The fossil land and freshwater snails of Gündlkofen (Middle Miocene, Germany)

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Abstract

The molluscan fauna from the Middle Miocene (MN 5–6) fossil site of Gündlkofen in southern Germany was first reported by Gall (1980: Mitt. Bayer. Staatssamml. Paläont. hist. Geol., 20, 51–77). He listed 34 continental gastropod species, which were neither figured nor properly described in many cases. Here a revision of his identifications is presented, with a full description of the material and illustration of the best preserved specimens. Following this revision, 20 species are listed for Gündlkofen. Unfortunately, part of the original material was missing and the record of a few species could not be confirmed. The depositional environment seems to have been a temporary water body, like an oxbow lake, surrounded by a humid and warm forest and scrubland.

Key words: Caenogastropoda, Gastropoda, MN 5–6 European Mammal Neogene zones, Pulmonata

Introduction

The molluscan fauna from the Middle Miocene fossil site of Gündlkofen in southern Germany was reported by Gall (1980), who first described the site and listed 34 land and freshwater gastropod species from there. He also offered an age estimate for the site and conducted a paleoecological reconstruction based on the mollusks. Nevertheless, he neither figured nor properly described most of the snails in his work. Moreover, his identification of the larger snails was biased due to the bad preservation of the material, resulting in deformation of the shells. Further works present a fraction of the material from Gündlkofen, but, since they dealt only with very specific taxa (e.g., Schnabel 2006, 2007, for the family Filholiidae), a complete treatment of the material is still lacking. As such, a revision of Gall’s classification is presented here, with a full description of the material and illustration of the best preserved specimens.

Geological setting

As described by Gall (1980), all material from the Gündlkofen fossil site comes from a single fine sand/marl horizon, half meter thick, in a gravel pit located 750 m northwest of Gündlkofen (a small region part of the Bruckberg municipality in Bavaria, SW Germany). The site is located in the Molasse Basin of southern Germany. Based on fossil and lithological evidence, Gall (1980), following Meier (1965), related it to the lower section of the Nördlicher Völsschotter, which in turn is a member of the Upper Freshwater Molasse ("Obere Süßwassermolasse", OSM; Abdul Aziz et al. 2008). As such, Gall (1980) suggested an age of roughly 15 Ma for the site, correlating it with the Middle Silvana-beds ("Silvanaschichten") and the Langhian/Badenian stages (Middle Miocene; MN 5–6 European Mammal Neogene zones). For a more thorough description of the site’s lithology and age correlation see Gall (1980).
Material and methods

All the material from Gündlkofen is housed at the collection of the Bayerische Staatsammlung für Paläontologie und Geologie (BSPG; Munich, Germany) under the record number BSPG 1952 XVIII. All available specimens were analyzed; a list of the examined material follows each species description. Preservation of most of the material is very poor. In order to facilitate future comparative work, here is offered the identification of the material according to Gall (1980) and a brief description of the available specimens for each species. Selected specimens were examined by scanning electronic microscopy (SEM) in the Staatliches Museum für Naturkunde Stuttgart (SMNS; Stuttgart, Germany). Shell measurements abbreviations: H = shell length; D = greatest shell width; h = aperture/operculum height; d = aperture/operculum width.

Unfortunately, part of the original material was missing and the record of some species could not be confirmed. The following lots, as listed by Gall (1980), could not be found: BSPG 1952 XVIII 9 and 55, *Triptychia* cf. *obliqueplicata* (Sandberger); BSPG 1952 XVIII 13, *Serrulina ptycholarynx* (Boettger); BSPG 1952 XVIII 19, *Orcula* sp.; BSPG 1952 XVIII 24, *Triptychia* cf. *bacillifera* (Sandberger); BSPG 1952 XVIII 52, *Triptychia* (Milne-Edwardsia?) sp. Part of this missing material was analyzed by Nordsieck (1981b) and Schnabel (2006). Nordsieck (1981b) studied the *Serrulina ptycholarynx* from Gündlkofen and classified it as a new subspecies: *Serrulastra (Serruplica) ptycholarynx galli* Nordsieck. Schnabel (2006) analyzed the rest of the material: (1) he described a new subspecies, *T. solida schaireri* Schnabel, for Gall’s *T. cf. obliqueplicata*; (2) he described a new species, *T. teutonica* Schnabel, for Gündlkofen, but it is impossible to tell to which (if any) of Gall’s species he is referring to; (3) finally, he indicates a *Triptychia (?)* n. sp. 5, referring specifically to Gall’s *Triptychia (Milne-Edwardsia?)* sp.

Finally, some taxonomic remarks should be made: (1) The classification of Bouchet et al. (2005) is followed here, treating the genus *Archaeozonites* Sandberger (and the Archaeozonitinae) as Gastrodontoidea incertae sedis (rather than its traditional allocation within Zonitidae). (2) The traditional subspecific division of the *Cepaea* Held species treated herein is avoided. A more cautious approach is preferred until these taxa have received proper revisionary work. Moreover, the poor preservation of the specimens hampers a precise taxonomic determination at species level, thus making classification at subspecies level even more tentative (see Discussion chapter below). (3) There is uncertainty about the position of the genus *Tropidomphalus* Pilsbry, normally assigned either to Eloniidae or Helicidae (Zilch 1959–1960; Binder 2008; Moser et al. 2009). Here the latter was preferred, in accordance with Binder (2008). (4) The Euglandininae, in which *Palaeoglandina* Wenz belongs, were commonly classified within Oleacinidae, but were moved to Spiraxidae by Thompson (2010). This decision is followed here.

Systematics

Caenogastropoda

Superfamily Littorinoidea

Family Pomatiidae

Genus *Pomatias* Studer

*Pomatias consobrina* (Sandberger, 1874)

(Figs. 1–2)

*Cyclostoma consobrinum* Sandberger, 1874: 606 (pl. 29, fig. 33a [non 33b–c]).


*Pomatias consorbinum* [sic] Kókay, 2006: 34 (pl. 4, fig. 3).

Material examined. BSPG 1952 XVIII 17 (14 spcm., 29 opercula), 44 (1 spcm.).

Description. Shell medium-sized, trochiform. Protoconch (~1½ whorl) smooth; transition to teleoconch clear.
Teleoconch sculpture reticulated, with stronger spiral ribs and weaker axial ribs; distance between spiral ribs equal to twice their width; distance between axial ribs roughly equal to their width. Whorl profile greatly convex; spire stepped. Suture deep. Aperture rounded. Umbilicus narrow. Operculum with spiral growth.

Previous identification of the material. Gall (1980: Nr. 32 and 33): respectively, Pomatias consobrinum (Sandberger) and Pomatias sp.

Discussion. The present specimens compare well with P. consobrina, being easily identified by its size and strong reticulate sculpture (Stworzewicz 1995; Kókay 2006). The species is known from the Middle Miocene (MN 5–8) of Germany, Hungary and Austria (Schlickum 1976; Kókay 2006).

Paleoecological remarks. Recent species live in forests or shrublands, with more humid soil where they can burrow (Welter-Schultes 2012).

Superfamily Rissooidea

Family Bithyniidae

Genus Bithynia Leach

Bithynia sp. (Fig. 3)

Material examined. BSPG 1952 XVIII 18 (3 opercula).

Previous identification of the material. Gall (1980: Nr. 34): Bithynia (Bithynia) cf. glabra (Zieten).

Discussion. The only fossils of this genus in the material from Gündlkofen are opercula; their overall shape and concentric growth pattern indicate the genus Bithynia, but identification at species level is impossible.

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

Pulmonata

Hygrophila

Superfamily Planorboidea

Family Planorbidae

Genus Gyraulus Charpentier

Gyraulus sp. (Figs. 4–5)

Material examined. BSPG 1952 XVIII 16 (1 spcm.).

Previous identification of the material. Gall (1980: Nr. 30): Gyraulus (Gyraulus) trochiformis cf. kleini (Gottschick & Wenz).

Discussion. The single specimen from Gündlkofen is a juvenile and, due to its poor preservation (lacking protoconch sculpture) and the known conchological variation in the genus (Meier-Brook 1983; Rasser 2013), classification beyond genus level is presently not possible.

Paleoecological remarks. Recent Gyraulus are found in various habitats, so their use in paleoecological
analysis is limited; still, they usually thrive in richly vegetated, shallow standing or slow-flowing waters, sometimes even temporary water bodies (Welter-Schultes 2012).

**Stylommatophora**

**Superfamily Clausiliioidea**

**Family Clausiliidae**

**Clausiliidae indet.**

(Figs. 6–8)

**Material examined.** BSPG 1952 XVIII 36 (1 spcm.), 37 (6 spcm.).

**Previous identification of the material.** Gall (1980: Nr. 19 and 20): respectively, *Pseudidyla moersingensis* (Boettger) and Clausiliidae gen. et sp. indet.

**Discussion.** Due to the very fragmentary nature of the present specimens, a more precise identification is not feasible. Nevertheless, it should be noted that there are two distinct morphs of spire tops: one larger, with higher whorls (Fig. 6), and one smaller, with the whorls more closely packed together and growing more quickly in width (Fig. 7). There is also a single apertural fragment (Fig. 8) that was identified by Gall (1980) as *Pseudidyla moersingensis* (Boettger), a species known from the Middle to Late Miocene of Germany (Nordsieck 1981a, 1982). Its overall shape and dentition seem to indicate the genus *Pseudidyla* (Boettger 1877), but due to the fragmentary nature of the present specimens, it is impossible to safely assign them to *P. moersingensis*.

Moreover, Gall (1980: Nr. 18) also lists another clausiliid, *Serrulina ptycholarynx* (Boettger), for Gündlkofen; however, as explained above, the lot unfortunately could not be found at the BSPG collection. It should be noted, however, that Nordsieck (1981b) classified Gall’s *S. ptycholarynx* as a new subspecies, *Serrulastra (Serruplica) ptycholarynx galli* Nordsieck, and figures the holotype (pl. 8, fig. 18), which consists in a fragmentary body whorl with an intact aperture. The shell sculpture, aperture shape and dentition is congruent with the group of genera *Serrulastra* Nordsieck, *Serrulina* Mousson and *Serrulella* Nordsieck in Zilch. The distinction between these genera, (and their myriad of subgenera, species and subspecies) is very tenuous and classification of fragmentary fossil material is thus further complicated. As such, the validity of this subspecies should be taken carefully.

Finally, the only thing that can be safely said about the clausiliids from Gündlkofen is that they represent two species, one probably belonging to the genus *Pseudidyla* and the other to *Serrulastra* or *Serrulina* and likely the species *S. ptycholarynx*.

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

**Family Filholiidae**

**Genus Triptychia** Sandberger

**Triptychia** sp.

(Fig. 9)

**Material examined.** BSPG 1952 XVIII 53 (16 spcm.).

**Description.** Shell medium-sized, multispiral, sinistral; spire conical, with early spire slightly concave. Protoconch (~2 whorls) smooth, bulbous; transition to teleoconch clear. Teleoconch sculptured by orthocline axial ribs; distance between ribs roughly equal to rib width. Suture shallow, but well-marked. Whorl profile flat.

**Previous identification of the material.** Gall (1980: Nr. 24): *Triptychia* sp.

**Discussion.** The few sinistral spire fragments clearly belong to *Triptychia* due to their overall conical profile, flattened whorls and a shallow but well-marked suture. Unfortunately, it is impossible to proceed further in the
identification, since the aperture region (with the most important diagnostic features) is not preserved. As explained above, Gall (1980) and Schnabel (2006) list three *Triptychia* species each for Gündlkofen, but their identification differs in all cases. Unfortunately, the lots that would contain these specimens could not be found at the BSPG collection. Nevertheless, the present specimens compare well with the *Triptychia (?)* n. sp. 5 of Schnabel (2006), which is the *Triptychia (Milne-Edwardsia?)* sp. of Gall (1980).

**Paleoecological remarks.** Filholiidae is a completely fossil family. It is usually suggested that filholiids were mostly wood-dwelling animals preferring humid and warm forests (Schnabel 2007).

**Superfamily Cochlicopoidea**

**Family Cochlicopidae**

**Genus Azeca Fleming**

*Azeca cf. lubricella Boettger, 1870*  
(Fig. 10)

*Azeca lubricella* Boettger, 1870: 292.  
*Azeca (Azeca) lubricella lubricella*: Wenz, 1923: 1092.  
*Azeca lubricella lubricella*: Schlickum, 1976: 8 (pl. 1, fig. 21).  

**Material examined.** BSPG 1952 XVIII 45 (2 spcm.).

**Previous identification of the material.** Gall (1980: Nr. 29): *Azeca cf. lubricella lubricella* Boettger.

**Discussion.** The present specimens are simply apertural fragments, where two teeth (one columellar and one palatal) can be seen. While the aperture shape and dentition seem to clearly indicate the genus *Azeca*, identification beyond that remains rather tentative. Still, the dentition of the present specimens agree very well with *Azeca lubricella*, a species typical from the Silvana-beds in the Middle Miocene of Southern Germany (Schlickum 1976).

**Paleoecological remarks.** The single recent species in the genus, *Azeca goodalli* (Férussac), lives in leaf litter in woodlands or shrublands, often with calcareous soil (Welter-Schultes 2012). Schlickum (1976) states that *A. lubricella* specifically may have lived on the immediate vicinity of a water body.

**Superfamily Gastrodontoidea**

**Gastrodontoidea indet.**  
(Fig. 11)

**Material examined.** BSPG 1952 XVIII 38 (4 spcm.).

**Description.** Shell small, discoid; spire depressed. Teleoconch sculptured by axial ribs; distance between ribs equal to width of rib. Suture well-marked. Aperture apparently circular. Umbilicus wide, deep.

**Previous identification of the material.** Gall (1980: Nr. 5): *Aegopinella subnitens* (Klein).

**Discussion.** The present specimens are extremely poorly preserved and any attempt on identification beyond this level would be very tentative. Gall (1980) justified his identification by means of the teleoconch sculpture, made of axial and spiral ribs. Nevertheless, this sculpture cannot be observed; only axial ribs are visible.

**Gastrodontoidea incertae sedis**

**Subfamily Archaeozonitinae**

**Genus Archaeozonites Sandberger**
Archaeozonites sp.
(Figs. 12–13)

Material examined. BSPG 1952 XVIII 2 (1 spcm.), 42 (1 spcm.), 43 (1 spcm.), 50b (1 spcm.).

Description. 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 width of rib. Suture weakly marked. Spire trochiform; whorls profile flattened to slightly convex. Umbilicus wide, deep.

Previous identification of the material. Gall (1980: Nr. 2, 3, 4 and, in part, 13): respectively, Archaeozonites cf. costatus costatus Sandberger, Archaeozonites costatus subcostatus Sandberger, Archaeozonites sp. and Tropidomphalus sp.

Discussion. The present specimens, despite very deformed or fragmentary, show the main diagnostic features of the genus Archaeozonites: the strong ribs, the flattened whorl profile, weakly marked suture, the broad conical profile of the spire and a wide umbilicus. Nevertheless, the poor preservation precludes going further than genus level in the classification and the differentiation in two subspecies as Gall (1980) proposed is not possible. Nevertheless, the specimens from Gündlkofen resemble the Central European Miocene species A. costatus (Sandberger) and A. laticostatus (Sandberger), mainly due to their sculpture pattern. The genus is known in Europe from the Middle Eocene to the Late Pliocene (Zilch 1959–1960).

Paleoecological remarks. As a fossil genus, any paleoecological inference must remain tentative. Nevertheless, Lueger (1981) considers that A. laticostatus lived under leaves or between rocks in moist forests.

Superfamily Helicoidea

Family Elonidae

Genus Klikia Pilsbry

Klikia cf. coarctata (Klein, 1853)
(Fig. 14)

Helix coarctata Klein, 1853: 206 (pl. 5, fig. 6).
Klikia (Apula) coarctata coarctata: Wenz, 1923: 534.
Klikia (Apula) coarctata: Schlickum, 1976: 17 (pl. 4, fig. 60); Kókay, 2006: 92.
Klikia (Apula) cf. coarctata coarctata: Gall, 1980: 60.
Klikia cf. coarctata: Salvador, 2013b: 161 (figs. 6–9).

Material examined. BSPG 1952 XVIII 7 (1 spcm.).


Previous identification of the material. Gall (1980: Nr. 14); Klikia (Apula) cf. coarctata coarctata (Klein).

Discussion. The single specimen from Gündlkofen, despite being slightly deformed, compares fittingly with K. coarctata, a species from the Middle Miocene of southern Germany (MN 5–6; Klein 1853; Schlickum 1976; Salvador 2013b). However, a more certain identification is not possible, since one of the main features of this species, a covered umbilicus (Klein 1853; Harzhauser & Binder 2004), cannot be observed.

Paleoecological remarks. As a fossil genus, comparison with living relatives is somewhat tentative. Nevertheless, Lueger (1981) suggested that species in this genus preferred drier environments.

Family Helicidae

Genus Cepaea Held
Cepaea cf. eversa Deshayes, 1851
(Figs. 15–16)

Helix eversa Deshayes, 1851: 395 (pl. 1, figs. 5–7).
Cepaea eversa eversa: Wenz, 1923: 617.
Cepaea eversa larteti: Gall, 1980: 60.
Cepaea eversa: Hir & Kökay, 2004: 89.

Material examined. BSPG 1952 XVIII 8 (19 spcm.)


Previous identification of the material. Gall (1980: Nr. 15): Cepaea eversa larteti (Boissy).

Discussion. The present specimens from Sandelzhausen compare reasonably well with C. eversa and can be differentiated from the specimens of C. cf. sylvestrina Schlotheim (see below) by a larger size, a higher spire, a rounder aperture and one quarter to one half additional whorl. Nevertheless, the specimens of C. eversa from Gündlkofen are always larger, also with half whorl more, than typical specimens. Nevertheless, as common in the genus, C. eversa seems to be a very variable species regarding shell morphology (Hir & Kökay 2004). It is a frequent species in Middle Miocene (MN 5–7) deposits of Central and Western Europe (Hir & Kökay 2004).

Paleoecological remarks. Recent Cepaea have too broad a range of habitats (Welter-Schultes 2012) to be useful for a paleoenvironmental analysis.

Cepaea cf. sylvestrina Schlotheim, 1820
(Figs. 17–18)

Helix sylvestrina Schlotheim, 1820: 99.
Cepaea sylvestrina sylvestrina: Wenz, 1923: 690.
Cepaea silvana silvana: Gall, 1980: 61.

Material examined. BSPG 1952 XVIII 49 (10 spcm.)


Previous identification of the material. Gall (1980: Nr. 16): Cepaea silvana silvana (Klein).

Discussion. The specimens from Gündlkofen compare reasonably well with C. sylvestrina, but are slightly larger, with one quarter to one half additional whorl when compared to typical C. sylvestrina; nevertheless, this species seem to be quite variable morphologically. Cepaea silvana Klein, another common species in the German Middle Miocene, is even smaller, with fewer whorls and a more rounded overall profile, and might be simply a morphological extreme of C. sylvestrina.

Paleoecological remarks. As C. cf. eversa above.

Cepaea sp.

Material examined. BSPG 1952XVIII 19 (4 spcm.).

Previous identification of the material. Gall (1980: Nr. 17): Cepaea sp.

Discussion. These few protoconch and spire top fragments cannot be confidently assigned to any particular species of Cepaea.
Genus *Tropidomphalus* Pilsbry

*Tropidomphalus cf. incrassatus* (Klein, 1853)
(Figs. 19–20)

*Helix inflexa* Klein, 1847: 71 (pl. 1, fig. 12).
*Helix incrassata* Klein, 1853: 208 (pl. 5, fig. 6).
*Tropidomphalus (Pseudochloritis) incrassatus incrassatus* Wenz, 1923: 510; Schlickum, 1976: 16 (pl. 4, fig. 56).
*Tropidomphalus (Pseudochloritis) incrassatus incrassatus* Gall, 1980: 59.
*Tropidomphalus (Pseudochloritis) zelli* Gall, 1980: 60.
*Tropidomphalus* sp.: Gall, 1980: 60.
*Tropidomphalus (Pseudochloritis) incrassatus* Kókay, 2006: 90 (pl. 34, figs. 12–14).
*Pseudochloritis incrassata* Binder, 2008: 172 (pl. 3, figs. 2–4, pl. 6, fig. 2).
*Tropidomphalus cf. incrassatus* Salvador, 2013b: 164 (figs. 18–21).

**Material examined.** BSPG 1952 XVIII 5 (7 spcm.), 6 (1 spcm.), 50 (3 spcm.), 51 (2 spcm.).

**Description.** Shell large, 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 wide.

**Previous identification of the material.** Gall (1980: Nr. 11, 12 and 13): respectively, *Tropidomphalus (Pseudochloritis) incrassatus incrassatus* (Klein), *Tropidomphalus (Pseudochloritis) zelli* (Kurr) and *Tropidomphalus* sp.

**Discussion.** *T. incrassatus* is considered to belong to the subgenus *Pseudochloritis* Boettger, recently elevated to genus status by Binder (2008). Nevertheless, as Salvador (2013b) questioned the delimitation and the usefulness of the subgenus *Pseudochloritis*, here the allocation in *Tropidomphalus* is maintained.

The present specimens, despite their poor preservation, seem to conform well to the great morphological variation shown by *Tropidomphalus incrassatus* (Binder 2008), a species known from the Middle Miocene of Central Europe (Kókay 2006; Binder 2008). All specimens show varying degrees of deformation that alter the overall shell shape, size and proportions; this may have led Gall (1980) to identify a large deformed specimen as *T. zelli* (Kurr). For more details on preservation and their impact on taxonomy see the Discussion chapter below.

**Paleoecological remarks.** Binder (2008) considers the shell of *Tropidomphalus*, based mainly on the angulation of the body whorl and prosocline aperture, an adaptation for ground-dwelling by reducing water loss in drier environments. Moser *et al.* (2009) suggest that the genus inhabited drier and more open habitats, having a “way of life like strong-shelled Balkanese representatives of Ariantinae”.

Superfamily Limacoidea

Family Limacidae

Genus *Limax* Linnaeus

*Limax* sp.
(Fig. 21)

**Material examined.** BSPG 1952 XVIII 3 (15 spcm.), 39 (19 spcm), 40 (7 spcm.).

**Description.** Shell small, vestigial, oval; shell width ~2/3 length. Nucleus slightly bent laterally; nucleus region higher than remainder of shell. Shell with marked concentric growth lines.

**Previous identification of the material.** Gall (1980: Nr. 6, 7 and 8): respectively, *Limax* sp., *Milax* sp. and *Parmacella* sp.

**Discussion.** The shells of limacids are vestigial and internal and thus of very limited taxonomical value. As
such, the identification of the present material cannot proceed further than genus level. The genus *Limax* is known in Europe from the Late Oligocene onwards (Zilch 1959–1960).

Gall (1980) identified some specimens as belonging to the genera *Parmacella* Cuvier and *Milax* Grey. The shell of *Parmacella* slugs are also vestigial, but exhibit a very characteristic inflated and prominent protoconch. This diagnostic feature is not present in the specimens from Gündlkofen. The shells of *Milax* are inflated and markedly convex, with a central elevated nucleus, features that cannot be seen in the present specimens.

**Paleoecological remarks.** Recent *Limax* species occupy a variety of habitats, but usually live in damp leaf litter (Welter-Schultes 2012).

Superfamily Punctoidea

Family Discidae

Genus *Discus* Fitzinger

*Discus* sp.

(Fig. 22)

**Material examined.** BSPG 1952 XVIII 41 (3 spcm.).

**Description.** Shell diminutive, discoid. Protoconch (~1¼ whorl) flat, smooth; transition to teleoconch clear. Teleoconch sculptured by fine but well-marked parallel prosocline ribs; distance among ribs equal to width of rib. Whorl profile convex. Suture well-marked. Whorls regularly growing.

**Previous identification of the material.** Gall (1980: Nr. 9): *Discus* sp.

**Discussion.** The material is very fragmentary, but a generic assignment is possible by the distinct shell shape and sculpture pattern. Moreover, the well-marked sculpture compare well with *D. pleuradrus* (Bourguignat), a species widespread during the Middle and Upper Miocene of Central Europe (Böttcher et al. 2009).

**Paleoecological remarks.** Recent European species live in damp woodlands or grasslands (Welter-Schultes 2012).

Superfamily Pupilloidea

Family Chondrinidae

Genus *Granaria* Held

*Granaria* sp.

(Fig. 23)

**Material examined.** BSPG 1952 VIII 46 (1 spcm.), 47 (2 spcm.).

**Description.** Shell small, with acuminated spire top. Protoconch (1½ whorl) narrow, rounded, smooth; transition to teleoconch unclear. Whorl profile convex. Suture deep. Teleoconch sculptured by regularly distributed, very fine prosocline ribs; distance between ribs approximately twice rib width.

**Previous identification of the material.** Gall (1980: Nr. 31): *Cochlostoma* sp.

**Discussion.** Only spire fragments remain and thus a more precise identification is not possible. The regular whorl growth and the fine, straight and regular ribs indicate the genus *Granaria* (Höltke & Rasser 2013). Moreover, the present specimens are indistinguishable from the *Granaria* sp. described from the Middle Miocene (MN 5) of Sandelzhausen, southeastern Germany (Salvador 2014).

**Paleoecological remarks.** Recent *Granaria* species prefer dry and open habitats, usually calcareous (Welter-Schultes 2012).
Family Helicodiscidae

Genus Lucilla Lowe

Lucilla subteres (Clessin, 1877)  
(Fig. 24)

Helix (Patula) subteres Clessin, 1877: 35.  
Patula subteres: Clessin, 1885: 76 (pl. 7, fig. 6).  
Pyramidula subteres: Wenz, 1923: 1062.  
Helicodiscus (Hebetodiscus) subteres: Schlickum, 1976: 11 (pl. 2, fig. 35); Schlickum, 1979: 68 (fig. 2); Gall, 1980: 65; Kókay, 2006: 74 (pl. 27, figs. 14–16).

Material examined. BSPG 1952 XVIII 4 (1 spcm.).

**Description.** Shell diminutive, discoid, with flattened spire. Protoconch (~1¼ whorl) flat, apparently smooth; transition to teleoconch unclear. Teleoconch smooth, but with well-marked growth lines. Whorl profile convex. Suture well-marked, deep. Whorls regularly growing. Aperture round. Umbilicus wide.

**Previous identification of the material.** Gall (1980: Nr. 28): Helicodiscus (Hebetodiscus) subteres (Clessin).

**Discussion.** The present specimen compares well to *L. subteres* known from Miocene (MN 5–6) sites of Southern Germany and Hungary (Schlickum 1976, 1979; Kókay 2006). The species of *Lucilla* were usually classified in the genus *Helicodiscus* Morse and, more specifically, in the subgenus *Hebetodiscus* H.B. Baker. *Hebetodiscus*, however, was later considered a distinct genus by Bequaert & Miller (1973), which, in turn, was then regarded as a synonym of *Lucilla* by Falkner et al. (2002). As such, some authors (e.g., Hubricht 1985; Hotopp et al. 2010) state that this whole *Helicodiscus* complex should be revised. Until then, the current approach of treating *Lucilla* as a distinct genus (e.g., Moser et al. 2009; Gargominy et al. 2011; Welter-Schultes 2012) is followed here.

**Paleoecological remarks.** The two recent European *Lucilla* species are subterranean (*L. scintilla* Lowe is even blind), living deeper in the soil than other land snails (Welter-Schultes 2012). If the extinct species shared this habit, the increased difficulty for their preservation would explain the scarce fossil record of the genus.

Superfamily Testacelloidea

Family Oleacinidae

Genus Pseudoleacina Wenz

Pseudoleacina sp.  
(Fig. 25)

Material examined. BSPG 1952 XVIII 15 (1 spcm.).

**Description.** Shell small, fusiform with bulbous body whorl. Teleoconch apparently sculptured by marked axial ribs only directly below suture. Suture well-marked but not too deep, slightly incised. Body whorl very large. Aperture greatly elongated vertically. Umbilicus imperforate.

**Previous identification of the material.** Gall (1980: Nr. 26): Pseudoleacina sp.

**Discussion.** As remarked by Gall (1980), the present specimen does not conform well to any other Miocene species of *Pseudoleacina*, mainly by its large size and bulbous body whorl. Gall (1980) also called attention to the sculpture pattern: strong axial ribs only present right below the suture; this feature is known only in *Pseudoleacina rakosdensis* (Gaál), from the Sarmatian (MN 7–8) of Rákós, Romania (Gaál 1911; Kókay 2006). Despite this fact, the poor preservation of the present specimen precludes a more confident determination.

**Paleoecological remarks.** *Pseudoleacina* is a fossil genus, but like the rest of the family it might have been a malacophagous predator (Barker & Efford 2004). Moreover, most authors consider *Pseudoleacina* species as hygrophilic woodland inhabitants (e.g., Lueger 1981; Harzhauser & Binder 2004; Harzhauser & Tempfer 2004), but some (e.g., Gall 1980) consider it a calciphilic and xerophilic species.
Family Spiraxidae

Genus *Palaeoglandina* Wenz

*Palaeoglandina* cf. *gracilis* (Zieten, 1830)

(Fig. 26)

*Limnaea gracilis* Zieten, 1830: 39 (pl. 30, fig. 3).
*Poiretia (Palaeoglandina) gracilis gracilis* Wenz, 1923: 839.
*Palaeoglandina gracilis porrecta* Gall, 1980: 64.

**Material examined.** BSPG 1952 XVIII 14 (3 spcm.).

**Description.** Shell large, fusiform; greatest width on last whorl. Teleoconch sculptured by regularly distributed, well-marked coarse ribs; distance between ribs equal to rib width. Aperture drop-shaped, vertically elongated; no apparent callus. Peristome simple, but slightly thickened on columellar region. Umbilicus imperforated.

**Previous identification of the material.** Gall (1980: Nr. 25): *Palaeoglandina gracilis porrecta* (Gobanz).

**Discussion.** The fragmentary and deformed preservation of the present material precludes a more precise identification. Nevertheless, the specimens are reminiscent of *P. gracilis* by their broad shell, strong sculpture and elongated aperture. *Palaeoglandina gracilis* is known from the Late Oligocene to the Middle Miocene (MN 7) of Central Europe (Salvador 2013b).

**Paleoecological remarks.** The genus *Palaeoglandina* is known since the Paleocene, being widespread throughout Europe and becoming extinct in the Early Pleistocene (Zilch 1959–1960; Esu et al. 1993). Likely, as the recent species in the family, *Palaeoglandina* was a malacophagous predator (Barker & Efford 2004); some authors (e.g., Moser et al. 2009) even suggested that it should have displayed the same lifestyle and habitat as the recent North American *Euglandina rosea* (Férussac), living on the leaf litter or on trees, with a wide habitat tolerance (Hubricht 1985; Davis et al. 2004).

Family Testacellidae

Genus *Testacella* Draparnaud

*Testacella schuetti* Schlickum, 1967

(Fig. 27)

*Testacella schuetti* Schlickum, 1967: 63 (fig. 1); Harzhauser et al., 2008: 53 (figs. 7.2–7.3); Nardi & Bodon, 2011: 159 (table 3).
*Testacella (Testacella) schuetti* Schütt, 1967: 218 (fig. 19).
*Testacella zelli* Gall, 1980: 56.

**Material examined.** BSPG 1952 XVIII 22 (5 spcm.).

**Description.** Shell small, ear-shaped, vestigial; shell width ~3/5 shell length. Apex pointed, curved. Shell with well-marked growth lines. Aperture elongated, oval; parietal and columellar region greatly thickened.

**Previous identification of the material.** Gall (1980: Nr. 1): *Testacella zelli* Klein [sic].

**Discussion.** The shell is vestigial in this monotypic family and, therefore, is of very limited taxonomical value. Despite being slightly larger, the present specimens compare well with *T. schuetti* by its oval aperture, low shell and a pointed but curved apex. The species is known from few Middle Miocene (Sarmatian, MN 7–8) sites of the Styrian Basin and North-Alpine Foreland Basin (type locality: Hollabrunn, Austria; Schlickum 1967; Harzhauser et al. 2008). As such, the present record is the oldest for the species.

**Paleoecological remarks.** Recent *Testacella* are voracious predators, feeding on earthworms, gastropods and centipedes, and live mainly underground, thus requiring a moist soil cover (Barker & Efford 2004). This burrowing habit should make preservation in the fossil record difficult.
FIGURE 22. Discus sp., juvenile (BSPG 1952 XVIII 41; D = 1.5 mm).
FIGURE 23. Granaria sp. (BSPG 1952 XVIII 47; H = 1.6 mm).
FIGURE 24. Lucilla subteres (BSPG 1952 XVIII 4; D = 1.7 mm).
FIGURE 25. Pseudoleacina sp. (BSPG 1952 XVIII 15; H = 16.3 mm, D = 6.2 mm).
FIGURE 26. Palaeoglandina gracilis (BSPG 1952 XVIII 14; H = 38.2 mm, D = 22.3 mm, h = 28.2 mm, d = 14.5 mm).
FIGURE 27. Testacella schuetti (BSPG 1952 XVIII 22; H = 4.7 mm, D = 2.7 mm).

FIGURE 1. Pomatias consobrina (BSPG 1952 XVIII 17; H = 15.8 mm, D = 14.1 mm).
FIGURE 2. Pomatias consobrina, operculum (BSPG 1952 XVIII 17; h = 7.3 mm, d = 6.3 mm).
FIGURE 3. Bithynia sp., operculum (BSPG 1952 XVIII 18; h = 3.3 mm, d = 2.4 mm).
FIGUREs 4–5. Gyraulus sp., juvenile (BSPG 1952 XVIII 16; H = 0.4 mm, D = 0.7 mm).
FIGURE 6. Clausiliidae indet., spire fragment (BSPG 1952 XVIII 37; H = 2.9 mm).
FIGURE 7. Clausiliidae indet., spire fragment (BSPG 1952 XVIII 37; H = 2.3 mm).
FIGURE 8. Clausiliidae indet. (possibly Pseudidyla), aperture fragment (BSPG 1952 XVIII 36; h = 2.3 mm, d = 1.3 mm).
FIGURE 9. Tripychia sp. (BSPG 1952 XVIII 53; H = 10.2 mm, D = 5.1 mm).
FIGURE 10. Azeca cf. lubricella, aperture fragment (BSPG 1952 XVIII 45; h = 2.0 mm).
FIGURE 11. Gastrodontoidea indet. (BSPG 1952 XVIII 38; D = 9.0 mm).
FIGUREs 12–13. Archaeaconites sp. (BSPG 1952 XVIII 42; H = 17.6 mm, D = 28.6 mm).
FIGURE 14. Klikia cf. coarctata (BSPG 1952 XVIII 7; D = 7.8 mm).
FIGURES 15–16. Cepaea cf. eversa (BSPG 1952 XVIII 8; H = 20.3 mm; D = 27.4 mm; h = 10.3 mm; d = 14.3 mm).
FIGURES 17–18. Cepaea cf. sylvestrina (BSPG 1952 XVIII 49; H = 16.4 mm; D = 25.2 mm; h = 9.1 mm; d = 13.5 mm).
FIGURES 19–20. Tropidomphalus cf. incrassatus (BSPG 1952 XVIII 5; H = 14.1 mm; D = 28.8 mm; h = 11.7 mm; d = 17.7 mm).
FIGURE 21. Limax sp. (BSPG 1952 XVIII 3; H = 5.9 mm, D = 3.7 mm).
Discussion

**Taxonomy and preservation.** The preservation of the larger specimens from many OSM fossil sites may present some problems for taxonomy (Gall 1973; Moser et al. 2009; Salvador 2013b). The fossils can be compressed or inflated, producing a more flattened or rounded overall appearance and thus hampering a precise taxonomic determination at species level. As remarked by Gall (1973) for the helicids of Sandelzhausen (MN 5), a locality just a few kilometers away from Gündlkofen, a “blown-up” specimen of species “A” might appear as a member of the more spherical species “B”. Nevertheless, this bias is often not considered when identifying the larger fossil snails, and authors end up identifying or describing many species or subspecies more than actually present (e.g., Gall 1972).

In the case of Gündlkofen this preservation bias affects the specimens of *Palaeoglandina*, *Archaeozonites*, *Cepaea* and *Tropidomphalus*. As such, here a great care was taken when identifying the specimens, using characters other than overall shell shape and using material from the original descriptions (and later revisions) of other Middle Miocene sites from Southern Germany (housed at the SMNS and BSPG). Nevertheless, the identification beyond genus level must unfortunately remain tentative.

Largely due to this preservation bias, Gall (1980) slightly overestimated the number of species in Gündlkofen, listing 34 species for the site. This number was reduced to 20 in the present work. Nevertheless, it should be noted that the lots of five of Gall’s supposed species could not be found, as explained above, so the actual number of species in Gündlkofen could be a little higher.

**Remarks on the paleoenvironment.** The molluscan fauna from Gündlkofen is remarkable for the near absence of freshwater species: only a single *Gyraulus* sp. and three opercula of *Bithynia* sp. were recovered. The lack of other hygrophilous microgastropods such as the Carychiinae and Succineidae, commonly found in the German Miocene (e.g., Strauch 1977), is also striking. *Gyraulus* and *Bithynia* are usually related to still (and often temporary) waters (Welter-Schultes 2012), which, together with features of the site’s lithology, led Gall (1980) to propose that Gündlkofen represents an environment like an oxbow lake.

Gall (1980) defined the mollusks of Gündlkofen as a relatively hygrophilic assemblage. The present work agrees with this statement, since most of the genera prefer more humid conditions; land snail habitats tend not to vary much in genus level, facilitating comparisons with the recent fauna (Barker 2001; Cook 2001; Pearce & Örstan 2006) and thus being very useful for environmental reconstructions. As such, the area seems to have been covered with a damp and warm forest and scrubland (Gall 1980). Nevertheless, a few species more oriented towards drier (such as *Tropidomphalus* cf. *incrassatus* and perhaps also *Cepaea* cf. *evera*) or rockier environments (likely *Palaeoglandina* and *Milax*; Gall 1980) occur in a considerable number, possibly indicating a variety of habitats near the site. Since most of these species have sturdier shells, they could have been transported from farther away.

Finally, the most obvious comparison of the fossil molluscan fauna from Gündlkofen is with Sandelzhausen, a neighboring and nearly coeval site (Salvador 2013a, 2013b, 2014; Salvador & Rasser submitted). Gall (1980) already examined this relationship and the present work largely agrees with his findings. After the present revision Gündlkofen shares nearly 80% of its land snail genera and 40% of its species with Sandelzhausen; this percentage is a little lower than that given by Gall (1980), but still meaningful. Nevertheless, Sandelzhausen has also attracted different hygrophilous species to its riparian zone, e.g., *Succinea minima* Klein and members of the genus *Carychium* O.F. Müller (Salvador 2013b, 2014), due to its richer freshwater environment (Gall 1972; Moser et al. 2009; Salvador & Rasser submitted). As these conditions seem not to be present in Gündlkofen (Gall 1980), some differences in faunal compositions will inevitably be found; moreover, Gündlkofen appears to be slightly younger than Sandelzhausen (Gall 1980), which could also account for differences in their faunas.

**Acknowledgements**

I am deeply grateful to Alexander Nützel (BSPG) for lending the Gündlkofen material housed at his institution; to Hartmut Nordsieck (Senckenberg Forschungsinstitut und Naturmuseum Frankfurt) and Thomas Schnabel (BG/BRG Amstetten) for the help in tracking down the missing material; to Karin Wolf-Schwenninger (SMNS) for the SEM images; to Thomas A. Neubauer (Naturhistorisches Museum Wien) for the revision and comments that
greatly improved the article; and to my supervisors, Michael W. Rasser (SMNS) and James H. Nebelsick 
(Universität Tübingen), for the support. This work was supported by a doctorate grant from CNPq (Conselho 
Nacional de Desenvolvimento Científico e Tecnológico, Brazil).

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générale et particulière des mollusques terrestres et fluviatiles, tant des espèces que l'on trouve aujourd'hui vivantes, que 
des dépouilles fossiles de celles qui n'existent plus; classés d'après les caractères essentiels que présentent ces animaux et 

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