BIOTA, PALAEOENVIRONMENTS AND BIOSTRATIGRAPHY OF CONTINENTAL OLIGOCENE DEPOSITS OF THE SOUTH GERMAN MOLASSE BASIN (PENZBERG SYNCLINE)

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ABSTRACT. Six charophyte, 13 mollusc, four ostracod and nine fish otolith taxa are taxonomically described, and one fruit, one seed and two foraminiferal taxa are briefly noted from the Lower Cyrena Beds and the Lower Coloured Molasse of the Sindelsdorf section near Penzberg (approximately 50 km south of Munich). Our palaeoecological and lithological data from the Lower Cyrena Beds suggest a delta plain with lagoons, estuaries, slowly flowing rivers, lakes and swamps. Faunal and floral elements of the Lower Coloured Molasse indicate lacustrine environments. The gastropod *Tympanotonos* and the tropical to subtropical fish fauna (Eleotridae, Ambassidae and Cyprinodontidae) suggest a warm, at least subtropical climate. Furthermore, *Tympanotonos* suggests comparisons with Recent molluscan faunas of the mangrove swamps of the West African coast, and thus hints at mangrove vegetation bordering the coasts of the Upper Bavarian Molasse Sea. A biostratigraphical classification for the Oligocene Molasse deposits of the Penzberg Syncline is established for the first time based on otoliths and charophytes. The Lower Cyrena Beds are attributed to the newly defined otolith zone OT-O1/2 and probably correspond to the oldest part of the *Chara microcera* Zone. The lowermost part of the Lower Coloured Molasse can be correlated both with otolith zone OT-O2 and the *Chara microcera* Zone. The Sindelsdorf section lies within the Rupelian–Chattian transition zone and thus the chronostratigraphic age is approximately 29–28 Ma.

KEY WORDS: continental Oligocene, South German Molasse Basin, charophytes, molluscs, ostracods, fish otoliths.

CONTINENTAL deposits of Oligocene age in the South German Molasse Basin are herein considered on a broad palaeontological basis for the first time. The section studied, situated in the Penzberg Syncline (Text-figs 1–2), is 170 m thick and can be correlated with the Lower Cyrena Beds (Lower Brackish-Water Molasse) and the lowermost part of the Lower Coloured Molasse (Lower Freshwater Molasse) (Text-fig. 3). Charophytes, molluscs, ostracods and fish otoliths are taxonomically described, and fruits, seeds and foraminifers are briefly noted. Our palaeoecological analysis suggests varying environments in a tropical to subtropical climate. Biostratigraphical analysis based on the charophyte flora and fish otoliths suggests a latest Rupelian and/or earliest Chattian age for the succession.

Previous studies of charophytes and fish otoliths from the lower Chattian of the Marienstein and Murnau synclines in the Southern German Molasse Basin include those published in Reichenbacher and Schwarz (1997), Uhlig *et al.* (2000) and Reichenbacher and Uhlig (2002). The Oligocene molluscs from this region have been studied by Zöbelein (1952, 1955, 1957), Hölzl (1957, 1962) and Barthelt (1989), and the ostracods by Witt (1967) and Müller (1985). However, none of these publications dealt with the Lower Cyrena Beds in the Penzberg Syncline.

Barthelt (1989) considered the depositional environment represented by the Lower Brackish-Water Molasse. She reconstructed a complex deltaic environment, and suggested the presence of mangrove vegetation based on distinctive mollusc species. Uhlig *et al.* (2000) and Reichenbacher and Uhlig (2002) supported this interpretation.

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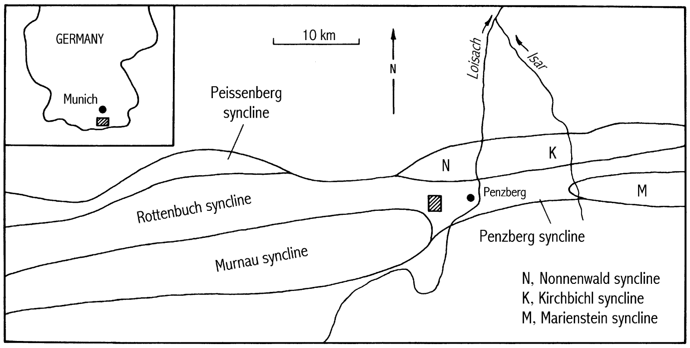
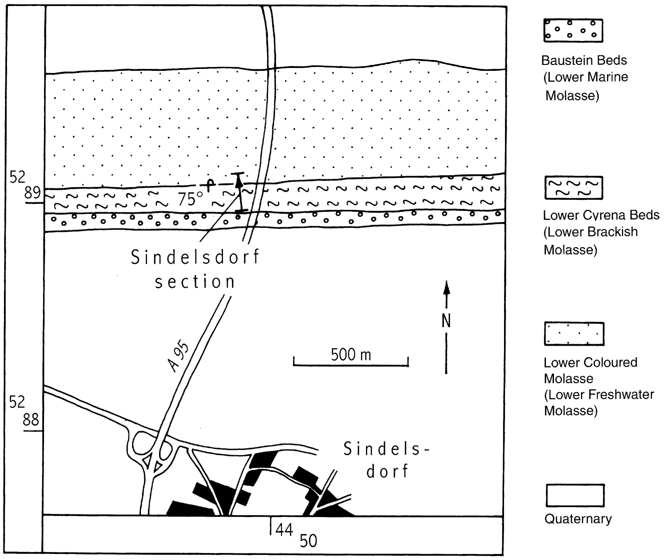


TEXT-FIG. 1. Map of the Folded Molasse in Upper Bavarica; hatched is the location of the Sindelsdorf section (for details, see Text-fig. 2).

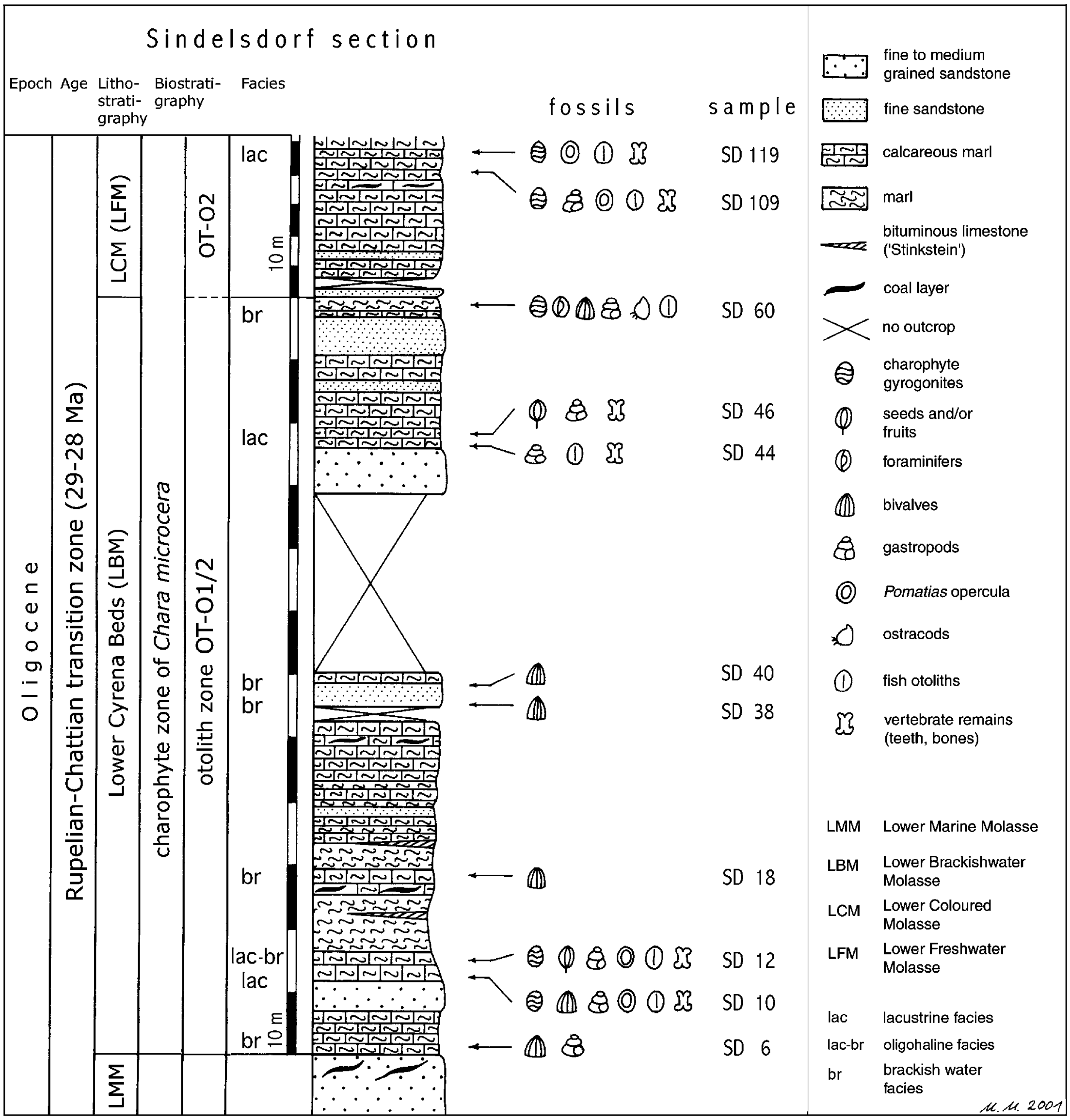


TEXT-FIG. 2. Simplified geological map around the Sindelsdorf section (according to Schmidt-Thomé and Doben 1979; Hesse and Stephan 1991).

GEOLOGICAL SETTING

Sedimentation in the South German Molasse Basin started at the Eocene/Oligocene transition. In the Early Oligocene marine sediments accumulated (Lower Marine Molasse) (Lemcke 1988, pp. 16–21). At the beginning of the Late Oligocene, the sea receded to the area east of Munich. In the transition zone between the fluvial deposits of the Lower Freshwater Molasse in the west and the marine facies in the east, the sediments of the Lower Brackish-Water Molasse developed, including the Upper Bavarian vitrains (‘Pechkohle’) (Geissler 1975; Barthelt 1989). In the Miocene, the southernmost parts of these Molasse deposits were sheared from the northern basement by the rising alpine nappes, and were compressed into a series of synclines with an east-west orientation (Lemcke 1988, p. 69).

One of these synclines is the Penzberg Syncline in Upper Bavaria (Text-fig. 1). It extends 20 km in an east–west direction and about 3 km in a north–south direction. The Sindelsdorf section discussed herein is situated in the south-western part of the syncline (Text-fig. 2). In this section, the Baustein Beds (Lower



TEXT-FIG. 3. Chronostratigraphy, lithostratigraphy, biostratigraphy, and facies of the Sindelsdorf section with the location of the fossiliferous layers.

Marine Molasse), the Lower Cyrena Beds (Lower Brackish-Water Molasse) and the Lower Coloured Molasse (Lower Freshwater Molasse) crop out. The beds are overturned, strike 80–95° and dip 70–80° south.

The Lower Cyrena Beds and the lowest part of the Lower Coloured Molasse of the Sindelsdorf section were studied. The former comprise intercalated marls and fine sandstones, and are dominated by calcareous marls. Fine- to medium-grained sandstones, bituminous limestones ('Stinksteine') and coal occur rarely. Furthermore, there are some 'brackish horizons' with shell fragments of *Polymesoda subarata subarata* (formerly *Cyrena*) and/or *Tympanotonos margaritaceus* (Text-fig. 3). The lower boundary of the Lower Cyrena Beds is drawn lithostratigraphically at the base of the first calcareous marl overlying the sandy Baustein Beds. The upper boundary is at the top of the uppermost 'brackish horizon' (in agreement with Doben and Frank 1983, p. 32 and Hesse and Stephan 1991, p. 100). The Lower Cyrena Beds in the Sindelsdorf section are 121 m thick. The lowermost part of the Lower Coloured Molasse is again dominated by calcareous marls with intercalated fine sandstones and marls. Only one coal layer was encountered (Text-fig. 3). The thickness of the Lower Coloured Molasse is about 1200 m in the Penzberg Syncline (Hesse and Stephan 1991, p. 105). Only the lowermost 52 m was investigated for this paper.

MATERIAL AND METHODS

Following construction during 1969–1970 of highway A95 between Munich and Garmisch-Partenkirchen, the Lower Cyrena Beds and the lowest part of the Lower Coloured Molasse in the south-western part of the Penzberg Syncline have been very well exposed. In 2000 a 180-m section of this outcrop was investigated. Altogether 17 samples were collected; 14 of these (each weighing 7 kg) were examined by screen-washing. After treatment with a 5 per cent solution of hydrogen peroxide, the samples were washed through 0·1 mm, 0·3 mm and 2·0 mm sieves and the microfossils recovered were picked out by hand under a stereomicroscope. Six samples proved to be barren. The other eight samples mainly yielded charophytes, molluscs, ostracods and fish otoliths.

The scanning electron microscope (SEM) images of the charophytes and ostracods figured herein were taken at the Institute for Palaeontology and Historical Geology in Munich. The SEM images of fish otoliths were prepared at the Laboratory for Electron Microscopy at the Technical University in Karlsruhe and those of the molluscs with a digital SEM (type Leo) at the Zoological Institute and Zoological Museum at the University of Hamburg.

SYSTEMATIC PALAEONTOLOGY

All of the specimens described are housed in the Bavarian State Collection for Palaeontology and Geology. They have been assigned registration numbers BSP 2001 VI 1–68. Synonyms were chosen with regard to their importance for the development of the species and/or generic name.

Class CHAROPHYCEAE G. M. Smith, 1938 emend. Schudack, 1993

Remarks. Charophytes (stoneworts) are submerged aquatic plants, forming a separate class of the green algae. Today they occur throughout the world where they usually grow at depths of a few metres in freshwater and brackish habitats. During sexual reproduction they produce oospores, which calcify in some genera and are then called gyrogonites. The earliest known charophytes are of Devonian age.

Order CHARALES Lindley, 1836
Suborder CHARINAE Feist and Grambast-Fessard, 1991
Family CHARACEAE Richard ex C. Agardh, 1824 emend. Martin-Closas and Schudack, 1991

Genus CHARA Linnaeus, 1753

Type species. Chara tomentosa Linnaeus, 1753.

Chara tornata Reid and Groves, 1921

Text-figure 4A–C

- * 1921 *Chara tornata* Reid and Groves, p. 187, pl. 5, figs 1–3.
- 1959 *Grambastichara tornata* (Reid and Groves); Horn af Rantzien, p. 70, pl. 4, figs 1–6.
- 1985 *Grambastichara tornata* (Reid and Groves) Horn af Rantzien; Schwarz, p. 28, pl. 3, fig. 11; pl. 4, figs 1–11.
- 1988 *Grambastichara tornata* (Reid and Groves) Horn af Rantzien; Schwarz, p. 159, pl. 1, fig. 8.
- 1993 *Chara tornata* Reid and Groves; Schwarz, p. 45, pl. 1, figs 4–5.

1997 *Chara tornata* Reid and Groves; Reichenbacher and Schwarz, p. 178, figs 10–11.
1997 *Chara tornata* Reid and Groves; Schwarz, p. 15, pl. 2, figs 7–13.

Material. Forty-five gyrogonites obtained from SD 60. Only nine of 60 individuals (15 per cent) are well preserved. The remaining gyrogonites are preserved without the apical centre or are heavily corroded.

Description. The apex is rounded showing a disruption in the periapical region. The spiral cells are flat, without distinct modifications in the periapical region. In the apical centre the width visibly increases, whereas the thickness decreases occasionally. No ornamentation was observed. The basal region is usually rounded, occasionally slightly pointed, showing a superficial basal pore.

Measurements (n = 9): length 600–775 μm; width 387–575 μm; isopolarity index 1·3–1·74; number of convolutions 9–12; width of spiral cells 50–75 (112) μm.

Remarks. Similar to *Stephanochara ungeri* Feist-Castel, 1977, but differs in having distinctly increased and usually concave spiral cells in the apical centre.

Genus RHABDOCHARA Mädler, 1955 emend. Grambast, 1957

Type species. *Rhabdochara langeri* (Ettingshausen, 1872) Mädler, 1955.

Rhabdochara exigua Schwarz, 1988

Text-figure 4D–F

* 1988 *Rhabdochara exigua* Schwarz, p. 166, pl. 3, figs 1–5.
1993 *Rhabdochara exigua* Schwarz; Schwarz, p. 48, pl. 1, fig. 10.
1997 *Rhabdochara exigua* Schwarz; Schwarz, p. 20, pl. 4, figs 1–2.

Material. Two hundred and seventy-four gyrogonites were obtained from SD 109 (273 individuals) and SD 119 (one individual). Only five per cent are well preserved; the remainder have lost the apical centre or are completely deformed.

Description. The apex is truncated. Spiral cells are concave, without distinct modifications in the periapical and apical regions. About 25 per cent of the lime shells show protruding double fluted sutures. In a very small percentage of individuals there are weakly developed, interrupted ridges along the central axis of the spiral cells. The basal region is usually tapered or rounded. No basal pore was observed. It probably lies at the bottom of a funnel filled with sediment.

Measurements (n = 13): length 650–875 μm; width 525–750 μm; isopolarity index 1·07–1·36; number of convolutions 8–10; width of spiral cells (n = 7) 87–125 μm.

Genus STEPHANOCHARA Grambast, 1959

Type species. *Stephanochara compta* Grambast, 1959.

Stephanochara aff. *pinguis* Grambast ex Riveline, 1986

Text-figure 4O–Q

aff. * 1986 *Stephanochara pinguis* Grambast; Riveline, p. 54, pl. 19, figs 7–10.
aff. 1986 *Stephanochara pinguis* Grambast; Breuer and Feist, pl. 3, fig. 11.
aff. 1997 *Stephanochara pinguis* Grambast ex Riveline; Schwarz, p. 22, pl. 4, fig. 6.

Material. Thirty-three gyrogonites obtained from SD 12. Only six (18 per cent) are well preserved, 16 (48 per cent) have lost the apical centre, and 11 (33 per cent) are stonecores.

Description. The apex is truncated. Spiral cells are flat to convex. In the periapical region, spiral cells are thinned and weakly to moderately narrowed. In the apical centre, both the thickness and width of the spiral cells are either constant or increase. No ornamentation was observed. The basal region is rounded or tapered. The basal pore lies at the bottom of a small funnel.

Measurements (n = 6): length 850–1075 μm; width 750–950 μm; isopolarity index 1·08–1·21; number of convolutions 9–10; width of spiral cells (n =5) 100–137 μm.

Remarks. This species resembles *Nitellopsis merianii* forma *globula* (this paper), but has a completely different basal plate. In addition, the morphology of the apex (Text-fig. 4O) is clearly different from that of *Nitellopsis*. Two individuals are broken in the basal region showing a small pyramidal to cylindrical basal plug (Text-fig. 4Q). *Stephanochara ungeri* Feist-Castel, 1977 is very similar to the material studied here but its gyrogonites are smaller. According to shape and size it most closely resembles *Stephanochara pinguis*, although this has a prominent apical swelling. Feist *et al*. (1994) described a comparable species with less prominent apical swelling as *S*. aff. *pinguis* from the upper Stampian (MP 23) in the Ebro Basin (Spain).

Genus SPHAEROCHARA Mädler, 1952 emend. Grambast, 1962

Type species. *Sphaerochara hirmeri* (Rásky, 1945) Mädler, 1952.

Sphaerochara ulmensis (Straub, 1952) Grambast, 1962

Text-figure 4G–I

* 1952	*Chara ulmensis* Straub, p. 470, pl. A, fig. 19.
1962	*Sphaerochara ulmensis* (Straub); Grambast, p. 77.
1985	*Sphaerochara ulmensis* (Straub) Grambast; Schwarz, p. 41, pl. 9, figs 1–9.
1988	*Sphaerochara ulmensis* (Straub) Grambast; Schwarz, p. 170, pl. 5, figs 5–6.
1993	*Sphaerochara ulmensis* (Straub) Grambast; Schwarz, p. 48, pl. 1, fig. 12.
1997	*Sphaerochara ulmensis* (Straub) Grambast; Reichenbacher and Schwarz, p. 182, figs 19–20.
1997	*Sphaerochara ulmensis* (Straub) Grambast; Schwarz, p. 24, pl. 4, fig. 10.

Material. Approximately 1400 gyrogonites obtained from SD 109 and seven from SD 119. About 25 per cent of the gyrogonites from SD 109 are well preserved. The others have lost the apical centre or are corroded. Complete deformations are rare. All gyrogonites from SD 119 are severely deformed.

Description. The apex is usually rounded, rarely pointed. Thickness of spiral cells varies from concave to convex. In the periapical region, spiral cells visibly decrease in thickness and width. In the apical centre, they widen and often become thicker. Distinct swelling is rarely seen. Some of the gyrogonites have ridges along the central axis of the spiral cells, which disappear in the apical region. The basal region is normally rounded and has a superficial basal pore.

Measurements (n = 30): length 425–625 μm; width 375–537 μm; isopolarity index 1·09–1·35; number of convolutions 9–12; width of spiral cells (n = 5) 50–62 μm.

Remarks. Berger (1986, 1992) proposed to combine *S. hirmeri*, *S. granulifera*, *S. ulmensis* and perhaps *S. inconspicua* as *Sphaerochara* group *hirmeri*.

Genus NITELLOPSIS Hy, 1889

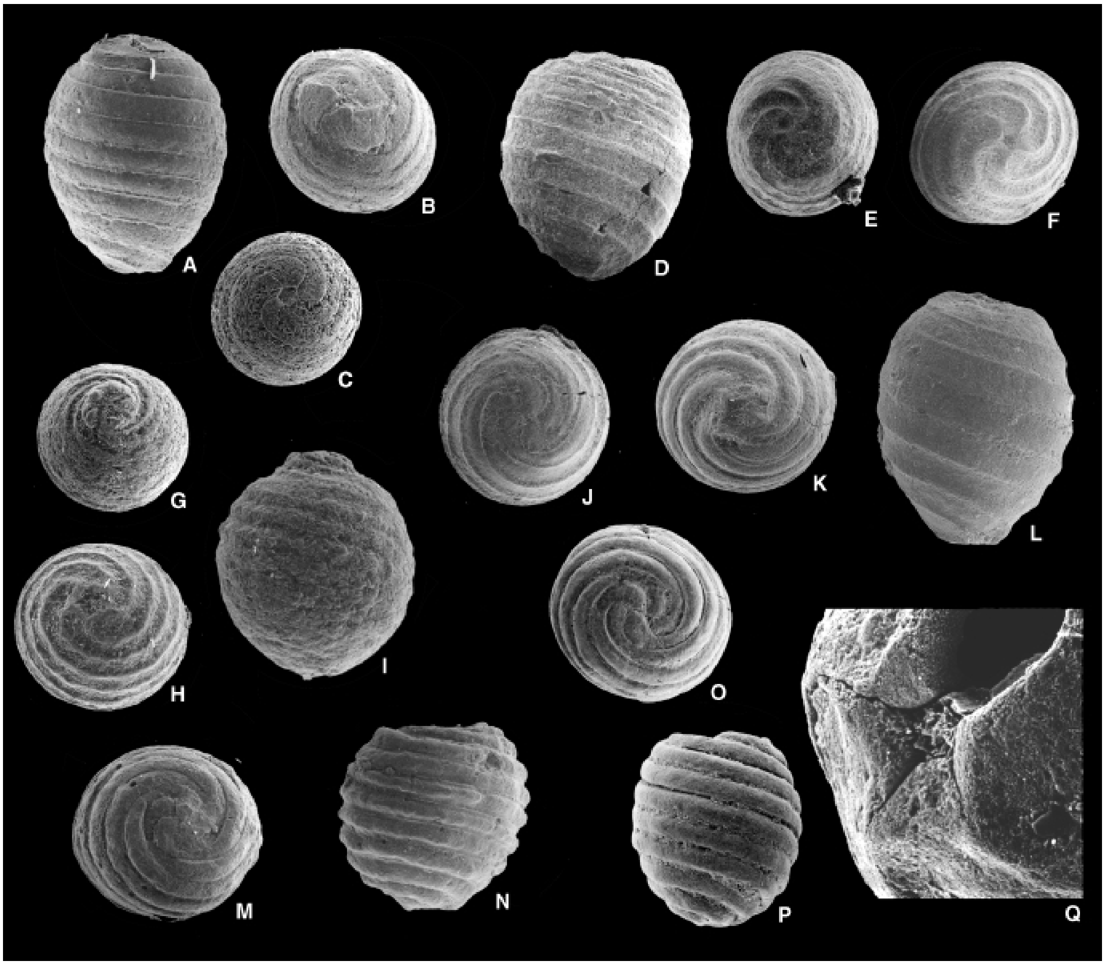
Subgenus TECTOCHARA (L. and N. Grambast, 1954) Grambast and Soulié-Märsche, 1972

Type species. *Nitellopsis* (*Tectochara*) *merianii* (Al. Braun ex Unger, 1850) Grambast and Soulié-Märsche, 1972.

Nitellopsis (*Tectochara*) *merianii* (Al. Braun ex Unger, 1850) Grambast and Soulié-Märsche, 1972

Text-figure 4J–L

* 1850	*Chara meriani* Al. Braun ex Unger, p. 34.
1972	*Nitellopsis* (*Tectochara*) *meriani* (Al. Braun ex Unger); Grambast and Soulié-Märsche, p. 3.



TEXT-FIG. 4. A–C, *Chara tornata* Reid and Groves, 1921, BSP 2001 VI 1–3, SD 60, gyrogonite in lateral (A, ×50), apical (B, ×44) and basal (C, ×32) views. D–F, *Rhabdochara exigua* Schwarz, 1988, BSP 2001 VI 4–6, SD 109, gyrogonite in lateral (D, ×42), apical (E, ×35) and basal (F, ×35) views. G–I, *Sphaerochara ulmensis* (Straub, 1952) Grambast, 1962, BSP 2001 VI 7–9, SD 109, gyrogonite in apical (G, ×41), basal (H, ×50) and lateral (I, ×50) views. J–L, *Nitellopsis* (*Tectochara*) *merianii* (Al. Braun ex Unger, 1850) Grambast and Soulié-Märsche, 1972, BSP 2001 VI 10–12, SD 109, gyrogonite in apical (J, ×25), basal (K, ×25) and lateral (L, ×30) views. M–N, *Nitellopsis* (*Tectochara*) *merianii* forma *globula* (Mädler, 1955) Soulié-Märsche *et al.*, 1997, BSP 2001 VI 13–14, SD 10, gyrogonite in apical (M, ×25) and lateral (N, ×23) views. O–Q, *Stephanochara* aff. *pinguis* Grambast ex Riveline, 1986, BSP 2001 VI 15–17, SD 12, gyrogonite in apical (O, ×25), lateral (P, ×27) and basal (Q, ×145) views.

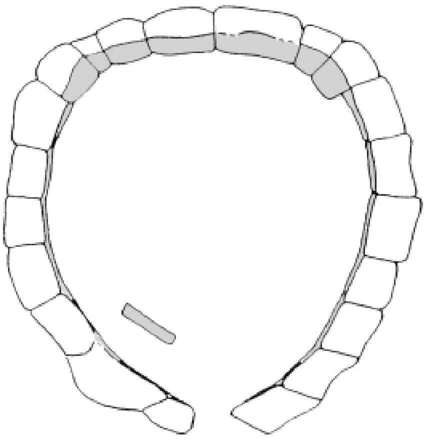
1985 *Nitellopsis* (*Tectochara*) *meriani* (Braun ex Unger) Grambast and Soulié-Märsche; Schwarz, p. 45, pl. 11, figs 1–7.

1988 *Nitellopsis* (*Tectochara*) *meriani* (Braun ex Unger) Grambast and Soulié-Märsche; Schwarz, p. 174, pl. 5, figs 9–11.

1993 *Nitellopsis* (*Tectochara*) *meriani* (Braun ex Unger) Grambast and Soulié-Märsche; Schwarz, p. 49, pl. 1, fig. 11.

1997 *Nitellopsis* (*Tectochara*) *meriani* (Braun ex Unger) Grambast and Soulié-Märsche; Reichenbacher and Schwarz, p. 180, figs 23–25.

1997 *Nitellopsis* (*Tectochara*) *meriani* (Braun ex Unger) Grambast and Soulié-Märsche; Schwarz, p. 30, pl. 6, figs 7–8.



TEXT-FIG. 5. *Nitellopsis* (*Tectochara*) *merianii* forma *globula* (Mädler, 1955) Soulié-Märsche *et al.*, 1997; oriented section showing the basal plug inside the gyrogonite; ×86.

1997 *Nitellopsis* (*Tectochara*) *merianii merianii* (Al. Braun ex Unger) Grambast and Soulié-Märsche; Soulié-Märsche *et al.*, p. 146, fig. 5.
1997 *Nitellopsis* (*Tectochara*) *merianii* (Alex. Braun ex Unger) Grambast et Soulié-Märsche; Berger, p. 774.

Material. Eight hundred and forty-three gyrogonites obtained from SD 109 (820 specimens) and SD 119 (23 individuals). In SD 109 about 30 per cent of the gyrogonites are well preserved, about 30 per cent have lost the apical centre and the remainder are deformed. In SD 119 only two individuals are well preserved, 16 have lost the apical centre and five are deformed.

Description. The apex is truncated. Spiral cells vary in thickness from concave to convex. They increase in thickness towards the apical truncation, where they are usually convex, rarely flat. In the periapical region, spiral cells usually become visibly narrower and decrease slightly in thickness. In the apical centre, spiral cells generally remain flat, whereas they may widen distinctly. An increase in thickness in the apical centre is rare and swelling is nearly absent. No ornamentation was observed. The basal region is tapered with the basal pore at the bottom of a funnel.

Measurements (n = 25): length 950–1175 μm; width 800–975 μm; isopolarity index 1·05–1·28 (mean value 1·18); number of convolutions 7–10; width of spiral cells (n = 10) 125–187 μm.

Remarks. The material investigated clearly belongs to *Nitellopsis* (*Tectochara*) *merianii* but differs from the type in generally lacking a distinct apical swelling. However, Soulié-Märsche *et al.* (1997) and Berger (1997) described *N.* (*T.*) *merianii merianii* of similar morphology from the Miocene of North Thailand.

Nitellopsis (*Tectochara*) *merianii* forma *globula* (Mädler, 1955), Soulié-Märsche *et al.*, 1997

Text-figure 4M–N

* 1955 *Tectochara meriani globula* Mädler, p. 281, pl. 23, figs 6–11.
1988 *Nitellopsis* (*Tectochara*) *globula* (Mädler) Grambast and Soulié-Märsche; Schwarz, p. 176, pl. 5, figs 7–8.
1997 *Nitellopsis* (*Tectochara*) *globula* (Mädler) Grambast and Soulié-Märsche; Reichenbacher and Schwarz, p. 180, figs 21–22.
1997 *Nitellopsis* (*Tectochara*) *globula* (Mädler) Grambast and Soulié-Märsche; Schwarz, p. 31, pl. 6, figs 10–11.
1997 *Nitellopsis* (*Tectochara*) *merianii* forma *globula* (Mädler); Soulié-Märsche *et al.*, p. 148, pl. 7, figs A–I.
2000 *Nitellopsis* (*Tectochara*) *merianii* forma *globula* (Mädler); Uhlig *et al.*, p. 509, pl. 2, figs 5–6.

Material. One hundred and fifty-four gyrogonites obtained from SD 10. About 40 per cent are well preserved and about 40 per cent are deformed. Deformation frequently affects the apical region, where the apical centre is collapsed. In the remaining gyrogonites, the apex is lacking.

Description. The apex is truncated, rarely rounded. Spiral cells are flat to convex, narrower in the periapical region and thin out slightly to distinctly. In the apical centre, thickness of spiral cells remains constant or may swell, and the width may increase. No ornamentation was observed. The basal region is rounded or tapered. The basal pore lies at the bottom of a small to very small funnel.

Measurements (n = 46): length 850–1175 μm; width 800–1075 μm; isopolarity index 0·98–1·21 (mean value 1·1); number of convolutions 9–11; width of spiral cells (n = 10) 125–150 μm.

Remarks. Resembling *Stephanochara* aff. *pinguis*, some individuals of *N. merianii* forma *globula* were subject to additional examination. We made orientated sections that enabled us to demonstrate the very thin basal plug typical of *Nitellopsis* (Text-fig. 5).

Berger (1997) proposed to include the subspecies *globula*, *helvetica* and *huangi* in *N.* (*T.*) group *merianii*. We prefer to use *N.* (*T.*) *merianii* forma *globula* because it differs from *N.* (*T.*) *merianii* statistically by its more globular shape (see mean value of isopolarity index).

Phylum MOLLUSCA Cuvier, 1797

Remarks. The bivalve and gastropod fauna investigated are described with special reference to the early ontogeny of shell formation. The morphology and dimensions of the embryonic shell (= protoconch I), i.e. the width of the initial cap-like onset and maximum diameter and ornament of the embryonic shell, are characterized. In cases of indirect evidence of development including a planktonic veliger stage, the height, maximum diameter and sculpture of the additional larval shell (= protoconch II) are included (cf. Kowalke 1998).

Class BIVALVIA Linnaeus, 1758
Superfamily UNIONIOIDEA Fleming, 1828
Family MARGARITIFERIDAE Kennard, Salisbury and Woodward, 1925
[= Margaritanidae Ortmann, 1911]

Genus MARGARITIFERA Schumacher, 1816

Type species. *Mya margaritifera* Linnaeus, 1758; Recent, Eurasia and North America.

Margaritifera inaequiradiata (Gümbel, 1861) Modell, 1931

Plate 1, figure 1

* 1861 *Unio inaequiradiata* Gümbel, p. 751.
1931 *Margaritifera inaequiradiata* (Gümbel); Modell, p. 66, pl. 13, figs 1–2; pl. 14, fig. 15a–b.
1931 *Margaritifera haushamensis* nova forma; Modell, p. 67, pl. 13, fig. 3.

Material. Two juvenile specimens from SD 10.

Description. The juvenile specimens measure up to 2 mm in maximum length and up to 1 mm in maximum height. Shells are characterised by a straight hinge margin. Sculpture around the umbo consists of irregular wavy folds, grading into regular closely spaced folds in the course of ontogeny. According to Modell (1931, pp. 66–67) these folds may decrease in adult shells, which then appear to be smooth.

Remarks. According to Barthelt (1989), *M. inaequiradiata* represents a typical species occurring in the Lower Brackish-Water Molasse, and specimens described by Modell (1931) as *M. geyeri* and *M. schneideri* may represent eco-phenotypes or tectonically compacted morphs.

Superfamily CORBICULOIDEA Gray, 1847
Family CORBICULIDAE Gray, 1847

Genus POLYMESODA Rafinesque, 1820

Type species. *Cyclas caroliniana* Bosc, 1801; Recent, North America.

Polymesoda subarata subarata (Schlotheim, 1820)

Plate 1, figure 2

*	1820	*Venulites subaratus* Schlotheim, p. 200.
	1822	*Cytherea*? *convexa*; Brongniart, p. 284.
	1957	*Polymesoda convexa* (Brongniart); Hölzl, p. 10, pl. 1, figs 1–5, 9–10; pl. 7, fig. 1.
	1957	*Polymesoda convexa cordata*; Hölzl, p. 15, pl. 1, figs 7–8.
	1957	*Polymesoda convexa maxima*; Hölzl, p. 16, pl. 1, fig. 6.

Material. Twenty-nine articulated juvenile specimens measuring less than 1 mm in length from SD 6 (one specimen) and SD 60 (28 specimens); several adult shells from SD 18, SD 38 and SD 40.

Description. Adult shells measure up to 40 mm in length. These are characterised by closely spaced concentric growth lines and occasionally occurring growth rugae. Prodissoconchs of juveniles are corroded and sculpture is not preserved. Prodissoconch I is separated from prodissoconch II by a groove-like depression in the shell. Prodissoconch I measures 0·07 mm in the length of the straight hinge of the hatched veliger (D-line) and about 0·1 mm in maximum diameter. Prodissoconch II measures about 0·1 mm in height and 0·14–0·15 mm in maximum diameter. The transition to the teleoconch is characterised by a thickening of the shell and by the onset of the adult sculpture.

Remarks. Kadolsky (1995) discussed in detail the nomenclatural context and taxonomy of the *subarata* group in the European Oligocene and Miocene.

The prodissoconch reflects a planktotrophic veliger stage. Embryonic (prodissoconch I) and larval shell (prodissoconch II) are morphologically distinct. The prodissoconch of *P. subarata sowerbii* (Basterot, 1825) differs from that of *P. s. subarata* by having slightly larger dimensions of prodissoconch II, while prodissoconch I is of equal size as in *P. s. subarata*. Prodissoconch II of *P. s. sowerbii* measures 0·19–0·21 mm in maximum diameter, and this size reflects a slightly longer veliger stage than in the case of *P. s. subarata*. The prodissoconch morphology of *P. s. sowerbii* has been described in material from Aquitanian brackish-water sediments of northern Greece by Harzhauser and Kowalke (2001).

Class GASTROPODA Cuvier, 1797
Order LITTORINIMORPHA Golikov und Starobogatov, 1975
Superfamily RISSOOIDEA Gray, 1847
Family HYDROBIIDAE Troschel, 1857

Genus HYDROBIA Hartmann, 1821

Type species. *Helix acuta* Drapanaud, 1801; Recent, western Europe.

Hydrobia sp.

Plate 1, figures 3–4

Material. Eleven specimens from SD 60.

Description. The conical shell, comprising 5–6 rounded whorls, measures up to 4 mm in height and 2·5 mm in width. The low conical protoconch has 2·2–2·5 whorls, measuring 0·23–0·26 mm in maximum diameter. Sculpture is not preserved. The first whorl measures 0·06 mm in the width of the initial cap and 0·14–0·15 mm in maximum diameter. Transition to the teleoconch is characterised by a slight thickening and by the onset of the adult sculpture of prosocyrt growth lines.

Remarks. The dimensions of the protoconch reflect a short planktotrophic larval phase. In the course of the veliger stage a larval shell comprising about one whorl was secreted. The shape of the protoconch and the nature of the morphological change to the teleoconch are very similar to that of the Recent European brackish-water species *H. ulvae* (Pennant, 1777) (Kowalke 1998, p. 72, pl. 10, fig. 1).

Barthelt (1989) described a *Hydrobia*, which occurs in rock-forming abundance within the Lower Brackish-Water Molasse and could be conspecific with the material described here. This species was tentatively assigned by Barthelt to *H. ventrosa* (Montagu, 1803), but this is a Recent species and most likely not conspecific with the Oligocene *Hydrobia* sp. However, species determination is not possible, owing to the poor preservation and lack of diagnostic characters.

Superfamily LITTORINOIDEA Gray, 1840
Family POMATIASIDAE Stimpson, 1860

Genus POMATIAS Studer, 1789
Subgenus POMATIAS (NEOBEMBRIDGIA) Kadolsky, 1988

Type species. *Pomatias* (*Neobembridgia*) *moguntinum* Kadolsky, 1988; Upper Oligocene of the Mainz Basin, Germany.

Pomatias (*Neobembridgia*) *antiquum antiquum* (Brongniart, 1810*a*)

* 1810 *Cyclostoma elegans antiquum* Brongniart, p. 365, pl. 22, fig. 1.
v 1952 *Pomatias antiquum antiquum* (Brongniart) *pro parte*; Zöbelein, p. 38.
v 1958 *Pomatias antiquum antiquum* (Brongniart) *pro parte*; Zöbelein, pp. 46–48.

Material. Twenty fragments of opercula from SD 10 (three fragments), SD 12 (nine fragments), SD 109 (six fragments) and SD 119 (two fragments).

Description. The operculum has up to four narrow coils. It is characterised by two marginal grooves separated by a narrow keel beneath the outer opercular margin. Coils rapidly increased in size during ontogeny. The outer portion of the coils is sculptured by a narrow border. Complete opercula of this species have been described by Uhlig *et al.* (2000, p. 510, text-fig. 7).

Remarks. The subgenus *Neobembridgia* is distinguished from the typical subgenus by the morphology of the operculum: *Pomatias* (*Pomatias*) is characterised by having only one marginal groove.

Order CERITHIIMORPHA Golikov and Starobogatov, 1975
Superfamily TURRITELLOIDEA Lovén, 1846
Family TURRITELLIDAE Lovén, 1846

Genus PROTOMA Baird, 1870

Type species. *Turritella cathedralis* Brongniart, 1810*b*; Burdigalian of southern France.

Protoma diversicostata (Sandberger, *in* Gümbel 1861)

* 1861 *Turritella diversicostata* Sandberger, p. 746.
1962 *Protoma diversicostata* (Sandberger); Hölzl, p. 141, pl. 8, fig. 14.
1989 *Protoma diversicostata* (Sandberger); Barthelt, p. 37, pl. 12, fig. 3.

Material. Three juvenile specimens from SD 6.

Description. The protoconch is not preserved. Sculpture of the flattened teleoconch whorls consists of ten fine spiral carinae, which are regularly distributed all over the whorls with regular spaces between them (approximately 0·4 mm in adult whorls). Two carinae in the mid portion of the whorls are more strongly developed.

Remarks. *Protoma diversicostata* is distinguished from Oligocene species of the genus *Turritella* by having more flattened whorls.

Superfamily CERITHIOIDEA Férussac, 1819
Family POTAMIDIDAE H. and A. Adams, 1854

Genus POTAMIDES Brongniart, 1810*b*

Type species. *Cerithium lamarkii* Brongniart, 1810*b*; Oligocene of Europe.

Potamides sp.

Plate 1, figures 5–6

Material. Eleven juvenile specimens from SD 60.

Description. Juvenile specimens measure up to 3 mm in height and comprise about seven whorls. The protoconch of some individuals is preserved, comprising 1·75 whorls, measuring 0·25 mm in height and 0·2–0·22 mm in maximum diameter. The embryonic shell has 0·8–1 rounded whorls measuring 0·16–0·18 mm in maximum diameter. The width of the initial cap of the embryonic shell amounts to 0·06–0·07 mm. A straight thickening marks the transition to the larval shell. The protoconch is terminated by a slightly sinuous thickening. Onset of the teleoconch is indicated by the formation of two spiral carinae in the median portion of the whorls, with the abapical one more strongly developed. On the second teleoconch whorl, both carinae are about equally strong. On the third whorl, two additional weaker carinae are developed below and above the suture. The posterior three carinae are crossed by 10–12 orthocline to slightly opisthocline axial ribs. The intersection points of spiral and axial sculpture are thickened tubercles, which can be elongated to short spines. The base of the last whorl is sculptured by three, weak spiral carinae. The aperture is broken. It has angular outline, and it is characterised by a prominent short anterior canal and by a weak fold located in the median portion of the columella.

Remarks. The protoconch of *Potamides* sp. is indicative of a yolk-rich embryogenesis reflected by a large embryonic shell, and a subsequent short planktotrophic veliger stage, during which a larval shell comprising 0·75 of a whorl was secreted. The early teleoconch is distinguished from that of juvenile *Granulolabium* spp. by the earlier onset of axial sculpture and by the lack of secondary spiral cords.

We refrain from assigning our material to the type species *P. lamarkii* Brongniart, 1810*b* (cf. Hölzl 1957; Barthelt 1989) because *P. lamarkii* represents a direct developer and it is characterised by a larger protoconch (cf. Kadolsky 1995, p. 15, fig. 15, pl. 2, figs 15–16; Kowalke 2001*a*).

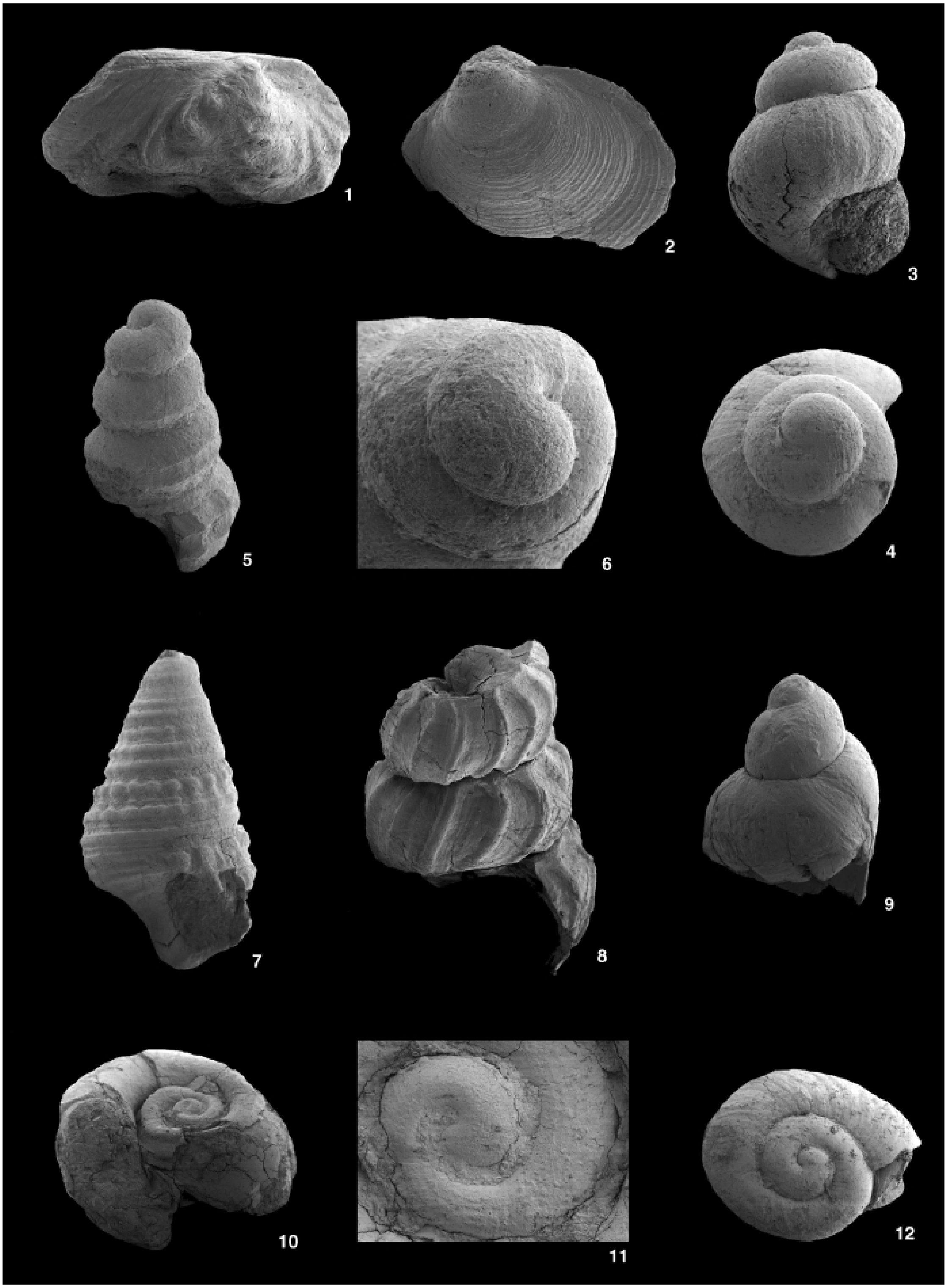
Genus GRANULOLABIUM Cossmann, 1889

Type species. *Cerithium plicatum* Bruguière, 1792; Aquitanian of southern France.

EXPLANATION OF PLATE 1

Fig. 1. *Margaritifera inaequiradiata* (Gümbel, 1861), BSP 2001 VI 18, SD 10, lateral view; ×28.
Fig. 2. *Polymesoda subarata subarata* (Schlotheim, 1820), BSP 2001 VI 19, SD 60, lateral view; ×120.
Figs 3–4. *Hydrobia* sp., BSP 2001 VI 20–21, SD 60. 3, apertural view; ×92. 4, apical view; ×118.
Figs 5–6. *Potamides* sp., BSP 2001 VI 22–23, SD 60. 5, lateral view; ×73. 6, apical view of the protoconch; ×180.
Fig. 7. *Granulolabium* cf. *plicatum* (Briguière, 1789), BSP 2001 VI 24, SD 60, apertural view; ×250.
Fig. 8. Thiaridae gen. et spec. indet., BSP 2001 VI 25, SD 10; ×30.
Fig. 9. *Radix* sp., BSP 2001 VI 26, SD 10; ×25.
Figs 10–11. *Planorbarius* sp., BSP 2001 VI 27–28, SD 10. 10, ×13. 11, detailed view of the protoconch; ×56.
Fig. 12. Stylommatophora sp. cf. *Zonites* sp., BSP 2001 VI 29, SD 12, apical view; ×12.

PLATE 1



REICHENBACHER *et al.*, Oligocene molluscs

Granulolabium cf. *plicatum* (Bruguière, 1789)

Plate 1, figure 7

* 1789	*Cerithium plicatum* Bruguière, p. 488.
1989	*Pirenella plicata* (Bruguière); Barthelt, p. 39, pl. 12, fig. 2.
v 2001	*Granulolabium plicatum* (Bruguière); Harzhauser and Kowalke, p. 276, fig. 4.2–5.

Material. Approximately 200 juvenile specimens from SD 60.

Description. The juvenile specimens measure up to 4 mm in height and consist of about five teleoconch whorls. The protoconch is not preserved. Whorls are sculptured by four primary spiral carinae. The posteriormost three are crossed by 16–18 weak axial folds or weak ribs. Intersection of the spiral and axial sculpture is coincident with more or less strongly developed tubercles. Each of the spiral carinae has one secondary spiral thread. The posteriormost thread is most strongly developed. The base of the last whorl has three spiral carinae.

Remarks. Kadolsky (1984) and Kowalke (2001*b*) discussed the nomenclature of the genera *Granulolabium* and *Pirenella*. The protoconch of *G. plicatum* from the Aquitanian of the Mesohellenic Trough (northern Greece) had a planktotrophic veliger stage (cf. Harzhauser and Kowalke 2001).

Genus TYMPANOTONOS Schumacher, 1817

Type species. *Murex fuscatus* Linnaeus, 1758; West African coast.

Tympanotonos margaritaceus (Brocchi, 1814)

1814	*Muricites margaritaceus* Brocchi, p. 477, pl. 9, fig. 24.
1989	*Tympanotonus margaritaceus* (Brocchi); Barthelt, p. 39, pl. 12, fig. 1.
v 2001	*Tympanotonos margaritaceus* (Brocchi); Harzhauser and Kowalke, pp. 278–279, fig. 5.7–9.

Material. Seven compacted juvenile specimens from SD 6 and five adult fragmented specimens from SD 60.

Description. The shells measure up to 30 mm in height and consist of ten flat teleoconch whorls. Sculpture consists of three noded spiral carinae crossed by weak axial ribs. The strongest developed posteriormost and the spiral carina in the median portion of the whorls have a weaker secondary spiral thread. Just above the posterior suture an additional weak tuberculate spiral cord is evident. The aperture is characterised by a thickened, extended peristome. The columella has a median fold. A single known protoconch of this species is found on a specimen from the Hausham syncline (material from the collection of B. Reichenbacher). It comprises 1·75 rounded whorls and measures *c*. 0·18 mm in maximum diameter. Sculpture is not preserved. The first whorl measures 0·05 mm in the width of the initial cap and 0·12–0·13 mm in maximum diameter. The protoconch is terminated by a slightly sinuous thickening.

Remarks. The protoconch is indicative of a planktotrophic larval stage. *Tympanotonos margaritaceus* resembles the modern *T. fuscatus* Linnaeus, 1758 from the West African coast. *T. fuscatus* is distinguished by the development of the axial sculpture on the early teleoconch and by the strongest development of the second posterior spiral carina, instead of the posteriormost in *T. margaritaceus* (cf. Wittibschlager 1983; Kadolsky 1995). We refrain from separating *T. margaritaceus* from *Tympanotonos* and assigning this species to *Mesohalina* Wittibschlager, 1983, based on sculptural characteristics (see also discussion in Harzhauser and Kowalke 2001).

Family THIARIDAE Troschel, 1857

THIARIDAE gen. et sp. indet.

Plate 1, figure 8

Material. Three specimens from SD 10.

Description. The fragmented specimens measure 2 mm in maximum height. Sculpture of the moderately rounded teleoconch whorls consists of 10–12 strong, sickle-shaped collabral ribs. Apex and aperture are not preserved.

Remarks. Two species described as *Melanoides mayeri* (Gümbel, 1861) and *M. winkleri* (Mayer-Eymar, 1861) from brackish-water deposits of Bavaria more likely resemble Potamididae (cf. Wolff 1897, p. 289, pl. 25, fig. 22 a–b). These species are characterised by spiral and axial sculpture and are not conspecific with the material described here. Eocene Thiaridae within the genus *Melanotarebia* Bandel and Kowalke, 1997, from Tethyan coastal swamps are distinguished in having about equally strong spiral and axial teleoconch sculpture (Bandel and Kowalke 1997). Recent Thiaridae within the genera *Melanoides* Olivier, 1804, and *Sermyla* H. and A. Adams, 1854, with a similar shell outline differ in having a reticulate sculpture. *Thiara* Röding, 1798 is distinguished by the formation of spines. *Stenomelania* Fischer, 1885, with its reduced sculptural elements, is characterised by having a much more slender shell (Kowalke 1998). The shell morphology of our material and the occurrence in fluvial facies indicate a relationship with the family Thiaridae.

Subclass HETEROSTROPHA Fischer, 1885
Order PULMONATA Cuvier, 1797
Suborder BASOMMATOPHORA Keferstein, 1864
Family LYMNAEIDAE Gray, 1842
Genus RADIX Montfort, 1810

Type species. *Helix auricularia* Linnaeus, 1758; Recent, Europe.

Radix sp.

Plate 1, figure 9

Material. Thirty-one juvenile specimens from SD 10 (7 specimens), SD 12 (5 specimens), SD 44 (7 specimens), SD 46 (3 specimens) and from SD 109 (9 specimens).

Description. The juvenile specimens measure up to 4 mm in height and comprise up to four whorls. The aperture of the large last whorl is not completely preserved. The protoconch consists of 1·5 slightly rounded whorls, which rapidly increase in diameter. The protoconch measures 0·6–0·7 mm in height and 0·19 mm in the width of the initial cap. The protoconch is terminated by a weak, straight thickening of the shell. The onset of the adult shell is indicated by the presence of closely spaced growth lines.

Remarks. According to Barthelt (1989) *Radix* frequently occurs in the seam sections of the Lower Brackish-Water Molasse.

Family PLANORBIDAE Gray, 1840
Genus PLANORBARIUS Froriep, 1806

Type species. *Helix corneus*, Linnaeus, 1758; Recent, Europe.

Planorbarius sp.

Plate 1, figures 10–11

Material. One juvenile specimen from SD 10.

Description. The planispirally coiled shell measures 2·88 mm in maximum diameter and consists of 2·75 fragmented whorls. The first whorl measures 0·14 mm in the width of the initial cap and 0·5 mm in maximum diameter. The first whorl is ornamented by an indistinct pattern of fine grooves and folds. The protoconch is terminated by a straight thickening of the shell. The onset of the adult shell is indicated by the formation of spiral striae.

Remarks. We refrain from assigning this poorly preserved single juvenile specimen to a species.

Suborder STYLOMMATOPHORA A. Schmidt, 1855

Stylommatophora sp. cf. *Zonites* sp.

Plate 1, figure 12

Material. Ten specimens from SD 10 (two specimens), SD 12 (three specimens), SD 44 (three specimens) and SD 109 (two specimens).

Description. The fragmented shells consist of 2·5 rather planispirally coiled whorls. The maximum diameter of the shells amounts to 3 mm. The first whorl measures 0·2 mm in the width of the initial cap of the embryonic shell and 0·8–0·9 mm in maximum diameter. The onset of the adult shell is indicated by the formation of regular growth lines. The teleoconch appears to be smooth aside from the growth lines.

Stylommatophora sp. cf. *Cepaea* sp.

Material. Two specimens from SD 44.

Description. The fragmented low conical shell consists of three slightly rounded whorls. The first whorl measures 0·2 mm in the width of the initial cap of the embryonic shell and 0·5–0·6 mm in maximum diameter. The adult shell is characterised by irregular weak axial folds, which are restricted to the posterior half of the whorls.

Remarks. The genus *Zonites* Montfort, 1810 (type species *Helix algirus* Linnaeus, 1758, Recent, southern France) has been reported from the Bavarian Oligocene by Barthelt (1989). A second stylommatophoran species represented by individuals with up to about three whorls may belong to the genus *Cepaea* Held, 1837, with the Recent type species *Helix nemoralis* Linnaeus, 1758, from Europe. However a clear attribution of the present early ontogenetic shells of stylommatophoran species to adult individuals is not possible.

Class OSTRACODA Latreille, 1806

Remarks. Ostracods (Maxillopoda, Crustacea) are known to have existed since at least the Ordovician (Hou *et al*. 1996). Their small, calcified, bivalved carapaces are easily fossilized and exhibit many features of taxonomic value. Unfortunately, specimens of three of the four species described here were preserved exclusively as complete carapaces filled with hard sediment, and many had been compressed. Attempts to empty the carapaces were unsuccessful, and some of the valves broke along fractures. Poor preservation and the paucity of specimens made gender determination impossible.

Superfamily CYPRIDOIDEA Baird, 1845
Family CANDONIDAE Kaufmann, 1900
Subfamily PARACYPRIDINAE Sars, 1923

Genus PHLYCTENOPHORA Brady, 1880

Type species. *Phlyctenophora zealandica* Brady, 1880, p. 33, pl. 3, fig. 1a–m.

Phlyctenophora grosdidieri Stchepinsky, 1963

Plate 2, figures 1–9

* 1963 *Phlyctenophora grosdidieri* Stchepinsky, p. 155, pl. 1, figs 8–13.
v 1985 *Phlyctenophora grosdidieri* Stchepinsky; Müller, p. 12, pl. 1, figs 1–3.
v 1990 *Phlyctenophora* aff. *grosdidieri* Stchepinsky; Kreuzer, fig. 3.

Material. One hundred and twelve adult and 18 juvenile carapaces (26 very damaged, 11 internal casts) from SD 60.

Description. Smooth, elongated carapaces, maximum height just anterior to midlength. Greatest width at approximately middle of carapace. Left valve overlaps right valve except in hinge area. Anterior end broadly rounded, posterior end pointed, ventral margin straight or slightly concave. Dimensions of broad morphotypes (n = 30): length 686–784 μm; height 313–372 μm; width 254–313 μm; h/l 0·410–0·514. Dimensions of intermediate morphotypes (n = 6): length 705–754 μm; height 333–352 μm; width 264–352 μm; h/l 0·442–0·500. Dimensions of slender morphotypes (n = 42): length 686–803 μm; height 303–392 μm; width 196–264 μm; h/l 0·431–0·541.

Remarks. *P. grosdidieri* is the most abundant of the species recovered. Since no single valves could be obtained, internal characters such as marginal pores, inner margins, and vestibulae were not investigated. The central muscle scars have been revealed on a few internal casts. Stchepinsky (1963) did not mention these scars in his original description of the species. Those of the material described here correspond to the muscle scars of *P.* aff. *zealandica* in Morkhoven (1963, p. 82, figs 113–114), a species closely related to the type species, and to those of extant *P. mesembria* and *P. polygona* (Wouters 1999). Although no measurements were provided in the original description, Stchepinsky's (1963) figures correspond well with the material from Sindelsdorf (see also Müller 1985, p. 12).

Approximately 30 per cent of the *Phlyctenophora* specimens correspond to Stchepinsky's description of *P. grosdidieri* in all characters that could be examined, and to some of the material of Müller (1985) and Kreuzer (1990). These specimens are hereby referred to as the 'broad morphotype' (Pl. 2, figs 1–3).

Some 40 per cent of the specimens differ from the broad morphotype in being markedly more slender in dorsal view, in having more pointed anterior and posterior ends in dorsal view, and in featuring a slightly modified outline in lateral view: a more concave ventral margin, a dorsal area that is not evenly rounded (instead exhibiting a hump), and a more pointed posterior end. They are easily distinguished from the broad morphotype and are here categorized as the 'slender morphotype' (Pl. 2, figs 4–6). Both morphotypes are linked by several specimens showing transitional character states, which are referred to here as the 'intermediate morphotype' (Pl. 2, figs 7–9). Figures in Stchepinsky's original description also show different outlines in lateral view: figures 9 and 11–13 on his plate 1 represent the broad morphotype, while figures 8 and 10 represent the slender morphotype.

Besides *P. grosdidieri*, Müller (1985) distinguished a form he determined as *P.* aff. *grosdidieri*, considering it to be a possible new species identified by its less pointed posterior end in lateral view. A re-examination of his material showed that intermediate forms of this character also occur. Furthermore, his specimens also show the variation in outline (lateral view) and width described here, including intermediate forms. Müller did not mention the width of carapaces for either of his *Phlyctenophora* forms.

In conclusion, the species *P. grosdidieri* Stchepinsky, 1963 shows great variability in carapace outline, the extreme forms of which are linked by intermediate ones. The Early–Late Chattian phylogenetic development from one form to another suggested by Müller (1985, p. 12) has to be rejected, because of their common occurrence here in one bed of the Early Chattian age. Eighteen specimens belong to different juvenile stages. Because of this small number, the height/length-ratios of different ontogenetic stages could not be distinguished. The presence of juveniles indicates autochthonous deposition.

Family LEPTOCYTHERIDAE Hanai, 1957

Genus LEPTOCYTHERE Sars, 1925

Type species. *Cythere pellucida* Baird, 1850 (described by Sars, 1925).

Leptocythere cf. *lacertosa* Hirschmann, 1912

Plate 2, figures 10–13

* 1912	*Cythere lacertosa* Hirschmann, p. 53, figs 36–39.
1929	*Leptocythere lacertosa* (Hirschmann); Klie, p. 281.
1971	*Leptocythere lacertosa* (Hirschmann); Whatley *et al*., p. 404, pl. 1.
v 1985	*Limnocythere* sp. A; Müller, p. 29, pl. 5, figs 15–19.

Material. 18 adult carapaces (length 372–45 0 μm, height 196–254 μm, h/l 0·500–0·579) and one juvenile carapace (length 362 μm, height 176 μm) from SD 60.

Description. A small *Leptocythere* with a dorsal margin distinctly inclined towards posterior end. Greatest height at the anterior end of the hinge. Greatest width distinctly posterior to midlength in lateral view. Anterior end broadly rounded, posterior end slightly more pointed. Anterior margin compressed, thus appearing beak-shaped in dorsal view (Pl. 2, fig. 11). Posterior margin less compressed, featuring three ridges almost parallel to posterior outline, the outer one of which forms a prominent posterodorsal edge (Pl. 2, figs 10–11). The ridges make the posterior end look terraced in ventral view (Pl. 2, fig. 12). The mid-ventral indentation almost completely covered by ventromedian lateral bulges. V-shaped dorsomedian sulci present. Valve surface slightly reticulated with many shallow pits; a former more prominent reticulation has probably been eroded away.

Remarks. With respect to the ornamentation, the material is very similar to *Leptocythere psammophila* Guillaume, 1976; however, *L. psammophila* belongs to the middle to large species of the genus 550–650 μm in length, whereas *L. lacertosa* does not exceed a length of 450 μm. As internal characters could not be examined, the determination is given in open nomenclature.

Family CYTHERIDEIDAE Sars, 1925

Genus CYTHERIDEA Bosquet, 1852
Subgenus CYTHERIDEA Bosquet, 1852

Type species. *Cytheridea* (*Cytheridea*) *muelleri* (Münster, 1830) described by Brady and Norman 1889 (p. 172).

EXPLANATION OF PLATE 2

Figs 1–3. *Phlyctenophora grosdidieri* Stchepinsky, 1963, broad type, BSP 2001 VI 30–32, SD 60; ×60. 1, right valve. 2, left valve. 3, dorsal view, anterior to left.

Figs 4–6. *Phlyctenophora grosdidieri* Stchepinsky, 1963, intermediate type, BSP 2001 VI 33–35, SD 60; ×60. 1, right valve. 2, left valve. 3, dorsal view, anterior to left.

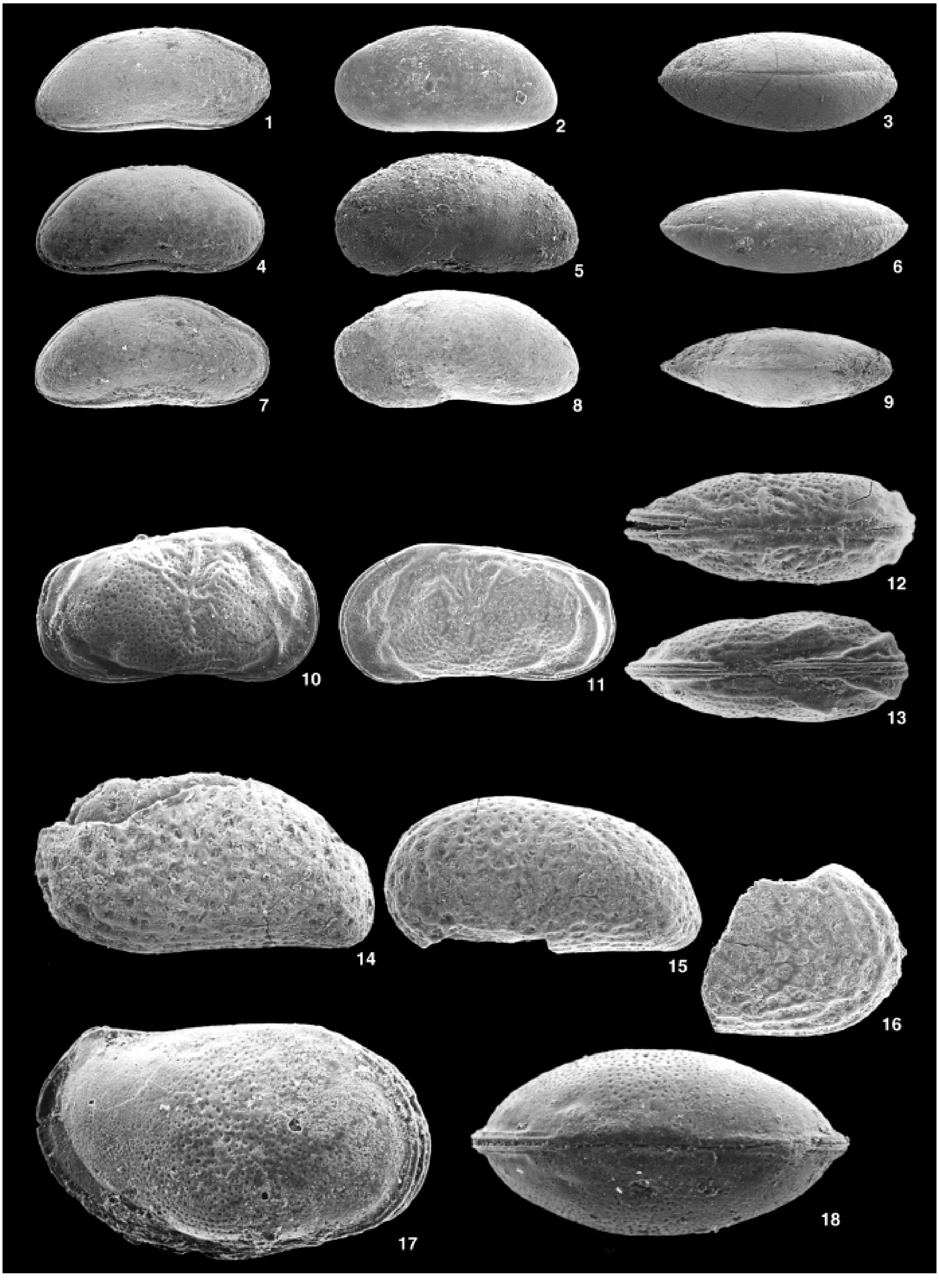
Figs 7–9. *Phlyctenophora grosdidieri* Stchepinsky, 1963, slender type, BSP 2001 VI 36–38, SD 60; ×60. 1, right valve. 2, left valve. 3, dorsal view, anterior to left.

Figs 10–13. *Leptocythere* cf. *lacertosa* Hirschmann, 1912, BSP 2001 VI 39–42, SD 60; ×100. 10, right valve. 11, left valve. 12, dorsal view, anterior to left. 13, ventral view, anterior to left.

Figs 14–16. *Cytheridea* cf. *bavarica* Goerlich, 1953, BSP 2001 VI 43–45, SD 60; ×75. 14, left valve, juvenile. 15, left valve, adult. 16, fragment of right valve, adult.

Figs 17–18. *Palmoconcha* cf. *turbida* Müller, 1912, BSP 2001 VI 46–47, SD 60; ×100. 17, right valve. 18, dorsal view, anterior to left.

PLATE 2



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Cytheridea (*Cytheridea*) cf. *bavarica* Goerlich, 1953

Plate 2, figures 14–16

* 1953	*Cytheridea* (*Cytheridea*) *bavarica* Goerlich, p. 133, figs 26–29.
v 1985	*Cytheridea bavarica* Goerlich; Müller, p. 16, figs 8–10.
v 1967	*Cytheridea bavarica* Goerlich; Witt, pp. 86, 94, 96, 100.

Material. SD 60: one left valve, ventral margin partly destroyed (length 750 μm, height *c*. 370 μm); one left valve, juvenile, dorsal margin partly destroyed (length 666 μm, height 343 μm); two fragments of right valve.

Description. A *Cytheridea* with many pits, irregularly spread over the entire carapace. Dorsal margin evenly inclined towards the posterior end apart from a weak indentation at midlength. Ventral margin straight, anterior end broad, posterior end pointed.

Remarks. The posteroventral spines described by Müller (1985) for some of his specimens of *C. bavaria* are not present. The similar species *C. muelleri* (Münster 1830) differs in height/length ratio and in the size and distribution of the pits. The specimens described here correspond to those from the Bavarian Molasse described by Witt (1967) (collection material examined). Nevertheless, the poor preservation of the few specimens recovered only allows a determination in open nomenclature.

Family LOXOCONCHIDAE Sars, 1925

Genus PALMOCONCHA Swain and Gilby, 1974

Type species. *Palmoconcha laevimarginata* Swain and Gilby, 1974, p. 325, pl. 5, figs 10–13.

Palmoconcha cf. *turbida* Müller, 1912

Plate 2, figures 17–18

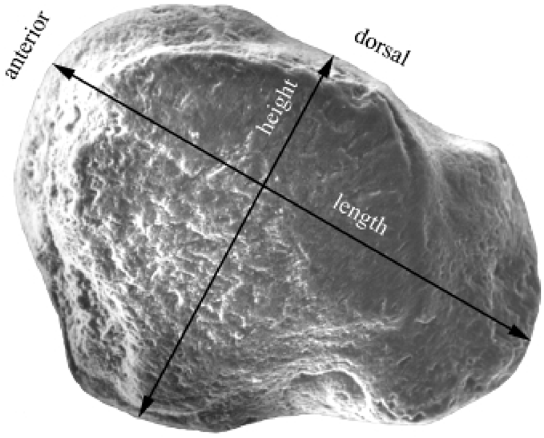
* 1894	*Loxoconcha levis* Müller, p. 344, pl. 27, figs 8, 19, 22; pl. 28, fig. 8 (junior homonym of *L. levis* Brady, 1870).
1912	*Loxoconcha turbida* (nom. nov.), G. W. Müller; Müller, p. 308.
non 1962	*Loxoconcha* cf. *turbida* Müller; Bassiouni, p. 57, pl. 7, fig. 11.
1981	*Lindisfarnia turbida*; Horne and Kilenyi, p. 107.
non 1981	*Loxoconcha* cf. *turbida* G. W. Müller; Uffenorde, p. 178, pl. 9, figs 3, 12.
1985	*Palmoconcha turbida*; Horne and Whatley, p. 158.

Material. Sixteen carapaces (adult) from SD 60 (length 588–686 μm, height 333–401 μm, h/l 0·543–0·679).

Description. A *Palmoconcha* with the typical rhomboidal outline in lateral view. Dorsal margin straight, anterodorsal edge not very prominent, anterior end widely rounded. Posterodorsal margin inclined slightly behind a weak indentation, forming a prominent posterior angle; posterior end narrowly rounded. Ventral and dorsal margin only parallel at midregion. Flat marginal rim exceeding almost the complete free margin except in anteroventral area (most prominent posteriorly). Both valves equal in length, left valve overlapping right valve only midventrally. In dorsal view, anterior end more pointed than posterior end. Greatest width at midlength. Carapace evenly arched laterally with a punctate ornamentation. Adductor muscle scars as described for the genus (Athersuch *et al*. 1989).

Remarks. In all characters that could be investigated, the material corresponds to *L. turbida* (Müller 1894, 1912). As internal characters could not be examined, the determination is given in open nomenclature.

The specimens identified as *L.* cf. *turbida* in Bassiouni (1962) and Uffenorde (1981) are characterized by a more strongly developed posterior marginal rim and a less prominent posterodorsal edge.



TEXT-FIG. 6. Measurements and terminology of the lapillus of a cyprinid fish.

Supraorder TELEOSTEI Müller, 1844

Remarks. Teleost fishes have three pairs of aragonitic bodies (= otoliths) in the auditory system of their skulls. According to its exact position in the auditory system, the otolith is termed a lapillus, asteriscus or sagitta. Commonly, palaeontologists use the term otolith for the sagitta, which is the largest otolith in nearly all teleost families. However, there are exceptions: in cyprinid fish the largest otolith is the lapillus (Text-fig. 6). Sagittae of different taxa differ in shape, size and other morphological features, and thus can be used for species identification (Koken 1884). Their taxonomic classification is based on studies of comparative morphology of the sagittae of recent fish species (cf. Nolf 1985; Smale *et al.* 1995).

Order CYPRINIFORMES Bleeker, 1859
Family CYPRINIDAE Cuvier, 1817

Genus *incertae sedis*

'genus Cyprinidarum' sp.

Text-figure 7A–D

v 1997 'genus Cyprinidarum' sp. 1.; Reichenbacher and Schwarz, tab. 1, fig. 57.
v 2002 'genus Cyprinidarum' sp.; Reichenbacher and Uhlig, tab. 8, pl. 1, fig. 9.

Material. Fifty-nine lapilli, among them 50 from SD 10, one from SD 12, six from SD 109, and two from SD 119.

Description. Shapes of the lapilli are ovate or slightly trapeziform; some have a weakly pointed posterior end. The outer face is convex and covered with fine grooves. A shallow, narrow line looking like a V or U extends in the posterior part of the outer face. The inner face is rather smooth and flat, but in some specimens also convex-concave. A prominent furrow is situated anteriorly and builds up a suture between outer and inner face. The furrow may extend to the middle of the dorsal rim. In some lapilli the dorsal rim shows a well-developed projection near the junction of this furrow (Text-fig. 7D). Other lapilli show a straighter dorsal rim (Text-fig. 7A–B). The ventral rim may be rounded (Text-fig. 7C–D) or has a prominent projection in the middle (Text-fig. 7A–B). Its posterior end is straight or slightly convex or (rarely) concave (Text-fig. 7A).

Measurements: Length 0·5–1·5 mm; height 0·4–1·1 mm; l/h 1·1–1·5.

Remarks. The general shape of the lapilli described herein corresponds well with those of Recent cyprinid taxa (e.g. Chardon and Vandewalle 1992, Text-fig. 11.3; Martini and Reichenbacher 1997, pl. 1, figs 3, 6).

Taxonomic determination is possible only to family level, owing to the lack of studies of lapilli morphology on cyprinid taxa of lower rank. Differences in the morphology as described above, and also differences in sizes, lead to the assumption that two or more taxa may be present.

Our lapilli represent one of the oldest records of cyprinids in Europe (cf. Böhme 2000). Additional cyprinid lapilli of the same age (transition zone Lower/Upper Oligocene) have been described from lacustrine deposits of the Mainz Basin (Mödden *et al.* 2000, as 'genus Cyprinidarum' sp. A). They differ from our material because of their more elongate posterior end. A few fossil cyprinid lapilli of the same and slightly younger age have been figured from the Lower Brackish-Water Molasse of the Murnau and Hausham synclines (North Alpine Foreland Basin) (Reichenbacher and Schwarz 1997; Reichenbacher and Uhlig 2002). They may belong to the same taxa as our material. Apart from these records, fossil cyprinid lapilli are known only from Early Miocene and younger deposits (Menzel and Becker-Platen 1981; Martini 1983; Reichenbacher 1988; Gaudant 1989; Reichenbacher and Mödden 1996; Gaudant *et al.* 2002; Sach *et al.* 2003).

Order ESOCIFORMES Bleeker, 1859
Family UMBRIDAE Bleeker, 1859

Genus PALAEUMBRA Weiler, 1973

Type species. *Palaeumbra moguntina* Weiler, 1973.

Palaeumbra moguntina Weiler, 1973

Text-figure 7E–F

* v 1973 *Palaeumbra moguntina* Weiler, p. 456, figs 1–2.
v 1996 *Palaeumbra moguntina* Weiler; Reichenbacher and Mödden, p. 94, pl. 3, figs D–I.
v 2000 *Palaeumbra moguntina* Weiler; Mödden *et al.*, p. 350, fig. 4L.
v 2000 *Palaeumbra moguntina* Weiler; Reichenbacher, p. 63, pl. 1, figs 10–12.
v 2000 *Palaeumbra moguntina* Weiler; Uhlig *et al.*, p. 508, pl. 1, figs 6–7.
v 2002 *Palaeumbra moguntina* Weiler; Reichenbacher and Uhlig, pl. 1, figs 1–2.

Material. Fourteen sagittae, among them 11 from SD 10 and three from SD 44.

Description. The sagittae are characterised by a slightly rectangular, but rounded shape and a convex outer face. The dorsal rim is moderately rounded and shows a weakly developed posterodorsal angle. At the posteroventral transition, a distinct edge or a small projection to the back is present. The ventral rim is regularly rounded. The prominent rostrum is long, massive and anteriorly pointed. A small antirostrum may also be present; it is rounded or pointed. The sulcus is straight. A thick colliculum clearly divides the sulcus in the ostium and cauda, which are both approximately the same length. A marked Crista superior and Crista inferior extend from the posterior part of the ostium to the end of the cauda. No colliculi are present in the cauda. The specimens found in sample SD 44 (Text-fig. 7E) are characterised by a steeply dropping posterior rim and thus have a more rectangular and less rounded shape than the specimens in sample SD 10.

Length 0·95–2·55 mm; height 0·74–1·63 mm; l/h 1·3–1·5; l/h increasing with length of sagitta.

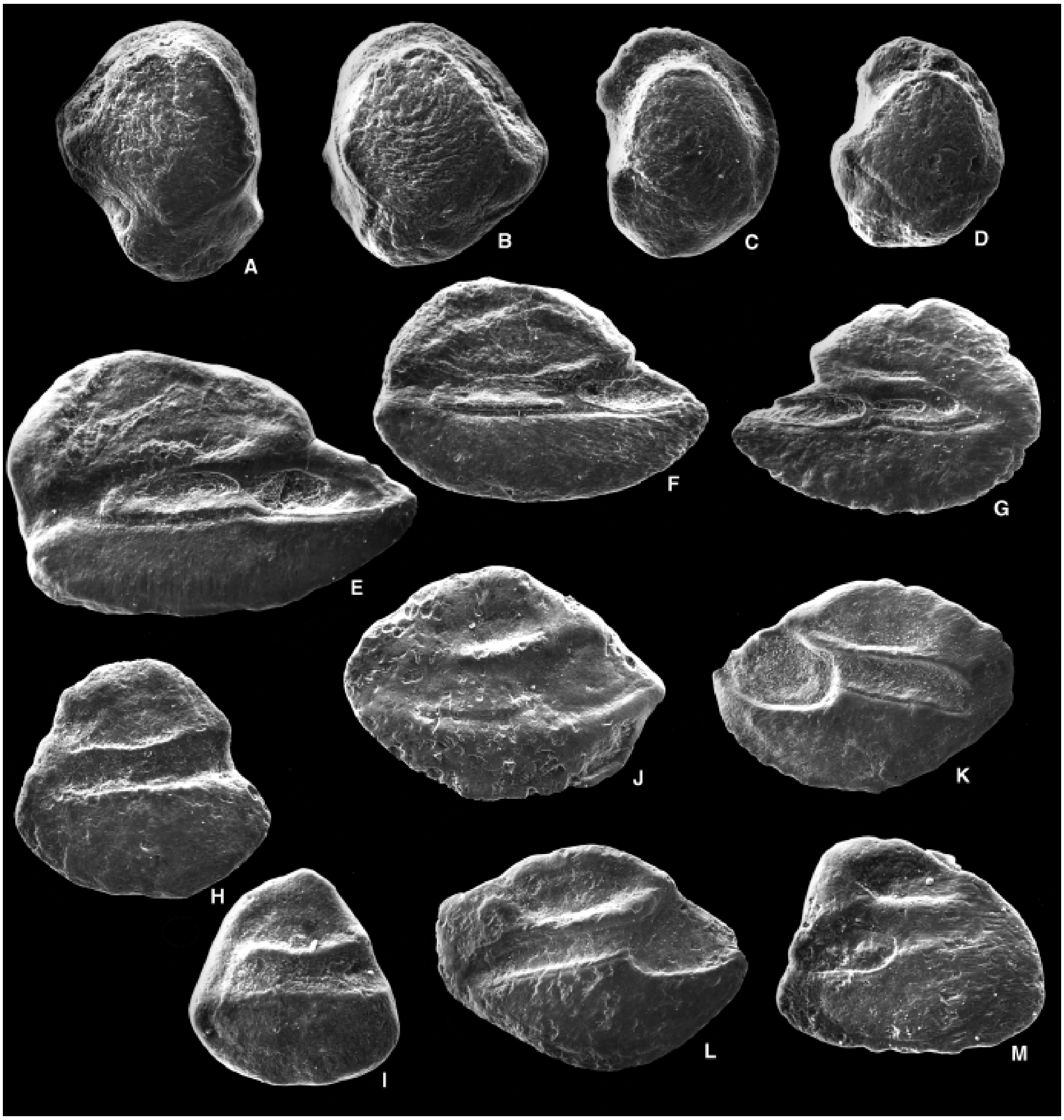
Remarks. *P. moguntina* is the only known species of the fossil genus *Palaeumbra*.

Genus *incertae sedis*

'genus Umbridarum' *crassus* (Weiler, 1963)

Text-figure 7G

* v 1963 Otol. (inc. sed.) *crassus* n. sp.; Weiler, p. 15, figs 28–29.
v 1996 'genus Umbridarum' *crassus* (Weiler); Reichenbacher and Mödden, p. 94, pl. 3, figs K–M.
v 1997 'genus Umbridarum' *crassus* (Weiler); Reichenbacher and Philippe, p. 406, figs 4F–L, 6A–F.



TEXT-FIG. 7. A–D, 'genus Cyprinidarum' sp., BSP 2001 VI 48–51, SD 10, outer faces of left (A, ×40) and right (B–D, ×50) lapilli. E–F, *Palaeumbra moguntina* Weiler, 1973, BSP 2001 VI 52–53, SD 10, left sagittae; ×20. G, 'genus Umbridarum' *crassus* (Weiler, 1963), BSP 2001 VI 54, SD 10, right sagitta; ×30. H–I, *Palaeolebias symmetricus* (Weiler, 1963), BSP 2001 VI 55–56, SD 109, left sagittae; ×50, ×40. J, 'genus Apogonidarum' sp./aff. *kosdensis* (Schubert, 1912), BSP 2001 VI 57, SD 12, left sagitta; ×25. K, *Dapalis rhomboidalis* Stinton, *in* Stinton and Kissling 1968, BSP 2001 VI 58, SD 12, right sagitta; ×15. L, *Dapalis carinatus* Stinton, *in* Stinton and Kissling 1968, BSP 2001 VI 59, left sagitta; ×15. M, 'genus Percoideorum' sp., BSP 2001 VI 60, SD 10, right sagitta; ×50.

v 2000 'genus Umbridarum' *crassum* (Weiler); Mödden *et al.*, p. 350, fig. 4M.
v 2000 'genus Umbridarum' *crassus* (Weiler); Reichenbacher, p. 63, pl. 1, fig. 9.
v 2000 'genus Umbridarum' *crassus* (Weiler); Uhlig *et al.*, p. 508, pl. 1, fig. 5.
v 2002 'genus Umbridarum' *crassus* (Weiler); Reichenbacher and Uhlig, pl. 1, fig. 6.

Material. Eight sagittae from SD 10.

Description. Elongate to ovate sagittae, generally with a pronounced hump on the posterior part of the outer face. Dorsal rim, posterior rim and ventral rim are regularly rounded and crenulated. The rostrum is rather long and pointed, the antirostrum pronounced. A colliculum divides the straight sulcus in a rather narrow cauda and a somewhat wider ostium. Crista superior and Crista inferior are well developed and extend from the posterior part of the ostium to the end of the cauda.

Length 1·0–2·05 mm; height 0·67–1·46 mm; l/h 1·4–1·5.

Remarks. The species differs from *Palaeumbra moguntina* by the rounded transition between posterior and ventral rim, the presence of 1–3 small colliculi within the cauda, and a more pointed rostrum.

Order ATHERINIFORMES Rosen, 1964
Family CYPRINODONTIDAE Agassiz, 1834

Genus PALAEOLEBIAS Reichenbacher, *in* Reichenbacher and Weidmann 1992

Type species. *Palaeolebias semicircularis* Reichenbacher, *in* Reichenbacher and Weidmann 1992.

Palaeolebias symmetricus (Weiler, 1963)

Text-figure 7H–I

* v 1963	Otol. (Cyprinodontidarum) *symmetricus* Weiler, p. 14, figs 23–26.
v 1992	*Palaeolebias symmetricus* (Weiler); Reichenbacher and Weidmann, p. 18, figs 4–5.
v 1997	*Palaeolebias symmetricus* (Weiler); Reichenbacher and Philippe, p. 408, fig. 7A–H.
v 1997	*Palaeolebias symmetricus* (Weiler); Reichenbacher and Schwarz, table 3, fig. 38.
v 2000	*Palaeolebias symmetricus* (Weiler); Reichenbacher, p. 77, pl. 1, figs 5–8.
v 2002	*Palaeolebias symmetricus* (Weiler); Reichenbacher and Uhlig, pl. 1, fig. 12.

Material. Six sagittae (five from SD 109 and one from SD 119).

Description. This species is characterised by its triangular, symmetrical shape and the broad but short rostrum. The sulcus is indistinctly divided in a very small ostium and a long, straight cauda. Some colliculi are present in the cauda.

Length 0·49–0·87 mm; height 0·49–0·88 mm; l/h 0·9–1·0.

Remarks. *P. symmetricus* differs from all known *Palaeolebias* species by its typical symmetrical shape.

Order PERCIFORMES Bleeker, 1859
Family AMBASSIDAE Boulenger, 1904

Genus DAPALIS Gistel, 1848

Type species. *Dapalis minutus* (Blainville, 1817).

Dapalis carinatus Stinton, *in* Stinton and Kissling 1968

Text-figure 7L

* v 1968	*Dapalis carinatus* Stinton, *in* Stinton and Kissling, p. 148, pl. 1, fig. 3.
v 1992	*Dapalis carinatus* Stinton and Kissling; Reichenbacher and Weidmann, p. 32, pl. 6, figs 7–12, 16.
v 2000	*Dapalis* sp.; Uhlig *et al*., p. 508, pl. 1, fig. 9.
v 2002	*Dapalis carinatus* Stinton and Kissling; Reichenbacher and Uhlig, pl. 1, figs 4–5.

Material. Four sagittae from SD 12.

Description. *D. carinatus* has an elongate to ovate shape. The short and somewhat truncated posterior rim and the relatively narrow ostium (compared with other *Dapalis* species) are the characteristic features of this taxon. For a detailed description, see Reichenbacher and Weidmann (1992).

Length 1·47–2·94 mm; height 1·01–2·13 mm; l/h 1·4.

Dapalis rhomboidalis Stinton, *in* Stinton and Kissling 1968

Text-figure 7K

* v 1968 *Dapalis rhomboidalis* Stinton, *in* Stinton and Kissling, p. 149, pl. 1, fig. 4.
v 1992 *Dapalis rhomboidalis* Stinton and Kissling; Reichenbacher and Weidmann, p. 33, pl. 6, figs 1–6.
v 2000 *Dapalis* sp.; Uhlig *et al*., pl. 1, fig. 10.
v 2002 *Dapalis rhomboidalis* Stinton and Kissling; Reichenbacher and Uhlig, pl. 1, fig. 3.

Material. A single sagitta from SD 12.

Description. *D. rhomboidalis* has a more rounded shape than *D. carinatus*, and especially a deeply rounded ventral rim. In addition, the lower rim of the ostium of *D. rhomboidalis* is more concave and thus the ostium is relatively larger. For a detailed description, see Reichenbacher and Weidmann (1992).

Length 2·7 mm; height 1·95 mm; l/h 1·4.

Family APOGONIDAE Jordan and Gilbert, 1882

Genus *incertae sedis*

'genus Apogonidarum' sp./aff. *kosdensis* (Schubert, 1912)

Text-figure 7J

aff. * 1912 *Otolithus* (*Percidarum*?) *kósdensis* Schubert, p. 126, fig. 2.
aff. 1981 'genus Apogonidarum' *kosdensis* (Schubert); Nolf, p. 157.
v 1997 'genus Apogonidarum' sp./aff. *kosdensis* (Schubert); Reichenbacher and Schwarz, table 1, figs 35–37.
aff. v 1999 'genus Apogonidarum' *kosdensis* (Schubert, 1912); Nolf and Reichenbacher, p. 189, pl. 1, figs 4–8; pl. 3, figs 1–4.

Material. A single sagitta from SD 12.

Description. The sagitta has an ovate shape. Inner and outer faces are slightly convex. The regularly rounded dorsal rim is highest in the middle. The regularly rounded ventral rim leads to the rather short rostrum, which is pointed. The sulcus is situated in the middle of the sagitta and slightly concave. The large ostium is U-shaped and its lower rim bends upwards. The cauda is short and has a well-marked crista inferior.

Length 1·71 mm; height 1·26 mm; l/h 1·36.

Remarks. This taxon differs from the middle Eocene species 'genus Apogonidarum' *kosdensis* mainly by the less rounded posterior part of the sagitta and the shorter rostrum. Owing to its higher dorsal rim and the relatively wider ostium it can also be distinguished from 'genus Apogonidarum' sp. 1 described from the Murnau Syncline (Reichenbacher and Uhlig 2002).

Family ELEOTRIDAE Gill, 1861

Genus *incertae sedis*

'genus Eleotridarum' sp.

Material. A single sagitta from SD 12 and one from SD 44.

Description. Both sagittae are poorly preserved and partly broken. The shape is rectangular with a small posterodorsal and a prominent praeventral projection. The sulcus has the typical gobioid shape and is, as typical for eleotrids, opened anteriorly.

Length 2·0–2·7 mm; height 1·55–2·1 mm; l/h 1·3.

Remarks. The specimens differ from other fossil eleotrid species because of their narrow praedorsal part.

Genus *incertae sedis*

'genus Percoideorum' sp.

Text-figure 7M

aff. v 1999 'genus Percoideorum' sp.; Nolf and Reichenbacher, p. 190, pl. 1, fig. 14; pl. 3, fig. 12.

Material. One complete and two incomplete sagittae of approximately the same sizes from SD 10.

Description. Sagittae with a triangular shape, but not symmetrical because the highest part of the dorsal rim is situated at the anterior part of the sagitta. The sulcus is situated in the middle of the sagitta, and shifts upwards posteriorly. It is clearly divided in an ovate ostium and a short straight cauda. The crista superior is well developed and accentuates the deepening of the dorsal area.

Length 0·73 mm; height 0·59 mm; l/h 1·24.

Remarks. A similar taxon was described from the Middle Eocene of Hungary but it is more symmetrical in shape and has a more pointed rostrum. Both taxa probably belong to an extinct family and genus of the Percoidei.

ASSOCIATED FLORAL AND FAUNAL ELEMENTS

Seeds of *Stratiotes* cf. *websteri* (Zinndorf, 1901) were found in layers SD 12 and 46, and fruits of *Celtis lacunosa* (Reuss, 1861) Kirchheimer, 1957 in SD 12. In SD 60 two foraminiferal taxa occur: *Quinqueloculina* sp. and *Ammonia kiliani* (Andreae, 1884). In several layers (SD 10, 12, 44, 46, 109 and 119) there are remains of mammalian teeth and bones.

PALAEOENVIRONMENTS

The taxa deriving from the Lower Cyrena Beds of the Sindelsdorf section (SD) are indicative of freshwater, brackish and marine habitats. Taxa from the Lower Coloured Molasse support terrestrial and freshwater environmental interpretations (Table 1).

Because of the mainly good preservation of the fish otoliths and the charophyte gyrogonites, as well as the existence of gastropod protoconchs, we postulate that the fossils from the Sindelsdorf section reflect autochthonous embedding. This is also supported by the bivalves and ostracods, which preserve both valves, and because of the mutual occurrence of juvenile and adult ostracods. However, the foraminifers and the single apogonid otolith are corroded and poorly preserved, and were probably transported from a marine environment nearby.

For each layer of the Sindelsdorf section investigated, we reconstructed the palaeoenvironment based on the presence of specific fossil assemblages. Freshwater organisms are found in SD 10, 44, 46, 109 and 119, whereas brackish faunal elements predominate in SD 6, 18, 38, 40 and 60. Layer SD 12 has a fossil assemblage of intermediate character, suggesting a water body of very low salinity (oligohaline).

Freshwater environments

In layer SD 10 the aquatic gastropod fauna consists of the species *Radix* sp., *Planorbarius* sp. and one representative of the Thiaridae. Bivalves are represented by *Margaritifera inaequiradiata*. Recent and

TABLE 1. Fossil taxa from the Sindelsdorf section and their preferred environments. The number of specimens is bracketed. a, abundant; LBM, Lower Brackish-Water Molasse; LCM, Lower Coloured Molasse; LFM, Lower Freshwater Molasse.

Lithostratigraphy		Lower Cyrena Beds (LBM)									LCM (LFM)	
Sample		SD 6	SD 10	SD 12	SD 18	SD 38	SD 40	SD 44	SD 46	SD 60	SD 109	SD 119
Charophytes	*Chara tornata*									◕ (45)		
	Rhabdochara exigua										● (273)	● (1)
	Stephanochara aff. *pinguis*			? (33)								
	Sphaerochara ulmensis										● (1400)	● (7)
	Nitellopsis (*T.*) *merianii*										● (820)	● (23)
	N. (*T.*) *merianii* f. *globula*		● (154)									
Molluscs	*Margaritifera inaequiradiata*		● (2)									
	Polymesoda s. subarata	◔ (1)			◔ (a)	◔ (a)	◔ (a)			◔ (28)		
	Hydrobia sp.									◐ (11)		
	Pomatias a. antiquum		⊕ (3)	⊕ (9)							⊕ (6)	⊕ (2)
	Protoma diversicostata	◔ (3)										
	Potamides sp.									◔ (11)		
	Granulolabium cf. *plicatum*									◔ (200)		
	Tympanotonos margaritaceus	◔ (7)								◔ (5)		
	Thiaridae gen. et sp. indet.		◕ (3)									
	Radix sp.		◕ (7)	◕ (5)				◕ (7)	◕ (3)		◕ (9)	
	Planorbarius sp.		● (1)									
	cf. *Zonites* sp.		⊕ (2)	⊕ (3)				⊕ (3)			⊕ (2)	
	cf. *Cepaea* sp.							⊕ (2)				
Ostracods	*Phlyctenophora grosdidieri*									◔ (130)		
	Leptocythere cf. *lacertosa*									◐ (19)		
	Cytheridea (*C.*) cf. *bavarica*									◔ (2)		
	Palmoconcha cf. *turbida*									◔ (16)		
Pisces	'genus Cyprinidarum' sp.		● (50)	● (1)							● (6)	● (2)
	Palaeumbra moguntina		● (11)					● (3)				
	'genus Umbridarum' *crassus*		● (8)									
	Palaeolebias symmetricus										◕ (5)	◕ (1)
	Dapalis carinatus			◕ (4)								
	Dapalis rhomboidalis			◕ (1)								
	'genus Apogonidarum' sp.			○* (1)								
	'genus Eleotridarum' sp.			◕ (1)				◕ (1)				
	'genus Percoideorum' sp.		? (3)									
Fruits, Seeds	*Stratiotes* cf. *websteri*			◕ (a)					● (a)			
	Celtis lacunosa			⊕ (a)								
Foraminifera	*Quinqueloculina* sp.									○* (a)		
	Ammonia kiliani									◔* (a)		

habitats: ⊕ terrestrial ● freshwater ◕ freshwater and brackish
◐ brackish ◔ brackish and marine ○ marine

* most probably transported

fossil species of *Planorbarius* and *Margaritifera* are restricted to freshwater habitats, but *Radix* tolerates slightly brackish conditions, and Thiaridae also settle in estuaries. *Margaritifera inaequiradiata* is known from fluvial sediments (Smith 2001), whereas *Radix* sp. and *Planorbarius* sp. characterise stagnant waters and quiet tributary creeks of rivers (Wenz and Zilch 1959–60). Thiaridae, which are today restricted to the tropics and warmer subtropics, can be found in both running and stagnant waters and are known from these habitats at least since the Middle Eocene (Bandel and Kowalke 1997*a*; Bandel and Riedel 1998). The fish fauna consists of cyprinids (carps) and umbrids. Recent cyprinids and umbrids live predominantly in lakes and rivers. The fossil taxa *Palaeumbra moguntina* and ‘genus Umbridarum’ *crassus* described herein are mainly known from lacustrine sediments (Reichenbacher and Philippe 1997; Mödden *et al.* 2000). The charophyte flora consists of the single species *Nitellopsis* (*Tectochara*) *merianii* forma *globula*. This taxon is frequently found in European Tertiary lacustrine sediments (e.g. Schwarz 1985, 1988; Schwarz and Reichenbacher 1989). Generally, rich occurrences of charophytes indicate a very shallow depth of water (< 5 m). In conclusion, faunal and floral elements of SD 10 support a low energy, shallow freshwater environment. This is confirmed by lithofacies as layer SD 10 is represented by a slightly silty, fairly dark brown calcareous marl.

In layers SD 44 and 46, *Radix* sp. represents the only element of the aquatic molluscan fauna. Additionally, the freshwater fish *Palaeumbra moguntina* (Umbridae) and an eleotrid species are present in SD 44. In SD 46 *Stratiotes* cf. *websteri* frequently occurs. We suggest a lacustrine palaeoenvironment for layers SD 44 and 46. The lithofacies is similar to that of SD 10.

In layers SD 109 and 119, *Radix* sp. only occurs in the former. In both layers the fish fauna comprises cyprinids and cyprinodontids (toothcarps), the latter occurring within the Sindelsdorf section for the first time. Recent cyprinodontids are distributed in the European Mediterranean in very shallow marine waters, as well as in brackish and fresh waters (e.g. Villwock 1977; Reichenbacher and Sienknecht 2001). The fossil species *Palaeolebias symmetricus* has been described from lacustrine to slightly brackish deposits of southern France, the Mainz Basin and the Molasse Basin (Reichenbacher and Philippe 1997; Reichenbacher 2000; Reichenbacher and Uhlig 2002). The charophyte flora comprises *Rhabdochara exigua*, *Sphaerochara ulmensis* and *Nitellopsis* (*Tectochara*) *merianii*, which co-occur in both layers. In SD 109 charophytes are particularly abundant. This charophyte assemblage typically characterises freshwater habitats (Schwarz 1985, 1988; Reichenbacher and Schwarz 1997). We suggest a lacustrine, well-aerated, shallow (< 5 m) and oligotrophic environment. The pale colour of the marls also indicates a more oxygenated environment than before.

Remains of organisms indicative of terrestrial habitats (cf. Table 1) are restricted to the freshwater assemblages and most probably have been washed in from the adjacent mainland.

Brackish environments with very low salinity (oligohaline)

In SD 12 *Radix* sp. represents the only element of the aquatic molluscan fauna. The fish fauna contains representatives of the families Ambassidae (glassfishes) and Eleotridae (sleepers), and, rarely, a cyprinid (freshwater) and an apogonid (primarily marine element that is most probably allochthonous). Recent ambassids and eleotrids are well known from tropical littoral and estuarine waters (e.g. Nelson 1994). *Dapalis rhomboidalis* and fossil eleotrid taxa are known from both brackish and lacustrine Oligocene Molasse sediments (Reichenbacher and Weidmann 1992). However, it is evident that the lacustrine fish taxa of the underlying layer SD 10 (see Text-fig. 3) are rare (cyprinids) or absent (umbrids) in SD 12. The flora is, aside from the ecologically variable *Stephanochara* aff. *pinguis*, characterised by mass accumulations of seeds of *Stratiotes* cf. *websteri*. Recent *Stratiotes* is restricted to stagnant freshwater lakes that are rich in nutrients (Wendelberger 1986, p. 45), but it is possible that Oligocene *Stratiotes* also occurred in slightly brackish habitats. Owing to the absence of freshwater fish, layer SD 12 probably accumulated in a slightly brackish (oligohaline) environment. The lithofacies is very similar to that of SD 10.

Brackish environments

In SD 6 the aquatic molluscan fauna is characterised by the gastropods *Tympanotonos margaritaceus* and *Protoma diversicostata*, and by the bivalve *Polymesoda s. subarata*. The genus *Tympanotonos* belongs to the generally euryhaline cerithioidean family Potamididae, whose Recent and fossil representatives are known from a broad variety of brackish and brackish-marine habitats. However, Recent *Tympanotonos* is restricted to intertidal biotopes (e.g. Barthelt 1989; Harzhauser and Kowalke 2001; Kowalke 2001*a*, *b*). Thus, *Tympanotonos* is indicative of lagoons, mud flats and estuaries with mangrove vegetation (Elouard and Rosso 1977; Brown 1980; Bandel and Kowalke 1999). Recent representatives of the genera *Protoma* and *Polymesoda* inhabit euryhaline habitats. Recent *Protoma* species are found in subtidal habitats of the South Atlantic, and Recent *Polymesoda* species characterise the littoral marine zone of the tropical and subtropical Americas, occurring in intertidal to shallow subtidal habitats (cf. Barthelt 1989). Fossil representatives of these suspension feeders are known from lagoons, where they preferentially inhabit sandy-silty substrates (Kowalke and Bandel 1996). The grey, silty calcareous marl of SD 6 indicates a similar environment.

Layers SD 18, 38, and 40 represent the so-called brackish horizons mentioned above. The fauna consists exclusively of mass populations of *Polymesoda s. subarata* and suggests a brackish habitat, most probably a lagoon or an estuary. The absence of *Tympanotonos margaritaceus* may indicate, in contrast to the conditions in SD 6, a slightly deeper, subtidal depositional environment. The grey, silty calcareous marl of SD 18 suggests a lagoonal environment, whereas the grey calcareous fine-grained sandstone of SD 38 and 40 probably accumulated in an estuarine environment.

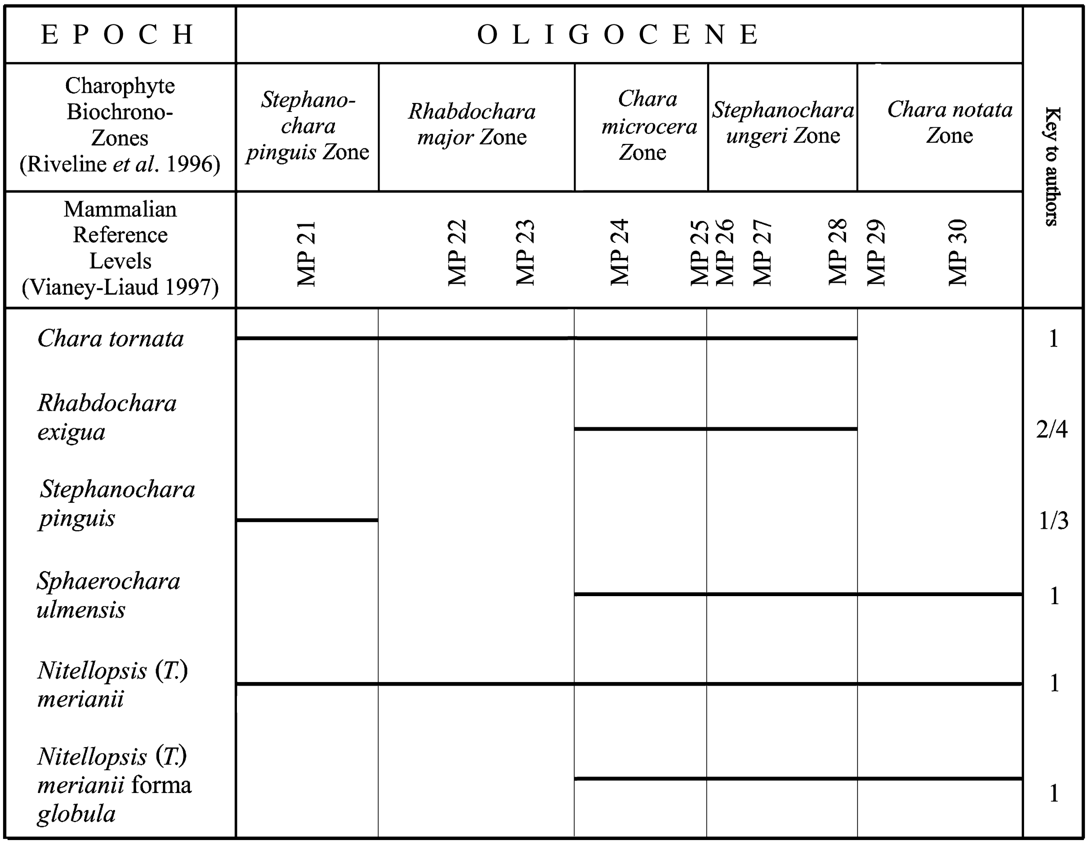
The most diverse molluscan fauna of the section is present in SD 60. *Polymesoda s. subarata*, *Tympanotonos margaritaceus*, *Potamides* sp., and frequently *Granulolabium* cf. *plicatum* as well as *Hydrobia* sp. occur. Recent Potamididae-Hydrobiidae associations are widespread in estuaries, the landward portion of mudflats, and coastal swamps (Kowalke 1998; Bandel and Kowalke 1999). We suggest a corresponding environment for layer SD 60. The slightly higher diversity of the potamidid fauna compared to SD 6 may point to a more structured and ecologically more differentiated coastal swamp environment (cf. Harzhauser and Kowalke 2002). The charophyte flora is only represented by *Chara tornata*, a species which is largely insensitive to changes in salinity (Schwarz 1985, 1988; Reichenbacher and Schwarz 1997). The ostracod fauna consists of *Phlyctenophora grosdidieri*, *Leptocythere* cf. *lacertosa*, *Cytheridea* cf. *bavarica* and *Palmoconcha* cf. *turbida*. Living and fossil species of *Phlyctenophora*, *Cytheridea* and *Palmoconcha* are known to occur in brackish to epi-neritic habitats (van Morkhoven 1963). Clearer evidence for the palaeoenvironment is provided by the extant species *Leptocythere lacertosa*, which has been shown to inhabit mainly estuarine zones (Athersuch *et al.* 1989). Foraminifers also occur in SD 60 and are represented by *Quinqueloculina* sp. and *Ammonia kiliani*. However, owing to their strongly corroded shells we assume that they are not autochthonous. The entire fauna and flora clearly suggest a brackish environment. Moreover, the molluscs and the ostracod *Leptocythere* cf. *lacertosa* point to an estuarine biotope, which also fits well with the fairly dark grey, slightly silty marl lithofacies.

PALAEOCLIMATE

Among the molluscs *Tympanotonos* represents a thermophile, stenotherm element. The fish fauna contains taxa of families that today are mainly distributed in the tropical realm (Eleotridae, Ambassidae) or the Mediterranean area (Cyprinodontidae). These occurrences indicate a warm, at least subtropical climate. Furthermore the molluscan fauna, especially owing to the presence of *Tympanotonos*, is highly reminiscent of Recent faunas from mangrove swamps of the West African coast (Elouard and Rosso 1977; Brown 1980; Bandel and Kowalke 1999). Our data support the assumptions of Barthelt (1989) who postulated a mean annual temperature of around 20°C and mangrove vegetation for the Lower Brackish-Water Molasse of southern Germany.

BIOSTRATIGRAPHY

Opercula of the terrestrial gastropod *Pomatias antiquum*, which we found at the base (layers SD 10 and 12) and at the top (SD 109 and 119) of the Sindelsdorf section are considered to be significant for the Chattian (Zöbelein 1953). According to Zöbelein (1953) the whole of the section studied should correspond to the Chattian. Further biostratigraphical data derives from the investigation of fish otoliths and charophytes, and suggests an age very close to the Rupelian/Chattian boundary (see Text-fig. 3).



1, Riveline (1986, p. 208); 2, Schwarz (1988, p. 179); 3, Feist *et al.* (1994, p. 28); 4, Schwarz (1997, p. 50)

TEXT-FIG. 8. Biostratigraphic ranges of charophyte species.

Biostratigraphy of the Lower Coloured Molasse

The Lower Coloured Molasse of the Sindelsdorf section can be attributed to the otolith zone OT-O2 of the western Paratethys (Reichenbacher 1999) owing to the presence of *Palaeolebias symmetricus*. Zone OT-O2 covers the time interval of the Mammalian Reference Level MP 24 and corresponds to the Late Rupelian and Early Chattian.

The charophyte flora is also biostratigraphically significant. The first occurrences of *R. exigua*, *S. ulmensis* and *N.* (*T.*) *merianii* forma *globula* occur within the *Chara microcera* Zone (Text-fig. 8). In addition, *R. exigua* is restricted to the *Chara microcera* Zone or to the succeeding *Stephanochara ungeri* Zone (cf. Text-fig. 8). *S. ungeri* should be present in the latter zone, but is absent from our material. We suggest that this is because of stratigraphical age (and not due to ecological conditions) because the otolith zonation clearly points to an age corresponding to the *Chara microcera* Zone.

Biostratigraphy of the Lower Cyrena Beds

In the Lower Cyrena Beds of the Sindelsdorf section, the type species of otolith zone OT-O2, *Palaeolebias symmetricus*, is absent. Its absence is probably a result of stratigraphical age rather than ecological conditions, because we found ‘genus Umbridarum’ *crassus* in layer SD 10. This species occurs in European localities of zone OT-O2, often together with *P. symmetricus* (e.g. Reichenbacher and Philippe 1997; Mödden *et al.* 2000). If the Lower Cyrena Beds of the Sindelsdorf section covered zone OT-O2 we would expect *P. symmetricus* at least in SD 10. However, we also cannot recognize the preceding zone OT-O1, which is defined by the first and last occurrence of *Dapalis angustus* (cf. Reichenbacher 1999). Additionally, *D. carinatus* and *D. rhomboidalis* (appearing in SD 12) are so far unknown from zone OT-O1. Consequently, we introduce the new otolith zone OT-O1/2, 'genus Umbridarum' *crassus* Interval Zone herein. Its lower limit is defined by the absence of *Dapalis angustus* and its upper limit by the first occurrence of *Palaeolebias symmetricus*. This zone also probably covers the first occurrences of *D. carinatus* and *D. rhomboidalis*. Zone OT-O1/2 spans a time interval between zones OT-O1 and OT-O2. With regard to the charophyte biostratigraphy of the Sindelsdorf section (see below), zone OT-O1/2 should correspond to the *Chara microcera* Zone and thus can be correlated with the Mammalian Reference Level MP 24.

The charophytes have very low diversity in the Lower Cyrena Beds. However, *N.* (*T.*) *merianii globula*, present in SD 10, indicates an age not older than the *Chara microcera* Zone (cf. Text-fig. 8). It should be noted that it is not clear at present if *S.* aff. *pinguis* has any relationship to *S. pinguis*. To date *S. pinguis* is known only from the *S. pinguis* Zone of the Early Rupelian (cf. Text-fig. 8), and *S.* aff. *pinguis* only from a locality in Spain corresponding to the Mammalian Reference Level MP 23 (Feist *et al.* 1994).

CONCLUSIONS

Our palaeoecological and lithological data from the Lower Cyrena Beds of the Penzberg Syncline suggest the following environments: lagoon (SD 6, ?18), estuary (SD ?38, ?40, 60), slowly flowing river (SD 10) and lakes (SD 12, 44, 46). Swamp habitats are indicated by the presence of coal debris within the Sindelsdorf section (see Text-fig. 3).

Similar connections of marine-brackish and limno-fluvial sediments can be observed in Recent delta plains (cf. Füchtbauer 1988, pp. 891–892; Barthelt 1989, pp. 61–63). A deltaic environment for the Lower Cyrena Beds is especially supported by the molluscan fauna because we have found with *Polymesoda*, *Hydrobia* and *Potamides* gastropods with a planktonic larval development, with a conspicuous yolk-rich embryogenesis and a subsequent short planktotrophic larval stage. Thus we conclude that the larvae found suitable habitats in the very near vicinity (cf. Bandel and Kowalke 1999) and that a highly structured littoral zone with a broad variety of convenient habitats was available.

The Lower Coloured Molasse of the Penzberg Syncline has yielded fish otoliths for the first time. All faunal and floral elements (SD 109, 119) indicate a lacustrine environment. According to Barthelt (1989, pp. 56, 57) and Bachmann and Müller (1991, p. 271) the Lower Coloured Molasse accumulated in an extended meandering river system, building a landward continuation of the delta plain. The biota of the layers SD 109 and 119 most probably derive from stagnant waters of abandoned channels of this river system.

The gastropod *Tympanotonos* and the obviously tropical to subtropical fish fauna (Eleotridae, Ambassidae and Cyprinodontidae) suggest a warm, at least subtropical climate. Furthermore *Tympanotonos* indicates affinities with Recent molluscan faunas of the mangrove swamps of the West African coast, and thus hints at mangrove vegetation bordering the coasts of the Upper Bavarian Molasse Sea.

It was possible to establish a biostratigraphical classification for the Lower Cyrena Beds and for the lowermost part of the Lower Coloured Molasse of the Penzberg Syncline. The whole section covers the *Chara microcera* Zone. We introduced a new otolith zone OT-O1/2 for the Lower Cyrena Beds. We correlated the Lower Coloured Molasse with otolith zone OT-O2, which is known to contain the Mammalian Reference Level MP 24. The absolute age of the Sindelsdorf section is probably between 28·0 and 29·0 Ma (cf. Schmidt-Kittler *et al.* 1997; Reichenbacher 1999). The Lower Cyrena Beds of the Penzberg Syncline are the same age as, or slightly older than the Lower Cyrena Beds of the Murnau Syncline to the south-west (cf. Uhlig *et al.* 2000).

For the first time we report the charophyte *Stephanochara* aff. *pinguis* from a section in the North Alpine Molasse Basin. Its absence from previously described localities of similar age may be due to the rarity of MP 23 and MP 24 localities in Europe. However, it also should be taken into consideration that *S.* aff. *pinguis* differs from *N.* (*T.*) *merianii* forma *globula* mainly because of its basal plate. We cannot preclude that *S.* aff. *pinguis* might have been described as *N.* (*T.*) *merianii* forma *globula* in previous publications.

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