THE FOSSIL CONTINENTAL MOLLUSKS IN THE UPPER FRESHWATER MOLASSE (MIDDLE MIOCENE) OF THE DISTRICTS OF BIBERACH, RAVENSBURG AND NEU-ULM, GERMANY

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ABSTRACT – The present work is a taxonomical study of the continental mollusks collected in several fossil outcrops in the districts of Biberach and Ravensburg (SE Baden-Württemberg state) and Neu-Ulm (SW Bavaria state), Germany, by one of the authors (V.J.S.) in the years 1983-2013. All these fossil sites are of Middle Miocene age (European Mammal Neogene zones MN 5 and MN 6) and belong to the Upper Freshwater Molasse (“Obere Süßwassermolasse” or OSM), in the North Alpine Foreland Basin of southern Germany. The molluscan fauna of these sites counts with 17 gastropod and three bivalve species: *Tinnyea laureae*, *Pomatias* sp., *Bithynia* sp., *Theodoxus* sp., *Galba* cf. *G. dupuyiana*, *Lymnaea dilatata*, *Gyraulus applanatus*, *Planorbarius cornu*, *Opeas minutum*, Clausiliidae indet., *Triptychia* sp., *Archaeozonites costatus*, *Klikia* sp., *Pseudochloritis incrassata*, *Palaeotachea renevieri*, *Megalotachea silvana*, *Deroceras* sp., *Margaritifera flabellata*, *Unio kirchbergensis* and *Sphaerium* aff. *S. rivicola*. Finally, a few paleoenvironmental remarks are offered.

Key words: Bivalvia, European Mammal Neogene Zones MN5 and MN 6, Gastropoda, OSM, Pulmonata.

RESUMO – O presente trabalho é um estudo taxonômico dos moluscos continentais coletados em diversos afloramentos fossilíferos nos distritos de Biberach e Ravensburg (SE do Estado de Baden-Württemberg) e Neu-Ulm (SO do Estado de Bayern), Alemanha, por um dos autores (V.J.S.) durante os anos 1983-2013. Tais afloramentos datam do Mioceno Médio (zonas neógenas de mamíferos europeus MN5 e MN 6), pertencendo ao grupo “Obere Süßwassermolasse” (OSM) da bacia Alpina do Norte. A malacofauna dessas localidades conta com 17 espécies de gastrópodes e três de bivalves: *Tinnyea laureae*, *Pomatias* sp., *Bithynia* sp., *Theodoxus* sp., *Galba* cf. *G. dupuyiana*, *Lymnaea dilatata*, *Gyraulus applanatus*, *Planorbarius cornu*, *Opeas minutum*, Clausiliidae indet., *Triptychia* sp., *Archaeozonites costatus*, *Klikia* sp., *Pseudochloritis incrassata*, *Palaeotachea renevieri*, *Megalotachea silvana*, *Deroceras* sp., *Margaritifera flabellata*, *Unio kirchbergensis* e *Sphaerium* aff. *S. rivicola*. Adicionalmente, são oferecidos alguns comentários sobre o paleoambiente das localidades estudadas.

Palavras-chave: Bivalvia, zonas neógenas de mamíferos europeus MN 5 e MN 6, Gastropoda, OSM, Pulmonata.

INTRODUCTION

Sach (1999) described several Middle Miocene fossil sites in the district of Biberach, Baden-Württemberg state, SW Germany, with his main focus being the lithology, sedimentology, biostratigraphy and the fossil mammals of the region. This author also listed many mollusk-bearing sites, but, since they were not the objective of his study, he did not provide a formal treatment of them. These mollusks are also listed, but not described nor figured, in a recently

published catalogue of Early/Middle Miocene fossil sites in southern Germany (Sach, 2014). This catalogue also brings species lists of a few other newly discovered mollusk-bearing fossil sites in the neighboring districts of Ravensburg, in Baden-Württemberg, and Neu-Ulm, in Bavaria State (Figure 1), preliminarily listed by Sach (2014). Herein is presented a taxonomical analysis of these fossil continental mollusks, which are represented by 17 gastropod and three bivalve species, alongside with some paleoenvironmental remarks.

MATERIAL AND METHODS

The mollusk-bearing fossil sites in the districts of Biberach, Ravensburg and Neu-Ulm can be seen in Figure 1, as named by Sach (1999, 2014). The Middle Miocene fossil sites studied here are detailed below.

Biberach District

Wannenwaldtobel 1: 48°01'50.88"N, 09°50'01.14"E; boulder horizon of the Ries impact ("Brockhorizont" in the original), 603.5 m above sea level (a.s.l.); Mammal Neogene zones MN 5/6 (transition).

Wannenwaldtobel 2: coordinates as Wannenwaldtobel 1; calcareous marl and marlstone horizon ("Kalkmergel" in the original), 610.0 m a.s.l.; additional fine-sand horizon with bivalves (*Margaritifera flabellata*) at ~609 m a.s.l.; Mammal Neogene zones MN 5/6 (transition).

Tobel Oelhalde-Nord: 48°02'24.95"N, 09°49'52.03"E; two fine-grained sand horizons with reworked OSM components, 604.6 m and 612.5 m a.s.l.; Mammal Neogene zones MN 5/6 (transition).

Tobel Oelhalde-Süd: 48°02'16.08"N, 09°49'47.06"E; fine-sand horizon with reworked OSM components, 596.3 m a.s.l.; additional fine-grained sand horizon with bivalves (*Margaritifera flabellata*) at 600.2 m a.s.l.; Mammal Neogene zones MN 5/6 (transition).

Edelbeuren-Schlachtberg: 48°05'21.38"N, 10°01'17.71"E; two fine-grained sand horizons with reworked OSM components, ~583 m a.s.l.; Mammal Neogene zone MN 5.

Binnrot: 48°03'49.01"N, 10°03'07.94"E; fine-sand horizons with reworked OSM components, 571.3–572.7 a.s.l.; additional sandy horizon with bivalves (*Sphaerium* aff. *rivicola*) at ~577 m a.s.l.; Mammal Neogene zone MN 5.

Bonlanden: 48°04'03.71"N, 10°04'11.04"E; fine-sand horizon with reworked OSM components, 564.9 m a.s.l.; Mammal Neogene zone MN 6.

Edelbeuren-Maurerkopf: 48°05'40.82"N, 10°01'51.93"E; two fine-sand horizons with reworked OSM components, 559.5–563.0 m a.s.l.; Mammal Neogene zone MN 5.

Heselsberg (Ochsenhausen-Heselsberg): 48°04'11.19"N, 9°57'23.48"E; fine-gravel horizon ("Erolzheimer Sande" at "Baustelle Remmele" in the original) with reworked OSM components, ~607 m a.s.l.; and 48°04'05.33"N, 9°57'27.72"E; fine-sand horizon ("Baustelle Harsch" in the original) with reworked OSM components, ~620 m a.s.l.; Mammal Neogene zone MN 5 (both fossil sites).

Auttagershofen: 48°11'56.49"N, 10°01'04.74"E; calcareous marl horizon, ~531 m a.s.l.; Mammal Neogene zone MN 5.

Ravensburg District

Burgerbachtobel 1: 47°48'03.26", N 9°26'59.22"E (close to the border of Ravensburg and Bodenseekreis districts); calcareous marl and fine-sand horizons with reworked OSM components, ~580 m a.s.l.; Mammal Neogene zone MN 6; Schmalegger Tobel: 47°48'25.21", N 9°32'16.14"E; fine-sand horizons with reworked OSM components, ~510 m above sea level; Mammal Neogene zone MN 6.

Lattentobel: 47°49'49.70", N 9°25'57.63"E; fine-sand horizons with reworked OSM components, ~610 m; Mammal Neogene zone MN 6.

Neu-Ulm District

Altstadt-Untereichen: 48°09'29.47"N, 10°06'39.93"E; fine-sand horizons with reworked OSM components, ~562–566 m a.s.l.; additional fine-sand horizon with bivalves (*Margaritifera flabellata*) at ~570 m a.s.l.; Mammal Neogene zone MN 5.

The largest portion of the fossil material studied here derives from the localities Wannenwaldtobel 2, Edelbeuren-Maurerkopf, Burgerbachtobel 1 and Altstadt-Untereichen. Together, these four sites have so far yielded numerous fossils of mammals, other vertebrate groups, non-mollusk invertebrates (insects, crustaceans and ostracods) and plants (Sach, 1999, 2014). There are some additional sites in these districts that also bear mollusk fossils (Sach, 1999, 2014), but the material was too fragmentary and was not collected and thus, could not be studied here. As such, the records for the following sites could not be confirmed in the present work: Biberach: Awengen (*Lymnaea* sp., *Cepaea* sp.) and Oberstetten (*Cepaea* sp.); Ravensburg: Ibacher Tobel, Horber-/Staigertobel, Aichertobel and Weiler Sandkeller (*Unio* sp. vel *Margaritifera* sp.) and Höll-Tobel (?*Tropidomphalus* sp., *Margaritifera* cf. *flabellata*). The sites Schwendi-Tobel and Brunnentobel, in Ravensburg, despite harboring mollusks (Sach, 1999, 2014), were excluded from the present work, since their location and stratigraphical data remain unknown.

All the material from the above mentioned fossil sites, which is housed in the collection of the Staatliches Museum für Naturkunde Stuttgart (SMNS; Stuttgart, Germany), was analyzed for the present work. A list of the examined material follows each species description. The specimens were collected during the years of 1983 to 2013 by V.J. Sach; for more details, see Sach (1999). Systematic arrangements follow Bouchet *et al.* (2005) and Nordsieck (2014). Selected specimens were examined by scanning electronic microscopy (SEM) in the SMNS; shell measurements were obtained either with a digital caliper or with the aid of computer software. The following shell measurements abbreviations are used throughout the text: **H**, shell height; **D**, shell greatest width; **h**, operculum height; **L**, shell length (bivalves).

GEOLOGICAL SETTING

All the studied fossil sites date from the Middle Miocene (European Mammal Neogene zones MN 5 and MN 6) and belong to the stratigraphical unit known as the Upper Freshwater Molasse ("Obere Süßwassermolasse" in German, or OSM). More specifically: four sites (Bonlanden, Burgerbachtobel 1, Lattentobel and Schmalegger Tobel) are deemed to belong to the MN 6 zone; three sites (Wannenwaldtobel 1+2, Tobel Oelhalde-Süd and Tobel Oelhalde-Nord) belong to the transitional period MN 5/6; the remaining sites date from the MN 5 zone. For a more thorough

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

description of each fossil site, as well as the lithology of the fossiliferous sediments, their lithostratigraphic position and biostratigraphy, see Sach (1999, 2014) and Sach *et al.* (2003).

SYSTEMATIC PALEONTOLOGY

Class GASTROPODA Cuvier, 1795

Clade CAENOGASTROPODA Cox, 1960

Superfamily CERITHIOIDEA Fleming, 1822

Family PACHYCHILIDAE P. Fischer & Crosse, 1892

Tinnyea Hantken, 1887

Tinnyea lauraea (Mathéron, 1843)

(Figures 2A-B)

1843 *Melania lauraea* Mathéron, p. 291, pl. 36, figs. 23-24.

1927 *Melanatria escheri turrita*: Berz & Jooss, p. 206.

1953 *Brotia (Tinnyea) escheri*: Papp, p. 128, pl. 3, fig. 29; Schlickum, 1976, p. 4, pl. 1, fig. 9; Mikuz & Pavsic, 2000, p. 44, pl. 1, figs. 1-8.

2014 *Brotia escheri*: Sach, p. 23.

Material examined. SMNS 101648 (seven specimens).

Occurrence. Altenstadt-Untereichen.

Description. Shell medium-sized to large, turreted, with regularly growing whorls. Protoconch not preserved. Teleoconch sculpture by parallel oblique axial ribs on first whorls (distance between axial ribs roughly twice their width) and by both axial and spiral cords on the remaining whorls (distance between cords roughly equal to three times their width). First spiral cord on each whorl stronger, with spike-like protuberances when it meets with axial ribs. Whorls profile convex. Suture well-marked, but not too deep.

Discussion. As pointed out by Kadolsky (1995), the name *T. escheri* (Brongniart, 1823) is a *nomen nudum*. The first valid name for the species is *T. lauraea*. This species is known in the fossil record of Central Europe from the Oligocene to the Pliocene, but is rarer in the early and middle Miocene (Harzhauser *et al.*, 2002). Nevertheless, it is known from the coeval nearby locality of Oggenhausen (Berz & Jooss, 1927). **Paleoecological remarks.** This species is known from freshwater and oligohaline sediments (Kóky, 2006).

Superfamily LITTORINOIDEA Children, 1834

Family POMATIIDAE Newton, 1891

Pomatias Studer, 1789

Pomatias sp.

Material examined. SMNS 101678 (one operculum).

Occurrence. Burgerbachtobel 1.

Discussion. A single fragmentary operculum can be assigned to *Pomatias* by its spiral growth pattern, but identification beyond genus level is presently not possible.

Superfamily RISSOOIDEA Gray, 1847

Family BITHYNIIDAE Gray, 1857

Bithynia Leach, 1818

Bithynia sp.

(Figure 2C)

1999 *Bithynia* sp.: Sach, p. 24; Sach *et al.*, 2003, p. 6; Sach, 2014, p. 27.

Material examined. SMNS 101539 (>100 operculum).

Occurrence. Edelbeuren-Maurerkopf.

Discussion. Only opercula remain; their overall shape and concentric growth pattern indicate the genus *Bithynia*, but identification at species level is impossible.

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

Clade NERITIMORPHA Golikov & Starobogatov 1975

Family NERITIDAE Lamarck, 1809

Theodoxus Montfort, 1810

Theodoxus sp.

(Figure 2D)

2014 *Theodoxus crenulatus*: Sach, p. 25.

Material examined. SMNS 101649 (one specimen).

Occurrence. Altenstadt-Untereichen.

Discussion. The color pattern is preserved in this single fragment; this distinctive pattern allows the assignment to the genus *Theodoxus*. Despite a more precise identification at species level not being possible, it should be remarked that *Theodoxus crenulatus* (Klein, 1853) is a very common and widespread species in the middle and late Miocene of Central Europe and exhibits a great variation in color pattern (*e.g.* Harzhauser *et al.*, 2012).

Paleoecological remarks. The habitat range of recent *Theodoxus* species is ample, so its use for paleoecological inferences is very limited; nevertheless, all species are intolerable to drought and seem to prefer rocky substrates (Bandel, 2001; Zettler *et al.*, 2004; Bunje, 2005; Welter-Schultes, 2012).

PULMONATA Cuvier, 1814

Clade HYGROPHILA

Superfamily LYMNAEOIDEA Rafinesque, 1815

Family LYMNAEIDAE Rafinesque, 1815

Galba Schrank, 1803

Galba cf. *G. dupuyiana* (Noulet, 1854)

(Figure 2E)

1999 *Galba* sp.: Sach, p. 16; Sach *et al.*, 2003, p. 9; Sach, 2014, p. 37.

1999 *Lymnaea* cf. *L. armaniacensis*: Sach, p. 24; Sach *et al.*, 2003, p. 6; Sach, 2014, p. 27.

Material examined. SMNS 101540 (43 specimens), 101541 (one specimen), 101542 (one specimen), 101543 (one specimen), 101544 (eight specimens), 101545 (nine specimens).

Occurrence. Wannenwaldtobel 2, Edelbeuren-Maurerkopf and Auttagershofen.

Description. Shell small ($H < 1$ cm), lymnaeiform; shell width $\sim 1/2$ shell height. Transition proto- to teleoconch unclear. Teleoconch smooth, except for well-marked growth lines. Suture deep, well-marked. Whorls profile convex. Aperture oval, narrow, elongated. Peristome simple. Imperforate.

Discussion. Only broken and/or deformed spires remain in the present material, but they are reminiscent of *Galba dupuyiana*, a common species known throughout the middle Miocene of West and Central Europe (Kókay, 2006). The present specimens compare especially well with the taller and more elongated forms reported from the German early/middle Miocene sites of Oggenhausen and Sandelzhausen (Böttcher *et al.*, 2009; Salvador & Rasser, 2014).

Paleoecological remarks. The single recent European species, *Galba truncatula* (O.F. Müller, 1774), inhabits both permanent and temporary water bodies, usually on the margins (Chapuis *et al.*, 2007; Welter-Schultes, 2012).

Lymnaea Lamarck, 1799

Lymnaea dilatata (Noulet, 1854)

(Figures 2F-G)

1854 *Limnea dilatata* Noulet, p. 107.

1921 *Limnaea (Radix) dilatata*: Ehrhart & Jooss, p. 4.

1923 *Radix (Radix) socialis dilatata*: Wenz, p. 1277; Seemann, 1926, p. 92.

1999 *Lymnaea dilatata*: Sach, p. 16; Fischer, 2000, p. 136, figs. 1-2; Binder, 2002, p. 165, pl. 1, fig. 7a; Sach *et al.*, 2003, p. 6; Binder, 2004, p. 192, pl. 1, fig. 7; Kowalke & Reichenbacher, 2005, p. 630, figs. 9.4-9.5; Sach, 2014, p. 23; Salvador & Rasser, 2014, p. 189, figs. 8-9).

1999 *Lymnaea* sp.: Sach, p. 20.

1999 *Tudorella conica*: Sach, p. 24; Sach *et al.*, 2003, p. 6.

2006 *Radix dilatata*: Kókay, p. 52, pl. 17, fig. 14; Neubauer *et al.*, 2014, supplementary material 1.

Material examined. SMNS 101598 (~80 specimens), 101599 (~50 specimens), 101600 (one specimens), 101601 (three specimens), 101602 (one specimen), 101603 (two specimens), 101604 (six specimens), 101605 (three specimens), 101606

(one specimen), 101647 (seven specimens), 101680 (one specimen), 101682 (one specimen).

Occurrence. Wannenwaldtobel 2, Tobel Oelhalde-Süd, Bonlanden, Heselsberg, Edelbeuren-Maurerkopf, Burgerbachtobel 1 and Altenstadt-Untereichen.

Description. Shell large, lymnaeiform; spire acuminate, proportionately small. Transition proto- to teleoconch unclear. Teleoconch smooth, except for growth lines. Suture well-marked. Whorls profile slightly convex. Body whorl proportionately large. Peristome simple. Imperforate.

Discussion. *Lymnaea dilatata* is known from the whole Miocene of West and Central Europe (Binder, 2004; Kó kay, 2006). Some authors (e.g. Wenz, 1923; Kó kay, 2006) have placed the species in the genus *Radix* Montfort, 1810, but, as remarked by Fischer (2000), it is more reminiscent of *Lymnaea*. The single specimen previously identified as *Pomatias conicus* (Klein, 1853) by Sach (1999) and Sach *et al.* (2003) is a spire apex of *L. dilatata*.

Paleoecological remarks. Recent *Lymnaea* thrive in richly vegetated, shallow standing or slow-flowing waters, being commonly found in temporary water bodies (Glöer, 2002; Welter-Schultes, 2012).

Superfamily PLANORBOIDEA Rafinesque, 1815

Family PLANORBIDAE Rafinesque, 1815

Gyraulus Charpentier, 1837

Gyraulus applanatus (Thomae, 1845)
(Figures 2H-I)

1845 *Planorbis applanatus* Thomae, p. 150.

1851 *Planorbis dealbatus* Braun, p. 1134.

1923 *Gyraulus* (*Gyraulus*) *trochiformis applanatus*: Wenz, p. 1579.

1923 *Gyraulus* (*Gyraulus*) *trochiformis dealbatus*: Wenz, p. 1591.

1970a *Gyraulus trochiformis applanatus*: Schlickum, p. 148, pl. 10, fig. 6; Schlickum, 1970b, p. 180.

1964 *Gyraulus trochiformis dealbatus*: Schlickum, p. 15, pl. 2, fig. 35; Steininger *et al.*, 1973, p. 451, pl. 9, figs. 11a,b; Reichenbacher, 1989, pl. 1, fig. 11; Kó kay, 2006, p. 57, pl. 19, fig. 15.

2005 *Gyraulus applanatus*: Kowalke & Reichenbacher, p. 631, figs. 9.1-9.3; Kó kay, 2006, p. 56, pl. 19, figs. 13-14; Neubauer *et al.*, 2014, supplementary material 1.

1995 *Gyraulus dealbatus*: Kadolsky, p. 40, fig. 47; Binder, 2004, p. 193, pl. 2, figs. 1a-c; Neubauer *et al.*, 2014, supplementary material 1; Salvador & Rasser, 2014, p. 192, figs. 16-23.

Material examined. SMNS 101544 (17 specimens), 101545 (~30 specimens), 101546 (~40 specimens), 101547 (one specimen).

Occurrence. Wannenwaldtobel 2 and Edelbeuren-Maurerkopf.

Description. Shell very small ($D < 5$ mm), pseudodextral, planispiral; shell height ~1/3 shell width. Protoconch sculpture not preserved; transition to teleoconch unclear. Teleoconch smooth, except for growth lines. Spire depressed. Suture deep, well-marked. Whorls somewhat rapidly growing, especially body whorl. Body whorl rounded, with very faint keel on median portion. Aperture arrowhead-shaped. Peristome simple, sharp. Umbilicus wide, shallow.

Discussion. The present specimens compare well with *Gyraulus applanatus* by the aperture shape, rapidly growing whorls and a rounded body whorl profile with a faint keel on its median portion. This species has not been reported by Sach (1999, 2014) for any of the localities. *Gyraulus applanatus* is known from the very early to middle Miocene of Germany and Austria (Gottschick & Wenz, 1916; Kadolsky, 1995; Binder, 2004; Kowalke & Reichenbacher, 2005). There is some morphological variation within this species and transitional forms between it and *G. dealbatus*, as reported by previous authors (Gottschick & Wenz, 1916; Kowalke & Reichenbacher, 2005; Salvador & Rasser, 2014). This led Kowalke & Reichenbacher (2005) to synonymize both species. The present specimens from Biberach are mostly juvenile or fragmentary; the small number of adult specimens does not seem to present much variation.

Paleoecological remarks. Recent *Gyraulus* are found in many habitats, limiting their use in paleoecological analysis. Still, they usually inhabit shallow richly-vegetated standing or slow-flowing waters, sometimes even temporary water bodies (Welter-Schultes, 2012).

Planorbarius Duméril, 1806

Planorbarius cornu (Brongniart, 1810)
(Figure 2J)

1810 *Planorbis cornu* Brongniart, p. 371, pl. 22, fig. 6.

1923 *Coretus cornu cornu*: Wenz, p. 1426.

1966 *Planorbarius cornu*: Schlickum, p. 326, pl. 13, fig. 27; Schlickum, 1970a, p. 149, pl. 10, fig. 7; Reichenbacher, 1989, p. 172, pl. 1, fig. 10; Binder, 2004, p. 193, pl. 2, figs. 2-3; Neubauer *et al.*, 2014, supplementary material 1; Salvador & Rasser, 2014, p. 193, figs. 26-28.

1999 *Coretus* cf. *C. cornu*: Sach, p. 16.

1999 *Coretus* sp. Sach, p. 17.

2006 *Planorbarius cornu cornu*: Kó kay, p. 58, pl. 20, fig. 6; Böttcher *et al.*, 2009, p. 239, figs. 2.4-2.6.

2003 *Planorbarius* cf. *P. cornu*: Sach *et al.*, p. 6; Sach, 2014, p. 23.

Material examined. SMNS 101571 (>100 specimens), 101572 (>100 specimens), 101573 (three specimens), 101574 (>100 specimens), 101575 (13 specimens), 101576 (one specimen), 101577 (two specimens), 101578 (one specimen), 101579 (one specimen), 101580 (four specimens), 101581 (five specimens), 101646 (eight specimens).

Occurrence. Wannenwaldtobel 2, Tobel Oelhalde-Nord, Tobel Oelhalde-Süd, Edelbeuren-Schlachtberg, Bonlanden, Edelbeuren-Maurerkopf and Altenstadt-Untereichen.

Description. Shell large, sinistral, planispiral; shell height ~1/3 shell width. Spire very depressed. Suture deep, well-marked. Whorls regularly growing. Whorl profile rounded. Aperture rounded. Umbilicus very wide, deep. Unfortunately, due to poor preservation, proto- and teleoconch sculpture cannot be observed.

Discussion. The present specimens, despite the poor preservation, compare well with *Planorbarius cornu*, a morphologically variable species known from the middle Eocene to the late Miocene of France, Germany (especially abundant in the OSM) and Czech Republic (Schlickum, 1970a; Kóky, 2006). As pointed out by Harzhauser *et al.* (2014), this long time span could indicate the presence of more than one species. Until this species complex has been the target of revisionary work, we prefer a more conservative identification as *P. cornu*.

Paleoecological remarks. Recent *Planorbarius* are found in typically richly-vegetated standing or slow-moving waters (Glöer, 2002; Welter-Schultes, 2012).

Clade STYLOMMATOPHORA A. Schmidt, 1855
Superfamily ACHATINOIDEA Swainson, 1840
Family SUBULINIDAE P. Fischer & Crosse, 1877

Opeas Albers, 1850

Opeas minutum (Klein, 1853)
(Figure 2K)

1853 *Bulimus minutus*: Klein, p. 212, pl. 5, fig. 9.
1923 *Opeas minutum*: Wenz, p. 872; Seemann, 1926, p. 92; Kóky, 2006, p. 80, pl. 30, fig. 16; Harzhauser *et al.*, 2014, p. 28, pl. 9, figs. 3-5, 7.
1976 *Opeas (Opeas) minutum*: Schlickum, p. 14, pl. 3, fig. 46.

Material examined. SMNS 101551 (one specimen).

Occurrence. Edelbeuren-Maurerkopf.

Description. Shell small, with regularly growing whorls. Protoconch large, rounded, dome-shaped, apparently smooth; transition to teleoconch unclear. Teleoconch apparently smooth. Whorls profile slightly convex. Suture well-marked but not too deep.

Discussion. *Opeas minutum* is easily diagnosed by the small size of its subulinid shell. Although this single specimen is a spire apex, it compares extremely well with material from other Miocene fossil sites in Germany. The species is known from the early/middle Miocene of Hungary, Germany, Austria and Switzerland (Schlickum, 1976; Kóky, 2006; Harzhauser *et al.*, 2014) and has not been reported by Sach (1999, 2014) for the present locality.

Paleoecological remarks. Recent *Opeas* are found in tropical and subtropical regions worldwide (Zilch, 1959-1960; Willig, 2013).

Superfamily CLAUSILIOIDEA J.E. Gray, 1855
Family CLAUSILIIDAE Gray, 1855

Clausiliidae indet.
(Figures 2L-M)

2003 Clausiliidae indet.: Sach *et al.*, p. 6; Sach, 2014, p. 27.

Material examined. SMNS 101549 (one specimen), 101550 (four specimens).

Occurrence. Edelbeuren-Maurerkopf.

Discussion. The sinistral shell and rounded whorl profile (Figure 2L), as well as the sculpture pattern on the apertural fragment (Figure 2M), point to a clausiliid. Unfortunately, with the present material a more precise determination is not possible.

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

Family FILHOLIIDAE Wenz, 1923

Triptychia Sandberger, 1875

Triptychia sp.
(Figure 2N)

Material examined. SMNS 101548 (one specimen).

Occurrence. Edelbeuren-Maurerkopf.

Description. Shell sinistral, with conical profile. Protoconch dome-shaped; transition to teleoconch unclear. Teleoconch sculpture not preserved. Whorl profile slightly convex. Suture deep, well-marked, slightly incised.

Discussion. The conical sinistral shell with its flat whorl profile agrees very well with the genus *Triptychia*. Nevertheless, it is presently impossible to proceed further than this in the classification of the material.

Paleoecological remarks. It is usually suggested that filholiids were mostly wood-dwelling animals, preferring humid and warm forests (Schnabel, 2007, and references therein).

Superfamily ZONITOIDEA Mörch, 1864
Family ZONITIDAE Mörch, 1864

Archaeozonites Sandberger, 1872

Archaeozonites costatus Sandberger, 1875
(Figures 2O-P)

1875 *Archaeozonites costatus*: Sandberger, p. 604; Schlickum, 1976, p. 18, pl. 5, fig. 66; Rasser *et al.*, 2013, p. 440.

1921 *Zonites (Aegopis) costatus*: Ehrat & Jooss, p. 3; Wenz, 1923, p. 254; Seemann, 1926, p. 91.

1999 *Valvata* sp.: Sach, p. 22; Sach, 2014, p. 31.

2006 *Aegopis costatus*: Kóky, p. 77, pl. 29, figs. 11-12.

2002 *Miozonites costatus*: Binder, p. 168, pl. 1, figs. 14-16, pl. 3, fig. 8, pl. 7, fig. 3, pl. 8, fig. 4; Harzhauser *et al.*, 2014, p. 33, pl. 10, figs. 13-19.

Material examined. SMNS 101556 (three specimens), 101557 (one specimen), 101558 (one specimen), 101559 (three specimens).

Occurrence. Edelbeuren-Schlachtberg, Binnrot and Edelbeuren-Maurerkopf.

Description. Shell large ($D > 2$ cm), helicoid, with broad conical spire and regularly growing whorls. Protoconch (~1 whorl) flattened, sculptured by fine riblets that grow coarser towards teleoconch. Teleoconch sculptured by numerous strong parallel prosocline ribs; distance between ribs equal to rib's width; ribs apparently absent on lower portion of whorls. Suture weakly marked. Whorls profile flattened; body whorl with a strong keel. Aperture oval. Umbilicus broad, deep.

Discussion. Despite the somewhat distorted preservation of the body whorl and aperture, the present specimens compare fittingly with *Archaeozonites costatus*, a species known from the early and middle Miocene of Central Europe (Kó kay, 2006) and common in the Silvana-beds ("Silvanaschichten") of southwestern Germany (MN 5-6; Schlickum, 1976). The single specimen of *Valvata* sp. reported by Sach (1999, 2014) is a misidentification of a fragment of *A. costatus*.

Paleoecological remarks. As a fossil genus, any paleoecological inference is tentative; still, Lueger (1981) considered that *Archaeozonites laticostatus* (Sandberger, 1885), also from the Miocene of Central Europe, lived under leaves or between rocks in moist forests.

Superfamily HELICOIDEA Rafinesque, 1815
Family ELONIDAE Gittenberger, 1977

Klikia Pilsbry, 1895

Klikia sp.
(Figure 2Q)

1999 *Klikia coarctata*: Sach, p. 24; Sach *et al.*, 2003, p. 6; Sach, 2014, p. 27.

Material examined. SMNS 101552 (~85 specimens), 101645 (four specimens), 101681 (one specimen).

Occurrence. Edelbeuren-Maurerkopf, Heselsberg and Altenstadt-Untereichen.

Description. Shell medium-sized ($D > 1$ cm), depressed, multispiral. Suture well-marked, moderately deep. Whorls closely-packed, regularly increasing in size. Aperture crescent-shaped. Peristome reflexed.

Discussion. Despite the extremely poor preservation, the shell's discoid shape, size and the large number of narrowly coiled whorls indicate the genus *Klikia*. Nevertheless, identification beyond genus level is impossible.

Paleoecological remarks. Lueger (1981) suggested that species in this fossil genus preferred drier environments.

Family HELICIDAE Rafinesque, 1815

Pseudochloritis Boettger, 1909

Pseudochloritis incrassata (Klein, 1853)
(Figures 3A-C)

1846 *Helix inflexa* Klein [*non* von Zieten, 1832], p. 71, pl. 1, fig. 12.

1853 *Helix incrassata* Klein, p. 208, pl. 5, fig. 6.

1923 *Tropidomphalus* (*Pseudochloritis*) *incrassatus* *incrassatus*: Wenz, p. 510; Seemann, 1926, p. 91; Schlickum, 1976, p. 16, pl. 4, fig. 56.

1980 *Tropidomphalus* (*Pseudochloritis*) *incrassatus* *incrassatus*: Gall, p. 59.

1999 *Tropidomphalus* sp.: Sach, p. 16; Sach *et al.*, 2003, p. 9.

1999 *Tropidomphalus* aff. *zellii*: Sach, p. 21; Sach *et al.*, 2003, p. 6; Sach, 2014, p. 23.

2006 *Tropidomphalus* (*Pseudochloritis*) *incrassatus*: Kó kay, p. 90, pl. 34, figs. 12-14.

2008 *Pseudochloritis incrassata*: Binder, p. 172, pl. 3, figs. 2-4, pl. 6, fig. 2; Rasser *et al.*, 2013, p. 434, pl. 4, fig. 12; Harzhauser *et al.*, 2014, p. 35, pl. 12, figs. 9-16, 19-24; Hó ltke & Rasser, 2015, p. 1, figs. 4.3, 5.1-5.2, 6.11-6.12.

2008 *Tropidomphalus* (*Pseudochloritis*) *incrassatus*: Gó rka, p. 107, figs. 3.1-3.4.

Material examined. SMNS 101582 (28 specimens), 101583 (10 specimens), 101584 (one specimen), 101585 (four specimens), 101586 (five specimens), 101587 (three specimens), 101588 (one specimen), 101589 (one specimen), 101590 (one specimen), 101591 (two specimens), 101592 (one specimen), 101593 (two specimens), 101594 (two specimens), 101595 (two specimens), 101596 (two specimens), 101597 (>100 specimens), 101607 (one specimen), 101624 (three specimens), 101644 (eight specimens).

Occurrence. Wannenwaldtobel 1, Wannenwaldtobel 2, Tobel Oelhalde-Nord, Tobel Oelhalde-Süd, Edelbeuren-Schlachtberg, Binnrot, Edelbeuren-Maurerkopf, Heselsberg, Schmalegger Tobel and Altenstadt-Untereichen.

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

Discussion. The present specimens conform well to *P. incrassata*, a species known from the middle Miocene of Central Europe (Binder, 2008; Salvador, 2014). There is some uncertainty regarding the position of this genus, which is either assigned to Helicidae (Ariantinae) or to Elonidae (Zilch, 1959-1960; Binder, 2008; Moser, *et al.*, 2009; Nordsieck, 2014; Hó ltke & Rasser, 2015).

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

Palaeotachea Jooss, 1912

Palaeotachea renevieri (Maillard, 1892)
(Figures 2R-T)

1892 *Helix* (*Macularia*) *renevieri* Maillard, p. 43, pl. 3, fig. 18.

1923 *Cepaea renevieri*: Wenz, p. 652.

1954 *Cepaea* cf. *C. renevieri*: Zöbelein, p. 156.

1999 *Cepaea* sp.: Sach, p. 23; Sach, 2014, p. 31.

Material examined. SMNS 101560 (34 specimens), 101561 (24 specimens), 101562 (three specimens), 101563 (one specimen), 101564 (two specimens), 101565 (two specimens), 101566 (three specimens), 101567 (one specimen), 101568 (one specimen), 101569 (five specimens), 101570 (four specimens).

Occurrence. Tobel Oelhalde-Nord, Tobel Oelhalde-Süd, Bonlanden, Edelbeuren-Maurerkopf, Heselsberg, Auttagershofen and Burgerbachtobel 1.

Description. Shell medium-sized ($D > 1$ cm), $\sim 4/4$ whorls, helicoid, with overall flattened profile and very faint keel; whorls quickly but regularly growing; shell length $\sim 2/3$ its width. Protoconch flattened; transition to teleoconch unclear. Suture well-marked. Body whorl slightly bent downwards near the aperture. Aperture small, prosocline, circular. Peristome lightly thickened and slightly reflexed. Imperforate. On one specimen (SMNS 101563) it is possible to observe, under UV light, vestiges of three colored fine parallel spiral bands, the topmost one on the middle to upper portion of the whorl, the other two regularly spaced on the basal portion of whorl.

Discussion. *Palaeotachea renevieri* can be identified by its small size, a small circular aperture, a thickened but not reflexed peristome and a somewhat flattened shell profile with a faint keel. The species is known from the middle and late Miocene of Southern Germany and Switzerland (Wenz, 1923; Zöbelein, 1954). The observed trifasciate banding pattern is recurrent in Miocene helicids (e.g. Górka, 2008; Salvador, 2013).

Paleoecological remarks. As a fossil genus, paleoecological implications are not possible. Recent *Cepaea* Held, 1838 and allied species inhabit a broad range of habitats (Welter-Schultes, 2012).

Megalotachea Pfeffer, 1930

Megalotachea silvana (Klein, 1853)
(Figures 2U-W)

1853 *Helix silvana* Klein, p. 205, pl. 5, fig. 2.

1923 *Cepaea silvana silvana*: Wenz, p. 667; Schlickum, 1976, p. 17, pl. 4, figs. 62-63; Reichenbacher, 1989, p. 165, pl. 2, figs. 17-19.

1999 *Cepaea silvana*: Sach, p. 16; Sach *et al.*, 2003, p. 6; Kóky, 2006, p. 93, pl. 36, figs. 2-3; Rasser *et al.*, 2013, p. 440; Sach, 2014, p. 23.

Material examined. SMNS 101608 (>100 specimens), 101609 (one specimen), 101610 (two specimens), 101611 (one specimen), 101612 (one specimen), 101613 (two specimens), 101614 (one specimen), 101615 (two specimens), 101616 (two specimens), 101617 (three specimens), 101618 (four specimens), 101619 (six specimens), 101620 (five specimens), 101621 (three specimens), 101622 (eight specimens), 101623 (34 specimens), 101625 (19 specimens), 101626 (35 specimens), 101627 (10 specimens), 101643 (16 specimens).

Occurrence. Wannenwaldtobel 1, Wannenwaldtobel 2, Tobel Oelhalde-Nord, Tobel Oelhalde-Süd, Edelbeuren-Schlachtberg, Binnrot, Bonlanden, Edelbeuren-Maurerkopf, Heselsberg, Auttagershofen, Burgerbachtobel 1 and Altenstadt-Untereichen.

Description. Shell large ($D > 2$ cm), $4/4-4\frac{1}{2}$ whorls, helicoid; whorls regularly growing. Protoconch flattened, smooth; transition to teleoconch unclear. Teleoconch smooth, except for growth lines. Whorl profile flat on first whorls; more convex on later ones. Suture well-marked. Body whorl slightly bent downwards. Aperture prosocline, crescent-shaped; callus faint. Peristome markedly thickened and reflexed. Imperforate.

Discussion. The present specimens compare fittingly with *Cepaea silvana*, a common species in the German Early/Middle Miocene, mainly due to their more rounded aperture and their greatly reflexed peristome. The specimens show a broad size range: $H = 14.9 \pm 2.0$ mm (max = 19.0 mm, min = 13.0 mm), $D = 21.9 \pm 1.9$ mm (max = 28.0 mm, min = 19.2 mm). Still, the poor preservation of the fossils, with many internal molds and deformed specimens, precludes a precise description of morphological variation in other shell characters.

Paleoecological remarks. Same as *Palaeotachea renevieri*, above.

Superfamily LIMACOIDEA Lamarck, 1801
Family AGRIOLIMACIDAE H. Wagner, 1935

Deroceras Rafinesque, 1820

Deroceras sp.
(Figure 3D)

1999 *Limax* sp.: Sach, p. 16; Sach *et al.*, 2003, p. 6; Sach, 2014, p. 27.

Material examined. SMNS 101553 (eight specimens), 101554 (>100 specimens), 101555 (22 specimens), 101677 (~ 40 specimens).

Occurrence. Wannenwaldtobel 2, Edelbeuren-Maurerkopf and Burgerbachtobel 1.

Description. Shell small ($H < 1$ cm), vestigial, oval; shell width $\sim 2/3$ length. Nucleus slightly bent laterally; nucleus region higher than remainder of shell. Shell with marked concentric growth lines.

Discussion. The vestigial shells of slugs are of very limited

Figure 2. **A**, *Tinnyea lauraea* (SMNS 101648, specimen #1, from Altenstadt-Untereichen; H = 11.3 mm). **B**, *Tinnyea lauraea* (SMNS 101648, specimen #2, from Altenstadt-Untereichen; H = 16.0 mm). **C**, *Bithynia* sp., operculum (SMNS 101539, from Edelbeuren-Maurerkopf; h = 3.7 mm). **D**, *Theodoxus* sp. (SMNS 101649, from Altenstadt-Untereichen; fragment width = 4.5 mm). **E**, *Galba* cf. *G. dupuyiana* (SMNS 101540, from Wannenwaldtobel 2; H = 8.2 mm). **F-G**, *Lymnaea dilatata* (SMNS 101601, from Wannenwaldtobel 2; H = 17.8 mm, D = 11.1 mm). **H**, *Gyraulus applanatus* (SMNS 101546, specimen #1, from Wannenwaldtobel 2; D = 2.5 mm). **I**, *G. applanatus* (SMNS 101546, specimen #2, from Wannenwaldtobel 2; D = 2.9 mm). **J**, *Planorbarius cornu* (SMNS 101573, from Wannenwaldtobel 2; D = 19.0 mm). **K**, *Opeas minutum*, spire apex (SMNS 101551, from Edelbeuren-Maurerkopf; H = 1.8 mm). **L**, Clausiliidae indet., spire apex (SMNS 101550, from Edelbeuren-Maurerkopf; H = 0.7 mm). **M**, Clausiliidae indet., fragment of body whorl, apertural region (SMNS 101550, from Edelbeuren-Maurerkopf; fragment width = 2.1 mm). **N**, *Triptychia* sp., spire apex (SMNS 101548, from Edelbeuren-Maurerkopf; H = 2.6 mm). **O-P**, *Archaeozonites costatus* (SMNS 101559, from Edelbeuren-Schlachtberg; H = 17.3 mm, D = 27.0 mm). **Q**, *Klikia* sp. (SMNS 101552, from Edelbeuren-Maurerkopf; D = 11.2 mm). **R-T**, *Palaeotachea renevieri* (SMNS 101562, from Heselsberg; H = 11.2 mm, D = 17.1 mm). **U-W**, *Megalotachea silvana*, unusually large specimen (SMNS 101609, from Bonlanden; H = 19.0 mm, D = 28.0 mm).

taxonomical value and, therefore, identification of the present specimens cannot proceed further than genus level. As pointed by Harzhauser *et al.* (2014), fossil *Deroceras* are known since the Miocene, but are often identified as either *Limax* Linnaeus, 1758 or *Milax* Gray, 1855.

Paleoecological remarks. *Deroceras* is known from a broad range of habitats, from the more usual open grasslands to forests, including wetlands and anthropically disturbed areas (Welter-Schultes, 2012; Rowson *et al.*, 2014).

Class BIVALVIA Linnaeus, 1758

Order UNIONOIDA Stoliczka, 1871

Family MARGARITIFERIDAE Henderson, 1929 (1910)

Margaritifera Schumacher, 1816

Margaritifera flabellata (Goldfuss, 1837)
(Figures 3E-G)

Synonymy. See Schneider & Prieto (2011) and complement: 1970 *Plicatibaphia flabellata*: Starobogatov, p. 61.

1999 *Unio* sp. vel *Margaritifera* sp.: Sach, p. 16; Sach *et al.*, 2003, p. 6; Sach, 2014, p. 27.

2014 *Unio* sp. vel *Margaritifera* sp.: (in part) Sach, p. 81.

1999 *Margaritifera flabellata*: Sach, p. 20; Sach, 2014, p. 30.

2011 *Margaritifera (Pseudunio) flabellata*: Schneider & Prieto, p. 4, figs. 3-6.

2012 *Plicatibaphia bavarica*: Grim *et al.*, p. 19, pl. 1.

Material examined. SMNS 101629 (three specimens), 101630 (five specimens), 101631 (two specimens), 101632 (three specimens), 101633 (seven specimens), 101634 (two specimens), 101635 (three specimens), 101636 (two specimens), 101637 (three specimens), 101638 (one specimen), 101639 (one specimen), 101640 (two specimens), 101656 (~10 specimens).

Occurrence. Wannenwaldtobel 2, Tobel Oelhalde-Nord, Tobel Oelhalde-Süd, Edelbeuren-Schlachtberg, Binnrot, Bonlanden, Edelbeuren-Maurerkopf, Heselsberg, Burgerbachotobel 1, Schmalegger Tobel, Lattentobel and Altenstadt-Untereichen.

Description. Valve elliptical to reniform; middle third of valve length slightly compressed in height; ~35% longer than taller. Shell inflated, width ~40% of total shell length. External surface frequently smooth, sometimes covered by traces of growth lines and deep and worn plicae at posterior margin of valves. Internal surface smooth, without scars preserved. Umbones wide and low, ~20% of total valve length and ~5% of total valve height, located between anterior and middle third of shell length. Ligament external, long and narrow, length ~60% of total shell length. Right hinge composed by two pseudocardinal teeth, disposed anteriorly to umbones axis, on a dental shelf; dental shelf triangular, located between anterior and dorsal shell margins; shape approximately fusiform; length ~60% of total valve height; anterior tooth long and narrow, length ~30% of dental shelf length, laminar, distanced from posterior

tooth ~1.5 times its own width; posterior tooth short and rounded, ~1/2 anterior tooth total length. Left hinge with two pseudocardinal teeth, disposed anteriorly to umbones axis, on a dental shelf; dental shelf triangular, wide, length ~90% of total valve height; anterior tooth long, length same as dental shelf width, pyramidal, dorsal to middle portion wide and strong, middle and anterior portion laminar, away from posterior tooth *ca.* twice its own width; posterior tooth strong and wide, triangular and flat, length same as anterior tooth, greatest width ~10% total dental shelf length.

Discussion. *Margaritifera flabellata* is characteristic of the late Miocene in a wide range of Central European localities and shows a constancy of overall shell forms (Kóky, 2006; Schneider & Prieto, 2011). Moreover, this species shows some variety in shell ornamentation, which is deemed to be due to preservation issues rather than related to distinct environmental conditions (Schneider & Prieto, 2011).

Paleoecological remarks. Recent European *Margaritifera* species inhabit fast flowing and well oxygenated waters (Harzhauser & Tempfer, 2004), with the larger *M. auricularia* (Spengler, 1793) usually occurring in large rivers (Welter-Schultes, 2012). The fossil *M. flabellata* more closely resembles the recent *M. margaritifera* (Linnaeus, 1758), which usually is found in clear running waters (Welter-Schultes, 2012). Apparently, the conditions in the present sites during the Miocene were very favorable to *M. flabellata*: the species is widespread, occurring in nearly all the mollusk-bearing localities presented here (Table 1), reasonably abundant and reaches large sizes; moreover, there is an equal proportion of articulated and disarticulated specimens, indicating that the species is autochthonous. Given the environmental interpretation of the sites (Sach, 1999; see also discussion section below), *M. flabellata* seems to have had different preferences than its living relatives. Moreover, this species is also known from some paludal Miocene environments (Schneider & Prieto, 2011).

Family UNIONIDAE Fleming, 1828

Unio Philipsson, 1788

Unio kirchbergensis Krauss, 1852
(Figures 3J-K)

1852 *Unio kirchbergensis* Krauss, p. 152, figs. 5a-c; Pictet, 1855, p. 529; Lea, 1870, p. 65.

2014 *Unio* sp. vel *Margaritifera* sp.: (in part) Sach, p. 81.

Material examined. SMNS 101650 (one specimen).

Occurrence. Altenstadt-Untereichen.

Description. Valve elliptical, ~40% longer than taller. Valve width ~20% of total valve length. External surface mostly smooth, with traces of growth lines on middle and ventral portions. Internal surface smooth, without scars preserved. Umbones wide and low, ~25% of total valve length and ~5% of total valve height, located between anterior and middle third of length. Left hinge with two cardinal teeth disposed parallel

Figure 3. A-C, *Pseudochloritis incrassata* (SMNS 101585, from Edelbeuren-Schlachtberg; H = 15.3 mm, D = 26.0 mm). D, *Deroceras* sp. (SMNS 101554, from Edelbeuren-Maurerkopf; H = 9.5 mm, D = 6.1 mm). E, *Margaritifera flabellata*, left valve (SMNS 101656, from Altenstadt-Untereichen; L = 66.0 mm). F-G, *M. flabellata*, respectively, lateral (right valve) and dorsal view of closed specimen (SMNS 101632, from Edelbeuren-Schlachtberg; L = 65.1 mm). H, *M. flabellata*, detail of right hinge (SMNS 101633, specimen #1, from Edelbeuren-Schlachtberg; scale bar = 1 cm). I, *M. flabellata*, detail of left hinge (SMNS 101633, specimen #2, from Edelbeuren-Schlachtberg; scale bar = 1 cm). J-K, *Unio kirchbergensis*, respectively, external and internal view of left valve (SMNS 101650, from Altenstadt-Untereichen; L = 48.8 mm). L-M, *Sphaerium* aff. *S. rivicola*, respectively, external and internal view of left valve (SMNS 101628, specimen #1, from Binnrot; L = 7.7 mm). N, *Sphaerium* aff. *S. rivicola*, right valve (SMNS 101628, specimen #2, from Binnrot; L = 10.7 mm). O, *Sphaerium* aff. *S. rivicola*, right valve (SMNS 101628, specimen #3, from Binnrot; L = 10.3 mm).

to umbones axis, on a dental shelf. Dental shelf long and straight, length ~90% of total valve height, located between dorsal and anterior margins; shape follows that of valve's margins. Anterior tooth triangular, flat, ~35% shorter than dental shelf width, posterior end wider than anterior; touches posterior end of posterior tooth; greatest width ~30% of total dental shelf length; distant from posterior by roughly its own width. Posterior tooth long, wide; length equal to dental shelf width; greatest width ~55% of total dental shelf length.

Discussion. This single specimen is externally identical to a much worn *Margaritifera flabellata*, but the hinge is well-preserved and its proportions are very peculiar. The anterior tooth is very flat and triangular, while in *M. flabellata* it is pyramidal with disproportional sides. The posterior tooth is broad, occupying almost the entire posterior portion of the dental shelf area, while *M. flabellata* presents a posterior tooth with roughly half this size. The present specimen compares fittingly with the syntypes of *Unio kirchbergensis* (SMNS 25504/2005), a species known only from its type locality, Kirchberg an der Iller (southern Germany), from the late early Miocene Kirchberg Formation.

Paleoecological remarks. Recent *Unio* species have a wide range of habitats; nevertheless, they are more usually found in rivers, avoiding small water bodies, and do not tolerate desiccation (Welter-Schultes, 2012).

Order VENEROIDA H. Adams & A. Adams, 1856
Family SPHAERIIDAE Deshayes, 1855 (1820)

Sphaerium Scopoli, 1777

Sphaerium aff. *S. rivicola* (Lamarck, 1818)
(Figures 3L-O)

Synonymy. See Schneider & Prieto (2011) and complement: 1999 *Sphaerium* sp.: Sach, p. 22; Sach, 2014, p. 31. 2011 *Sphaerium* (*Amesoda*) *rivicola*: Schneider & Prieto, p. 9, figs. 7A-C.

Material examined. SMNS 101628 (four specimens).

Occurrence. Binnrot.

Description. Valve triangular to elliptical, ~30% longer than taller. Valves flattened, width ~10% of total shell length. External surface with growth lines. Internal surface not observable due to poor preservation. Umbones wide and low, prominent from shell outline, located on the middle of anterior portion of valve; ~25% valve total length and ~10% total valve height. Ligament external, long and narrow; ~50% total valve length. Hinge poorly preserved; cardinal tooth not observable; lateral tooth on middle portion of both sides of dorsal margin.

Discussion. Lueger (1979) reported the first Late Miocene record of this species from Vienna Basin, Austria, justifying his identification as *Sphaerium rivicola*, a recent species, due to the species' occurrence as Pleistocene fossils. Later, Schneider & Prieto (2011) reported the species from the Late Miocene of southern Germany. The present specimens

are very similar in overall shape and proportions to those reported by Lueger (1979) and Schneider & Prieto (2011), being much more reminiscent of those reported by the latter. The present specimens are anteroventrally elongated, with less pronounced umbones, while Lueger's are nearly round, with a posterior carina and pronounced umbones. Conchological features apart, geographical and stratigraphical distributions are still problematic: *S. rivicola* is a recent European species. It is well known that recent freshwater bivalves can have broad geographical distributions, throughout rivers and others small water bodies (e.g. Pereira *et al.*, 2014), but ca. 15 Ma separate the recent *S. rivicola* from the fossils. Therefore, here we prefer a more conservative classification of the present material, linking the present material to the specimens of Schneider & Prieto (2011), due to their shared similarity in conchological features and stratigraphical and geographical proximity. A thorough revision of all the available fossil material is necessary to a better definition of *Sphaerium* morphotypes occurring in the European Miocene.

Paleoecological remarks. The valves are poorly preserved and disarticulate and the numbers of specimens is too small for any taphonomical inference. Recent *Sphaerium* species show a remarkable tolerance to wide ranges of dissolved oxygen in water, from rapid and well-oxygenated waters to temporary and hypoxic water bodies (Cummings & Graf, 2010; Welter-Schultes, 2012).

DISCUSSION

The poor preservation of part of the material studied here is problematic for taxonomy; therefore, for fragmentary and/or deformed specimens and internal molds identification could not proceed further than genus level (or family level for the clausiliid). Table 1 lists all the fossil sites in the districts of Biberach, Ravensburg and Neu-Ulm and the species found in each one. Table 1 also lists the abundance of each species for each site, but it should be noted that the collection of the molluscan specimens was not controlled for this and techniques for recovering microgastropods (usually abundant in other Miocene outcrops in southern Germany) were not used.

The species list presented here (Table 1) is consistent with those presented by Sach (1999, 2014). Nevertheless, some new occurrences were also noted here: *Gyraulus applanatus*, *Opeas minutum*, *Archaeozonites costatus*, *Palaeotachea renevieri*, *Triptychia* sp. and *Unio kirchbergensis*. Moreover, a few misidentifications listed by Sach (1999, 2014) and Sach *et al.* (2003) were rectified here: the single specimen previously identified as *Pomatias conicus* is a spire apex of *Lymnaea dilatata* and, likewise, the single specimen of *Valvata* sp. is a misidentification of a fragment of *Archaeozonites costatus*.

Sach (1999) presented a paleoenvironmental interpretation of the fossiliferous horizons of the Biberach district, proposing a large meandering river system surrounded by alluvial and gallery forests. This interpretation was based upon the cross-stratification lithology of the finely grained sandy sediments and on the evaluation of the fossil remains found, especially

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

Species	BIBERACH									RAVENSBURG			NEU-ULM
	A	B	C	D	E	F	G	H	I	J	K	L	M
CAENOASTROPODA													
<i>Bithynia</i> sp.							xxx		S				
<i>Pomatias</i> sp.										x			
<i>Tinnyea laurae</i>													x
NERITIMORPHA													
<i>Theodoxus</i> sp.													x
HYGROPHILA													
<i>Galba</i> cf. <i>G. dupuyana</i>	xxx						x		x				
<i>Gyraulus applanatus</i>	xxx						x						
<i>Lymnaea dilatata</i>	x		x			x	xxx	x		x			x
<i>Planorbis cornu</i>	x	x	x	x		x	x	x	x				x
STYLOMATOPHORA													
<i>Archaeozonites costatus</i>				x	x		x						x
Clausiliidae indet.							x						
<i>Deroceras</i> sp.	x			S		xx	xxx			xx			
<i>Klikia</i> sp.						S	xxx	x		S			x
<i>Megalotachea silvana</i>	xx	xx	xx	xx	x	xx	xxx	x	x	x			xx
<i>Opeas minutum</i>							x						
<i>Palaeotachea renevieri</i>		xx	xx			xx	xx	x	x	x			
<i>Pseudochloritis incrassata</i>	x	x	x	xx	x		xxx	x		S	x		x
<i>Triptychia</i> sp.							x						
BIVALVIA													
<i>Margaritifera flabellata</i>	x	x	x	x	x	x	x	x		x	x	x	x
<i>Sphaerium</i> aff. <i>S. rivicola</i>					x								
<i>Unio kirchbergensis</i>													x

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

The molluscan freshwater fauna, as already observed by Sach (1999), is consistent with rivers, oxbow lakes and ponds. *Bithynia* and the freshwater pulmonates indicate still or slow-flowing waters, including perhaps short-lived shallow water bodies. This is in accordance with the slow-flowing streams and ponds proposed by Sach (1999), with *Bithynia* and the freshwater pulmonates inhabiting the well vegetated areas close to the margins.

In the immediate vicinity of the water bodies, there were humid alluvial and gallery forests that went through periodical floods (Sach, 1999). These forests would have provided favorable conditions for the land snails (*Opeas*, the clausilioids and supposedly *Archaeozonites*) that prefer warmer and more humid environments. There is also indication, mainly based on plant and mammal remains, of drier forests and open areas (Sach, 1999), but, despite snails of such habitats being rather common

in other German Miocene sites (e.g. Randeck Maar; Salvador *et al.*, 2015), there is no such fauna in the present material. The two fossil genera *Pseudochloritis* and *Klikia* supposedly inhabited more exposed areas (Lueger, 1981; Binder, 2008; Moser *et al.*, 2009) and they are very abundant in one of the sites studied here, namely Edelbeuren-Maurerkopf. These areas would be located farther away from the water bodies (and perhaps on raised ridges; Sach, 1999).

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