Early Miocene land and freshwater gastropods from the karst fissure filling Tomerdingen 1 (southern Germany)

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Early Miocene land and freshwater gastropods from the karst fissure filling Tomerdingen 1 (southern Germany)

Dietrich Kadolsky

Abstract

The mollusc fauna recovered from the fissure filling Tomerdingen 1 (southern Germany, 11 km NW Ulm) consists of six species of freshwater and land gastropods which are revised and figured. All except *Triptychia tomerdingensis* n. sp. (Clausilioidea, Filholididae) were already known from the Ulm Beds and Ehingen Beds in the area. The mammals of Tomerdingen 1 have been assigned to the early part of mammal zone MN 1; it is assumed that the molluscs, which occurred in a different, mammal-free rock matrix, have a similar age. The faunal assemblage of Tomerdingen 1 represents a new local mollusc assemblage zone, characterized by the presence of *Triptychia tomerdingensis* n. sp. Ties of the mollusc assemblages of the Ulm Beds and underlying Ehingen Beds with the mammal biozonation are discussed. The Tomerdingen assemblage is overlain by the Eggingen assemblage which is associated with mammal subzone MN 2a, possibly extending into late MN 1, and includes the majority of recorded mollusc occurrences; Tomerdingen is preceded by the Ehingen assemblage, from which no mammal evidence is known.

K e y w o r d s : Non-marine molluscs, mammal biostratigraphy, mollusc assemblage zones, Ulm Beds, taxonomy, *Triptychia tomerdingensis* n. sp.

1. Introduction

This study is Contribution No. 15 by the author in the series "Non-marine and marginally marine mollusc faunas in the European Tertiary". The aim of this series is to document newly discovered as well as already published faunas or material in need of better documentation and taxonomic revision. Faunas described or listed a long time ago often need also a review of the stratigraphic context and accompanying faunas, which taxonomic specialists often tended to neglect. Stratigraphic subdivision, formation names and biostratigraphic non-mollusc evidence have often considerably advanced since the initial (and sometimes only) publication of a mollusc fauna. In particular, high-resolution biozonations for non-marine Tertiary sediments in Europe based on mammals are now well established. This fact offers the chance to refine the age ranges and thus the temporal succession of terrestrial and freshwater mollusc species, where they co-occur with well-dated mammal faunas. One such occurrence is the fissure filling locality Tomerdingen 1, exposed in the now abandoned Tomerdingen quarry (southern Germany, Baden-Württemberg, ca. 11 km NW of Ulm), where Upper Jurassic limestones had been exploited for cement manufacture. The fissure filling was first described by Seemann & Berckhemer (1930), who provided also a list of mollusc species. Their material is present in the Staatliches Museum für Naturkunde in Stuttgart and is here revised. Also a mammal fauna was first listed by Seemann & Berckhemer (1930). Subsequently selected mammal species have been studied in greater detail (Dietrich 1931; Tobien 1939, 1963, 1970, 1974, 1975; Ziegler 1989, 1990a, 1990b; Werner 1994). The biostratigraphic age of the Tomerdingen mammal fauna is early mammal zone MN1 (Tobien 1974; de Bruijn et al. 1992; Werner 1994) of early Aquitanian age.

2. Geological setting

The geological setting is here summarized mainly according to Seemann & Berckhemer (1930). The fossiliferous fissure was exposed in the communal limestone quarry of the town of Tomerdingen, located ca. 500 m S of Tomerdingen in Baden-Württemberg (ca. 48° 28′ 41″ N, 9° 54′ 19″ E) at a surface elevation of ca. 630 m. The bedrock is Late Jurassic strongly fractured limestone. In the quarry, a monocline striking 65−70° juxtaposes massive and stronger fractured limestones poor in fossils in the W against downthrown coarsely bedded more fossiliferous limestones in the E, which show less fracturing. Two sets of fractures exist, striking 20−25° and 110−115°. Most fractures are infilled by Tertiary materials which is commonly a dark brown loam with limonitic concretions ("Bohnerz"). The loam rarely yielded Tertiary fossils, of which Seemann & Berckhemer (1930) unfortunately gave no details.

According to Werner (1994), there is a fissure "Tomerdingen 1" with a Middle Oligocene (i.e. Rupelian)

rhinoceratid reported by DIETRICH (1931), and a fissure "Tomerdingen 2", which contained the Aquitanian mammals and gastropods first mentioned by SEEMANN & BERCKHEMER (1930), of which the gastropods are the subject of the present study. This statement is incomprehensible, since DIETRICH (1931) stated expressly that the rhinoceratid remains derived from the fissure described by SEEMANN & BERCKHEMER (1930), and that the new rhinoceratid taxon indicated an early Aquitanian age. Thus, only one mammal bearing fissure exists, which will be referred to simply as "Tomerdingen 1".

The fissure is located in the massive limestones in the western part of the quarry, striking 20–25°. Its fill differed from that of the other fissures in that hardly any Bohnerz was present. When observed at the quarry face, the fissure opened only 4 m below the surface and widened downwards up to 1.5 m. SEEMANN & BERCKHEMER (1930) assume that it reached the present-day surface in an area of the quarry, where the limestone was already removed. The fill was rather heterogenous: limestone rubble with Jurassic fossils; fragments of sinter crusts formed on the fissure wall and then detached; fine-grained sandy and marly, rarely fat, grey-greenish clays with vertebrates; grey-greenish, non-glauconitic fine sand devoid of fossils; lumps of coaly greyish-black marl; lighter coloured marly limestone with mollusc shells; fine to coarse-grained glauconitic sand with fish remains. The latter originated from the Upper Marine Molasse (OMM = Obere Meeresmolasse), which is now absent in the area.

The bones were mostly off white to light brownish, and rarely brown. Most gastropod shells have a dark grey stain which may be finely dispersed organic matter or pyrite.

The difference in rock type between the ossiferous and the gastropod-bearing rocks means that the mammal fauna is not necessarily coeval with the gastropod fauna. The multitude of rock types, of which the OMM sands are clearly younger than both the mammal and the gastropod faunal associations, suggests a complex fill history, which is moreover different from the infill process of adjacent fissures. SEEMANN & BERCKHEMER's (1930) description does not allow to reconstruct this history, and with the quarry now being built over, this history can no longer be deciphered. The authors observed vertical striation on the fissure walls, to which in places bone breccia adhered to. They interpreted this as evidence of downgliding of fissure infill, possibly caused by widening of the fissure below. SEEMANN & BERCKHEMER (1930) described also horizontal flutes in the fissure wall which were caused by streaming water.

A remarkable feature of most gastropod shells is their microfracturing (Fig. 1). These fractures are curved, equidistant, of equal strength and run parallel to each other. Often they curve around the umbilical area. An explanation cannot be given here.

Fig. 1. Microfractures in a shell of *Palaeotachea subsulcosa* (SMNS 61397) from the fissure infill Tomerdingen 1. Scale 2 mm.
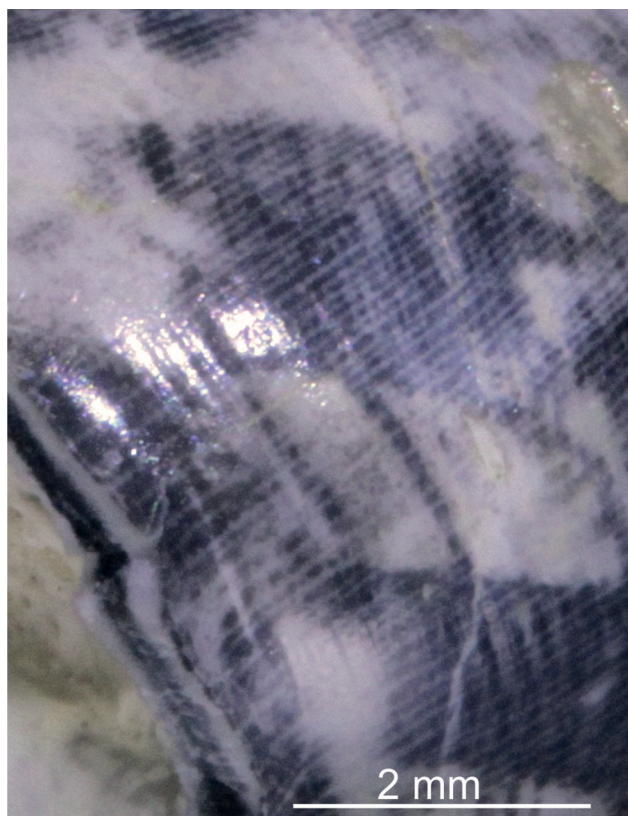
3. Materials and methods

Molluscs from Tomerdingen 1 and reference specimens were inspected under a binocular microscope Wild M5. Some specimens were drawn with the aid of a drawing tube. All were photographed by the author with a Canon EOS 500D camera, and the illustrations were processed with HeliconFocus and Corel software.

The specimens mentioned in this paper are housed in the following institutions: BSPG = Bayerische Staatssammlung für Paläontologie und Geologie, München; K = Collection of the author; MUWI = Museum Wiesbaden; NHMB = Naturhistorisches Museum Basel; SMNS = Staatliches Museum für Naturkunde Stuttgart; SMF = Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt a. M.

4. Systematic palaeontology

The sequence of species follows the systematic arrangement of BOUCHET et al. (2017), to which is referred to for the taxonomic categories above family level.

The synonymy lists include primarily references to occurrences in Tomerdingen and in the Ulm Beds (Ulmer Schichten, which are part of the upper Lower Freshwater Molasse (= USM = Untere Süßwassermolasse)). Further references are included in brackets, when they were indispensable for the taxonomy or nomenclature of the species in question.

4.1. Aquatic gastropods

Family Lymnaeidae RAFINESQUE 1815

Subfamily Lymnaeinae RAFINESQUE 1815

Stagnicola cf. *subovatus* (ZIETEN, 1832)
Pl. 1, Fig. 1

cf. * 1832 *Limnaea subovata* ZIETEN: 39, pl. 30, fig. 2.
cf. v 1872 *Limneus subovatus*. – SANDBERGER: pl. 21, fig. 6.
cf. v 1875 *Limneus subovatus*. – SANDBERGER: 453.
cf. 1923 *Radix (Radix) subovata* [*subovata*]. – WENZ: 1291–1308 [partim].
v 1930 *Radix (Radix) subovata*. – SEEMANN & BERCKHEMER: 22.

M a t e r i a l : Two specimens (SMNS 61400/1 (internal mould), SMNS 61401/1 (preserved shell, Pl. 1, Fig.1)

R e m a r k s . The better preserved specimen from Tomerdingen (Pl. 1, Fig.1) is close to *Stagnicola subovatus* but differs by the broader last whorl (Pl. 1, Fig. 1b). Because of the low number of specimens of lymnaeids from the Ulm Beds available for study, the variability of *Stagnicola subovatus* is not sufficiently understood. Therefore, the Tomerdingen specimens are only tentatively attributed to this species.

"*Lymnaea*" *subovata* is here assigned to *Stagnicola*, because it is more elongate than recent *Radix* species, the middle whorls are much flatter in outline and the height : width ratio of the middle whorls is higher than in *Radix* species. In the genus *Stagnicola* JEFFREYS, 1830, *S. subovatus* is a representative of a relatively ventrose lineage.

D i s t r i b u t i o n : ZIETEN (1832) described *Stagnicola subovatus* from the Ulm Beds of Niederstotzingen. Subsequent authors, particularly SANDBERGER (1875) and WENZ (1923) added many more localities in the Ulm Beds as well as in the underlying Ehingen Beds. Outside the Ulm area, WENZ (1923) in his compilation, listed many more localities in Germany, France, Spain, Switzerland and the Czech Republic, ranging in age from "Sannoisian" (i.e. early Rupelian) to Burdigalian. WENZ's treatment and synonymy need to be re-assessed. For example, WENZ (1923) treated "*Lymnaea*" *pachygaster* THOMÄ, 1845 as conspecific with *S. subovatus*, stating that *S. subovatus* "is hardly separable from *pachygaster*". The differences, however, are clear in fully grown specimens, which in *S. pachygaster* have a more inflated and relatively larger last whorl than in *S. subovatus*. As the dimensions and proportions of the middle whorls of *S. pachygaster* are almost identical to those of *S. subovatus*, *S. pachygaster* is also placed in the genus *Stagnicola* and treated preliminarily as a separate species until the variability of *S. subovatus* from the population in the type region is better understood.

Family Planorbidae RAFINESQUE, 1815

Subfamily Planorbinae RAFINESQUE, 1815

Tribe Planorbini RAFINESQUE, 1815

Gyraulus applanatus (THOMÄ, 1845)
Pl. 1, Fig. 2

(*v 1845 *Planorbis applanatus* THOMÄ: 155).
(* 1847 *Planorbis declivis* A. BRAUN in SANDBERGER: 43, foot note (indication: *P. applanatus* THOMÄ, 50)).
(v 1872 *Planorbis declivis* SANDBERGER: pl. 25, fig. 9).
v 1875 *Planorbis declivis* – SANDBERGER: 370, 424, 453, 491–492, pl. 25, fig. 9–9e.
1923 *Gyraulus (Gyraulus) trochiformis applanatus*. – WENZ: 1579–1588.
v 1930 *Gyraulus trochiformis applanatus*. – SEEMANN & BERCKHEMER: 22.

M a t e r i a l : One specimen; nos. SMNS 61398 and SMNS 61399 were given for two parts of the same specimen, now glued together.

D i s t r i b u t i o n : *Gyraulus applanatus* was described from the Wiesbaden Formation (mammal zone MN 2a, Aquitanian) from the vicinity of Wiesbaden in the Mainz Basin. It is a widespread species in the Mainz Basin, ranging from the Oppenheim Formation (MN 1) to the Wiesbaden Formation and probably also into younger formations. According to WENZ (1923), G. *applanatus* is widely distributed in formations of Chattian and Aquitanian age, and more sporadically in Burdigalian strata. Closely related and, according to RASSER & SALVADOR (2019), conspecific is *Gyraulus kleini* GOTTSCHICK & WENZ, 1916, described from and common in the Silvana Beds (Burdigalian to Langhian) of the North Alpine Foredeep.

Tribe Coretini GRAY, 1847

Planorbarius cornu (BRONGNIART, 1810)
Pl. 1, Figs. 3, 4

(*v 1810 *Planorbis cornu* BRONGNIART: 371, pl. 22, fig. 6).
(*v 1845 *Planorbis solidus* THOMÄ: 153).
(*v 1845 *Planorbis corniculum* THOMÄ: 154, pl. 4, fig. 7).
* 1872 *Planorbis subteres* SANDBERGER: pl. 21, fig. 5.
(1875 *Planorbis cornu*. – SANDBERGER: 370, 424, 452).
1875 *Planorbis cornu* var. *subteres* SANDBERGER: 452, pl. 21, fig. 5–5b.
1923 *Coretus cornu cornu*. – WENZ: 1426–1449 [partim] (+ syn. *solidus* THOMÄ, 1845, *corniculum* THOMÄ, 1845, *subteres* SANDBERGER, 1872, and others).
v 1930 *Coretus cornu cornu*. – SEEMANN & BERCKHEMER: 22.

M a t e r i a l : Three specimens (SMNS 61402/1, SMNS 61403/1, SMNS 61404/1).

R e m a r k s : Two variants occur in Tomerdingen 1: Fig. 3 depicts a specimen with a relatively high shell, wide last whorl and correspondingly narrower umbilicus. Fig. 4 depicts a flatter shell with more slowly increasing whorls and wider umbili-

cus. Similar variants are observed in other populations which are treated as conspecific because it seems unlikely that two closely related forms occurring together are truly separate species. THOMÄ (1845) named the high-shelled variant *P. solidus* and the flatter, more evolute form *P. corniculum*; both occur often together, e.g.: Calcaire d'Étampes in the Paris Basin (late Rupelian, type region): Itteville (coll. LOZOUET & MAESTRATI); Wiesbaden Formation in the Mainz Basin (Aquitanian), Wiesbaden (MUWI) and Mainz–Weisenauer Straße 5 (SMF); Silvana Beds in the North Alpine Foredeep (Burdigalian), Zwiefaltendorf (coll. KADOLSKY ex SCHLICKUM).

D i s t r i b u t i o n : BRONGNIART (1810) described *Planorbarius cornu* from several localities in the Meulières de Montmorency and the Calcaire d'Étampes (Paris Basin), which are placed in mammal zone MP 24 (late Rupelian). Younger *Planorbarius* populations received several additional names, but separate species or named subspecies are since long not recognized (WENZ 1923 and pers. obs., see under Remarks). WENZ (1923) cited localities in Germany, France, Spain, Switzerland and the Czech Republic, ranging in age from the "Sannoisian" (early Rupelian) to the Burdigalian.

4.2. Terrestrial gastropods

Family Filholiidae WENZ, 1923

Triptychia tomerdingensis n. sp.
Pl. 1, Figs. 5–9

v   1930 *Pomatias* (*antiquum*?). – SEEMANN & BERCKHEMER: 22 [non *Cyclostoma elegans antiquum* BRONGNIART, 1810].

v   1930 *Triptychia* (*Triptychia*) *antiqua*. – SEEMANN & BERCKHEMER: 22 [non *Clausilia antiqua* ZIETEN, 1832].

v   2006b *Triptychia* (*Triptychia*) *antiqua*. – SCHNABEL: 136 [partim, non pl. 1, figs. 2, 3; locality Tomerdingen only; non *Clausilia antiqua* ZIETEN, 1832].

E t y m o l o g y : After the type locality Tomerdingen.

H o l o t y p e : SMNS 61408 (Pl. 1, Fig. 5).

P a r a t y p e s : SMNS 61399/1 (fragment, labelled "*Pomatias* (*antiquum*?)", Pl. 1, Fig. 8), 61407/8 (middle whorls; Pl. 1 Fig. 7). 61408/3 (middle and final whorls, peristome partly preserved). 61409/3 (last whorls without preserved peristome). 61410/1 (protoconch and middle whorls, Pl. 1, Fig. 6).

T y p e   l o c a l i t y : SW Germany, fissure Tomerdingen 1 in Tomerdingen quarry; ca. 11 km NW Ulm. (ca. 48° 28′ 41″ N, 9° 54′ 19″ E).

T y p e   h o r i z o n : Lacustrine limestone, dislodged in fissure Tomerdingen 1, here interpreted as derived from the Ulm Beds, mammal zone MN 1, Aquitanian.

D i a g n o s i s : A medium-sized *Triptychia* species with a club-shaped shell, ca. 60 strong collabral ribs per whorl, a relatively rounded aperture with a small, indistinct sinulus, and a strongly lipped and expanded peristome.

D e s c r i p t i o n : Shell ca. 22 mm high (reconstructed from combination of the holotype with a paratype apical fragment, see Pl. 1, Fig. 9) and 7.1 mm wide (holotype), club-shaped, with a very narrow or closed umbilicus. Protoconch smooth, ca.

three moderately convex whorls. First teleoconch whorl with very weak collabral orthocline riblets grading into strong ribs of fairly regular strength, which persist up to the peristome and to the umbilical area without becoming weaker. Per whorl there are ± 60 ribs. These ribs are rounded in cross-section and narrower than their interstices; their shape is orthocline and slightly convex; at the suture they thicken and render the suture crenellate. The height : width ratio of the visible part of the middle whorls varies between 0.25 and 0.36. Teleoconch whorls almost flat in profile, separated by a slightly deepened suture. Aperture pear-shaped, adapically terminating in a weak sinulus. Peristome continuous, thickened and expanded, with a strong parietal callus. Supracolumellar ("parietal") lamella not observed due to rock matrix; middle and abapical columellar lamellae equally strong in the middle whorls; in the adult aperture the abapical lamella is stronger; both reach the peristome.

R e m a r k s : SEEMANN & BERCKHEMER (1930) mistook the collabral ribbing of a fragment of *Triptychia tomerdingensis* for the spiral ribbing of pomatiids.

Triptychia antiqua (ZIETEN, 1832) is more slender, less club-shaped and has finer ribbing; its aperture is more elongate and the sinulus larger. It is often larger than *T. tomerdingensis*, although the material of *T. tomerdingensis* is insufficient to describe variability. The height : width ratio of the late middle whorls of *T. antiqua* is higher, up to 0.5. Three specimens of *T. antiqua* from the Ulm Beds in the neotype locality Thalfingen are figured for comparison on Pl. 1, Figs. 12–14.

T. tomerdingensis is, for its broad and club-shaped, a strongly ribbed shell with a low height : width ratio of the middle whorls including the late ones, similar to *T. conoidea* FISCHER & WENZ, 1914 and *T. emmerichi* WENZ, 1912. Unfortunately all material of these species was held in WENZ's collection, which was destroyed in the air bombardments of Frankfurt a. M. in 1943/1944. *Triptychia conoidea* (Pl. 1 Fig. 11) is least well known, as the aperture was not described. The figured shell is 26 mm high and 8.8 mm wide. *T. conoidea* occurs in the Kaltennordheim Formation in the Rhön Mountains whose age is "young Early Miocene" (MARTINI 2011). The holotype and sole known specimen of *T. emmerichi* (Pl. 1, Fig. 10) is 19.4 mm high and 7.6 mm wide; on the last whorl there are 38 flattened ribs. The middle columellar lamella is weaker than the abapical one, which alone reaches the peristome. *T. emmerichi* occurs in the Wiesbaden Formation of Budenheim in the Mainz Basin, which is dated Aquitanian, mammal biozone MN 2a.

D i s t r i b u t i o n : Only known from the type locality.

Family Zonitidae MÖRCH, 1864

Subfamily Archaeozonitinae PFEFFER, 1930

R e m a r k s : HAUSDORF (in BOUCHET et al. 2017: 365, 387) included Archaeozonitinae in the family Gastrodontidae, citing similarities with *Poecilozonites* BOETTGER, 1884 (recent, Bermudas) and *Zonitoides* (*Ventricallus*) PILSBRY, 1946 (recent, N. America). According to HAUSDORF, „no characters are known by which the group [Archaeozonitinae] can be distinguished from the Gastrodontidae". This statement is only true, if it is amended to "consistently distinguished". All gastrodontids are much smaller than all archaeozonitines except *Omphalosagda* SANDBERGER, 1872, which is indeed similar in size and shape to *Ventricallus*, but *Ventricallus* differs in having a much narrower

umbilicus, a callous peristome and sometimes an internal fold in basal or palatal position (PILSBRY 1946: 458−471). None of the archaeozonitines exhibits a thickened peristome or any folds. No such (or any other) differences exists between Archaeozonitinae and Zonitidae, which are a preferable relation because there is no size difference and no geographical separation; modern zonitid species occur in SE Europe.

Archaeozonites cf. *subangulosus* (ZIETEN, 1832)
Pl. 2, Figs. 1, 2

cf. *   1832 *Helix subangulosa* ZIETEN: 41, pl. 31, fig. 2.
cf.   1872 *Archaeozonites subangulosus*. − SANDBERGER: pl. 21, fig. 15.
cf.   1875 *Archaeozonites subangulosus*. − SANDBERGER: 463 (Ref. pl. 21, fig. 15−15a).
cf.   1923 *Zonites (Aegopis) subangulosus*. − WENZ: 260−262 [pars, excl. syn. *risgoviensis* JOOSS, 1912].
v   1930 *Zonites (Aegopis) subangulosus*. − SEEMANN & BERCKHEMER: 22.

M a t e r i a l : 2 Fragments (SMNS 61405/1, SMNS 61406/1).

R e m a r k s : The identification is preliminary due to the incomplete state of preservation. Size, shape of the last whorl, sculpture and the narrow umbilicus are consistent with *Archaeozonites subangulosus*. Other archaeozonitids of similar size have a wider umbilicus.

D i s t r i b u t i o n of *A. subangulosus*: The species was described from the lacustrine limestone of Ulm, i.e. the Ulm Beds. It is also reported from the underlying Ehingen Beds (Late Oligocene) and the Hochheim Formation (formerly Landschneckenkalk; Late Oligocene) of the Mainz Basin, and from several localities in the the Lower Freshwater Molasse (Aquitanian?) of Switzerland.

Family Helicidae RAFINESQUE, 1815

Subfamily Helicinae RAFINESQUE, 1815

Palaeotachea subsulcosa (THOMÄ, 1845)
Pl. 2, Figs. 3–6

*   1832 *Helix globulosa* ZIETEN: 38, pl. 29, fig. 3 [non *Helix globulosa* FÉRUSSAC, 1821].
*   1832 *Helix rugulosa* ZIETEN: 38, pl. 29, fig. 5 [non *Helix rugulosa* RISSO, 1826].
(*v   1845 *Helix subsulcosa* – THOMÄ: 130, pl. 2, fig. 3a–c).
(v   1858 *Helix subsulcosa*. – SANDBERGER: pl. 4 fig. 10).
(v   1858 *Helix (Archelix) subsulcosa*. – SANDBERGER: 38, pl. 4, fig. 10–10b).
(*   1862 *Helix colorata* (BRAUN) SANDBERGER: pl.35, fig. 8 [non *Helix colorata* MOUSSON, 1849]).
*v   1872 *Helix quadrifasciata* SANDBERGER: pl. 21, fig. 9 [non *Helix quadrifasciata* DE SERRES, 1840, nec LE GUILLOU, 1842].
*v   1872 *Helix crepidostoma* SANDBERGER: pl. 21, fig. 10.
v   1872 *Helix rugulosa*. – SANDBERGER: pl. 21, fig. 11.
(1872 *Helix colorata*. – SANDBERGER: pl. 22, fig. 22 [non *Helix colorata* MOUSSON, 1849]).

(v   1872 *Helix subsulcosa*. – SANDBERGER: pl. 22, fig. 23).
v   1875 *Helix (Coryda) rugulosa*. – SANDBERGER: 381, 456, pl. 21, fig. 11, 11a (type), pl. 22, fig. 23–23b (var. *subsulcosa*), pl. 22, fig. 22–22b (var. *colorata*).
v   1875 *Helix (Coryda) rugulosa* typus. – SANDBERGER: 381, 456, pl. 21, fig. 11, 11a.
(v   1875 *Helix (Coryda) rugulosa* var. *subsulcosa* − SANDBERGER : 381, pl. 22, fig. 23–23b).
v   1875 *Helix (Coryda) crepidostoma* SANDBERGER: 456 (Ref. pl. 21, fig. 10, 10a (type), pl. 21 fig. 9, 9a (var. *quadrifasciata*).
        1923 *Cepaea rugulosa rugulosa*. – WENZ: 653−663 [partim, excl. syn. *wradzidloi* ZINNDORF, 1901 and *convexitesta* JOOSS, 1912]).
(1923 *Cepaea rugulosa subsulcosa*. – WENZ: 664−667).
        1930 *Cepaea subsulcosa crepidostoma*, – WENZ: 3030 (subspecies rank conditionally proposed).
        1930 *Cepaea subsulcosa subsulcosa*. – WENZ: 3030 (new syn.: *Helix rugulosa* ZIETEN 1832, non RISSO, 1826).
v   1930 *Cepaea rugulosa rugulosa*. – SEEMANN & BERCKHEMER: 22 (mainly f. *crepidostoma*, occasionally *rugulosa* s.str.).
(cf.   1936 *Cepaea (Cepaea) subsulcosa* – WENZ: 231).
v   1972 *Cepaea (Cepaea) subsulcosa*. − MÜLLER: 57, 59 (cf.), 131, 132, 133, 134, 136, 137 (cf.), 138, 192−194, fig. 13, tab. 7.
(cf. v   2008 *Cepaea (Palaeotachea)* cf. *subsulcosa*. − KADOLSKY: 91).

M a t e r i a l : 17 specimens (nos. SMNS 61396/1, SMNS 61397/1, SMNS 61411/1 – SMNS 61426/1).

R e m a r k s : ZIETEN (1832) described *Helix globulosa* and *H. rugulosa* from the Ulm Beds of Ulm and Niederstotzingen, respectively. However, both names are unavailable as junior primary homonyms. Nonetheless the name *H. rugulosa* had been widely used until WENZ (1930) discovered the homonymy and replaced the name *H. rugulosa* with the next younger name *Helix subsulcosa* THOMÄ, 1845. This name is based on material from "Hochheim" in the Mainz Basin; its stratigraphic occurrence was believed to be the "Landschneckenkalk" (now Hochheim Formation, Late Oligocene), but is actually the lower part of the "Cerithienschichten" (now Oppenheim Formation, Early Miocene, mammal zone MN1) (KADOLSKY 1989; OTT et al. 2009; SCHÄFER & KADOLSKY 2015).

SANDBERGER (1875) recognized that *H. rugulosa* ZIETEN and *H. subsulcosa* were conspecific, but maintained them as varieties without differentiating them from each other. In addition he introduced a new species, *H. crepidostoma*, for certain forms of the Ulm Beds without differentiating them from „*Helix rugulosa*". His description and figure indicate that the overall shape of *H. crepidostoma* was more conical, the outline of the middle whorls very flat and the ribbing much weaker. The latter is in most syntypes merely a preservation issue, but there is also one well-preserved syntype, which indeed shows a weak ribbing. The shell shape, convexity of the middle whorls and ribbing strength are variable and overlap widely in populations both from the Oppenheim Formation and the Ulm Beds; consequently there is no basis for a taxonomic differentiation.

In the specimens from Tomerdingen the ribbing is usually weak, which may be a diagenetic effect. The shells have five well-developed pigment bands, while in other populations unbanded shells can be common. The Tomerdingen shells are relatively small, because in Tomerdingen the animals terminated growth already at 4.2 whorls and formed the expanded

and thickened lip of adult individuals, whereas elsewhere the animals did so when they reached about five whorls. This phenomenon is not uncommon in Helicidae, e.g. in *Palaeotachea maguntina* (DESHAYES) it is very strongly developed (author's observations).

D i s t r i b u t i o n : WENZ (1923) applied a rather extended species concept and recognized three subspecies, then named *Cepaea rugulosa rugulosa* (Rupelian to Aquitanian: S. Germany, Mainz Basin, Switzerland, France), C. *rugulosa eurabdota* (FONTANNES, 1884) (Chattian: SE France) and C. *rugulosa subsulcosa* (Chattian to Aquitanian: Mainz Basin). Topotypes, resp. syntypes of the Rupelian taxa *Helix wrazidloi* ZINNDORF, 1901 and *Cepaea convexitesta* JOOSS, 1912 have been examined and found to be incorrectly synonymized with "*Cepaea rugulosa rugulosa*", while a taxonomic distinction between *rugulosa/ crepidostoma* from the Ulm area and *subsulcosa* s.str. from the Mainz Basin is not confirmed in this study. Thus a taxonomic review of the *Palaeotachea subsulcosa* complex is required. To date the author has examined material and can confirm the following *Palaeotachea* populations as belonging to *P. subsulcosa*: Gaimersheim 2 karst fissure filling (BSPG, MÜLLER 1972) of MP 27 age; possibly Oberleichtersbach doline filling (KADOLSKY 2008) of MP 30 age; probably Paulhiac (small specimens: NHMB, WENZ 1936) of MN 1 age; Hochheim-Flörsheim, lower Oppenheim Formation (SMF, SMNS, BSPG, K; syntypes of *Helix subsulcosa* in MUWI) of MN1 age; Ehingen (MUWI, BSPG) of Late Oligocene age; in the Ulm Beds of MN 2 age: Eggingen (MUWI, syntypes of *Helix crepidostoma*), Thalfingen (SMNS), Donaurieden (SMF, K), Ulm-Michelsberg (holotype of *Helix quadrifasciata*, MUWI).

5. Discussion

5.1. Depositional environment

The shells contain a whitish to beige or light grey calcareous rock matrix, indicating a lacustrine carbonate deposit. In the Ulm Beds, molluscs have typically been collected from such rocks, although more argillaceous layers commonly exist, too. Mammals are typically recovered from the latter. This and the clay content indicate increased terrigenous influx. Absence of these terrigenous materials in the limestone layers could indicate greater distance from the shores, probably due to higher water levels. In such situation, shells of land snails can still be swept in; if air-filled, they are capable of long-distance drift. The aquatic gastropods lived close to their burial place, because their shells do not normally fill with air after death.

5.2. Stratigraphy

WENZ (1916, 1918) characterized the sediment complex in the Lower Freshwater Molasse (Untere Süßwassermolasse = USM) of the Ulm area by mollusc associations (Fig. 2). Later he extended the concept of his Rugulosa Beds including the divisions into Lower and Upper Rugulosa-Schichten into the entire North Alpine Foredeep (Molasse Basin) and beyond (WENZ 1923−1930). These terms, as well as the terms Omphalosagda Beds and Ramondi Beds, were understood as biostratigraphic assemblage zones, but were also applied to the sediments assigned to these zones. For the Ulm area, he introduced also the lithostratigraphic terms Thalfingen Beds and Öpfingen Beds, which designate different facies belts of the Ulm Beds. The index fossils for the Rugulosa Beds as given by WENZ (1916) are shown in Fig. 2 with modernized nomenclature. To this list this author has added the occurrences of *Triptychia* species, and, following the

Age	Stratigraphic subdivisions by Wenz (1916, 1918)				Index fossils			Stratigraphy this paper			
					Wenz 1916 (modified)		Additions this paper	Lithostra-tigraphy	Mammal zones	Mollusc assemblage zones	Mollusc localities
Aquitanian	Rugulosa-Schichten	Upper	Omphalo-sagda-Schichten	Thal-finger Sch.	Öpfin-ger Sch.	*Omphalosagda subrugulosa* (Quenstedt), *Tropidomphalus minor* Fischer & Wenz, *Palaeotachea eckingensis* (Sandberger), *Triptychia ulmensis* (Sandberger), *Eualopia eckingensis* (Sandberger), *Oxyloma peregrina suevica* (Wenz), *Zilchiola gracilis* (Sandberger), *Viviparus pachystoma* (Sandberger), *Meiopomatias bisulcatus* (Zieten)	*Triptychia antiqua* (Zieten), *Agalactochilus inflexus* (Zieten)	Ulmer Schichten [Ulm Beds]	MN 2a	Eggingen	Altsteußlingen, Beiningen, Donaurieden, Eggingen (historical outcrop), Frankenhofen, Langenau-Göttingen, Ulm-Lehr, Niederstotzingen, Oberdischingen, Öpfingen, Ulm (Buckenrain, Kuhberg, Michelsberg)
			Palaeotachea subsulcosa **(Thomä)**, *Janulus gyrorbis* (Klein), ***Archaeozonites subangulosus*** **(Zieten)**			(Strata and faunas from this interval in the Ulm area were not known to Wenz (1916, 1918))		***Triptychia tomerdingensis*** **n.sp.**		MN 1	Tomerdingen	Tomerdingen 1
								?		MP 30	?	
Chattian		Lower	Ramondi-Schichten			*Wenzia ramondi* (Brongniart), *Pachycarocollina bouilletii* (Boissy), *Palaeotachea hortulana* (Thomä), *Neobembridgia antiqua antiqua* (Brongniart)	*Triptychia escheri* (Sandberger), *Triptychia suevica* (Sandberger), *Galactochiloides ehingensis* (Klein)	Ehinger Sch. [Ehingen Beds]	MP 26?	Ehingen	Ehingen (Am Schiff), Ehingen-Berg

Fig. 2. Stratigraphy of the Ulm Beds and Ehingen Beds. Bold: index fossils found in Tomerdingen1.

taxonomic revision of Kadolsky et al. (2016), of *Agalactochilus inflexus* (Zieten, 1832) and *Galactochiloides ehingensis* (Klein, 1846). Wenz (1916) had synonymized the two latter and listed them under the name "*Galactochilus inflexum* (= *ehingense*)" as being present in the entire "Rugulosa-Schichten".

The index fossils present in Tomerdingen 1 are shown in bold in Fig. 2. Evidently, none of the index fossils of the Omphalosagda-Schichten and Ramondi-Schichten have been found in Tomerdingen, nor have any of the four *Triptychia* species. The mammal faunas provide additional insight into the relationship of the Tomerdingen molluscs with the Ulm and Ehingen Beds:

Although many localities in the Ulm area have yielded mammals, co-occurring molluscs have surprisingly rarely been reported, and vice versa. The most important exception is the historical outcrop near Eggingen. Its mammal fauna has been placed in the early part of mammal zone MN 2a (Werner 1994). Its mollusc fauna is clearly an assemblage of the Omphalosagda Beds, with the index fossils *Omphalosagda subrugulosa*, *Agalactochilus inflexus*, *Tropidomphalus minor*, *Palaeotachea eckingensis*, *Eualopia eckingensis*, *Triptychia antiqua*, *Meiopomatias bisulcatus* and *Zilchiola gracilis* being present (Wenz 1923−1930). The mollusc associations of the "Omphalosagda-Schichten" in many localities are relatively uniform. Therefore the age of this assemblage is assumed to be equivalent to the MN 2a mammal zone throughout, with a possible extension into the upper part of MN 1. In Fig. 2, last column, all mollusc-bearing localities with 2 or more of the index fossils are listed.

The Ehingen Beds have not yielded mammals. Their index molluscs are known from various Oligocene localities elsewhere; most age-specific is *Neobembridgia antiqua antiqua* (Brongniart, 1810). It had been described from the Calcaire d'Étampes of the Paris Basin, which lies in mammal zone MP 24. In Ehingen the species seems to be slightly more evolved (see Kadolsky 2015 for a review of *Neobembridgia antiqua antiqua*) and co-occurs with *Wenzia ramondi*, which is not known older than MP 26; therefore, the Ehingen mollusc fauna may have an MP 26 age. This age refers only to the mollusc-bearing beds; the entire Ehingen Beds may comprise a larger time span, but positive evidence is missing. Werner (1994) assigned mammal faunas of the zones MP 30 to MN 2a to the Ulm Beds. The molluscs associated with MP 30 mammals at Eggingen-Erdbeerhecke and Eggingen-Mittelhart 1, in chocolate-brown marls, are not documented. In MN 1 the Tomerdingen1 molluscs represent a new assemblage zone, currently only characterized by *Triptychia tomerdingensis* n. sp.

The Tomerdingen1 molluscs are not necessarily coeval with the mammals, as they occur in a different, mammal-free rock matrix. Nonetheless a similar age, i.e. in the early part of MN 1, is likely and is adopted in this paper for the following reason:

The Tomerdingen 1 locality lies north of the present-day continuous cover of Ulm Beds, indicating an originally much wider distribution of this formation to the north. The Ulm Beds rise gently to the north and thus are subjected to northward increasing erosion. Erosion would mostly occur from top down, i.e. the oldest parts of the Ulm Beds would be eroded last. In any case it is very likely that material from the bottom of the Ulm Beds would have slid into the fissure. This seems to have occurred after transgression of the OMM in the Tomerdingen area. The OMM may have encountered only a remnant of the basal part of the Ulm Beds and was subsequently also erosionally removed. The fissure infill occurred most likely after the beginning removal of the OMM, when material from both formations were still present in the vicinity of Tomerdingen.

6. Conclusions

There is only one fossiliferous fissure in Tomerdingen quarry (contrary to Werner 1994), which is designated Tomerdingen 1.

The molluscs from the Tomerdingen1 karst fissure are freshwater and land gastropods deposited in carbonatic lake sediments.

Although the Tomerdingen 1 molluscs occur in a rock type different from the rock matrix containing mammals, their age is likely to be similar, i.e. the early part of mammal zone MN 1 (early Aquitanian).

The mollusc association of Tomerdingen1 is to date the only representative of a new local assemblage zone between the overlying Eggingen assemblage zone with *Omphalosagda subrugulosa* (mammal zone MN 2a, perhaps extending into late MN 1) and the underlying Ehingen assemblage zone with *Neobembridgia antiqua antiqua* (possibly MP 26). The Tomerdingen mollusc assemblage zone is characterized by the presence of *Triptychia tomerdingensis* n. sp. and the absence of all index gastropods of the other assemblage zones.

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Plate 1

(1a−1d) *Stagnicola* cf. *subovatus* (Zieten, 1832). Tomerdingen 1. SMNS 61401. In Fig. 1b the outline of a specimen of *Stagnicola subovatus* from the Ulm Beds of Thalfingen is superimposed; this was illustrated by Sandberger, 1872, pl. 21, fig. 6 (SMNS 22178) as *Limneus subovatus*.

(2a−2d) *Gyraulus applanatus* (Thomä, 1845). Tomerdingen 1. SMNS 61398.

(3a−3d) *Planorbarius cornu* (Brongniart, 1810). Tomerdingen 1. SMNS 61402.

(4a−4d) *Planorbarius cornu* (Brongniart, 1810). Tomerdingen 1. SMNS 61403.

(5a−5d) *Triptychia tomerdingensis* n. sp. Holotype. Tomerdingen 1. SMNS 61407a.

(6a−6c) *Triptychia tomerdingensis* n. sp. Paratype. Tomerdingen 1. SMNS 61410.

(7a−7d) *Triptychia tomerdingensis* n. sp. Paratype. Tomerdingen 1. SMNS 61407b.

(8a, 8b) *Triptychia tomerdingensis* n. sp. Paratype. Tomerdingen 1. SMNS 61399. Listed by Seemann & Berckhemer (1930) as *Pomatias* (*antiquum*?).

(9) *Triptychia tomerdingensis* n. sp. Composite of the specimens in Pl. 1, Figs. 5a and 6b.

(10) *Triptychia emmerichi* Wenz, 1912. Holotype. Budenheim quarry near Mainz, Wiesbaden Formation, Aquitanian (MN2a). Copy of the original figure (Wenz 1912: fig. 3).

(11) *Triptychia conoidea* Fischer & Wenz, 1914. Holotype. Theobaldshof near Kaltennordheim (Rhön), early Miocene. Copy of the original figure (Fischer & Wenz 1914: fig. 2).

(12) *Triptychia antiqua* (Zieten, 1832). Neotype (Schnabel 2006). Thalfingen, Ulm Beds. SMF 151479, collection K. Fischer. Original of Zilch (1960, fig. 1433) and Schnabel (2006, pl. 1, fig. 2).

(13) *Triptychia antiqua* (Zieten, 1832). Thalfingen, Ulm Beds. MUWI, unregistered. Original of Sandberger 1872 (pl. 21, fig. 14, 14a) and Schnabel (2006, pl. 1, fig. 3).

(14) *Triptychia antiqua* (Zieten, 1832). Thalfingen, Ulm Beds. MUWI, unregistered. Original of Sandberger (1875: 460).
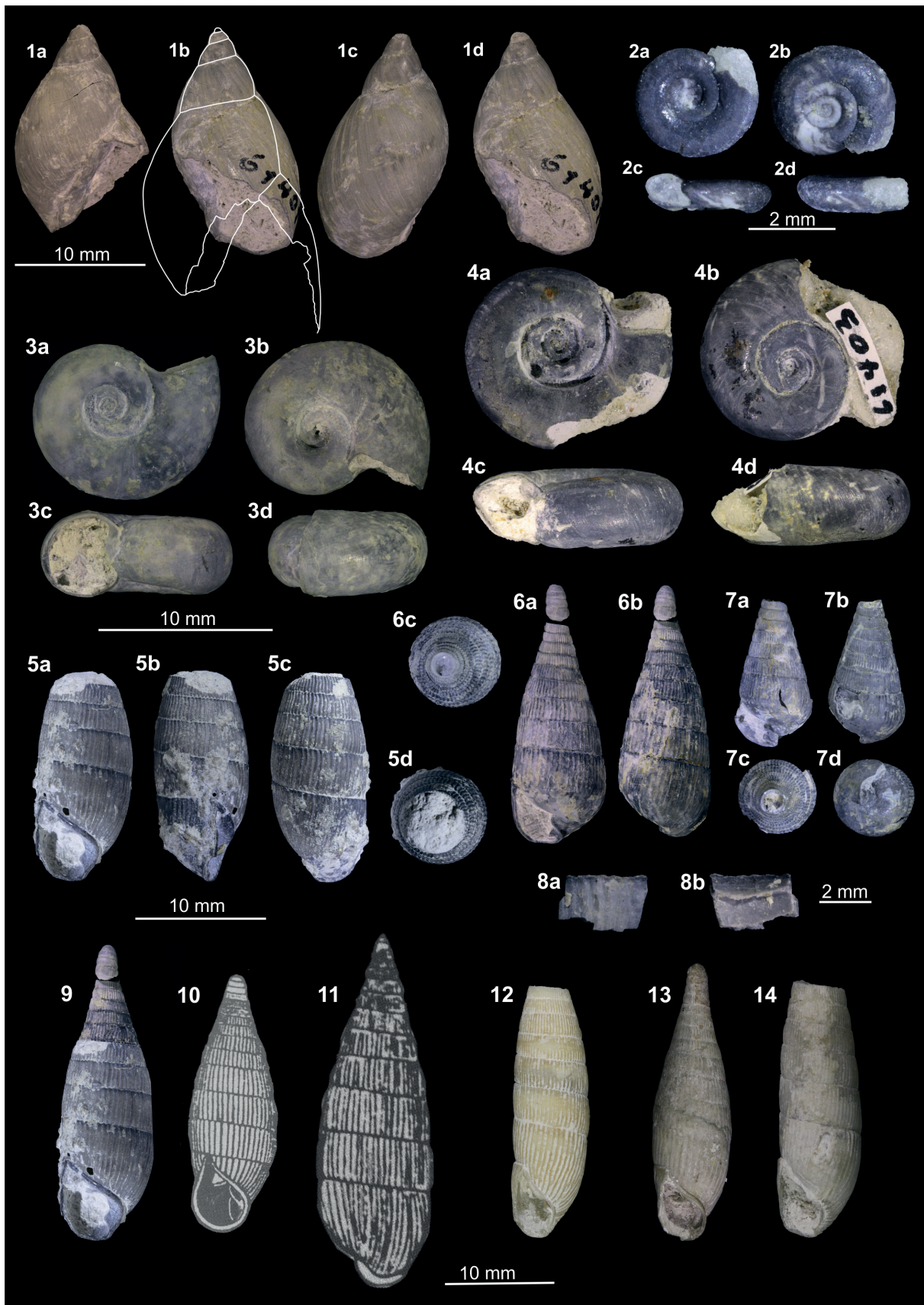
Plate 2

(1a−1c) *Archaeozonites* cf. *subangulosus* (Zieten, 1832). Tomerdingen 1. SMNS 61405.
(2a−2c) *Archaeozonites* cf. *subangulosus* (Zieten, 1832). Tomerdingen 1. SMNS 61406.
(3a−3e) *Palaeotachea subsulcosa* (Thomä, 1845). Tomerdingen 1. SMNS 61396.
(4a−4e) *Palaeotachea subsulcosa* (Thomä, 1845). Tomerdingen 1. SMNS 61397.
(5a−5d) *Palaeotachea subsulcosa* (Thomä, 1845). Tomerdingen 1. SMNS 61415.
(6a−6e) *Palaeotachea subsulcosa* (Thomä, 1845). Tomerdingen 1. SMNS 61412.