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FOSSIL MOLLUSCS FROM THE MIDDLE MIOCENE OF ÖHNINGEN, SOUTHWESTERN GERMANY

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ABSTRACT: Herein, we revise an extensive set of mollusc fossils from the Upper Freshwater Molasse deposits of Öhningen palaeolake (SW Germany; Middle Miocene, MN7). Based on material housed in paleontological collections in Europe and North America, we present the first thorough systematic account of the phylum from this historic locality. A total of ten species were identified from Öhningen: three freshwater gastropods (*Lymnaea dilatata* Noulet, 1854, *Gyraulus* cf. *applanatus* (Thomä), *Planorbarius mantelli* (Dunker)), two terrestrial gastropods (*Granaria* cf. *schuebleri* (Klein), *Palaeotachea sylvestrina* (Schlotheim)), and five bivalves (*Anodonta splendens* Goldfuss, *A. lavateri* (Münster), *Pseudunio flabellatus* (Goldfuss), *"Dreissena"* sp., *Pisidium escheri* (Mayer-Eymar, 1865)). Three freshwater and five terrestrial gastropod genera mentioned in older literature could not be found in the available material. Ours is the first report of a Dreissenidae from Öhningen.

KEY WORDS: Bivalvia; Hygrophila; palaeolake; Stylommatophora; Upper Freshwater Molasse

INTRODUCTION

The Middle Miocene continental deposits of Öhningen ("Oeningen" in early literature) in south-western Germany are famous for the diversity of their fossil flora and insect fauna (HANTKE 1954, SELMEIER 1990, FIKÁČEK & SCHMIED 2013). It is likewise famous for the fossil giant salamander *Andrias scheuchzeri* (Holl, 1831), which was first described as a human fossil from before the Biblical deluge. The outcrops have been known since the 16th century, when Augustinian monks collected and sold the fossils (SELMEIER 1990, LUTZ et al. 1999). Scientific studies of the fossils from Öhningen were pioneered by the Swiss geologist and naturalist Oswald Heer in the mid-19th century, focusing on the fossil flora (LUTZ et al. 1999).

The mollusc fossils from Öhningen have never been systematically studied. Previous authors usually only offered brief lists of taxa or species counts, but those are not consistent with one another. RUTTE (1956) synthesised all knowledge about Öhningen and provided the most extensive list of fossil molluscs to date by compiling all previous records from the literature (namely, HEER 1865, 1879, SANDBERGER 1870–1875, SCHALCH 1883, BÖHNDEL 1916, WENZ 1923–1930, SEEMANN 1929, HANTKE 1954). RUTTE (1956) listed 23 gastropod (including land and freshwater) and three bivalve species. However, as RUTTE (1956) simply transcribed the identifications of previous authors, some taxa were listed more than once under different names. Most later publications about Öhningen did not highlight

the molluscs (e.g., SELMEIER 1990, who simply alluded to a count of only four species of gastropods and bivalves combined), although GIERSCH (2004) listed the mollusc taxa found in the outcrops he studied.

Herein, we revise an extensive mollusc material from Öhningen available in palaeontological collections, presenting the first systematic account of this phylum from this locality and depicting all species found.

GEOLOGICAL SETTING

The town of Öhningen is located on the western edge of Lake Constance (Bodensee), bordering Switzerland (Fig. 1). The historical fossiliferous outcrops were located northeast of the town on the small mountain Schienerberg (47°40'30"N, 08°55'50"E). There, Miocene freshwater sediments occur in two lithostratigraphic units. The more extensive one comprises sediments of the Upper Freshwater Molasse (Obere Süßwassermolasse, in German, abbreviated OSM), a thick sequence with riverine and lake sediments that derived from the uprising Alpine mountain chain in the south (RUTTE 1956, LUTZ et al. 1999). The locality Bohlinger Schlucht at the northern slope of Schienerberg (partly known as Schrotzburg) comprises Middle Miocene sediments attributed to the Mammal Neogene Zone MN6 (Badenian), to MN7 (Sarmatian) (Langhian/Serravallian; GIERSCH 2004) with vertebrate and plant remains (GIERSCH 2004; see UHL et al. 2006 for review). They are collectively designated Öhningen Beds (Öhninger Schichten), with the subunits Balmensande and Krokodilschichten (RUTTE 1956, LUTZ et al. 1999).

The Öhningen Beds were penetrated by a volcanic pipe that led to the formation of a maar lake with a diameter of at least 1 km (RUTTE 1956). In this lake, the so called Öhninger Kalk (Öhningen Limestone) was deposited with numerous molluscs and the famous giant salamander *Andrias scheuchzeri*. They were exploited in two historical quarries, the Oberer Steinbruch at Salenhof, and the Unterer Steinbruch at Ziegelhof. The age of the maar lake sediments is interpreted as MN7 (Sarmatian), but this remains uncertain (TOBIEN 1986). More detailed descriptions of the geology and lithology of Öhningen can be found elsewhere (STAUBER 1937, HANTKE 1954, RUTTE 1956, RIETSCHEL et al. 1985, SELMEIER 1990, LUTZ et al. 1999). Unfortunately, only a few of the molluscs studied herein have precise locality data on their labels, but we assume that most – if not all – of them come from the maar lake limestones, i.e., Öhninger Kalk.

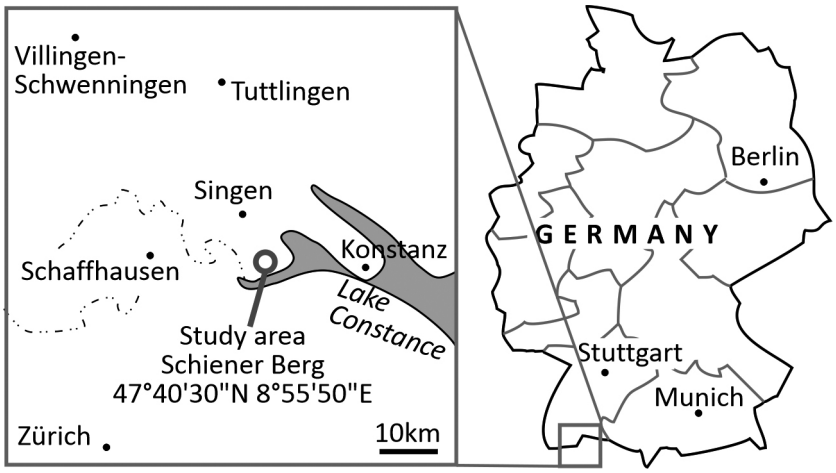


Fig. 1. Map showing the study locality

CHECKLIST OF MOLLUSCS

The list of mollusc species from Öhningen compiled by RUTTE (1956) is reproduced below, split into freshwater and terrestrial gastropods, and bivalves; the species are listed in alphabetical order within each category. However, as remarked above, some species appear more than once on this list due to conflicting identifications, since RUTTE (1956) simply transcribed the identifications of all previous authors. Species names according to current taxonomy (BINDER 2008, HÖLTKE & RASSER 2013, NEUBAUER et al. 2014, RASSER & SALVADOR 2019, MOLLUSCABASE 2022) are provided within square brackets when applicable.

Gastropods (freshwater)

(1) *Ancylus deperditus deperditus* Desmarest, 1814 [*Ferrissia deperdita* (Desmarest, 1814)]
(2) *Ferrissia* n. sp. [*sensu* HANTKE 1954]
(3) *Melanopsis kleinii kleinii* Kurr, 1856
(4) *Planorbis* (*Gyraulus*) *trochiformis kleini* (Gottschick et Wenz, 1916) [*Gyraulus* cf. *applanatus* (Thomä, 1845)]
(5) *Planorbis cornu cornu* (Brongniart, 1810) [*Planorbarius cornu* (Brongniart, 1810)]
(6) *Planorbis cornu mantelli* (Dunker, 1848) [*Planorbarius mantelli* (Dunker, 1848)]
(7) *Radix* (*Radix*) *socialis dilatata* (Noulet, 1854) [*Lymnaea dilatata* Noulet, 1854]
(8) *Radix subovata* (von Zieten, 1832)
(9) *Theodoxus* (*Calvertia*) *crenulatus crenulatus* (Klein, 1853) [*Theodoxus crenulatus* (Klein, 1853)]

Gastropods (terrestrial)

(10) *Abida antiqua antiqua* (von Zieten, 1832) [*Granaria* cf. *schuebleri* (Klein, 1846)]
(11) *Campylaea* (*Dinarica*) *insignis* (von Zieten, 1832) [*Pseudochloritis insignis* (von Zieten, 1832)]
(12) *Cepaea eversa larteti* (de Boissy, 1840) [*Megalotachea turonensis* (Deshayes, 1832)]
(13) *Cepaea? silvana* (Klein, 1853) [*Palaeotachea? silvana* (Klein, 1853)]
(14) *Cepaea silvana silvana* (Klein, 1853) [*Palaeotachea silvana* (Klein, 1853)]
(15) *Cepaea sylvestrina geniculata* (Sandberger, 1875) [*Palaeotachea sylvestrina* (Schlotheim, 1820)]
(16) *Cepaea* sp. [*sensu* HANTKE 1954; likely *Palaeotachea* sp.]
(17) *Goniodiscus* (*Goniodiscus*) *pleuradra pleuradra* (Bourguignat, 1881) [*Discus pleuradrus* (Bourguignat, 1881)]
(18) *Klikia* (*Klikia*) *giengensis giengensis* (Klein, 1846)
(19) *Klikia* sp.
(20) *Milax* (*Milax*) *gracilior* (Sandberger, 1875) [the *Limax* sp. reported later by GIERSCH (2004) likely refers to this taxon]
(21) *Tropidomphalus* (*Pseudochloritis*) *incrassatus incrassatus* (Klein, 1853) [*Pseudochloritis incrassata* (Klein, 1853)]
(22) *Tropidomphalus* (*Pseudochloritis*) *zelli* (Kurr, 1856) [*Pseudochloritis incrassata* (Klein, 1853)]
(23) *Zonites* (*Aegopis*) *costatus* (Sandberger, 1875) [*Archaeozonites costatus* Sandberger, 1875]

Bivalves

(24) *Anodonta lavateri* (Münster, 1837) [*Unio lavateri* Münster, 1837]
(25) *Unio flabellatus* (Goldfuss, 1837) [*Pseudunio flabellatus* (Goldfuss, 1837)]
(26) *Pisidium escheri* (Mayer-Eymar, 1865)

MATERIAL AND METHODS

A large number of museum collections likely to contain mollusc fossils from Öhningen were contacted by the authors. Only a small number of collections housed such fossils and, of those, seven could be accessed for the present study: ETHZ – Geological and Paleontological Collection, Eidgenössische Technische Hochschule Zürich (Zurich, Switzerland); MCZ – Museum of Comparative Zoology, Harvard University (Cambridge, USA); MGH – Museum Geowissenschaften Heidelberg, Ruprecht-Karls-Universität Heidelberg (Heidelberg, Germany); NHMUK – Natural History Museum (London, UK); PIMUZ – Paläontologisches Institut und Museum, Universität Zürich (Zurich, Switzerland); RMK – Rosgartenmuseum Konstanz (Konstanz, Germany); SMNS – Staatliches Museum für Naturkunde Stuttgart (Stuttgart, Germany).

The material of these collections consists largely of samples collected in the late 19th and early 20th centuries, usually lacking precise locality and/or stratigraphic data. All the available material from those collections is reported herein under each species entry. The species are listed below in systematic order (starting with gastropods), following the classification of BOUCHET & ROCROI (2010) for Bivalvia and BOUCHET et al. (2017) for Gastropoda. Every species is figured and discussed, including data on their diagnostic features and distribution, as well as their taxonomy and palaeoecology when pertinent. A brief chresonymy section is provided for each species, including solely studies pertaining to Öhningen.

SYSTEMATIC PALEONTOLOGY

GASTROPODA

Hygrophila

Superfamily Lymnaeoidea

Family Lymnaeidae

Genus *Lymnaea* Lamarck, 1799

Lymnaea dilatata Noulet, 1854

Figs 2–3

Limnaeus pachygaster – SCHALCH 1883: p. 68.
Limnaeus dilatatus – SEEMANN 1929: p. 75.
Radix (*Radix*) *socialis dilatata* – HANTKE 1954: p. 86.
Lymnaea dilatata – RUTTE 1956: p. 164.
Radix subovata – RUTTE 1956: p. 164.
Radix socialis dilatata – GIERSCH 2004: p. 14.

Material examined: ETHZ 8046 (ca. 30 spcm), ETHZ 8047 (>100 spcm, in part ex Lavater colln.), ETHZ 13492 (1 spcm, from "Oberer Bruch"), NHMUK IP G3747 (2 spcm), NHMUK IP G3750 (ca. 10 spcm), NHMUK IP G3751 (>20 spcm), NHMUK IP G3752b (3 spcm), NHMUK IP OR62686 (1 spcm), NHMUK IP OR63747 (2 spcm), NHMUK IP OR63750 (ca. 10 spcm), NHMUK IP OR63751 (>30 spcm), NHMUK IP OR63752a (ca. 10 spcm), MCZ IPGA-8856 (1 spcm), MGH unnumbered (1 spcm, from "bituminöser Mergelschiefer" [bituminous marl slate]), PIMUZ unnumbered (10 spcm; public exhibition), PIMUZ unnumbered (1 spcm, ex J.J. Scheuchzer colln.), RMK unnumbered (1 spcm; public exhibition: "Leinersaal"), SMNS 106844 (2 spcm).
Remarks: The poor preservation of most specimens (the fossils are usually flattened, e.g., Fig. 3) hampers identification, but they are likely to represent *L. dilatata*, a widespread species reported from the entire duration of the Miocene of Central and West Europe (SALVADOR et al. 2015a). Specimens of *L. dilatata* from the OSM deposits of Randeck Maar, in SW Germany, show similar flattened preservation (SALVADOR et al. 2015a), being sometimes identified as a bivalve's valve in earlier works and/or museum collections.

Superfamily Planorboidea

Family Planorbidae

Genus *Gyraulus* Charpentier, 1837

Gyraulus cf. *applanatus* (Thomä, 1845)

Fig. 4

Planorbis laevis – SEEMANN 1929: p. 75.
[?] *Bulimus* – HANTKE 1954: p. 86 (operculum).
Planorbis (*Gyraulus*) *trochiformis kleini* – RUTTE 1956: p. 164.

Material examined: ETHZ 8046 (>50 spcm, in part ex Lavater colln.), ETHZ 8047 (>250 spcm, in part ex Lavater colln., in part from "Untersee"), ETHZ 13492 (ca. 20 spcm), NHMUK IP G2687 (9 spcm), NHMUK IP G3103 (>30 spcm, ex J.E. Lee colln, presented Oct/1885), NHMUK IP G3750 (ca. 10 spcm), NHMUK IP G3752a (>50 spcm), NHMUK IP G3752b (>50 spcm), NHMUK IP G20934 (>20 spcm), NHMUK IP G23497 (ca. 10 spcm), NHMUK IP OR62687 (8 spcm), NHMUK IP OR63752a (>50 spcm), NHMUK IP OR63752b (ca. 15 spcm), PIMUZ unnumbered (15 spcm; public exhibition), RMK unnumbered (5 spcm; public exhibition: "Leinersaal"), SMNS 106846 (5 spcm), SMNS 106847 (1 spcm), SMNS 106848 (>50 spcm), SMNS 106851 (>100 spcm).
Remarks: Although the preservation of the specimens is very poor, being flattened and deformed, they very probably represent *G. applanatus*, commonly found in deposits from the German Miocene (RASSER & SALVADOR 2019).

The operculum alluded to by HANTKE (1954: 86, "Deckel von *Bulimus*") could refer to specimens of *Gyraulus applanatus*. As the Öhningen fossils of this planorbid are often completely flattened, they might appear at a first glance as the opercula of some terrestrial snails common in the German Miocene (e.g., *Pomatias* spp.).

Genus *Planorbarius* Duméril, 1806

Planorbarius mantelli (Dunker, 1848)

Figs 5–6

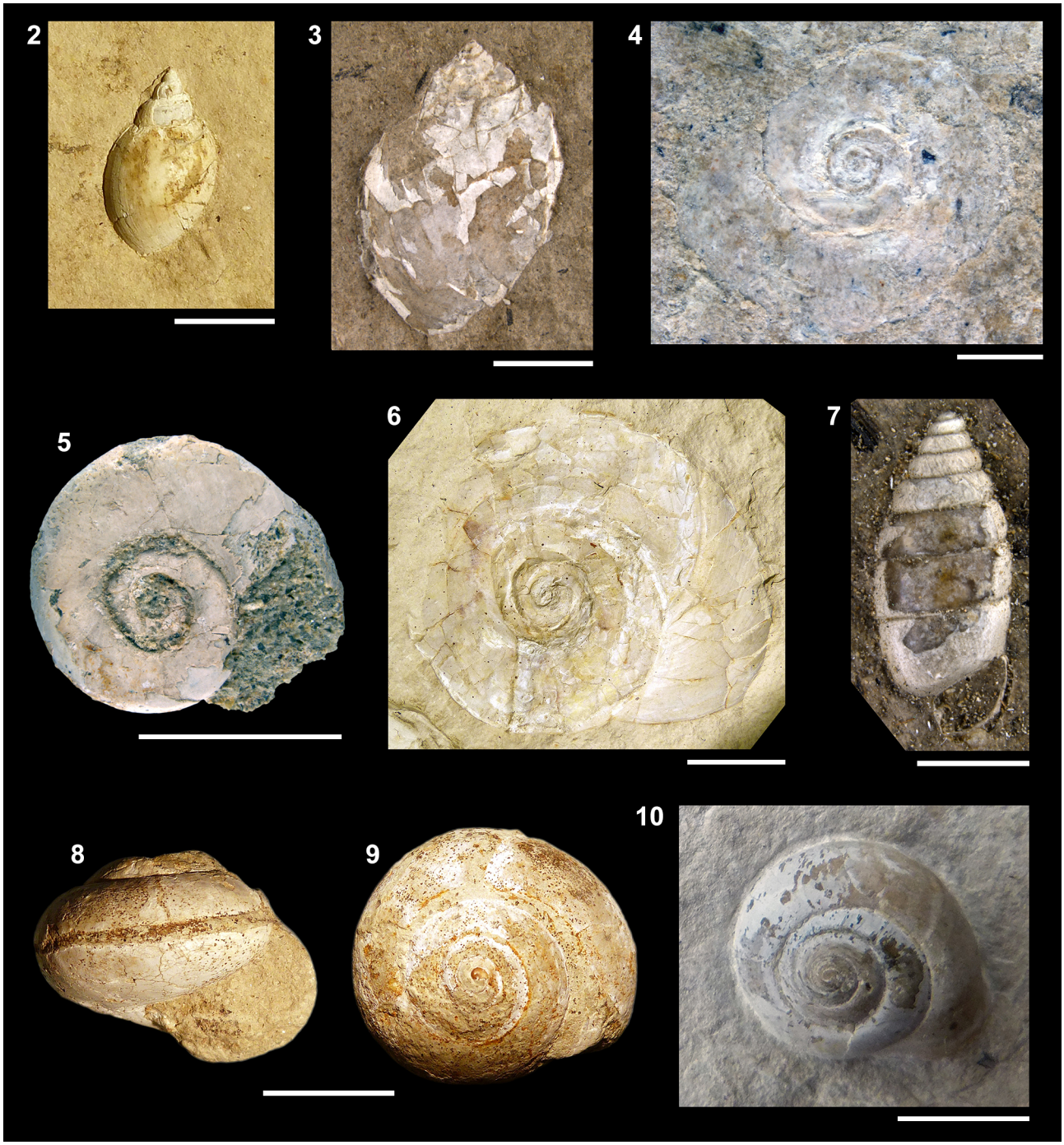
Planorbarius solidus – SCHALCH 1883: p. 68.
Coretus cornu mantelli – WENZ 1923: p. 1452.
Planorbis cornu var. *Mantelli* – SEEMANN 1929: p. 75.
Planorbarius cornu mantelli – HANTKE 1954: p. 86.
Planorbis cornu cornu – RUTTE 1956: p. 164.
Planorbis cornu mantelli – RUTTE 1956: p. 164.
Planorbarius cornu spp. – GIERSCH 2004: p. 14.

Material examined: ETHZ 8046 (3 spcm), ETHZ 8047 (15 spcm, in part ex Lavater colln.), NHMUK IP G3750 (1 spcm), PIMUZ unnumbered (ex J. J. Scheuchzer colln.), SMNS 106843 (1 spcm), SMNS 106849 (2 spcm).
Remarks: There are a few relatively better-preserved specimens (e.g., Fig. 5) to allow species identification. The shell's characteristic planispiral shape, relatively large size, and whorl growth pattern allows the identification as *P. mantelli*. This species is recorded from the late Early to the Late Miocene of Central Europe and has been usually treated in earlier literature as a synonym of *P. cornu* (Brongniart, 1810), which occurs from the Late Oligocene to Early Miocene (HARZHAUSER et al. 2014).

Stylommatophora
Superfamily Pupilloidea
Family Chondrinidae
Genus *Granaria* Held, 1838
***Granaria* cf. *schuebleri* (Klein, 1846)**
Fig. 7

Abida antiqua antiqua – SEEMANN 1929: p. 75.
Abida antiqua antiqua – RUTTE 1956: p. 165.
? *Abida* sp. – GIERSCH 2004: p. 14.

Material examined: ETHZ 8047 (4 spcm, from "Untersee"), PIMUZ unnumbered (1 spcm; public exhibition), SMNS 106845 (1 spcm), SMNS 106846 (1 spcm).



Figs 2–10. Gastropods from the Öhningen region: 2–3 – *Lymnaea dilatata* Noulet, 1854, scale bar 5 mm (2 – ETHZ 8047 (ex Lavater colln.), 3 – SMNS 106844, example of flattened specimen); 4 – *Gyraulus* cf. *applanatus* (Thomä, 1845), scale bar 1 mm, SMNS 9555-2008, flattened specimen; 5–6 – *Planorbarius mantelli* (Dunker, 1848), scale bar 10 mm (5 – SMNS 9541-2008, 6 – ETHZ 8047 (ex Lavater colln.), example of flattened specimen); 7 – *Granaria* cf. *schuebleri* (Klein, 1846), scale bar 5 mm, SMNS 9553-2008; 8–10 – *Palaeotachea sylvestrina* (Schlotheim, 1820), scale bar 5 mm (8–9 – ETHZ 8047, 10 – NHMUK IP OR63748)

Remarks: The apertural teeth and lamellae are the most important diagnostic shell features for identifying chondrinids (Gittenberger 1973, Höltke & Rasser 2013). Unfortunately, those were not preserved in the presently available specimens. However, in their overall shell and whorl profiles, as well as the fine axial sculpture, the fossils from Öhningen are very reminiscent of *G. schuebleri*. This species in known from the Late Miocene to Early Pliocene of southern Germany (Höltke & Rasser 2013).

Superfamily Helicoidea

Family Helicidae

Genus *Palaeotachea* Jooss, 1912

***Palaeotachea sylvestrina* (Schlotheim, 1820)**
Figs 8–10

Helix (*Macularia*) *silvana* – Seemann 1929: p. 75.
Helix (*Macularia*) *subvermiculata* – Seemann 1929: p. 75.
Cepaea? *Silvana* – Hantke 1954: p. 86.
Cepaea sp. – Hantke 1954: p. 86.
Cepaea eversa larteti – Rutte 1956: p. 165.
Cepaea? *silvana* – Rutte 1956: p. 165.
Cepaea silvana silvana – Rutte 1956: p. 165.
Cepaea silvestrina geniculata – Rutte 1956: p. 165.
Cepaea sp. – Rutte 1956: p. 165.
Cepaea silvana silvana – Giersch 2004: p. 14.
Cepaea sylvestrina sylvestrina – Giersch 2004: p. 14.
Cepaea eversa larteti – Giersch 2004: p. 14.

Material examined: ETHZ 8047 (7 spcm), NHMUK IP G3752b (1 spcm), NHMUK IP OR63748a (1 spcm), NHMUK IP OR63748b (1 spcm), SMNS 106850 (4 spcm).
Remarks: While most specimens are poorly preserved and deformed, a few fossils are in better condition (Figs 8–10), allowing identification. Given the size of the fossil shells and the proportionately large body whorl (when compared to Miocene congeners), the specimens can be identified as *P. sylvestrina*. This species is known from the Middle and Late Miocene of Central Europe (Höltke & Rasser 2016).

BIVALVIA

Superfamily Unionoidea

Family Unionidae

Genus *Anodonta* Lamarck, 1799

***Anodonta splendens* (Goldfuss, 1837)**
Figs 11, 16

Unio splendens Goldfuss, 1837: p. 183, pl. 132, fig. 7.
Anodonta Heerii Mayer-Eymar in Heer 1865: p. 351.
Anodonta Heeri [sic] – Schalch 1883: p. 68.

Material examined: NHMUK IP OR63750 (1 spcm, ex Bruckmann colln), NHMUK IP OR74964 (2 spcm, ex van Breda colln), PIMUZ unnumbered (1 spcm; public exhibition), RMK unnumbered (1 spcm, from "Oberer Bruch", public exhibition: "Leinersaal"), SMNS 107351 (1 spcm), SMNS 107348 (1 spcm), SMNS 107359 (1 spcm).
Remarks: The specimens are mostly flattened, though the valves were preserved in their entirety. Some specimens were preserved in "butterflied" position, with articulated valves (e.g., Fig. 11; though the hinge was not fully preserved), indicating that this species was autochthonous or at least parautochthonous in Öhningen paleolake.

The valves bear traces of concentric lines and have a slightly elongated ovate shape, with the hinge positioned more posteriorly in comparison to the other unionoids below. The overall shape and position of the hinge fit the description of *A. splendens*, originally described from Öhningen (Goldfuss 1837). Goldfuss (1837) described this species as being taller and shorter than *A. lavateri* (see below), externally ornamented by concentric striae and presenting more posteriorly positioned umbones. Based on the presently examined specimens, *A. splendens* further differs from *A. lavateri* in having a longer shell, about 2 to 2.5 times longer than tall.

Furthermore, in all likelihood, *Anodonta heerii* Mayer-Eymar, 1865, described (but not illustrated) from Schrotzburg near Öhningen as being smaller than *A. lavateri* (Heer 1865) but having broader valves, probably represents the same taxon as *A. splendens* (absent from the work of Heer 1865). We thus consider *A. heerii* a taxon inquirendum and potential junior synonym of *A. splendens*.

We use the name *A. splendens* here as it is understood in the palaeontological literature (e.g., Bulić & Jurišić-Polšak 2009). However, *Anodonta splendens* Goldfuss, 1837 is a junior homonym of *Anodonta splendens* De Cristofori & Jan, 1832, an extant species from central Africa (considered a junior synonym of *Chambardia rubens* (Lamarck, 1819); Daget 1998). There is presently no replacement name available for *A. splendens* Goldfuss, 1837 or case to retain the name. A few other later names (*A. anatinoides* Klein, 1846, *A. heeri* Locard, 1893, *A. sandbergeri* Locard, 1893) have been considered junior synonyms of *A. splendens*, but those synonymies remain uncertain (see also *A. lavateri* below).

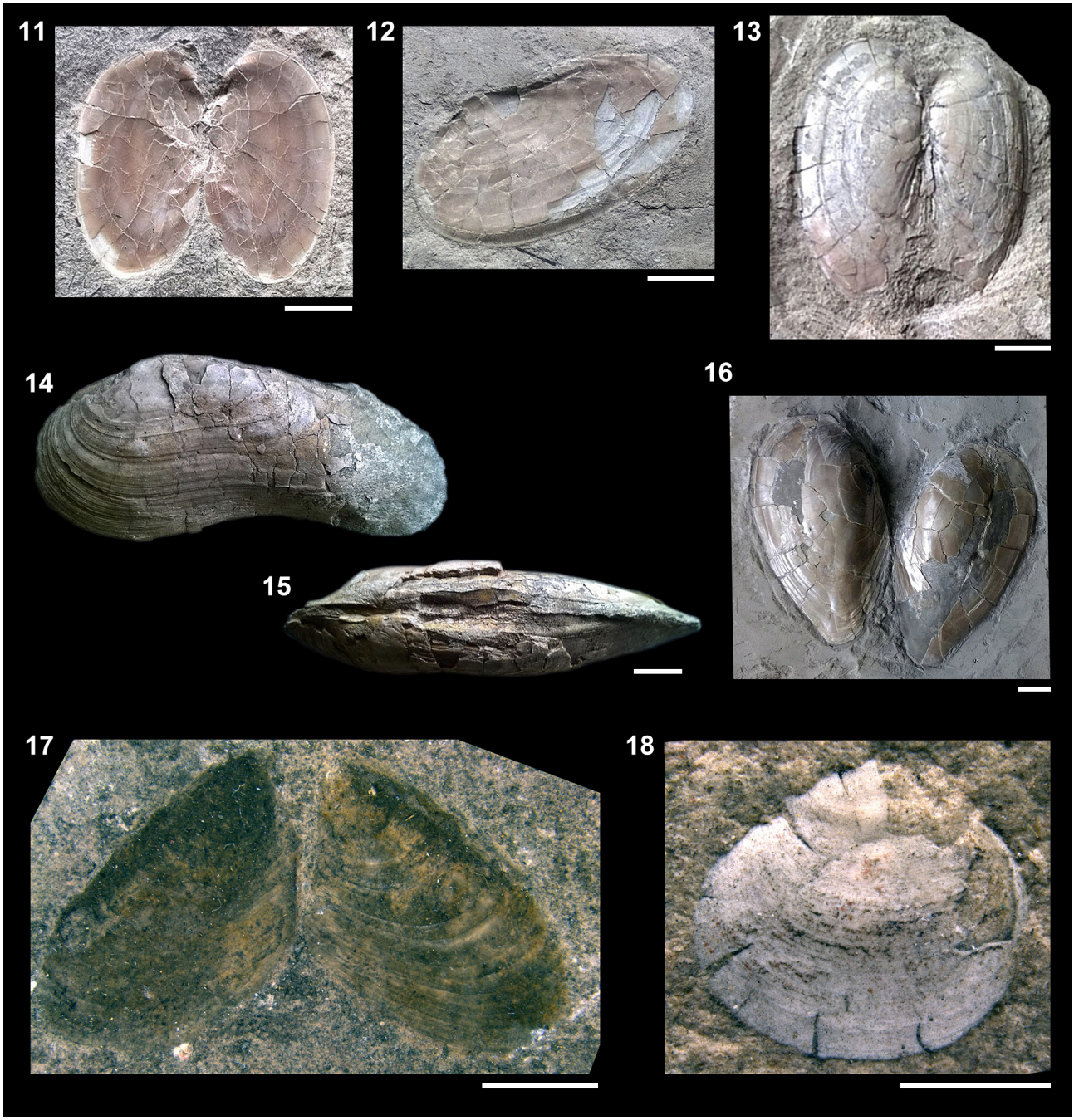
***Anodonta lavateri* (Münster, 1837)**
Figs 12–13

Unio Lavateri Münster in Goldfuss 1837: p. 182, pl. 132, fig. 6.
Anodonta Lavateri – Heer 1865: p. 351.
Anodonta Lavateri – Sandberger 1875: p. 570.
Anodonta Lavateri – Schalch 1883: p. 68.
Anodonta Lavateri – Seemann 1929: p. 75.
Unio lavateri – Hantke 1954: p. 86.

Anodonta lavateri – RUTTE 1956: p. 165.
Unio lavateri – GIERSCH 2004: p. 14.

Material examined: ETHZ 8046 (ca. 30 spcm, in part ex Lavater colln., in part ex Th, Würtenberger), MGH unnumbered (ca. 20 spcm), NHMUK IP G3069 (1 spcm), NHMUK IP G23495 (9 spcm, ex Murchinson colln), NHMUK IP G23496 (ca. 20 spcm, ex Murchinson colln), NHMUK IP G23497 (6 spcm), NHMUK IP OR63750 (ca. 20 spcm, ex Bruckmann colln), NHMUK IP OR74964 (ca. 15 spcm, ex van Breda colln), PIMUZ unnumbered (ca. 10 spcm; public exhibition), PIMUZ unnumbered (8 spcm, ex J. J. Scheuchzer colln.), RMK unnumbered (>10 spcm, from "Oberer Bruch", public exhibition: "Leinersaal"), SMNS 107350 (2 spcm), SMNS 107360 (1 spcm).

Remarks: The shell has an elongated-ovate shape, reaching up to 45 mm in length. The fossils were



Figs 11–18. Bivalves from the Öhningen region: 11 – *Anodonta splendens* (Goldfuss, 1837), scale bar 10 mm, SMNS 107359; 12–13 – *Anodonta lavateri* (Münster, 1837), scale bar 10 mm (12 – SMNS 107351, 13 – SMNS 107360, from the "stone pit" near Öhningen); 14–15 – *Pseudunio flabellatus* (Goldfuss, 1837), scale bar 10 mm, SMNS 9791-2008, from Schiener Berg; 16 – *Anodonta splendens* (Goldfuss, 1837), scale bar 10 mm, SMNS 23316; 17 – "*Dreissena*" sp., scale bar 5 mm, SMNS 107354; 18 – *Pisidium escheri* (Mayer-Eymar, 1865), scale bar 1 mm, RMK FTEm 810, from "Oberer Bruch"

largely preserved in butterflied position (indicating autochthonous or at least parautochthonous burial), but the hinge and other features are not visible. In its overall shape, as well as the somewhat irregular arrangement of the growth lines, the present fossils fit the original description and illustration of *A. lavateri*. This species was originally described from Öhningen, with elongated and narrow valves, with the posterior margin ending in an acuminated shape, being ~1.5 longer than high, presenting concentric striae and depressed whorls (Goldfuss 1837). Some of the specimens studied here differ slightly from the original description in having a longer shell, up to twice longer than tall, presenting a discreet posterior slope, and being more inflated.

Sandberger (1875) questioned the validity of this species due to the poor preservation of the specimens and similarity to other fossil *Anodonta* spp. from Öhningen, so its status remains uncertain. Comparing the specimens examined here with the original descriptions (Goldfuss 1837), however, indicates the presence of two *Anodonta* morphotypes in Öhningen. A revision is needed as the original descriptions mix features present in both morphotypes and provides incomplete data on shell proportions. Also, it is well known that environmental and physiological features can affect the shell shape of unionids (e.g., Fassatoui et al. 2014), so a future revision with better preserved specimens can help to elucidate this. Thus, we prefer to err on the side of caution and maintain both species as valid here until a thorough revision becomes possible.

Family Margaritiferidae

Genus *Pseudunio* F. Haas, 1910

***Pseudunio flabellatus* (Goldfuss, 1837)**
Figs 14–15

Unio (*Iridea*) *flabellatus* – Sandberger 1875: p. 568, pl. 30, figs. 1, 2.
Unio flabellatus – Schalch 1883: p. 68.
Unio (*Iridea*) *flabellatus* – Seemann 1929: p. 75.
Margaritana flabellate – Hantke 1954: p. 86.
Unio flabellatus – Rutte 1956: p. 165.

Material examined: NHMUK IP G23498 (3 spcm), NHMUK IP OR63093 (1 spcm, ex Bruckmann colln), NHMUK IP OR63462 (1 spcm), PIMUZ unnumbered (2 spcm, ex J. J. Scheuchzer colln.), SMNS 107357 (1 spcm), SMNS 107349 (2 spcm), SMNS 107356 (3 spcm), SMNS 107352 (2 spcm).
Remarks: A large (up to 90 mm) equivalve and inequilateral shell with an elongated ovate shape that becomes more tapered at the posterior margin; growth lines are well-marked, but their strength as well as the interval between them are irregular. At the posterior region of the shell, there are two transverse folds which are broad but very low, visible on the ventral half of the valve (preserved only in one specimen). Despite the relatively good preservation of some fossils (e.g., Figs 14–15), the hinge region is not visible in them.

The specimens can be identified as *Pseudunio flabellatus*, a widespread species in the Miocene of Europe (see revision by Schneider & Pietro 2011). It is considered that the dispersal of this species throughout Central Europe was due to warming temperatures during the Miocene Climatic Optimum (Scholz et al. 2007). Given the preservation of some specimens in life position, this species can be considered autochthonous in Öhningen.

Superfamily Dreissenoidea

Family Dreissenidae

Genus *Dreissena* Van Beneden, 1835

***"Dreissena"* sp.**
Fig. 17

Material examined: NHMUK IP G23498 (2 spcm), SMNS 107354 (1 spcm).
Remarks: The valves are flattened and embedded in the marl in the best-preserved specimen (Fig. 17); the hinge and the adductor muscle scar are not visible. The size of the fossil, the elongated mytiliform shape of the valves, and the concentric growth lines that become more oblique towards the edge of the valves, are reminiscent of the genus *Dreissena*. Nevertheless, the classification of European fossil dreissenids at the generic level is uncertain, with a handful of poorly defined genera in need of revision (Neubauer et al. 2015). As such, and considering the preservation of the present fossils (and the lack of visibility of hinge characters), we opted for a provisional classification as "*Dreissena*" sp.

Superfamily Sphaerioidea

Family Sphaeriidae

Genus *Pisidium* C. Pfeiffer, 1821

***Pisidium escheri* (Mayer-Eymar, 1865)**
Fig. 18

Cyclas escheri Mayer-Eymar in Heer 1865: p. 349, fig. 199.
Pisidium priscum – Sandberger 1875 [in part]: p. 570, pl. 30, fig. 6.
Pisidium escheri – Hantke 1954: p. 86.
Pisidium escheri – Rutte 1956: p. 165.

Material examined: RMK FTEm 810 (1 spcm, from "Oberer Bruch", public exhibition: "Leinersaal").
Remarks: Only one fragmentary and poorly preserved specimen was found, but its inequilateral valve bearing soft and irregular growth lines allows its identification. The *Pisidium* fossils from Öhningen

were previously identified as either *P. escheri* (by HANTKE 1954) or *P. priscum* (Eichwald, 1830). The latter was described from Miocene deposits in Ukraine, but is more widespread in Europe, while the former was described from Schrotzburg near Öhningen but has been considered a synonym of *P. priscum* (SANDBERGER 1875).

The fossils from Öhningen (the present one plus the original illustration in HEER 1865) are significantly different from *P. priscum*, and more similar to fossil representatives of *P. amnicum* (O. F. Müller, 1774) from the Middle/Late Miocene of Hammerschmiede, Bavaria (SCHNEIDER & PRIETO 2011). According to SANDBERGER (1875), *P. priscum* is considered to be more inequilateral and have stronger sculpture in relation to *P. amnicum*. The specimens from Öhningen, therefore, do not fit the definition of *P. priscum* and thus, we reinstate *Cyclas escheri* Mayer-Eymar, 1865 as a valid species, presently classified as *Pisidium escheri* (Mayer-Eymar, 1865). We note, however, that further revisionary work is needed to better define its relationship with *P. amnicum*.

DISCUSSION

MOLLUSC FAUNA

Overall, the preservation of the fossils from Öhningen is poor. Most specimens have been flattened during fossil diagenesis, resulting in a vast loss of diagnostic morphological features. Very few specimens have been preserved in "3D", and of those, many consist of internal molds. Even so, there is a good number of reasonably well-preserved specimens to allow species identification (Figs 2–18). A large number of bivalve specimens have been preserved in life position (i.e., with valves closed; e.g., Figs 14–15) or in "butterflied" position (i.e., with valves spread, but articulated; Figs 11, 13, 16, 17), indicating autochthonous or parautochthonous origin and little to no transport to fossilisation site.

The present paper is the first report of a dreissenid from Öhningen, as well as the first study in over a century to reconsider *Anodonta splendens*. Overall, ten species of molluscs were identified herein: five gastropods (three freshwater and two terrestrial) and five bivalves. It is difficult to interpret this low mollusc diversity (especially of land snails) in comparison to other Miocene freshwater deposits in southern Germany (e.g., SALVADOR et al. 2015a), given the paucity of fossils and information regarding Öhningen mollusks. Judging from the palaeontological collections analysed, there seems to have been a strong bias towards collecting plant and insect fossils from Öhningen.

There are further taxa mentioned in the older literature that could not be found in the available material. The freshwater taxa include two operculate snails (*Melanopsis kleinii* and *Theodoxus crenulatus*) and two pulmonate limpets (*Ferrissia deperdita* and the supposed *Ferrissia* n. sp. sensu HANTKE 1954). The terrestrial taxa include *Archaeozonites costatus*, *Discus pleuradrus*, *Klikia giengensis*, *Milax gracilior*, *Pseudochloritis insignis* and/or *P. incrassata*. The absence of these species in our material could be due to: (1) misidentification by previous authors, especially of poorly preserved specimens; for instance, specimens that were overall similar to *Pseudochloritis* spp. but that in fact belong to *Palaeotachea sylvestrina* (as assessed by shape of the protoconch and lack of sculpture); and/or (2) the absence of voucher specimens from those earlier studies in the present collections.

PALAEOENVIRONMENT

According to a palaeoenvironmental reconstruction based on sedimentological data, the sediments of Öhningen were deposited in a maar lake (ca. 1–2 km in diameter and at least 100 m deep), with episodic events of high salinity and shallow waters in the littoral (LUTZ 1997, LUTZ et al. 1999). The lake apparently had no tributaries for its whole duration (HANTKE 1965, GAUDANT 1980). The climate in Öhningen during the existence of the lake was described as moderately warm, with a mean annual temperature of 15.5–16.5 °C (warmest month 24 °C, coldest month 8–11 °C), and very humid, with an annual precipitation of 1,300–1,500 mm (HANTKE 1954, MAI 1995, LUTZ 1997, UHL et al. 2006).

The mollusc fauna of Öhningen can be interpreted in that scenario via an actualistic palaeoecological approach (RASSER et al. 2019); for that, we only consider those species whose presence we could confirm. The freshwater snails reported here are commonly found in lakes, especially in well-vegetated littoral areas (WELTER–SCHULTES 2012, RASSER et al. 2019). In any event, they would likely not tolerate the high salinity episodes proposed in the literature (LUTZ 1997, LUTZ et al. 1999), as suggested for a similar case in the Middle Miocene Lake Steinheim (RASSER & COVICH 2014, and references therein).

The bivalves indicate a calm sedimentation environment given their preservation in life position or butterflied position. Living representatives of the bivalve genera treated herein have in common the trait of inhabiting soft bottoms in more littoral (and preferably calmer) waters in well-oxygenated lakes, though *Pseudunio* is more typical of fluvial environments (FECHTER & FALKNER 1989, NUTTALL 1990,

Harzhauser & Mandic 2010, Thorp & Rogers 2010, Schneider & Prieto 2011, Welter-Schultes 2012). *Dreissena* spp., however, are more typically attached to harder substrates in both riverine and lacustrine settings (Nuttall 1990, Harzhauser & Mandic 2010), which could explain its rarity in Öhningen. *Pseudunio* and *Pisidium* are also typical of hard carbonate-rich waters (Schneider & Prieto 2011), which is in accordance with Öhningen's palaeoenvironment.

One unusual feature of Öhningen in comparison to other OSM lake settings is the large number of bivalves preserved. In other Middle Miocene lakes in southern Germany, bivalves are very scarce or completely absent (e.g., Salvador 2013, Salvador et al. 2015a). In contrast, bivalve assemblages similar to the present one have been reported from some OSM fluviatile deposits (Schneider & Prieto 2011, Salvador et al. 2015b; though none are coeval with Öhningen). So, it is expected that the palaeoenvironment at Öhningen would be particularly amenable to bivalves, though the reasons for that remain uncertain. In contrast, it could be a matter of fossilisation and preservation at Öhningen when compared to other localities.

The dearth of land snail species does not allow a thorough interpretation of the environment surrounding the palaeolake in Öhningen, though some facets can be garnered. Species of *Palaeotachea* are considered to be generalists, inhabiting a wide array of microhabitats (Rasser et al. 2019), so its presence does not add much to our analysis. Members of the genus *Granaria*, on the other hand, usually inhabit dry open areas, including rocky (calcareous) habitats (Höltke & Rasser 2013, Rasser et al. 2019), so a suitable environment could be expected around the palaeolake.

CONCLUDING REMARKS

Our analysis of the available mollusc material from Öhningen has simultaneously yielded a more restricted list of species than known in the literature, while also identifying new occurrences ("*Dreissena*" sp.) and reinstating obsolete taxa (*Pisidium escheri*). It is clear that a rich fossiliferous locality such as Öhningen would greatly benefit from renewed excavations to better assess the mollusc diversity in the palaeolake and its surroundings, enable the taxonomic revision of the problematic bivalve taxa, and improve the palaeoecological and palaeoenvironmental reconstructions of this past environment.

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