

Early Miocene (Ottangian) Mollusca of the Western Paratethys—ontogenetic strategies and palaeo-environments

Mollusques du Miocène inférieur (Ottangien) de la partie ouest de la Paratéthys—Stratégies ontogénétiques et paléoenvironnements

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Abstract

Early ontogenetic shells of 25 species of brackish water and freshwater molluscs from the Ottangian (Lower Miocene) Oncophora Beds (Lower Bavaria, South Germany) and Kirchberg Formation (Upper Bavaria, South Germany) are described for the first time. Taxonomic implications are discussed. The investigated bivalves (Cardiidae and Dreissenidae) were characterised by an indirect development with inclusion of a planktonic veliger stage. Among the gastropods only three species of the genus *Ctyrokia* Schlickum, 1965 were characterised by veliger larvae, all the other gastropod species were direct developers, which hatched as crawling young. The species *Agapilia schlickumi* nov. sp. (Neritidae), *Nematurella pseudozilchi* nov. sp. and *Nematurella strauchi* nov. sp. (Hydrobiidae) are introduced. Our study revealed the co-occurrence of 10 molluscan species in the Oncophora Basin of Lower Bavaria and the Kirchberg Basin of Upper Bavaria and thus indicates similar oligohaline to mesohaline coastal swamp milieus for both depositional environments. The presence of planktonic larval development in gastropods indicates a connection to the open sea.

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Résumé

Des coquilles juvéniles de 25 espèces de mollusques des eaux saumâtres et lacustres sont décrites pour la première fois des couches à Oncophora de Basse Bavière (Allemagne) et des couches de Kirchberg de Haute Bavière, toutes deux d'âge Ottangien (Miocène inférieur). Les conséquences taxonomiques sont discutées. Les bivalves étudiés (Cardiidae et Dreissenidae) étaient caractérisés par un développement de type indirect, incluant un stade planctonique (larve veligère). Parmi les gastéropodes, seules trois espèces du genre *Ctyrokia* Schlickum, 1965 étaient caractérisées par l'existence de larves veligères. Toutes les autres espèces de gastéropodes avaient un développement direct, les jeunes ayant dès l'éclosion un mode de vie benthique. Les espèces *Agapilia schlickumi* nov. sp. (Neritidae), *Nematurella pseudozilchi* nov. sp. et *Nematurella strauchi* nov. sp. (Hydrobiidae) sont créées. Notre étude confirme l'existence d'un milieu semblable, correspondant à un marécage côtier oligohalin et mésohalin, pendant le dépôt des couches à Oncophora et des couches de Kirchberg qui ont en commun dix espèces de mollusques. La présence de gastéropodes ayant un développement larvaire planctonique indique une connexion avec la mer ouverte.

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Keywords: Mollusca; Early ontogenetic shells; Ottangian; Western Paratethys; Brackish water

Mots clés : Mollusques ; Coquilles juvéniles ; Ottangien ; Paratéthys ouest ; Eaux saumâtres

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1. Introduction

The deposition of brackish water sediments during the Late Otnangian (Early Miocene) of the Western Paratethys resulted from the regression of the Molasse Sea, which had covered an area from Switzerland in the West to Austria and the Czech Republic in the East since the Late Eggenburgian (Upper Marine Molasse). The Late Otnangian regression initiated the development of shallow brackish basins with a corresponding sedimentation, the Upper Brackish Molasse (Čtyroký et al., 1973; Rögl, 1998). In the Molasse Basins of Southern Germany and Upper Austria, which are part of the Western Paratethys, two regional basins and deposits characterised by a predominantly endemic brackish mollusc fauna are well known: In the east the Oncophora Basin of Lower Bavaria with the Oncophora Beds, and in the west the Kirchberg Basin of Upper Bavaria with the Kirchberg Formation (Fig. 1).

Rzehak (1882) originally defined the Oncophora Beds as a brackish sequence in South Moravia, characterised by the abundant brackish bivalve “*Oncophora*” (= *Rzehakia*). Suess (1891) and most of the following authors used the term Oncophora Beds for Late Otnangian series in Lower Bavaria and Upper Austria with a similar brackish mollusc fauna. The Oncophora Beds comprise 40–60 m sediment in Lower Bavaria and 15–25 m in Upper Austria. For Bavaria the Oncophora Beds are divided into seven units based on lithological and palaeontological data (Wittmann, 1957; Schlickum, 1964; Schlickum and Strauch, 1968; Reichenbacher, 1993): Mehlsande, which have been deposited in deeper waters, and the diachroneous shallow water units Schillhorizont, Glimmersande, Aussüßungshorizont, Schillsande, Uniosande and Lakustrische Schichten. In Austria the Oncophora Beds are reduced, represented by the occurrence of Mehlsande (Reichenbacher, 1993).

A lithologic and biostratigraphic subdivision of the Kirchberg Formation at the type-locality Illerkirchberg near Ulm has been given by Kranz (1904, 1905), and was substantially confirmed by Schlickum (1963), who presented a comprehensive work mainly on the molluscs (1960–1971). Based on mollusc-, ostracod-, charophyte- and fish-assemblages, Reichenbacher (1988, 1989); Schwarz and Reichenbacher (1989) and Reichenbacher and Schwarz (1990) presented detailed palaeoecological and biostratigraphical analyses of the Kirchberg Formation at and near the type-locality Illerkirchberg near Ulm. The Kirchberg Formation comprises up to 25 m and is divided into eight units (horizons 1–8, from basis to top), which names reflect their most prominent fossil assemblages. Horizon 1 is divided in the southern Flusssand-1-Horizon and the northern Viviparen-Horizon. Horizon 2 comprises the Spariden-Horizon, which is only locally present, and the (overlying) Congerien-Horizon. Horizon 3 can be distinguished into a lower part (*Clupeonella humilis*-Horizon) and an upper part (*Dapalis curvirostris*-Horizon). The *Unio*-/*Anodonta*-Horizon and the Bithynien-/*Stephanochara ungeri*-Horizon are Horizons 4 and 5, and the Bithynien-/*Gobius multipinnatus*-/*Dapalis crassirostris*-Horizon and the Flusssand-2-Horizon present Horizons 6 and 7. The uppermost Horizon 8 is the *Aphanius*-Gobiiden-Horizon.

Schlickum and Strauch (1968); Büchi and Schlanke (1977); Lemcke (1984, 1988); Zöbelein (1985); Doppler (1989); Reichenbacher (1993) and Reichenbacher et al. (1998) have discussed the palaeogeographic relations between the Oncophora Basin of Lower Bavaria and the Kirchberg Basin of Upper Bavaria (Fig. 1). In the course of the latest Otnangian/earliest Karpatian major freshwater influx led to a lacustrine environment and to the end of the Upper Brackish Molasse. The overlying deposits belong to the Upper Freshwater Molasse.

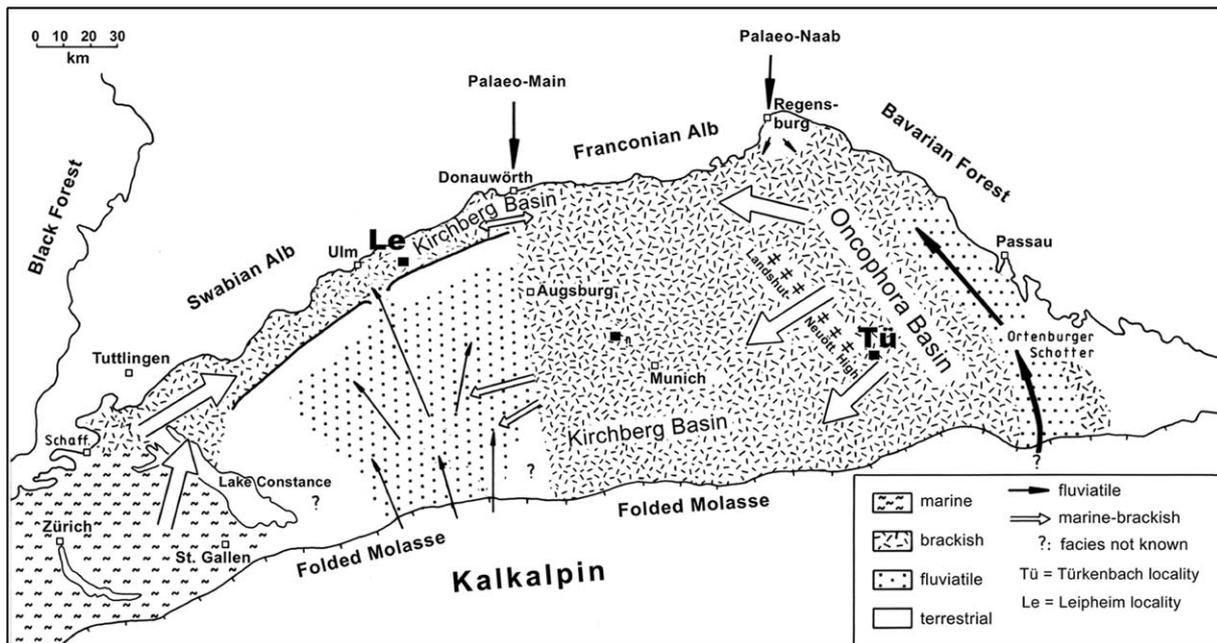


Fig. 1. Geographic situation and Late Otnangian palaeogeography in the Western Paratethys. After Reichenbacher (1993), modified.

Fig. 1. Situation géographique et paléogéographie à l'Otnangien terminal de la partie ouest de la Paratéthys. D'après Reichenbacher (1993), modifié.

The mollusc faunas of both the Oncophora Beds and the Kirchberg Formation were up to now only known with regard to the dissoconch and teleoconch morphologies. They are described herein for the first time with special reference to their prodissoconchs and protoconchs. An interpretation of the modes of early ontogenetic development of the taxa is presented, and systematic and ecological inferences are discussed.

2. Materials and methods

The studied molluscs comprise specimens, which were collected by one of us (B.R.) in the years 1984–1992, and further specimens, which are kept in the Bavarian State Collection (BSP). Additional material for comparison (types of the collection Schlickum, Senckenberg-Museum Frankfurt, SMF) was investigated. Our material from the Kirchberg Formation derives from the type-locality Illerkirchberg (near Ulm) and from an outcrop near Leipheim (Fig. 1). The molluscs from the Oncophora Beds mainly come from the outcrop of the Türkenbach River, near Marktl (Fig. 1). Detailed information concerning all mentioned localities is given in Reichenbacher (1989, 1993). Figured specimens are deposited in the Bavarian State Collection Munich (BSP 2003 II 1–38).

Molluscan shells of all ontogenetic stages have been extracted from clayey and marly sediments after processing with H₂O₂, drying and fractionating by sieves. Micromorph molluscs with preserved protoconchs have been mounted on stubs, sputtered with gold and have been investigated with the aid of scanning electron microscopy (digital scan “Leo”).

The investigated bivalves were characterised by an indirect mode of early ontogeny—for terminology and measurements of bivalve prodissoconchs see also Malchus (1985). The prodissoconchs consist of an embryonic shell (prodissoconch I) and a larval shell (prodissoconch II). Embryonic and larval shell are separated by a more or less prominent thickened rim on the shell and they furthermore can be differentiated by sculptural pattern. The maximum diameter of prodissoconch I, the length of the straight hinge of the hatched veliger (D-line), the maximum diameter and the height of the prodissoconch are measured (Table 1). The prodissoconch is terminated by a thickened rim on the shell and the onset of the dissoconch is usually indicated by the formation of a regular adult sculpture.

The investigated gastropods were characterised by two modes of early ontogenetic development—for terminology

and measurements of gastropod protoconchs see also Kowalke (1998): (1) Indirect mode with an embryogenesis reflected by a small embryonic shell measuring less than 0.15 mm in maximum diameter and less than 0.05 mm in the width of the initial cap. In this case a subsequent more or less extended larval stage was present, during which the larva was free swimming and feeding on phytoplankton. During this larval stage a shell has been secreted, which could be distinguished from the embryonic shell and which is terminated by a sinuous rim or sinusigera notch. This is reflected by a thickened apertural rim of a pediveliger, which was ready for metamorphosis. (2) Direct development without additional larval stage. In this case a large and bulbous embryonic shell is present, which usually measures more than 0.15 mm in maximum diameter and more than 0.05 mm in the width of the initial cap (Table 2).

3. Systematic palaeontology

Class Bivalvia Linnaeus, 1758

Superfamily Cardioidea Lamarck, 1809

Family Cardiidae Lamarck, 1809

Remarks: According to a recent comprehensive cladistic analysis of cardiid bivalves by Schneider (1998a, 1998b) the family Cardiidae comprises the subfamilies Clinocardiinae, Fragininae, Tridacninae and Lymnocardiinae that were confirmed to be a monophyletic group based on anatomical and shell characters.

Subfamily Lymnocardiinae Stoliczka, 1871

Remarks: Lymnocardiinae are known as fossils since the Early Oligocene. The subfamily includes 73 genera (Neveškaja et al., 2001), most of which became extinct, except for four Recent genera (see e.g. Keen, 1969; Vokes, 1980; Basch, 1990; Schneider, 1998a, 1998b). The Recent representatives settle shallow marine and brackish-marine to oligohaline habitats. Relic faunas of the diverse Paratethyan lineage characterise the delta portion of large rivers, like Danube, Don and Wolga, flowing into the Black Sea and the Caspian Sea (Gillet, 1946; Stanley, 1979).

Genus *Limnopagatia* Schlickum, 1963.

Type-species: *Cardium friabile* Krauss, 1852 from the Ottnangian of the Kirchberg Formation.

Diagnosis: *Limnopagatia* species measure 10–25 mm in length and up to 21 mm in height. The valves appear oval to subangular-shaped. Sculpture of the adult valve consists of 24–32 ribs. The small narrow hinge is slightly bent. It com-

Table 1

Prodissoconch (P) dimensions of the bivalves studied herein (in mm)

Dimensions des coquilles juvéniles (P) des bivalves étudiés (en mm)

	PI (d)	D-line (l)	P II (d)	P II (h)
<i>L. schmieri</i> Schlickum, 1964	0.09	0.05	0.2	0.08–0.09
<i>L. schuetti</i> Schlickum, 1962	0.08	0.06	0.22	0.1–0.11
<i>M. amygdaloides</i> (Dunker, 1848)	0.08	0.05	0.21	0.07–0.08
<i>Mytilopsis clavaeformis</i> (Krauss, 1852)	0.09–0.1	0.06	0.2–0.24	0.07–0.08
<i>Mytilopsis rottensis</i> (Ammon, 1888)	0.13–0.14	0.08	0.21–0.22	0.08

Table 2

Protoconch dimensions of the gastropods studied herein (in mm)
 Dimensions des coquilles juvéniles des gastéropodes étudiés (en mm)

	Protoconch-whorls	Protoconch diameter	First whorl(d)	Initial cap(w)
<i>A. schlickumi</i> nov. sp.	1.25	0.45	0.4	0.1
<i>T. cyrtocelis</i> (Krauss, 1852)	1.2–1.3	0.47–0.5	0.38–0.42	0.13–0.16
<i>H. frauenfeldi</i> (Hoernes, 1856)	1.25–1.3	0.34	0.29	0.08
<i>Hydrobia</i> cf. <i>semiconvexa</i> Sandberger, 1874	1.5	0.34	0.26	0.04
<i>C. hoelzli</i> (Schlickum, 1964)	1.8–1.9	0.23–0.25	0.13–0.14	0.02–0.03
<i>C. ammoni</i> Schlickum, 1965	2.5	0.33	0.13	0.02
<i>C. conoidea</i> (Krauss, 1852)	2.5	0.32	0.12–0.13	0.02–0.03
<i>C. zoebelini</i> Schlickum, 1970a	1–1.1	0.29–0.31	0.26–0.28	0.06–0.07
<i>N. bavarica</i> (Sandberger, 1874)	1.25–1.3	0.32–0.35	0.25–0.27	0.07–0.08
<i>N. convexula</i> Schlickum and Strauch, 1967	1.25–1.4	0.32–0.34	0.25–0.28	0.04
<i>N. klemmi</i> Schlickum, 1964	1	0.2	0.2	0.05–0.06
<i>N. pappi</i> Schlickum, 1960	1.25	0.29–0.3	0.24–0.25	0.06–0.07
<i>N. pseudozilchi</i> sp. n.	1.2	0.27–0.28	0.22–0.23	0.05–0.06
<i>N. strauschi</i> sp. n.	1.25	0.36	0.27	0.07
<i>N. zilchi</i> Schlickum, 1960	1.2–1.25	0.3–0.33	0.25–0.27	0.07–0.08
<i>Bithynia</i> cf. <i>glabra</i> (Zieten, 1830)	1.25	0.38	0.31–0.32	0.1
<i>M. impressa impressa</i> Krauss, 1852	1.5	0.26	0.23	0.08
<i>L. dilatata</i> (Noulet, 1854)	1	0.6	0.6	0.2
<i>S. armaniacensis</i> (Noulet, 1857)	1	0.54	0.54	0.18
<i>S. praebouiletti</i> (Schlickum, 1970a)	1	0.4	0.4	0.11–0.12
<i>G. applanatus</i> (Thomae, 1845)	1	0.18	0.18	0.05
<i>F. wittmanni</i> (Schlickum, 1964)	/	0.49–0.5	/	/

prises two cardinal teeth in each valve. The anterior tooth of the right valve and the posterior tooth of the left valve are reduced. In the right valve, one lamella-shaped posterior lateral tooth, which converges to the umbo is present, but the dorsal margin is functioning as a second (upper) posterior lateral tooth. Furthermore, the right valve has one or two anterior lateral teeth, a short lower one and a weakly developed or reduced upper one. The left valve bears one lamella-shaped anterior tooth. Only in *L. friabilis* also a long posterior lateral tooth is present, but in other species only a short thickened rim of the dorsal margin is functioning as a posterior lateral tooth (for more details cf. Schlickum, 1963).

Remarks: *Limnopagetia* can be distinguished from *Cerastoderma* due to its reduced hinge and the two-layered shell (Neveškaja et al., 2001). Right valves can easily be recognised as *Limnopagetia* by their dorsal margin functioning as a posterior upper lateral tooth. *Limnopappia* differs from *Limnopagetia* by its more reduced hinge.

Limnopagetia schmieri Schlickum, 1964.

Fig. 2(1–4).

1964. *L. schmieri* nov. sp. - Schlickum, p. 28–29, Pl. 4, Figs. 68 and 69.

1967. *L. schmieri* Schlickum - Schlickum, Figs. 5–10.

1971. *L. schmieri* Schlickum - Schlickum, Pl. 3, Fig. 40.

1973. *L. schmieri* Schlickum - Steininger et al., p. 511–512, Pl. 24, Fig. 7.

Material: Oncophora Beds, Glimmersande: Hitzenau near Wimbach (three paratypes, BSP 1964 I 14); Rott (five specimens, BSP 1964 XXVIII 148, 1980 XXIX 14); Aussüssungshorizont: Türkenbach (75 juvenile specimens ex coll. Reichenbacher, BSP II 39, and the figured specimen BSP 2003 II 1).

Description: Rounded-subtriangular-shaped, up to 14 mm length and 13 mm height, shell slightly domed and moderately thick, slightly inequilateral (posterior margin longer), juveniles strongly inequilateral; about 32 flattened scaly ribs with narrow or very narrow spaces between them, juveniles with keel in the posterior portion of the valve.

The prodissoconch measures 0.2 mm in maximum diameter and 0.08–0.09 mm in height. Prodissoconch I measures 0.09 mm in maximum diameter and 0.05 mm in the length of the straight hinge of the hatched veliger (D-line). The folded surface is characterised by a fine groove–ridge pattern. Prodissoconch I is terminated by a prominent swelling, followed by a slight depression. The onset of the larval shell is indicated by the formation of regular growth lines. Prodissoconch II is terminated by a thickened rim of the shell. The onset of the adult shell is indicated by the formation of closely spaced growth lines and ribs.

Remarks: The similar species *L. modelli* differs from *L. schmieri* due to its equilateral and more rounded-shaped valves, the broader umbo and the better rounded ribs. *L. modelli* is known from the Schillhorizont, Glimmersande, Schill-sande, Uniosande and Lakustrische Schichten of the Oncophora Beds, whereas in the Aussüssungshorizont mainly *L. schmieri* is present. Schlickum (1964) supposed that *L. modelli* had evolved from *L. schmieri*, due to the more reduced hinge of *L. modelli*. The type-species is distinguished by its rounded quadrangular shell, which is characterised by fewer ribs.

Neveškaja et al. (2001) assigned *L. schmieri* and *L. modelli* to the genus *Cerastoderma* Poli, 1795, which is not confirmed by our investigations. The reduced hinge and the two-layered shell, the formation of scales representing remnants

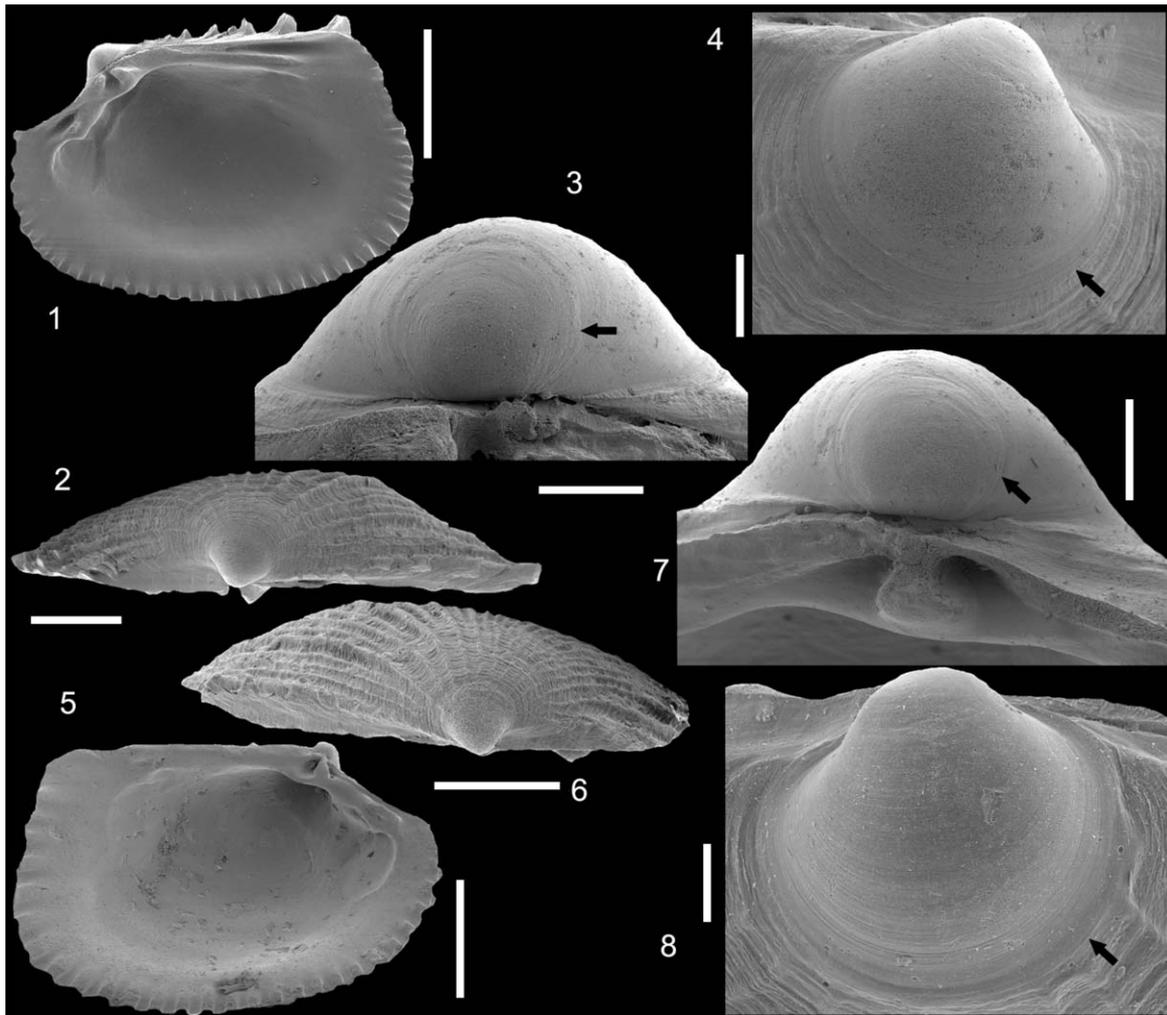


Fig. 2. Lymnocaridinae Stoliczka, 1871. 1–4. *L. schmiereri* Schlickum, 1964. 1, 2, specimen BSP 2003 II 1, Aussüßungshorizont of Türkenbach (Oncophora Beds). 3, prodissoconch of the same specimen, with detailed view of prodissoconch I; the arrow is indicating the transition from prodissoconch I to prodissoconch II. 4, prodissoconch of the same specimen; the arrow is indicating the transition from the prodissoconch to the adult shell. 5–8. *L. schuetti* Schlickum, 1962. 5, 6, specimen BSP 2003 II 2, Aussüßungshorizont of Türkenbach. 7, 8, prodissoconch of specimen BSP 2003 II 3, Aussüßungshorizont of Türkenbach. 7, the arrow is indicating the transition from prodissoconch I to prodissoconch II. 8, the arrow is indicating the transition from the prodissoconch to the adult shell. Scale bars: 1, 5, 6 = 0.5 mm; 2 = 0.2 mm; 3, 4, 7, 8 = 0.05 mm.

Fig. 2. Lymnocaridinae Stoliczka, 1871. 1–4. *L. schmiereri* Schlickum, 1964. 1, 2, spécimen BSP 2003 II 1, Aussüßungshorizont de Türkenbach (Oncophora Beds). 3, prodissoconque du même spécimen, avec une vue détaillée de la prodissoconque I; la flèche montre la transition entre la prodissoconque I et la prodissoconque II. 4, prodissoconque du même spécimen; la flèche montre la transition entre la prodissoconque I et la coquille adulte. 5–8. *L. schuetti* Schlickum, 1962. 5, 6, spécimen BSP 2003 II 2, Aussüßungshorizont de Türkenbach. 7, 8, prodissoconque du spécimen BSP 2003 II 3, Aussüßungshorizont de Türkenbach. 7, la flèche montre la transition entre la prodissoconque I et la prodissoconque II. 8, la flèche montre la transition entre la prodissoconque I et la coquille adulte. Barres d'échelle : 1, 5, 6 = 0.5 mm ; 2 = 0,2 mm ; 3, 4, 7, 8 = 0,05 mm.

of the reduced third layer, as well as the general outline of the shell clearly indicate an affiliation to *Limnopageta*.

Genus *Limnopappia* Schlickum, 1962.

Type-species: *Limnopappia schuetti* Schlickum, 1962 from the Ottnangian of the Kirchberg Formation.

Diagnosis: Valves oval-shaped, up to 15 mm length and up to 12 mm height; slightly domed; shell moderately thick; umbo very small and hardly emerging; 32–35 ribs. Hinge delicate and more or less elongated, each valve has only one cardinal tooth (which may be reduced in adult specimens) and one (lower) posterior lateral tooth, lamella-shaped. The right valve has two anterior lateral teeth converging to the umbo, the lower one stronger developed than the upper one. The left

valve is characterised by only one lamella-shaped anterior lateral tooth (see also Schlickum, 1962).

Remarks: According to Schlickum (1962) the morphology of the hinge closely resembles that of *Cerastoderma*. Thus Schlickum (1962) assumed that *Limnopappia* evolved from *Cerastoderma* after reduction of the hinge. In fact, the differences between *Cerastoderma* and *Limnopappia* are very clear, as the valves of *Limnopappia* are less domed, their umbo is smaller and hardly emerging, and their hinge is reduced. *Limnopappia* differs from *Limnopageta* by its smaller size, and the presence of only one (or no) cardinal tooth (instead of two in *Limnopageta*). Right valves of *Limnopappia* can easily be distinguished from *Limnopageta* due to their slightly

better developed upper anterior lateral teeth. Furthermore, right valves of *Limnopappia* do not reveal a dorsal margin functioning as an upper posterior lateral tooth as in *Limnopageta*.

Limnopappia schuetti Schlickum, 1962

Fig. 2(5–8).

?1888. *Cardium kraussi* Mayer - Ammon, p. 11, Figs. 8–10.

1962. *L. schuetti* nov. sp. - Schlickum, p. 110–112, Figs. 1 and 2.

1962. *Limnopappia kuiperi* nov. sp. - Schlickum, p. 112–113, Fig. 3.

1964. *Limnopappia kuiperi kuiperi* Schlickum - Schlickum, p. 31–32, Pl. 5, Fig. 72.

1964. *Limnopageta kuiperi sauerzopfi* nov. ssp. - Schlickum, 32, Pl. 5, Figs. 73 and 74.

1970b. *L. schuetti* Schlickum - Schlickum, p. 154–155, Pl. 10, Fig. 17.

1973. *L. schuetti* Schlickum - Steininger et al., p. 515, Pl. 24, Fig. 4a–c.

1989. *L. schuetti* Schlickum - Reichenbacher, Pl. 2, Figs. 10 and 11.

Material: Kirchberg Formation, Viviparen-Horizon: Unterkirchberg (holotype, collection Schlickum M 1200, SMF). Oncophora Beds, Aussüssungshorizont: Türkenbach (30 specimens ex coll. Reichenbacher, BSP 2003 II 40, and the figured specimens BSP 2003 II 2–3).

Description: The small thin shell measures up to 10 mm in the length and up to 8 mm in width. The only moderately bent shell has rounded rectangular shape. The small umbo is slightly emerging. Sculpture of the dissoconch consists of 32 slightly bent roundish ribs with broad gaps. The ribs may be elongated to very short spines. The delicate elongated hinge is characterised by a reduction of the second cardinal tooth in adult specimens, whereas it is present in juveniles.

The prodissoconch measures 0.22–0.23 mm in maximum diameter and 0.1–0.11 mm in height. Prodissoconch I measures 0.08 mm in maximum diameter and 0.06 mm in the length of the D-line. Ornament of the embryonic shell is not preserved. Prodissoconch I is terminated by a swelling and a subsequent slight depression in the shell. The onset of prodissoconch II is indicated by the formation of growth lines. The prodissoconch is terminated by a thickened rim of the shell. The onset of the dissoconch is indicated by the formation of the regular adult sculpture of closely spaced growth lines and ribs.

Remarks: *L. schuetti* Schlickum, 1962, which according to Schlickum (1962) is restricted to the Viviparen-Horizon of Unterkirchberg (Kirchberg Formation), was scarcely distinguished from *L. kuiperi* by its slightly larger size and by its more elongated suboval shape. Comparative analysis of the holotype of *L. schuetti* and specimens of *L. kuiperi* from the Aussüssungshorizont of Türkenbach exhibited few differences: The cardinal tooth of the holotype is slightly weaker developed; however this feature differs even during the onto-

genetic development of a single specimen. The slightly elongated shape is also present in specimens of *L. kuiperi* from the Aussüssungshorizont of Türkenbach. Specimens from Türkenbach are characterised by slightly more bent shells. The minor differences most probably indicate that *L. kuiperi* represents a synonym of *L. schuetti*.

“*Cardium kraussi*” from the Oncophora Beds as described by Ammon (1888) probably corresponds to *L. schuetti*. In this case the species name “*kraussi*” would gain priority. We have not seen the original material of Ammon and a definite assignment is hardly possible on the basis of comparison with the figures in Ammon (Figs. 8–10). Schlickum (1964: 31) had attributed “*C. kraussi*” to his subspecies *L. kuiperi sauerzopfi*. Schlickum (1964) introduced the subspecies *L. k. sauerzopfi* Schlickum, 1964 comprising morphs with slightly emerging umbo. We do not follow this separation of a subspecies, because it is not possible to distinguish the morphs with stronger emerging umbo, connected to those with only scarcely emerging umbo by intermediate morphs (cf. discussion in Reichenbacher, 1993).

The prodissoconch of *L. schuetti* from the Aussüssungshorizont of Türkenbach differs from that of *Limnopageta modelli* by a smaller embryonic shell and by its larger larval shell, which documented a less yolk rich embryogenesis and a subsequent longer stay within the plankton.

Superfamily Dreissenoidae Gray in Turton, 1840

Family Dreissenidae Gray in Turton, 1840

Subfamily Dreisseninae Gray in Turton, 1840

Remarks: According to a revision of Nuttall (1990) the Dreisseninae comprise the genera *Dreissena* van Beneden, 1835 (including three subgenera), *Congeria* Partsch, 1835, *Mytilopsis* Conrad, 1858 and probably also *Prodreissena* Rovereto, 1898. The infaunal *Dreissenomya* Fuchs, 1870 with two subgenera is placed within an own subfamily Dreissenomyinae. *Mytilopsis* first occurred in the European Eocene and its Recent distribution naturally comprises the Western Hemisphere, but it has been introduced to Asia by man (Nuttall, 1990). *Dreissena*, *Congeria* and *Dreissenomya* first occurred in the Late Miocene of the Paratethys. The latter two genera became extinct during the Late Miocene and Pliocene while *Dreissena* is still present as an exclusively freshwater dweller. *Dreissena* and *Congeria*, which many of the paratethyan species of *Mytilopsis* have been assigned to, can easily be distinguished from *Mytilopsis*. *Dreissena* with similar shape of the shell differs by the lack of a characteristic apophysis beneath or below the septum. *Congeria* with apophysis fused to the septum furthermore differs by its large quadrate to rhomboidal thick shell.

Genus *Mytilopsis* Conrad, 1858.

Type-species: The recent species *Mytilus leucophaetus* Conrad, 1831 from the eastern USA.

Mytilopsis amygdaloides (Dunker, 1848).

Fig. 3(5–7).

1848. *Congeria amygdaloides* nov. sp. - Dunker, p. 162, Pl. 21, Figs. 8 and 9.

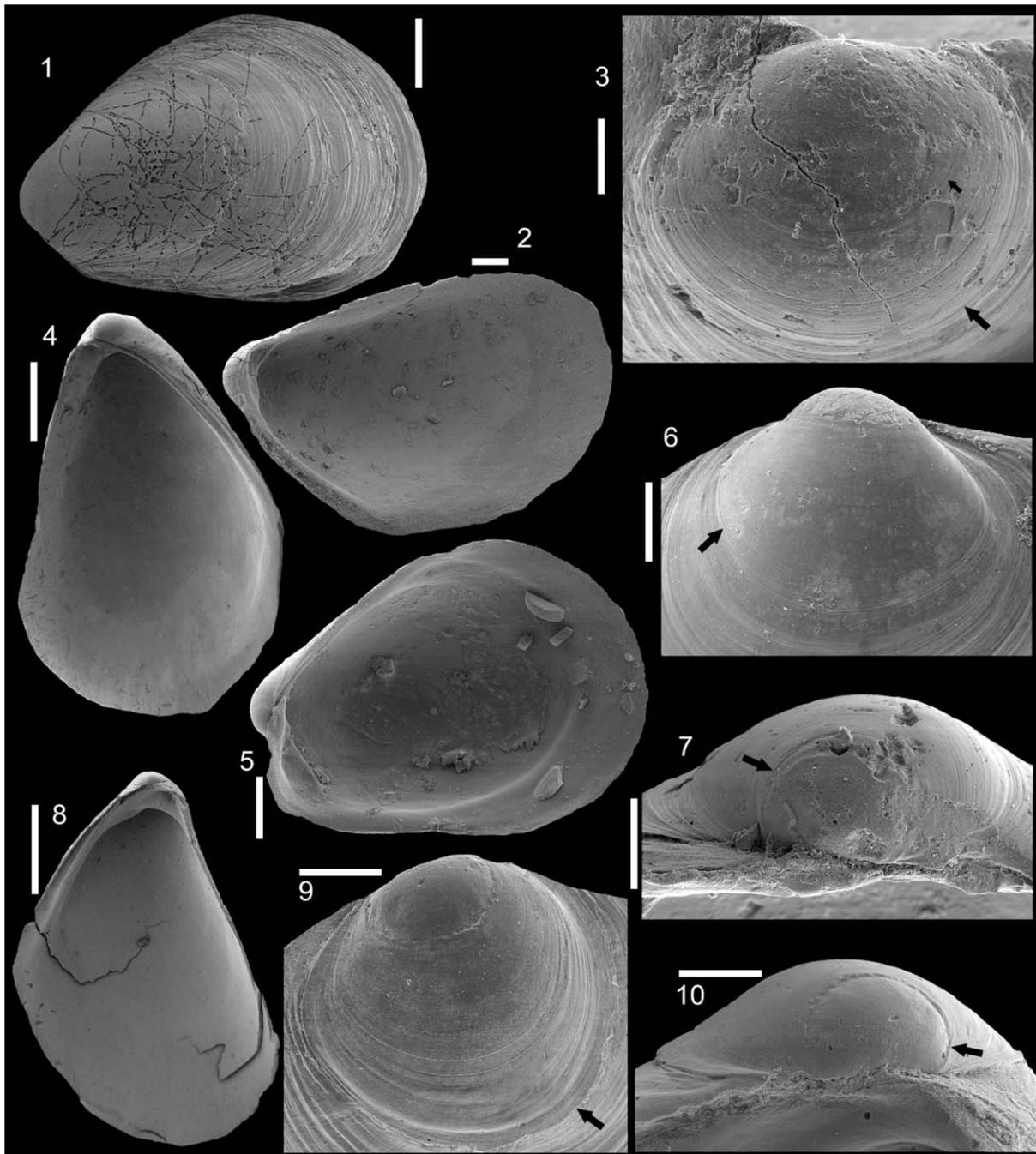


Fig. 3. *Mytilopsis* Conrad, 1858. 1–4. *Mytilopsis rottensis* (Ammon, 1888). 1, 2, specimen BSP 2003 II 4, Congerien-Horizon of Leipheim (Kirchberg Formation). 3, same specimen; detailed view of the prodissococonch; the transition from prodissococonch I to prodissococonch II is marked by a small arrow, and the larger arrow is indicating the transition from the prodissococonch to the adult shell. 4, specimen BSP 2003 II 5, Aussüßungshorizont of Türkenbach (Oncophora Beds). 5–7. *M. amygdaloides* (Dunker, 1848). 5, specimen BSP 2003 II 6, Congerien-Horizon of Leipheim. 6, same specimen, prodissococonch; the arrow is indicating the transition from the prodissococonch to the adult shell. 7, prodissococonch of specimen BSP 2003 II 7, from Leipheim with detail of prodissococonch I; the arrow is indicating the transition from prodissococonch I to prodissococonch II. 8–10. *Mytilopsis clavaeformis* (Krauss, 1852). 8, specimen BSP 2003 II 8, Congerien-Horizon of Leipheim. 9, the arrow is indicating the transition from the prodissococonch to the adult shell. 10, the arrow is indicating the transition from prodissococonch I to prodissococonch II. Scale bars: 4, 8 = 0.5 mm; 1, 2, 5 = 0.2 mm; 3, 6, 7, 9, 10 = 0.05 mm.

Fig. 3. *Mytilopsis* Conrad, 1858. 1–4. *Mytilopsis rottensis* (Ammon, 1888). 1, 2, spécimen BSP 2003 II 4, Congerien-Horizon de Leipheim (Kirchberg Formation). 3, le même spécimen ; vue détaillée de la prodissococonque ; la transition entre la prodissococonque I et la prodissococonque II est indiquée par la petite flèche, et la grande flèche indique la transition entre la prodissococonque et la coquille adulte. 4, spécimen BSP 2003 II 5, Aussüßungshorizont de Türkenbach (Oncophora Beds). 5–7. *M. amygdaloides* (Dunker, 1848). 5, spécimen BSP 2003 II 6, Congerien-Horizon de Leipheim. 6, le même spécimen, prodissococonque ; la flèche indique la transition entre la prodissococonque et la coquille adulte. 7, prodissococonque du spécimen BSP 2003 II 7, de Leipheim avec détail de la prodissococonque I ; la flèche indique la transition entre la prodissococonque I et la prodissococonque II. 8–10. *Mytilopsis clavaeformis* (Krauss, 1852). 8, spécimen BSP 2003 II 8, Congerien-Horizon de Leipheim. 9, la flèche indique la transition entre la prodissococonque et la coquille adulte. 10, la flèche indique la transition entre la prodissococonque I et la prodissococonque II. Barres d'échelle : 4, 8 = 0,5 mm ; 1, 2, 5 = 0,2 mm ; 3, 6, 7, 9, 10 = 0,05 mm.

1852. *Dreissena amygdaloides* (Dunker) - Krauss, p. 145–146.

1966. *C. amygdaloides* Dunker - Schlickum, p. 328, Pl. 13, Figs. 32–37.

1970a. *C. amygdaloides* Dunker - Schlickum, p. 151–152, Pl. 10, Fig. 11.

1970b. *C. amygdaloides* Dunker - Schlickum, p. 181, Pl. 3, Figs. 15 and 16.

1971. *C. amygdaloides* Dunker - Schlickum, Pl. 2, Figs. 15 and 16.

1973. *C. amygdaloides* Dunker - Steininger et al., p. 525, Pl. 27, Fig. 2.

1989. *C. amygdaloides* Dunker - Reichenbacher, Pl. 1, Fig. 15.

1990. *M. amygdaloides* (Dunker) - Nuttall, Pl. 5, Figs. 11–13.

Material: Kirchberg Formation, Congerien-Horizon: Leipheim (29 specimens ex coll. Reichenbacher, BSP II 41, and the figured specimens BSP 2003 II 6–7; 22 specimens ex coll. Schlickum, BSP 1964 XXVIII 149; five specimens, BSP 1979 XXVI 19–23); Oberkirchberg (67 specimens, BSP 1955 XXIX 17, BSP 1965 IX 4).

Description: The medium sized valve has oval almond shape. It is characterised by distinct growth lines. A weak subsided apophysis beneath the septum is present. The stout umbo is curving only slightly prosogy. Some individuals are characterised by a colour pattern of thick brown bands on white ground.

The prodissoconch measures 0.21 mm in maximum diameter and 0.07–0.08 mm in height. Prodissoconch I measures 0.08 mm in maximum diameter and 0.05 mm in the length of the D-line. Prodissoconch I is terminated by a thickened rim on the shell. The onset of prodissoconch II is indicated by a slight groove and by the formation of dense growth lines. The prodissoconch is terminated by a slight groove in the shell and by a thickened rim. The groove is accompanied by indistinct short ribs. The early dissoconch bears strong concentric folds.

Mytilopsis clavaeformis (Krauss, 1852).

Fig. 3(8–10).

1852. *Dreissena clavaeformis* nov. sp. - Krauss, p. 146–149, Pl. 3, Fig. 4.

1966. *Congeria clavaeformis* Krauss - Schlickum, p. 327, Pl. 13, Figs. 30 and 31.

1970a. *C. clavaeformis* Krauss - Schlickum, p. 150–151, Pl. 10, Fig. 10.

1971. *C. clavaeformis* Krauss - Schlickum, Pl. 2, Fig. 14.

1973. *C. clavaeformis* - Steininger et al., p. 526–527, Pl. 27, Fig. 4.

1989. *C. clavaeformis* Krauss - Reichenbacher, Pl. 1, Fig. 14.

Material: Kirchberg Formation, Congerien-Horizon: Leipheim (19 specimens ex coll. Reichenbacher, BSP II 42, and the figured specimen BSP 2003 II 8; 11 specimens ex coll. Schlickum, BSP 1964 XXVIII 150; 38 specimens, BSP

1979 XXVI 24); Oberkirchberg (26 specimens, BSP 1955 XXIX 18). Oncophora Beds, Schillsande: Türkenbach (44 specimens ex coll. Reichenbacher, BSP II 43); Aussüßungshorizont: Türkenbach (125 specimens ex coll. Reichenbacher, BSP II 44).

Description: The considerably large valve measures up to 30 mm in length and up to 13 mm in width. The lower margin of the valve is curving concave in the anterior portion, the posterior portion is domed. It is characterised by a colour pattern of brown radial stripes that may be curving zigzag in shape. The acute umbo is bent slightly prosogy. The shell lacks a sharp keel. A weak apophysis beneath the septum is present.

The prodissoconch measures 0.23–0.24 mm in maximum diameter and 0.07–0.08 mm in height. Prodissoconch I measures 0.09–0.1 mm in maximum diameter and 0.06 mm in the length of the D-line. It is ornamented by a groove–ridge pattern and it is terminated by a slight groove in the shell. The onset of prodissoconch II is indicated by the formation of closely spaced growth lines. The prodissoconch is terminated by a slight groove in the shell and by accompanying sculpture of densely arranged short axial ribs measuring about 0.02–0.03 mm in length. The early dissoconch is characterised by the formation of strong concentric folds.

Remarks: *M. clavaeformis* differs from *M. amygdaloides* by its more angular shape, the thin valve, the slightly smaller prodissoconch I and by its larger prodissoconch II, which reflects a longer stay within the plankton. It differs from *M. rottensis* with similar dissoconch by its less slender outline with less pointed umbilical region and by lacking a sharp keel, the considerably smaller prodissoconch I but slightly larger prodissoconch II.

Mytilopsis rottensis (Ammon, 1888).

Fig. 3(1–4).

1888. *Dreissena amygdaloides* var. *Rottensis* - Ammon, p. 12–13, Figs. 17 and 18.

1888. *D. amygdaloides* Dunker - Ammon, p. 12, Fig. 16.

1888. *Dreissena sub-Basteroti* nov. sp. - Ammon, p. 13–14, Figs. 19–21.

1964. *Congeria rottensis* (Ammon) - Schlickum, 25, Pl. 4, Figs. 56–65.

1964. *Congeria schuetti* nov. sp. - Schlickum, p. 24–25, Pl. 4, Fig. 55.

1973. *C. rottensis* (Ammon) - Steininger et al., p. 525–526, Pl. 27, Fig. 3.

Material: Kirchberg Formation, Congerien-Horizon: Leipheim (56 specimens ex coll. Reichenbacher, BSP 2003 II 45, and the figured specimen BSP 2003 II 4). Oncophora Beds, Schillsande: Türkenbach (two specimens ex coll. Reichenbacher, BSP 2003 II 46); Eitzenham (12 specimens ex coll. Schlickum, BSP 1964 XXVIII 151); Entholz (62 specimens ex coll. Schlickum, BSP 1964 XXVIII 152); Aussüßungshorizont: Türkenbach (seven specimens ex coll. Reichenbacher, BSP 2003 II 47, and the figured specimen BSP 2003 II 5); Stadel Rott (150 specimens, BSP 1980 XXIX

21). Additionally, the holotype of *M. schuetti*, collection Schlickum M 1123 (SMF), from the Schillsande was investigated.

Description: The medium sized moderately thin valve measures up to about 20 mm in length and up to about 10 mm in width. It has an elongated elliptical shape with a pointed anterior portion. The anterior margin is curving slightly convex. Some individuals are characterised by a keel near the anterior margin of the shell, with a very steep inclination to the anterior margin. The acute umbo is curving more or less spirogyr. Sculpture consists of fine growth lines. A colour pattern of irregular brown wavy stripes may be present. A distinct apophysis is present beneath the septum.

The prodissoconch measures 0.21–0.22 mm in maximum diameter and 0.08 mm in height. Prodissoconch I is bulbous and measures 0.13–0.14 mm in maximum diameter and about 0.08 mm in the length of the D-line. Prodissoconch I is terminated by a slightly thickened rim on the shell. The onset of prodissoconch II is indicated by the formation of closely spaced concentric growth lines. The early dissoconch bears strong concentric folds.

Remarks: *M. rottensis* differs from the similar *M. clavaeformis* by its more slender shape with a more acute umbo. *M. amygdaloides* differs by its considerably thicker valve without pointed margin and by lacking a distinct keel. *M. rottensis* differs from *M. amygdaloides* and *M. clavaeformis* by its considerably larger prodissoconch I, which reflected a yolk rich embryogenesis. Specimens of *M. rottensis* from the Congerien-Horizon of the Kirchberg Formation regarding the prodissoconch morphology fully correspond to the investigated specimens from the Oncophora Beds.

Schlickum (1964) mentioned the conchological variability of *M. rottensis*. Investigations of the holotype of *M. schuetti*, which according to Schlickum (1964) was restricted to the Schillhorizont, yielded no significant differences compared to *M. rottensis* (cf. Reichenbacher, 1993). Regarding the morphology of the shell, the holotype of *M. schuetti* mediates between morphs of *M. rottensis* from the Schillsande and from the Aussüssungshorizont, and it is thus regarded as conspecific.

Class Gastropoda Cuvier, 1797

Subclass Neritimorpha Golikov and Starobogatov, 1975

Superfamily Neritoidea Rafinesque, 1815

Family Neritidae Rafinesque, 1815

Subfamily Neritinae Rafinesque, 1815

Genus *Agapilia* Harzhauser and Kowalke, 2001.

Type-species: *Nerita picta* Férussac, 1825, from the Early Miocene of southern France.

Agapilia schlickumi nov. sp.

Fig. 4(1, 2)

1964. *Clithon (Vittoclithon) pictus pictus* (Férussac) - Schlickum, p. 4, Pl. 1, Figs. 1 and 2.

1970a. *Clithon (Vittoclithon) pictus pictus* (Férussac) - Schlickum, p. 146, Pl. 10, Figs. 1 and 2.

1971. *Clithon (Vittoclithon) pictus* (Férussac) - Schlickum, Pl. 1, Fig. 1.

1973. *Clithon (Vittoclithon) pictus* (Férussac) - Steininger et al., p. 387, Pl. 1, Fig. 8.

Material: Oncophora Beds, Schillsande: Bergham (15 specimens, BSP 1964 XXVIII 153); Aussüssungshorizont: Türkenbach (holotype, BSP 2003 II 9; eight paratypes, BSP 2003 II 39); Hitzenu (35 specimens, BSP 1964 XXVIII 154).

Derivation of name: Named in honour of W. Richard Schlickum, an enthusiastic worker on the fauna of the Bavarian Molasse.

Type horizon and locality: Silty marls of the Upper Ottnangian Aussüssungshorizont of the Oncophora Beds at Türkenbach (Lower Bavaria).

Description: The rounded to subangular convolute shell measures up to 9 mm in height and up to 7.5 mm in width. The flanks of adult whorls are slightly flattened causing the characteristic outline of the shell. A colour pattern of dense dark brown wavy to zigzag shaped stripes on cream white ground is present. The stripes are curving sinuously on the flanks of the whorls. The half moon shaped aperture is characterised by a rounded outer lip. Sculpture consists of closely spaced growth lines. The columellar septum bears a callus pad. The columellar edge is slightly curving. It bears a prominent tooth in its anterior third, which extends into the interior columellar portion, and up to eight weaker additional teeth.

The protoconch measures up to 0.45 mm in maximum diameter. It comprises 1.25 inflated rounded whorls. The initial cap measures 0.1 mm in width. The protoconch is terminated by a slightly thickened rim of the shell. The onset of the teleoconch is indicated by the formation of closely spaced growth lines.

Remarks: The protoconch is indicative of a direct development without a larval stage. The investigated material derives from the Aussüssungshorizont of Türkenbach.

Differences: *Agapilia picta* (Férussac, 1825) from the Aquitanian and Burdigalian of South France and from the Aquitanian of Greece with a very similar teleoconch differs by its minor size and by a protoconch morphology which reflected an indirect development including a free planktonic larval stage (Harzhauser and Kowalke, 2001: Figs. 2.5–10). *A. pachii* (Hörnes, 1856) from the Karpatian of the Korneuburg Basin (Austria) differs by its stronger angular teleoconch and by a protoconch which is indicative of an indirect development (Harzhauser and Kowalke, 2001: Figs. 2.3, 4, 11 and 12). *Theodoxus* differs by its elongated shell with rounded flanks, by weaker callus, by the lack of coarse dentition and by the lack of the characteristic colour pattern and by the formation of axial threads sculpturing the early teleoconch.

Genus *Theodoxus* Montfort, 1810.

Type-species: The recent species *Nerita fluviatilis* Linnaeus, 1758, from Europe and North Africa.

Theodoxus cyrtocelis (Krauss, 1852).

Fig. 4(3–7).

1852. *Neritina cyrtocelis* nov. sp. - Krauss, p. 144–145.

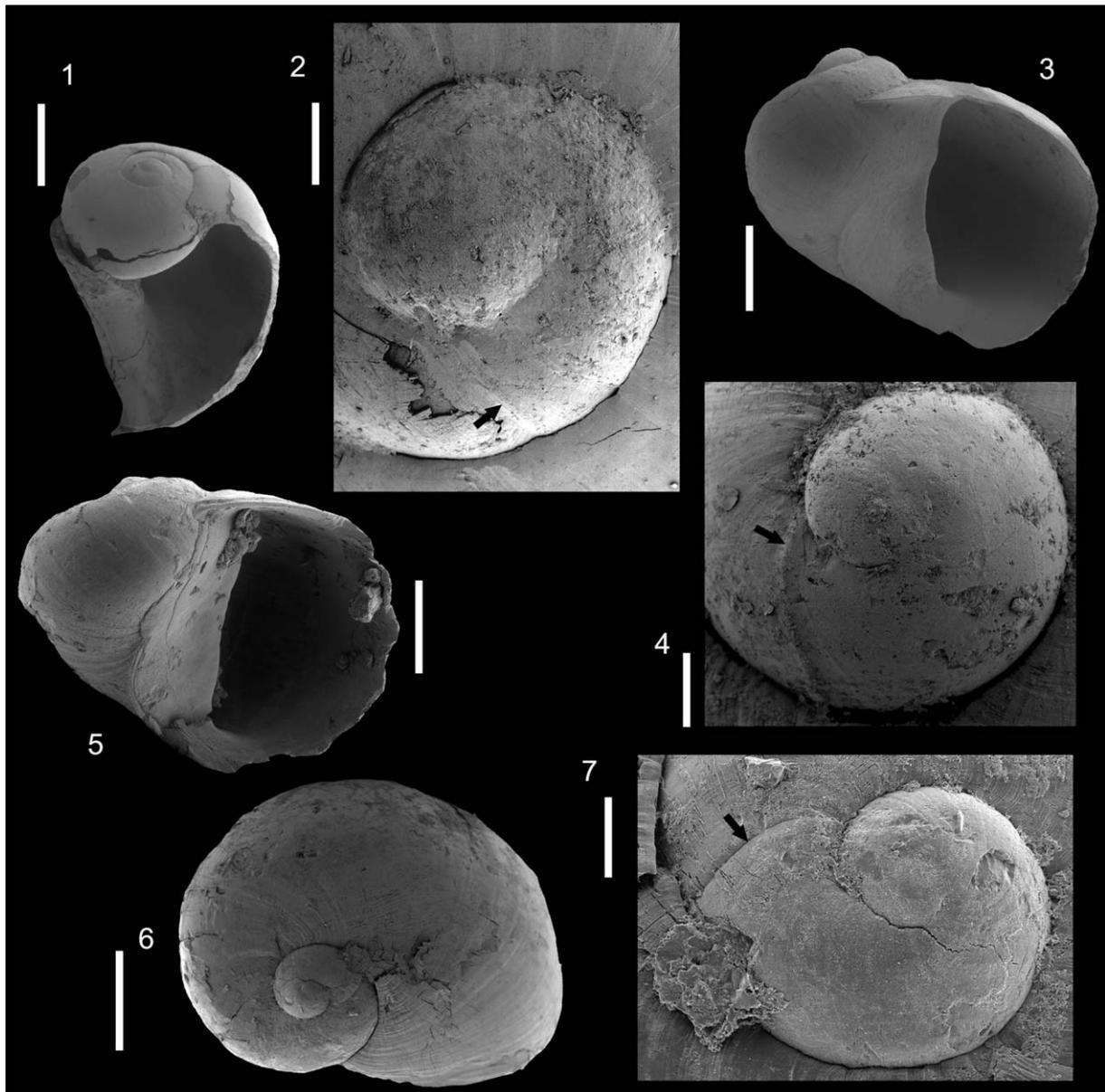


Fig. 4. *Agapilia* Harzhauser and Kowalke, 2001; *Theodoxus* Montfort, 1810. **1, 2.** *A. schlickumi* nov. sp. **1**, holotype, BSP 2003 II 9, Ausüstungshorizont de Türkenbach. **2**, same specimen, detailed apical view of the protoconch; the arrow is indicating the transition from the protoconch to the teleoconch. **3–7.** *T. cyrtocelis* (Krauss, 1852). **3**, specimen BSP 2003 II 10, Congerien-Horizon of Leipheim. **4**, protoconch of the same specimen; the arrow is indicating the transition from the protoconch to the teleoconch. **5, 6**, specimen BSP 2003 II 11, Ausüstungshorizont de Türkenbach, apertural and apical view. **7**, same specimen with detailed apical view of the protoconch; the arrow is indicating the transition from the protoconch to the teleoconch. Scale bars: 1 = 1 mm; 3, 5, 6 = 0.5 mm; 2, 4, 7 = 0.1 mm.

Fig. 4. *Agapilia* Harzhauser et Kowalke, 2001 ; *Theodoxus* Montfort, 1810. **1, 2.** *A. schlickumi* nov. sp. **1**, holotype, BSP 2003 II 9, Ausüstungshorizont de Türkenbach. **2**, le même spécimen, vue apicale détaillée de la protoconque ; la flèche indique la transition entre la protoconque et la téléconque. **3–7.** *T. cyrtocelis* (Krauss, 1852). **3**, spécimen BSP 2003 II 10, Congerien-Horizon de Leipheim. **4**, protoconque du même spécimen ; la flèche indique la transition entre la protoconque et la téléconque. **5, 6**, spécimen BSP 2003 II 11, Ausüstungshorizont de Türkenbach, vues aperturale et apicale. **7**, le même spécimen avec une vue apicale détaillée de la protoconque ; la flèche indique la transition entre la protoconque et la téléconque. Barres d'échelle : 1 = 1 mm ; 3, 5, 6 = 0,5 mm ; 2, 4, 7 = 0,1 mm.

1964. *Theodoxus* (*Theodoxus*) *cyrtocelis* (Krauss) - Schlickum, p. 4–5, Pl. 1, Figs. 3–6.

1970b. *Theodoxus* (*Theodoxus*) *cyrtocelis* (Krauss) - Schlickum, p. 147, Pl. 10, Figs. 3 and 4.

1971. *Clithon* (*Vittoclithon*) *pictus* (Férussac) - Schlickum, Pl. 3, Fig. 26.

1973. *Theodoxus* (*Theodoxus*) *cyrtocelis cyrtocelis* (Krauss) - Steininger et al., p. 388, Pl. 1, Fig. 10a, b.

1989. *T. cyrtocelis cyrtocelis* (Krauss) - Reichenbacher, Pl. 1, Figs. 1 and 2.

Material: Kirchberg Formation, Congerien-Horizon: Leipheim (53 specimens ex coll. Reichenbacher, BSP 2003 II

48, and the figured specimen BSP 2003 II 10; 17 specimens, BSP 1964 XXVIII 155). Oncophora Beds, Schillsande: Türkenbach (55 specimens ex coll. Reichenbacher, BSP 2003 II 49); Aussüßungshorizont: Türkenbach (100 specimens ex coll. Reichenbacher, BSP 2003 II 50, and the figured specimen BSP 2003 II 11).

Description: The elongated oval neritid shell with only slightly emerging spire measures up to 7.5 mm in height and up to 8.5 mm in width. The variable colour pattern consists of irregular light dots and stripes on dark ground. The aperture is characterised by a rounded outer lip and by a straight to slightly curving columella which bears regular fine dentition. The protoconch comprises 1.2–1.3 inflated whorls. It measures 0.47–0.5 mm in maximum diameter. The initial cap measures 0.13–0.16 mm in width. The protoconch is smooth aside from irregular folds. It is terminated by a prominent thickened rim of the shell. The onset of the teleoconch is indicated by the formation of dense growth lines and indistinct spiral threads.

Remarks: The protoconch is indicative of a direct development without a free larval stage. *T. c. cyrtocelis* differs from *A. schlickumi* sp. n. by an elongated shell, its larger, less rounded protoconch, by the less thickened apertural rim in the transition to the teleoconch and by the formation of fine spiral threads sculpturing the early teleoconch.

Subclass Caenogastropoda Cox, 1959

Order Littorinimorpha Golikov and Starobogatov, 1975

Superfamily Risssooidea Gray, 1847

Family Hydrobiidae Troschel, 1856

Genus *Hydrobia* Hartmann, 1821.

Type-species: The recent species *Cyclostoma acutum* Draparnaud, 1805, from the Mediterranean Sea.

Hydrobia frauenfeldi (Hörnes, 1856).

Fig. 5(1, 2)

1856. *Paludina frauenfeldi* nov. sp. - Hörnes, p. 582, Pl. 47, Fig. 18.

1971. *H. frauenfeldi* (Hörnes) - Schlickum, Pl. 3, Fig. 27.

1973. *H. frauenfeldi* (Hörnes) - Steininger et al., p. 390, Pl. 2, Fig. 2.

Material: Oncophora Beds, Aussüßungshorizont: Türkenbach (50 specimens ex coll. Reichenbacher, BSP 2003 II 51, and them the figured specimen BSP 2003 II 12).

Description: The small slender shell with acute spire is characterised by seven to eight slightly rounded whorls with moderately incised sutures. It measures up to 6 mm in height. The elongated body whorl forms about 50% of the total height of the shell. The drop shaped aperture is characterised by a pointed parietal portion. The columellar lip is bent. A narrow slit-like umbilicus is present.

The protoconch comprises 1.25–1.3 rounded whorls. It measures 0.34 mm in maximum diameter. The first whorl measures 0.29 mm in maximum diameter and 0.08 mm in the width of the initial cap. The protoconch is ornamented by a fine groove–ridge pattern. It is terminated by a prominent thickened rim of the shell. The onset of the teleoconch is indicated by the formation of closely spaced regular growth lines.

Remarks: The protoconch is indicative of a direct development without a free larval stage.

H. frauenfeldi represents an ubiquitous hydrobiid, which appeared in the Ottnangian and is reported until the Early Pannonian of the Paratethys (Harzhauser and Kowalke, 2002).

Hydrobia cf. *semiconvexa* Sandberger, 1874.

Fig. 5(3, 4).

1874. *H. semiconvexa* sp. n. - Sandberger: p. 561.

1966. *H. semiconvexa* Sandberger - Schlickum, p. 323, Pl. 12, Figs. 6–8.

1970b. *H. semiconvexa* Sandberger - Schlickum, p. 177, Pl. 3, Fig. 2.

1971. *H. semiconvexa* Sandberger - Schlickum, Pl. 3, Figs. 2 and 3.

1973. *H. semiconvexa* Sandberger - Steininger et al., p. 391, Pl. 2, Fig. 2.

1989. *H. semiconvexa* Sandberger - Reichenbacher, Pl. 2, Fig. 8.

Material: Kirchberg Formation, Congerien-Horizon: Leipheim (10 specimens ex coll. Reichenbacher, BSP 2003 II 52, and the figured specimen BSP 2003 II 13).

Description: The slender shell with tower to cylindrical shape comprises seven rounded whorls, which are separated by deep sutures. The penultimate and the last whorl have a more cylindrical outline than the apex. The egg-shaped aperture is characterised by a pointed parietal edge and by a bent peristome. The protoconch comprises 1.5 slightly rounded whorls measuring 0.34 mm in maximum diameter and 0.04 mm in the width of the initial cap. Sculpture is not preserved. Ornament consists of a very fine groove–ridge pattern. The protoconch is terminated by a prominent thickened rim of the shell. The onset of the teleoconch is indicated by the formation of closely spaced orthocone growth lines.

Remarks: The protoconch is indicative of a direct development. *H. semiconvexa* differs from *H. frauenfeldi* with about equal size by more rounded whorls separated by deeper sutures, the egg-shape of the aperture, the bent peristome and by its protoconch with a smaller embryonic shell, but comprising a quarter of a whorl more.

Genus *Ctyrokia* Schlickum, 1965.

Type-species: *Euchilus hoelzli* Schlickum, 1964 from the Ottnangian of Bavaria.

Ctyrokia ammoni Schlickum, 1965.

Fig. 6(1, 2).

1965. *C. ammoni* nov. sp. - Schlickum, p. 100–101, Fig. 1.

1973. *C. ammoni* Schlickum - Steininger et al., p. 396, Pl. 3, Fig. 6.

Material: Oncophora Beds, Aussüßungshorizont: Türkenbach (one specimen ex coll. Reichenbacher, BSP 2003 II 53, and the figured specimen BSP 2003 II 21).

Description: The elongated conical shell measures up to 7 mm in height and up to 3.5 mm in width. It comprises up to eight flat whorls, separated by only slightly incised sutures. According to Schlickum (1965) distinct spiral keels and grooves may be present. The body whorl amounts about 60%

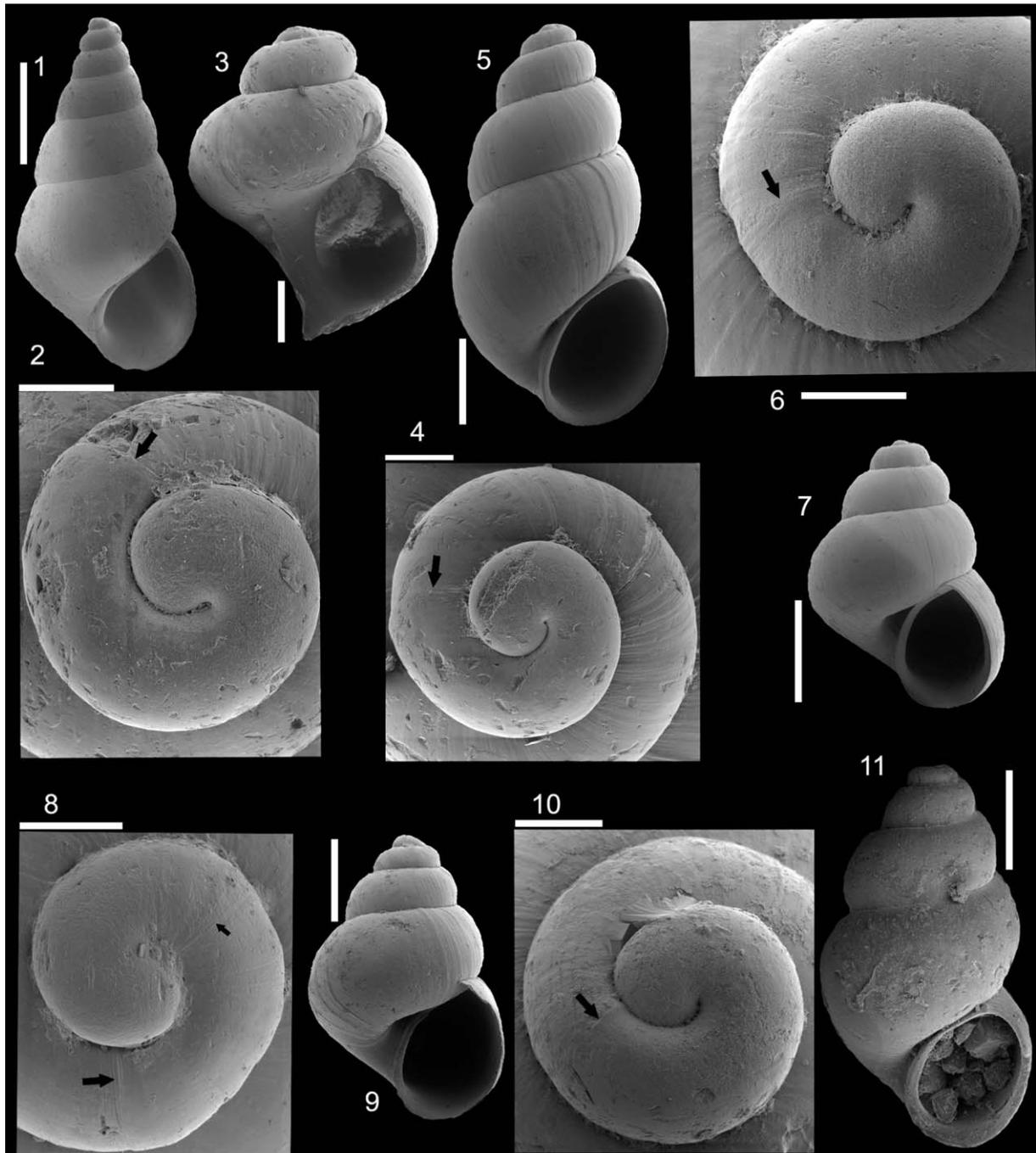


Fig. 5. *Hydrobia* Hartmann, 1821 and *Nematurella* Sandberger, 1874. **1, 2.** *H. frauenfeldi* (Hörnes, 1856). **1.** specimen BSP 2003 II 12, Aussüßungshorizont of Türkenbach. **2.** same specimen, apical view of the protoconch; the arrow is indicating the transition from the protoconch to the teleoconch. **3, 4.** *Hydrobia* cf. *semiconvexa* Sandberger, 1874. **3.** specimen BSP 2003 II 13, Congerien-Horizon of Leipheim. **4.** same specimen, apical view of the protoconch; the arrow is indicating the transition from the protoconch to the teleoconch. **5, 6.** *N. pseudozilchi* nov. sp. **5.** holotype, BSP 2003 II 14, Aussüßungshorizont of Türkenbach. **6.** same specimen, apical view of protoconch; the arrow is indicating the transition from the protoconch to the teleoconch. **7, 8.** *N. zilchi* Schlickum, 1960. **7.** juvenile specimen, BSP 2003 II 15, Congerien-Horizon of Leipheim. **8.** same specimen, apical view of protoconch; a small arrow points to the first occurrence of growth lines on the embryonic shell; the subsequent part has most probably formed during an embryogenesis supported by nurse egg feeding; the larger arrow is indicating the transition from the protoconch to the teleoconch. **9, 10.** *N. convexula* Schlickum and Strauch, 1967. **9.** specimen BSP 2003 II 16, Congerien-Horizon of Leipheim. **10.** same specimen, apical view of protoconch; the arrow is indicating the transition from the protoconch to the teleoconch. **11.** *N. klemmi* Schlickum, 1964, paratype, SMF 172150/8 (ex coll. Schlickum, 10897). Scale bars: 1 = 1 mm; 5, 7, 9, 11 = 0.5 mm; 3 = 0.2 mm; 2, 4, 6, 8, 10 = 0.1 mm.

Fig. 5. *Hydrobia* Hartmann, 1821 et *Nematurella* Sandberger, 1874. **1, 2.** *H. frauenfeldi* (Hörnes, 1856). **1.** spécimen BSP 2003 II 12, Aussüßungshorizont de Türkenbach. **2.** le même spécimen, vue apicale de la protoconque ; la flèche indique la transition entre la protoconque et la téléoconque. **3, 4.** *Hydrobia* cf. *semiconvexa* Sandberger, 1874. **3.** spécimen BSP 2003 II 13, Congerien-Horizon de Leipheim. **4.** le même spécimen, vue apicale de la protoconque ; la flèche indique la transition entre la protoconque et la téléoconque. **5, 6.** *N. pseudozilchi* nov. sp. **5.** holotype, BSP 2003 II 14, Aussüßungshorizont de Türkenbach. **6.** le même spécimen, vue apicale de la protoconque ; la flèche indique la transition entre la protoconque et la téléoconque. **7, 8.** *N. zilchi* Schlickum, 1960. **7.**

of the total height of the shell. The elongated egg-shaped aperture is pointed in its parietal portion. The straight columella is slightly thickened by callus.

The protoconch comprises 2.5 slightly rounded whorls. It measures 0.33 mm in maximum diameter and 0.35 mm in height. The embryonic shell comprises one whorl. It measures 0.13 mm in maximum diameter and 0.02 mm in the width of the initial cap. The embryonic shell is characterised by a very small initial cap and by an inflated subsequent embryonic whorl. The transition to the larval shell is indicated by a groove-like incision in the shell. The larval shell is smooth aside from indistinct growth lines. The protoconch is terminated by a sinuous thickened rim of the shell. The early teleoconch is sculptured by slightly prosocyrte growth lines.

Remarks: The protoconch is indicative of a free larval stage. After hatching from the eggs, veliger larvae spent a longer time within the plankton, during which about one and a half additional whorls have been secreted. The larvae fed on phytoplankton. The syntopic species *C. hoelzli* differs by its less slender shell and by its smaller protoconch comprising 0.6–0.7 whorls less. The investigated specimens in this study verify that *C. ammoni* co-occurred within the Aussüsungshorizont of Türkenbach.

Ctyrokia conoidea (Krauss, 1852).

Fig. 6(8–10).

1852. *Paludina conoidea* nov. sp. - Krauss, p. 141–142, Pl. 3, Fig. 1.

1965. *C. conoidea* (Krauss) - Schlickum, p. 99, 101.

1966. *C. conoidea* (Krauss) - Schlickum, p. 325, Pl. 13, Figs. 23 and 24.

1973. *C. conoidea* (Krauss) - Steininger et al., p. 397, Pl. 3, Fig. 5.

1989. *C. conoidea* (Krauss) - Reichenbacher, Pl. 2, Fig. 4.

Material: Kirchberg Formation, Congerien-Horizon: Leipheim (25 specimens ex coll. Reichenbacher, BSP 2003 II 54, and the figured specimens BSP 2003 II 25–26).

Description: The small conical egg-shaped thick shell measures up to 4.8 mm in height and up to 3 mm in width. It comprises about six slightly rounded whorls. A slight keel in the median portion of the whorls is present in one specimen. The teleoconch is characterised by a prominent colour pattern of variable more or less broad yellowish to brown stripes. About four to eight stripes per whorl are present. The body whorl amounts about 70% of the total height of the shell. The large aperture has egg-shape to subangular shape. The straight columella bears a slight callus. The columellar edge is bent.

The protoconch comprises 2.5 rounded whorls measuring 0.32 mm in maximum diameter and 0.35 mm in height. The first whorl measures 0.12–0.13 mm in maximum diameter and 0.02–0.03 mm in the width of the initial cap. The transi-

tion to the larval shell is not visible. The protoconch is terminated by a sinuous rim on the shell.

Remarks: The dimensions of the first whorl indicate an indirect development including a planktonic veliger stage. The protoconch closely resembles that of *C. ammoni*, which is slightly larger in diameter. It differs by lacking the prominent incision following the embryonic shell, which is present in *C. ammoni*. The teleoconch differs from that of *C. ammoni* by the considerably broader shell and by its less rounded outline with an indicated keel. *C. hoelzli* differs by its smaller larval shell reflecting a shorter stay within the plankton. *C. conoidea* differs from all other described species of *Ctyrokia* by its considerably lower shell with slowly increasing whorls and by its prominent colour pattern. *C. conoidea* is restricted to the Kirchberg Formation.

Ctyrokia hoelzli (Schlickum, 1964).

Fig. 6(3–7).

1964. *E. hoelzli* nov. sp. - Schlickum, p. 10–11, Pl. 1, Fig. 21.

1965. *C. hoelzli* (Schlickum) - Schlickum, p. 99–100.

1971. *C. hoelzli* (Schlickum) - Schlickum, Pl. 3, Fig. 35.

1973. *C. hoelzli* (Schlickum) - Steininger et al., p. 396, Pl. 3, Fig. 2.

Material: Kirchberg Formation, Congerien-Horizon: Leipheim (one specimen ex coll. Reichenbacher, BSP 2003 II 55, and the figured specimen BSP 2003 II 22); Oncophora Beds, Aussüsungshorizont: Türkenbach (10 specimens ex coll. Reichenbacher, BSP 2003 II 56, and the figured specimen BSP 2003 II 23).

Description: The small egg-shaped conical shell measures up to 6.1 mm in height and up to 3.8 mm in width. The shell comprises seven flat whorls which are separated by only slightly incised sutures. The body whorl forms about 70% of the total height of the shell. The drop shaped to elongated egg-shaped aperture is characterised by a pointed parietal edge. The straight columella is slightly thickened by callus in adult specimens. The columellar lip is bent.

The protoconch comprises 1.8–1.9 slightly rounded whorls. It measures 0.23–0.25 mm in maximum diameter and 0.21–0.22 mm in height. The embryonic shell comprises one whorl measuring 0.13–0.14 mm in maximum diameter and 0.02–0.03 mm in the width of the initial cap. The transition to the larval shell is characterised by a thickening followed by a slight incision. The larval shell is smooth aside from indistinct growth lines. The protoconch is terminated by an indistinct sinuous slightly thickened rim of the shell. The onset of the teleoconch is indicated by the formation of prosocyrte growth lines.

Remarks: The protoconch is indicative of a free planktotrophic larval stage. *C. hoelzli* differs from *C. ammoni* by

spécimen juvénile, BSP 2003 II 15, Congerien-Horizon de Leipheim. **8**, le même spécimen, vue apicale de la protoconque ; la petite flèche indique l'apparition des lignes de croissance sur la coquille embryonnaire ; la partie subséquente a été probablement formée pendant l'embryogénèse ; la grande flèche indique la transition entre la protoconque et la téléconque. **9**, **10**. *N. convexula* Schlickum et Strauch, 1967. **9**, spécimen BSP 2003 II 16, Congerien-Horizon de Leipheim. **10**, le même spécimen, vue apicale de la protoconque ; la flèche indique la transition entre la protoconque et la téléconque. **11**. *N. klemmi* Schlickum, 1964, paratype, SMF 172150/8 (ex coll. Schlickum, 10897). Barres d'échelle : 1 = 1 mm ; 5, 7, 9, 11 = 0,5 mm ; 3 = 0,2 mm ; 2, 4, 6, 8, 10 = 0,1 mm.

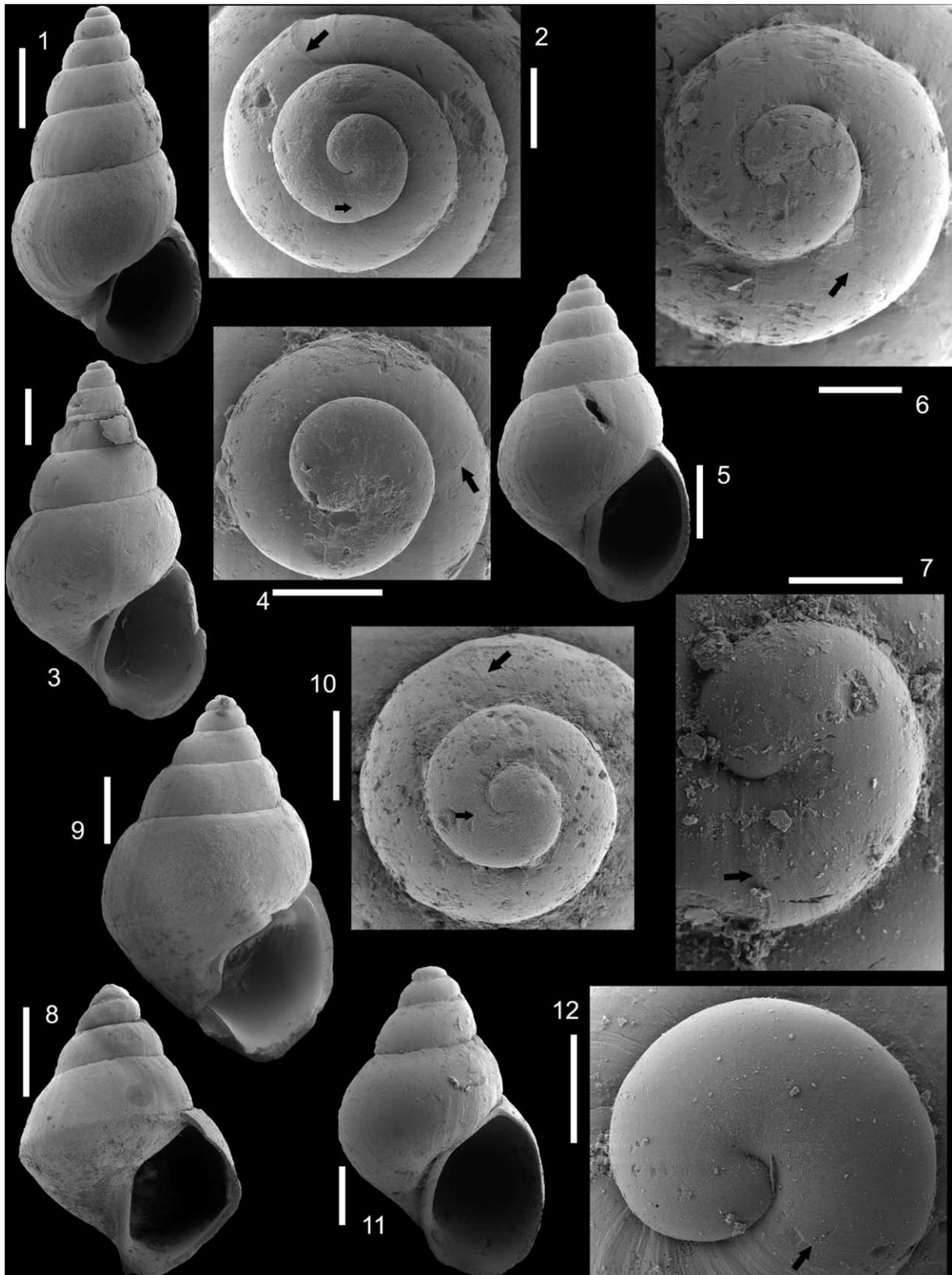


Fig. 6. *Ctyroikia* Schlickum, 1965. **1, 2.** *C. ammoni* Schlickum, 1965. **1**, specimen BSP 2003 II 21, Aussüßungshorizont of Türkenbach. **2**, same specimen, apical view of protoconch; a slight depression in the shell accompanied by a subsequent slight thickening indicate the transition from the embryonic shell to the larval shell (small arrow); the larger arrow indicates the transition from the protoconch to the teleoconch. **3–7.** *C. hoelzli* (Schlickum, 1964). **3**, specimen BSP 2003 II 22, Congerien-Horizon of Leipheim. **4**, protoconch of the same specimen; the arrow is indicating the transition from the protoconch to the teleoconch. **5**, specimen BSP 2003 II 23, from the Aussüßungshorizont of Türkenbach. **6**, same specimen, apical view of protoconch; the arrow is indicating the transition

its smaller protoconch, which is indicative of a shorter larval stage. The protoconch of *C. hoelzli* is slightly wider than high, whereas the protoconch of *C. ammoni* is slightly higher than wide. The dimensions of the embryonic shells are equal with exception of the transition to the larval shell, which is characterised by a slighter incision in case of *C. hoelzli*. The adult shell of *C. hoelzli* is slightly broader than that of *C. ammoni*.

C. hoelzli has originally been described from the Mehlsande and Schillhorizont of the Süßbrackwassermolasse of Lower Bavaria (Schlickum, 1964) and it co-occurred in the Aussüßungshorizont of Türkenbach. Specimens from the Congerien-Horizon of Leipheim with corresponding protoconch morphology verified the presence of *C. hoelzli* in the Kirchberg Formation from where it has not been reported up to now.

Ctyrokia zoebeleini Schlickum, 1970.

Fig. 6(11, 12).

1970b. *C. zoebeleini* nov. sp. - Schlickum, p. 177–178, Pl. 3, Figs. 5 and 6.

Material: Kirchberg Formation, Congerien-Horizon: Leipheim (10 specimens ex coll. Reichenbacher, BSP 2003 II 57, and the figured specimens BSP 2003 II 27–28).

Description: The small elongated egg-shaped shell with acute apex measures up to 5.4 mm in height and 3.1 mm in width. It comprises up to six flat to slightly rounded whorls, which are separated by only slightly incised sutures. Adult specimens may bear very weak spiral threads and grooves. The large body whorl forms about 75% of the total height of the shell. The large acute egg-shaped aperture is characterised by a straight slightly thickened columella and by a bent columellar edge.

The protoconch comprises 1–1.1 whorls measuring 0.29–0.31 mm in maximum diameter. The first whorl measures 0.26–0.28 mm in maximum diameter and 0.06–0.07 mm in the width of the initial cap. The transition to the teleoconch is indicated by the formation of closely spaced orthoclin to slightly prosoclyt growth lines.

Remarks: *C. zoebeleini* differs from all other described *Ctyrokia* spp. by its direct development without an inclusion

of a planktonic larval stage. The teleoconch closely resembles that of *C. hoelzli*. The teleoconch of *C. zoebeleini* differs from that of *C. hoelzli* by its slightly more slender outline and by the larger and higher aperture.

Genus *Nematurella* Sandberger, 1874.

Type-species: *Nematurella flexilabris* Sandberger, 1874 from the Badenian of Tramelan (Switzerland).

Nematurella bavarica (Sandberger, 1874).

Fig. 7(3–5).

1874. *Hydrobia bavarica* nov. sp. - Sandberger, p. 576.

1960. *Nematurella schuetti* nov. sp. - Schlickum, p. 211, Pl. 19, Fig. 12.

1960. *Nematurella scholli* nov. sp. - Schlickum, p. 207–208, Pl. 18, Figs. 6 and 7.

1973. *N. scholli* Schlickum - Steininger et al., p. 391, Pl. 2, Fig. 5.

1989. *Nematurella* cf. *bavarica* (Sandberger) - Reichenbacher, Pl. 2, Fig. 3.

Material: Kirchberg Formation, Congerien-Horizon: Leipheim (30 specimens ex coll. Reichenbacher, BSP 2003 II 58, and the figured specimens BSP 2003 II 18–19); unhorizontated: Günzburg (four syntypes of *N. bavarica* ex coll. Schlickum, S 10060, = paratypes of *N. schuetti*, SMF 266717/4).

Description: The slender shell has five moderately rounded whorls measuring slightly more than 3 mm in height. The apex has strongly conical outline, whereas the penultimate and the ultimate whorl are elongated cylindrical in shape. The height/width-ratio of the shell amounts 1.6–1.8. The teleoconch whorls appear to be smooth. A well developed umbilicus is present in juvenile specimens. It becomes slit-like with the formation of the last teleoconch whorl. The last whorl forms about 70% of the total height of the shell.

The protoconch comprises 1.25–1.3 slightly rounded low whorls measuring 0.32–0.35 mm in maximum diameter. The first whorl measures 0.25–0.27 mm in maximum diameter and 0.07–0.08 mm in the width of the initial cap. The embryonic shell is apparently smooth. The protoconch is termi-

from the protoconch to the teleoconch. 7, detail of the embryonic shell of specimen BSP 2003 II 24, Congerien-Horizon of Leipheim; the arrow is indicating the transition from the embryonic shell to the larval shell. 8–10. *C. conoidea* (Krauss, 1852). 8, specimen BSP 2003 II 25, Congerien-Horizon of Leipheim; the teleoconch is characterised by a weak keel in the median portion of the whorls. 9, specimen BSP 2003 II 26, Congerien-Horizon of Leipheim. 10, same specimen, apical view of protoconch; the transition from the embryonic shell to the larval shell is indicated by a weak rim (small arrow); the larger arrow indicates the transition from the protoconch to the teleoconch. 11, 12. *C. zoebeleini* Schlickum, 1970. 11, specimen BSP 2003 II 27, Congerien-Horizon of Leipheim. 12, protoconch of specimen BSP 2003 II 28, Congerien-Horizon of Leipheim; the protoconch is indicative of a direct development and the arrow is indicating the transition from the protoconch to the teleoconch. Scale bars: 1, 3, 5, 8, 9, 11 = 0.5 mm; 2, 4, 10, 12 = 0.1 mm; 6, 7 = 0.05 mm.

Fig. 6. *Ctyrokia* Schlickum, 1965. 1, 2. *C. ammoni* Schlickum, 1965. 1, spécimen BSP 2003 II 21, Aussüßungshorizont de Türkenbach. 2, le même spécimen, vue apicale de la protoconque ; une légère dépression de la coquille suivie d'un léger épaississement indique la transition entre la coquille embryonnaire et la coquille larvaire (petite flèche) ; la grande flèche indique la transition entre la protoconque et la téléconque. 3–7. *C. hoelzli* (Schlickum, 1964). 3, spécimen BSP 2003 II 22, Congerien-Horizon de Leipheim. 4, protoconque du même spécimen ; la flèche indique la transition entre la protoconque et la téléconque. 5, spécimen BSP 2003 II 23, Aussüßungshorizont de Türkenbach. 6, le même spécimen, vue apicale de la protoconque ; la flèche indique la transition entre la protoconque et la téléconque. 7, détail de la coquille embryonnaire du spécimen BSP 2003 II 24, Congerien-Horizon de Leipheim ; la flèche indique la transition de la coquille embryonnaire à la coquille larvaire. 8–10. *C. conoidea* (Krauss, 1852). 8, spécimen BSP 2003 II 25, Congerien-Horizon de Leipheim ; la téléconque est caractérisée par une légère carène dans la partie médiane des spires. 9, spécimen BSP 2003 II 26, Congerien-Horizon de Leipheim. 10, le même spécimen, vue apicale de la protoconque ; la transition entre la coquille embryonnaire et la coquille larvaire est indiquée par un petit dépôt (petite flèche) ; la grande flèche indique la transition entre la protoconque et la téléconque. 11, 12. *C. zoebeleini* Schlickum, 1970. 11, spécimen BSP 2003 II 27, Congerien-Horizon de Leipheim. 12, protoconque du spécimen BSP 2003 II 28, Congerien-Horizon de Leipheim ; la protoconque montre un développement direct et la flèche indique la transition entre la protoconque et la téléconque. Barres d'échelle : 1, 3, 5, 8, 9, 11 = 0,5 mm ; 2, 4, 10, 12 = 0,1 mm ; 6, 7 = 0,05 mm.

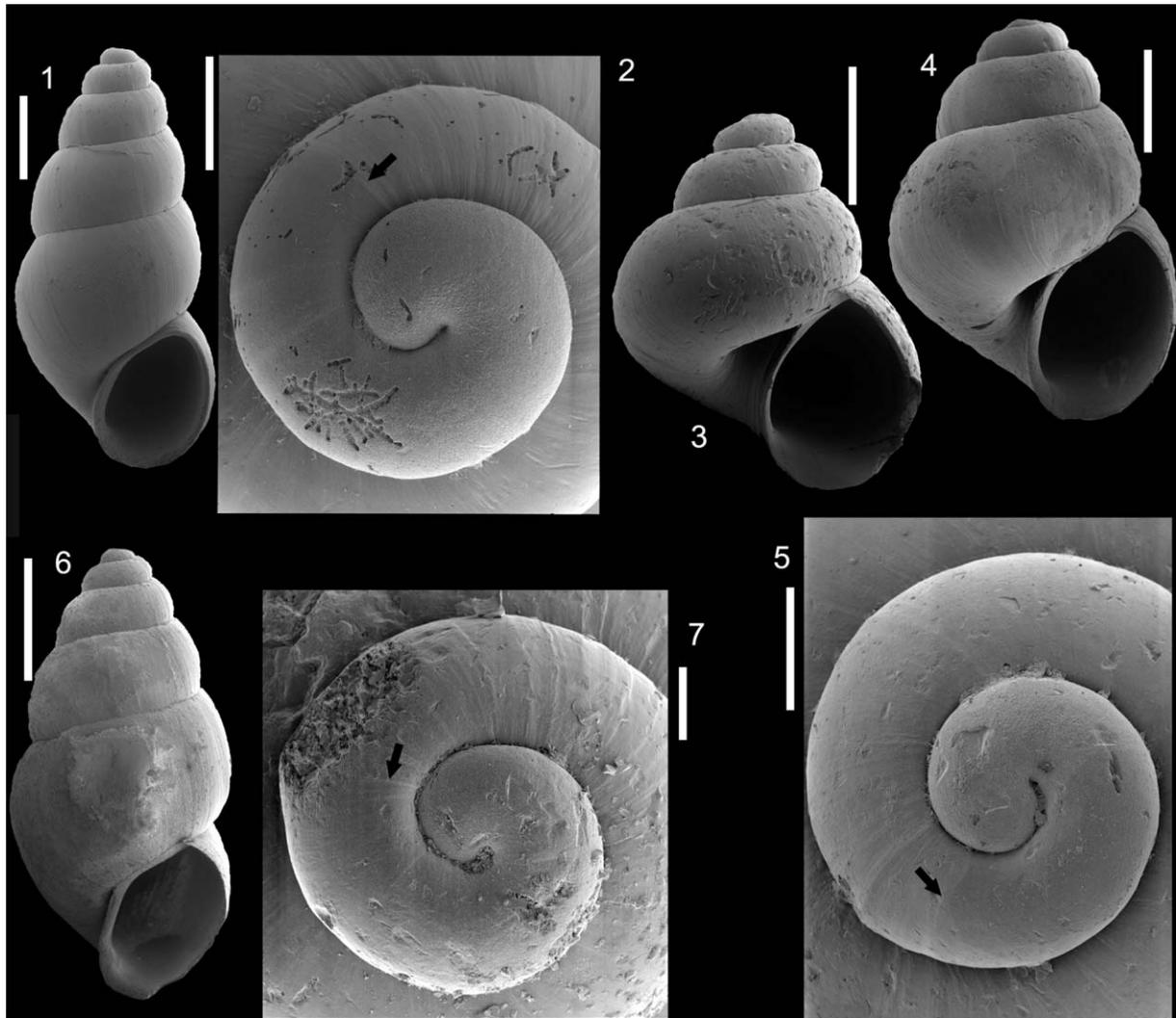


Fig. 7. *Nematurella* Sandberger, 1874. **1, 2.** *N. pappi* Schlickum, 1960. **1**, specimen BSP 2003 II 17, Aussüssungshorizont of Türkenbach. **2**, same specimen, apical view of protoconch; the arrow is indicating the transition from the protoconch to the teleoconch. **3–5.** *N. bavarica* (Sandberger, 1874). **3**, specimen BSP 2003 II 18, Congerien-Horizon of Leipheim. **4**, specimen BSP 2003 II 19, Congerien-Horizon of Leipheim, with formation of cylindrical shape in the course of the fourth whorl. **5**, protoconch of the same specimen; the arrow is indicating the transition from the protoconch to the teleoconch. **6, 7.** *N. strauchi* nov. sp. **6**, holotype, BSP 2003 II 20, Congerien-Horizon of Leipheim. **7**, protoconch of the same specimen as in Fig. 6, apical view; the arrow is indicating the transition from the protoconch to the teleoconch. Scale bars: 1, 3, 4, 6 = 0.5 mm; 2, 5, 7 = 0.1 mm.

Fig. 7. *Nematurella* Sandberger, 1874. **1, 2.** *N. pappi* Schlickum, 1960. **1**, spécimen BSP 2003 II 17, Aussüssungshorizont de Türkenbach. **2**, le même spécimen, vue apicale de la protoconque ; la flèche indique la transition entre la protoconque et la téléconque. **3, 5.** *N. bavarica* (Sandberger, 1874). **3**, spécimen BSP 2003 II 18, Congerien-Horizon de Leipheim. **4**, spécimen BSP 2003 II 19, Congerien-Horizon de Leipheim, avec la formation de formes cylindriques dans la quatrième spire. **5**, protoconque du même spécimen ; la flèche indique la transition entre la protoconque et la téléconque. **6, 7.** *N. strauchi* nov. sp. **6**, holotype, BSP 2003 II 20, Congerien-Horizon de Leipheim. **7**, protoconque du même spécimen que la Fig. 6, vue apicale ; la flèche indique la transition entre la protoconque et la téléconque. Barres d'échelle : 1, 3, 4, 6 = 0,5 mm ; 2, 5, 7 = 0,1 mm.

nated by a slightly thickened sharp rim of the shell. The onset of the teleoconch is indicated by the formation of closely spaced orthoclin growth lines.

Remarks: The protoconch is indicative of a direct development without a free larval stage. It differs from the protoconch of *N. zilchi* by its larger size, whereas the teleoconch of *N. zilchi* is larger in size. The adult shell of *N. bavarica* is slightly larger and more slender than that of *N. klemmi*. The protoconch of *N. bavarica* is also slightly larger. The morphology of the teleoconch is similar to that of *N. pappi*, differs by its slightly larger size, the less slender outline with

less rounded whorls. The protoconch is larger than that of *N. pappi*.

Schlickum (1961) recognised that his species *N. schuetti* is conspecific with *N. bavarica*. Comparative analysis of the protoconch morphologies of two paratypes from Günzburg and specimens from the Kirchberg Formation yielded no differences and thus supports the status of conspecifics. *N. scholli* from the Flusssand-1-/Viviparen-Horizon is represented by morphs with slightly more flattened whorls, which also occur within type-material of *N. bavarica* from Günzburg and which are within the variability of *N. bavarica*.

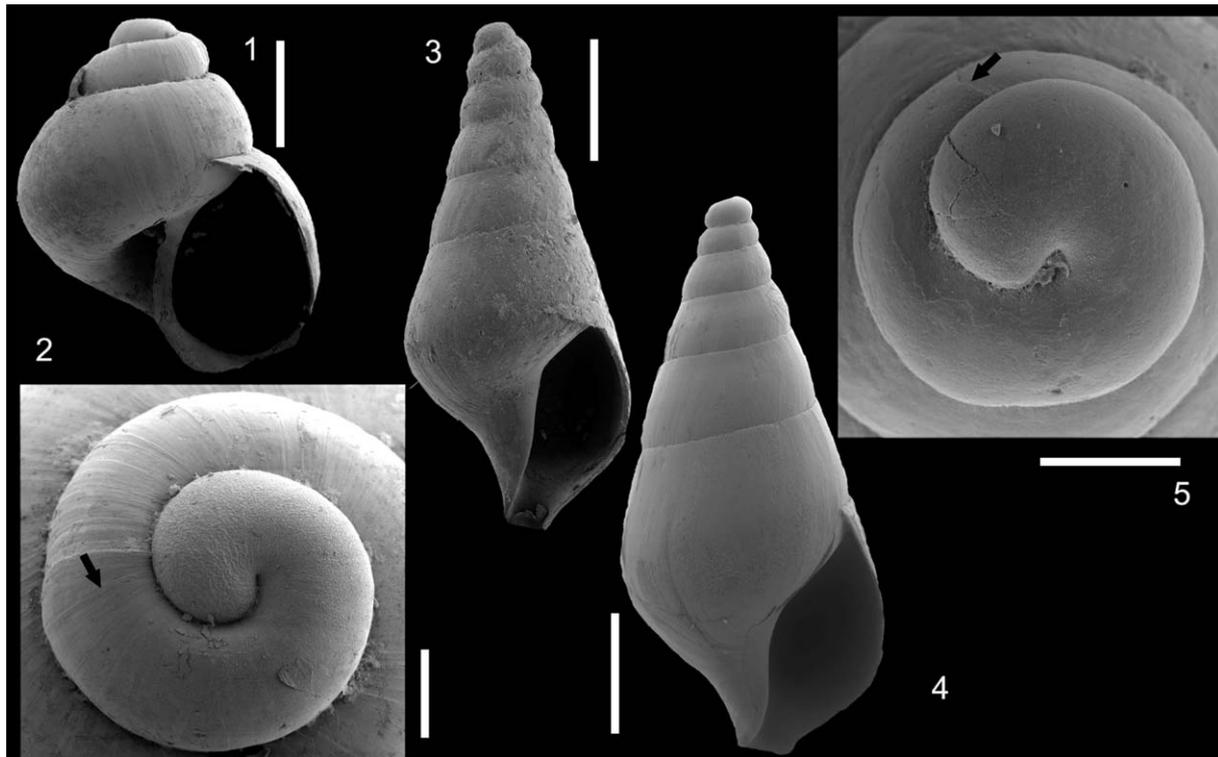


Fig. 8. *Bithynia* Leach in Abel, 1818; *Melanopsis* Férussac, 1819. 1, 2. *Bithynia* cf. *glabra* (Zieten, 1830). 1, specimen BSP 2003 II 29, Congerien-Horizon of Leipheim. 2, same specimen, apical view of protoconch; the arrow is indicating the transition from the protoconch to the teleoconch. 3–5. *M. impressa impressa* Krauss, 1852. 3, slender morph, BSP 2003 II 30, Congerien-Horizon of Leipheim. 4, specimen BSP 2003 II 31, Aussüssungshorizont of Türkenbach. 5, same specimen, apical view of protoconch; the arrow is indicating the transition from the protoconch to the teleoconch. Scale bars: 1, 3, 4 = 0.5 mm; 2, 5 = 0.1 mm. Fig. 8. *Bithynia* Leach in Abel, 1818; *Melanopsis* Férussac, 1819. 1, 2. *Bithynia* cf. *glabra* (Zieten, 1830). 1, spécimen BSP 2003 II 29, Congerien-Horizon de Leipheim. 2, le même spécimen, vue apicale de la protoconque ; la flèche indique la transition entre la protoconque et la téléoconque. 3–5. *M. impressa impressa* Krauss, 1852. 3, morphyte mince, BSP 2003 II 30, Congerien-Horizon de Leipheim. 4, spécimen BSP 2003 II 31, Aussüssungshorizont de Türkenbach. 5, le même spécimen, vue apicale de la protoconque ; la flèche indique la transition entre la protoconque et la téléoconque. Barres d'échelle : 1, 3, 4 = 0,5 mm ; 2, 5 = 0,1 mm.

A subadult specimen from the Congerien-Horizon of Leipheim differs by a considerably smaller protoconch comprising only one whorl measuring 0.04 mm in the width of the initial cap and 0.24 mm in maximum diameter. The protoconch is terminated by a slightly thickened rim of the shell. Probably a second species with identical teleoconch morphology like *N. bavaria* existed, distinctive only by its protoconch morphology.

Nematurella convexula Schlickum and Strauch, 1967.

Fig. 5(9, 10).

1960. *Nematurella* cf. *makowskyi* Rzehak - Schlickum, Pl. 19, Figs. 13 and 14.

1967. *N. convexula* nov. sp. - Schlickum and Strauch, p. 173–174.

1971. *N. convexula* Schlickum and Strauch - Schlickum, Pl. 1, Fig. 5 (holotype).

1973. *N. convexula* Schlickum and Strauch - Steininger et al., p. 392, Pl. 392, Pl. 2, Fig. 8.

1989. *N. convexula* Schlickum and Strauch - Reichenbacher, Pl. 1, Fig. 2.

Material: Kirchberg Formation, Congerien-Horizon: Leipheim (40 specimens ex coll. Reichenbacher, BSP 2003 II 59, and the figured specimen BSP 2003 II 16; four paraty-

poids BSP 1967 XXIV 25); Bithynien-/Gobius *multipinnatus*-/Dapalis *crassirostris*-Horizon: Leipheim (two specimens ex coll. Reichenbacher).

Description: The small spindle shaped thick shell measures up to 3 mm in height. The height/width-ratio of the shell amounts 1.8–1.9. It consists of five well rounded whorls, which are separated by deep sutures. The shell is sculptured by growth lines and regularly arranged, closely spaced varices. The last whorl forms about 60–70% of the total height of the shell. A slit-like umbilicus is present, which is well developed in juvenile specimens. The roundish to inclined egg-shaped aperture with slightly pointed posterior portion is slightly detached from the spire. It is characterised by a slightly thickened peristome, which is bent in the anterior and columellar portion.

The protoconch comprises 1.25–1.4 low whorls rapidly increasing in diameter. It measures 0.32–0.34 mm in maximum diameter. Embryonic ornament consists of a very fine groove–ridge pattern. The first whorl measures 0.04 mm in the width of the initial cap and 0.25–0.28 mm in maximum diameter. It is terminated by a slightly thickened rim on the shell. The onset of the teleoconch is indicated by the formation of closely spaced regular growth lines.

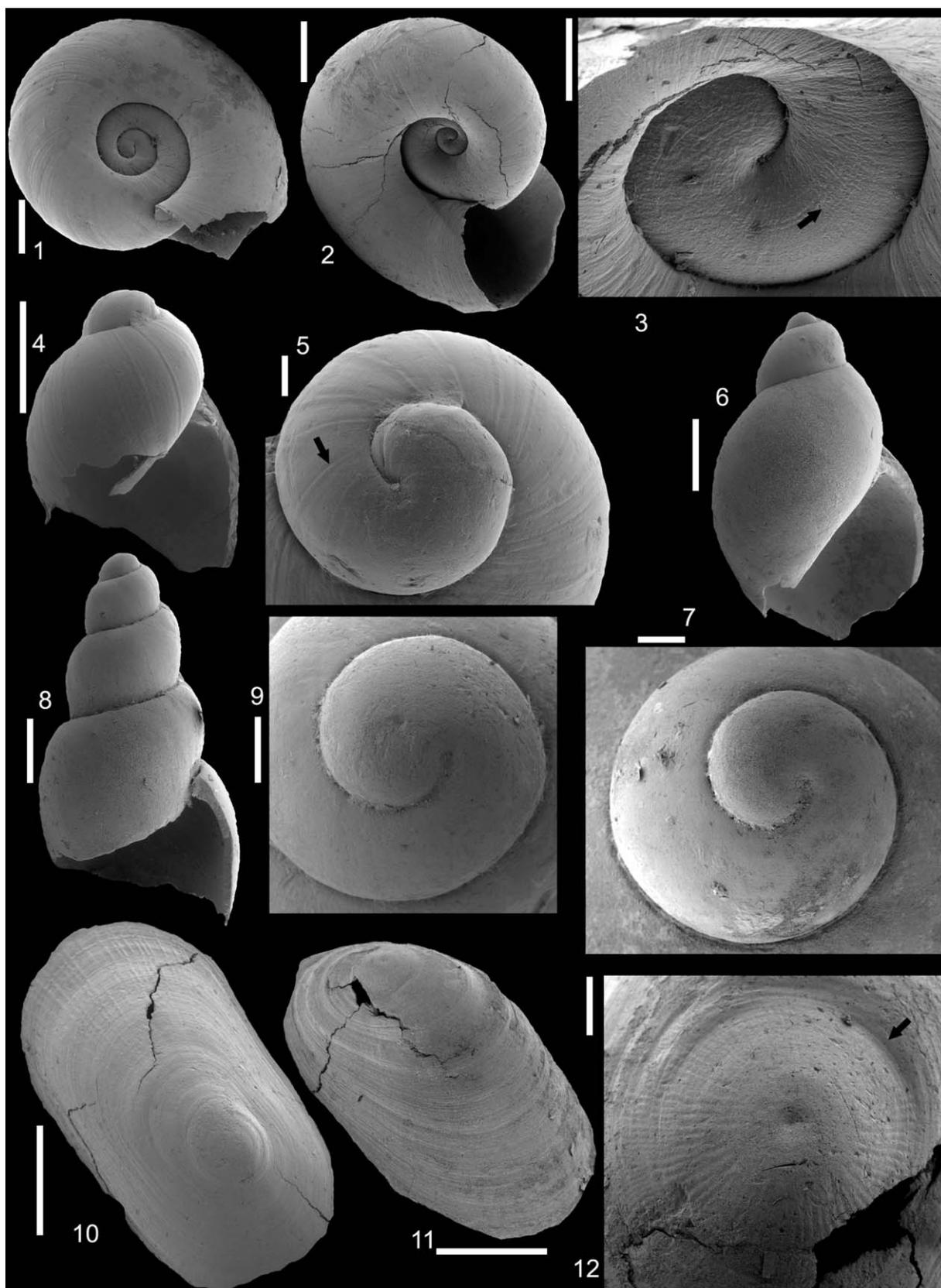


Fig. 9. Basommatophora Keferstein, 1864. 1–3. *G. applanatus* (Thomae, 1945). 1, specimen BSP 2003 II 32, Aussüßungshorizont of Türkenbach, apical view. 2, specimen BSP 2003 II 33, Aussüßungshorizont of Türkenbach, umbilical view. 3, same specimen, umbilical view of protoconch; the arrow is indicating the transition from the protoconch to the teleoconch. 4, 5. *L. dilatata* (Noulet, 1854). 4, specimen BSP 2003 II 34, Congerien-Horizont of Leipheim. 5, same specimen, apical view of protoconch; the arrow is indicating the transition from the protoconch to the teleoconch. 6, 7. *S. armaniacensis* (Noulet, 1857). 6,

Remarks: *N. convexula* differs from *N. klemmi* by slightly more rounded whorls and thus deeper sutures and a conspicuously small rounded aperture (cf. Schlickum and Strauch, 1967). *N. convexula* furthermore differs by its slightly larger size comprising half a whorl more and by characteristic fine varices which are regularly arranged all over the teleoconch whorls and which are absent in *N. klemmi*. The protoconch of *N. convexula* differs by its smaller initial cap but considerably larger diameter of the first whorl.

The holotype of *N. convexula* had previously been assigned to *N. cf. makowskyi* Rzehak, 1882 by Schlickum (1960), but *N. makowskyi* differs by its much larger size, the flattened less rounded whorls and thus elongated spindle shaped shell with acute apex.

N. convexula within the Kirchberg Formation appeared to be restricted to the Congerien-Horizon (Schlickum and Strauch, 1967; Schlickum, 1971; Reichenbacher, 1989), but could now also be confirmed from the Bithynien-/Gobius multipinnatu -/Dapalis crassirostris-Horizon at Leipheim.

Nematurella klemmi Schlickum, 1964.

Fig. 5(11).

1964. *N. klemmi* nov. sp. - Schlickum, p. 7–8, Pl. 1, Fig. 14.

1973. *N. klemmi* Schlickum - Steininger et al., p. 392, Pl. 2, Fig. 6.

Material: Oncophora Beds, Uniosande: Woching/Danube (eight paratypes ex coll. Schlickum S 10897, SMF 172150/8; further four paratypes, BSP 1964 I 18).

Description: The small low spindle shaped thick shell with stout apex has up to 4.5 well rounded whorls measuring up to 2.5 mm in height. The whorls are smooth aside from growth lines. The height/width-ratio of the shell amounts 1.8–1.9. The last whorl forms 70–75% of the total height of the shell. A slit-like umbilicus is present. The aperture is slightly detached from the spire. It has inclined egg-shape with a rounded base and a slightly pointed posterior portion. The peristome is slightly thickened and slightly bent in its anterior and columellar portion.

The protoconch is not well preserved. The first whorl measures 0.05–0.06 mm in the width of the initial cap and 0.2 mm in maximum diameter. A slight thickening of the shell is terminating the protoconch.

Nematurella pappi Schlickum, 1960.

Fig. 7(1, 2).

1960. *N. pappi* nov. sp. - Schlickum, p. 206–207, Pl. 18, Figs. 4 and 5.

1973. *N. pappi* Schlickum - Steininger et al., p. 391, Pl. 2, Fig. 4.

Material: Oncophora Beds, Aussüssungshorizont: Türkenbach (50 specimens ex coll. Reichenbacher, BSP 2003 II 60, and the figured specimen BSP 2003 II 17); Grub near Kirn (five paratypes, BSP 1964 XXVIII, further 40 specimens, BSP 1960 I 234); Mühlberg (150 specimens, BSP 1964 XXVIII 156); Stadl Rott/Brombach (18 specimens, BSP 1961 I 22, further 140 specimens, BSP 1964 XXVIII 157); Hutterer/Eggldham (31 specimens, BSP 1961 I 20, further 280 specimens, BSP 1964 XXVIII 158).

Description: The slender shell comprises 5.5 rounded whorls measuring up to 2.5 mm in height. Sculpture consists of closely spaced prosoclin growth lines. The last whorl forms 50–60% of the total height of the shell. The small aperture has inclined egg-shape. It is characterised by a slightly pointed posterior portion. The columellar edge is bent.

The protoconch has 1.25 slightly rounded whorls measuring 0.29–0.3 mm in maximum diameter. The first whorl measures 0.06–0.07 mm in the width of the initial cap and 0.24–0.25 in maximum diameter. The initial 0.7–0.8 whorls are characterised by a distinct groove–ridge pattern. The last quarter of the embryonic shell has irregularly arranged growth lines. The protoconch is terminated by a prominent thickened rim of the shell. The onset of the teleoconch is indicated by the formation of closely spaced growth lines.

Remarks: The protoconch is indicative of a direct development. It is distinguished from all other described *Nematurella* spp. by the distinctly coarser groove–ridge pattern which is ornamenting the initial embryonic shell.

Nematurella pseudozilchi nov. sp.

Fig. 5(5, 6).

Material: Oncophora Beds, Aussüssungshorizont: Türkenbach (holotype, BSP 2003 II 14, five paratypes, BSP 2003 II 40).

Derivation of name: The species name refers to the similarity of the teleoconch morphology to *N. zilchi* from the Kirchberg Formation.

specimen BSP 2003 II 35, Aussüssungshorizont of Türkenbach. 7, same specimen, apical view of protoconch. 8, 9. *S. praebouletti* Schlickum, 1970. 8, specimen BSP 2003 II 36, Aussüssungshorizont of Türkenbach. 9, same specimen, apical view of protoconch. 10–12. *F. wittmanni* (Schlickum, 1964). 10, specimen BSP 2003 II 37, Aussüssungshorizont of Türkenbach, apical view. 11, specimen BSP 2003 II–38, Aussüssungshorizont of Türkenbach, lateral view. 12, same specimen, apical view of protoconch; the arrow is indicating the transition from the protoconch to the teleoconch. Scale bars: 1, 4, 6, 8, 10, 11 = 0.5 mm; 2 = 0.2 mm; 5, 7, 9, 12 = 0.1 mm; 3 = 0.05 mm.

Fig. 9. Basommatophora Keferstein, 1864. 1–3. *G. applanatus* (Thomae, 1945). 1, spécimen BSP 2003 II 32, Aussüssungshorizont de Türkenbach, vue apicale. 2, spécimen BSP 2003 II 33, Aussüssungshorizont de Türkenbach, vue ombilicale. 3, le même spécimen, vue ombilicale de la protoconque ; la flèche indique la transition entre la protoconque et la téléconque. 4, 5. *L. dilatata* (Noulet, 1854). 4, spécimen BSP 2003 II 34, Congerien-Horizon de Leipheim. 5, le même spécimen, vue apicale de la protoconque ; la flèche indique la transition entre la protoconque et la téléconque. 6, 7. *S. armaniacensis* (Noulet, 1857). 6, spécimen BSP 2003 II 35, Aussüssungshorizont de Türkenbach. 7, le même spécimen, vue apicale de la protoconque. 8, 9. *S. praebouletti* Schlickum, 1970. 8, spécimen BSP 2003 II 36, Aussüssungshorizont de Türkenbach. 9, le même spécimen, vue apicale de la protoconque. 10–12. *F. wittmanni* (Schlickum, 1964). 10, spécimen BSP 2003 II 37, Aussüssungshorizont de Türkenbach, vue apicale. 11, spécimen BSP 2003 II 38, Aussüssungshorizont de Türkenbach, vue latérale. 12, le même spécimen, vue apicale de la protoconque ; la flèche indique la transition entre la protoconque et la téléconque. Barres d'échelle : 1, 4, 6, 8, 10, 11 = 0,5 mm ; 2 = 0,2 mm ; 5, 7, 9, 12 = 0,1 mm ; 3 = 0,05 mm.

Type-horizon and type-locality: Silty marls of the Upper Ottangian Aussüssungshorizont at Türkenbach (Oncophora Beds).

Description: The solid slender shell comprises four slightly rounded elongated whorls. The holotype measures 2.45 mm in height and 1.2 mm in width. The whorls are separated by deeply incised sutures. The last whorl forms 70% of the total height of the shell. The inclined aperture is slightly detached from the spire. It has egg-shape with slightly pointed posterior portion. It is characterised by a bent basal and columellar lip.

The protoconch comprises 1.2 slightly rounded low whorls measuring 0.27–0.28 mm in maximum diameter. The first whorl measures 0.22–0.23 mm in maximum diameter and 0.05–0.06 mm in the width of the initial cap. Ornament consists of a very fine groove–ridge pattern. The protoconch is terminated by a thickened rim on the shell. The onset of the teleoconch is indicated by a closely spaced arrangement of strong varices and by the formation of closely spaced orthoclin growth lines.

Remarks: *N. pseudozilchi* has similar teleoconch morphology like *N. zilchi* from the Kirchberg Formation, but differs by its considerably smaller size. The shell of *N. pseudozilchi* is slightly more slender, the height/width-ratio amounts 2–2.2. The protoconch of *N. pseudozilchi* is well distinguished by its considerably smaller dimensions, by lacking an embryonic umbilicus and a characteristic change in the embryonic sculpture. Thus the protoconch of *N. pseudozilchi* is not indicative of a nurse egg or nurse embryos nutrition as typically occurred in *N. zilchi*.

Nematurella strauchi nov. sp.

Fig. 7(6, 7).

Material: Kirchberg Formation, Congerien-Horizon: Leipheim (holotype BSP 2003 II 20).

Derivation of name: Named after Friedrich Strauch, Münster, who worked on the stratigraphy and molluscan fauna of the Bavarian Molasse.

Type horizon and type-locality: The holotype derives from the Upper Ottangian Congerien-Horizon of the Kirchberg Beds at Leipheim.

Description: The thin shelled holotype measures 3.16 mm in height and 1.52 mm in width. The height/width-ratio of the shell amounts 2. It comprises five slightly rounded whorls separated by incised sutures. The body whorl forms about 60% of the total height of the shell. Sculpture consists of closely spaced orthoclin growth lines. The narrow egg-shaped slightly detached aperture is characterised by a thin bent peristome.

The protoconch comprises 1.25 slightly rounded whorls measuring 0.36 mm in maximum diameter. The first whorl measures 0.27 mm in maximum diameter and 0.07 mm in the width of the initial cap. Sculpture is not preserved. The protoconch is terminated by a thickened rim of the shell. The onset of the teleoconch is indicated by the formation of closely spaced growth lines.

Remarks and differences: The protoconch is indicative of a direct development. The teleoconch resembles that of *N. bavarica*, but differs by its very thin shell, less rounded whorls thus less deeply incised sutures and by a more slender aperture. The protoconch differs by its more inflated first whorl. *N. strauchi* sp. n. differs from *N. pappi* by its less slender outline, the thin shell, and by its larger protoconch. *N. flexilabris* differs by its slightly more slender shell with higher body whorl and by a larger and broader aperture. *N. zoebeleini* Schlickum, 1960 differs by its larger size, the higher body whorl and by its less inclined aperture (Schlickum, 1960: p. 208–209, Pl. 18.8). *N. zilchi* differs by its larger shell with more rounded whorls separated by deeper sutures, and by its larger rounded thickened aperture. The protoconch differs by its considerably larger diameter. The transition to the teleoconch is not accompanied by varices like in *N. zilchi*. *N. irenae* Schlickum, 1964 differs by its large elongated spindle shaped shell with well rounded whorls and by its large aperture, which is slightly detached from the spire (Schlickum, 1964: p. 8, Pl. 1.15).

Nematurella zilchi Schlickum, 1960.

Fig. 5(7, 8).

1960. *N. zilchi* nov. sp. - Schlickum, p. 209–211, Pl. 19, Figs. 10 and 11.

1966. *N. zilchi* Schlickum - Schlickum, p. 223–324, Pl. 12, Figs. 9–18.

1973. *N. zilchi* Schlickum - Steininger et al., p. 393, Pl. 2, Fig. 10.

1989. *N. zilchi* Schlickum - Reichenbacher, Pl. 2, Fig. 1.

Material: Kirchberg Formation, Congerien-Horizon: Leipheim (six specimens ex coll. Reichenbacher, BSP 2003 II 61, and the figured specimen BSP 2003 II 15); Bithynien-/Gobius *multipinnatus*-/Dapalis *crassirostris*-Horizon: Leipheim (23 juvenile specimens ex coll. Reichenbacher, BSP 2003 II 62).

Description: The solid shell comprises five to six rounded whorls measuring up to 5 mm in height. The height/width-ratio of the shell amounts 1.8–1.9. The last two to three whorls are higher, less rounded, more elongated and thus the early shell has low conical shape while the last whorls have elongated spindle shape. According to Schlickum (1960) the shell is somewhat variable, with individuals from the *Clupeonella humilis*-/Dapalis *curvirostris*-Horizon having less rounded whorls with less acute spire. The whorls are separated by deep sutures. The last whorl forms about 70% of the total height of the shell. The slightly thickened aperture has rounded egg-shape. It is characterised by a pointed posterior portion which is slightly detached from the shell.

The protoconch comprises 1.2–1.25 slightly rounded low whorls measuring 0.3–0.33 mm in maximum diameter. The first whorl measures 0.25–0.27 mm in maximum diameter and 0.07–0.08 mm in the width of the initial cap. A distinct embryonic umbilicus is present. Ornament consists of a fine groove–ridge pattern on the initial 0.7 whorls of the embryonic shell. This portion is terminated by a slight thickening

of the shell. The subsequent part of the embryonic shell is characterised by fine growth lines. The protoconch is terminated by a thickened rim on the shell. The onset of the teleoconch is indicated by a closely spaced arrangement of varices and by the formation of closely spaced orthoclin growth lines.

Remarks: The protoconch is indicative of a direct development without a free larval stage. The change of sculpture after about 0.7 whorls of the embryonic shell and the presence of fine growth lines on the last half whorl of the embryonic shell may indicate an embryogenesis supported by nurse egg or nurse embryos. A similar development has been described in recent rissoids from the North Atlantic by Warén (1996).

The protoconch differs from that of *N. convexula* with about equal size by its considerably wider initial cap, from those of *N. bavarica* and *N. strauchii* nov. sp. by its smaller size. *N. zilchi* is similar to the type-species *N. flexilabris* Sandberger, 1874, from Switzerland, but differs by its broader shell with larger more rounded aperture (see Schlickum, 1960: Pl. 18.1).

Genus *Staliopsis* Rzehak, 1893.

Type-species: *Staliopsis moravica* Rzehak, 1893 from the Ottnangian of Moravica.

Remarks: The formerly used genus name *Euchilus* Sandberger, 1872 represents a synonym of *Nystia* Tournouër, 1869 (cf. discussion in Schlickum, 1968).

Subgenus *Staliopsis* Rzehak, 1893.

Staliopsis dehmi (Schlickum, 1961).

1961. *Euchilus dehmi* nov. sp. - Schlickum, p. 64, Pl. 3, Fig. 3.

1964. *E. dehmi* Schlickum - Schlickum, p. 9–10, Pl. 1, Fig. 19.

1971. *Staliopsis (Staliopsis) dehmi* (Schlickum) - Schlickum, Pl. 3, Fig. 31.

1973. *Staliopsis (Staliopsis) dehmi* (Schlickum) - Steinger et al., p. 394–395, Pl. 2, Fig. 15.

Material: Oncophora Beds, Schill-Horizon: Branzmühl (six paratypes, BSP 1961 I 423–428, further seven specimens, BSP 1961 I 429); Mistelbach (one specimen, BSP 1964 XXV III 159).

Description: The thick slender conical-ovate shell has up to six whorls with acute apex measuring up to 4.5 mm in width and up to 3 mm in height. Whorls are only moderately rounded, separated by deep sutures and sculptured by very fine more or less evident spiral ribs. The last whorl amounts 70–75% of the total height of the shell. The subangular aperture has a slightly callous columella with a bent columellar edge and it is surrounded by a prominent varix-like thickening.

The protoconch is not well preserved. The initial 2.5 whorls of the shell measure 0.3 mm in maximum diameter. The first whorl measures 0.13 mm in maximum diameter. The width of the initial cap amounts 0.06 mm. Transition from the Protoconch to the teleoconch is not preserved.

Remarks: Dimensions of protoconchs of the investigated specimens from Branzmühl are indicative of an indirect devel-

opment including a free planktotrophic larval stage. The protoconch is distinguished from similar early ontogenetic shells of *C. conoidea* and *C. ammoni* by slightly smaller larval shells but a considerably wider initial cap. The protoconch of *C. hoelzli* differs by comprising 0.6–0.7 whorls less and by its considerably smaller initial cap.

S. dehmi differs from the similar *S. grimmi* by its considerably smaller size, more slender shell, lower last whorl and smaller aperture. *S. puisseguri* (Schlickum, 1965) from Lower Bavaria is similar but differs by its considerably smaller shell with shorter spire and by the very large last whorl, well rounded to the base, with large aperture (Schlickum, 1965: p. 103, Figs. 2 and 3).

Staliopsis grimmi (Schlickum, 1961).

1961. *Euchilus grimmi* nov. sp. - Schlickum, p. 64, Pl. 3, Fig. 3.

1964. *E. grimmi* Schlickum - Schlickum, p. 10, Pl. 1, Fig. 20.

1971. *Staliopsis (Staliopsis) grimmi* (Schlickum) - Schlickum, Pl. 3, Fig. 33.

1973. *Staliopsis (Staliopsis) grimmi* (Schlickum) - Steinger et al., p. 395, Fig. 14.

Material: Oncophora Beds, Aussüssungs-Horizon: Hitzenau/Simbach (three paratypes, BSP 1961 430–433); Bergham (three specimens, BSP 1961 I 434).

Description: The thick ovate-conical shell with acute spire consists of up to six moderately rounded whorls measuring up to 7.5 mm in height and up to 5 mm in width. The whorls are separated by moderately incised sutures and are sculptured by more or less evident fine spiral ribs or cords. The last whorl amounts more than 75% of the total height of the shell. The large subangular aperture is characterised by a callous columella with a bent columellar edge. A varix-like thickening is surrounding the aperture.

Remarks: *Staliopsis edlaueri* (Schlickum, 1963) from the Kirchberg Beds with a similar shell outline differs by its thinner shell, the shorter, low conical spire and by deeper incised sutures (cf. Schlickum, 1963: p. 3–4, Pl. 1, Fig. 1).

Family Bithyniidae Gray, 1857

Genus *Bithynia* Leach in Abel, 1818.

Type-species: The recent European species *Paludina tentaculata* Linnaeus, 1758.

Bithynia cf. *glabra* (Zieten, 1830).

Fig. 8(1, 2).

1830. *Cyclostoma glabrum* nov. sp. - Zieten, p. 42, Pl. 31, Fig. 9.

1874. *Bythinia* [sic!] *gracilis* (Zieten) - Sandberger, p. 561, Pl. 28, Fig. 16.

1964. *Bithynia glabra* (Zieten) - Schlickum, p. 9.

1966. *B. glabra* (Zieten) - Schlickum, p. 324, Pl. 12, Fig. 22.

1989. *Bithynia* cf. *glabra* (Zieten) - Reichenbacher, Pl. 1, Fig. 4.

Material: Kirchberg Formation, Bithynien-/Gobius *multipinnatus*-*Idapalis crassirostris*-Horizon: Leipzig (two

juvenile specimens ex coll. Reichenbacher, BSP 2003 II 63, among them the figured specimen BSP 2003 II 29).

Description: The egg-shaped shell with conical spire measures up to 9.5 mm in height and up to 6.5 mm in width. It comprises five to six slightly rounded whorls, which are separated by moderately incised sutures. The body whorl forms about 60% of the total height of the shell. The rounded to egg-shaped aperture may be slightly detached from the shell. The protoconch comprises 1.25 slightly rounded whorls measuring 0.38 mm in maximum diameter and 0.23 mm in height (in the visible part). The first whorl measures 0.31–0.32 mm in maximum diameter and 0.1 mm in the width of the initial cap. The first whorl is ornamented by a fine groove–ridge pattern. The last quarter whorl is sculptured by irregular growth lines. The protoconch is terminated by a thickened rim of the shell. The onset of the teleoconch is indicated by the formation of closely spaced growth lines.

Remarks: *B. dunkeri* Gude, 1913 which co-occurred in the Kirchberg Formation (Schlickum, 1966: p. 324, Pl. 12.19–21) differs by its broad shell with larger body whorl, larger aperture, by the more flattened whorls and by its stouter apex.

Order Cerithiimorpha Golikov and Starobogatov, 1975

Superfamily Cerithioidea Férussac, 1819

Family Melanopsidae H. and A. Adams, 1854

Genus *Melanopsis* Férussac, 1807.

Type-species: The recent species *Buccinum praemorsum* Linnaeus, 1758 from South Spain and North Africa.

Melanopsis impressa impressa Krauss, 1852.

Fig. 8(3–5).

1852. *M. impressa* nov. sp. - Krauss, p. 143, Pl. 3, Fig. 3.

1874. *M. impressa* Krauss - Sandberger, p. 558, Pl. 31, Fig. 8.

1964. *M. impressa impressa* Krauss - Schlickum, p. 11, Pl. 2, Figs. 23–25.

1973. *M. impressa impressa* Krauss - Steininger et al., p. 404–405, Pl. 4, Figs. 6 and 7.

1989. *M. impressa impressa* Krauss - Reichenbacher, Pl. 2, Fig. 6.

Material: Kirchberg Formation, Congerien-Horizon: Leipheim (two specimens ex coll. Reichenbacher, BSP 2003 II 64, and the figured specimen BSP 2003 II 30); Oncophora Beds, Aussüßungshorizont: Türkenbach (50 specimens ex coll. Reichenbacher, BSP 2003 II 65, and the figured specimen BSP 2003 II 31).

Description: The melanopsid shell measures up to 30 mm in height and up to 15 mm in width. It comprises about 10 whorls. Juvenile and subadult specimens bear an acute spire. The large body whorl forms up to 80% of the total height of the shell (in adult specimens). The oblique oval aperture is characterised by a prominent columellar callus and by a distinct anterior notch. The protoconch comprises about 1.5 rounded whorls. It measures 0.26 mm in maximum diameter and 0.24 mm in height. The first whorl measures 0.23 mm in maximum diameter and 0.08 mm in the width of the initial cap. A distinct embryonic umbilicus is present. Ornament con-

sists of a very fine wrinkled pattern. The protoconch is terminated by a thickened rim on the shell.

Remarks: The protoconch is indicative of a direct development. Morphology and ornament are very similar to that of Recent and Pannonian melanopsids as described by Kowalke (1998); Harzhauser et al., (2002). The following juvenile teleoconch is smooth, but can be differentiated from the protoconch by its less rounded whorls, by lacking a wrinkled ornament, and by a regular sculpture of closely spaced sinuous growth lines. We found this species for the first time within the Congerien-Horizon, where considerably slender morphs (Fig. 8(3)) occur. These morphs are probably pointing to sub-optimal conditions influenced by higher salinities. These morphs however show no further conchological differences that would justify a separation from the typical *M. impressa impressa*. Especially the protoconch morphologies are identical.

Specimens assigned to *M. impressa* with identical teleoconch morphology without preserved protoconchs already appeared in the Aquitanian of the Mesohellenic Trough (Greece) as described by Harzhauser and Kowalke (2001).

Subclass Heterostropha Fischer, 1885

Order Pulmonata Cuvier, 1817

Suborder Basommatophora Keferstein, 1864

Superfamily Lymnaeoidea Rafinesque, 1815

Family Lymnaeidae Rafinesque, 1815

Genus *Lymnaea* Lamarck, 1799.

Type-species: The Recent European species *Helix stagnalis* Linnaeus, 1758.

Lymnaea dilatata (Noulet, 1854).

Fig. 9(4, 5).

1854. *L. dilatata* nov. sp. - Noulet, p. 107.

1964. *Radix socialis dilatata* (Noulet) - Schlickum, p. 14–15, Pl. 2, Fig. 33.

1966. *Radix (socialis) dilatata* (Noulet) - Schlickum, p. 326, Pl. 13, Fig. 26.

1989. *R. socialis dilatata* (Noulet) - Reichenbacher, Pl. 1, Fig. 9.

2000. *L. dilatata* (Noulet) - Fischer, p. 136, Figs. 1 and 2.

2002. *L. dilatata* (Noulet) - Binder, p. 165, Pl. 1, Fig. 7a, b.

Material: Kirchberg Formation, Congerien-Horizon: Leipheim (one figured specimen, BSP 2003 II 34); Bithynien-/Gobius *multipinnatus*-/Dapalis *crassirostris*-Horizon: Leipheim (one specimen ex coll. Reichenbacher, BSP 2003 II 66).

Description: The medium sized lymnaeid shell measures up to 16 mm in height and up to 11 mm in width. The large body whorl forms more than 80% of the total height of the shell. The protoconch comprises about one bulbous whorl measuring 0.6 mm in maximum diameter and 0.2 mm in the width of the initial cap. The first half whorl is characterised by a slightly folded surface. The transition to the teleoconch is indicated by the formation of fine growth lines accompanied by slight varices.

Remarks: *L. dilatata* differs from *Stagnicola armaniacensis* by its much broader shell and by the larger increase of the diameter of the whorls. The protoconch differs by its considerably wider initial cap.

L. dilatata considerably differs from *Radix* Montfort, 1810, with the type-species *Helix auricularia* Linnaeus, 1758 (see Wenz and Zilch, 1959–1960: p. 96, Fig. 303), regarding the higher acute spire and the less extended aperture. This species has formerly been considered as a subspecies of *L. socialis* (Zieten, 1830) from the Late Miocene of SW Germany, which is not followed here (see discussions in Fischer, 2000; Binder, 2002).

Genus *Stagnicola* Jeffreys, 1830.

Type-species: The Recent European species *Stagnicola palustris* (Müller, 1774).

S. armaniacensis (Noulet, 1857)

Fig. 9(6, 7).

1857. *Limnaea armaniacensis* nov. sp. - Noulet, p. 22.

1964. *Stagnicola* (*Stagnicola*) *armaniacensis* (Noulet) - Schlickum, p. 13–14, Pl. 2, Fig. 31.

1989. *S. armaniacensis* (Noulet) - Reichenbacher, Pl. 2, Fig. 7.

Material: Oncophora Beds, Aussüßungshorizont: Türkenbach (one figured specimen, BSP 2003 II 35); Bergham (three specimens, BSP 1964 XXVIII 160–162); Woching (six specimens, BSP 1964 XXVIII 163–168).

Description: The moderately slender lymnaeid shell measures up to about 30 mm in height and up to 11 mm in width. The body whorl forms about 70% of the total height of the shell. The protoconch comprises about one slightly rounded whorl measuring 0.54 mm in maximum diameter. The width of the initial cap amounts 0.18 mm. The transition to the teleoconch is indistinct.

Remarks: The protoconch of *S. armaniacensis* differs from that of *S. praebouiletti* by its wider shell with higher body whorl and by its larger protoconch.

Stagnicola praebouiletti Schlickum, 1970.

Fig. 9(8, 9).

1964. *Stagnicola* (*Stagnicola*?) *bouiletti* - Schlickum, p. 14, Pl. 2, Fig. 32 [non Michaud, 1855].

1970c. *S. praebouiletti* nov. sp. - Schlickum, p. 92, Figs. 12–17.

1973. *Stagnicola* (*Stagnicola*) *praebouiletti* Schlickum - Steininger et al., p. 451, Pl. 9, Fig. 10.

Material: Oncophora Beds, Aussüßungshorizont: Türkenbach (one figured specimen, BSP 2003 II 36).

Description: The very slender thin shell has elongated spindle shape with an acute spire. It comprises about eight flat to slightly rounded whorls. The body whorl forms about 40% of the total height of the shell. According to Sandberger (1875) the shell measures more than 40 mm in height. The elongated egg-shaped aperture is characterised by an acute parietal edge. The protoconch comprises about one slightly rounded whorl measuring 0.4 mm in maximum diameter. The

width of the initial cap amounts 0.11–0.12 mm. The transition to the teleoconch is indistinct.

Superfamily Planorboidea Rafinesque, 1815

Family Planorbidae Rafinesque, 1815

Genus *Gyraulus* Charpentier, 1837.

Type-species: The Recent European species *Gyraulus albus* (Müller, 1774).

Gyraulus applanatus (Thomae, 1845).

Fig. 9(1–3).

1845. *Planorbis applanatus* nov. sp. - Thomae, p. 150.

1964. *Gyraulus trochiformis dealbatus* (Braun) - Schlickum, p. 15, Pl. 2, Fig. 35.

1970a. *G. trochiformis applanatus* (Thomae) - Schlickum, p. 148–149, Pl. 10, Fig. 6.

1970b. *G. trochiformis applanatus* (Thomae) - Schlickum, p. 180.

1973. *G. trochiformis dealbatus* (Braun) - Steininger et al., p. 451–452, Pl. 9, Fig. 11a, b.

1989. *G. trochiformis dealbatus* (Braun) - Reichenbacher, Pl. 1, Fig. 11.

Material: Kirchberg Formation, Bithynien-/Gobius multipinnatus-/Dapalis crassirostris-Horizon: Leipheim, Illerkirchberg (10 specimens ex coll. Reichenbacher, BSP 2003 II 67); Oncophora Beds, Aussüßungshorizont: Türkenbach (two specimens ex coll. Reichenbacher, figured, BSP 2003 II 32–33).

Description: The planorbid shell measures up to 3 mm in maximum diameter. It is smooth aside from closely spaced regular growth lines. The protoconch comprises about one whorl. The initial cap which is partly covered by the succeeding whorl measures about 0.05 mm in width. The maximum diameter of the first whorl amounts 0.18 mm in the visible part. The embryonic shell is characterised by a wrinkled surface which causes a fine groove–ridge pattern. Additional sculpture consists of about 10 fine spiral threads. The transition to the adult shell is indistinct, indicated by the successive onset of dense growth lines and by the decrease of the embryonic sculpture.

Remarks: Schlickum (1970a) mentioned the variability of the “stems” *applanatus* (Thomae), with more rapidly increasing whorls, and *dealbatus* (Braun), with regularly increasing narrow whorls. Our material reveals both types, connected by transitional morphs. We consider them as conspecific, thus *G. applanatus* represents the valid name of the species.

Genus *Ferrissia* Walker, 1903.

Type-species: The recent North American species *Ancylus rivularis* Say, 1817.

Ferrissia wittmanni (Schlickum, 1964).

Fig. 9(10–12).

1964. *Ancylus wittmanni* nov. sp. - Schlickum, p. 15–17, Pl. 2, Figs. 36–38.

1973. *A. wittmanni* Schlickum - Steininger et al., p. 453, Pl. 10, Fig. 1a, b.

1989. *F. wittmanni* (Schlickum) - Reichenbacher, Pl. 1, Fig. 8.

Material: Oncophora Beds, Ausstüßungshorizont: Türkenbach (two specimens ex coll. Reichenbacher, figured, BSP 2003 II 37–38).

Description: The cap like shell measures up to 12 mm in length and 8.5 mm in width. It is smooth aside from distinct growth lines. Juvenile specimens are characterised by axial threads. The teleoconch shape is variable. Some individuals are characterised by very slender, elongated oval teleoconchs with very narrow aperture. The cap like flat protoconch has roundish to slightly elongated shape. It measures 0.49–0.5 mm in maximum diameter. The initial (median) portion, which central part is depressed and it is characterised by a folded surface. The outer portion is sculptured by closely spaced prominent axial threads.

Remarks: Individuals from the Sarmatian of St. Margarethen (Austria, Central Paratethys) with corresponding morphology of the protoconch and teleoconch could not be distinguished and are considered as conspecific (Harzhauser and Kowalke, 2002).

4. Discussion and conclusions

The investigated bivalves of the Kirchberg Formation and of the Oncophora Beds were characterised by larval shells indicative of indirect development including planktonic veliger stages. Veliger larvae were free swimming and feeding on phytoplankton as indicated by the larval shells with regular growth lines, well demarcated from the embryonic shells. Among the lymnardiines the prodissoconch of *L. schuetti* is distinguished from that of *L. schmieri* by a smaller embryonic shell, but larger larval shell, which documented a longer stay within the plankton. This could explain the far distribution of *L. schuetti*, which co-occurred within the Oncophora Beds and within the Kirchberg Formation, whereas *L. schmieri* was restricted to the Oncophora Beds. From this sequence *L. schuetti* has been described as *L. kuiperi* by Schlickum (1962), which according to our investigations represents a synonym of *L. schuetti*.

Limnopageta and *Limnopappia* evolved from a *Cerastoderma*-like ancestor after reduction of the hinge and of the third shell layer. *Cerastoderma* was absent from the Oncophora Beds, even the brackish-pliohaline strata (e.g. Mehlsande) lack any records of *Cerastoderma* spp. Contrary, *Cerastoderma* was widely distributed in the Congerien-Horizon of the Kirchberg Formation. This could indicate an immigration of *Cerastoderma* from the Molasse Basin of Eastern Switzerland into the Kirchberg Basin (see Fig. 1), which most probably coincided with the Transgressive Cycle 3 of the Swiss Upper Marine Molasse (Reichenbacher, 1993).

The genus *Mytilopsis* (Dreissenidae) is present by the three species *Mytilopsis rottensis*, *M. amygdaloides* and *M. clavaeformis*, which had formerly been assigned to *Congerina* or *Dreissena* but could be distinguished from those genera by

shell characteristics. The *Mytilopsis* spp. could well be differentiated by their protoconch morphologies. *M. rottensis* (= *C. schuetti* according to Schlickum, 1964) and *M. clavaeformis* co-occurred within the Oncophora Beds and Kirchberg Formation.

Among the gastropods the neritid genus *Theodoxus* is characterised by a direct development without an inclusion of a free larval stage. *T. cyrtocelis* has a similar bulbous protoconch like its modern congener *T. fluviatilis*, indicative of a yolk rich embryogenesis, probably supported by nurse egg feeding, with subsequent hatching of crawling young. Globular to subangular neritid shells, which had been attributed to *Clithon* by previous authors (e.g. Schlickum, 1964, 1970, 1971), were recognised to belong to the genus *Agapilia*, and *A. schlickumi* nov. sp. could be differentiated from the type-species *A. picta* from the Aquitanian of the Mediterranean with similar teleoconch morphology by investigations of the protoconch. The protoconch reflected a direct development, whereas the type-species was characterised by planktonic veliger larvae (Harzhauser and Kowalke, 2001). *A. schlickumi* nov. sp. most probably migrated to the Oncophora Basin of Lower Bavaria from the Central Paratethys due to the absence of this species in the Kirchberg Formation.

The hydrobiids *Hydrobia* cf. *semiconvexa* from the Kirchberg Formation and its counterpart *H. frauenfeldi* from the Oncophora Beds could well be separated by the dimensions and sculpture of their embryonic shells. The genus *Nematurella* is presented by the species *N. convexula*, *N. bavarica*, *N. zilchi* and *N. strauschi* nov. sp. in the Kirchberg Formation and *N. klemmi*, *N. pappi* and *N. pseudozilchi* nov. sp. in the Oncophora Beds. The species seemingly have morphologically similar counterparts (see remarks in the systematic part), which however are well separated by their protoconch morphologies (Table 2). *Nematurella* spp. are characterised by protoconchs indicating a direct development with hatching of crawling young; in case of *N. zilchi* this development was most probably supported by nurse egg feeding.

Ctyroikia (Hydrobiidae) represents the only gastropod genus of the investigated gastropod fauna with species reflecting an indirect development with inclusion of a free planktonic veliger stage. The low conical shape of the protoconchs and the morphology of the sinusigera are similar to Mid-Miocene Rissooidea from the Central Paratethys, e.g. *R. turricula* and *R. clotho*, and recent representatives from the North Atlantic and from the Mediterranean Sea, such as *Peringia ulvae*, *Rissoa guerini*, *R. dolium* (Kowalke, 1998: Pl. 9, Figs. 6 and 7, Pl. 10, Fig. 1; Kowalke and Harzhauser, 2004: Fig. 4). *C. ammoni* and *C. hoelzli* could be differentiated by comparison of the protoconch morphologies. *C. ammoni* was characterised by a larger multispiral larval shell, indicating a longer stay within the plankton. However *C. ammoni* was restricted to the Oncophora Beds most probably by ecological reasons, whereas *C. hoelzli* co-occurred within the Kirchberg Formation, from where it could be reported within this study for the first time. *C. conoidea* and *C. zoebeleini* were restricted to the Kirchberg Formation. *C.*

Table 3
Distribution of the species during the late Otnungian
Distribution des espèces du Otnungien terminal

	Kirchberg Basin	Oncophora Basin (LB)
<i>Cerastoderma sociale</i> (Krauss, 1852)	x	
<i>Cerastoderma solitarium</i> (Krauss, 1852)	x	
<i>Limnopagetia friabilis</i> (Krauss, 1852)	x	
<i>Limnopagetia bavarica</i> (Ammon, 1888)		x
<i>Limnopagetia ganssi</i> (Schlickum, 1970)	x	
<i>L. modelli</i> Schlickum, 1964		x
<i>Limnopagetia reconditum</i> (Mayer, 1876)	x	
<i>L. schmiereri</i> Schlickum, 1964		x
<i>L. schuetti</i> Schlickum, 1962	x	x
<i>M. amygdaloides</i> (Dunker, 1848)	x	
<i>Mytilopsis clavaeformis</i> (Krauss, 1852)	x	x
<i>Mytilopsis rottensis</i> (Ammon, 1888)	x	x
<i>A. schlickumi</i> sp. n.		x
<i>T. cyrtocelis</i> (Krauss, 1852)	x	x
<i>H. frauenfeldi</i> (Hoernes, 1856)		x
<i>Hydrobia</i> cf. <i>semiconvexa</i> Sandberger, 1874	x	
<i>C. hoelzli</i> (Schlickum, 1964)	x	x
<i>C. ammoni</i> Schlickum, 1965		x
<i>C. conoidea</i> (Krauss, 1852)	x	
<i>C. zoebeleini</i> Schlickum, 1970	x	
<i>N. bavarica</i> (Sandberger, 1874)	x	
<i>N. convexula</i> Schlickum and Strauch, 1967	x	
<i>N. klemmi</i> Schlickum, 1964		x
<i>N. pappi</i> Schlickum, 1960		x
<i>N. pseudozilchi</i> sp. n.		x
<i>N. strauchi</i> sp. n.	x	
<i>N. zilchi</i> Schlickum, 1960	x	
<i>S. dehmi</i> (Schlickum, 1961)		x
<i>S. grimmi</i> (Schlickum, 1961)		x
<i>Bitynia</i> cf. <i>glabra</i> (Zieten, 1830)	x	x
<i>M. impressa impressa</i> Krauss, 1852	x	x
<i>L. dilatata</i> (Noulet, 1854)	x	
<i>S. armaniacensis</i> (Noulet, 1857)	x	x
<i>S. praebouiletti</i> (Schlickum, 1970)		x
<i>G. applanatus</i> (Thomae, 1845)	x	x
<i>F. wittmanni</i> (Schlickum, 1964)	x	x

conoidea with similar protoconch dimensions like *C. ammoni* is distinguished by its slightly smaller embryonic shell and by its broad conical teleoconch. This species differs also by its prominent colour pattern of broad yellowish to brown stripes. *C. zoebeleini* differs in the unique feature of direct development with hatching of crawling young, as it could easily be distinguished from all other present *Ctyrokia* spp. with planktotrophic development. The presence of planktonic larvae in *Ctyrokia* enabled a far distribution of the genus, which has also been reported from contemporaneous deposits of Moravia (Steininger et al., 1973).

The molluscan faunas of the Kirchberg Formation and of the Oncophora Beds indicate a similar depositional environment. Ten species of the herein investigated material were recognised to co-occur in both sequences (Table 3). A connection of the depositional environments during the late Otnungian is feasible, as it is also indicated by fish faunas (Reichenbacher, 1993) (Fig. 1). A restricted shallow coastal

milieu with reduced water energy and salinity is indicated. Plant remnants are evident. However a connection to the open sea is indicated by the presence of planktotrophic larval development in gastropods.

The oligohaline taxa to freshwater dwellers like *Melanopsis* or pulmonates (*Lymnaea*, *Stagnicola*, *Gyraulus*, *Ferrissia*), predominantly frequent within the Upper Otnungian Aussüssungshorizont and Lakustrische Schichten, are usually absent from mesohaline waters with more than 5 ppt salinity (Remane and Schlieper, 1971). Thus a primarily oligohaline to freshwater milieu with occasional increase of salinity is probable. *A. schlickumi* nov. sp. is particularly frequent in the restricted milieu of the Aussüssungshorizont. This indicates that *A. schlickumi* preferred oligohaline conditions, whereas early Early Miocene as well as Karpatian species of *Agapilia* typically inhabited brackish to brackish-marine biotops, i.e. an outer estuarine mud flat milieu (Harzhauser and Kowalke, 2001; Harzhauser, 2002).

The conspicuous absence of any potamidid species from the Otnungian of the Western Paratethys could confirm the interpretation of a brackish water milieu with low salinities (oligohaline to mesohaline). But this absence most probably is also caused by other factors than only by low salinities, e.g. the restricted connection or barrier to the Central Paratethys during the middle to late Otnungian. Strata which have been assigned to a brackish milieu, e.g. Schillhorizont and Glimmersande also lack Potamididae. On the other hand potamidids are ubiquitous faunal elements during the Early and Middle Miocene of the Central Paratethys and of the Mediterranean (Harzhauser and Kowalke, 2001; Kowalke, 2003) and euryhaline Recent *Potamides* settles a multitude of oligohaline to hypersaline habitats of the Mediterranean (Kowalke, 2001). Thus the absence of potamidids in the late Otnungian of the Western Paratethys remains enigmatic.

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