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Fossil land and freshwater gastropods from the Miocene of Hohenmemmingen, Germany

RODRIGO B. SALVADOR, OLAF HÖLTKE & MICHAEL W. RASSER

Abstract

Herein we present an account of the fossil terrestrial and freshwater gastropods from the locality of Hohenmemmingen (Baden-Württemberg state, SW Germany) based on museum collections. The fossil outcrops belong to the Silvana Beds of the Upper Freshwater Molasse, being of Early/Middle Miocene age. In total, 23 gastropod species, all pulmonates, are documented in the material (whereas 33 species had been previously reported in the literature): five freshwater species and 18 terrestrial. From an actualistic palaeoecological approach, this palaeo-environment featured a humid and warm forest cover, with a well-vegetated and likely shallow water body.

Key words: Pulmonata, Silvana Beds, Upper Freshwater Molasse.

1. Introduction

The Silvana Beds (“Silvanaschichten” in German) are a unit of the Upper Freshwater Molasse (“Obere Süßwassermolasse” in German; abbreviated OSM) that outcrop at several localities in southern Germany (e.g., SANDBERGER 1870–1875; WENZ 1923–1930; NEUBAUER et al. 2015; HÖLTKE et al., 2016). These beds are particularly notable for their abundant molluscan fossils (e.g., SALVADOR et al. 2015; SALVADOR & RASSER 2016), but many of the localities with outcrops are known only from the older literature. One of them is Hohenmemmingen, in the municipality of Giengen an der Brenz (Heidenheim district, Baden-Württemberg state, SW Germany; Fig. 1)

Fossil mollusks from Hohenmemmingen were mentioned by some authors (KLEIN 1846; SANDBERGER 1858–1863, 1870–1875), but a comprehensive faunal list was only provided much later, by GOTTSCHICK & WENZ (1916). These authors reported 32 gastropod species and one poorly preserved bivalve; later, WENZ (1923–1930), in his compilation work, repeated this information with a few revisions in taxonomic attribution and a new record of one species. After these accounts, the material has been scarcely mentioned again in the literature until HÖLTKE et al. (2016) compiled a list of species from this locality for a biogeographic analysis using museum specimens. Herein, we add material from other collections, offering an updated classification of the species and illustrating several of the

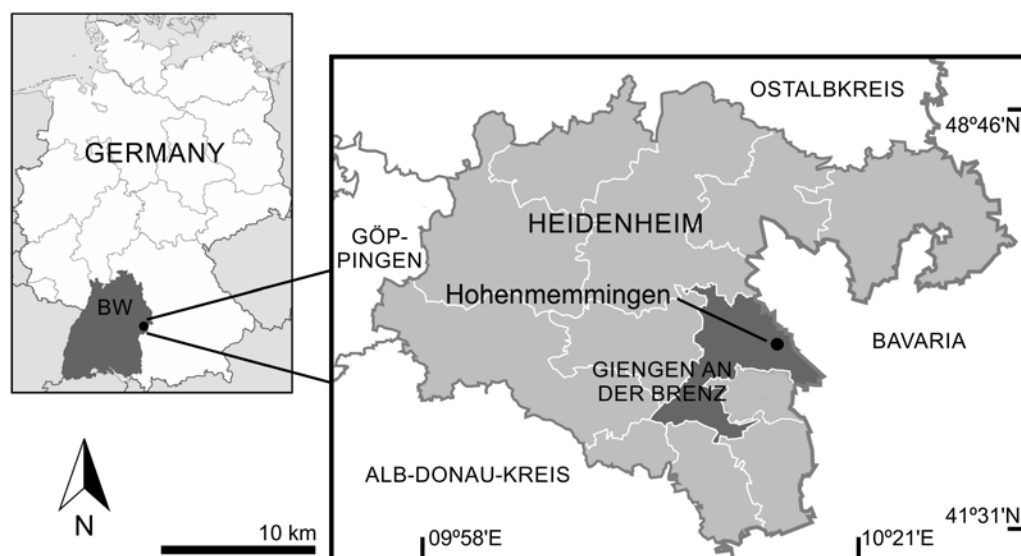


Fig. 1. Map showing the locality of Hohenmemmingen, part of the municipality of Giengen an der Brenz, Heidenheim district, Baden-Württemberg state (BW), Germany.

Table 1. List of all molluscan species reported from the Silvana Beds of Hohenmemmingen. The species whose records have been confirmed in the present work are accompanied by the collection number(s) of the studied material. Species whose record is only known from the literature are indicated accordingly.

Species	Figure(s)	Material studied / References
CAENOCASTROPODA		
PACHYCHILIDAE		
<i>Tinnyea lauraea</i> (Mathéron, 1843)		Wenz (1923)
BITHYNIIDAE		
<i>Bithynia glabra</i> (Zieten, 1832)	—	Gottschick & Wenz (1916), as synonym <i>B. gracilis</i> Sandberger, 1872; see Salvador et al. (2016b)
PULMONATA: ELLOBIOIDEA		
ELOBIIDAE		
<i>Carychium nouleti</i> Bourguignat, 1857	—	Gottschick & Wenz (1916), as synonym <i>C. gibbum</i> Sandberger, 1875; see Strauch (1977)
PULMONATA: HYGROPHYLA		
LYMNAEIDAE		
<i>Lymnaea dilatata</i> Noulet, 1854	Fig. 2.1	GPIT/GA/3929 (3 spec.), GPIT/GA/3964 (3 spec.), GPIT/GA/3999 (1 spec.), GPIT/GA/4049 (5 spec.), GPIT/GA/4068 (2 spec.), SMNS 107257 (7 spec.)
<i>Radix socialis</i> (Zieten, 1832)	Fig. 2.2	SMNS 107235 (3 spec.), SMNS 107328 (>20 spec.)
PLANORBIDAE		
<i>Ferrissia deperdita</i> (Desmarest, 1814)	—	Gottschick & Wenz (1916)
<i>Gyraulus albertanus</i> (Clessin, 1877)	—	Gottschick & Wenz (1916)
<i>Gyraulus applanatus</i> (Thomä, 1845)	Fig. 2.3	GPIT/GA/3935 (5 spec.), GPIT/GA/3981 (5 spec.), GPIT/GA/3986 (>20 spec.), GPIT/GA/3993 (4 spec.), GPIT/GA/4043 (>20 spec.), GPIT/GA/4061 (>20 spec.), SMNS 107329 (5 spec.), SMNS 107330 (8 spec.)
<i>Hippeutis subfontanus</i> (Clessin, 1887)	Fig. 2.4	GPIT/GA/3984 (1 spec.), SMNS 107331 (7 spec.)
<i>Planorbarius mantelli</i> (Dunker, 1848)	Fig. 2.5	GPIT/GA/3971 (>20 spec.), GPIT/GA/04078 (>30 spec.), SMNS 107335 (18 spec.), SMNS 107336 (>20 spec.), SMNS 107339 (2 spec.), SMNS 107346 (>20 spec.)
<i>Segmentina larteti</i> (Noulet, 1854)	—	Gottschick & Wenz (1916)
PULMONATA: STYLOMMATOPHORA		
SUCCINEIDAE		
<i>Oxyloma minima</i> (Klein, 1853)	—	GPIT/GA/4070 (2 spec.)
COCHLICOPIDAE		
<i>Azeca lubricella</i> O. Boettger, 1870	Fig. 3.3	SMNS 107333 (2 spec.)
<i>Hypnophila loxostoma</i> (Klein, 1853)	—	GPIT/GA/4060 (1 spec.)
CHONDRINIDAE		
<i>Granaria noerdingensis</i> (Klein, 1846) vel <i>G. subfusiformis</i> (Sandberger, 1875)	—	Gottschick & Wenz (1916) and Wenz (1923), respectively; <i>G. noerdingensis</i> is a <i>nomen dubium</i> according to Höltnke & Rasser (2013)
GASTROCOPTIDAE		
<i>Gastrocopta acuminata</i> (Klein, 1846)	Fig. 3.5	SMNS 67428 (2 spec.), SMNS 67431 (1 spec.)
<i>Gastrocopta nouletiana</i> (Dupuy, 1850)	Fig. 3.6	SMNS 67404 (1 spec.), SMNS 107347 (12 spec.)
STROBILOPSIDAE		
<i>Strotilops uniplicata</i> (Braun in Walchner, 1851)	—	Gottschick & Wenz (1916)
VALLONIIDAE		
<i>Acanthinula trochulus</i> (Sandberger, 1872)	—	Gottschick & Wenz (1916)

Species	Figure(s)	Material studied / References
VERTIGINIDAE		
<i>Vertigo callosa</i> (Reuss, 1849)	—	Gottschick & Wenz (1916)
CLAUSILIIDAE		
<i>Pseudidyla moersingensis</i> (O. Boettger, 1877)	Fig. 3.2	SMNS 66932 (1 spec.), SMNS 66937 (1 spec.), GPIT/GA/04015 (4 spec.)
SUBULINIDAE		
<i>Opeas minutum</i> (Klein, 1853)	—	BSPG 1966 XXVI (1 spec.), GPIT/GA/4071 (5 spec.)
OLEACINIDAE		
<i>Palaeoglandina gracilis</i> (Zieten, 1832)	—	BSPG no nr. (1 spec.), GPIT/GA/3965 (4 spec.), SMNS 67013 (1 spec.), SMNS 107337 (1 spec.), SMNS 107343 (1 spec.)
DISCIDAE		
<i>Discus pleuradrus suevicus</i> Gottschick & Wenz, 1916	—	Gottschick & Wenz (1916); Wenz (1923)
<i>Discus euglyphoides</i> (Sandberger, 1872)	—	GPIT/GA/04014 (>20 spec.)
OXYCHILIDAE		
<i>Aegopinella subnitens</i> (Klein, 1853)	—	Gottschick & Wenz (1916)
ZONITIDAE		
<i>Archaeozonites costatus</i> Sandberger, 1872	—	GPIT/GA/03998 (1 spec.), SMNS 65268 (1 spec.), SMNS 65632 (1 spec.), SMNS 107340 (2 spec.)
AGRIOLIMACIDAE		
<i>Deroceras</i> sp.	Fig. 3.1	SMNS 107332 (1 spec.)
VITRINIDAE		
<i>Vitrina suevica</i> Sandberger, 1872	—	Gottschick & Wenz (1916)
ELONIDAE		
<i>Apula coarctata</i> (Klein, 1853)	Fig. 3.4	SMNS 66292 (1 spec.)
<i>Klikia giengensis</i> (Klein, 1846)	—	GPIT/GA/4072 (6 spec.), SMNS 66278 (1 spec.)
HELICIDAE		
<i>Palaeotachea silvana</i> (Klein, 1853)	—	BSPG 11955 IV 71 (1 spec.), GPIT/GA/3935 (1 spec.), GPIT/GA/3947 (10 spec.), GPIT/GA/3951 (8 spec.), GPIT/GA/3954 (5 spec.), GPIT/GA/3967 (1 spec.), GPIT/GA4001 (5 spec.), GPIT/GA4009 (3 spec.), GPIT/GA/4010 (7 spec.), SMNS 66655 (3 spec.), SMNS 66841 (1 spec.), SMNS 107338 (2 spec.), SMNS 107341 (>20 spec.), SMNS 107343 (2 spec.), SMNS 107344 (5 spec.), SMNS 107245 (3 spec.), SMNS 107346 (1 spec.)
<i>Palaeotachea turonensis</i> (Deshayes, 1831)	Fig. 3.8	SMNS 66797 (2 spec.), SMNS 66804 (2 spec.)
<i>Pseudochloritis incrassata</i> (Klein, 1853)	—	GPIT/GA/3953 (5 spec.), GPIT/GA/3968 (3 spec.), GPIT/GA/04080 (12 spec.), SMNS 66148 (2 spec.), SMNS 66227 (1 spec.)
HELICODONTIDAE		
<i>Protodrepanostoma involutum</i> (Thomä, 1845)	—	GPIT/GA/3988 (1 spec.)
HYGROMIIDAE		
<i>Leucochroopsis kleinii</i> (Klein, 1846)	Fig. 3.7	GPIT/GA/3947 (2 spec.), SMNS 65947 (2 spec.), SMNS 107334 (>20 spec.)
BIVALVIA		
SPHAERIIDAE		
<i>Sphaerium?</i> sp	—	Gottschick & Wenz (1916)

Hohenmemmingen fossils for the first time. This work is part of our research group's goal of "rescuing" information on all Silvana Beds outcrops, bringing them back to light in a modern context and, more importantly, making this information available to the entire scientific community.

Abbreviations: Institutions: BSPG = Bayerische Staatssammlung für Paläontologie und Geologie (Munich, Germany); GPIT = Department of Geosciences, Eberhard Karls Universität Tübingen (Tübingen, Germany; formerly Geologisch-Paläontologisches Institut Tübingen); SMNS = Staatliches Museum für Naturkunde Stuttgart (Stuttgart, Germany). Shell measurements: H = shell height (parallel to coiling axis); D = greatest shell width (perpendicular to H).

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2. Geological setting

Hohenmemmingen lies at the northern margin of the Molasse Basin in southern Germany, which is a part of the North Alpine Foreland Basin. As mentioned above, the mollusk-bearing sediments around Hohenmemmingen belong to the unit known as OSM, which lies over the OBM unit (Upper Brackish Molasse). The transition between these two units is indistinct and the faunal composition indicates that the brackish environment of the OBM went through a gradual "freshening" (PIPPÉRR & REICHENBACHER 2017). The OSM unit, as the name implies, is characterized by freshwater sediments, dated as late Early to Middle Miocene (REICHENBACHER et al. 2013; SANT et al. 2017).

The sediments at Hohenmemmingen belong, more specifically, to a sub-unit of the OSM known as Silvana Beds (GOTTSCHICK & WENZ 1916). These beds are characterized by (and receive their name from) the presence of the helcid *Palaeotachea silvana* (KLEIN, 1853), but several other gastropod taxa are also typical of these strata (e.g., ESU 1999). The molluscan fauna of Hohenmemmingen is typical of the Silvana Beds and thus supports a late Early to early Middle Miocene age for the sediments (European mammal Neogene zone MN 5, although no mammalian remains are known). Unfortunately, there are no current outcrops known, so only literature data is presently available for this locality. According to FRAAS (1869) and GOTTSCHICK & WENZ (1916), the Silvana Beds in Hohenmemmingen consist of limestone that was seldom banked

and occurred mostly as strongly weathered and irregular nodules (termed as "Knauer" in GOTTSCHICK & WENZ 1916).

3. Material and methods

The material studied for the present account consists exclusively of specimens from historical museum collections (see Table 1 for a full list of studied lots). This includes some of the voucher material of GOTTSCHICK & WENZ (1916), which was deposited in the SMNS, Germany. Unfortunately, not all of their material has been preserved to this day. A good portion of GOTTSCHICK's voucher material was housed in the SMNS, and WENZ's private collection was in Frankfurt a. M.; together, these collections must have contained all the originals of GOTTSCHICK & WENZ (1916), but a good portion of the SMNS and WENZ's collection were lost during World War II (ZILCH 1960; SALVADOR et al. 2016a).

The best preserved gastropod species found are illustrated herein; images were obtained either with a Leica auto-montage apparatus or with a scanning electron microscope (SEM) at the SMNS. The main shell measurements were taken either with a digital caliper (for the larger specimens) or with the software ImageJ (RASBAND 2012) and Leica Application Suite (LAS, v.3.8.0).

4. Results and discussion

In total, 23 gastropod species, all belonging to the Pulmonata, were found in the material from Hohenmemmingen available in museum collections. Five of these are freshwater species, while the remaining are terrestrial; a full species list can be found in Table 1 (classification follows BOUCHET & ROCROI 2005 and NORDSIECK 2014). These species are all common finds in coeval sediments from several other outcrops of the Silvana Beds. Therefore, we will refrain from giving a full description of the material here, since these species have been extensively explored and illustrated elsewhere (e.g., HARZHAUSER et al. 2014; SALVADOR et al. 2015, 2016c; SALVADOR & RASSER 2016). Examples of the best preserved specimens found in the present material are displayed in Figs. 2 and 3.

From the species listed by GOTTSCHICK & WENZ (1916), twelve could not be confirmed with the material available (Table 1). One special case that deserves further notice concerns the *Gyraulus* species reported by GOTTSCHICK & WENZ (1916): *G. applanatus* (THOMÄ, 1845), *G. dealbatus* (A. BRAUN, 1851) and *G. kleini* GOTTSCHICK & WENZ, 1916. GOTTSCHICK & WENZ (1916) reported that these species are linked by a series of intermediate forms, which was also observed in the present material. The specimens of these



Fig. 2. Fossil freshwater gastropods from Hohenmemmingen. **1.** *Lymnaea dilatata*, SMNS 107257 (H = 12.7 mm, D = 6.5 mm). **2.** *Radix socialis*, SMNS 107235 (H = 19.1 mm, D = 13.0 mm). **3a.** *Gyraulus applanatus*, SMNS 107330/1 (H = 1.1 mm, D = 4.3 mm). **3b.** *Gyraulus applanatus*, SMNS 107330/2 (D = 4.1 mm). **3c.** *Gyraulus applanatus*, SMNS 107330/3 (D = 3.9 mm). **4a.** *Hippeutis subfontanus*, SMNS 107331/1 (H = 0.7 mm, D = 3.4 mm). **4b.** *Hippeutis subfontanus*, SMNS 107331/2 (D = 2.6 mm). **5a–c.** *Planorbarius mantelli*, SMNS 107335 (H = 8.1 mm, D = 22.6 mm).

Gyraulus species display a large amount of morphological variation, with the extremes described as distinct species, but with numerous intermediate forms; this phenomenon has also been observed in conspecifics from other OBM and OSM localities (e.g., KOWALKE & REICHENBACHER 2005; SALVADOR & RASSER 2014; SALVADOR et al. 2016b). As a result, *Gyraulus dealbatus* is considered a synonym of *G. applanatus* (KOWALKE & REICHENBACHER 2005; SALVADOR et al. 2016b); the status of *G. kleini* still remains uncertain, but it agrees with intermediate forms in the spectrum of morphological variation seen in *G. applanatus*.

From an actualistic palaeoecological approach, it can be surmised that the Miocene Hohenmemmingen environment featured a humid and warm forest cover, as indicated by most terrestrial gastropod genera. In special, *Discus*, *Leucochroopsis* and *Opeas* are considered very good indicators of this type of environment. No species with particular affinity for drier and more open habitats were recorded in the present material (but the literature cites *Granaria*; Table 1), although *Apula* is considered a potential representative of this environment in the literature; absence of other commonly xerophile genera, like

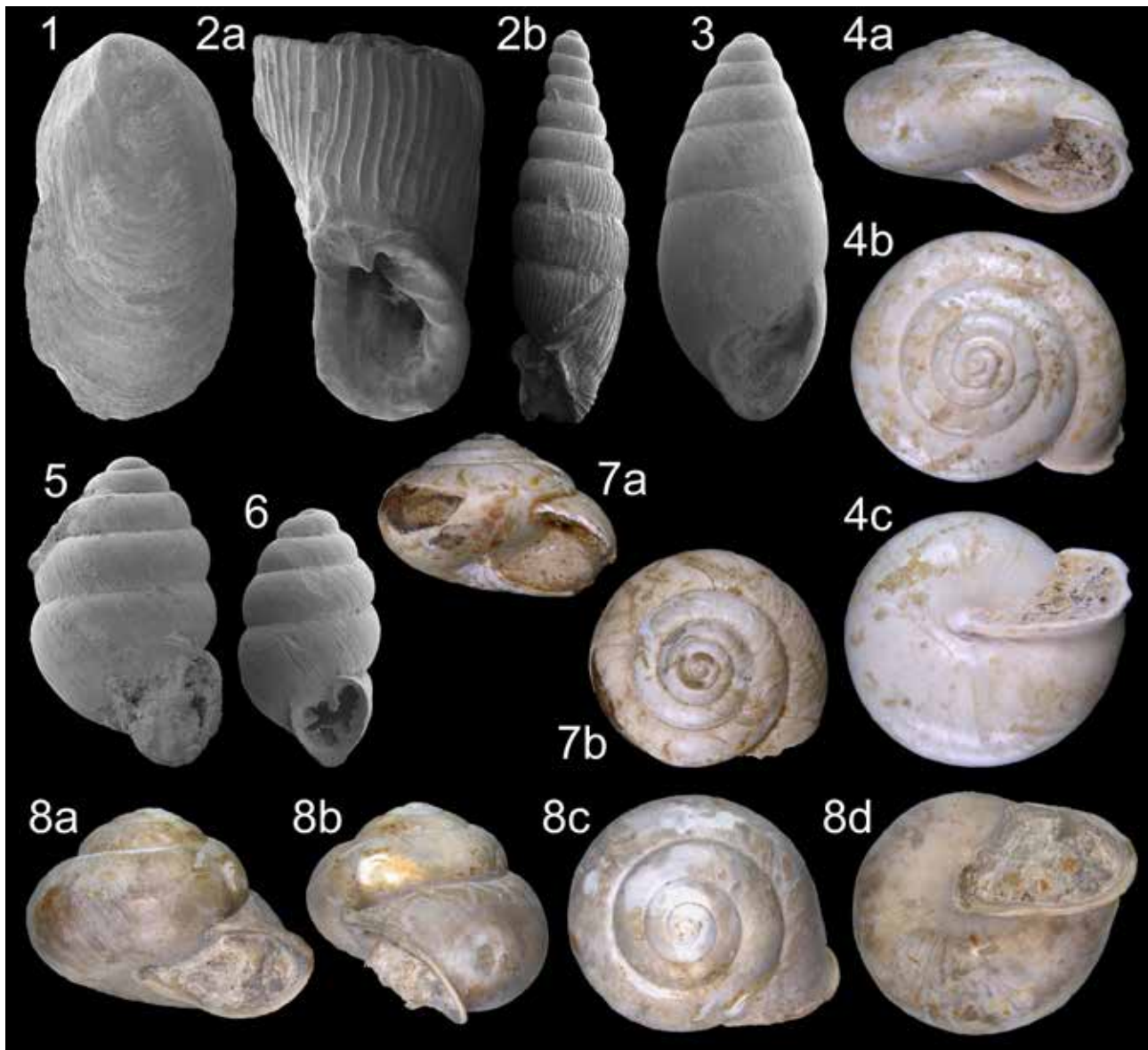


Fig. 3. Fossil terrestrial gastropods from Hohenmemmingen. **1.** *Deroceras* sp., SMNS 107332 (H = 6.0 mm). **2a.** *Pseudidyla moersingensis*, SMNS 66932 (H = 4.2 mm). **2b.** *Pseudidyla moersingensis*, SMNS 66937 (H = 8.7 mm, D = 2.6 mm). **3.** *Azeca lubricella*, SMNS 107333 (H = 4.6 mm, D = 2.1 mm). **4a–c.** *Apula coarctata*, SMNS 66292 (H = 7.9 mm, D = 11.9 mm). **5.** *Gastrocopta acuminata*, SMNS 67428 (H = 2.7 mm, D = 1.6 mm). **6.** *Gastrocopta nouletiana*, SMNS 107347/1 (H = 2.2 mm, D = 1.2 mm), shown in scale with *G. acuminata*. **7a, b.** *Leucochroopsis kleinii*, SMNS 65947 (H = 6.0 mm, D = 8.9 mm). **8a–d.** *Palaeotachea turonensis*, SMNS 66797 (H = 24.2 mm, D = 31.8 mm).

Vallonia and *Pupilla*, is also meaningful. The freshwater species all indicate a slow-moving or stagnant water body and the presence of *Hippeutis* in particular is a good indication of well-vegetated and likely shallow waters. Moreover, representatives of the terrestrial hygrophilic *Oxyloma* are usually found on the vegetation belt surrounding the

water. A full discussion of the ecological affinities of these fossil genera can be found in SALVADOR & RASSER (2014) and SALVADOR et al. (2015, 2016c), based on the habitat requirements of Recent congeners (e.g., KERNEY et al. 1983; WELTER-SCHULTES 2012).

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