



# New gastropod assemblages from the Early/Middle Miocene of Riedensheim and Adelschlag-Fasanerie, southern Germany

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With 4 figures, 1 table and 2 appendices

**Abstract:** This work presents a taxonomic study and paleoecological reconstructions of the continental gastropod assemblages from two new Miocene localities in the German part of the North Alpine Foreland Basin, Bavaria. Riedensheim (next to the town of Rennertshofen) and Fasanerie (next to the town of Adelschlag). The fossil rich deposits belong to the Upper Freshwater Molasse (OSM), correlated to the regional biostratigraphic unit C+D (Burdigalian/Langhian; MN 5 in the European mammal Neogene zone). 17 gastropod species (almost exclusively pulmonates) were found in Adelschlag-Fasanerie and 35 species in Riedensheim. 13 species are shared by both assemblages. Of these, the following species have their distribution expanded in Germany: *Azeca peneckeii*, *Carychium (Carychium) galli*, *Vitrea ammoni* and *Urticicola perchteae*; and possibly also *Stagnicola* cf. *praebouiletti* and *Truncatellina* cf. *pantherae*. Paleoecological reconstructions indicate a rich freshwater gastropod community in Riedensheim, with a well-vegetated area immediately surrounding the water body (which diminished in size with time), and a surrounding environment dominated by humid forest. The fauna from Adelschlag-Fasanerie, which was much impoverished in comparison, might represent flood plain and fluvial channel deposits. Finally, a comparison to the molluscan faunas of coeval and nearby localities (Adelschlag, Attenfeld, Sandelzhausen and Undorf) is provided.

**Key words:** Burdigalian/Langhian, Caenogastropoda, Karpatian/Badenian, Pulmonata, Upper Freshwater Molasse.

## 1. Introduction

The North Alpine Foreland Basin (NAFB) is well known for its rich and diverse Miocene fossil record. Its youngest part, the Upper Freshwater Molasse (“Obere Süßwassermolasse”, in German; abbreviated OSM), contains a large number of vertebrate-bearing localities (e.g., HEISSIG 1997; KÄLIN & KEMPF 2009; ABDUL-AZIZ et al. 2010; BÖHME & ILG 2003). The invertebrate fossils, however, have usually received less attention, despite the importance of mollusks in paleoenvironmental reconstructions and biostratigraphy (e.g., HARZHAUSER et al. 2008; MOSER et al. 2009a).

Fossil samples were recently collected from two new Miocene Bavarian localities: Riedensheim (in the municipality of Rennertshofen) and Fasanerie (in the

municipality of Adelschlag). These two sites are not accessible anymore, but have delivered rich fossil assemblages presently under study. A first taxonomical contribution dealing with the continental gastropods and their paleoecological and biostratigraphic context is presented here.

## 2. Geological setting

The two fossil sites presented in this paper, Riedensheim and Adelschlag-Fasanerie, belong to the OSM. Geographically, they are located at the northern margin of the basin at the border to the Franconian Alb (Fig. 1). Rich vertebrate and invertebrate faunas were recently discovered at both localities.

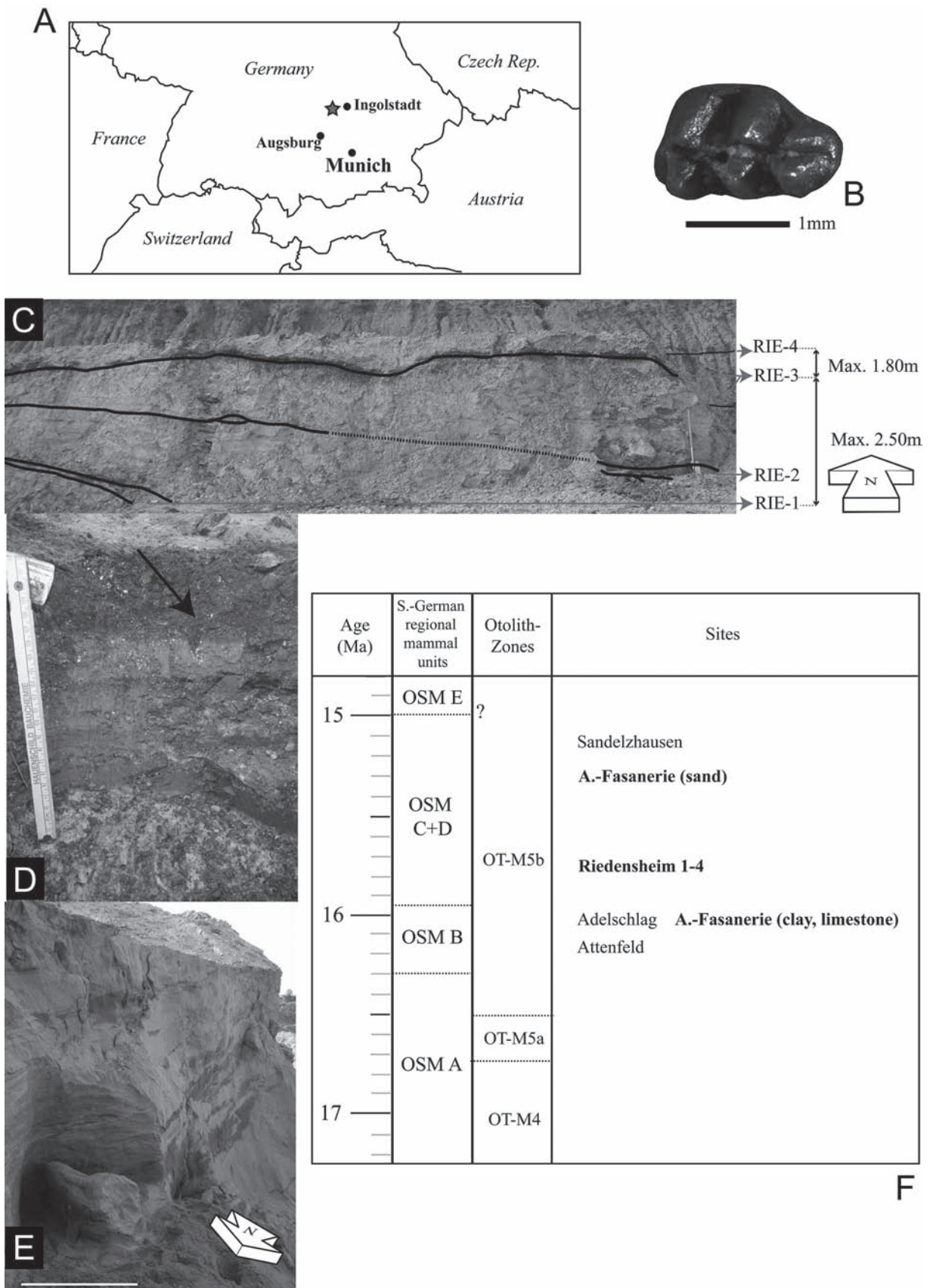


Fig. 1.

## 2.1. Adelschlag-Fasanerie

The sand pit was located at the hamlet Fasanerie (48°51' N, 11°12' E) northwest of the town of Adelschlag. The pit is presently filled up and excavations are not possible anymore. It was in the paleontological limelight in 2012 due to the discovery of a well-preserved skull of the proboscidean *Gomphotherium* BURMEISTER, 1837. An intensive study of the deposits followed, leading, among other works, to the sampling of the molluscs studied herein (SAUER 2013). Most of the gastropods presented here stem from one of the deepest exposed layers (location A in SAUER 2013), an approximately 12 cm thick layer of reddish to brownish clay (named here as “Adelschlag-Fasanerie clay”). This layer was unconformably overlain by sandy and vertebrate-rich strata which provided also some rare and fragile, but complete, gastropod specimens (named here as “Adelschlag-Fasanerie sand”). Finally evidence of gastropod-enriched freshwater limestones in the profile is provided by displaced blocks (named here as “Adelschlag-Fasanerie limestone”). According to earlier observations by one of the authors (CM), these limestones occurred below the clay deposits in adjacent pits and therefore form the base of the reported sedimentary sequence.

## 2.2. Riedensheim

The pit “Riedensheim III” of the company Hoffmann Mineral was recently opened for mining of siliceous earth. It is located 650 m north of the small town of Riedensheim (48°45'N, 11°07'E), and 6.5 km northwest of Neuburg on the Danube. Several meters of Miocene sand and marls were exposed below Quaternary loess loams. The strata laid unconformably on Cretaceous siliceous earth and sandstones of the Upper Cretaceous Wellheim Formation (SCHNEIDER et al. 2013). Due to the progression of mining, the strata have been removed in the meantime. Four gastropod-enriched marly layers were sampled in 2014. Although post-depositional

karst phenomena disturbed the horizontal layering of the strata, the samples studied here could be ordered from the bottom (layer Riedensheim 1) to the top (layer Riedensheim 4) (Fig. 1). The layer Riedensheim 2 had a laterally changing facies; its eastern part was more sandy while the western part was marly. As the horizon could be clearly tracked through the whole section despite of facial changes, all findings from this layer were merged under the label Riedensheim 2. The gastropods presented here stem from layers 1, 2 (including the sandy facies) and 4.

## 2.3. Biostratigraphy

The biozonation of the German Upper Freshwater Molasse is based on the presence/absence of mammalian taxa (e.g., DEHM 1955; HEISSIG 1997; BÖHME et al. 2002; ABDUL-AZIZ et al. 2008, 2010). The rodent species, in particular, are of first importance for detailed biostratigraphy in this area. Seven faunal units (OSM A to F) are now defined for the Older and Middle Series (*sensu* DEHM 1955), and have their equivalents in the taxon range-based zonation of the Swiss part of the NAFB (KÄLIN & KEMPF 2009).

### 2.3.1. Adelschlag-Fasanerie

At present, no biostratigraphically significant mammalian fossil has been obtained from the location A, but fish otoliths correlate it to the later part of the otolith zone OT-M5 (REICHENBACHER, personal communication in SAUER 2013). The mammals obtained from the sand unconformably overlying this level correlate to the OSM C+D (SAUER 2013). The rare isolated teeth of the cricetid rodent *Megacricetodon* aff. *bavaricus* FAHLBUSCH, 1964 are clearly larger than the tooth recorded from Langenmoosen (OSM B), and more similar to what was observed in Sandelzhausen, for instance (OSM C+D).

The few *Megacricetodon* FAHLBUSCH, 1964 remains documented in Adelschlag (see also below), a local-

**Fig. 1.** **A** – Map showing the localities of Adelschlag-Fasanerie and Riedensheim (red star). **B** – Left upper first molar of *Megacricetodon* aff. *bavaricus* (Riedensheim 4). **C** – View of the gastropod-rich layers from Riedensheim (RIE-4 and part of RIE-3 are in a second exposure in the background). **D.** Adelschlag-Fasanerie, locality A (the arrow indicates the sampled layer). **E** – Adelschlag-Fasanerie sand, during the excavation of the *Gomphotherium* skull (scale: 1 m). **F** – Biostratigraphic correlation of Adelschlag-Fasanerie (abbreviated “A.-Fasanerie”) and Riedensheim, as well as the localities discussed in the text. Undorf is not considered because of the lack of sufficient biostratigraphic information, but the presence of the rodent *Keramidomys* allows the exclusion of OSM A. The correlations follow REICHENBACHER et al. (2013).

ity sampled in the 1950s (at approximately the same height above sea level as Adelschlag-Fasanerie but 1.8 km distant), do not contradict an assignment to the OSM B or early OSM C+D. The two teeth found there belonging to m2 and m3 are unfortunately not of high biostratigraphic value and belong to the uppermost size range, similar to the tooth from Langenmoosen (OSM B). They also fall within the variation range from Roßhaupten (base of OSM C+D, after HEISSIG 1997; for measurements, see FAHLBUSCH 1964). The fossils obtained from Roßhaupten are derived from dark, organic rich, sandy marl rich in gastropods (REICHENBACHER et al. 2004). This lithological description resembles the observations made at the location A (sensu SAUER 2013) from Adelschlag-Fasanerie. Therefore, the duration of the hiatus between the marly deposits and the erosive base of the sand in Adelschlag-Fasanerie cannot be precisely determined.

### 2.3.2. Riedensheim

At present, the few findings of mammal fossils do not allow for a precise biostratigraphic assignment of this locality. The uppermost layer Riedensheim 4 yielded a first upper molar of *Megacricetodon* aff. *bavaricus* (Fig. 1B). Its size (2 mm x 1.23 mm) is in the lower range of specimens from the Sandelzhausen locality (WESSELS & REUMER 2009) and, thus, allows for a preliminary correlation to the OSM C+D. Based on this specimen only, a more precise relative dating of Riedensheim 4 is not possible. Vertebrate-enriched layers have been recently sampled in the sandy layers underlying the deposits considered herein, as well as a marly layer that cannot be confidently correlated to any of the layers discussed herein. While lacking gastropods, the large amount of *Megacricetodon* teeth found allows us to correlate the beginning of the sedimentation in Riedensheim to the base of OSM C+D. All four available M1 teeth are clearly smaller than the tooth from Riedensheim 4. For this reason it is reasonable to correlate the layers 1-4 to the first half of the OSM C+D (Fig. 1).

The absolute dating of the pre-Riesian OSM deposits is a much-debated subject. While ABDUL-AZIZ et al. (2010) propose an age roughly ranging from 15.8 to 17.1 Ma (mostly Karpatian), other studies consider these dates are somewhat too old (REICHENBACHER et al. 2013 and references therein), and define the biozone between ca. 15 and 16 Ma (Badenian). Regarding these discrepancies and the lack of sufficient material in the gastropod-enriched layers, a more precise dating is presently not possible.

## 2.4. Additional information on the studied OSM localities

The faunal composition of several neighboring and nearly coeval localities are compared to the locality of Riedensheim and Adelschlag-Fasanerie. The following preliminary biostratigraphic succession is suggested (from the oldest to the youngest): Attenfeld, Adelschlag/Adelschlag-Fasanerie clay, Adelschlag-Fasanerie sand/Riedensheim 1-4, Sandelzhausen. The Undorf localities cannot be arranged in this system due to the uncertainties mentioned below.

### 2.4.1. Adelschlag

As noted before, the Adelschlag locality is geographically very close to Adelschlag-Fasanerie, and might be a stratigraphical equivalent to the marly part of the latter. Emending MAYR (1979), REICHENBACHER et al. (2004) proposed a slightly younger stratigraphic age of Adelschlag with regard to Attenfeld. Their proposal is based on the evolutionary stage of the dormouse *Miodyromys* KRETZOI, 1943 compared to the representatives of the OSM B, more precisely from Langenmoosen. The gastropods reported by REICHENBACHER et al. (2004) from this locality are revised in the present work, based on SEM images (Appendix 2: Table 1). Nearly all gastropod species are freshwater taxa; a single terrestrial species was reported.

### 2.4.2. Attenfeld

The clay pit is situated approximately 4 km north of Neuburg (REICHENBACHER et al. 2004), and is thus close to Riedensheim. The locality can be correlated to OSM B. As above, the gastropods listed by REICHENBACHER et al. (2004) were re-identified (Appendix 2: Table 1). Only freshwater snails are known from this locality.

### 2.4.3. Sandelzhausen

The molluscan fauna from Sandelzhausen was studied by GALL (1972) and MOSER et al. (2009a) and revised by SALVADOR (2013a, 2013b, 2015) and SALVADOR & RASSER (2014). The locality has been intensively excavated and studied, and a rich literature dealing with the taxonomy of the fossils, their age and paleoecology, as well as the geology of the site, is now available (see MOSER et al. 2009b, and references therein for an overview). Sandelzhausen correlates to OSM C+D.

### 2.4.4. Undorf

The molluscan fauna from Undorf (near Regensburg) was studied by CLESSIN (1877, 1885, 1892, 1911) and

never revised, although a single species was later described by FALKNER (1974). CLESSIN presented a profile of the mollusk-bearing locality (CLESSIN 1911), but without clearly mentioning the exact location. It is thus difficult to correlate these data with the small mammal finds from Undorf reported by FAHLBUSCH (1964). The literature also reports fossil vertebrates excavated along the railway track, with a large diversity of large mammals and other vertebrates (e.g., RINNERT 1956). The small mammal finds do not help much with the relative dating, because the stratigraphical ranges of the species are too long (*Democricetodon* FAHLBUSCH, 1964, *Eumyarion* THALER, 1966, *Keramidomys* HARTENBERGER, 1966, *Neocometes similis* FAHLBUSCH, 1966; FAHLBUSCH 1975; SCHÖTZ 1981; PRIETO 2010). It should be noted that many taxa from Undorf described by CLESSIN (1877, 1885, 1892, 1911) were considered doubtful by WENZ (1923-1930) and are therefore excluded from the present faunal composition analysis. The single new species described later (*Spermodea candida* FALKNER, 1974) was also excluded, since it is not known if it is synonymous with one of CLESSIN's species (CLESSIN 1877, 1885, 1892, 1911).

### 3. Material and methods

All the gastropod material found in the new localities of Adelschlag-Fasanerie and Riedensheim is reported here. The sediments were screen-washed (smallest sieve 0.4 mm) after dissolution in a low concentrated H<sub>2</sub>O<sub>2</sub> solution. The specimens are housed at the collections of the Bayerische Staatssammlung für Paläontologie und Geologie (BSPG; Munich, Germany) and the Staatliches Museum für Naturkunde Stuttgart (SMNS; Stuttgart, Germany). The material analyzed is fully listed in Appendix 1.

The classification used here follows BOUCHET et al. (2005) and NORDSIECK (2014). All species found are figured. Further data on their diagnostic features is provided on the discussion section of each species. Specimens were measured either with a digital caliper or with the aid of computer software (Leica Application Suite [LAS] v.3.8.0 and ImageJ). The following abbreviations are used throughout the article for shell measurements: H = shell height; D = shell greatest diameter; h = operculum height; w = operculum width.

### 4. Systematic Paleontology

Caenogastropoda  
 Superfamily Littorinoidea  
 Family Pomatiidae  
 Genus *Pomatias* STUDER, 1789

*Pomatias* sp.  
 (Fig. 2A)

**Occurrence:** Riedensheim 2 (1 operculum).

**Discussion:** This single ellipsoid operculum presenting a sub-central nucleus and spiral growth pattern is consistent with the genus *Pomatias*. Classification beyond genus level is not possible.

Superfamily Truncatelloidea  
 Family Bithyniidae  
 Genus *Bithynia* LEACH, 1818  
*Bithynia* sp.  
 (Figs. 2B-C)

**Occurrence:** Adelschlag-Fasanerie sand (6 opercula), Riedensheim 1 (6 opercula) and Riedensheim 2 (1 specimen + 1 operculum).

**Discussion:** A single shell fragment and some opercula remains. The sturdy shell with strongly convex whorls and the tear-shaped operculum (with a central nucleus and concentric growth pattern) are consistent with the genus *Bithynia*, but do not allow further classification.

Family Hydrobiidae  
 Genus *Pseudamnicola* PAULUCCI, 1878  
*Pseudamnicola suevicus* (GOTTSCHICK, 1928)  
 (Fig. 2D)

- 1928 *Amnicola suevica* GOTTSCHICK, p. 148, pl. 2, figs. 7a-c.  
 1976 *Pseudamnicola convexa suevica* [sic]. – SCHLICKUM, p. 3, pl. 1, fig. 6.  
 2014 *Pseudamnicola convexa suevica* [sic]. – NEUBAUER et al., supplementary material 1.

**Occurrence:** Adelschlag-Fasanerie clay (16 specimens), Riedensheim 4 (>30 specimens).

**Discussion:** This genus can be identified by its hydrobiid shell with few whorls, with rapidly-expanding whorls and a large oval aperture; the adults are of a very small size. The present specimens compare very well to the syntypes of *Pseudamnicola suevicus* (SMNS 15817), a species known only from Zwiefaltendorf (MN 5-6, Germany; SCHLICKUM 1976). This species is often treated as a subspecies of *Pseudamnicola convexus* (SANDBERGER, 1875), which was originally described from Ehingen (MN 5, Germany; also reported from other localities in Central Europe), but is insufficiently defined. *Pseudamnicola convexus* may well be the senior name for this species, but addressing this issue is beyond the scope of the present work.

The genus *Pseudamnicola* should be treated as masculine, following *Amnicola* GOULD & HALDEMAN, 1840 (FALKNER et al. 2002).

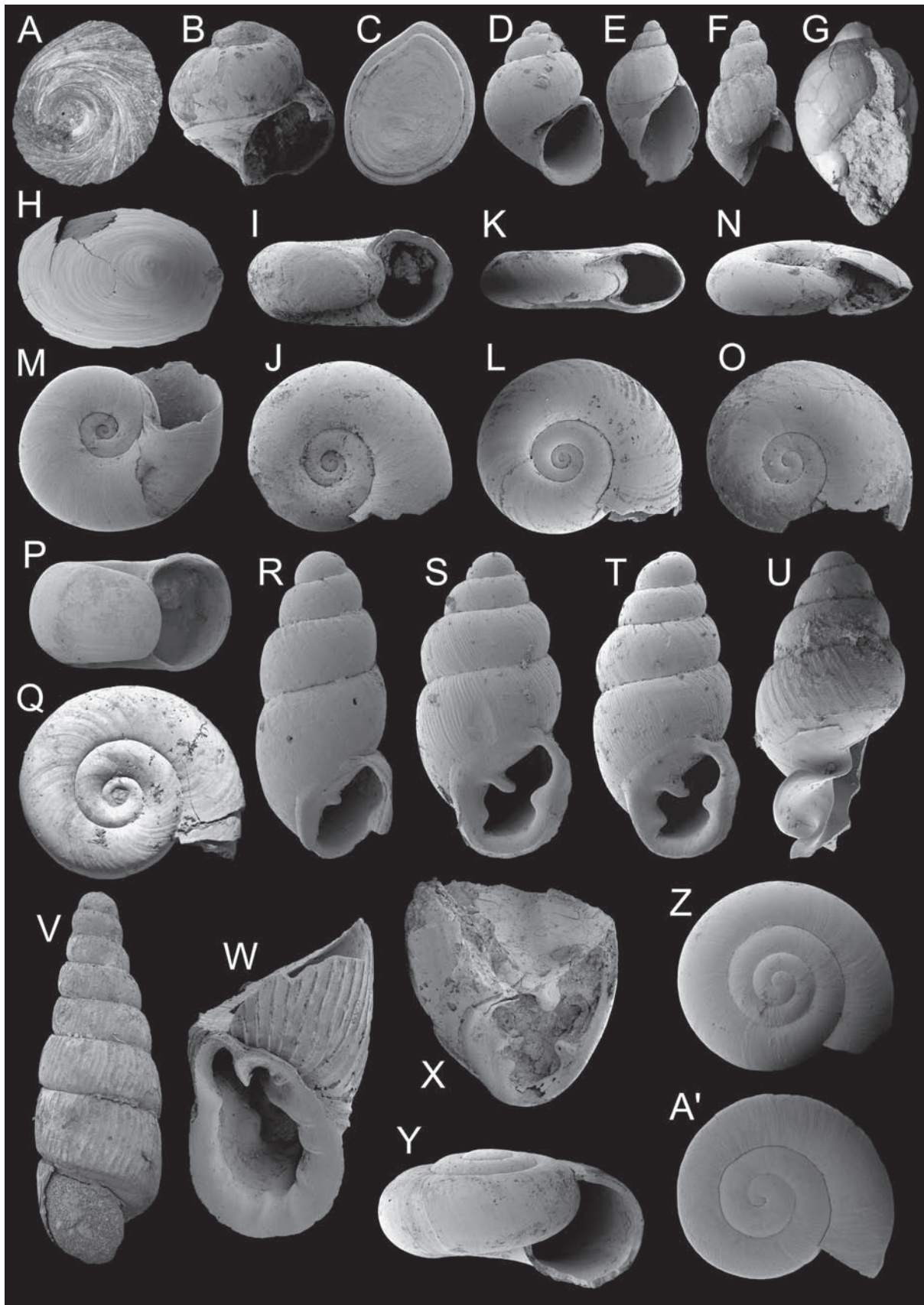


Fig. 2.

Pulmonata  
 Hygrophila  
 Superfamily Lymnaeoidea  
 Family Lymnaeidae  
 Genus *Galba* SCHRANK, 1803  
*Galba dupuyiana* (NOULET, 1854)  
 (Fig. 2E)

- 1854 *Limnea Dupuyiana* NOULET, p. 108.  
 1872 *Limneus Laurillardianus* SANDBERGER, pl. 28, figs. 27-27b [non *laurillardianus* NOULET 1854].  
 1875 *Limneus Dupuyianus*. – SANDBERGER, p. 543.  
 1923 *Radix (Radix) dupuyana* [sic]. – WENZ, p. 1242.  
 2000 *Galba (Galba) dupuyiana*. – FISCHER, p. 135, fig. 4.  
 2006 *Galba dupuyana* [sic]. – KÓKAY, p. 50, pl. 16, figs. 14-16.  
 2009 *Galba dupuyiana*. – BÖTTCHER et al., p. 239, figs. 2/1-2.  
 2014 *Galba dupuyiana*. – NEUBAUER et al., supplementary material 1.  
 2014 *Galba dupuyiana*. – SALVADOR & RASSER, p. 188, figs. 1-7.

**Occurrence:** Adelschlag-Fasanerie clay (>30 specimens), Riedensheim 1 (>30 specimens), Riedensheim 2 (>40 specimens) and Riedensheim 4 (>50 specimens).

**Discussion:** The present specimens compare well to *G. dupuyiana*, with large, round and rapidly-expanding whorls. The species was originally described from Sansan (MN6, France; FISCHER 2000), but is known throughout the Middle Miocene of Western and Central Europe (KÓKAY 2006). There are two distinct extreme morphological varieties (a broader and a slender form) of this species known from other coeval sites in Germany (BÖTTCHER et al. 2009; SALVADOR &

RASSER 2014), but in the present material only the broader form is present.

Genus *Stagnicola* JEFFREYS, 1830  
*Stagnicola cf. praebouiletti* (SCHLICKUM, 1970c)  
 (Fig. 2F)

- 1964 *Stagnicola (Stagnicola?) bouiletti*. – SCHLICKUM, p. 14, pl. 2, fig. 32 [non MICHAUD 1835].  
 1970c *Stagnicola praebouiletti* SCHLICKUM, p. 92, figs. 12-17.  
 1973 *Stagnicola (Stagnicola) praebouiletti*. – STEININGER et al., p. 451, pl. 9, fig. 10.  
 1993 *Stagnicola praebouiletti*. – REICHENBACHER, table 13.  
 2005 *Stagnicola praebouiletti*. – KOWALKE & REICHENBACHER, p. 631, figs. 9.8-9.9.  
 2014 *Stagnicola praebouiletti*. – NEUBAUER et al., supplementary material 1.

**Occurrence:** Riedensheim 2 (1 specimen).

**Discussion:** This single specimen has a very slender lymnaeiform shell, with a tall spire, tall whorls, deep suture and regularly growing whorls. The material is poorly preserved, but it compares well to *Stagnicola praebouiletti*, a species originally described from the Bavarian Oncophora Beds (from the Upper Brackish Molasse, or OBM). Due to the younger age and fragmentary nature of the present specimen, this identification remains tentative.

Genus *Lymnaea* LAMARCK, 1799  
*Lymnaea dilatata* NOULET, 1854  
 (Fig. 2G)

**Fig. 2.** Fossil gastropods. **A** – *Pomatias* sp., operculum (BSPG 2014 XIX 095; Riedensheim 2; h = 4.6 mm, w = 4.0 mm). **B** – *Bithynia* sp. (BSPG 2014 XIX 039; Riedensheim 2; H = 1.7 mm, D = 1.6 mm). **C** – *Bithynia* sp., operculum (BSPG 2014 XIX 012; Riedensheim 1; h = 2.7 mm, w = 2.1 mm). **D** – *Pseudamnicola suevicus* (BSPG 2014 XIX 086; Riedensheim 4; H = 1.8 mm, D = 1.2 mm). **E** – *Galba dupuyiana* (BSPG 2014 XIX 061; Riedensheim 4; H = 4.8 mm). **F** – *Galba cf. praebouiletti* (BSPG 2014 XIX 037; Riedensheim 2; H = 3.6 mm). **G** – *Lymnaea dilatata* (BSPG 2013 XXVI; Adelschlag-Fasanerie; H = 22.9 mm). **H** – *Ferrissia deperdita* (BSPG 2014 XIX 009; Riedensheim 1; H = 3.3 mm, D = 2.3 mm). **I** – *Gyraulus albertanus* (BSPG 2014 XIX 054; Riedensheim 4; H = 1.2 mm, D = 2.6 mm). **J** – *Gyraulus albertanus* (BSPG 2014 XIX 080; Riedensheim 4; D = 2.9 mm). **K** – *Gyraulus applanatus* (BSPG 2014 XIX 075; Riedensheim 4; H = 1.1 mm, D = 3.2 mm). **L** – *Gyraulus applanatus* (BSPG 2014 XIX 060; Riedensheim 4; D = 3.0 mm). **M** – *Gyraulus applanatus*, specimen with predation mark (BSPG 2014 XX 004; Adelschlag-Fasanerie; D = 2.2 mm). **N** – *Hippeutis subfontanus* (BSPG 2014 XIX 055, spcm. #1; Riedensheim 4; H = 0.6 mm, D = 1.8 mm). **O** – *Hippeutis subfontanus* (BSPG 2014 XIX 055, spcm. #2; Riedensheim 4; D = 1.6 mm). **P** – *Planorbarius cornu* (BSPG 2014 XIX 079, spcm. #1; Riedensheim 4; H = 3.4 mm, D = 5.8 mm). **Q** – *Planorbarius cornu* (BSPG 2013 XXVI; Adelschlag-Fasanerie; D = 21.2 mm). **R** – *Carychium eumicrum* (BSPG 2014 XIX 083; Riedensheim 4; H = 1.2 mm). **S** – *Carychium galli* (BSPG 2014 XIX 087, spcm. #1; Riedensheim 4; H = 1.6 mm). **T** – *Carychium galli* (BSPG 2014 XIX 087, spcm. #2; Riedensheim 4; H = 1.7 mm). **U** – *Carychium nouleti*, broken specimen showing sinuous internal lamella (BSPG 2014 XX 001; Adelschlag-Fasanerie; H = 1.4 mm). **V** – *Pseudidyla moersingensis* (BSPG 2014 XIX 042; Riedensheim 2; H = 6.4 mm). **W** – *Pseudidyla moersingensis*, aperture fragment (BSPG 2014 XIX 066; Riedensheim 4; H = 3.3 mm, D = 1.8 mm). **X** – *Azeca peneckeii*, aperture fragment (BSPG 2014 XIX 064; Riedensheim 4; H = 2.4 mm, D = 2.1 mm). **Y** – *Vitrea ammoni* (BSPG 2014 XIX 059; Riedensheim 4; H = 1.7 mm, D = 3.1 mm). **Z** – *Vitrea ammoni* (BSPG 2014 XIX 085; Riedensheim 4; D = 3.6 mm). **A'** – *Pseudochloritis* sp., spire apex fragment (BSPG 2014 XIX 021; Riedensheim 2; D = 8.3 mm).

- 1854 *Limnea dilatata* NOULET, p. 107.  
 1923 *Radix (Radix) socialis dilatata*. – WENZ, p. 1277.  
 2000 *Lymnaea dilatata*. – FISCHER, p. 136, figs. 1-2.  
 2006 *Radix dilatata*. – KÓKAY, p. 52, pl. 17, fig. 14.  
 2014 *Radix dilatata*. – NEUBAUER et al., supplementary material 1.  
 2014 *Lymnaea dilatata*. – SALVADOR & RASSER, p. 189, figs. 8-9.

**Material examined:** BSPG 2013 XXVI (8 spcm.); 2014 XIX 007 (14 spcm.), XIX 040 (1 spcm.), XIX 049 (4 spcm.), XIX 071 (15 spcm). SMNS 101695 (1 spcm.).

**Occurrence:** Adelschlag-Fasanerie limestone (8 specimens), Riedensheim 1 (14 specimens), Riedensheim 2 (1 specimen) and Riedensheim 4 (19 specimens).

**Discussion:** *Lymnaea dilatata* is diagnosed by its large lymnaeid shell, with an acuminate and proportionately small spire, rapidly-expanding and slightly convex whorls, a somewhat oval body whorl and a large ellipsoid aperture. This species is known from the entire Miocene of Western and Central Europe (BINDER 2004; KÓKAY 2006).

#### Superfamily Planorboidea

##### Family Planorbidae

##### Genus *Ferrissia* WALKER, 1903

##### *Ferrissia deperdita* (DESMAREST, 1814)

(Fig. 2H)

- 1814 *Ancylus deperditus* DESMAREST, p. 19, pl. 1, fig. 14.  
 1923 *Pseudancylus deperditus deperditus*. – WENZ, p. 1692.  
 1976 *Ferrissia deperdita*. – SCHLICKUM, p. 7, pl. 1, fig. 20.  
 2006 *Ferrissia deperdita*. – KÓKAY, p. 60, pl. 20, fig. 15, pl. 21, fig. 1.  
 2014 *Ferrissia deperdita*. – HARZHAUSER et al., p. 17, pl. 5, figs. 1, 2, 5, 12,  
 2014 *Ferrissia deperdita*. – NEUBAUER et al., supplementary material 1.  
 2014 *Ferrissia deperdita*. – SALVADOR & RASSER, p. 191, fig. 11.

**Occurrence:** Riedensheim 1 (2 specimens) and Riedensheim 2 (1 specimen).

**Discussion:** The present specimens show a shell apex slightly bent to the side; the cap-like protoconch is smooth, gradually transitioning to the teleoconch, which bears well-marked growth lines. Given this pattern and age, the specimens compare well to *F. deperdita*, a species known from the Middle Miocene of Hungary, Austria, southern Germany, Switzerland and France (SCHLICKUM 1976; KÓKAY 2006; HARZHAUSER et al. 2014).

##### Genus *Gyraulus* CHARPENTIER, 1837

##### *Gyraulus albertanus* (CLESSIN, 1877)

(Figs. 2I-J)

- 1877 *Planorbis albertanus* CLESSIN, p. 40.  
 1923 *Gyraulus (Gyraulus) albertanus*. – WENZ, p. 1541.  
 1972 *Gyraulus (Gyraulus) albertanus*. – GALL, p. 16.  
 2009a *Menetus (Dilatata) albertanus*. – MOSER et al., p. 46.  
 2014 *Gyraulus albertanus*. – NEUBAUER et al., supplementary material 1.  
 2014 *Gyraulus albertanus*. – SALVADOR & RASSER, p. 191, figs. 12-15.

**Occurrence:** Adelschlag-Fasanerie clay (>20 specimens), Riedensheim 1 (15 specimens), Riedensheim 2 (>30 specimens) and Riedensheim 4 (>20 specimens).

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

**Discussion:** *Gyraulus albertanus*, when compared to coeval congeners, is diagnosed by its proportionately larger size (shell height ca. half the shell diameter), a more overall rounded shell profile, quickly growing whorls and a large and round aperture. The species is known from several Early/Middle Miocene OSM localities (e.g., CLESSIN 1877; SALVADOR & RASSER 2014).

##### *Gyraulus applanatus* (THOMAE, 1845)

(Figs. 2K-M)

- 1845 *Planorbis applanatus* THOMAE, p. 150.  
 1851 *Planorbis dealbatus*. – BRAUN, p. 1134.  
 1923 *Gyraulus (Gyraulus) trochiformis applanatus*. – WENZ, p. 1579.  
 1923 *Gyraulus (Gyraulus) trochiformis dealbatus*. – WENZ, p. 1591.  
 1964 *Gyraulus trochiformis dealbatus*. – SCHLICKUM, p. 15, pl. 2, fig. 35.  
 1970a *Gyraulus trochiformis applanatus*. – SCHLICKUM, p. 148, pl. 10, fig. 6.  
 1970b *Gyraulus trochiformis applanatus*. – SCHLICKUM, p. 180.  
 1973 *Gyraulus trochiformis dealbatus*. – STEININGER et al., p. 451, pl. 9, fig. 11a-b.  
 1989 *Gyraulus trochiformis dealbatus*. – REICHENBACHER, p. 172, pl. 1, fig. 11.  
 1995 *Gyraulus dealbatus*. – KADOLSKY, p. 40, fig. 47.  
 2004 *Gyraulus dealbatus*. – BINDER, p. 193, pl. 2, figs. 1a-c.  
 2005 *Gyraulus applanatus*. – KOWALKE & REICHENBACHER, p. 631, figs. 9.1-9.3.  
 2006 *Gyraulus applanatus*. – KÓKAY, p. 56, pl. 19, figs. 13-14.  
 2006 *Gyraulus trochiformis dealbatus*. – KÓKAY, p. 57, pl. 19, fig. 15.  
 2014 *Gyraulus applanatus*. – NEUBAUER et al., supplementary material 1.  
 2014 *Gyraulus dealbatus*. – NEUBAUER et al., supplementary material 1.



- 2014 *Gyraulus dealbatus*. – SALVADOR & RASSER, p. 192, figs. 16-23.

**Occurrence:** Adelschlag-Fasanerie clay (>80 specimens), Adelschlag-Fasanerie sand (8 specimens), Riedensheim 1 (>20 specimens), Riedensheim 2 (>50 specimens) and Riedensheim 4 (>120 specimens).

**Discussion:** The present specimens are well within the common conchological variation of *G. applanatus*, reported for several sites in Germany (GOTTSCHICK & WENZ 1916; KOWALKE & REICHENBACHER 2005; SALVADOR & RASSER 2014). There are two extreme forms, the typical *G. applanatus* (flattened shell, regularly growing whorls, more closely packed together, with a well-marked carina on the laterobasal portion of the body whorl, and a smaller aperture, shaped as an arrowhead) and the typical *G. dealbatus* (BRAUN, 1851) (with a more rounded shell profile, with rapidly growing whorls, with all intermediate steps. As such, KOWALKE & REICHENBACHER (2005) synonymized the two species, a decision which is followed here.

Genus *Hippeutis* CHARPENTIER, 1837  
*Hippeutis subfontanus* (CLESSIN, 1877)  
 (Figs. 2N-O)

- 1877 *Planorbis (Hippeutis) subfontanus* CLESSIN, p. 39.  
 1923 *Hippeutis (Hippeutis) subfontanus subfontanus*. – WENZ, p. 1648.  
 1976 *Hippeutis subfontaneus subfontaneus* [sic]. – SCHLICKUM, p. 6, pl. 1, fig. 17.  
 2014 *Hippeutis subfontanus*. – NEUBAUER et al., supplementary material 1.

**Occurrence:** Riedensheim 4 (5 specimens).

**Discussion:** The genus *Hippeutis* is easily recognizable by its flattened and angular shell profile (it is round in early whorls, though), slightly incised suture and arrowhead-shaped aperture. The present specimens compare well with *H. subfontanus* (syntypes SMNS 106434), a species known from coeval and nearby localities from the Silvana Beds (“Silvanaschichten”, in German) of the OSM (WENZ 1923; SCHLICKUM 1976).

Genus *Planorbarius* DUMÉRIL, 1806  
*Planorbarius cornu* (BRONGNIART, 1810)  
 (Figs. 2P-Q)

- 1810 *Planorbis cornu* BRONGNIART, p. 371, pl. 22, fig. 6.  
 1923 *Coretus cornu cornu*. – WENZ, p. 1426.  
 1966 *Planorbarius cornu*. – SCHLICKUM, p. 326, pl. 13, fig. 27.  
 1970a *Planorbarius cornu*. – SCHLICKUM, p. 149, pl. 10, fig. 7.  
 1989 *Planorbarius cornu*. – REICHENBACHER, p. 172, pl. 1, fig. 10.

- 2004 *Planorbarius cornu*. – BINDER, p. 193, pl. 2, figs. 2-3.  
 2006 *Planorbarius cornu cornu*. – KÓKAY, p. 58, pl. 20, fig. 6.  
 2009 *Planorbarius cornu cornu*. – BÖTTCHER et al., p. 239, figs. 2.4-2.6.  
 2014 *Planorbarius cornu*. – NEUBAUER et al., supplementary material 1.  
 2014 *Planorbarius cornu*. – SALVADOR & RASSER, p. 193, figs. 26-28.

**Occurrence:** Adelschlag-Fasanerie limestone (>30 specimens), Adelschlag-Fasanerie clay (>40 specimens), Adelschlag-Fasanerie sand (5 specimens), Riedensheim 1 (>20 specimens), Riedensheim 2 (>30 specimens) and Riedensheim 4 (>50 specimens).

**Discussion:** Despite the fact that, for the vast majority of the present specimens, only the first whorls are preserved, the shell characteristic shape and unique sculpture enables the identification as *P. cornu*. This characteristic sculpture consists of a protoconch (ca. 1 whorl) sculptured by spiral lines of regularly organized circular pits (giving the impression of a reticulated pattern under light microscopy), transitioning abruptly to the teleoconch, which is sculptured by spiral striae on the first ca. 1½ whorl and smooth on the rest (except for growth lines).

*Planorbarius cornu* is especially abundant in the OSM and the sturdy nucleus of its shell favors preservation. The species is known from a long time span, ranging from the Middle Eocene to the Late Miocene of France, Germany and the Czech Republic (SCHLICKUM 1970a; KÓKAY 2006), which likely indicates an agglomerate of species under the same name. As such, until this species complex has received a much-needed revisionary work, this species is better classified as *P. cornu sensu lato*.

Eupulmonata

Superfamily Ellobioidea

Family Ellobiidae

Genus *Carychium* O.F. MÜLLER, 1773  
*Carychium eumicrum* BOURGUIGNAT, 1857  
 (Fig. 2R)

- 1857 *Carychium eumicrum* BOURGUIGNAT, p. 253.  
 1923 *Carychium eumicron eumicron* [sic]. – WENZ, p. 1187.  
 1977 *Carychium (Carychiella) eumicron* [sic]. – STRAUCH, p. 159, pl. 14, figs. 13-15, pl. 17, fig. 53, pl. 19, fig. 76.  
 1999a *Carychium eumicrum*. – STWORZEWICZ, p. 264, figs. 5-6.  
 2006 *Carychium (Carychiella) eumicron eumicron* [sic]. – KÓKAY, p. 48, pl. 16, fig. 5.  
 2014 *Carychium eumicrum*. – HARZHAUSER et al., p. 19, pl. 6, figs. 6, 7, 10.  
 2015 *Carychium (Carychiella) eumicron* [sic]. – SALVADOR, p. 38, fig. 1.

**Occurrence:** Riedensheim 4 (5 specimens).

**Description:** Shell diminutive, pupiform to fusiform, narrow. Protoconch (~1 whorl) dome-shaped, smooth; transition to teleoconch unclear. Teleoconch smooth, except by fine growth lines. Whorl profile convex. Suture well-marked, deep. Aperture ellipsoid; parietal lamella well-marked; median palatal tooth very faint. Peristome narrow, very weakly reflexed. Umbilicus rimate, very shallow.

**Discussion:** *Carychium eumicrum* is easily diagnosed by its much smaller size than other Carychiinae. Other diagnostic characters include a much slenderer shell, a lack of teleoconch sculpture, a less developed aperture (with a narrow and very weakly reflexed peristome) and the apertural dentition (with a well-marked parietal lamella and a very faint median palatal tooth). This species is known from Central Europe from the Late Oligocene to Middle Miocene (STRAUCH 1977; STWORZEWICZ 1999a).

*Carychium (Carychium) galli* SALVADOR, 2015  
(Figs. 2S-T)

2015 *Carychium (Carychium) galli*. – SALVADOR, p. 39, figs. 2-4.

**Occurrence:** Adelschlag-Fasanerie clay (12 specimen), Riedensheim 1 (2 specimens), Riedensheim 2 (7 specimens) and Riedensheim 4 (>100 specimens).

**Discussion:** This species was previously known only from its type locality in Sandelzhausen (MN 5), Germany. It is diagnosed mainly by displaying a simple internal lamella (columellar apparatus) (SALVADOR 2015). This species is similar to *Carychium nouleti* BOURGUIGNAT, 1857, known from many Miocene localities throughout Central Europe, which can be distinguished mainly by bearing a sinuous internal lamella (STRAUCH 1977; STWORZEWICZ 1999a). Other useful diagnostic characters of *C. galli* are a usually slenderer and smaller shell, the more defined and spaced axial sculpture, the more angular shape of the peristome and a strong and distinct palatal tooth (SALVADOR 2015). The presence of a simple vs. sinuous internal lamella is an important character for taxonomy, separating two large subgeneric groups (STRAUCH 1977).

The presents specimens, though low in number, show a similar variation in overall shell shape as seen in Sandelzhausen (SALVADOR 2015), going from a broader form to a narrower one, with many intermediate forms. Both fossil and recent *Carychium* species are known for a large amount of conchological variability in overall shell shape and in the whorls' height and relative proportions (BULMAN 1990; STWORZEWICZ 1999a).

*Carychium (Saraphia) nouleti* BOURGUIGNAT, 1857  
(Fig. 2U)

1857 *Carychium nouleti* BOURGUIGNAT, figs. 9-10.  
1923 *Carychium nouleti nouleti*. – WENZ, p. 1195.

1923 *Carychium nouleti gibbum*. – WENZ, p. 1197.  
1977 *Carychium (Saraphia) nouleti*. – STRAUCH, p. 162, pl. 15, figs. 24-27, pl. 18, fig. 61, pl. 20, fig. 83.  
1999a *Carychium nouleti*. – STWORZEWICZ, p. 269, figs. 19-22.

**Occurrence:** Adelschlag-Fasanerie clay (6 specimens).

**Discussion:** These few larger specimens of *Carychium* are reminiscent of the shells of *C. nouleti* reported from the Middle Miocene of Opole, Poland (STRAUCH 1977), in both size and overall shape. Shell shape is somewhat reminiscent of the smaller *C. galli*, but the clearest diagnostic feature is the sinuous internal lamella (columellar apparatus) (see also the discussion of *C. galli* above). The species is known throughout the Miocene of Europe and Algeria (STRAUCH 1977).

Stylommatophora  
Superfamily Clausilioidea  
Family Clausiliidae

Genus *Pseudidyla* BOETTGER, 1877

*Pseudidyla moersingensis* (BOETTGER, 1877)  
(Figs. 2V-W)

1877 *Clausilia (Pseudidyla) mörsingensis* BOETTGER, p. 89, pl. 3, figs. 32-34.  
1923 *Pseudidyla moersingensis moersingensis*. – WENZ, p. 791.  
1981 *Pseudidyla moersingensis*. – NORDSIECK, p. 107.  
2007 *Pseudidyla moersingensis*. – NORDSIECK, p. 136.  
2015 *Pseudidyla moersingensis*. – SALVADOR, p. 47, figs. 19-22.

**Occurrence:** Riedensheim 1 (9 specimens), Riedensheim 2 (>20 specimens) and Riedensheim 4 (>100 specimens).

**Discussion:** The present material consists of spire and aperture fragments. The shell is sinistral, with an acuminate apex; the protoconch (ca. 2 whorls) is rounded and smooth, transitioning abruptly to a teleoconch sculpture by well-marked sinuous axial ribs that become stronger towards the aperture; the body whorl is non-apostrophic, with two crests on its basal surface (the lower one stronger than the upper) and a slight furrow between them; the aperture is roughly oval, with a small rounded area between parietal lamella and palatal region; the peristome is greatly reflexed.

The following apertural barriers are always present: a strong and vertical parietal lamella; a columellar lamella (leading to the clausilium); a basal lamella (beginning deeper on the body whorl inner surface); two folds preceding the columellar lamella and one fold preceding basal lamella; a principal lamella (deeper on the body whorl's inner palatal surface). Other apertural barriers are not always present, such as one to two basal folds, one supracolumellar fold and one infraparietal fold. Weak fold-like marks are sometimes present on the palatal region.

Due to the overall shell profile and especially the apertural shape and barriers, the specimens can be identified as

*Pseudidyla moersingensis*. This species is known from the late Early to early Late Miocene of Germany (NORDSIECK 1981).

Superfamily Cochlicopoidea  
Family Cochlicopidae  
Genus *Azeca* FLEMING, 1828  
*Azeca penecke* ANDREAE, 1892  
(Fig. 2X)

- 1891 *Azeca Boettgeri* PENECKE, p. 364, pl. 21, figs. 8a-b [non ANDREAE 1884].  
1892 *Azeca penecke* ANDREAE, p. 435.  
1923 *Azeca penecke*. – WENZ, p. 1095.  
2014 *Azeca penecke*. – HARZHAUSER et al., p. 20, pl. 6, figs. 8, 11, 13-14.

**Occurrence:** Riedensheim 4 (>30 specimens).

**Discussion:** Although the specimens are fragmentary, several entirely preserved apertures permit identification to species level. The triangular aperture (columellar and parietal regions of peristome meet at an angle of ca. 90°) with a complete and thickened peristome, alongside the dentition of the present specimens (with four teeth), is diagnostic for *Azeca penecke* (HARZHAUSER et al. 2014b). This dentition consists of a median parietal tooth, a low palatal tooth and two columellar teeth; the parietal tooth is stronger than the others, which are all of similar size.

*Azeca penecke* was previously known only from the early Middle Miocene of the Rein Basin, Austria (HARZHAUSER et al. 2014b). The palatal tooth seems to be stronger in the specimens from the Rein Basin, but this could represent intraspecific morphological variation. As such, the present record considerably expands the distribution of the species.

Superfamily Gastrodontoidea  
Family Pristilomatidae  
Genus *Vitrea* FITZINGER, 1833  
*Vitrea ammoni* (CLESSIN, 1894)  
(Figs. 2Y-Z)

- 1894 *Hyalina Ammoni* CLESSIN, p. 29.  
1923 *Vitrea ammoni*. – WENZ, p. 292.

**Occurrence:** Riedensheim 1 (1 specimen), Riedensheim 2 (3 specimens) and Riedensheim 4 (>80 specimens).

**Discussion:** The present material compares well to the original description and syntypes (SMNS 106363, 106364) of *V. ammoni*, a species known only from the geographically close and likely coeval site of Undorf (WENZ 1923). These syntypes, however, seem to belong to several species (and maybe even genera), as remarked by CLESSIN (1894) himself. The present material compares well to a syntype which was

alone in the lot (SMNS 106364) and thus likely is the one to which the original description refers to.

Superfamily Helicoidea  
Family Helicidae  
Genus *Pseudochloritis* BOETTGER, 1909  
*Pseudochloritis* sp.  
(Fig. 2A')

**Occurrence:** Riedensheim 1 (9 specimens), Riedensheim 2 (5 specimens) and Riedensheim 4 (11 specimens).

**Discussion:** Identification as *Pseudochloritis* is possible due to the characteristic flattened early whorls and sculpture (protoconch of ca. 1¼ whorl, large in relation to following whorl, sculptured by fine striae dotted with weak papillae, transitioning gradually to the teleoconch, which is sculptured by thickened growth lines and irregular weak furrows, with regularly arranged papillae). It is impossible to proceed further than genus level in the identification, but *P. incrassata* (KLEIN 1853) is very commonly found in coeval sites (e.g., SALVADOR 2013; SALVADOR et al. 2015b).

Genus *Megalotachea* PFEFFER, 1930  
*Megalotachea silvana* (KLEIN, 1853)  
(Figs. 3A-C)

- 1853 *Helix silvana* KLEIN, p. 205, pl. 5, fig. 2.  
1923 *Cepaea silvana silvana*. – WENZ, p. 667.  
1976 *Cepaea silvana silvana*. – SCHLICKUM, p. 17, pl. 4, figs. 62-63.  
1989 *Cepaea silvana silvana*. – REICHENBACHER, p. 165, pl. 2, figs. 17-19.  
2006 *Cepaea silvana*. – KÓKAY, p. 93, pl. 36, figs. 2-3.  
2013 *Cepaea silvana*. – RASSER et al., p. 440.

**Occurrence:** Adelschlag-Fasanerie sand (1 specimen).

**Remarks:** The present specimen conforms well to *M. silvana* (syntype SMNS 22738) in size and overall shell shape and proportions. This species is very common in the OSM, lending its name to the Silvana Beds.

Genus *Palaeotachea* JOOSS, 1912  
*Palaeotachea renevieri* (MAILLARD, 1892)  
(Figs. 3D-F)

- 1892 *Helix (Macularia) Renevieri* MAILLARD, p. 43, pl. 3, fig. 18.  
1923 *Cepaea renevieri*. – WENZ, p. 652.  
1954 *Cepaea* cf. *renevieri*. – ZÖBELEIN, p. 156.

**Occurrence:** Adelschlag-Fasanerie sand (1 specimen).

**Remarks:** This species is identified by its small size, small circular aperture, flattened shell profile and faint keel. *Palaeotachea renevieri* is known from the Middle and Late Miocene of southern Germany and Switzerland (WENZ 1923; ZÖBELEIN 1954).

*Megalotachea* vel *Palaeotachea* sp.

**Occurrence:** Riedensheim 1 (1 specimen) and Riedensheim 4 (4 specimens).

**Discussion:** Some few fragments of spire apices from the Riedensheim locality cannot be assigned precisely to either *Megalotachea* or *Palaeotachea*. Both genera occur in Adelschlag-Fasanerie (see above), but there are no complete specimens from Riedensheim.

Family Hygromiidae

Genus *Leucochroopsis* BOETTGER, 1908

*Leucochroopsis* sp.

(Fig. 3G)

**Occurrence:** Riedensheim 2 (5 specimens) and Riedensheim 4 (5 specimens).

**Remarks:** The assignment of the present fragmentary specimens to the genus *Leucochroopsis* is possible by the following characters: a depressed conical spire; the rounded basal portion of the shell; regularly growing and smoothly keeled whorls; a crescent-shaped aperture; and teleoconch sculpture pattern (fine regularly distributed scales, giving the impression of prosocline axial striae). Further identification in the species level is not possible, but the present specimens are reminiscent (in overall shell shape and proportions) of *L. kleinii* (KLEIN, 1847), a common species in the German Silvana Beds.

Genus *Urticicola* LINDHOLM, 1927

*Urticicola perchtae* SALVADOR, 2013b

(Figs. 3H-I)

2009a *Hygromiidae* gen. indet. sp. 2. – MOSER et al., p. 50.

2009 *Leucochroopsis* sp. – BÖTTCHER, p. 241, figs. 13-14.

2013b *Urticicola perchtae* SALVADOR, p. 168, figs. 28-32.

**Occurrence:** Riedensheim 4 (2 specimens).

**Discussion:** The profile of the whorls (with a smooth but prominent keel-like angulation), the depressed spire and the teleoconch sculpture (regularly distributed and vertically elongated fine scales), allow the identification as *Urticicola perchtae*. The species was previously known only from the German fossil outcrops of Sandelzhausen (type locality) and Oggenhausen (SALVADOR 2013b), coeval with Riedensheim.

Superfamily Limacoidea

Family Agriolimacidae

Genus *Deroceras* RAFINESQUE, 1820

*Deroceras* sp.

(Fig. 3J)

**Occurrence:** Adelschlag-Fasanerie sand (4 specimens), Riedensheim 2 (1 specimen) and Riedensheim 4 (4 specimens).

**Remarks:** Slug shells are vestigial and internal, having a very limited taxonomic value. Nevertheless, the present material (oval shell, with nucleus lightly bent laterally and concentric well-marked growth lines) compare well to specimens of the genus *Deroceras*. As remarked by HARZHAUSER et al. (2014), the genus is present in Europe since the Miocene, but the fossils are often identified as either *Limax* LINNAEUS, 1758 or *Milax* GRAY, 1855.

**Fig. 3.** Fossil gastropods. **A-C** – *Megalotachea silvana* (BSPG 2013 XXVI; Adelschlag-Fasanerie; H = 16.2 mm, D = 25.4 mm). **D-F** – *Palaeotachea renevieri* (BSPG 2013 XXVI; Adelschlag-Fasanerie; H = 12.5 mm, D = 16.7 mm). **G** – *Leucochroopsis* sp. (BSPG 2014 XIX 038; Riedensheim 2; H = 2.2 mm, D = 3.1 mm). **H** – *Urticicola perchtae* (BSPG 2014 XIX 063; Riedensheim 4; H = 2.1 mm, D = 3.1 mm). **I** – *Urticicola perchtae* (BSPG 2014 XIX 088; Riedensheim 4; D = 3.5 mm). **J** – *Deroceras* sp. (BSPG 2014 XIX 096; Riedensheim 2; H = 4.5 mm, D = 3.3 mm). **K** – *Vitrina suevica* (BSPG 2014 XIX 065; Riedensheim 4; H = 1.7 mm, D = 3.1 mm). **L** – *Vitrina suevica* (BSPG 2014 XIX 093; Riedensheim 4; D = 2.3 mm). **M** – *Discus pleuradrus* (BSPG 2014 XIX 084, spcm. #1; Riedensheim 4; H = 1.9 mm, D = 3.9 mm). **N** – *Discus pleuradrus* (BSPG 2014 XIX 084, spcm. #2; Riedensheim 4; D = 3.2 mm). **O** – *Granaria* sp. (BSPG 2014 XIX 091; Riedensheim 4; H = 1.7 mm, D = 1.6 mm). **P** – *Gastrocopta acuminata* (BSPG 2014 XIX 082; Riedensheim 4; H = 2.6 mm). **Q** – *Gastrocopta nouletiana* (BSPG 2014 XIX 077, spcm. #1; Riedensheim 4; H = 1.9 mm). **R** – *Gastrocopta nouletiana* (BSPG 2014 XIX 077, spcm. #2; Riedensheim 4; H = 2.2 mm). **S** – *Strobilops costata* (BSPG 2014 XIX 057; Riedensheim 4; H = 1.5 mm, D = 2.3 mm). **T** – *Strobilops uniplicata* (BSPG 2014 XIX 041; Riedensheim 2; H = 1.1 mm, D = 2.0 mm). **U** – *Negulopsis lineolata* (BSPG 2014 XIX 094; Riedensheim 4; H = 1.2 mm). **V** – *Truncatellina* cf. *pantherae* (BSPG 2014 XIX 089; Riedensheim 4; H = 1.0 mm, D = 0.9 mm).

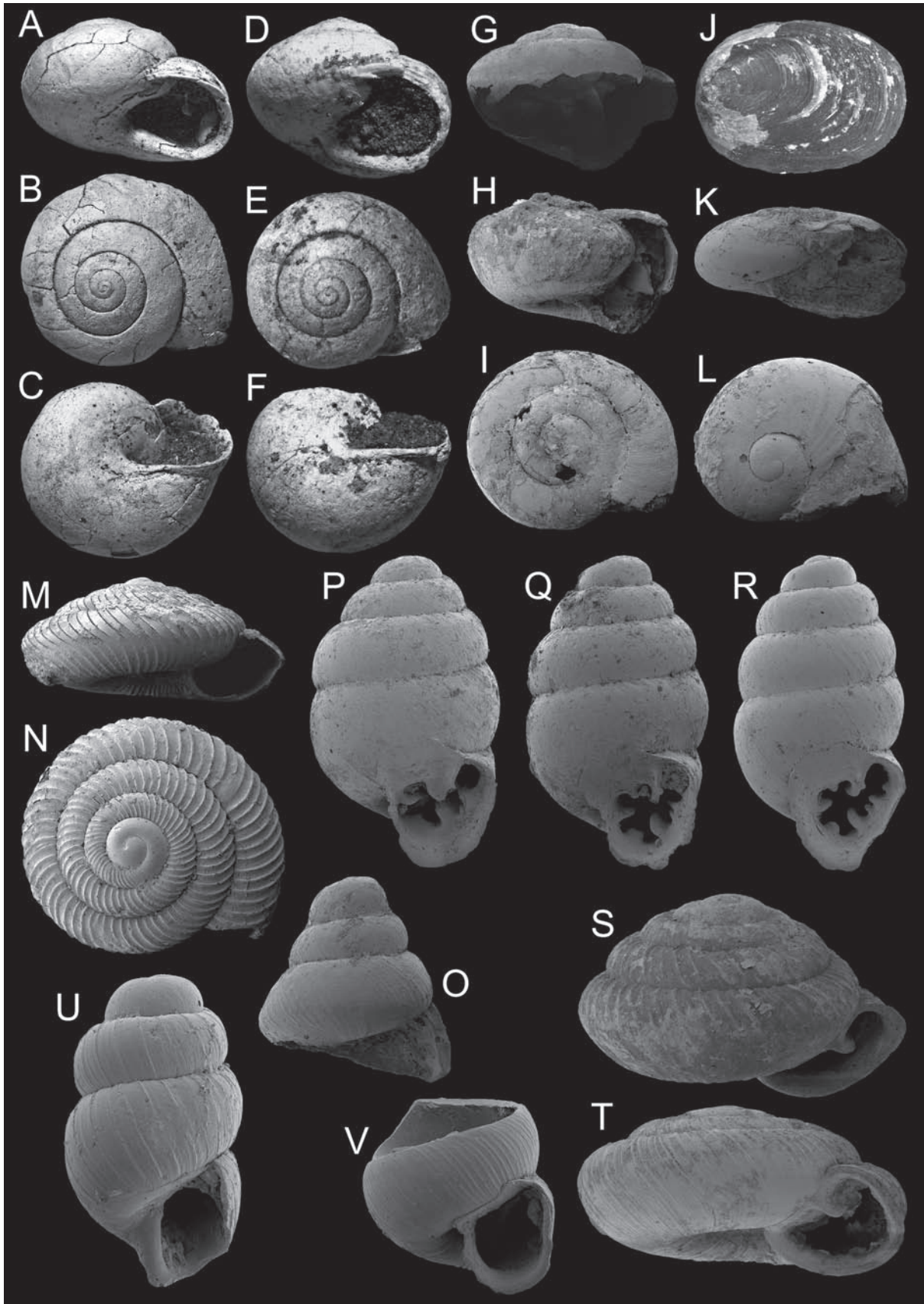


Fig. 3.

## Family Vitrinidae

Genus *Vitrina* DRAPARNAUD, 1801*Vitrina suevica* SANDBERGER, 1872

(Figs. 3K-L)

- 1872 *Vitrina suevica* SANDBERGER, pl. 29, figs. 27a-b.  
 1875 *Vitrina suevica*. – SANDBERGER, p. 602.  
 1923 *Vitrina suevica suevica*. – WENZ, p. 219.  
 1967 *Vitrina (Vitrina) suevica suevica*. – SCHÜTT, p. 213, fig. 17.

**Occurrence:** Riedensheim 4 (2 specimens).

**Discussion:** The present specimens have a discoidal shell, with a flattened spire and rapidly expanding whorls, a slightly incised suture and a protoconch (ca. 1 whorl) sculptured by spiral rows of punctae, which gradually transitions to a smooth teleoconch. They compare well to *Vitrina suevica* (holotype SMNS 106439). This species is known from a few Middle Miocene sites of southern Germany (SCHÜTT 1967).

## Superfamily Punctoidea

## Family Discidae

Genus *Discus* FITZINGER, 1833*Discus pleuradrus* (BOURGUIGNAT, 1881)

(Figs. 3M-N)

- 1881 *Helix pleuradra* BOURGUIGNAT, p. 53, pl. 3, figs. 67-72.  
 1923 *Gonyodiscus (Gonyodiscus) pleuradra pleuradra*. – WENZ, p. 341.  
 1942 *Gonyodiscus (Gonyodiscus) pleuradra pleuradra*. – WENZ & EDLAUER, p. 93.  
 1967 *Discus (Discus) pleuradrus*. – SCHÜTT, p. 213, fig. 16.  
 1976 *Discus (Discus) pleuradrus*. – SCHLICKUM, p. 12, pl. 2, fig. 37.  
 1981 *Discus (Discus) pleuradrus*. – LUEGER, p. 40, pl. 4, figs. 6-7.  
 2000 *Discus (Discus) pleuradra* [sic]. – FISCHER, p. 145, fig. 21.  
 2004 *Discus pleuradrus*. – HARZHAUSER & BINDER, p. 22, pl. 7, figs. 9-11.  
 2006 *Discus pleuradrus*. – KÓKAY, p. 75, pl. 28, figs. 3-4.  
 2009 *Discus pleuradrus*. – BÖTTCHER et al., p. 239, figs. 2.10-2.11.  
 2013 *Discus pleuradrus*. – RASSER et al., p. 439.  
 2014 *Discus pleuradrus*. – SALVADOR & RASSER, p. 195, figs. 32-33.

**Occurrence:** Adelschlag-Fasanerie clay (12 specimens), Riedensheim 2 (4 specimens) and Riedensheim 4 (>80 specimens).

**Discussion:** The present specimens show a discoid shell, with a low spire, regularly increasing whorls, a faint keel on median-upper portion of the body whorl and a wide umbilicus; the protoconch (ca. 1½ whorl) is flat and smooth, transitioning abruptly to the teleoconch, which is sculptured by strong prosocline ribs. The specimens compare well with

*D. pleuradrus*, a species known from the entire extent of the Miocene in Central and Western Europe, being especially common in the OSM (KÓKAY 2006; BÖTTCHER et al. 2009). Early and Late Miocene records could actually belong to other species, as remarked by MOSER et al. (2009a), thus restricting *D. pleuradrus* to the Middle Miocene of France, southern Germany and Austria (HARZHAUSER et al. 2014). Further revision is needed for this species complex.

## Superfamily Pupilloidea

## Family Chondrinidae

Genus *Granaria* HELD, 1838*Granaria* sp.

(Fig. 3O)

**Occurrence:** Adelschlag-Fasanerie clay (2 specimens), Riedensheim 2 (1 specimen) and Riedensheim 4 (10 specimens).

**Discussion:** The conical acuminated spire, regular whorl growth, convex whorls and the sculpture pattern (round and smooth protoconch of ca. 1½ whorl, transitioning abruptly to teleoconch, which is sculptured by very fine prosocline ribs) indicate the genus *Granaria* (HÖLTKE & RASSER 2013). Spires of *Granaria* are very common in coeval sites (e.g., SALVADOR 2015; SALVADOR et al. 2015a). Since no aperture was preserved, a more precise identification is impossible.

## Family Gastrocoptidae

Genus *Gastrocopta* WOLLASTON, 1878*Gastrocopta acuminata* (KLEIN, 1846)

(Fig. 3P)

- 1846 *Pupa acuminata* KLEIN, p. 75, pl. 1, fig. 19.  
 1923 *Gastrocopta (Albinula) acuminata acuminata*. – WENZ, p. 916.  
 1999b *Gastrocopta acuminata*. – STWORZEWICZ, p. 161, figs. 56-58.  
 2000 *Gastrocopta (Albinula) acuminata*. – MANGANELLI & GIUSTI, p. 60, pl. 1, figs. 1-6; pl. 2, figs. 1-7.  
 2015 *Gastrocopta acuminata*. – SALVADOR, p. 42, fig. 7.

**Occurrence:** Adelschlag-Fasanerie clay (4 specimens), Riedensheim 2 (2 specimens) and Riedensheim 4 (>40 specimens).

**Discussion:** The present specimens compare well to *G. acuminata* (syntypes SMNS 106361), diagnosed by a proportionately larger size than other coeval congeners and the shape of the anguloparietal lamella. The species occurs from the Middle Miocene to the Late Pliocene and perhaps even the Early Pleistocene (STWORZEWICZ 1999b; MANGANELLI & GIUSTI 2000).

*Gastrocopta nouletiana* (DUPUY, 1850)

(Figs. 3Q-R)

- 1850 *Pupa Nouletiana* DUPUY, p. 309, pl. 15, fig. 6.  
 1923 *Gastrocopta (Sinalbinula) nouletiana nouletiana*. – WENZ, p. 930.  
 1999b *Gastrocopta nouletiana*. – STWORZEWICZ, p. 163, figs. 59–61.  
 2015 *Gastrocopta nouletiana*. – SALVADOR, p. 43, figs. 8–11.

**Occurrence:** Riedensheim 4 (>100 specimens).

**Discussion:** The present specimens compare well to *G. nouletiana*, a frequent species throughout the Miocene European fossil record. The shells show some variation in overall shape, from more ovate (Fig. 3Q) to more slender ones (Fig. 3R), similar to what has been reported for other sites (e.g., SALVADOR 2015). The number and strength of the apertural barriers also vary, as common in the family; the total number of apertural barriers is usually eight in Riedensheim and seven in Adelschlag-Fasanerie (they lack the interpalatal tooth). The present apertural barriers are: suprapalatal tooth, upper palatal tooth, interpalatal tooth, lower palatal tooth, basal tooth, columellar lamella, infraparietal lamella, anguloparietal lamella (bifid, composed by a large and thick angular lamella, vertically positioned, and a narrow parietal lamella, folded towards the outer lip).

#### Family Strobilopsidae

Genus *Strobilops* PILSBRY, 1893

*Strobilops costata* (CLESSIN, 1877)

(Fig. 3S)

- 1877 *Strobilus costatus* (SANDBERGER MS) CLESSIN, p. 37.  
 1885 *Strobilus bilamellatus* CLESSIN, p. 79.  
 1915 *Strobilops (Strobilops) costata*. – WENZ, p. 79, textfig. 7, pl. 9, figs. 15–16.  
 1923 *Strobilops (Strobilops) costata*. – WENZ, p. 1041.  
 1967 *Strobilops (Strobilops) costata*. – SCHÜTT, p. 213, fig. 15.  
 1999b *Strobilops costata*. – STWORZEWICZ, p. 152, figs. 34–37.  
 2006 *Strobilops costata*. – KÓKAY, p. 72, pl. 26, figs. 11–13.  
 2006 *Strobilops costata bilamellata*. – KÓKAY, p. 72, pl. 26, figs. 14–15.

**Occurrence:** Riedensheim 4 (8 specimens).

**Discussion:** The present specimens have a conical-depressed shell, with whorls regularly growing, a slit-shaped aperture (bearing a strong median parietal tooth), a complete thickened and greatly reflexed peristome and a wide and deep umbilicus; the protoconch (ca. 1¼ whorl) is smooth and flattened, abruptly transitioning to the teleoconch, which is sculptured by strong widely spaced prosocline ribs. They compare well to *S. costata*, a species known from the Miocene of Central Europe (type locality Undorf) and reported to have some degree of morphological variation (STWORZEWICZ 1999b). The species *S. bilamellatus*, also from Undorf, is considered a synonym of *S. costata* (WENZ, 1915).

*Strobilops uniplicata* (BRAUN in WALCHNER, 1851)  
 (Fig. 3T)

- 1851 *Helix uniplicata* BRAUN in WALCHNER, p. 1138.  
 1885 *Strobilus planus* CLESSIN, p. 80, pl. 7, fig. 8.  
 1923 *Strobilops (Strobilops) uniplicata plana*. – WENZ, p. 1059.  
 1976 *Strobilops uniplicata plana*. – SCHLICKUM, p. 11, pl. 2, fig. 31.  
 1999b *Strobilops uniplicata*. – STWORZEWICZ, p. 156, figs. 44–45.  
 2006 *Strobilops uniplicata plana*. – KÓKAY, p. 71, pl. 26, figs. 7–8.

**Occurrence:** Riedensheim 2 (1 specimen).

**Discussion:** The present specimens have a discoid shell, with regularly growing whorls, a circular aperture (with a strong median parietal tooth), a complete thickened and reflexed peristome and a wide and deep umbilicus; the protoconch (ca. 1¼ whorl) is smooth and flattened, transitioning abruptly to the teleoconch, which is sculptured by well-marked prosocline ribs. They compare well to *S. uniplicata*, a species known from the Late Oligocene to the Middle Miocene of Central Europe (STWORZEWICZ 1999b). The species *S. plana* (from Undorf) is a subspecies of *S. uniplicata*.

#### Family Vertiginidae

Genus *Negulopsis* NORDSIECK, 2014

*Negulopsis lineolata* (SANDBERGER, 1872)

(Fig. 3U)

- 1843 *Bulimus lineolatus* A. BRAUN, p. 149 [*nomen nudum*].  
 1851 *Bulimus lineolatus* A. BRAUN, p. 1137 [*nomen nudum*].  
 1858 *Pupa cryptodus* “BRAUN” SANDBERGER, livr. 1, pl. 5, figs. 13–13c [non *Pupa cryptodonta* A. BRAUN 1843; *cryptodus* SANDBERGER is an unjustified emendation].  
 1858 *Pupa suturalis*. – SANDBERGER, livr. 1, pl. 6, figs. 1–1a [non *Bulimus suturalis* A. BRAUN 1851].  
 1858 *Pupa (Pupilla) suturalis* “BRAUN” SANDBERGER, livr. 2, p. 54 [non *Bulimus suturalis* A. BRAUN 1851].  
 1872 *Pupa lineolata* SANDBERGER, pl. 23, figs. 12–12b.  
 1872 *Pupa lineolate*. SANDBERGER, p. 397, p. 438.  
 1919 *Negulus suturalis gracilis* GOTTSCHICK & WENZ, p. 9, pl. 1, figs. 12–13.  
 1923 *Negulus suturalis suturalis*. – WENZ, p. 1024 [non A. BRAUN 1851].  
 1923 *Negulus suturalis gracilis*. – WENZ, p. 1027.  
 1999b *Negulus suturalis*. – STWORZEWICZ, p. 146, figs. 23–25 [non A. BRAUN 1851].  
 2004 *Negulus gracilis*. – HARZHAUSER & BINDER, p. 126, pl. 6, figs. 9–10.  
 2008 *Negulus gracilis*. – HARZHAUSER et al., p. 50, fig. 5.4.  
 2014 *Negulopsis suturalis*. – NORDSIECK, p. 175, fig. 13 [non A. BRAUN 1851].  
 2015a *Negulus suturalis*. – SALVADOR et al., p. 266, fig. 5C [non A. BRAUN 1851].

**Occurrence:** Riedensheim 4 (1 specimen).

**Remarks:** The very characteristic sculpture of this minute cylindrical-pupiform Miocene snail allows the identification as the species normally referred to as “*Negulus suturalis*” in the literature (STWORZEWICZ 1999b; HARZHAUSER et al. 2008; see the nomenclatural remarks below). The two Miocene fossil species occurring in Germany are “*N. suturalis*” and *N. gracilis*; the latter was originally described as a subspecies of the previous. HARZHAUSER & BINDER (2004) consider both species valid (based on whorl convexity and aperture height), using the name “*N. suturalis*” for Late Oligocene to Early Miocene forms and *N. gracilis* for Middle to Late Miocene forms. STWORZEWICZ (1999b), on a more thorough analysis, found no morphological differences between them and treat them as synonyms; a decision which is followed here. The new genus *Negulopsis* was recently created to allocate the European fossil species of *Negulus* (NORDSIECK 2014), widespread from the Eocene to Pliocene (ZILCH 1959-1960; ESU et al. 1993). Recent *Negulus* is exclusively African (BRUGGEN 1994).

**Nomenclature:** SANDBERGER (1875: 397) stated clearly and convincingly that A. BRAUN named this species *Pupa lineolata*, and that he applied the name *Bulimus suturalis* to the species *Acicula limbata* REUSS, 1849 [but actually to *A. filifera* SANDBERGER, 1862, which SANDBERGER (1875) synonymized with *A. limbata*]. WENZ (in FISCHER & WENZ, 1912) reinstated the name *suturalis* without providing any justification (there or in his subsequent publications); all later authors seem to have followed him uncritically. SANDBERGER (1872) made the name *lineolatus* available by providing a figure with a legend. *Bulimus suturalis* is available from A. BRAUN (1851) and is synonymous with *A. filifera*.

Finally, NORDSIECK (2014) defined the type species of the genus based on a misidentification, as explained above. As such, the type species of the genus *Negulopsis* NORDSIECK, 2014 is now fixed (under Article 70.3 ICZN) as *Pupa lineolata* SANDBERGER, 1872, misidentified as *Pupa suturalis* SANDBERGER, 1858 in the original designation by NORDSIECK (2014).

#### Genus *Truncatellina* LOWE, 1852

*Truncatellina* cf. *pantherae* HARZHAUSER & NEUBAUER  
in HARZHAUSER et al., 2014  
(Fig. 3V)

2014 *Truncatellina pantherae* HARZHAUSER & NEUBAUER  
in HARZHAUSER et al., 25, pl. 8, figs. 3-4, 13.

**Occurrence:** Riedensheim 4 (3 specimens).

**Discussion:** The present specimens can be assigned to the genus *Truncatellina* by the minute size, overall shape of the whorls, their growth pattern and sculpture (teleoconch sculptured by fine prosocline ribs), and the rounded trapezoid aperture, with a complete reflexed peristome. The identification beyond genus level is complicated by the fragmentary

nature of the material. Nevertheless, the lack of apertural barriers seems to indicate *T. pantherae*. The single preserved aperture is somewhat narrower than in *T. pantherae*, but this could represent morphological variation.

#### Genus *Vertigo* O.F. MÜLLER, 1773

*Vertigo angulifera* BOETTGER, 1884

(Fig. 4A)

- 1884 *Vertigo (Alaea) angulifera* BOETTGER, p. 271, pl. 4, figs. 10a-c.  
1923 *Vertigo (Vertilla) angulifera angulifera*. – WENZ, p. 1006.  
1967 *Vertigo (Vertilla) angulifera angulifera*. – SCHÜTT, p. 207, fig. 9.  
1998 *Vertigo angulifera*. – FINGER, p. 44, pl. 9, fig. H.  
1999b *Vertigo angulifera*. – STWORZEWICZ, p. 144, fig. 18.  
2008 *Vertigo angulifera*. – HARZHAUSER et al., p. 50, figs. 5.7-5.8.  
2014 *Vertigo angulifera*. – HARZHAUSER et al., p. 23, pl. 8, figs. 5-7.

**Occurrence:** Riedensheim 4 (13 specimens).

**Discussion:** The present specimens compare well in overall shell shape and apertural shape and barriers with *V. angulifera*. The minute ovate shell has a smooth protoconch (ca. 1¼ whorl), transitioning rather abruptly to a teleoconch sculptured by very fine prosocline ribs; the aperture is rounded trapezoid, with a weakly marked sinus (on the meeting of parietal and palatal regions of peristome) and four apertural lamellae (palatal, columellar, parietal and angular). *Vertigo angulifera* is known from the Early and Middle Miocene of Central Europe (HARZHAUSER et al. 2014).

#### *Vertigo callosa* (REUSS, 1849)

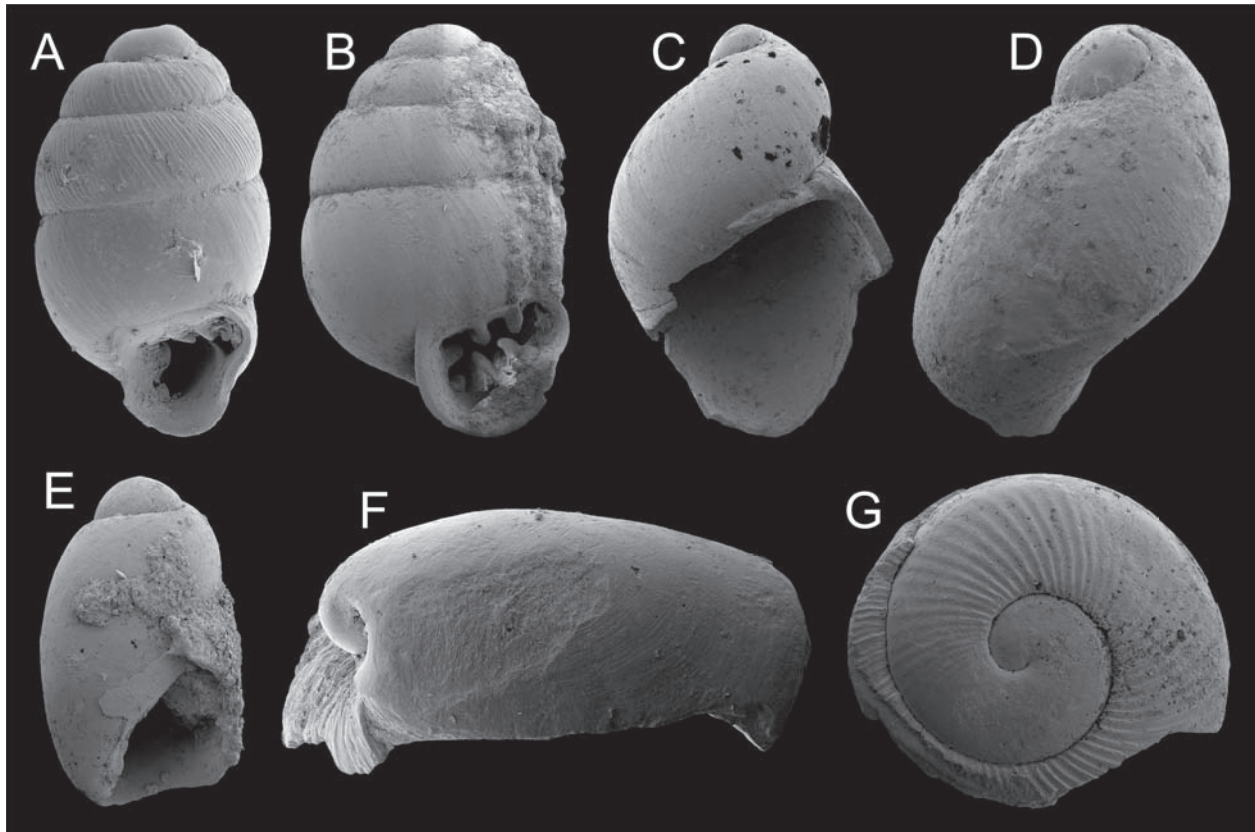
(Fig. 4B)

- 1849 *Pupa callosa* REUSS, p. 30, pl. 3, fig. 7.  
1923 *Vertigo (Vertigo) callosa*. – WENZ, p. 983.  
1999b *Vertigo callosa*. – STWORZEWICZ, p. 137, figs. 6-7.  
2015 *Vertigo callosa*. – SALVADOR, p. 45, figs. 17-18.

**Occurrence:** Adelschlag-Fasanerie clay (2 specimens).

**Discussion:** The present specimens compare well to the typical *Vertigo callosa*, a commonly found fossil that ranges from the Late Oligocene to the Late Miocene of Central Europe (STWORZEWICZ 1999b). This species is known for a large conchological variability in size, overall shell shape, aperture shape, and number and strength of the apertural barriers (STWORZEWICZ 1999b; SALVADOR 2015). The present specimens have a rounded triangular to trapezoid aperture, with six apertural barriers, namely: parietal lamella, angular lamella, upper palatal tooth, lower palatal tooth, basal tooth, columellar lamella; the angular lamella and upper palatal tooth are in close proximity to each other, forming a circular sinus.





**Fig. 4.** Fossil gastropods. **A** – *Vertigo angulifera* (BSPG 2014 XIX 092; Riedensheim 4; H = 1.4 mm). **B** – *Vertigo callosa* (BSPG 2014 XX 009; Adelschlag-Fasanerie; H = 1.7 mm). **C** – *Oxyloma minima* (BSPG 2014 XIX 056; Riedensheim 4; H = 2.5 mm). **D** – *Oxyloma minima* (BSPG 2014 XIX 078; Riedensheim 4; H = 2.5 mm). **E** – *Pseudoleacina* sp. (BSPG 2014 XIX 058; Riedensheim 4; H = 2.0 mm, D = 1.2 mm). **F** – *Testacella* sp. (BSPG 2014 XIX 081; Riedensheim 4; H = 2.5 mm). **G** – *Archaeozonites* sp., shell apex fragment (BSPG 2014 XIX 062; Riedensheim 4; D = 2.6 mm).

#### Superfamily Succineoidea

##### Family Succineidae

Genus *Oxyloma* WESTERLUND, 1885

*Oxyloma minima* (KLEIN, 1853)

(Figs. 4C-D)

- 1853 *Succinea minima* KLEIN, p. 205.  
 1923 *Succinea (Amphibina) minima minima*. – WENZ, p. 893.  
 1976 *Succinea (Hydrotropa?) minima*. – SCHLICKUM, p. 11, pl. 2, fig. 34.  
 2006 *Succinea minima*. – KÓKAY, p. 74, pl. 27, fig. 13.  
 2013b *Succinea minima*. – SALVADOR, p. 158, figs. 1-2.  
 2014 *Oxyloma minima*. – HARZHAUSER et al., p. 27, pl. 9, figs. 1-2, 6.

**Occurrence:** Adelschlag-Fasanerie clay (2 specimens), Riedensheim 4 (8 specimens).

**Discussion:** *Oxyloma minima* (syntypes SMNS 106410) is

easily identified in fossil samples by its succineiform shell, small size, whorls growth pattern and incised suture. The species is known from several localities throughout the Miocene of Central Europe (KÓKAY 2006).

#### Superfamily Testacelloidea

##### Family Oleacinidae

Genus *Pseudoleacina* WENZ, 1914

*Pseudoleacina* sp.

(Fig. 4E)

**Occurrence:** Riedensheim 4 (1 specimen).

**Discussion:** The rounded and slightly bulbous protoconch, the convex but nearly straight whorl profile and elongated aperture (with a prominently acuminate meeting of the parietal and palatal regions) are together reminiscent of the genus *Pseudoleacina*. Further identification is not possible.

Family Testacellidae  
 Genus *Testacella* DRAPARNAUD, 1801  
*Testacella* sp.  
 (Fig. 4F)

**Occurrence:** Riedensheim 4 (3 specimens).

**Discussion:** The vestigial ear-shaped shells of *Testacella* are very characteristic, bearing a pointed apex, quickly growing whorls, well-marked growth lines and an oval and elongated aperture, with thickened parietal and columellar regions. Only juvenile specimens were found in the present material, precluding identification to species level. Nevertheless, the overall shell shape (with a low shell and a pointed but curved apex) is reminiscent of *Testacella schuetti* SCHLICKUM 1967, a species known from a few Middle Miocene localities of Austria and SE Germany (HARZHAUSER et al. 2008; SALVADOR 2014).

Superfamily Zonitoidea  
 Family Zonitidae  
 Genus *Archaeozonites* SANDBERGER, 1872  
*Archaeozonites* sp.  
 (Fig. 4G)

**Occurrence:** Riedensheim 2 (2 specimens) and Riedensheim 4 (6 specimens).

**Discussion:** Only apical fragments are present; nevertheless, they show the main diagnostic features of the genus *Archaeozonites* (strong prosocline ribs, flattened whorl profile and weakly marked suture), allowing at least for genus level identification. The genus is known in Europe from the Middle Eocene to the Late Pliocene (ZILCH 1959-1960).

## 5. Discussion

The sedimentology of the outcrops offers the main clues about the paleoenvironment, but non-marine gastropods can help refine environmental reconstructions. Land snails, in particular, often show on the generic level a preference for one type of habitat (BARKER 2001; COOK 2001; PEARCE & ÖRSTAN 2006). As such, it is common for paleoecological reconstructions to use ecological data from Recent land snail genera as a guide for reconstructing the habitats of congeneric fossils (e.g., ALBESA et al. 1997; MOSER et al. 2009a). Some remarks concerning the gastropod paleohabitats in the Miocene sites of Riedensheim and Adelschlag-Fasanerie are thus given.

### 5.1. Riedensheim

The gastropod-bearing marly sediments are superim-

posed on fluvial sandy deposits that incised into the Cretaceous Wellheim Formation. The dark fossil-bearing layers are intercalated in olive-grey marls and silts containing centimeter-sized carbonate concretions and larger blocks of Cretaceous rocks up to ca. 30 cm in size. Thus, the fossil-bearing strata Riedensheim 1 to 4 probably represent oxbow lakes in which the aquatic gastropods lived and the land snails were deposited at river highstands or during flash floods. These are intercalated by floodplain deposits with possible pedogenic features (carbonate concretions). The large blocks indicate the existence of steep slopes in the vicinity that may have provided the more open area habitats needed by some of the snail species (see below).

In Riedensheim there seems to have been a rich freshwater gastropod community living in stagnant or slow moving permanent waters (such as oxbows), a well-vegetated area immediately surrounding it, and an environment dominated by humid woods beyond that (eventual patches of more open rocky or grassland areas should have existed beyond that). This reconstruction is explored in more detail below.

Regarding the freshwater environment, most of the Recent congeners can be found in many different environments, but they share a preference for richly vegetated, slow moving or standing water (WELTER-SCHULTES 2012). The appearance of *Hippeutis* in the topmost layer of the fossil-bearing strata, as well as the upward increase in land snail diversity, could point to shallowing.

Both *Carychium* and *Oxyloma* species are hygrophilous, living in very humid forests and meadows. Moreover, *Oxyloma* can be usually found in the reed belt surrounding water bodies (WELTER-SCHULTES 2012). The abundance of the diminutive and fragile *Carychium galli* seems to point to a very richly vegetated and humid area. *Oxyloma minima*, which also has a remarkably fragile shell, was also found relatively frequently.

When comparing the composition of the molluscan fauna across the three different layers in Riedensheim (Table 1), it is possible to see an increase in terrestrial species richness from layers 1 to 4. This could be related to increasingly hospitable habitats for the land snails in the vicinities of the water body, to the shrinking and shallowing of the water body as mentioned above or to more frequent flood events.

The vast majority of land snail species in the Riedensheim fauna are inhabitants of humid forests, in particular *Discus* and *Vitrina* (KERNEY et al. 1983; WELTER-SCHULTES 2012). Furthermore, Recent *Negulus* species are only known from tropical African forests (BRUGGEN

**Table 1.** Occurrence of fossil gastropod species (and total number of specimens recovered) on each site and layer (an “\*” indicates that the number refers to opercula). The horizontal blank lines delimitates the groups Caenogastropoda, Basommatophora and Eupulmonata, in this order. Species are listed in the same order they appear on the text.

Species	Adelschlag-Fasanerie			Riedenschlag		
	limestone	clay	sand	1	2	4
<i>Pomatias</i> sp.					1*	
<i>Bithynia</i> sp.			6*	6*	1* + 1	
<i>Pseudamnicola suevicus</i>		16				>30
<i>Galba dupuyiana</i>		>30		>30	>40	>50
<i>Stagnicola</i> cf. <i>praebouiletti</i>					1	
<i>Lymnaea</i> cf. <i>dilatata</i>	8			14	1	19
<i>Ferrissia deperdita</i>				2	1	
<i>Gyraulus albertanus</i>		>20		15	>30	>20
<i>Gyraulus applanatus</i>		>80	8	>20	>50	>120
<i>Hippeutis subfontanus</i>						5
<i>Planorbarius cornu</i>	>30	>40	5	>20	>30	>50
<i>Carychium eumicrum</i>						5
<i>Carychium galli</i>		12		2	7	>100
<i>Carychium nouleti</i>		6				
<i>Pseudidyla moersingensis</i>				9	>20	>100
<i>Azeca peneckeii</i>						>30
<i>Vitrea ammoni</i>				1	3	>80
<i>Pseudochloritis</i> sp.				9	5	11
<i>Megalotachea silvana</i>			1			
<i>Palaeotachea renevieri</i>			1			
<i>Megalotachea</i> vel. <i>Palaeotachea</i>				1		4
<i>Leucochroopsis</i> sp.					5	5
<i>Urticicola perchtae</i>						2
<i>Deroceras</i> sp.			4		1	4
<i>Vitrea suevica</i>						2
<i>Discus pleuradrus</i>		12			4	>80
<i>Granaria</i> sp.		2			1	10
<i>Gastrocopta acuminata</i>		4			2	>40
<i>Gastrocopta nouletiana</i>						>100
<i>Strobilops costata</i>						8
<i>Strobilops uniplicata</i>					1	
<i>Negulopsis lineolata</i>						1
<i>Truncatellina</i> cf. <i>pantherae</i>						3
<i>Vertigo angulifera</i>						13
<i>Vertigo callosa</i>		2				
<i>Oxyloma minima</i>		2				8
<i>Pseudoleacina</i> sp.						1
<i>Testacella</i> sp.						3
<i>Archaeozonites</i> sp.					2	6

1994), but it is unclear how closely it is related to it *Negulopsis* and if an ecological comparison can be made. Some of the fossil genera are also supposed to inhabit humid forest, also tending towards warm environments, such as *Pseudoleacina*, *Pseudidyla*, *Leucochroopsis* and *Archaeozonites* (LUEGER 1981; HARZHAUSER & BINDER 2004; HARZHAUSER & TEMPFER 2004; NORDSIECK 2007). Other species can live both in forests and shrublands, provided it is a humid environment, such as those of the genera *Pomatias*, *Azeca* and *Testacella* (KERNEY & CAMERON 1979; BARKER & EFFORD 2004; WELTER-SCHULTES 2012; ROWSON et al. 2014).

Nevertheless, three genera are indicative of drier and more open habitats: *Granaria* and *Truncatellina*, which thrive on calcareous rocks and on meadows (WELTER-SCHULTES 2012; HÖLTKE & RASSER 2013), and supposedly the fossil genus *Pseudochloritis*, whose shell is considered an adaptation for reducing water loss (MOSER et al. 2009a). The scarcity and poor preservation of these taxa, however, indicate that such open habitats would be located further away from the deposits.

Finally, some recent genera (*Vitrea*, *Urticicola*, *Vertigo*, *Gastrocopta* and *Strobilops*) have too broad a range of habitats (WELTER-SCHULTES 2012) to be useful for a paleoenvironmental analysis (the latter two do not even have living native representatives in Europe). The slug *Deroceras* is also known from a broad range of habitats, including disturbed ones, provided they are humid (ROWSON et al. 2014).

It is also interesting to note the presence of two carnivorous species in the studied fauna. *Pseudoleacina* is a fossil genus, but its species likely were malacophagous, as are the remainder of the oleacinids (BARKER & EFFORD 2004). Recent *Testacella* feed mainly on earthworms, but gastropods and centipedes are also part of their diet (BARKER & EFFORD 2004; ROWSON et al. 2014). These two gastropods would surely have a broad range of prey to choose from in Riedensheim. No clear signs of predation by other malacophagous animals (such as holes on the shell, breakage followed by shell repair or anomalous growth etc.) were found in the present material.

## 5.2. Adelschlag-Fasanerie

The sedimentology of the basal layers of the sand pit points to a carbonate-rich freshwater lake. The initial lacustrine limestone precipitated during this phase was not exposed during sampling (it was seen only as a pile of rubble in one corner of the pit), which may explain the low diversity of the recorded fauna as a

sampling bias. Later, argillaceous sediments including the reddish to brownish clay were deposited, presumably indicating an increasingly shallow water body. A poorly sorted sandy gravel layer containing limonitic wood and bone debris marks the transition to the sandy layers overlying this deposit. The depositional system thus indicates the rapid transition from a flood plain environment to fluvial channel deposits.

The freshwater fauna is clearly dominated by *Gyraulus applanatus*, with comparatively few representatives of the other species. A considerable proportion of specimens of *G. applanatus* bear marks of shell breakage and further growth (Fig. 2M), which are commonly interpreted as the survival of these individuals after predation attempts. The pulmonate aquatic fauna is consistent with both temporary and perennial water bodies, but the presence of *Pseudamnicola* points to a perennial water body during the clay layer (Table 1). The impoverished aquatic fauna of the sand layer is consistent with the transition to fluvial channel deposits. As in Riedensheim, the presence of the hygrophilous genera *Carychium* and *Oxyloma* seem to indicate a well-vegetated area surrounding the water body. The remaining of the terrestrial fauna is not very useful for paleoecological analysis, but *Discus* at least is a reasonable indicator for humid forests.

## 5.3. Faunal composition

Comparing the overall faunas, 13 of the 17 species occurring in Adelschlag-Fasanerie are also known from Riedensheim (which has 35 species, considering all layers; Table 1). Given the possible biostratigraphic correlation explained above (OSM C+D), the most obvious comparison of these presently described snail faunas would be with the geographically close and nearly coeval localities of Adelschlag, Attenfeld, Sandelzhausen and Undorf (see also Table 2 of Appendix 2).

Riedensheim shares ca. 60% of its snail species with Sandelzhausen (reinterpreting the records of the genera *Limax* and *Milax* as *Deroceras* sp., as explained above), but only ca. 45% with Undorf. Similarly, Adelschlag-Fasanerie shares 12 of its species with Sandelzhausen and only eight with Undorf. As such, the presently studied faunas seem to have a greater affinity with Sandelzhausen. The species that occur only in Riedensheim and not in Sandelzhausen (*Negulopsis lineolata*, *Truncatellina* cf. *pantherae*, *Vertigo angulifera* and *Vitrea ammoni*) do not provide much information with respect to the paleoecological analysis. In contrast, species occurring only in Sandelzhausen, indicate a much more

diverse freshwater environment (see also MOSER et al. 2009b; SALVADOR & RASSER 2014).

Finally, the faunas of Adelschlag and Attenfeld (see the revised identification on Table 1 of Appendix 2) are restricted to freshwater species, all of which occur in Adelschlag-Fasanerie and/or Riedensheim. The comparison with these faunas underlines the expected affinities given the geographic and stratigraphic proximity of these two localities. The single terrestrial species found (*Opeas minutum* from Adelschlag) is recorded only from Undorf among the further localities discussed here.

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## Appendix 1

### List of analyzed material

All the material from Riedensheim and Adelschlag-Fasanerie available for each species is listed here. The order in which the species are presented below is the same as they appear in the main body of the text. Institutional abbreviations: BSPG = Bayerische Staatssammlung für Paläontologie und Geologie (Munich, Germany); SMNS = Staatliches Museum für Naturkunde Stuttgart (Stuttgart, Germany).

*Pomatias* sp.: BSPG 2014 XIX 095 (1 operculum).

*Bithynia* sp.: BSPG 2014 XIX 012 (4 opercula), XIX 039 (1 spcm., 1 operculum), XX 014 (2 opercula), XX 018 (3 opercula). SMNS 101684 (2 opercula), 101717 (1 operculum).

*Pseudamnicola suevicus* (GOTTSCHICK, 1928): BSPG 2014 XIX 086 (~20 spcm.), XX 003 (6 spcm.), XX 020 (4 spcm.). SMNS 101687 (6 spcm.), 101693 (6 spcm.).

*Galba dupuyiana* (NOULET, 1854): BSPG 2014 XIX 010 (~30 spcm.), XIX 018 (~30 spcm.), XIX 022 (5 spcm.), XIX 034 (7 spcm.), XIX 037 (1 spcm.), XIX 061 (~20 spcm.), XIX 067 (~20 spcm.), XX 010 (~30 spcm.). SMNS 101699 (8 spcm.).

*Stagnicola* cf. *praebouiletti* (SCHLICKUM, 1970c): BSPG 2014 XIX 037 (1 spcm.).

*Lymnaea dilatata* NOULET, 1854: BSPG 2013 XXVI (8 spcm.); 2014 XIX 007 (14 spcm.), XIX 040 (1 spcm.), XIX 049 (4 spcm.), XIX 071 (15 spcm.). SMNS 101695 (1 spcm.).

*Ferrissia deperdita* (DESMAREST, 1814): BSPG 2014 XIX 009 (2 spcm.), XIX 015 (1 spcm.).

*Gyraulus albertanus* (CLESSIN, 1877): BSPG 2014 XIX 001 (10 spcm.), XIX 014 (~30 spcm.), XIX 035 (2 spcm.), XIX 054 (4 spcm.), XIX 080 (~20 spcm.), XX 005 (~20 spcm.). SMNS 101683 (5 spcm.), 101708 (3 spcm.).

*Gyraulus applanatus* (THOMAE, 1845): BSPG 2014 XIX 002 (~20 spcm.), XIX 020 (~50 spcm.), XIX 029 (~40 spcm.), XIX 060 (~40 spcm.), XIX 075 (>50 spcm.), XX 004 (>50 spcm.), XX 016 (8 spcm.). SMNS 101686 (~30 spcm.), 101694 (~30 spcm.), 101706 (12 spcm.), 101709 (3 spcm.).

*Hippeutis subfontanus* (CLESSIN, 1877): BSPG 2014 XIX 055 (3 spcm.), XIX 068 (1 spcm.). SMNS 101704 (1 spcm.).

*Planorbarius cornu* (BRONGNIART, 1810): BSPG 2013 XXVI (~30 spcm.); 2014 XIX 008 (~20 spcm.), XIX 016 (8 spcm.), XIX 025 (6 spcm.), XIX 030 (~20 spcm.), XIX 053 (>50 spcm.), XIX 079 (>50 spcm.), XX 011 (~40 spcm.), XX 013 (1 spcm.), XX 017 (5 spcm.). SMNS 101685 (2 spcm.).

*Carychium eumicrum* BOURGUIGNAT, 1857: BSPG 2014 XIX 083 (3 spcm.). SMNS 101702 (2 spcm.).

*Carychium* (*Carychium*) *galli* SALVADOR, 2015: BSPG 2014 XIX 005 (2 spcm.), XIX 017 (4 spcm.), XIX 052 (6 spcm.), XIX 087 (>50 spcm.), XX 007 (7 spcm.). SMNS 101690 (5 spcm.), 101698 (~40 spcm.), 101707 (3 spcm.), 101713 (7 spcm.).

*Carychium nouleti* BOURGUIGNAT, 1857: BSPG 2014 XX 001 (1 spcm.), XX 019 (1 spcm.). SMNS 101719 (4 spcm.).

*Pseudidyla moersingensis* (BOETTGER, 1877): BSPG 2014 XIX 006 (9 spcm.), XIX 013 (16 spcm.), XIX 026 (1 spcm.), XIX 042 (9 spcm.), XIX 066 (~40 spcm.), XIX 074 (>50 spcm.). SMNS 101697 (12 spcm.).

*Azeca peneckeii* ANDREAE, 1892: BSPG 2014 XIX 064 (~20 spcm.), XIX 073 (14 spcm.).

*Vitrea ammoni* (CLESSIN, 1892): BSPG 2014 XIX 011 (1 spcm.), XIX 027 (3 spcm.), XIX 059 (~20 spcm.), XIX 085 (~30 spcm.). SMNS 101703 (12 spcm.), 101715 (15 spcm.).

*Pseudochloritis* sp.: BSPG 2014 XIX 003 (9 spcm.), XIX 021 (4 spcm.), XIX 031 (1 spcm.), XIX 072 (11 spcm.).

*Megalotachea silvana* (KLEIN, 1853): BSPG 2013 XXVI (1 spcm.).

*Palaeotachea renevieri* (MAILLARD, 1892): BSPG 2013 XXVI (1 spcm.).

*Megalotachea vel Palaeotachea* sp.: BSPG 2014 XIX 004 (1 spcm.), XIX 045 (2 spcm.), XIX 076 (2 spcm.).

*Leucochroopsis* sp.: BSPG 2014 XIX 023 (1 spcm.), XIX 038 (4 spcm.), XIX 050 (4 spcm.), XIX 090 (1 spcm.).

*Urticola perchtae* SALVADOR, 2013b: BSPG 2014 XIX 063 (1 spcm.), 2014 XIX 088 (1 spcm.).

*Deroceras* sp.: BSPG 2014 XIX 096 (1 spcm.), XIX 097 (2 spcm.), XX 015 (2 spcm.). SMNS 101716 (2 spcm.), 101718 (2 spcm.).

*Vitrina suevica* SANDBERGER, 1872: BSPG 2014 XIX 065 (1 spcm.), XIX 093 (1 spcm.).

*Discus pleuradrus* (BOURGUIGNAT, 1881): BSPG 2014 XIX 024 (1 spcm.), XIX 033 (3 spcm.), XIX 043 (~30 spcm.), XIX 084 (~30 spcm.), XX 012 (12 spcm.). SMNS 101696 (~20 spcm.).

*Granaria* sp.: BSPG 2014 XIX 036 (1 spcm.), XIX 044 (4 spcm.), XIX 091 (6 spcm.), XX 008 (2 spcm.).

*Gastrocopta acuminata* (KLEIN, 1846): BSPG 2014 XIX 019 (1 spcm.), XIX 028 (1 spcm.), XIX 051 (9 spcm.), XIX 082 (~20 spcm.), XX 002 (4 spcm.). SMNS 101705 (13 spcm.), 101714 (3 spcm.).

*Gastrocopta nouletiana* (DUPUY, 1850): BSPG 2014 XIX 048 (~30 spcm.), XIX 077 (~30 spcm.). SMNS 101700 (~20 spcm.), 101712 (~20 spcm.).

*Strobilops costata* (CLESSIN, 1877): BSPG 2014 XIX 057 (2 spcm.), XIX 070 (4 spcm.). SMNS 101692 (1 spcm.), 101711 (1 spcm.).

*Strobilops uniplicata* (BRAUN in WALCHNER, 1851): BSPG 2014 XIX 041 (1 spcm.).

*Negulopsis lineolata* (SANDBERGER, 1872): BSPG 2014 XIX 094 (1 spcm.).

*Truncatellina* cf. *pantherae* HARZHAUSER & NEUBAUER in HARZHAUSER et al., 2014: BSPG 2014 XIX 089 (3 spcm.).

*Vertigo angulifera* BOETTGER, 1884: BSPG 2014 XIX 047 (1 spcm.), XIX 092 (7 spcm.). SMNS 101701 (5 spcm.).

*Vertigo callosa* (REUSS, 1849): BSPG 2014 XX 009 (1 spcm.). SMNS 101688 (1 spcm.).

*Oxyloma minima* (KLEIN, 1853): BSPG 2014 XIX 056 (1 spcm.), XIX 078 (3 spcm.), XX 006 (1 spcm.). SMNS 101689 (1 spcm.), 101691 (3 spcm.), 101710 (1 spcm.).

*Pseudoleacina* sp.: BSPG 2014 XIX 058 (1 spcm.).

*Testacella* sp.: BSPG 2014 XIX 046 (1 spcm.), XIX 081 (2 spcm.).

*Archaeozonites* sp.: BSPG 2014 XIX 032 (2 spcm.), XIX 062 (2 spcm.), XIX 069 (4 spcm.).

## Appendix 2

**Table 1.** Gastropod species reported by REICHENBACHER et al. (2004) for the localities of Adelschlag and Attenfeld. The SEM images provided by these authors were used to offer a revised identification of the species (unfortunately, they did not figure *Bithynia* sp.).

REICHENBACHER et al. (2004)	Revised identification	Adelschlag	Attenfeld
<i>Belgrandiella?</i> sp.	<i>Pseudamnicola suevicus</i>	X	
<i>Bithynia</i> sp.	(not figured)	X	
<i>Lymnaea</i> sp.	<i>Galba dupuyiana</i>	X	X
<i>Omphiscola</i> sp.	<i>Opeas minutum</i>	X	
<i>Radix</i> sp.	<i>Lymnaea dilatata</i>	X	X
<i>Ferrissia</i> sp.	<i>Ferrissia deperdita</i>	X	X
<i>Gyraulus</i> sp. A	<i>Gyraulus applanatus</i>	X	X
<i>Gyraulus</i> sp. B	<i>Gyraulus albertanus</i>	X	
<i>Gyraulus</i> sp. C	<i>Gyraulus applanatus</i>	X	
<i>Hippeutis</i> sp.	<i>Hippeutis subfontanus</i>	X	
<i>Planorbarius</i> sp.	<i>Planorbarius cornu</i>	X	X

**Table 2.** Occurrence of gastropod species in the following localities: Adelschlag (Adels.), Adelschlag-Fasanerie (Ad.-Fasan.), Attenfeld (Atten.), Riedensheim, Sandelzhausen and Undorf. Species occurrence for Adelschlag and Attenfeld as reported by REICHENBACHER et al. (2004) and revised here (Appendix: Table 1); for Sandelzhausen as reported by SALVADOR (2013a, b, c) and SALVADOR & RASSER (2014); for Undorf by CLESSIN (1911), excluding dubious taxa (*sensu* WENZ 1923). Division of layers for Sandelzhausen follow MOSER et al. (2009a); a “?” indicates that the precise layer of origin is unknown.

Species	Adels.	Adelschlag-Fasanerie			Atten.	Riedensheim			Sandelzhausen		Undorf
		limestone	clay	sand		1	2	4	B-C2	C3-D1	
<i>Acanthinula trochulus</i>											x
<i>Acicula isselii</i>											x
<i>Archaeozonites costatus</i>											x
<i>Archaeozonites</i> sp.							x	x	x	x	
<i>Argna praeambula</i>											x
<i>Argna pseudoennea</i>											x
<i>Azeca peneckeii</i>								x			
<i>Bithynia gracilis</i>											x
<i>Bithynia</i> sp.	x			x		x	x			x	
<i>Carychium eumicrum</i>			x					x	?	?	x
<i>Carychium galli</i>						x	x	x		x	
<i>Carychium nouletii</i>			x								x
<i>Deroceras</i> sp.				x			x	x	?	?	x
<i>Discus pleuradrus</i>			x				x	x		x	
<i>Discus undorfensis</i>											x
<i>Emarginaria schaefferiana</i>											x
Endodontidae indet.										x	
<i>Ferrissia deperdita</i>	x				x	x	x		x		x
<i>Galba dupuyiana</i>	x		x		x	x	x	x	x	x	
<i>Gastrocopta acuminata</i>			x				x	x		x	x
<i>Gastrocopta nouletiana</i>								x	x	x	x
<i>Granaria grossecostata</i>									x	x	
<i>Granaria</i> sp.			x				x	x	x	x	
<i>Gyraulus albertanus</i>	x		x			x	x	x	x	x	
<i>Gyraulus applanatus</i>	x		x	x	x	x	x	x		x	x
<i>Helicodonta involuta</i>											x
<i>Helicodonta</i> sp.									?	?	
<i>Hippeutis subfontanus</i>	x							x			x
<i>Hippeutis</i> sp.										x	
<i>Janulus supracostatus</i>									?	?	x
<i>Klikia coarctata</i>										x	
<i>Klikia giengensis</i>											x
<i>Leucochroopsis kleini</i>										x	x
<i>Leucochroopsis</i> sp.							x	x			
<i>Lucilla subteres</i>									x		x
<i>Lymnaea dilatata</i>	x	x			x	x	x	x	x	x	x
<i>Megalotachea eversa</i>									x	x	
<i>Megalotachea silvana</i>				x							x
<i>Megalotachea sylvestrina</i>									x	x	
<i>Negulopsis lineolata</i>								x			x

