1915
Strobilops costata (Clessin, 1877) [with syn. *bilamellatus* Clessin, 1885]
Strobilops joossii (Gottschick, 1911)
Strobilops uniplicata A. Braun, 1851) [syn. *planus* Clessin, 1885]
Family Valloniidae Morse, 1864
Acanthinula? *imperforata* (Miller, 1907)
Acanthinula hesslerana Jooss, 1911a
Vallonia costata (Müller, 1774) [syn. *costataeformis* Jooss, 1912c]
Vallonia hoppla hoppla Gerber, 1996
Vallonia laxa Gerber, 1996
Vallonia lepida (Reuss, 1849) [syn. *moguntiaca* Wenz, 1915]
Vallonia sucyclophorella (Gottschick, 1911) [syn. *subcostata* Clessin, 1911]

Superfamily Enoidea B.B. Woodward, 1903 (1880)
Family Enidae B.B. Woodward, 1903 (1880)
Palaeomastus arneggensis (Miller, 1907)

SIGMURETHRA
Superfamily Clausilioidea Gray, 1855
Family Clausiliidae Gray, 1855
Clausiliidae *incertae sedis*
"*Clausilia*" *undatistria* (Boettger, 1877)
Subfamily Clausiliinae Gray, 1855
Emarginaria schaefferiana (Boettger, 1877)
Subfamily Laminiferinae Wenz, 1923
Laminifera arneggensis Miller, 1907
Laminifera excellens Jooss, 1927
Subfamily Eualopiinae H. Nordsieck, 1985
Neniopsis physoides (Miller, 1907)
Family Filholiidae Wenz, 1923
Triptychia antiquior (Miller, 1907)
Triptychia escheri (Sandberger, 1875)
Triptychia kleini Schnabel, 2006 [= *grandis* Klein, 1846]
Triptychia oligocaenica (Miller, 1907)
Triptychia randeckiana (Kranz, 1908)
Triptychia suevica (Sandberger, 1875)
Triptychia ulmensis (Sandberger, 1875)
?Family Palaostoidae Nordsieck, 1986
Palaeostoa? *suevica* (Miller, 1907)

Superfamily Testacelloidea Gray, 1840
Family Oleacinidae H. Adams & A. Adams, 1855
Pseudoleacina eburnea (Klein, 1953)
Pseudoleacina elongata (Miller, 1907) [with syn. *ovulina* Miller, 1907]
Palaeoglandina gracilis (Zieten, 1832) [syn. *antiqua* Klein, 1852]
Palaeoglandina gracilis insignis (Jooss, 1918b)
Palaeoglandina milleri (Pilsbry, 1909) [= *ovata* Miller, 1907]
Palaeoglandina wagneri (Miller, 1907)
Family Testacellidae Gray, 1840
Testacella zellii Klein, 1853

Superfamily Punctoidea Morse, 1864
Family Discidae Thiele, 1931 (1866)
Discus antiquus (Miller, 1907)
Discus costatus (Gottschick, 1911)
Discus diezi ulmensis (Jooss, 1918b)
Discus globosus (Miller, 1907)
Discus euglyphoides (Sandberger, 1872) [syn. *undorfensis* Clessin, 1894]
Discus wenzi (Jooss, 1918b)
Family Helicodiscidae H.B. Baker, 1927
Lucilla subteres (Clessin, 1877)
Family Punctidae Morse, 1864
Punctum pumilio Jooss, 1918b

Superfamily Gastrodontoidea Tryon, 1866
Family Gastrodontidae Tryon, 1866
Janulus gottschicki (Jooss, 1912c)
Janulus moersingensis (Jooss, 1918b)
Zonitoides suevicus (Jooss, 1918b)
Family Oxychilidae Hesse, 1927 (1879)
Oxychilus? *globosus* (Miller, 1907)
Subfamily Godwiniinae Cooke, 1921
Aegopinella procellaria (Jooss, 1918b)
Aegopinella subnitens (Klein, 1853)
Perpolita boettgeriana (Clessin, 1877)
*Perpolita subhammonis (*Gottschick, 1928)
Family Pristilomatidae Cockerell, 1891
Vitrea ammoni (Clessin, 1894)
Vitrea subdiaphana (Clessin, 1885)
***incertae sedis*: Family Grandipatulidae Pfeffer, 1930**
Grandipatula alsatica (Jooss, 1918a)

Superfamily Parmacelloidea P. Fischer, 1856 (1855)
Family Milacidae Ellis, 1926
Milax crassus (Clessin, 1894)
Milax diezi (Clessin, 1894)
Milax gracilior (Sandberger, 1875)
Milax sandbergeri (Clessin, 1885)

Superfamily Zonitoidea Mörch, 1864
Family Archaeozonitidae Pfeffer, 1930
Archaeozonites angulosus Miller, 1907
Archaeozonites? arneggensis (Miller, 1907)

Archaeozonites carinatus Miller, 1907
Archaozonites deplanatus Miller, 1907
Archaeozonites eocaenicus Miller, 1907
Archaeozonites praecostatus (Jooss, 1918b)
Miozonites algiroides badensis (Jooss, 1923)
Omphalosagda hydrobiarum (Jooss, 1911a)
Omphalosagda pyramidalis (Jooss, 1912a) [with syn. *risgoviensis* Jooss, 1912a, *carinata* Jooss, 1912]

Superfamily Limacoidea Lamarck, 1801
Family Limacidae Lamarck, 1801
Limax crassissimus Jooss, 1902
Limax lingulatus Sandberger, 1875
Family Vitrinidae Fitzinger, 1833
Vitrina suevica Sandberger, 1872

Superfamily Helicoidea Rafinesque, 1815
Family Elonidae Gittenberger, 1977, subfamily Eloninae Gittenberger, 1977; or family Helicidae Rafinesque, 1815, subfamily Ariantinae Mörch, 1864
Galactochilus braunii ehingensis (Klein, 1846) [syn. *suevicus* Sandberger, 1875]
Tropidomphalus (Pseudochloritis) alveus (Sandberger, 1875) [= *alveum* Jooss, 1918]
Tropidomphalus (Pseudochloritis) incrassatus (Klein, 1853) [with syn. *inflexa* C. Boettger, 1909, *dilatatus* Jooss, 1918b]
Tropidomphalus (Pseudochloritis) subtilistictus (Sandberger, 1875)
Tropidomphalus (Joossia) insignis (Zieten, 1832) [with syn. *steinheimensis* Klein, 1846, *maior* Miller, 1900]
Family Elonidae Gittenberger, 1977, subfamily Klikiinae, H. Nordsieck, 1986; or family Helicidae Rafinesque, 1815, subfamily Klikiinae H. Nordsieck, 1986
Apula coarctata (Klein, 1853) [with syn. *steinheimensis* Jooss, 1918b]
Klikia? *joossii* (Miller, 1907)
Klikia praeosculina (Miller, 1907) [with syn. *blaviana* Miller, 1907 and *leubii* Miller, 1907]
Family Helicidae Rafinesque, 1815
Subfamily Helicinae Rafinesque, 1815
Palaeotachea convexitesta (Jooss, 1912b) [with syn. *depressa* Jooss, 1912b]
Palaeotachea subsulcosa (Thomä, 1845) [syn. *crepidostoma* Sandberger, 1872]
Palaeotachea dentula (Quenstedt, 1867) [syn. *pachystoma* Klein, 1853, *lepida* Wenz, 1919]
Palaeotachea renevieri (Maillard, 1892) [syn. *coniuncta* Berz & Jooss, 1927]
Cepaea? *schneideri* Jooss, 1923 [sp. inquirenda]
Megalotachea elevata (Berz & Jooss, 1927)
Megalotachea eversa (Deshayes, 1851) [syn. *baumbergeri* Jooss, 1923]
Megalotachea silvana (Klein, 1853) [with syn. *subvermiculata* Sandberger, 1875]
Megalotachea sylvestrina (Schlotheim, 1820) [syn. *geniculata* Sandberger, 1872]
Megalotachea? joossi (Pfeffer, 1930)
Family Helicodontidae Kobelt, 1904
Protodrepanostoma invotutum angitortum Jooss, 1912c
Protodrepanostoma involutum deplanatum (Jooss, 1911b)
Family Hygromiidae Tryon, 1866
Subfamily Hygromiinae Tryon, 1866
Helicopsis? *suevica* Gottschick & Wenz, 1927
Leucochroopsis kleinii (Klein, 1846) [syn. *mucronata* Klein, 1846, *carinulata* Klein, 1853]
Leucochroopsis helicidarum (Jooss, 1918b) [species inquirenda]
Leucochroopsis apicalis (Reuss, 1860) [syn. *subapicalis* Sandberger, 1872]
Loganiopharynx constrictelabiatus (Miller, 1907)
Miodiscula miocaenica (Gottschick & Wenz, 1927)
Family Sphincterochilidae Zilch, 1960 (1910)
Wenzia fraasi (Jooss, 1912a)

Appendix 2: List of taxa by authorship

Here, the same list is ordered by author and date. See "References" section for the full citation. A '*' indicates an invalid nominal species/subspecies name because of subjective synonymy (see main text) and a '†' indicates that the species has a new name (see main text for more details).

Berz, K.C. & Jooss, C.H.
1927 *Cepaea renevieri coniuncta**
1927 *Cepaea renevieri elevata*

Boettger, C.R.
1909 *Pseudochloritis inflexa**

Boettger, O.
1877 *Clausilia (Emarginaria) schaefferiana*
1877 *Clausilia (Pseudidyla) undatistria*

Clessin, S.
1877 *Ancylus palustris**
1877 *Planorbis (Hippeutis) subfontanus*
1877 *Helix (Patula) subteres*
1877 *Hyalinia boettgeriana*
1877 *Strobilus costatus*
1885 *Lymnaea subtruncatula**
1885 *Amalia sandbergeri*
1885 *Strobilus bilamellatus**
1885 *Strobilus planus**
1885 *Hyalina subdiaphana*
1894 *Patula undorfensis**
1894 *Amalia crassa*
1894 *Amalia diezi*
1894 *Hyalina ammoni*
1911 *Acme flachi*
1913 *Helix* (*Vallonia) subcostata**

Dollfus, G.F.
1908 *Valvata (Cincinna) giraudi*

Fulton, H.C.
1915 *Helicina milleri*

GERBER, J.
1996 *Vallonia hoppla hoppla*
1996 *Vallonia laxa*

GEYER, D.
1914 *Pomatias salomoni*
1914 *Pomatias scalarinum saueri*
1914 *Neritina serratiliniformis*

GOTTSCHICK, F.
1911 *Patula (Charopa) costata*
1911 *Strobilus joossii*
1911 *Helix (Vallonia) subcyclophorella*
1921 *Hydrobia subventrosa*
1928 *Amnicola suevicus*
1928 *Zonitoides subhammonis*

GOTTSCHICK, F. & WENZ, W.
1916 *Gyraulus multiformis kleini*
1927 *Helicopsis suevica*
1927 *Trochoidea miocaenica*

JOOSS, C.H.
1902 *Pomatias ebfraasii*
1902 *Limax crassissimus*
1911a *Acanthinula hesslerana*
1911a *Omphalosagda hydrobiarum*
1911b *Helicodonta involuta deplanata*
1912a *Planoris crassus involutus**
1912a *Limnophysa amerbachensis amerbachensis**
1912a *Limnophysa amerbachensis gracilis*
1912a *Zonites (Archaeozonites) pyramidalis*
1912a *Zonites (Archaeozonites) risgoviensis risgoviensis**
1912a *Zonites (Archaeozonites) risgoviensis carinata**
1912a *Plebecula fraasi*
1912b *Ericia schneidi*
1912b *Palaeotachea convexitesta convexitesta*
1912b *Palaeotachea convexitesta depressa**
1912c *Pomatias (Rhabdotakra) excellens*
1912c *Helicodonta involuta angitorta*
1912c *Patula gottschicki*
1912c *Vallonia costataeformis**
1913 *Lymnaea turrita milleri*
1918a *Zonites* (*Grandipatula) alsatica*
1918b *Galactochilus alveum*
1918b *Zonites (Aegopis) praecostatus*
1918b *Janulus moersingensis*
1918b *Poietia (Palaeoglandina) gracilis insignis**
1918b *Klikia (Klikia) coarctata steinheimensis**
1918b *Hygromia (Trichiopsis) helicidarum*
1918b *Hyalinia (Hyalinia) procellaria*
1918b *Punctum pumilio*
1918b *Pyramidula (Gonyodiscus) wenzi*
1918b *Pyramidula (Gonyodiscus) ulmensis*
1918b *Tropidomphalus dilatatus*
1918b *Hyalinia (Polita) suevicus*
1923 *Zonites (Aegopis) algiroides badensis**
1923 *Cepaea eversa baumbergeri**
1923 *Cepaea schneideri**
1923 *Abida helicidarum*
1927 *Laminifera excellens*

KLEIN, A. VON
1846 *Melania bulimoides*
1846 *Pupa acuminata*
1846 *Pupa schuebleri*
1846 *Planorbis costatus*
1846 *Planorbis kraussii*
1846 *Planorbis laevis**
1846 *Helix mucronata**
1846 *Lymnaea socialis elongata**
1846 *Lymnaea socialis intermedia**
1846 *Lymnaea socialis striata**
1846 *Melania turrita**
1846 *Clausilia grandis*†
1846 *Helix steinheimensis**
1846 *Helix orbicularis*
1852 *Melania grossecostata**
1852 *Achatina antiqua**
1853 *Helix pachystoma**
1853 *Helix silvana*
1853 *Pupa quadridentata**
1853 *Helix carinulata**
1853 *Lymnaea turrita*
1853 *Helix subnitens*
1853 *Planorbis platystoma**
1853 *Glandina (Achatina) eburnea*
1853 *Succinea minima*
1853 *Testacella zellii*
1853 *Neritina crenulata*
1853 *Helix incrassata*

KRANZ, W.
1908 *Clausilia randeckiana*

KRAUSS, F.
1852 *Paludina conoidea*
1852 *Melanopsis impressa*
1852 *Neritina cyrtocelis*
1852 *Neritina obtusangula*
1852 *Neritina sparsa**
1852 *Paludina varicosa*†

MILLER, K.
1900 *Planorbis (Dilatata) kraussii scalaris**
1900 *Pupa (Torquilla) schuebleri pachygastra*†
1900 *Helix (Campylaea) insignis maior**
1907 *Hyalinia (Conulus) imperforata*
1907 *Archaeozonites angulosus*
1907 *Trochomorpha arneggensis*
1907 *Archaeozonites carinatus*
1907 *Archaeozonites eocaenicus*
1907 *Archaeozonites deplanatus*
1907 *Bithynia eocaenica*
1907 *Cionella exigua*†
1907 *Craspedopoma elegans*
1907 *Patula antiqua*
1907 *Patula globosa*
1907 *Lymnaea conica*
1907 *Lymnaea eocaenica*
1907 *Pupa bythiniformis*
1907 *Helix (Gonostoma) blaviana**
1907 *Helix joossii*
1907 *Helix (Gonostoma) leubii**
1907 *Helix (Gonostoma) praeosculina*
1907 *Laminifera arneggensis*
1907 *Helix constrictelabiata*
1907 *Megalomastoma dietleni*
1907 *Bulimus (Petraeus) arneggensis*

1907 *Clausilia (Balea?) physoides*
1907 *Hyalinia globosa*
1907 *Glandina wagneri*
1907 *Glandina ovata*†
1907 *Melania suevica*
1907 *Pomatias dubius*
1907 *Cyclotus scalaris*†
1907 ?*Helicina trochiformis*†
1907 *Glandina elongata*
1907 *Oleacina ovulina**
1907 *Clausilia antiquior*
1907 *Clausilia oligocaenica*

Nützel, A. & Bandel, K.
1993 *Gyraulus protocrescens*
1993 *Gyraulus rotundostomus*

Pfeffer, G.
1929 *Trachytachea joossi*

Pilsbry, H.A.
1909 *Poiretia milleri*

Salvador, R.B., Höltke, O., Rasser, M.W. & Kadolsky, D.
2015 (herein) *Granaria crassiventer*

Sandberger, F. von
1872 *Bithynia gracilis**
1872 *Helix crepidostoma**
1872 *Helix geniculata**
1872 *Helix subapicalis**
1873 *Strophostoma anomphalus capellinii*
1875 *Helix (Macularia) subvermiculata**
1875 *Limax lingulatus*
1875 *Pupa (Torquilla) subfusiformis*
1875 *Helix alveus*
1875 *Helix suevica**
1875 *Hydrobia semiconvexa*
1875 *Amalia gracilior*
1875 *Clausilia escheri*
1875 *Clausilia suevica*
1875 *Clausilia ulmensis*
1875 *Helix subtilisticta*
1875 *Vitrina suevica*

Schlickum, R.W.
1979 *Hydrocena (Hydrocena) trolli*

Schnabel, T.
2006 *Triptychia (Triptychia) kleini*

Schütze, E.
1907 (in Branca & Fraas) *Lymnaea truncatuliformis*
1907 (in Branca & Fraas) *Lymnaea brancai*
1907 (in Branca & Fraas) *Planorbis (Coretus) lincki*

Wenz, W.
1915 *Vallonia moguntiaca**
1919 *Cochlicopa milleri*
1919 *Viviparus suevicus*
1919 *Cepaea lepida*
1923 *Pomatias arneggensis*

Zieten, C.H. von
1832 *Helix insignis*
1832 *Pupa antiqua*

Appendix 3: Missing type material

Below are listed all nominal species-group taxa (in their original form) of which no type material could be identified in the SMNS collection. Part of this material could still be present in the SMNS but not identified as types, part may be deposited in other institutions, and part (or most) might have actually been lost. In a few cases, type material that had been inventoried in the SMNS collection could not be presently located. More specifically, the material listed below from the works of Gottschick, Wenz, Miller and Klein were probably in the Wenz collection in Frankfurt, which was destroyed during World War II (see also Zilch 1987). Furthermore, we have included below the new taxa which Sandberger (1870–1875) described from southern Germany. While Sandberger's collection is mostly stored in the MUWIE (or SMF) collection, he identified some specimens he studied as being kept in the "k. Naturaliensammlung zu Stuttgart" [royal collection of natural objects in Stuttgart]. Moreover, many specimens were provided to Sandberger by others (notably Wetzler, Probst and Miller), but it is not stated whether he just borrowed them or incorporated them into his collection. If he returned them to their original owners, Miller's collection is the only one to have been acquired by the SMNS.

aciculella Sandberger, 1875, *Caecilianella*
acieformis Klein, 1846, *Helix*
albertanus Clessin, 1877, *Planorbis*
alta Clessin, 1911b, *Acme*
alveus Sandberger, 1875, *Omphalosagda*
angulatus Clessin, 1877, *Planorbis (Gyrorbis)*
antiquata Clessin, 1913, *Pupa (Lauria?)*
antiquus Miller, 1907, *Pomatias*
aperta Sandberger, 1895, *Pupa*
applanata Miller, 1907, *Hyalinia*
arneggensis Miller, 1907, *Helix (Parachloraea)*
brevis Miller, 1907, *Clausilia*
bullatus Klein, 1846, *Limnaeus*
buxovillanum Wenz, 1923, *Cochlostoma (Obscurella)*
circumscisa Gottschick, 1920a, *Hyalinia (Gyralina)*
clessini Boettger, 1877, *Clausilia*
coarctata Klein, 1853, *Helix* [lot SMNS 43757/2005, lost]
conica Jooss, 1918b, *Klikia (Klikia) catantostoma*
conicum Klein, 1853, *Cyclostoma*
consobrinus Sandberger, 1875, *Cyclostomus*
costata Jooss, 1918b, *Palaeoglandina gracilis*
costatus Sandberger, 1875, *Archaeozonites*

deperditolacustris GOTTSCHICK, 1911, *Ancylus (Acroloxus)*
diezi CLESSIN, 1894, *Patula*
diezi CLESSIN, 1913, *Pupa (Alaea)*
diezi CLESSIN, 1913, *Strobilus*
distortus MILLER, 1900, *Planorbis (Armiger) costatus*
eckingensis SANDBERGER, 1875, *Clausilia*
ecostata SANDBERGER, 1875, *Melania Escheri*
ehingensis KLEIN, 1846, *Helix*
elegans KLEIN, 1853, *Achatina* [= *kleiniana* PILSBRY, 1909 nom.nov.]
ellipticus KLEIN, 1846, *Limnaeus*
elongata MILLER, 1900, *Gillia utriculosa*
elongata JOOSS, 1911b, *Limnophysa turrita*
elongata JOOSS, 1911b, *Melanopsis callosa*
erecta GOTTSCHICK, 1920a, *Hyalinia (Hyalinia) subnitens*
erecta GOTTSCHICK, 1919, *Vitrina (Vitrina) suevica*
excerpta CLESSIN, 1913, *Limnaea*
giengensis KLEIN, 1846, *Helix*
glabraeformis GOTTSCHICK, 1911, *Limnaea (Limnophysa)*
globula CLESSIN, 1913, *Pupa (Alaea)*
gracilis JOOSS, 1911b, *Cochlicopa (Zua) lubricella*
gracilis GOTTSCHICK & WENZ, 1919, *Negulus suturalis*
grossecostata KLEIN, 1852, *Melania* [lot SMNS 23909, lost]
grossecostata GOTTSCHICK & WENZ, 1919, *Torquilla schuebleri*
gyrorbis KLEIN, 1846, *Helix*
helvetica SANDBERGER, 1875, *Clausilia (Triptychia)*
heterodus MILLER, 1900, *Pupa (Pupilla)*
hildegardiae GOTTSCHICK, 1911, *Oleacina (Boltenia)*
inflata CLESSIN, 1913, *Pupa (Alaea)*
intermedia KLEIN, 1846, *Valvata multiformis*
kinkelini JOOSS, 1911a, *Limnaea*
kleiniana PILSBRY, 1909, *Poiretia* [nom. nov. for *Achatina elegans* KLEIN, 1853, non C.B. ADAMS, 1849]
kleinii KLEIN, 1846, *Helix*
kleinii KURR, 1856, *Melanopsis*
kurrii KLEIN, 1846, *Limnaeus*
lacustriformis JOOSS, 1913a, *Limnaea turrita*
latior GOTTSCHICK, 1921a, *Hippeutis subfontanus*
lentilii MILLER, 1900, *Pupa* [lot SMNS 45287/2005, lost]
lineolatum SANDBERGER, 1895, *Carychium*
longidens CLESSIN, 1913, *Pupa (Leucochila)*
loxostoma KLEIN, 1853, *Achatina*
maior MILLER, 1900, *Helix (Macularia) silvestrina*
maior JOOSS, 1912b, *Zonites (Archaeozonites) risgoviensis*
major GOTTSCHICK, 1928, *Amnicola suevicus*
major CLESSIN, 1885, *Clausilia (Serrulina) clessini*
major GOTTSCHICK & WENZ, 1916, *Cochlicopa subrimata*
major GOTTSCHICK, 1920b, *Vallonia subcyclophorella* [lot SMNS 45146/2005]
manca WENZ, 1919f, *Clausilia* [nom. nov. pro *Clausilia wetzleri* MILLER, 1907]
miliolum CLESSIN, 1913, *Pupa (Leucochila)*
milleri GOTTSCHICK & WENZ, 1919, *Vertigo angulifera*
minima GOTTSCHICK & WENZ, 1916, *Cochlicopa subrimata*
minima CLESSIN, 1913, *Pupa (Alaea)*
minor MILLER, 1900, *Helix (Macularia) silvestrina*
minor GOTTSCHICK, 1911, *Helix (Vallonia) subpulchella*
minor GOTTSCHICK, 1911, *Hyalinia (Polita) orbicularis*
minor KLEIN, 1846, *Limnaeus pereger*
minor MILLER, 1907, *Strophostoma anomphalus*
minutula CLESSIN, 1913, *Pupa (Isthmia)*
minutus KLEIN, 1846, *Bulimus*
miocaenica CLESSIN, 1913, *Pupa (Isthmia)*
moersingensis BOETTGER, 1877, *Clausilia (Pseudidyla)*
moguntina JOOSS, 1911b, *Limnophysa girondica*
muscicola CLESSIN, 1913, *Pupa (Alaea)*
nitidulus CLESSIN, 1877, *Planorbis (Gyraulus) dealbatus*
nobilis KLEIN, 1846 *Paludina*
noerdlingensis KLEIN, 1846, *Pupa* [*nomen dubium*, fide HÖLTKE & RASSER, 2013]
normalis GOTTSCHICK, 1921b, *Pseudamnicola pseudoglobulus*
nummulina SANDBERGER, 1875, *Helix*
oblongus CLESSIN, 1913, *Ancylus*
oepfingensis WENZ, 1918a, *Nematurella*
oxystoma KLEIN, 1846, *Planorbis*
paludinaeformis SANDBERGER, 1873, *Succinea* [nom. nov. pro *Succinea paludinoides* KLEIN, 1846]
paludinoides KLEIN, 1846, *Succinea*
palustriformis GOTTSCHICK, 1911, *Limnaea (Limnaea)*
parvulum GOTTSCHICK, 1920a, *Punctum propygmaeum*
perarmata GOTTSCHICK & WENZ, 1919, *Vertigo (Alaea) callosa*
perlabiata GOTTSCHICK & WENZ, 1919, *Pupilla*
physaeformis GOTTSCHICK, 1920c, *Aplexa subhypnorum*
planata GOTTSCHICK, 1921a, *Segmentina larteti*
planiuscula MILLER, 1907, *Paludina*
praelongata GOTTSCHICK & WENZ, 1916, *Limnaea (Radix) dilatata*
priscum WENZ, 1930, *Cochlostoma (Obscurella?)* [nom. nov. pro *Pomatias antiquus* MILLER, 1907]
procera GOTTSCHICK, 1920b, *Cochlicopa subrimata*
procera GOTTSCHICK & WENZ, 1916, *Leucochila acuminata*
quinquedentata JOOSS, 1911b, *Vertigo (Alaea) callosa*
radiatula SANDBERGER, 1872, *Valvata*
recedens GOTTSCHICK, 1920a, *Hyalinia (Hyalinia) subnitens*
rotundata KLEIN, 1846, *Valvata multiformis*
sandbergeri CLESSIN, 1894, *Patula (Charopa)*
scabiosa SANDBERGER, 1875, *Helix*
scalaris MILLER, 1900, *Carinifex multiformis*
scalaris GOTTSCHICK, 1920a, *Hygromia (Trichiopsis) kleini*
scalaris JOOSS, 1902, *Planorbis (Gyraulus) Zieteni*
septemgyratiformis GOTTSCHICK, 1911, *Planorbis (Gyrorbis)*
sexdentata GOTTSCHICK, 1920b, *Azeca*
silvana JOOSS, 1918b, *Pyramidula (Gonyodiscus)*
sparsisticta SANDBERGER, 1875, *Helix*
sparsistictum JOOSS, 1918b, *Tropidomphalus*
stagnaliformis CLESSIN, 1913, *Limnaea*
steinheimensis MILLER, 1900, *Bythinella*
steinheimensis GOTTSCHICK, 1921b, *Caspia(?)*
steinheimensis JOOSS, 1918b, *Poiretia (Palaeoglandina) gracilis*
steinheimensis MILLER, 1900, *Pupa (Pupilla)*
steinheimensis GOTTSCHICK, 1920b, *Vallonia lepida*
steinheimensis GOTTSCHICK & WENZ, 1919, *Vertigo (Alaea) callosa*
steinheimensis GOTTSCHICK, 1920a, *Vitrea (Vitrea) procrystallina*
steinheimensis JOOSS, 1912c, *Zonites subverticillus* [lot SMNS 45984/2005, lost]
subcarinatus GOTTSCHICK, 1921a, *Gyraulus hilgendorfi*
subconoideus JOOSS, 1912c, *Strobilus* [lot SMNS 45173/2005, on loan?]
subcostatus SANDBERGER, 1875, *Archaeozonites*
subcyclophorella GOTTSCHICK, 1911, *Helix (Vallonia)* [lot SMNS 15817, lost]
subhypnorum GOTTSCHICK, 1920c, *Aplexa*
subinvoluta SANDBERGER, 1875, *Helix*
subinvolutus GOTTSCHICK, 1921a, *Gyraulus multiformis applanatus kleini*
subkleini GOTTSCHICK, 1921a, *Gyraulus multiformis applanatus*
subleachi GOTTSCHICK, 1921b, *Bythinia gracilis*
submarginalis KLEIN, 1846, *Helix*
submuscorum GOTTSCHICK & WENZ, 1919, *Pupilla*

subpfeifferi Gottschick, 1920b, *Succinea (Amphibina) minima*
subpolita Gottschick, 1921b, *Acme (Platyla)*
subteres Sandberger, 1872, *Planorbis*
suevica Gottschick & Wenz, 1919, *Pupilla iratiana*
suevica Gottschick & Wenz, 1916, *Pyramidula (Gonyodiscus) supracostata*
suevica Gottschick & Wenz, 1919, *Vertigo (Alaea) protracta*
suevicus Sandberger, 1875, *Cyclostomus* [lot SMNS 61803, lost]
suevicus Sandberger, 1875, *Pomatias*
supracostata Sandberger, 1872, *Patula*
terrena Clessin, 1874, *Helix*
tridentiformis Gottschick, 1911, *Cionella (Azeca)*
trochulus Sandberger, 1875, *Hydrobia*
ulmensis Miller, 1907, *Cyclostomus*
ulmensis Wenz, 1918a, *Poiretia (Poiretia) rugulosa*
ulmensis Wenz, 1918a, *Torquilla subvariabilis*
umbilicata Jooss, 1918b, *Klikia (Klikia) coarctata*
undorfensis Boettger, 1877, *Clausilia (Pseudidyla) moersingensis*
undorfensis Clessin, 1894, *Hyalina*
undorfensis Clessin, 1877, *Limnaea*
undorfensis Clessin, 1913, *Pupa (Alaea)*
undorfensis Clessin, 1913, *Strobilus* [p. 104: *Strobilus curdoofensis*]
wetzleri Boettger, 1877, *Clausilia*
wetzleri Miller, 1907, *Clausilia*
zellii Kurr, 1856, *Helix*

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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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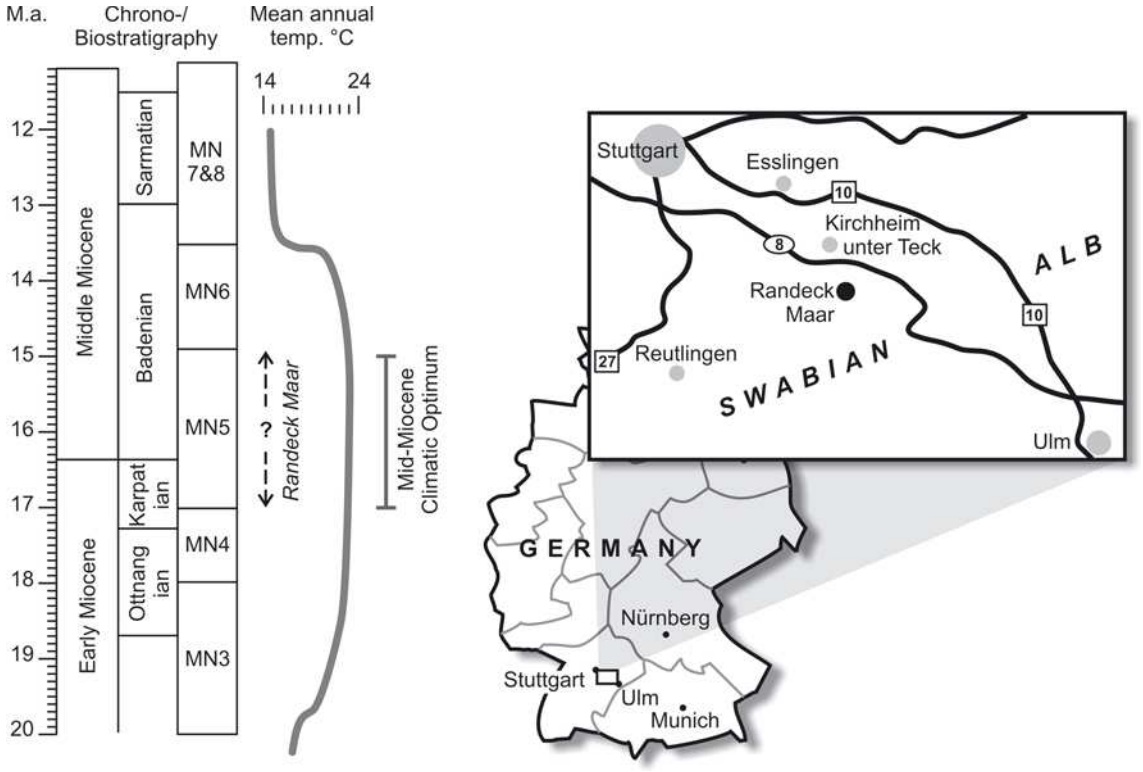

Fig. 1. Geography and stratigraphy of the Randeck Maar.

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,

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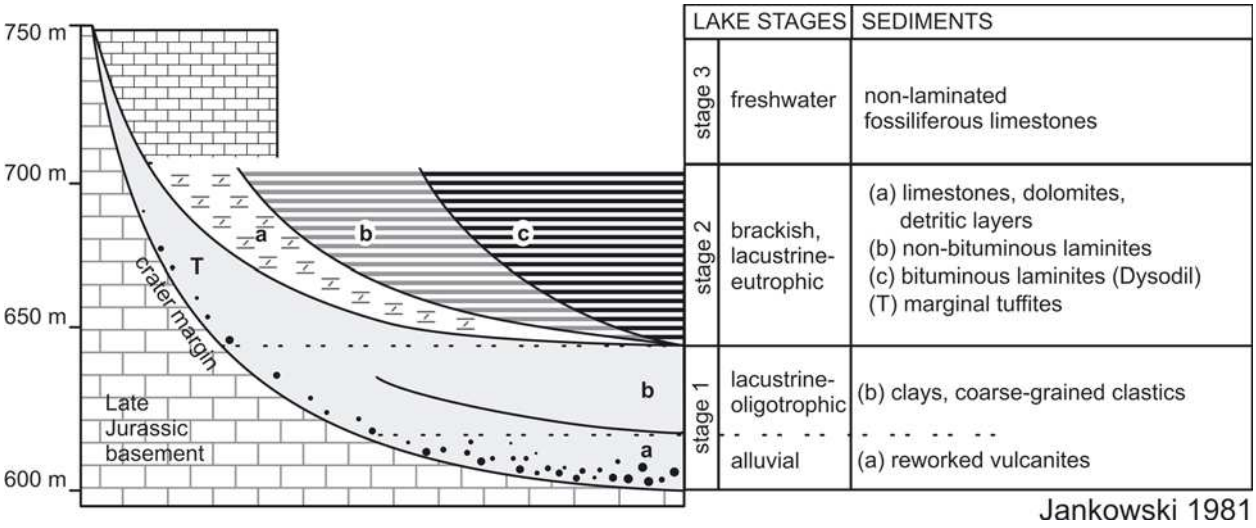

Fig. 2. Schematic cross section through the Randeck Maar sediments after Jankowski (1981). A "T" indicates the position of the light and dark tuffites. See Table 1 for the distribution of snails in the different facies types.

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.

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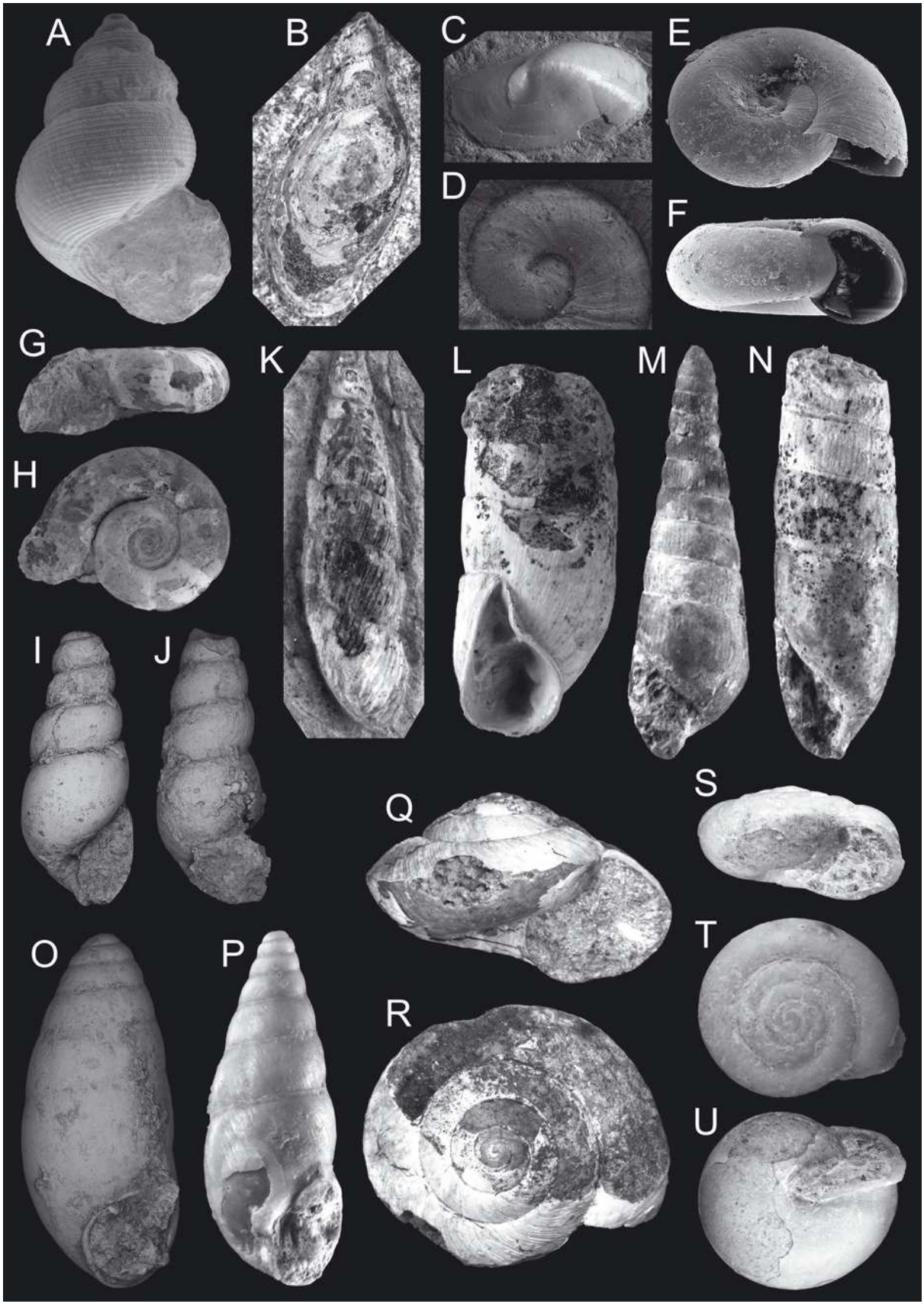

Fig. 3. Gastropods of the Randeck Maar.

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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.

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).

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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 lime-

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stones 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-*

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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 ~35°. Protoconch (~1½ whorls) round, apparently smooth; transition to teleoconch clear. Teleoconch sculptured by fine but well-marked, regularly arranged and closely spaced,

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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 Silvanabeds ("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).

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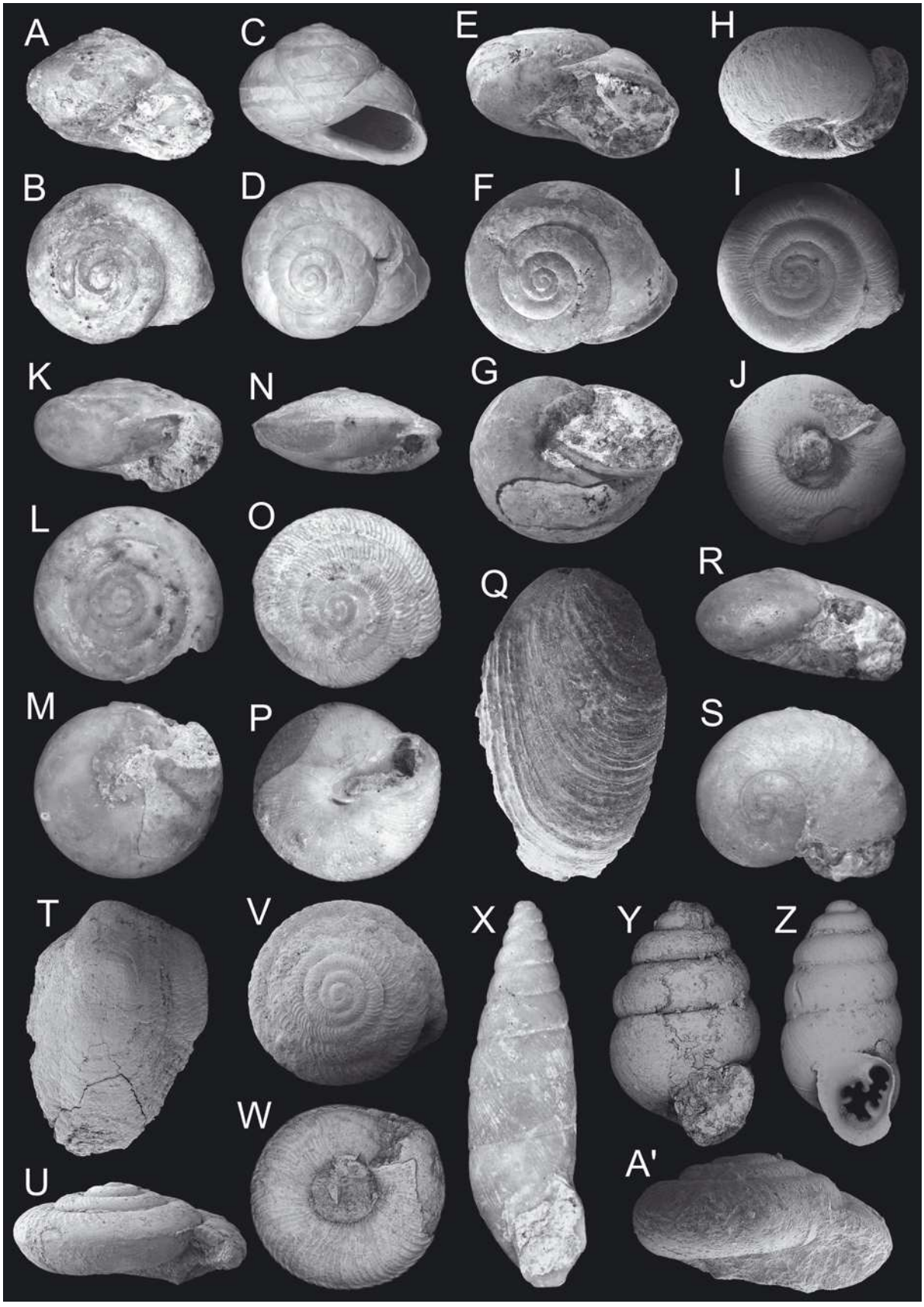

Fig. 4. Gastropods of the Randeck Maar (cont.).

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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.

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).

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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.

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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.

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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 acumi-

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nated 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.

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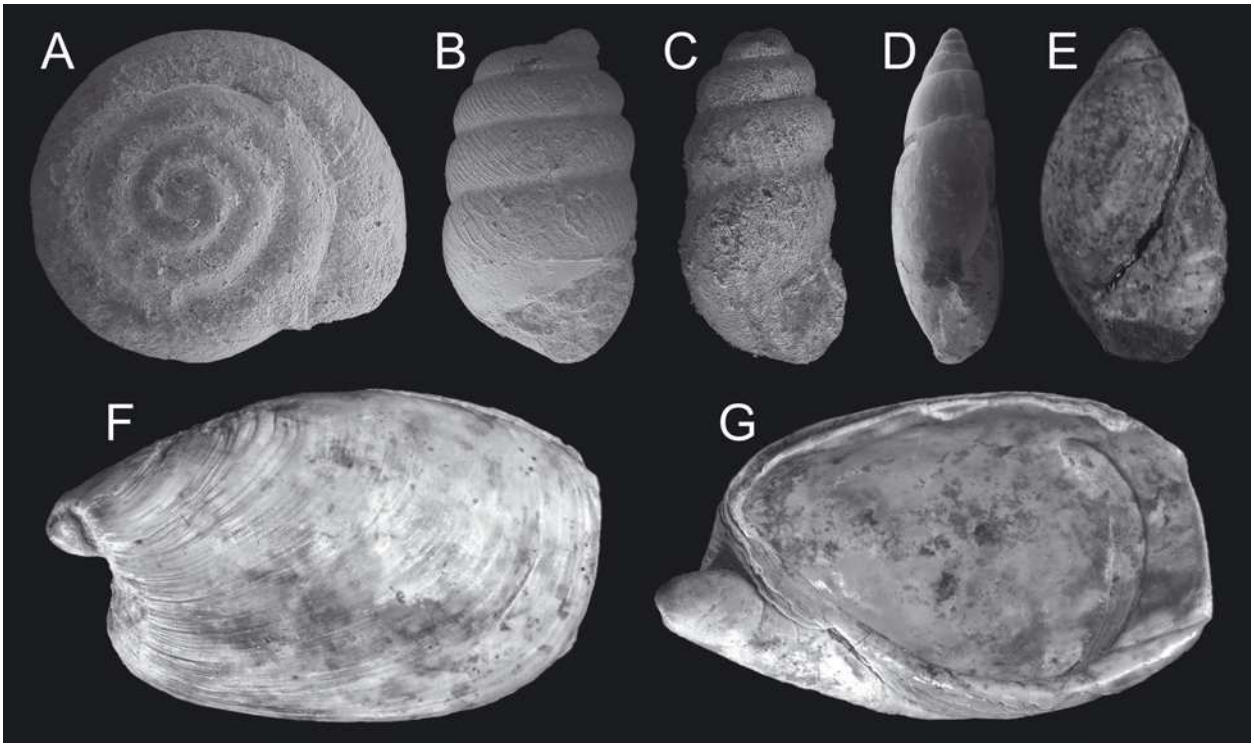

Fig. 5. Gastropods of the Randeck Maar (cont.).
A – *Vallonia* cf. *lepida* (SMNS 101185; H = 1.2 mm, D = 2.0 mm). **B –** ?*Truncatellina* sp. (SMNS 101181; H = 2.1 mm, D = 1.2 mm). **C –** *Negulus suturalis* (SMNS 101187; H = 1.5 mm, D = 0.7 mm). **D –** *Pseudoleacina eburnea* (SMNS 101164; H = 14.6 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

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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.

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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

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(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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Miocene land and freshwater gastropods of Mörsingen (Baden-Württemberg, South Germany).

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Abstract

The Miocene deposit of Mörsingen (Baden-Württemberg, South Germany) is located in the northern part of the North Alpine Foreland Basin. Lithostratigraphically, the sediments belong to the *silvana*-beds of the Upper Freswater Molasse (Obere Süßwassermolasse). The location contains freshwater sediments comprised of limestones and marl. Biostratigraphically, it lies within the mammal zone MN 5 (Badenian). For the first time, the continental gastropod fauna from this location is documented and illustrated in its entirety. A total of 9 freshwater and 35 terrestrial gastropod taxa could be identified from available specimens. Additionally, there are literature records for one additional freshwater and ten terrestrial species, of which no voucher material could be found. A new species, *Aegopinella moersingensis* n. sp., was identified in the material and is described here. From an actualistic perspective, the ecological preferences of the fossil assemblage of Mörsingen tends towards shaded and moist habitats with a dense forest cover, although more xerophile taxa are also present, indicating a variety of microhabitats in the vicinities. The freshwater species assemblage indicate stagnant or slow-flowing water, with the exception of a single taxon (*Esperiana*, presently absent from Central Europe) that lives in faster-moving streams and rivers. Fossils of taxa other than snails are rare in Mörsingen, including *Celtis* sp. (angiosperm), remains of freshwater bivalves, and undetermined ostracods.

Key words: *Aegopinella moersingensis* n. sp., Obere Süßwassermolasse, Upper Freshwater Molasse, Gastropoda, *silvana*-beds, Stylommatophora, Hygrophila.

1. Introduction

The village Mörsingen (48°13'57"N, 9°27'51"E) is a district ("Ortsteil") of Zwiefalten, Landkreis Reutlingen, Baden-Württemberg, southern Germany (Fig. 1). The Miocene deposit of Mörsingen is locality famous for the continental gastropod fossils of the Obere Süßwassermolasse (or Upper Freshwater Molasse, abbreviated OSM). From the middle of the 19th century to the beginning of the 20th century, large quantities of well-preserved material were extracted from this village's outcrops. Consequently, material from Mörsingen is present in the collections of several natural history collections. However, important material, including type and voucher specimens of published studies, has been lost or destroyed, potentially during World War II. This is the case, for instance, of the large collection of malacologist Wilhelm Wenz from Frankfurt am Main.

Historically, there were two sections in Mörsingen from where the fossil material originated. One was an in-operation clay pit and the other an area called Schneckengarten ("snail garden") by the local people. The name implies that the vast majority of fossils from Mörsingen were snails. Today, the Schneckengarten is agricultural land and the clay pit has been out of order and inaccessible at least since the post-war period, but it is still visible as a pronounced landmark.

Despite the wealth of gastropod fossils from Mörsingen, there has been no publication dealing exclusively with this fauna. Mörsingen is only mentioned in passing in the specialized literature, for example in Wenz (1923) or in Sandberger (1870-1875). The present work is therefore, the first to fully document the continental gastropods of

Mörsingen, describing and illustrating all fossils from that locality and including the description of a new species. Furthermore, we present discussions on the geology and the stratigraphic position of the sediments, as well as an actualist paleoenvironmental analysis.

2. Geological setting

Mörsingen is located on the northern part of the North Alpine Foreland Basin. The deposits studied herein are part of the OSM and, more specifically, belongs to the lithostratigraphic unit known as *silvana*-bed, named after the common fossil snail *Palaeotachea silvana* (Klein, 1853). The deposits are of Badenian age (Middle Miocene) and lie within the European land mammal zone MN 5 (Esu 1999).

The sediments consist of clay and marl with a disparity in the clay/limestone ratio. Given the lack of permanent outcrops today, the lithology of the snail-bearing sediments is poorly understood. Furthermore there is scarce information about it that can be extracted from the literature. However, in 2013, sedimentary samples could be taken from a local construction site in Mörsingen, which can aid in creating a better picture. The lithology consists of an alternation of limestone and marl and will be decribed in more detail in a future study.

3. Material and methods

Examined specimens are stored in the collections of Staatliches Museum für Naturkunde Stuttgart (SMNS, Stuttgart, Germany) and Naturmuseum Senckenberg (SMF, Frankfurt am Main, Germany).

Most specimens belong to the former collections of Bechter, Fischer, Gottschick, Jooss, Klein, Koch and Schütze (all in the SMNS); the remaining specimens are from unknown collectors/collections. New material collected from the above-mentioned construction site were washed from the matrix for examination and deposited in the SMNS collection.

Specimen examination was done under stereomicroscope and a few selected specimens were further examined under a scanning electron microscope at SMNS. The species list is presented below following the systematic classification of Bouchet et al. (2017), Wiese (2014) and Nordsieck (2014). For brevity and clarity, the synonymy provided herein only includes the original description and works that involve fossils from Mörsingen. We included information about type material and locality when available, a morphological description of the present specimens, paleoecology (per an actualistic genus-level interpretation; see Rasser et al., 2019), and a brief discussion when pertinent with information about taxonomy, geographic distribution and other features of notice.

Unfortunately, not all the species reported from Mörsingen in the literature could be confirmed (i.e., Wenz 1923, 1928; Gottschick & Wenz 1916; Schlickum 1976), as no voucher specimens could be found. Those species are listed in the last section of the present work in a tabular form, including their original report and their present systematic classification, as well as brief notes on palaeoecology.

4. Systematic paleontology

Gastropoda

Sorbeoconcha Ponder & Lindberg, 1997

Melanopsidae H. Adams & A. Adams, 1854

***Esperiana* Bourguignat, 1877**

***Esperiana kleinii* (Kurr, 1856) n. comb. (Fig. 2.1)**

1856 *Melanopsis kleinii* – Kurr: 42.

1976 *Melanopsis kleini kleini* Kurr – Schlickum, 18, pl. 5, fig. 65.

2018 *Esperiana kleinii* (Kurr, 1856) – Höltke et al., fig. 3.2.

Material: 12 specimens (SMNS J68.411, Jooss collection); 1 specimen (SMNS 107217). Type material is missing (Salvador et al. 2016).

Type locality: Zwiefalten and Andelfingen, Baden-Württemberg, Germany (Kurr 1856).

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Spindle-shaped shell with c. eight whorls. The whorls are flat, only the last one is slightly convex. The suture is very flat. From the first whorl until the beginning of the last one, the whorls grow in a regularly manner. The last whorl grows in an excessively manner and reaches c. 70 % of the total shell height. The periostome is obliquely-pear shaped. The margins are simple and sharp. The columellar margin forms a remarkable, callous thickening which runs up to the parietal region without interruption. The shell bears no sculpture. Unfortunately, the protoconch is broken on all available specimens. According to the examined specimens, the maximum shell height seems to be c. 18 mm.

Discussion: The species was originally placed in the genus *Melanopsis*. However, according to Glöer (2002) the genus *Melanopsis* has stepped whorls, which is not the case for the present species. Considering the flat whorls and suture of the present specimens, this species would be better allocated in the genus *Esperiana*, as *Esperiana kleinii* (Kurr, 1856) n. comb.

Paleoecology: Rivers and streams (Glöer 2002).

Pachychilidae P. Fischer & Crosse, 1892

***Tinnyea* Hantken, 1887**

***Tinnyea lauraea* (Matheron, 1842) (Fig. 2.2)**

1842 *Melania laurea* – Matheron: 291, pl. 36, figs 23– 24.

2018 *Tinnyea lauraea* (Matheron, 1842) – Höltke et al., fig. 3.3.

Material: 2 specimens (SMNS J68.392, Jooss collection); 10 specimens (SMNS J68.387, Jooss collection); 1 specimen (SMNS 107218).

Type locality: Vaucluse department, France (Matheron 1842).

Type stratum: Uncertain, possibly Miocene.

Description: Tower-shaped shell with regularly growing whorls. The protoconch and first teleoconch whorls are missing on all available specimens. The whorls are flat as well as the suture. Below the suture is a flattened, clearly distinct area which incorporates c. 1/3 of the whorl. The whorls bear distinct regularly arranged ophisthocyrt to ophistocline ribs. The distance between the ribs are c. twice the rib's width. Apart from this radial ribs, there are also weaker spiral lines present on the teleoconch whorls. The periostome is incomplete in all specimens. The columellar region has a thickened callus. The specimen is c. 29 mm in height.

Discussion: The species is mostly found in the literature as *Brotia escheri* (Brongniart in Cuvier & Brongniart, 1822). According to Kadolsky (1995) this is a *nomen nudum* and the correct name is *Tinnyea lauraea* (Matheron, 1842).

Paleoecology: The genus is extinct, but Kowalke (2004) suggested *Tinnyea* inhabited quiet waters or slow-flowing rivers.

Littorinimorpha Golikov & Starobogatov, 1975

Pomatiidae Newton, 1891 (1828)

***Pomatias* Studer, 1789**

***Pomatias conicus* (Klein, 1853) (Fig. 2.4)**

1853 *Cyclostoma conicum* – Klein: 21, pl. 5. fig. 14.

2018 *Pomatias conicus* (Klein, 1853) – Höltke et al., fig. 3.4.

Material: 3 specimens (SMNS 107220), 100 specimens (SMNS J68.040, Jooss collection), 23 specimens (SMNS J68.032, Jooss collection), 50 specimens (SMNS 4332/2008, Bechter collection), 9 specimens (SMNS 2018/2008). Type material is missing (Salvador et al. 2016).

Type locality: Herzogtum, Baden-Württemberg, Germany (Klein 1853).

Type stratum: Unknown, probably *silvana*-beds.

Description: Turbiniform dextral shell with 4-5 whorls. They are convex with deep sutures. The penultimate whorl is the most bulbuos one. The aperture has a simple peristome and it is obliquely-oval shaped. The shell has a slit-like umbilicus. The teleoconch bears strongly spiral rips and very weak regular arranged axial ribs. The height of the aperture makes up c. 40% of total shell height. The examined shell is c. 11.5 mm in height.

Discussion: The opercula of this species can often be found in fossil outcrops, like Randecker Maar in Baden-Württemberg, but they are very rare in Mörsingen.

Paleoecology: Mesophile habitats, in woods (Lueger 1981).

***Pomatias consobrinus* (Sandberger, 1875) (Fig. 2.3)**

1875 *Cyclostoma consobrinum* C. Mayer – Sandberger: 606, pl. 29, fig. 33a.

1910 *Cyclostoma consobrinum* – Fraas: 220, pl. 67, fig. 5.

2018 *Pomatias consobrinus* (Sandberger, 1875) – Höltke et al., fig. 3.5.

Material: 9 specimens (SMNS 107219, vouchers from Fraas 1910). 26 specimens (SMNS 4343/2008, Bechter collection); 3 specimens (SMNS 4348/2008, Bechter collection). Type material is missing (Salvador et al. 2016).

Type locality: The specimens illustrated by Sandberger (1875) came from Mörsingen, so it could be interpreted as the type-locality.

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Comparably large, turbiniform dextral shell. It consists of c. 4¾ convex wholrs which increase rapidly in size. The last whorl is the most bulbous one. The suture is relatively deep. The last whorl runs straight up to the aperture without turning down. The aperture has an oblique ovoid shape. It has a continuous periostome and is clearly separated from the rest of the shell. The periostome is simple apart from the columellar part which is slightly thickened. The shallow umbilicus is small and slit-like. The teleoconch bears weakly visible spiral lines. The protoconch is knobby and consists of c. 1¼ whorls, unsculptured. Maximum shell height is c. 18 mm.

Paleoecology: As *P. conicus* above.

***Bithynia* Leach, 1818.**

***Bithynia glabra* (Zieten, 1832) (Fig. 2.5)**

1832 *Cyclostoma glabrum* –Zieten: 42, pl. 31, fig. 9.

2018 *Bithynia glabra* (Zieten, 1832) – Höltke et al., fig. 3.6.

Material: 3 specimens (SMNS J68.154, Jooss collection), 1 specimen (SMNS 1970/2008, Schütze collection).

Type locality: Grimmelfingen, Baden-Württemberg, Germany (Zieten 1832).

Type stratum: Grimmelfinger Schichten, Lower/Middle Miocene.

Description: Small, trochiform shell with whorls rapidly increasing in size. It consist of c. 4 whorls with deep suture. The first teleoconch whorls are flatter whereas the two last ones are convex. The aperture region is not

completely preserved; it has an obliquely-oval to pyriform shape; periostome seemingly simple and sharp. No umbilicus. The teleoconch bears some straight growing lines with varying strength along the shell. The bulbuos protoconch consist of c. 0.5 whorls, being remarkably smooth when compared to the teleoconch. The protoconch has a slightly ivory-like appearance. Largest specimen is 4 mm high.

Paleoecology: In stagnant or slow-flowing waters (Glöer 2002).

Hygrophila Bouchet & Rocroi, 2005

Lymnaeidae Rafinesque, 1815

***Lymnaea* Lamarck, 1799**

***Lymnaea turrita* Klein, 1853 (Figs. 2.6, 2.7)**

1853 *Lymnaea turritus* – Klein: 220, pl. 5, fig. 17.

1913 *Lymnaea turrita* Klein emend Jooss milleri nov. var. – Jooss: 61, fig. 5,6.

Material: 2 specimens (Originals to Jooss 1913, SMNS 106409 & SMNS 196408)

Type locality: Andelfinger Berg near Andelfingen, Baden-Württemberg, Germany (Salvador et al. 2016).

Type stratum: *Silvana*-beds, Middle Miocene (Salvador et al. 2016).

Description: Relative large, spindle-shaped lymnaeiform shell, with c. 7 whorls. It has a tapered spire and comparably rapid growing whorls resulting in a large last whorl (c. 75% of total shell height). The whorls are only moderately convex and the suture is flat. The periostome is slightly ovoid with a simple and sharp margin. Only the columellar margin is reflected. The two insertions are connected by a distinct parietal callus. The knobby-shaped, incompletely-preserved, protoconch consits of c. 1¾ whorls and lacks sculpture.

Paleoecology: Standing or slow-moving waters, with rich vegetation (Welter-Schultes 2012).

***Radix* Montfort, 1810**

***Radix dilatata* (Noulet, 1854) (Fig. 2.8)**

1854 *Limnaea dilatata* Noulet – Noulet: 107.

2018 *Lymnaea dilatata* (Noulet, 1854) – Höltke et al., fig. 3.9

2018 *Radix dilatata* (Noulet, 1854) – MolluscaBase (2018).

Material: 2 specimens (SMNS J67.684, Jooss collection).

Type locality: Sansan, France (Noulet 1854).

Type stratum: Calcaires de L'Agenais, Lower Miocene.

Description: Large spindle-shaped shell with a high last whorl that makes up c. 75% of total shell height. The whorls rapidly-growing, only very weakly convex. The height of the aperture is c. 60% of shell height. The aperture is slightly pear-shaped. The periostome is simple. The shell lacks of sculpture. The protoconch is incompletely-preserve and consists of c. 1.5 whorls. No sculpture visible. Maximum shell height c. 42 mm.

Paleoecology: In stagnant or slow-flowing waters (Glöer 2002).

Planorbidae Rafinesque, 1815.

***Planorbarius* Duméril, 1806.**

***Planorbarius mantelli* (Dunker, 1848) (Fig. 2.9)**

1848 *Planorbis mantelli* – Dunker: 159, pl. 31, figs. 27.

2018 *Planorbarius mantelli* (Dunker, 1848) – Höltke et al., fig. 3.13.

Material: 4 specimens (SMNS 4437/2008, Bechter collection), 21 specimens (SMNS 2019/2008), 1 specimen (SMNS 2247/2008, Bechter collection), 1 specimen (SMNS 107221, Bechter collection), 30 specimens (SMNS 2248/2008, Bechter collection), 11 specimens (SMNS 4283/2008), 1 specimen (SMNS 4438/2008, Fleischer collection), 30 specimens (SMNS 2245/2008, Bechter collection).

Type locality: Günzburg, Bavaria, Germany (Dunker 1848).

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Flat planispiral shell. The spire is distinctly sunken under the upper margin of the subsequent whorl. The whorls increase rapidly in size, being convex with a deep suture. The teleoconch is covered by thin, irregularly spaced growing lines. These are crossed by hardly visible, more regularly-spaced spiral lines, mainly on the inner whorls. However, this sculptural features are not visible on all specimens. The bulbous protoconch consists of c. 1.5 whorls. The shell is c. 18 mm in width.

Paleoecology: Stagnant or slow-moving waters with rich vegetation (Glöer 2002; Welter-Schultes 2012).

***Gyraulus* Charpentier, 1837**

***Gyraulus applanatus* (Thomae, 1845) (Fig. 2.10)**

1845 *Planorbis applanatus* Thomae: 150.

1923 *Gyraulus* (*Gyraulus*) *trochiformis applanatus ludovici* (Noulet) – Wenz, 1588.

2018 *Gyraulus applanatus* (Thomä, 1845) – Höltke et al., fig. 3.12.

Material: 9 specimens (SMNS J67.780, Jooss collection).

Type locality: Wiesbaden and Mainz-Weisenau, Germany.

Type stratum: Upper Oligocene/Lower Miocene.

Description: Small planorbid shell with regularly increasing whorls. The shell consists of c. 4 convex whorls with a deep suture. The spire is sunken. The last whorl is c. twice as wide as the fore last one. The last whorl forms a blunt keel. The periostome is simple and sharp. The aperture has an arrow shape due to the keel of the last whorl. The width of the examined specimens is c. 3.9 mm.

Discussion: The species shows a reasonable degree of morphological variation, having several forms in its simonomy (see Rasser & Salvador 2019).

Paleoecology: In ponds, lakes and slow-flowing waters (Glöer 2002).

***Segmentina* Fleming, 1818**

***Segmentina lartetii* (Noulet, 1854) (Fig. 2.11)**

1854 *Planorbis Lartetii* Noulet – Noulet: 104-105.

2018 *Segmentina lartetii* (Noulet, 1854) – Höltke et al., fig. 3.14.

Material: 4 specimens (SMNS J67.909, Jooss collection).

Type locality: Sansan, France (Noulet 1854).

Type stratum: Middle Miocene (Fischer 2000).

Description: Small planorbid shells with sunken spire. The shell consist of c. 4¼ whorls rapidly increasing in size, resulting in a large last whorl which almost completely envelops the older ones. The suture is moderately shallow. The last whorl is ramp-like with a very flat basis. From the side, the shell looks a bit like an overturned bowl. The aperture region is not completely preserved in the present specimens, but is arrow-shaped. The shell is moderately umbilicated. The umbilicus has slightly oblique running margins. Protoconch flat, no sculpture is visible. The width of the shell is c. 3 mm.

Paleoecology: Vegetation-rich, muddy ponds and lakes (Glöer 2002).

***Ferrissia* Walker, 1903**

***Ferrissia deperdita* (Desmarest, 1814) (Fig. 2.12)**

1814 *Ancylus deperditus* – Desmarest: 19, pl. 1, fig. 14

2018 *Ferrissia deperdita* (Desmarest, 1814) – Höltke et al., fig. 3.10.

Material: 1 specimen (SMNS J67.925, Jooss collection).

Type locality: France (Desmarest 1814).

Type stratum: Unknown, possibly Miocene.

Description: Small limpet shell with an oval to elliptical outline. The basal margin of the shell is not completely preserved. The apex is not placed in the middle of the shell but offset in a backward position. The anterior part takes c. 2/3 of the shell length. The posterior and the anterior margin are convex. In lateral view, the anterior part of the shell is slightly convex; the posterior one is remarkably concave; the apex is relative flat and blunt. The teleoconch bears barely-visible closely-positioned concentric growth lines, more evident near the apex. The single specimen is c. 3.5 mm long and 2 mm wide.

Paleoecology: Stagnant or slow-moving waters (Glöer 2002).

Stylommatophora A. Schmidt, 1855

Azecidea Watson, 1920

Azeca* Fleming, *1828

***Azeca lubricella* O. Boettger, 1870 (Fig. 3.1.)**

1870 *Azeca lubricella* – O. Boettger: 291

2018 *Azeca lubricella* Boettger, 1870 – Höltke et al., fig. 4.2.

Material: 7 specimens (SMNS J67.234, Jooss collection). Type material is lost, but Schlickum (1976) designated a neotype.

Type locality: Tuchořice, Czech Republic (O. Boettger 1870).

Type stratum: European Mammal Zone MN3b**,** Eggengurgian, Early Miocene (Harzhauser et al. 2014).

Description: Ovoidshell of c. 6 whorls. Whorls and suture fairly flat. The last whorl about half total shell height. The aperture has an obliquepear shape. The periostome is slightly thickened, but not reflected. No umbilicus. The columellar region bears two fold-like teeth. On the parietal callus, there is also a strong tooth. The palatal margin contains a tooth, and dorsal to that, within the aperture, there is a second one, hardly visible. The teleoconch bears no sculpture apart from barely visible growth lines on the last whorl of some specimens. The protoconch is blunt and unsculptured. The shell height is c. 5 mm.

Paleoecology: Moist, herb-rich habitats in deciduous forests (Fechter & Falkner 1989).

***Hypnophila* Bourguignat, 1858**

***Hypnophila loxostoma* (Klein, 1853) (Fig. 3.2)**

1853 *Achatina loxostoma* – Klein: 214, pl. 5, fig. 12.

2018 *Hypnophila loxostoma* (Klein, 1853) – Höltke et al., fig. 4.3.

Material: 20 specimens (SMNS 2005/2008, Koch collection), 20 specimens (SMNS 1920/2008), 18 specimens (SMNS 2002/2008), 3 specimens (SMNS J67.255, Jooss collection). The type material is lost (Salvador et al. 2016).

Type locality: Mörsingen and Birk, Baden-Württemberg, Germany.

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Elongated ovoid shell, with c. 6 flat whorls rapidly increasing in size. Last whorl more than half the total shell height. The aperture has an obliquely-pear shape with a blunt and rounded periostome. No umbilicus. On the lower part of the columellar margin, near to the basal margin, there is a tooth-like callous thickening. The pronouncement of this feature seems to vary intraspecificaly. The columellar margin turns into a partietal callus which runs up to the upper insertion point. The height of the aperture is c. 35% of the total shell height. The teleoconch is smooth. The protoconch (c. 1¼ whorl) has a blunt apex and is also smooth. The shell height is c. 4 mm.

Discussion: Originally described as a full species, it was later deemed a subspecies (Gottschick & Wenz, 1916), being found in most of the literature in this form. Harzhauser et al. (2014) placed the species in the genus *Hypnophila* (Azecidae).

Paleoecology: Recent representatives of the family in Europe are found in a variety of habitats (Welter-Schultes 2012), making any paleoecological interpretation difficult.

Chondrinidae Steenberg, 1925.

***Granaria* Held, 1838**

***Granaria subfusiformis* (Sandberger, 1875) (Fig. 3.3, Fig. 5.4)**

1875 *Pupa subfusiformis* Sandberger – Sandberger: 598.

2018 *Granaria subfusiformis* (Sandberger, 1875) – Höltke et al., fig. 4.4.

Material: 2 specimens (SMNS 67.462, Jooss collection), 3 specimens (SMNS 16635). Type material is unknown.

Type locality: Sandberger (1875) named the following localities: Hausen near Ehingen/DonauMörsingen. In Bavaria: Denkendorf-Schönrunn; as well as Adelegg, a mountain which belongs partly to Bavaria and Baden-Württemberg.

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Pupiform to spindle-shaped shell. It consists of c. 8.5 whorls which are flat to slightly convex. The suture is moderately deep. The whorls expand in a regular manner. The oblique aperture is not complete in our specimens, but remains of a parietal callus and a parietal lamellae are visible, as well as a palatal tooth/lamella. The teleoconch bears fine prosocline ribs, more or less regularly arranged, becoming distinct from the fourth whorl on to the penultimate one. On the first teleoconch whorls and the body wholr, the ribs are barely visible. The distance between these ribs ranges from 0.5 to 2 times the ribs's width. The protoconch bears no sculpture. The size of the examined specimens is c. 7.5 mm height and c. 3 mm width.

Discussion: The species *G. subfusiformis* was named and described by Sandberger (1875) but without any illustration. It is the only *Granaria* species named from the *silvana*-beds. The type material of Sandberger (1875) is unknown. Until now, only fragments of *Granaria* were known from the *silvana*-beds, precluding species identification. According to that, Höltke & Rasser (2013) declared *G. subfusiformis* as *nomen dubium*. The presently figured specimen from Mörsingen allow a proper identification, despite its incomplete aperture. It differs from other German Miocene *Granaria* spp. as follows: 1) Differs from *G. schuebleri* (Klein, 1846) by alarger and more slender shell, with c. half fewer whorl. 2) Differs from *G. grossecostata* (Gottschick & Wenz, 1919) by a larger and more slender shell, with a shallower suture. 3) Differs from *G. helicidarum* (Jooss, 1923)

by a more slender shell. 4) Differs from *G. crassiventer* Salvador et al., 2016 by a smaller and more slender (more spindle-shaped) shell.

Paleoecology: Warm and dry habitats on calcareous grounds (Kerney et al. 1983).

Vertiginidae Fitzinger, 1833

***Gastrocopta* Wollaston, 1878**

***Gastrocopta acuminata* (Klein, 1846) (Fig. 3.4)**

1846 *Pupa acuminata* – Klein: 75, pl. 1, fig. 19.

2000 *Gastrocopta (Albinula) acuminata* (Klein, 1846) – Manganelli & Giusti, pl. 9, figs. 1– 3.

2018 *Gastrocopta acuminata* (Klein, 1846) – Höltke et al., fig. 4.5.

Material: 3 specimens (SMNS J67.427, Jooss collection), 3 specimens (SMNS J67.429, Jooss collection).

Type locality: Dächingen, Öpfingen and Hohenmemmingen, Baden-Württemberg, Germany.

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Pupiform shell of c. 4¾ whorls. Apart from the last one, the whorls are moderately convex. The last whorl has a more flattened profile. Suture moderately deep. The aperture has an oval to oblique oval shape, varying intraspecifically (see also Manganelli & Giusti, 2000a). A distinct parietal callus is present and the periostome is reflected. The umbilicus is small. The aperture contains five barriers (also varying intraspecifically in number and strength): one angulo-parietal lamellae that reaches the periostome, forming two tooth-like elevations; two palatal teeth; one columellar lamella; and one knob-shaped basal tooth. The teleoconch bears fine, regularly arranged prosocline growing lines. The protoconch consists of c. 1¼ whorls and bears no sculpture; it has a flat but slightly bulbous shape. Shell height is c. 3 mm.

Paleoecology: The genus *Gastrocopta* is extinct in Europe (Wedel 2008), but occurs elsewhere in the Palearctic, as well as the Nearctic (Zilch 1959–1960). As such, it has restricted use for paleoecology.

***Gastrocopta quadriplicata* (Braun, 1851) (Figs. 3.6, 5.7)**

1851 *Vertigo quadriplicata* – Braun: 1135.

2000 *Gastrocopta quadriplicata* (Braun, 1851) – Manganelli & Giusti, 72, pl. 8, figs. 1– 4.

2018 *Gastrocopta quadriplicata* (Braun, 1851) – Höltke et al., fig. 4.6.

Material: 2 specimens (SMNS J67.383, Jooss collection). Type material is lost, neotype selected by (Manganelli & Giusti (2000).

Type locality: Mainz Basin, Germany.

Type stratum: Uncertain, Upper Oligocene/Lower Miocene.

Description: Pupiform shell, of c. 4¾ regularly growing whorls, markedly convex. The penultimate whorl is the most bulbous one. Suture is narrow and deep. The aperture has an oval, slightly angular shape. The periostome is thin. The aperture contains four barriers: one angulo-parietal lamella that reaches all the way forward, bearing a slightl hook-shaped elevation on its outward portion; one columellar lamella stretching far back into the shell and ascending obliquely as well as two palatal teeth. Apart from the angulo-parietal, the other three end a little bit before reaching the periostome.Small slit-like umbilicus. The teleoconch bears very fine prosocline growing lines. The protoconch lacks sculpture (bumps on Pl.4, Fig.1 are just sediment); it has a bulbous shape and consists of c.1 ¼ whorls. Shell height is c. 3 mm.

Discussion: It can be distuingished from *G. acuminata* by its obliquely ascending columellar lamella and the weaker angulo-parietal lamella.

Paleoecology: As *G. acuminata* above.

Filholiidae Wenz, 1923

***Triptychia* Sandberger, 1875**

***Triptychia kleini* Schnabel, 2006 (Figs. 3.6, 3.7)**

1846 *Clausilia grandis* – Klein: 73, pl.1, fig. 16.

2006 *Triptychia kleini* – Schnabel: 147, pl. 3, fig. 32–34.

2018 *Triptychia kleini* Schnabel, 2006 – Höltke et al., fig. 4.8.

Material: 2 specimens Jooss collection (SMNS 107223; SMNS J68.554); 2 specimens (Bechter-collection SMNS 107222

Type locality: Zwiefalten, Baden-Württemberg, Germany.

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Sinistral turreted shell of up to 15 whorls, growing in regularly manner and having a flat profile. Suture flat; on the first 8 whorls, the suture runs remarkably oblique to the vertical shell axis, giving the impression that the upper part of the spire is slightly bent to the right (the effect is less prominent on juveniles). The aperture is relatively small compared to shell height (c. 28%). The peristome is slightly deflected. The palatal margin is slightly S-curved. The columellar margin runs arch-shaped into the parietal margin; from the latter, the sinulus is separated by a distinct crinkle. The aperture dentition consists of three folds: one parietal lamella, one columellar lamella, and one subcolumellar lamella. The parietal lamella is the highest one, being relatively thin; it runs more or less straight into the aperture. The coumellar lamella makes a remarkable crinkle and reaches the aperture in an obliquely manner. The subcolumellar lamella is the smallest one; it also runs more or less straight into the inner part of the aperture. The distance between the latter two lamellae is shorter than the distance between the parietal and columellar lamellae. The parietal lamella ends earlier than the other two lamellae, before the peristome. From the third to the eleventh whorl, the shell bears prominent regularly arranged axial ribs. On the younger whorls, only weak growth lines are visible. The large protoconch consists of c. 2½ whorls; it has a bulbous shape and lacks sculpture. The shell size is c. 39 mm.

Discussion: *Triptychia kleini* was proposed as a new name for the preoccupied *Clausilia grandis* (see Schnabel 2006 for details), which was used in the literature until then.

Paleoecology: Filholiids are extinct, but are hypothesized to have lived like their sister taxa Clausiliidae, on rock walls and trees (Nordsieck 2007).

***Triptychia teutonica* Schnabel, 2006**

2006 *Triptychia teutonica* – SCHNABEL: 172, pl. 8, figs. 97, 98.

Material: Holotype BSPG 1955 XXIX 16 (see Schnabel 2006, pl. 8, fig. 97); paratype SMF 264426 (see Schnabel, pl. 8, fig. 98).

Type locality: Mörsingen, Baden-Württemberg, Germany (Schnabel 2006).

Type stratum: *Silvana*-beds, Middle Miocene (Schnabel 2006).

Paleoecology: As *T. kleini* above.

***Triptychia* sp. (Fig. 2.8)**

Material: 1 incomplete specimen (SMNS 107223).

Description: Sinistral, clausilioid shell. The aperture is not preserved. The specimen consists of c. 8 flat whorls, with relative flat suture, positioned obliquely to the shell axis. The teleoconch bears more or less regular but weak growth lines, positioned obliquely to the shell axis. The protoconch is small and has a tip-like ("Zipfel-förmig") shape. The height of the specimen is c. 7 mm.

Discussion: Because of the incomplete preservation, especially lacking the taxonomic important apertural characters, a species determination is presently not possible. However, it seems to represent a distinct taxon from both *Tryptichia* spp. above.

Paleoecology: As *T. kleini* above.

Clausiliidae J.E. Gray, 1855

***Pseudidyla* O. Boettger, 1877**

***Pseudidyla moersingensis* (O. Boettger, 1877) (Fig. 3.9)**

1872 *Clausilia mörsingensis* – SANDBERGER: 598 [nomen nudum].

1877 *Clausilia mörsingensis* SANDBERGER – O. BOETTGER: table 2, fig. 32a–d.

2018 *Pseudidyla moersingensis* (O. BOETTGER, 1877) – HÖLTKE et al., fig. 4.7.

Material: 1 specimen (SMNS 107224). Type material is missing (Salvador et al. 2016).

Type locality: Mörsingen, Baden-Württemberg, Germany**.**

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Small sinistral turreted shell. The only specimen is incompletely preserved, consisting of c. 9¾ more or less regularly-growing flat whorls, with moderately deep sutures. The whorls bear radial ribs which are sometimes a little curved; the ribs begin on the third whorl, being very weak, but grow stronger from the fifth whorl onward. The height of the shell is c. 10 mm.

Paleoecology: Rock walls and trees, on a variety of habitats and climates (Nordsieck 2007).

Succineidae Beck, 1837

***Oxyloma* Westerlund, 1855**

***Oxyloma minima* (Klein, 1853) (Fig. 3.10)**

1853 *Succinea minima* – Klein: 205.

2016 Oxyloma minima (Klein, 1853) – Salvador et al.: 30-31, pl. 6, fig. 13.

2018 *Oxyloma minima* (Klein, 1853) – Höltke et al., fig. 4.1.

Material: 2 specimens (syntypes, SMNS 106410), 1 specimen (SMNS 15817, Gottschick collection), 3 specimens (SMNS 1973/2008, Miller collection).

Type locality: Near Mörsingen, Baden-Württemberg, Germany

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Small succineiform shell with a pointed ovoid shape. It consists of 2½ to 2¾ whorls increasing rapidly in size; the last whorl is very broad (up to 90% of total height). The suture is relatively deep. The height of the aperture is c. 75% of total shell height. The aperture is ovoid. The periostome is simple and sharp. The teleoconch is covered with thin growth lines. The protoconch (c. 1 whorl) is convex and has a blunt apex; it lacks sculpture. The maximum height of the examined specimens is c. 10 mm.

Paleoecology: Shore of rivers or lakes, often on very wet ground (Wiese 2014).

Ferussaciidae Bourguignat, 1883

***Cecilioides* Férussac, 1814**

***Cecilioides aciculella* (Sandberger, 1872) (Fig. 3.11)**

1853 *Achatina*? *acicula* – Klein: 215 [nomen nudum].

1872 *Caecilianella aciculella* Sandberger – Sandberger: pl. 29, fig. 15.

1875 Caecilianella aciculella Sandberger – Sandberger: 595.

2018 *Cecilioides aciculella* (Sandberger, 1872) – Höltke et al., fig. 4.9.

Material: 1 specimen (SMNS 107225). Type material is lost (Salvador et al. 2016).

Type locality: Birk near Mörsingen, Baden-Württemberg, Germany.

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Typical, tower-like shape similar to Recent *Cecilioides* spp. It has a blunt apex and c. 5¼ whorls. Whorls are only slightly convex, with a relative flat suture. The specimen is c. 3 mm high.

Paleoecology: Subterranean, in leaf litter, soil and among roots (Wiese 2014).

Subulinidae Fischer & Crosse, 1877

***Opeas* Albers, 1850**

***Opeas minutum* (Klein, 1853) (Figs. 3.12, 5.2, 5.3)**

1853 *Bulimus minutus* – Klein: 212, pl. 5, fig. 9.

1875 *Subulina minuta* – Sandberger: 596, pl. 29, fig. 16.

2018 *Opeas minutum* (Klein, 1853) – Höltke et al., fig. 4.10.

Material: 3 specimens (SMNS 67.042, Jooss collection), 1 specimen (SMNS 15817, Gottschick collection). Type material is lost (Salvador et al. 2016).

Type locality: Herzogtum, Baden-Württemberg, Germany.

Type stratum: Likely *Silvana*-beds, Middle Miocene.

Description: Spindle-shaped shell with c. 6 regularly growing whorls. The whorls are convex with an obliquely running deep suture. The periostome is simple and sharp. The aperture is obliquely pear shaped. Parietal callus present. The slit-like umbilicus is covered by the reflected columellar margin of the peristome. The teleoconch is sculptured by more or less regularly arranged straight to slightly curved growth lines, which are only visible under magnification (Pl. 4, Fig. 3). The protoconch consists of c. 1½ whorl, lacks sculpture, and has a bulbous shape. The height of specimen is c. 5 mm.

Paleoecology: Recent congeners are found in warm climates, in tropical and subtropical regions worldwide, living in leaf litter (Zilch 1959–1960; Willig et al. 2013).

Oleacinidae H. Adams & A. Adams, 1855

***Pseudoleacina* Wenz, 1914**

***Pseudoleacina eburnea* (Klein, 1853) (Fig. 3.13)**

1853 *Glandina eburnea* – Klein: 213, pl. 5, fig. 10.

1923 *Poiretia eburnea* (Klein) – Wenz: 857.

2016 *Pseudoleacina eburnea* (Klein, 1853) – Salvador et al.: 24, pl. 3, fig. 18.

2018 *Pseudoleacina eburnea (*Klein*,* 1853) – Höltke et al., fig. 4.12.

Material: 1 specimen (lectotype, SMNS 106386-a, designated by Salvador et al. 2016), 3 specimens (paralectotypes, SMNS 106386-b), 1 specimen (SMNS 107226).

Type locality: Near Mörsingen, Baden-Württemberg, Germany.

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Spindle-like shell with blunt apex and c. 5 whorls. Whorls are flat in profile and rapidly growing, resulting in a tall last whorl. Sutures flat. The last whorl runs obliquely downwards before reaching the aperture. The aperture occupies about half of the total shell height and it is slightly pear-shaped. The periostome is simple and sharp. The palatal margin runs down in a more or less straight manner. Umbilicus absent. The columellar forms a kind of spout approximately 1 mm above the shell basis. The shell bears very fine, slightly irregularly-arranged prosocline growth lines that are somewhat irregular. The protoconch is relatively large and bulbous, of c. 2 whorls, lacking sculpture. Maximum shell height is c. 11 mm.

Discussion: Gottschick (1911), when describing *P. eburnea*, noted that the species presented no spiral lines on its teleoconch, a fact that was later questioned by Lueger (1981). The present specimens, including the types, all lack spiral sculpture, in line with the observations of Gottschick (1911).

Paleoecology: Freshwater shore area and woods (Lueger 1981).

***Pseudoleacina kleiniana* (Pilsbry, 1909) (Fig. 3.14)**

1853 *Achatina elegans* – Klein: 214, pl. 5, fig. 11 [nomen nudum].

1909 *Poiretia kleiniana* – Pilsbry: 112.

2018 *Pseudoleacina kleiniana* (Pilsbry, 1909) – Höltke et al., fig. 4.13.

Material: 1 specimen (SMNS J67.037). Type material is lost (Salvador et al. 2016).

Type locality: Herzogtum, Baden-Württemberg, Germany.

Type stratum: Unknown, possibly *Silvana*-beds, Middle Miocene.

Description: Slender spindle-like shell with c. 4½ whorls. Whorls flat and rapidly growing; last whorl c. 75% of total shell height. Suture deep, obliquely positioned in relation to shell axis. The aperture is not fully preserved but the periostome seems to be simple and sharp. The aperture is narrow, oblique and slightly pear-shaped, higher than wide. The columella forms, on its base, a kind of spout. The teleoconch bears regularly-arranged prosocline growth lines. The protoconch has a blunt apex and a bulbous shape, consisting of c. 2 whorls and lacking sculpture. Examined specimen is 9 mm high.

Discussion: The slender shape and the relative distinct (under magnification) growth lines allows easy distinction from *Pseudoleacina eburnea*.

Paleoecology: See *P. eburnea* (Klein, 1853).

***Poiretia* Fischer, 1883**

***Poiretia taurinensis* (Sacco, 1886) (Fig. 3.15).**

1886 *Glandina taurinensis* – Sacco: 459, pl. 2 fig. 3.

2018 *Poiretia taurinensis* (Sacco, 1886) – Höltke et al., fig. 4.14.

Material: 1 specimen (SMNS 16635).

Type locality: Piemont, Italy (Sacco 1886).

Type stratum: Uncertain, Tertiary (Sacco 1886).

Description: Spindle-like, dextral shell. The flat whorls are rapidly growing resulting in a very high last whorl. This takes c. 88% of the total shell height. The sutures are flat. The last whorl doesn`t turn down before reaching the aperture. The height of the aperture takes more than the half (64%) of the total shell height. The periostome is simple and sharp. The aperture has a vertical elongated shape. No umbilicus is present. The columellar forms a kind of spout on its base. The teleoconch bears hardly visible, more or less regularly arranged prosocline growing

lines. However, on the last whorl they become even harder to detect. The protoconch is very flat and consists of c. 1 whorl. It lacks of scuplture.

The size of the determined specimen is 17 mm high and 8 mm wide at the widest point.

Paleoecology: According to Fechter & Falkner (1989), the only European species of *Poiretia* lives at the Adriatic coast from Monfalcone to Albania, as well as on the Gargano-Peninsula.

Helicodiscidae Pilsbry, 1927

***Lucilla* Lowe, 1852**

***Lucilla subteres* (Clessin, 1885) (Fig. 3.16)**

1885 *Patula subteres* – Clessin: 76, pl. 7, fig. 6.

2018 *Lucilla subteres (*Clessin*,* 1885) – Höltke et al., fig. 5.1.

Material: 2 specimens (SMNS 15817, Gottschick collection.

Type locality: Nittendorf (Undorf), Bavaria, Germany. Syntype (SMNS J68.501).

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Discoidal shell with relative low spire, of c. 4¼ regularly growing convex whorls. Suture remarkably deep. The periostome is simple and sharp; the two insertions are connected by a thin callous layer. The umbilicus is very wide, taking approximately 40% of the total shell width. The teleoconch bears more or less regularly-arranged fine growth lines. The protoconch is smooth and consists of c. 1½ whorl. Maximum diameter of the shell is c. 2 mm.

Paleoecology: Recent *Lucilla* spp. live in several kinds of habitats (see Kerney et al. 1983), making them innapropriate for paleoecology.

Discidae Thiele, 1931

***Discus* Fitzinger, 1833**

***Discus wenzi* (Jooss, 1918) (Fig. 3.17)**

1918 *Pyramidula wenzi* – Jooss: 291.

2016 *Discus wenzi* (Jooss, 1918) – Salvador et al., 40, fig. 2.4.

2018 *Discus wenzi* (Jooss, 1918) – Höltke et al., fig. 5.4.

Material: 1 specimen (syntype, SMNS 106447).

Type locality: Mörsingen, Baden-Württemberg, Germany.

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Discoidal shell, with elevated spire and c. 5¼ convex whorls, regularly increasing in size. The suture is remarkable deep. The aperture is of crescent shape. The periostome is sharp and simple. Umbilicus deep and wide. The teleoconch bears regularly-arranged distinct and pronounced prosocline ribs that extend into the umbilicus. The distance between ribs is approximately twice their width. The protoconch has a slightly bulbous shape and consists of c. 1¼ whorl, bearing no sculpture. The specimen is c. 4 mm in diameter.

Discussion: *Discus wenzi* can be distinguished from *D. euglyphoides* (Sandberger, 1872) by its more rounded base, smaller diameter, less prominent angulation (keel), higher spire, and more bulbous protoconch. Similarly, *D. wenzi* can be distinguished from *D. pleuradrus* (Bourguignat, 1881) by its higher spire, more prominent angulation on the body whol, and stronger ribs on the abapical portion of the body whorl.

Paleoecology: Extant congeners live in moist habitats like forests, mostly under stones or wood (Kerney et al. 1983; Welter-Schultes 2012).

***Discus euglyphoides* (Sandberger, 1872) (Fig. 3.18)**

1872 *Patula euglyphoides* – Sandberger: pl. 31, fig. 1.

1875 *Patula euglyphoides* – Sandberger: 583.

2018 *Discus euglyphoides* (Sandberger, 1872) – Höltke et al., fig. 5.2.

Material: 1 specimen (SMNS J65.809), 1 specimen (SMNS J65.806).

Type locality: Sandberger (1875) mentioned different localities. The specimens illustrated by him were from Leisacker near Neuburg an der Donau, Bavaria, Germany.

Type stratum: Probably *silvana*-beds, Middle Miocene.

Description: Discoidal shell with low spire, of c. 5 convex whorls increasing regularly in size. Suture is deep. The last whorl with a very pronounced keel, which runs up to the aperture but gets weaker a few millimeters before reaching it. The upper part of the last whorl runs ramp-like downwards to the keel. Below this keel, a very slight and narrow spiral channel has formed, which disappears when the keel gets weaker towards the aperture. Umbilicus deep and wide. The periostome is sharp and simple. The aperture has an obliquely-oval shape. The teleoconch bears regularly–arranged well-marked ribs, which extend in more or less uniform thickness into the umbilicus. The distance between ribs are c. twice their width. The protoconch has a slightly bulbous shape, having c. 1¼ whorl and lacking sculpture. The width of the specimen is c. 4.2 mm.

Discussion: See above for diagnosis from *D. wenzi*. *Discus euglyphoides* can be distinguished from *D. pleuradrus* by its prominent keel and flatter body whorl profile, as well as the stronger ribs on the abapical portion of the body whorl.

Paleoecology: As *D. wenzi* above.

***Discus pleuradrus* (Bourguignat, 1881) (Fig. 3.19)**

1881 *Helix pleuradra* – Bourguignat: 53, pl. 3, figs. 67-72.

2018 *Discus pleuradrus* (Bourguignat, 1881) – Höltke et al., fig. 5.3.

Material: 4 specimens (SMNS J65.787).

Type locality: Sansan, France.

Type stratum: Freshwater limestones of Sansan, Middle Miocene.

Description: Discoidal shell of c. 4 convex whorls, regularly increasing in size. The suture is deep. The aperture is oval to semicircular shape. The periostome is simple and sharp. Umbilicus deep and wide. The teleoconch bears well-marked prosocline ribs which are regularly arranged. On the abapical portion of the shell, these ribs become faint and slightly sigmoidal lines; towards the umbilical edge, the ribs become more strongly-marked again. The protoconch is bulbous, consisting of c. 1 whorl and lacking sculpture. The specimen is c. 4 mm wide.

Discussion: See above for diagnosis from the other *Discus* spp. that occur in Mörsingen.

Paleoecology: As *D. wenzi* above.

Oxychilidae Hesse, 1927

***Aegopinella* Lindholm, 1927**

***Aegopinella subnitens* (Klein, 1853) (Figs. 3.20, 5.1)**

1853 *Helix subnitens* – Klein: 210, pl. 5, fig. 7.

2018 *Aegopinella subnitens* (Klein, 1853) – Höltke et al., fig. 5.5.

Material: 5 specimens (SMNS J65.679, Jooss-collection), 6 specimens (SMNS J65.690, Jooss collection), 1 specimen (SMNS 107227).

Type locality: Zwiefalten, Baden-Württemberg, Germany.

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Flat shell of 4¼ whorls, with slightly raised spire. The whorls increase rapidly in size, resulting in a large and strongly convez last whorl. The suture is reasonably deep. The aperture is oblique and ovoid. The peristome is thin and sharp. Callus absent. Umbilicus open and wide; its width c. 33% of total shell width; margins of the umbilicus run obliquely abapically. The teleoconch bears very fine, regularly-arranged, prosocline growth lines, only visible under strong magnification. The protoconch is flat, smooth, and consists of c. 1–1¼ whorl. The maximum diameter of the examined specimens is c. 12 mm.

Discussion: Sandberger (1875) pointed out that the present species could represent juveniles of *Aegopinella orbicularis* (Klein, 1846) and, hence be synonymous with it. The original material of the latter, however, shows a narrower last whorl then the specimens discussed here. Also, the relative large size of *A. subnitens* when compared to its congener factors in favor of them being adult specimens. The shells of extant members of Oxychilidae often look very similar and identification without anatomical features is often difficult (Forcart 1957), especially with only a small series of specimens available.

Paleoecology: Typically moist habitats (Welter-Schultes 2012; Wiese 2014).

***Aegopinella moersingensis* n. sp. (Fig. 3.21; Fig. 4.14)**

Type material: Holotype, SMNS 107228 (Jooss collection).

Type locality: Mörsingen, Baden-Württemberg, Germany.

Type stratum: *Silvana*-beds, Middle Miocene.

Age: Karpatian–Badenian (MN5).

Etymology: The specific epithet alludes to the provenance of the species.

Diagnosis: Shell less wide (more compact), with a more elevated spire than congeners. Aperture ovoid, almost circular, positioned more obliquely (abapically).

Description: Slightly discoidal dextral shell, with relatively elevated spire for genus, of c. 4¾ whorls. Suture flat, well-marked. Whorls convex and somewhat rapidly growing. Body whorl presents a slight peripheral angulation near its base; from the suture to said angulation, the body whorl runs ramp-like abapically. Aperture obliquely ovoid in shape, nearly circular; periostome not completely preserved but seemingly simple and not reflected. Umbilicus deep, cylindrical, wide, taking c. 25% of shell width. Teleoconch bearing delicate and more or less regularlyarranged growth lines, which become fainter on the base of the shell. Protoconch blunt, flat, of c. 1½ whorl; it presents a rough surface, but it is unclear if thatdue to fossilization process. Holotype is 10 mm wide and 8 mm high.

Discussion: The only specimen available had a manuscript name (*A. subnitens elatior*) written on its label by Jooss, probably in 1912. We agree with Jooss that the present specimen is distinct enough from nominate *subnitens*, and propose the new species *Aegopinella moersingensis* n. sp. to allocate it. We refrain from using Jooss' manuscript name due to the pervasiveness of the epithet *elatior* among closely-related s *Aegopinella moersingensis* n. sp. differs from *A. subnitens* by its higher spire and the more obliquely positioned aperture, ovoid but almost circular in shape. It further differs from other Miocene *Aegopinella* spp. by its much higher spire, such as *A. denudata* (Reuss in Reuss & Meyer, 1849) (see Harzhauser et al. 2014: fig. 14D-G), *A. reussi* (Hörnes,1856) (see Harzhauser & Binder 2004: pl. 11, figs. 5-7), *A. vetusta* (Klika, 1891) (see Harzhauser et al.

2014: fig. 15A-C), *A. erecta* (Gottschick, 1920a) (see Höltke & Rasser 2017: fig. 3.18), and *A.*? *procellaria* (Jooss, 1918) (see below). Presently, *A. moersingensis* n. sp. is known only from Mörsingen.

Paleoecology: As *A. subnitens* above.

***Aegopinella*? *procellaria* (Jooss, 1918) (Fig. 3.22)**

1918 *Hyalina procellaria* – Jooss: 289.

2016 *Aegopinella*? procellaria (Jooss, 1918) – Salvador et al.: 32, pl.7, fig. 8.

2018 *Aegopinella? procellaria* (Jooss, 1918) – Höltke et al., fig. 5.6.

Material: 2 specimens (syntypes, SMNS 106419).

Type locality: Mörsingen, Baden-Württemberg, Germany.

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Discoidal flat shell, of c. 4¼ convex whorls, rapidly increasing in size. The last whorl builds up a very faint angulation. The suture is relatively deep. Directly below the suture, the whorls are flattened and form a kind of concave indentation (best observed on the last whorl). The aperture is oval shaped, positioned almost horizontally. The periostome is simple and sharp; the two insertions are connected by a thin callus. The umbilicus is deep and relatively narrow, taking only 14% of the total shell width. The teleoconch is smooth apart from barely perceptible growth lines. The protoconch is flat and smooth, of c.1½ whorl. The diameter of the shell is c. 8 mm.

Discussion: The systematic position of this species remain uncertain (Nordsieck 2014; Salvador et al. 2016)

Paleoecology: Uncertain, but presently it can be considered similar to *A. subnitens* (see above).

Gastrodontidae Tyron, 1866

***Janulus* Lowe, 1852**

***Janulus moersingensis* Jooss, 1918 (Fig. 3.23; Fig. 5.6)**

1918 *Janulus moersingensis* – Jooss: 289.

2016 *Janulus moersingensis* Jooss, 1918 – Salvador et al.: 31, pl. 6, fig. 15.

2018 *Janulus moersingensis* Jooss, 1918 – Höltke et al., fig. 5.8.

Material: 1 specimen (holotype, SMNS 106411), 1 specimen (SMNS J65.737, Jooss collection).

Type locality: Mörsingen, Baden-Württemberg, Germany.

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Small discoid shell with a flat spire, of c. 6 convex whorls, regularly increasing in size. The suture is remarkable deep. Shortly before the aperture, the last whorl slowly turns downwards. The periostome is simple and sharp; thin callus present. The aperture is crescent shape. The open and deep umbilicus takes c. 20% of the total shell width; its margins steeply run to the interior. The teleoconch bears regularly-arranged and closely-packed prosocline ribs; distance between ribs approximately their width. On the beginning of the teleoconch, the ribs are only weakly pronounced; after c. ¼ whorl, they become stronger and more distinct. The protoconch is flat, smotth, of c. 1½ whorls. The width of the shell is c. 6 mm.

Discussion: The present species is smaller than the similar and coeval *J. supracostatus*, also having c. 1 whorl less (Jooss 1918).

Paleoecology: Extant congeners live only on the Canary Islands and Madeira, in leaf litter or rocks among shrubs, ferns and trees in well-vegetated areas (Zilch 1959-1960; Seddon 2008).

Archaeozonitidae Pfeffer, 1930

***Archaeozonites* Sandberger, 1872**

***Archaeozonites costatus* Sandberger, 1875 (Fig. 4.1)**

1875 *Archaeozonites costatus* – Sandberger: 604.

2018 *Archaeozonites costatus* Sandberger, 1875 – Höltke et al., fig. 5.10.

Material: 5 specimens (SMNS 15817, Gottschick collection), 1 specimen (SMNS 2016/2008, Jooss-collection). 1 specimen (SMNS 17455). Type material is lost (Salvador et al. 2016).

Type locality: Mörsingen, Baden-Württemberg; Häder & Kutzenhausen (Dinkelscherben), Gutgrieder Graben near Peissenberg, Bavaria.

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Helicoid shell, of ca. 5 flattened and regularly growing whorls. The last whorl forms a distinct keel on its middle section, which extends to the aperture. The adapical part of the last whorl runs ramp-like down to the keel; abapical part convex. The suture is flat. The aperture has an oval shape, obliquely position in relation to shell axis. The periostome is simple and sharp. Umbilicus deep, with steep margins, taking about 20% of total width of shell. Above the keel line, the teleoconch is covered with distinct and regularly arranged prosocline ribs; below the keelthese are much more weakly marked. The protoconch is flat, smooth, relatively small, consisting of c. 1 whorl. The width of the shell is c. 16 mm.

Paleoecology: Probably forested areas (Binder 2002).

Helicodontidae Kobelt, 1904.

***Protodrepanostoma* Germain, 1929**

***Protodrepanostoma involutum* (Thomae, 1845) (Figs. 4.2; 4.13)**

1845 *Helix involuta* – Thomae: 144, pl. 2, fig. 8.

1872 *Helix scabiosa* – Sandberger: 584.

1923 *Helicodonta involuta involuta* (Thomae) – Wenz: 447.

1923 *Helicodonta involuta scabiosa* (Sandberger) – Wenz: 452.

2018 *Protodrepanostoma involutum* (Thomae, 1845) – Höltke et al., fig. 6.1.

Material: 8 specimens (SMNS 1957/2008), 1 specimen (SMNS 15817, Gottschick collection).

Type locality: Hochheim am Main, Hesse, Germany.

Type stratum: Upper Oligocene (Schäfer 2014).

Description: Discoid shell with flat sunken spire, of 4¾ slightly convex whorls, slowly increasing in size. Suture are very deep. The last whorl turns slowly down shortly before reaching the aperture. Aperture is crescent shape. The periostome is reflected, shield-like. Callus absent. The deep wide umbilicus takes c. 35% of the total shell width. The teleoconch bears distinct and dense regularly-arranged axial ribs. The slightly bulbous protoconch consists of c. 1¼ whorl, smooth, increasing rapidly in size (already after ¼ whorl, it reaches its maximum size). The width of the specimen is c. 4.5 mm.

Discussion: Specimens from the *silvana*-beds have been typically identified as *P. scabiosum*, which is sometimes (see synonymy above) treated as a subspecies of *P. involutum*, which is otherwise known from the late Oligocene to Early Miocene of Hochheim and Wiesbaden, Hesse, Germany. Previous authors (Clessin 1885; Gottschick & Wenz 1916) pointed out differences in the width of the umbilicus and the shell height to justify the separation in two subspecies or two species. However, in a large series of specimens in the SMNS (see synonymy above for

recent works), it becomes evident that this is just a small intraspecific variation and that there are in fact no meaningful conchological differences between *involutum* and *scabiosum*. Following Salvador et al. (2015), we consider *P. scabiosum* a junior synonym of *P. involutum*.

Paleoecology: Forests and hedges (Kerney et al. 1983).

?Helicodontidae Kobelt, 1904

Miodiscula Nordsieck, 2014

***Miodiscula disciformis* (Wenz, 1923) (Fig. 4.3)**

1919 *Helicodonta disciformis* – Wenz: 72.

1924 *Canariella disciformis* – Wenz: 16, pl. 2, figs. 1– 3.

2018 *Miodiscula disciformis* (Wenz, 1923) – Höltke et al., fig. 6.2.

Material: 2 specimens (SMNS J66.244, Jooss collection).

Type locality: Mörsingen, Baden-Württemberg, Germany.

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Slightly discoidal to somewhat heloic shell, with a medium-high spire, of c. 5¼ regularly growing whorls. Suture flat. Last whorl with a distinct angulation. Umbilicus open, small. Aperture elliptical. The teleoconch bears a widespread granulation, which is only visible under high magnification; portions of this granulation form larger knobs. Protoconch is apparently smooth and flat, but preservation state preclude the observation of exact number of whorls. The largest specimen is 13 mm wide and 9 mm high.

Discussion: Mörsingen is the type locality for this species (Wenz 1924), which was established as a new name for the preoccupied *Helix nummulina* Mayer-Eymar *in* Sandberger (1875). Originally assigned to the genus *Canariella* Hesse, 1918, this species was later transferred to *Miodiscula* Nordsieck, 2014, but its family allocation remains uncertain.

Paleoecology: As an extinct genus of unknown affinities, the present species cannot be used for paleoecological interpretations.

***Miodiscula miocaenica* (Gottschick & Wenz, 1927) (Fig. 4.4)**

1927 *Trochoidea miocaenica* – Gottschick & Wenz: 149, pl. 8, fig. 3.

2016 *Miodiscula miocaenica* (Gottschick & Wenz, 1927) – Salvador et al.: 31, pl. 6, fig. 14.

2018 *Miodiscula miocaenica* (Gottschick & Wenz, 1927) – Höltke et al., fig. 6.3.

Material: 1 specimen (syntype, SMNS 15817-131), 1 specimen (SMNS J68.551, Jooss collection).

Type locality: Mörsingen, Baden-Württemberg, Germany.

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Flattened helicoid shell, of c. 4¼ convex whorls. The last whorl builds up a remarkable and distinct keel in the middle of it. This keel runs up to the aperture. Below the suture, the upper part of the last whorl runs downward to the keel in a c. 45° angle. The last whorl reaches the aperture without turning down. The sutures are moderately deep. The periostome is not completely preserved but seems to be sharp and simple and not reflected. The two insertions are connected by a callous layer. However, only a remnant of this are already visible. The small umbilicus is slit-like to crescent shaped. It is slightly covered by a columellar callus. The teleoconch bears regularly arranged prosocline growing lines. On the first teleoconch whorls this growing lines are only weakly pronounced. They are getting stronger on the later ones. On the lower side of the shell, these growing lines are also only very faint. On the same side there is a hardly visible pattern of regularly arranged elongated-oval

shaped platelets. These platelets are also present on the other parts of the teleoconch but here they are even weaker and harder to see. The bulbous protoconch bears c. 1 ¼ whorls. It lacks of sculpture. The width of the shell is c. 5 mm.

Paleoecology: As *M. disciformis* above.

Elonidae Gittenberger, 1979

***lApula* C. R. Boettger, 1909**

***Apula coarctata* (Klein, 1853) (Fig. 4.5)**

1853 *Helix coarctata* – KLEIN: 206, pl. 5, fig. 3

1911 *Klikia coarctata* KLEIN –WENZ: 92, pl. 4, figs. 16–20.

Material: 9 specimens (SMNS J66.296, Jooss collection), 2 specimens (SMNS J66.296, Jooss collection). Type material is lost (Salvador et al. 2016).

Type locality: Mörsingen, Baden-Würrtemberg, Germany.

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Flat dextral shell with low spire. The shell has c. 5 whorls. The whorls are convex and show a regular increase in size. The suturs are comparablely flat. The last whorl has a very slightly keel which disappear shortly before the aperture. Shortly before the aperture, the last whorl slowly turns down. The aperture has a horseshoe-like shape and the peristome is reflected. The height of the aperture is c. ¾ of the total shell height. The insertions are connected by a thin callous layer. The umbilicus is closed by a columellar callus. The teleoconch bears very fine growing lines. The protoconch has a slightly bulbous shape and consists of c. 1.5 whorls. The embryonic whorls have hardy visible, regularly arranged rips on the surface. This can only be seen on some very well preserved specimens. The maximum shell diameter of the examined specimens is c. 12 mm.

Paleoecology: The genus likely inhabited a variety of habitats (Lueger 1981).

***Klikia* Pilsbry, 1895**

***Klikia catantostoma* (Sandberger, 1872) (Fig. 4.6; Fig. 5.5)**

1872 *Helix catantostoma* – Sandberger: pl. 29, fig. 6.

1875 *Helix catantostoma* – Sandberger: 587.

2018 *Klikia catantostoma* (Sandberger, 1872) – Höltke et al., fig. 6.5.

Material: 2 specimens (SMNS J66.304, Jooss collection), 2 specimens (SMNS J66.302, Jooss collection).

Type locality: Emerberg near Zwiefalten, Baden-Württemberg, Germany.

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Helicoid, dextral shell with very low spire. The 5 ¼ whorls grow slowly but in a regularly manner. The sutures are comparable flat. The whorls are convex and the last one builds up a slightly keel which disappeared in the last quarter of the whorl. The last whorl runs more or less straight up to the aperture. This is horseshoe-shaped with a reflected peristome. The two insertions seemed to be originally connected by a callous layer. Only remnants of this layer were preserved. The open and deep umbilicus is c. 1 mm in diameter. The umbilicus margins are running obliquely downwards and the umbilicus tapers in the deep. It is only little covered by the reflected columellar margin. The teleoconch is covered by regularly arranged, prominent small papillae which can only be seen under magnification. The slightly bulbous protoconch bears unregularly arranged folds and consists of c. 1 ¼ to 1.5 whorls. The maximum size of the examined specimens is c. 13 mm.

Paleoecology: The genus likely inhabited dry habitats (Lueger 1981).

***Klikia giengensis* (Klein, 1846) (Fig. 4.7)**

1846 *Helix giengensis* Krauss – Klein: 69, pl. 1, fig. 9.

1911 *Klikia giengensis* Krauss – Wenz: 85, pl. 4, figs. 6–8.

Material: 22 specimens (SMNS J66.276). Type material is lost (Salvador et al. 2016).

Type locality: Neue Steige near Hohenmemmingen and Michelsberg near Ulm, Baden-Württemberg, Germany.

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Small helicoid, dextral shell. There is a disparity in the shell height within this species. The shell consists of five whorls which grow in a regularly manner. They are convex and the sutures are relatively deep. The last whorl runs straight up to the aperture. This has a horseshoe-like shape. The peristome is distinctly reflected. The two insertions are connected by a thin callus. The width of the umbilicus reaches c. 33% of the total width. It is open and relative deep. The walls of the umbilicus are inclining downwards very weakly. The protoconch is small and consists of c. 1 whorl. It has no sculpture. The width of the shell is c. 9.4 mm.

Discussion: The species seems to have died out after the Mammal Zone MN5; it is not present in later OSM deposits (see also Wenz 1911).

Paleoecology: As *K. catantostoma* above.

***Klikia osculina* (Sandberger, 1875) (Fig. 4.8)**

1875 *Helix osculina* – Sandberger: 585.

2018 *Klikia osculina* (Sandberger, 1875) – Höltke et al., fig. 6.7.

Material: 1 specimen (SMNS J.66.251).

Type locality: Altheim near Ehingen/Donau, Baden-Württemberg, Germany.

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Dextral, helicoid shell with regularly increasing whorls. It consists of 4 ¾ whorls. The sutures of the two last whorls are moderately deep. The first whorls of the teleoconch have a much deeper suture. The last whorls runs straight up to the aperture without turning down. The aperture has an obliquely, horseshoe-like shape. The periostome is not completely preserved but seems to be reflected. The small umbilicus takes only 13 % of the total shell width. The umbilicus margins are obliquely running downwards. As it seems, the umbilicus was probably partly covered by a reflected columellar margin. The teleocnch bears regularly arranged small papillae as well as slightly irregular growing lines. The protoconch has a bulbous shape and consists of c. 1 whorl; lacks sculpture. The width of the shell is c. 8.6 mm.

Discussion: This species was not originally illustrated (Sandberger 1875). The present specimens, considering general morphology and teleoconch sculpture, fit well with the revision of Wenz (1911).

Paleoecology: As *K. catantostoma* above.

Hygromiidae Tyron, 1866

***Leucochroopsis* O. Boettger, 1908**

***Leucochroopsis kleinii* (Klein, 1846) (Fig. 4.9).**

1846 *Helix kleini* Krauss – Klein: 69, pl. 1, fig. 8.

Material: 25 specimens (SMNS 107229, Bechter collection), 6 specimens (SMNS J 65949, Jooss collection). Type material is missing (Salvador et al. 2016).

Type locality: Neue Steige near Hohenmemmingen, Baden-Württemberg, Germany.

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Helicoid shell ranging from higher to more flattened forms, of 4¾ to 5¼ whorls, rapidly increasing in size. The height of the last whorl takes c. 80% of the total shell height. The whorls are convex and the last one builds up a slight keel, which can vary intraspecifically from weak to strong. The suture is shallow in flatter specimens, but deeper in high-spired ones. The last whorl turns slightly downwards shortly before reaching the aperture. The aperture has a horseshoe-like shape. The periostome is simple and sharp. In the umbilicus region, the columellar margin is slightly reflected. Thin callus present. The small umbilicus is rimate, half covered. The teleoconch bears sometimes fine growing lines, often with regularly-arranged papillae on the shell surface (the papillae are not distributed evenly in each specimen and sometimes they are only present on the base of the shell). The convex protoconch is small and smooth, consisting of c. 1–1¼ whorl. The maximum shell diameter is c. 10 mm.

Discussion: Even though Lueger (1981) mentioned that the holotype would be in the SMNS collection, it could not be found in that institution and is considered lost (Salvador et al. 2016).

Paleoecology: Moist forested habitats (Lueger 1981).

Helicidae Rafinesque, 1815

***Pseudochloritis* C. R. Boettger, 1909**

***Pseudochloritis incrassata* (Klein, 1853) (Fig. 4.10)**

1853 *Helix incrassata* – Klein: 208, pl. 5, fig. 6.

1856 *Helix zelli* – von Kurr: 39.

2008 *Pseudochloritis incrassata* (Klein, 1853) – Binder: 172, pl. 3, figs. 2-3.

2018 *Pseudochloritis incrassata* (Klein, 1853) – Höltke et al., fig. 6.14.

Material: 16 specimens (SMNS 107230, Bechter collection).

Type locality: Zwiefaltendorf, "Bei der Birk", Baden-Württemberg, Germany. Possible syntypes: SMNS 22737 (Salvador et al. 2016).

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Helicoid low-spired shell (a few specimens can be more conical), of 4½ regularly–growing convex whorls. Suture deep. The last whorl turns obliquely abapically shortly before reaching the aperture. After an extralabial depression, the periostome increases in width, thickens, and reflects. The aperture has a crooked oval shape. Medium thick callous present. The umbilicus is deep, partially covered by the reflected columellar margin; its width is c. 15% of the total shell width. The teleoconch bears fine ribs and the microsculpture consists of little oval platelets. The protoconch also has these platelets, comprising c. 1¼ whorls. The maximum shell width in Mörsingen is c. 30 mm.

Discussion: The species has a high variability regarding the height of the spire and of the overall shell. For this reason, there are a lot of synonyms in the literature, like *Helix zelli* von Kurr, 1856. For a detailed discussion about this species see Binder (2008).

Paleoecology: As an extinct genus, it is difficult to assume its habitat preferences. However, previous authors have suggested, based on shell shape, that it inhabited open and dry habitats (Binder 2008; Moser et al. 2009).

***Palaeotachea* Jooss, 1912**

***Palaeotachea silvana* (Klein, 1853) (Fig. 4.11)**

1853 *Helix silvana* – Klein: 205, pl. 5, fig. 2.

2016 *Palaeotachea silvana* (Klein, 1853) – Höltke & Rasser: 244, fig. 5.5.

Material: 26 specimens (SMNS 107231, Bechter collection).

Type locality: Zwiefalten, Baden-Württemberg, Germany.

Type stratum: *Silvana*-beds, Middle Miocene.

Description: Helicoid shell with typical "*Cepaea*" shape, of 4¼ convex whorls, regularly growing in size. The shell shape ranges from low- to high-spired forms. The last whorl forms a very faint angulation that disappears c. ½ whorl before the aperture. The last whorl turns obliquely abapically shortly before reaching the aperture. The aperture has an oval shape. The periostome is reflected. Callus present. The umbilicus is covered by a columellar callus. On the columellar margin, there is often a knob-shaped thickening, the strength of which varies intraspecifically. The teleoconch bears very fine regularly-arranged growth lines. The relative flat protoconch consists of c. 1½ whorl and lacks sculpture. The average shell width in Mörsingen is c. 16 mm.

Discussion: This species is the index fossil of the *silvana*-beds and is often confused with the younger and similar *P. sylvestrina* (Schlotheim, 1820). Given the morphological variation within both species, they are difficult to distinguish. Apart from the biostratigraphy, the angle of spire can help identifying them: *P. silvana* has an average angle of around 100°, whereas in *P*. sylvestrina this value lies around 117° (Höltke & Rasser 2016).

Paleoecology: This species probably lived like the morphologically similar extant *Cepaea* spp. However, this genus is euryoecious (Lueger 1981) and thus, of limited used in paleoecology.

***Palaeotachea turonensis* (Deshayes, 1831) (Fig. 4.12)**

1831 *Helix turonensis* – Deshayes: 139, pl. 1, figs. 1, 2.

1840 *Helix larteti* – de Boissy: 75.

1851 *Helix eversa* – Deshayes *in* Férussac: 395, pl. 1, figs. 5–7.

2018 *Palaeotachea turonensis* (Deshayes, 1831) – Höltke et al., fig. 6.13.

Material: 2 specimens (SMNS J66.818).

Type locality: Touraine, France.

Type stratum: Faluns de Touraine, Miocene.

Description: Relatively large-sized bulbous helicoid shell of typical "*Cepaea"* shape. Shell consisting of 4¾ to 5 convex whorls, which grow in a regular manner. The suture is moderately deep. Before reaching the aperture, the last whorl turns obliquely abapically. The aperture has an oval shape, laterally elongated. The first part of the palatal margin runs more or less straight, while the lower part turns obliquely abapically. The periostome is reflected and remarkably thickened on the inner side. Thick parietal callus present. The umbilicus region is completely covered by columellar callus. The teleoconch bears fine regularly-arranged growth lines. The smooth protoconch consists of c. 1¼ relative flat whorl. Shell c. 24 mm wide.

Discussion: This species is widely distributed in the *silvana*-beds and coeval horizons. In Mörsingen, it is not as frequent as *P. silvana*. According to the literature See Höltke & Rasser 2016), this species seems to have died out in the OSM after the middle *silvana*-beds.

Paleoecology: As *P. silvana* above.

4. Literature records

Hydrobiidae Stimpson, 1865

***Pseudamnicola convexa suevica* (Gottschick, 1928)**

Reported by: Schlickum (1976: 3).

Paleoecology: Likely slow-flowing waters.

Vertiginidae Fitzinger, 1833

***Leucochlia nouletiana* (Dupuy, 1850)**

Reported by: Gottschick & Wenz (1916: 65).

Current allocation: *Gastrocopta nouletiana* (Dupuy, 1850).

Paleoecology: As *Gastrocopta acuminata* above.

Argnidae Hudec, 1965

***Argna oppoliensis* (Andreae, 1902)**

Reported by: Schlickum (1976: 10).

Paleoecology: Forests (Lueger 1981).

Vallonidae Morse, 1864

***Acanthinula trochulus* (Sandberger, 1872)**

Reported by: Gottschick & Wenz (1916: 67).

Paleoecology: Among dead leaves (Lueger 1981).

***Spermodea candida* Falkner, 1974**

Reported by: Schlickum (1976: 18).

Paleoecology: Congeners live in the leaf litter of deciduous forests, often near water (Welter-Schultes 2012; Wiese 2014).

Testacellidae Gray, 1840

***Testacella zelli* Klein, 1853**

Reported by: Wenz (1923: 213).

Paleoecology: In a variety of environments, burrowed in the soil (Fechter & Falkner 1989).

Gastrodontidae Tyron, 1866

***Janulus supracostatus* (Sandberger, 1872)**

Reported by: Wenz (1923: 304).

Paleoecology: As *Janulus moersingensis* above.

***Zonitoides suevicus* (Jooss, 1918)**

Reported by: Schlickum (1976: pl. 5, fig. 67).

Paleoecology: Moist habitats (Wiese 2014).

Hygromiidae Tyron, 1866

***Caracollina phacodes barreri* (Bourguignat, 1881)**

Reported by: Wenz (1923: 465).

Current allocation: *Praeoestophorella phacodes barreri* (Bourguignat, 1881) (see Nordsieck 2014).

Paleoecology: In dry habitats under stones and leave litter; extant congeners live in the Western Mediterranean and Middle Atlantic Islands (Fechter & Falkner 1989).

Clausiliidae J.E.Gray, 1855

***Pseudidyla undatistria* (O. Boettger, 1877**

Reported by: Wenz (1923: 793).

Remarks: Presently considered a nomem dubium (MolluscaBase, 2020).

Paleoecology: As *P. moersingensis* above.

Oleacinidae H. Adams & A. Adams, 1855

***Poiretia gracilis porrecta* (Gobanz, 1854)**

Reported by: Wenz (1923: 846).

Current allocation: *Palaeoglandina porrecta* (Gobanz, 1854).

Paleoecology: Genus died out in Pliocene (Zilch 1959-1960), so the ecology is unknown. Moser et al. (2009) suggested a lifestyle similar to present-day *Euglandina* spp.

Ellobiidae H. Adams & A. Adams in Pfeiffer, 1854

***Carychium nouleti gibbum* (Sandberger, 1872)**

Reported by: Wenz (1923: 1197).

Current allocation: *Carychium gibbum* Sandberger, 1875.

Paleoecology: Extant species can be found in a variety of habitats (Bogon 1990).

5. Conclusion

Overall, 35 different taxa of terrestrial gastropods, as well as nine different freshwater ones could be identified from Mörsingen based on museum and newly-collected specimens. In addition to that, ten additional terrestrial and one freshwater species are mentioned in the literature, albeit with no voucher material remaining. Given that most specimens retrieved from Mörsingen were more accidental finds than focused collection efforts, the presently-available specimens are heavily biased towards larger and sturdier shell.

Among the terrestrial genus-level taxa in Mörsingen, ten are entirely extinct and five are locally extinct in Central Europe today (*Janulus, Gastrocopta, Poiretia, Opeas, Hypnophila*). The remaining taxa have extant relatives present in the extant molluscan fauna of Central Europe. The ecological preferences of the land snails in Mörsingen range from drier habitats (e.g., *Granaria*) to very moist ones (e.g., *Leucochroopsis*), including species that lived in close contact with water bodies (e.g., *Oxyloma*). This indicates that a reasonable variety of habitats would have been present in that locality during the Miocene.

The freshwater snail fauna of Mörsingen includes the genus *Esperiana*, which is exinct in Central Europe today, and *Tinnyea*, a completely extinct genus. The remaining freshwater genera are still present in Central Europe. The vast majority of the species in Mörsingen would have preferred stagnant to slow-moving waters.

Accordingly, the sediments of Mörsingen were deposited in a lake environment surrounded by different terrestrial habitats; the closest area to the lake (judging by the scarcity of specimens of more xerophile species) would be more densily vegetated and humid. Apart from *Celtis* sp., ostracods and remains of freshwater bivalves, snails are the only fossils known from Mörsingen and for now the only ones available to guide the palecologically interpretation. Further studies on the ostracod fauna will certainly provide more information about the freshwater environment.

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Figure legend

Figure 1. Geographic position of Mörsingen.

Figure 2.

1. *Esperiana kleinii* (Kurr, 1856). Scale 5 mm. SMNS 107217.

2. *Tinnyea lauraea* (Matheron, 1842). Scale 10 mm. SMNS 107218.

3. *Pomatias consobrinum* (Sandberger, 1872)**.** Original Material of Fraas 1910. Scale 5 mm. SMNS 107219.

4. *Pomatias conica* (Klein, 1853). Scale 5 mm. SMNS 107220.

5. *Bithynia glabra* (Zieten, 1832). Scale: 1 mm (a); 200 mµ (b). SMNS J68.154.

6. & 7. *Lymnaea turrita* Klein, 1853. Original material to Jooss (1913). 6: Scale 10 mm. SMNS 106408 7: Scale 5 mm. SMNS 106409.

8. *Radix dilatata* (Noulet, 1854). Scale 10 mm. SMNS J67.684.

9. *Planorbarius mantelli* (Dunker, 1848). Scale 10 mm. SMNS 107221.

10. *Gyraulus dealbatus* (Braun, 1851). Scale: 1 mm (a & b); 200 mµ (d). SMNS J67.780.

11. *Segmentina lartetii* (Noulet, 1854). Scale: 1mm (a & b); 100 µm (c); 200 µm (d). SMNS J67.909.

12. *Ferrissia deperdita* (Desmarest, 1814). Scale: 1 mm (a); 200 µm (b). SMNS J67.925.

Figure 3.

1. *Azeca lubricella* O. Boettger, 1870. Scale 2 mm. SMNS J67.234.

2. *Hypnophila* loxostoma (Klein, 1853). Scale 500 µm. SMNS J67.255.

3. *Granaria subfusiformis* (Sandberger, 1875). Scale 2 mm. SMNS 16635.

4. *Gastrocopta acuminata* (Klein, 1846). Scale 1 mm. SMNS J67.427.

5. *Gastrocopta quadriplicata* (Braun, 1851). Scale 1 mm. SMNS J67.383.

6. *Triptychia kleini* Schnabel, 2006. Scale 2 mm. SMNS 107222.

7. *Triptychia kleini* Schnabel, 2006. Detail of the mouth. Scale 1 mm. SMNS J68.554.

8. *Triptychia* sp. Scale 2 mm. SMNS 107223.

9. *Pseudydila moersingensis* (O. Boettger, 1877). Scale 2 mm. SMNS 107224.

10. *Oxyloma minima* (Klein, 1853). Scale 500 µm. SMNS 15817.

11. *Cecilioides aciculella* (Sandberger, 1872). Scale 500 µm. SMNS 107225.

12. *Opeas minutum* (Klein, 1853). Scale 2 mm. SMNS J67.042.

13. *Pseudoleacina eburnea* (Klein, 1853). Scale 2 mm. SMNS 107226

14. *Pseudoleacina kleiniana* (Pilsbry, 1909). Scale 2 mm. SMNS J 67.037.

15. *Poiretia taurinensis* (Sacco, 1886). Scale 5 mm. SMNS 16635.

16. *Lucilla subteres* (Clessin, 1885). Scale 1 mm. SMNS 15817.

17. *Discus wenzi* (Jooss, 1918). Syntype. Scale 500 µm. SMNS 106447.

18. *Discus euglyphoides* (Sandberger, 1872). Scale 1 mm. SMNS J65.809.

19. *Discus pleuradrus* (Bourguignat, 1881). Scale 1 mm. SMNS J65.787.

20. *Aegopinella subnitens* (Klein, 1853). Scale 5 mm. SMNS 107227.

21. *Aegopinella moersingensis* n. sp. Scale 2 mm. SMNS 107228.

22. *Aegopinella*? *procellaria* (Jooss, 1918). Scale 2 mm. Syntype. SMNS 106419.

23. *Janulus moersingensis* Jooss, 1918. Scale 2 mm. Holotype. SMNS 106411.

Figure 4.

1. *Archaeozonites costatus* (Sandberger, 1872). Scale 4 mm. SMNS 17455.

2. *Protodrepanostoma involuta* (Thomae, 1845). Scale 1 mm. SMNS 15817.

3. *Miodiscula disciformis* (Wenz, 1919). Scale 5 mm. SMNS J66.244.

4. *Miodiscula miocaenica* (Gottschick & Wenz, 1927). Scale 1 mm. SMNS J68.551.

5. *Apula coarctata* (Klein, 1853). Scale 10 mm. SMNS J66.294.

6. *Klikia catanostoma* (Sandberger, 1872). Scale 10 mm. SMNS J66.304.

7. *Klikia giengensis* (Klein, 1846). Scale 4 mm. SMNS J66.276.

8. *Klikia osculina* (Sandberger, 1872). Scale 2 mm. SMNS J66.251.

9. *Leucochroopsis kleini* (Klein, 1846). Scale 10 mm. SMNS 107229.

10. *Pseudochloritis incrassata* (Klein, 1853). Scale 2 mm. SMNS 107230.

11. *Palaeotachea silvana* (Klein, 1853). Scale 5 mm. SMNS 107231.

12. *Palaeotachea turonensis* (Deshayes, 1831). Scale 4 mm. SMNS J66.818.

13. *Protodrepanostoma involuta* (Thomae, 1845). Detail oft he protoconch. Scale 100 µm. SMNS 15817.

14. Aegopinella moersingensis n. sp. Detail of the protoconch. Scale 500 mμ. SMNS 107228.

Figure 5.

1. *Aegopinella subnitens* (Klein, 1853). Detail of the protoconch. Scale 100 μm. SMNS 107227.

2. *Opeas minutum* (Klein, 1853). Detail of the protoconch. Scale 100 μm. SMNS J67.042.

3. *Opeas minutum* (Klein, 1853). Detail of the teleoconch. Scale 1 mm. SMNS J67.042.

4. *Granaria subfusiformis* (Sandberger, 1872). Detail of the protoconch. Scale 100 μm. SMNS 16635.

5. *Klikia catanostoma* (Sandberger, 1872). Detail of the protoconch. Scale 100 μm. SMNS J66.304.

6. *Janulus moersingensis* Jooss, 1918. Detail of the protoconch. Scale 100 μm. SMNS J65.737.

7. *Gastrocopta quadriplicata* (Braun, 1851). Detail of the protoconch. Scale 100 μm. SMNS J67.383.

Fig. 1 Geographic position

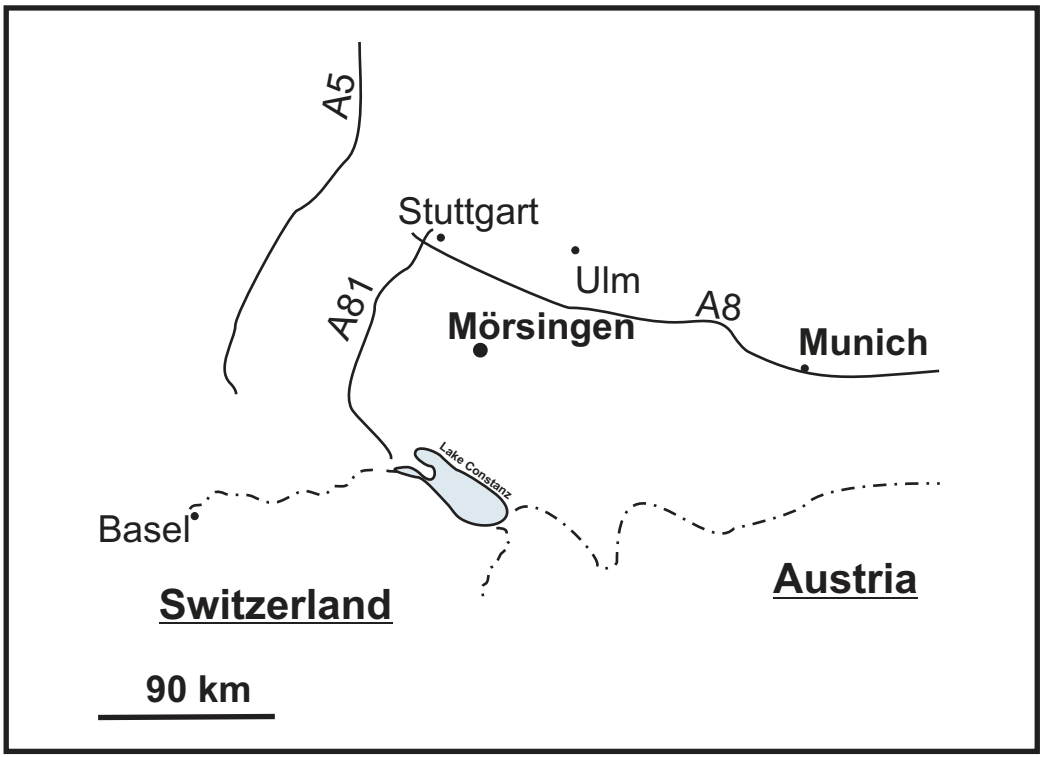

Figure 2

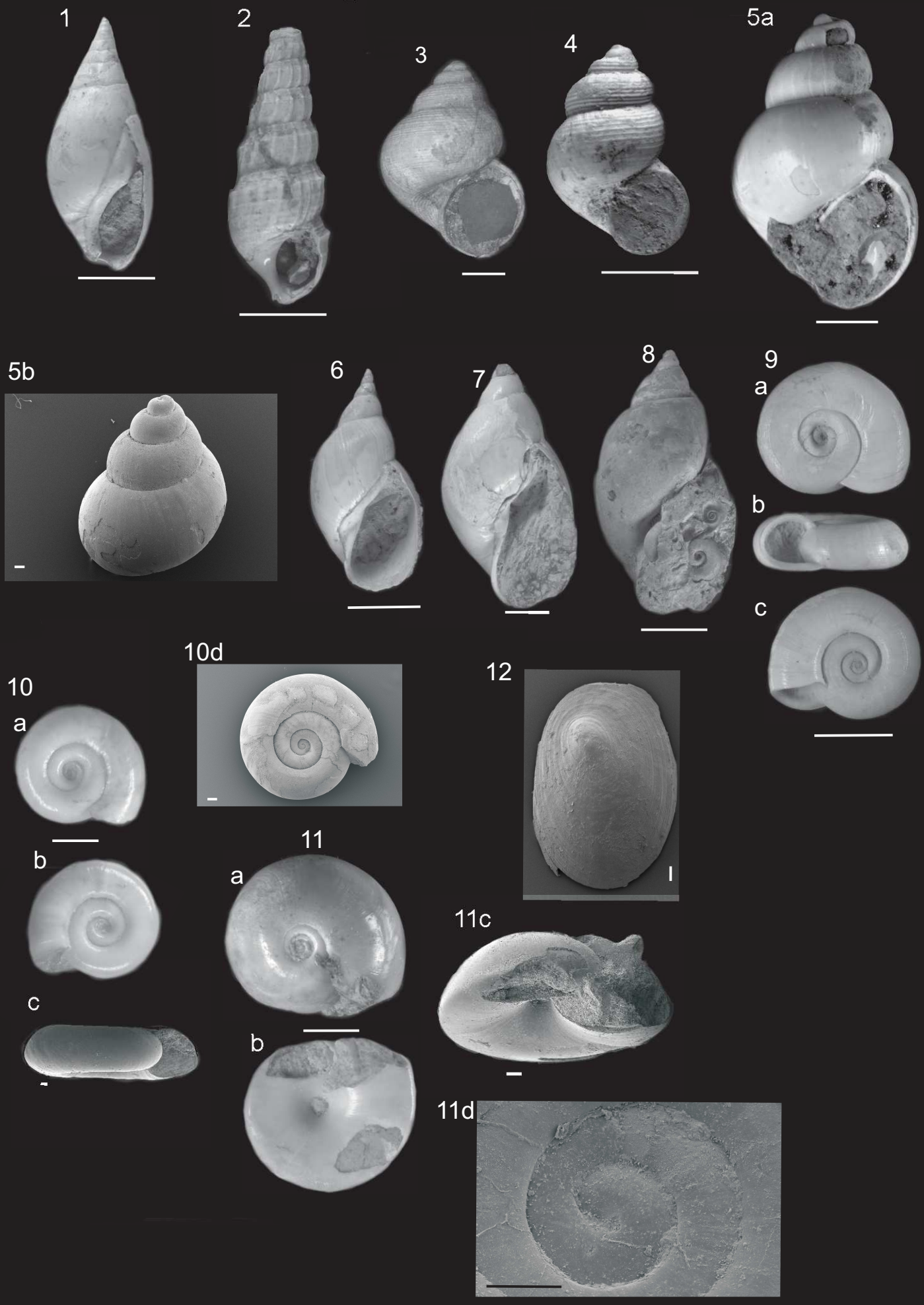

Figure 3

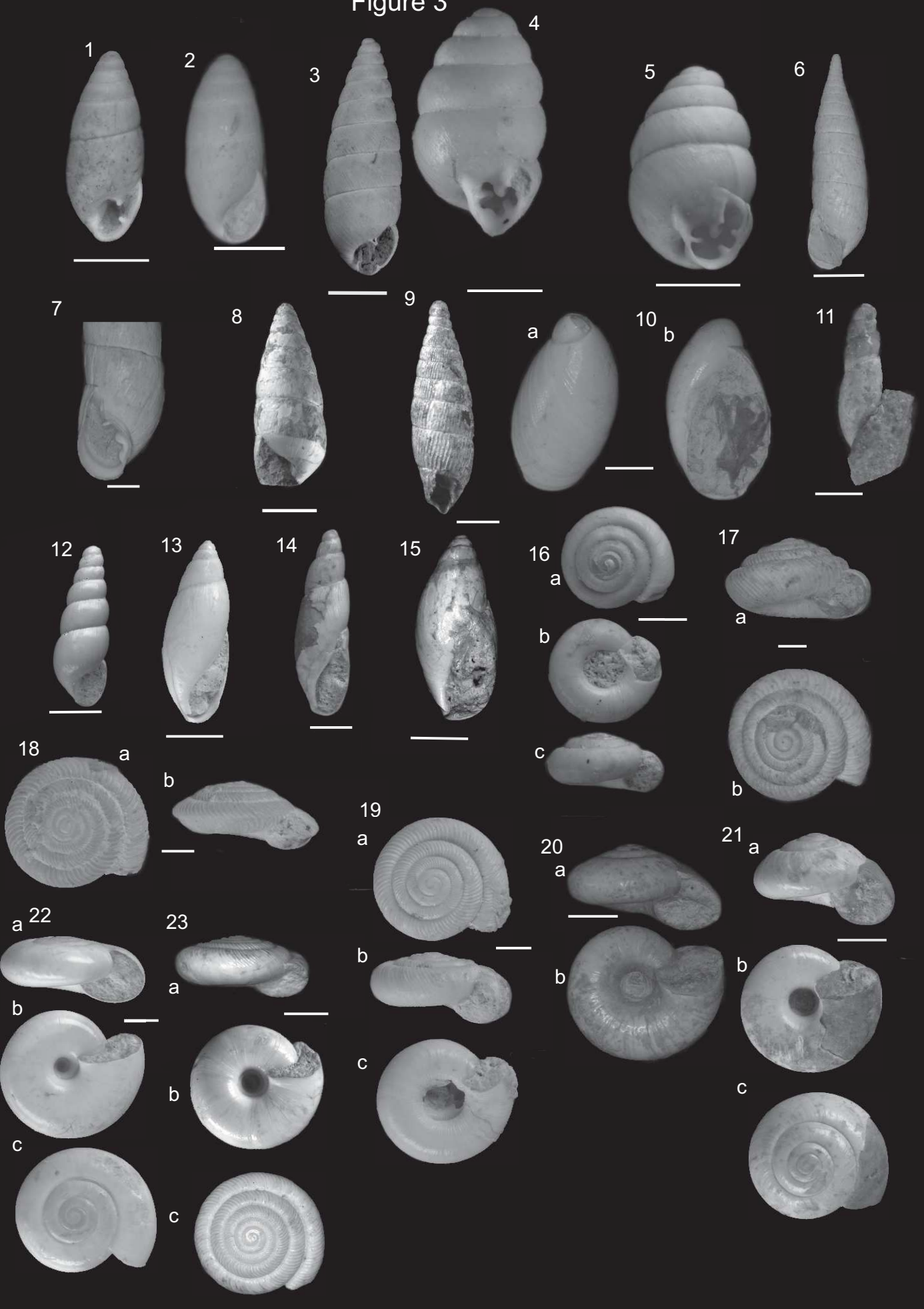
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Figure 4

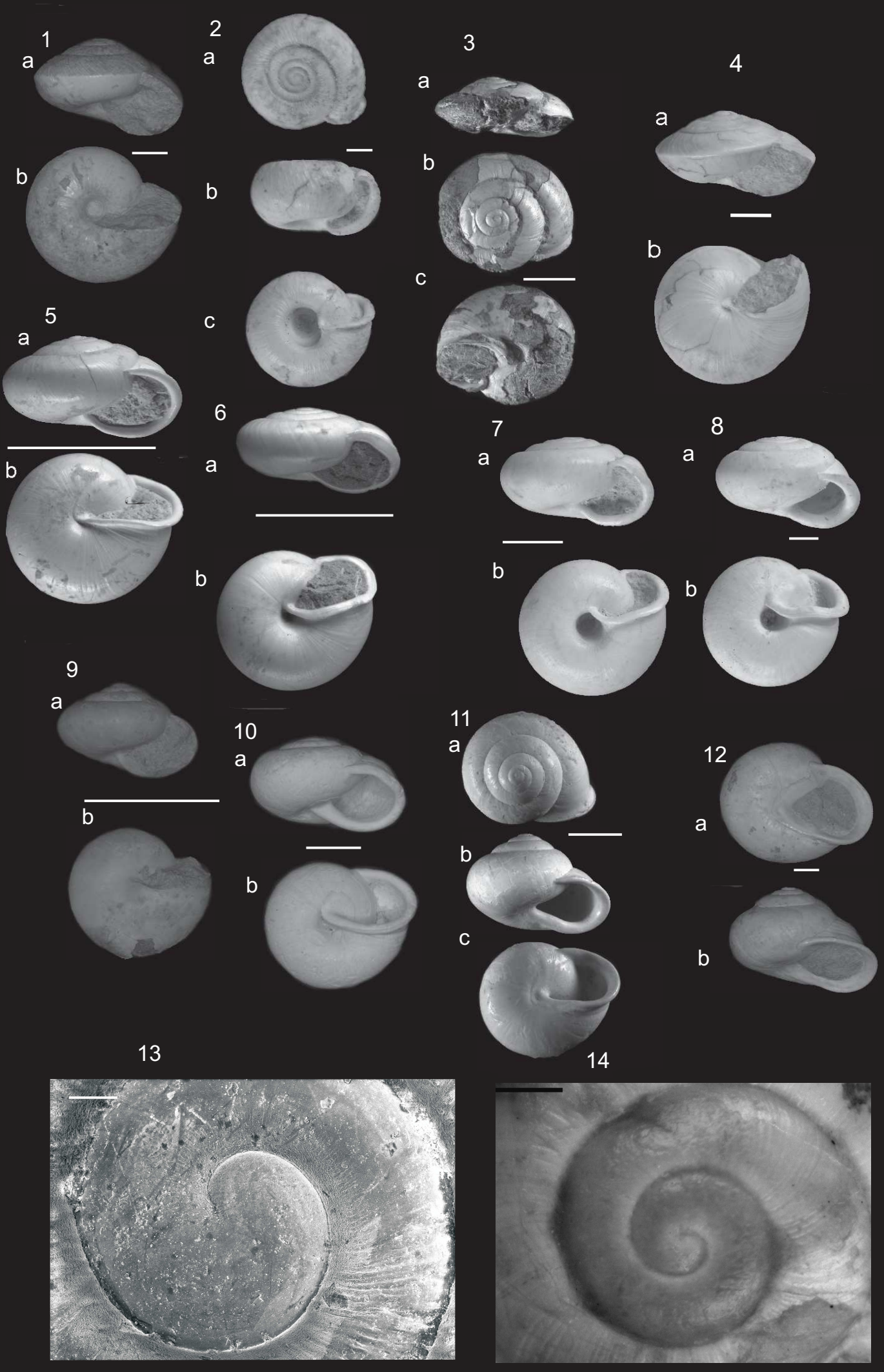

Figure 5

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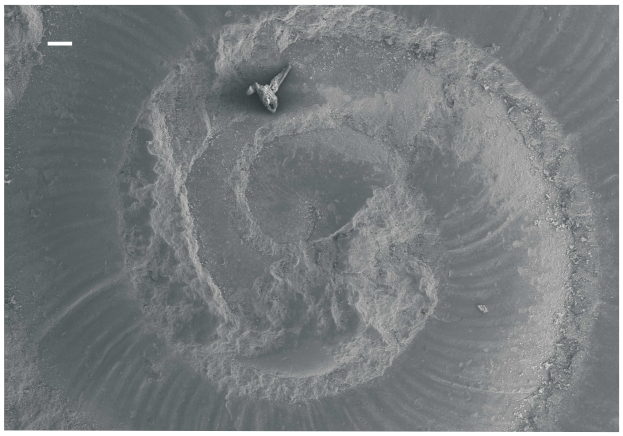

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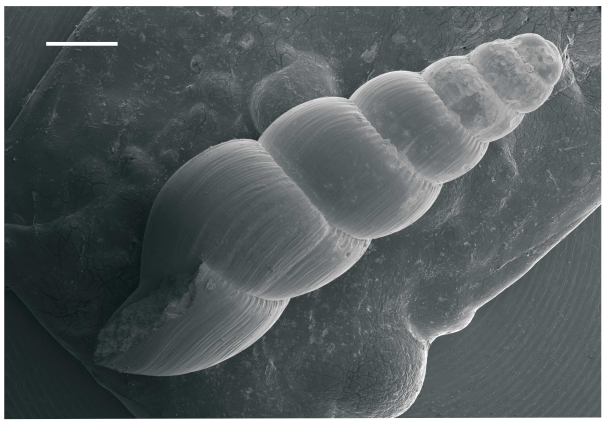

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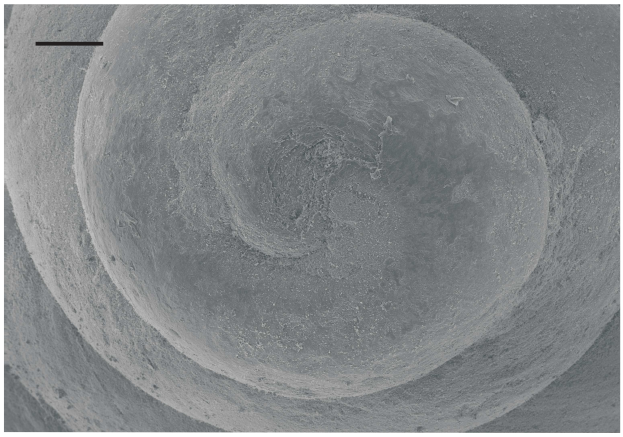

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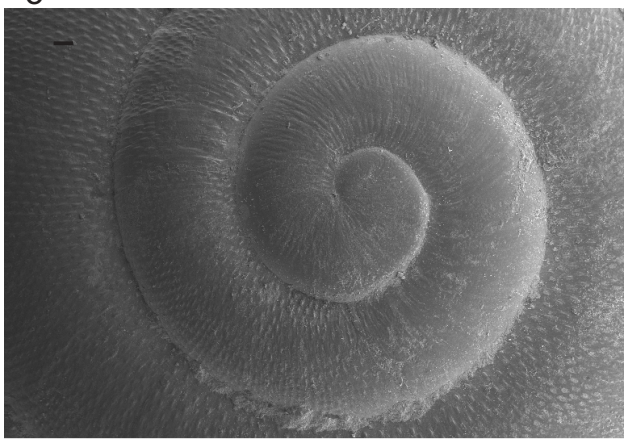

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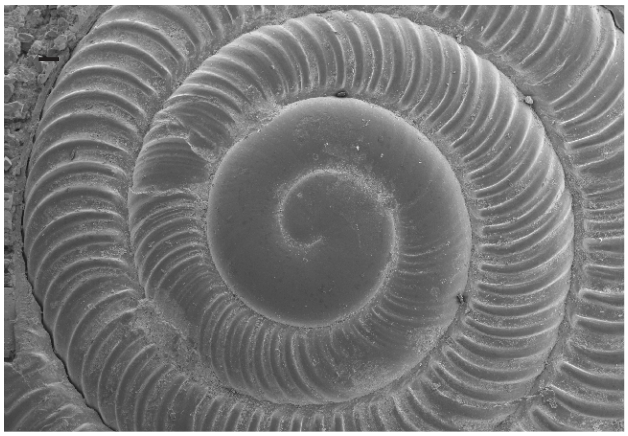

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