Studies on the side-branch planorbids (Mollusca, Gastropoda) of the Miocene crater lake of Steinheim am Albuch (southern Germany)

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Planorbid shells are abundant in the sediments of the fresh water lake of Steinheim am Albuch throughout its depositional history. They were studied repeatedly after Hilgendorf's (1867) initial work. He had all different morphs that appeared during the long lasting lake history related to a single founder species that developed into several lineages, one of which was designated as 'main-branch' with large conspicuous morphs. Most subsequent studies are concerned with that branch.

Based on new material and aided by SEM studies of the protoconchs, the small side-branch morphs have been restudied and evolutionary lineages are reconstructed. As a result the phylogenetic lineages of planorbids from lake Steinheim can be considered to have evolved from a single or up to three founder species.

The history of the planorbids of the Steinheim Basin shows a first immigration by species that normally lived in the ponds and creeks of the surrounding area. Subsequently a characteristic endemic fauna evolved which was separated by an effective barrier from further immigrants; this barrier remained active throughout the existence of the lake. The planorbids diversified differently within the three established branches. When the lake shrunk in size and changed in water chemistry due to evaporation, speciation accelerated. Chemical stress pushed an increasing diversity in shell shapes of planorbids as well as of some ostracodes during the *trochiformis* event. When the chemical stress was reduced again the extremes of the evolution were eradicated and speciation proceeded at a rate similar to prior of the event.

Two species are described as new: *Gyraulus protocrescens* sp. nov. and *G. rotundostomus* sp. nov.

Contents

Introduction

The fresh water lake sediments of Steinheim am Albuch are rich in well preserved snails. According to the literature one species of the genus *Gyraulus* (Planorbidae) which colonised the early lake, underwent a tremendous radiation. This radiation can be reconstructed by studying a unique complete fossil record. In more than a hundred years several authors have constructed different phylogenetic trees. Hilgendorf (1867) published the first one and established a 'main-branch' and two 'side-branches'. The main-branch comprises big morphs, most of which are very abundant. The side-branches comprise small planorbids, which are normally less abundant. After Hilgendorf (1867) research and discussion focussed on the main-branch.

Now new material from five sections with very dense sampling was available. The side-branch morphs were documented with SEM micrographs and the evolution of the side-branches was restudied.

The Steinheim Basin is a meteor crater. It is situated in the Late Jurassic limestones of southern Germany, at a distance of 40 km from the bigger Ries crater. Both craters are considered to be contemporary. The Ries has got a radiometric age of 14.8 Ma ± 0.7 Ma (Gentner et al., 1963).

The Steinheim Basin has an almost circular outline and a diameter of 3.5 km. It was originally 220 m deep. In its centre is an uplift, predominantly composed of allochthonous Late Jurassic limestones, called the Steinhirt-Klosterberg. It has a diameter of c. 800 m and rises 150 m above the bottom of the original crater.

The bottom of the crater was covered by a 40 to 50 m thick impact breccia, consisting predominantly of Late Jurassic rock debris. It than filled with water and became a lake. The preserved sediments of this lake reach a thickness of 30 to 40 m and consist of calcareous siltstones, arenites and limestones (Mensink, 1984). Part of the sediments were eroded subsequently so that today the original basin can be recognised again.

The duration of the lake's existence is unsure. The lake was situated in a karst area and thus the sedimentation rate is believed to have been low. There is no evidence for creeks debouching into the lake. According to the literature all water came from subterranean karst systems and from rain fall. The lake was thus rather isolated from other fresh water bodies. Reif (1984) and Gorthner (1992) estimate an existence of the lake between some hundreds of thousands of years and more than 1 million years. This is an extraordinary long time for a lake and especially for one of this small size.

The climate was subtropical and the vicinity of the lake was covered with forests populated by a diverse vertebrate fauna (Gregor, 1983; Janz, 1992).

The water level fluctuated so that the central uplift became an island periodically, but there is no evidence for a temporary drying out of the lake.

According to the literature the early lake was populated by a diverse mollusc fauna.

Most of its species became extinct subsequently. Only three species are thought to have survived: *Lymnaea dilatata* Noulet, 1854, *Pseudamnicola pseudoglobulus* (d'Orbigny, 1852) and *Gyraulus kleini* (Gottschick & Wenz, 1916). The tiny simple planorbid *G. kleini* has a wide distribution in the Miocene of southern Germany and is very similar to some Recent species of the genus *Gyraulus*. Whereas the shell shape of *L. dilatata* and *P. pseudoglobulus* remained relatively stable throughout the lake's history, *G. kleini* is considered to represent the stem species of an impressive species radiation. The morphological deviation of the different endemic species originating from these smooth planispiral shells goes very far, resulting in trochiform, uncoiled and ribbed morphs. Hilgendorf (1867) was the first to realise that the different morphs occur at different stratigraphic levels. Influenced by Darwin's theories he constructed a phylogenetic tree which is based on stratigraphic occurrence and similarity of the morphs. All the snails of his tree are known from Steinheim only, except of the assumed founder species *G. kleini*. The basic features of this tree have been confirmed by all subsequent authors who have examined larger amounts of material collected in stratigraphic order (Hyatt, 1880; Gottschick, 1911, 1920; Mensink, 1984).

Hilgendorf (1867) grouped the planorbids into one main-branch and two side-branches of evolutionary lines. The side-branch snails are small and in comparison to the main-branch morphs occur less commonly. Side-branch 1 is considered to be an offshoot of the main-branch. Side-branch 2 is said to be directly derived from the hypothetical stem species. Hilgendorf (1867) himself expressed doubts about this connection of side-branch 2. All later authors who accepted the monophyly of the Steinheim planorbids, however, took it for granted that the second side-branch is a direct offshoot of the stem species *G. kleini*.

Sediments and distribution of the gastropods

The sediments are calcareous and highly fossiliferous. Light-coloured, poorly lithified arenites and siltstones occur, as well as well-lithified carbonates (Mensink, 1984). The facies near the edges and the central uplift is more coarsely grained than that in the deeper more distal parts of the basin. Generally planorbids are rare in the deeper distal facies and more abundant at the edges. Probably the shallow water near the edges was the habitat of the planorbids and their occurrence in the distal facies at least partly resulted from transport over the relatively steep slopes. Obviously this transport did not mix up the zonation of the species which can be recognised in both facies types. In addition, the good preservation of snails in the deep water facies suggests that transport involved predominantly freshly sedimented material.

Because of the widespread parautochthony of the sediments there is no evidence for a primary ecological zonation.

Snails and ostracodes are very abundant throughout. Calcareous algae, especially charophytes are common too. Around the central uplift algal or/and bacterial mounds are present. Many of the lower beds are dominated by remains of charophytes. Although sprouts of charophytes are abundant, their oogonia, which normally have a better potential of fossilisation, are extremely rare. Another unusual feature is that the charophyte-remains are not preserved in calcite but in aragonite (Wolff & Füchtbauer, 1976). Phytoplankton is represented by diatomea and calcispheres. Faecal pellets and fish remains, especially teeth, are quite common.

Sedimentology and geochemistry reflect a changing, somewhat unusual, fresh water environment (Bajor, 1965; Wolff & Füchtbauer, 1976; Mensink, 1984). One remarkable feature is a widespread aragonitic cementation. The carbonates are enriched with heavy O^{18} and they have a low Ca/Mg-ratio, both interpreted as related to a high rate of evaporation (Bajor, 1965).

Since Hilgendorf (1867), the main-branch snails have been used as guide fossils. Each of the zones is defined by the first occurrence of a new morph. This endemic zonation was confirmed by many authors and only slightly changed (i.e. Mensink, 1984). The following zonation is used herein:

Zone of G. *supremus* (uppermost)
Zone of G. *revertens*
Zone of G. *oxystoma*
Zone of G. *trochiformis*
Zone of G. *sulcatus* (includes Hilgendorf's (1867) *discoideus* Zone)
Zone of G. *tenuis*
Zone of G. *steinheimensis*.
Zone of G. *kleini* (lowermost).

Material and methods

The information about the material is mostly from Janz (1992), who studied the ostracodes of the same samples utilised by us.

A total of 130 samples (washing residues) from five sections was sieved and the fraction > 0.5 mm was picked for snails. Fig. 1 shows the location of the sections in the basin.

The combined sections comprise a thickness of c. 23 m (Janz, 1992) from the lower *steinheimensis*-beds to the *supremus*-beds. The correlation of the sections is based on the main-branch planorbids and horizons with abundant leaf and with fish remains (Fig. 3).

Residues and specimens of gastropods are stored in the 'Staatliches Museum für Naturkunde' in Stuttgart (SMNS).

Sections

Section B

Topographical map TK 25 (1:25,000), map-sheet 7325 Heidenheim an der Brenz; co-ordinates R 3577920, H 5395010. Section B comprises 31 samples from the borehole B 26 of the Geological Survey of Baden-Württemberg. The samples are from a depth of 20.0-32.2 m. The drilling was done near the gymnasium of Steinheim am Albuch.

Section B contains the stratigraphically lowermost samples which were available for this study. They have been deposited close to the beginning of the lake's history. This is documented by a high amount of Late Jurassic rock debris deriving from the meteor impact. These samples already contain the first endemic morph G. *steinheimensis* (lowest *steinheimensis*- to *sulcatus*-beds). Section B is situated relatively far from

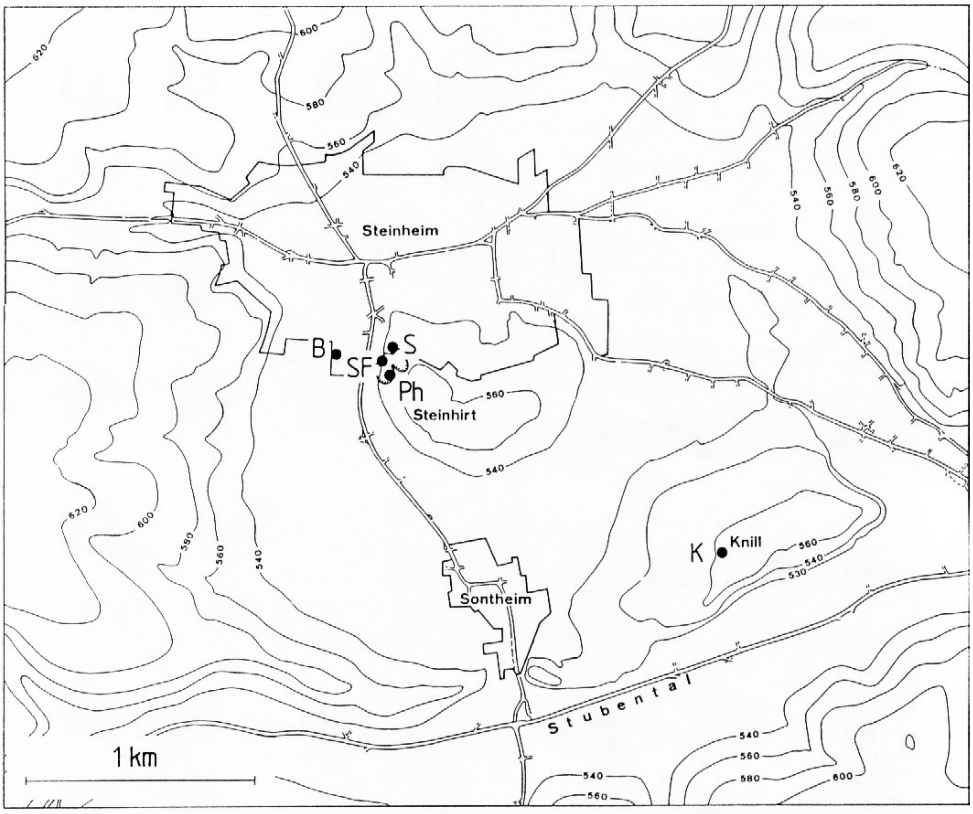

Fig. 1. Topographical map of the Steinheim Basin and the situation of the sampled sections (after Janz, 1992).

the central uplift so that the samples from its lower part display a fine grained, distal facies. The samples of the upper parts are more coarsely grained and they contain abundant remains of charophytes. These samples probably represent a lower stand of the water level.

Section SF

Same map-sheet, coordinates R 3578100, H 5394930. Section SF, comprising two sections with 18 samples all together (leg. Urlichs/Böttcher 1985), is an excavation for the funeral hall of Steinheim am Albuch (uppermost *steinheimensis*- to *sulcatus*-beds), is situated near the central uplift and displays a proximal facies.

Section S

Same map-sheet, coordinates R 3578120, H 5395060. Section S comprises 37 sam-

Fig. 2. Hilgendorf's original figure, published in 1867.
All morphs except No. 1 are endemic varieties of the species *Planorbis multiformis* (von Zieten, 1830). No. 1 is the stem species *Planorbis multiformis* (?) var. *aequeumbilicatus* (Hilgendorf, 1867) (= *Gyraulus kleini*), which has a widespread distribution in the Miocene of southern Germany. No. 2-11 are the main-branch morphs. They are relatively big (the phylogenetic tree is drawn at scale). The main-branch morphs are index fossils for the sediments of Steinheim. Names of the varieties: 2: *steinheimensis* (Hilgendorf, 1867); 3: *tenuis* (Hilgendorf, 1867); 4: *sulcatus* (Hilgendorf, 1867); 5: *discoideus* (Hilgendorf, 1867) [= *planorbiformis* (von Klein, 1847)]; 6: *trochiformis* (Stahl, 1824); 7: *oxystomus* (von Klein, 1847); 8 = *revertens* (Hilgendorf, 1867); 9: *supremus* (Hilgendorf, 1867); 10: *rotundatus* (von Klein, 1847); 11: *elegans* (Hilgendorf, 1867). Side-branch 1 is an offshoot of the main-branch and comprises *kraussii* (von Klein, 1847) = 12 and *pseudotenuis* (Hilgendorf, 1867) = 13. Side-branch 2, directly connected with the founder species, comprises No. 14-19: 14: *parvus* (Hilgendorf, 1867); 15: *minutus* (Hilgendorf, 1867); 16: *crescens* (Hilgendorf, 1867); 17: *triquetrus* (Hilgendorf, 1867); 18: *costatus* (von Klein, 1847); 18a: *costatus major* (Hilgendorf, 1867); 19: *denudatus* (Hilgendorf, 1867).

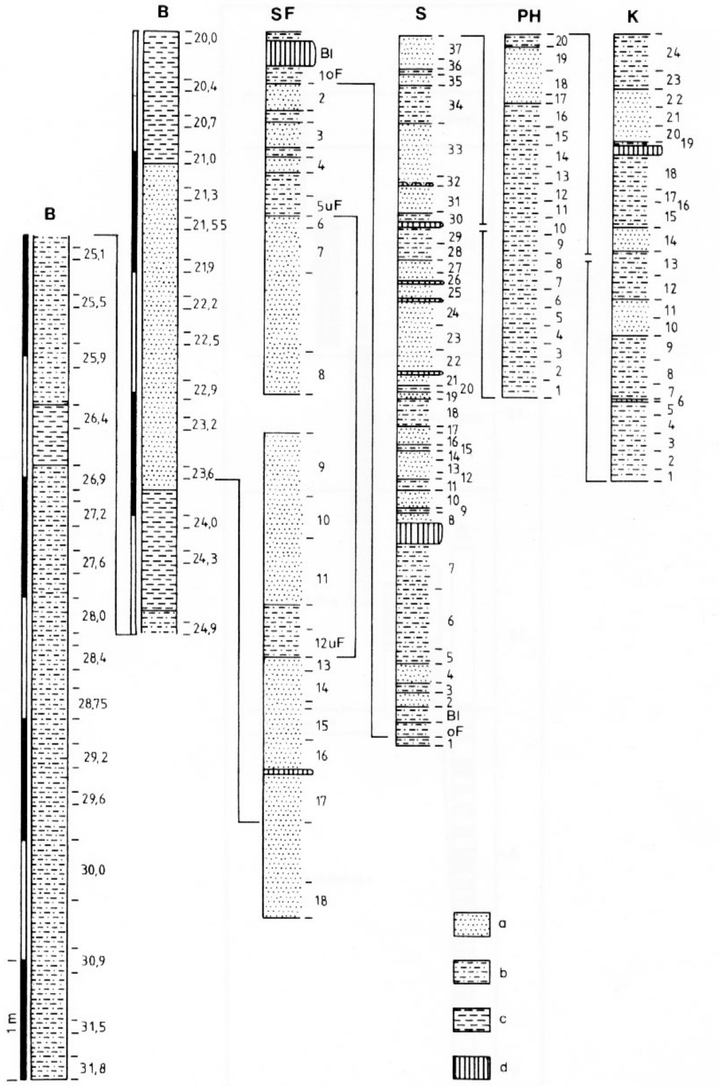

Fig. 3. Correlation and lithology of the sections: uF: lower fish layer, oF: upper fish layer, Bl: leaf layer, a: calcareous sand, b: calcisiltite with calcareous sand ('glue sand'), c: clayey calcisiltites, d): limestone, (after Janz, 1992).

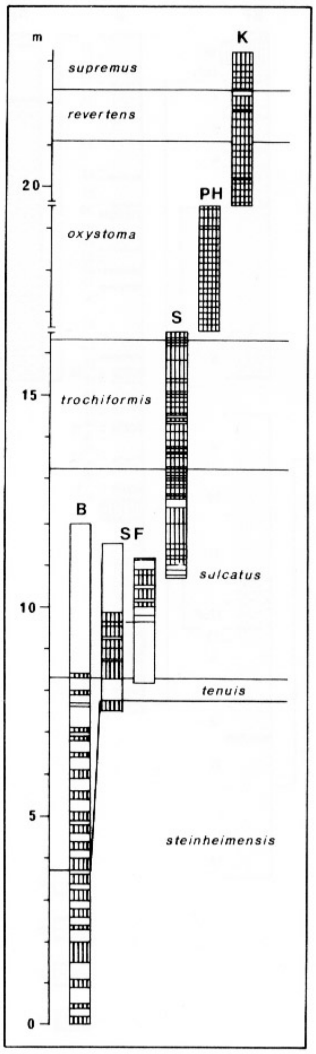

Fig. 4. Correlation of the sections with the guiding main-branch planorbids (modified after Janz, 1992).

ples (leg. Heizmann/Urlichs 1976) from an extension of the cemetery of Steinheim am Albuch (*sulcatus* to lowest *oxystoma* beds). It is situated near the central uplift and displays a proximal facies.

Section Ph

Same map-sheet, coordinates R 3578140, H 5394930. Section Ph comprises 20 samples (leg. Janz, 1989) from Pharion's Sandpit near the central uplift (*oxystoma* beds). It displays a proximal facies.

Section K

Same map-sheet, coordinates R 3579640, H 5394140. Section K comprises 18 samples (leg. Janz/Heizmann, 1989), from an excavation at the Knill. The Knill is a hill and the classical location for the uppermost beds of the Steinheim Basin (*oxystoma* to *supremus* beds). It is situated near the southeastern edge of the basin and displays a fine-grained facies.

Several thousands of individuals of side-branch planorbids have been picked. About 300 were documented with c. 1000 SEM-micrographs. Statistical methods like those employed by Mensink (1984) for the main-branch are not suitable for the side-branches, because side-branch morphs are less common and thus not available in large numbers. The fossil record here is less complete. Also, the important stem species of the side-branch snails provide too few characters that can be used effectively for statistical analysis. Mensink (1984) applied an univariate analysis for some biometrical characters of the main-branch planorbids. Recently Povel (this vol.) applied cluster analysis to Mensink's data set, which resulted in a different interpretation.

Herein the traditional typological method is used. The morphologies are compared from bed to bed. Similarity and transitional morphs are used as arguments for the reconstruction of phylogenetic connections. The authors see no reason to believe in an implicit superiority of a phylogenetical analysis based on statistical methods. The difference with previous authors who used the typological method lies in the use of the SEM (more characters, better illustrations) and in the dense sampling at new localities (sections B and SF).

Preservation

Usually the snails of the Steinheim Basin are very well preserved. Shells are not recrystallised and show original structures. Microsculptures are preserved on the shell surface in many cases. Some samples, however, contain only poorly preserved specimens due to corrosion and dolomitisation. Sometimes corrosion seems to occur selectively in some species. It was for instance nearly impossible to find an uncorroded *G. triquetrus* (Hilgendorf, 1867), whereas other species of the same sample were well preserved. It is also difficult in many samples to find an individual of *G. costatus* (von Klein, 1847) with preserved protoconch microsculpture. *G. costatus* is often yellowish in comparison with other species which also indicates a selective alteration. Perhaps these species lived in environments with a more aggressive early diagenesis. Gorthner (1984a) reported from the Recent Lake Ochrid that distinct chemical parameters of the sediments, such as the Ca/Mg-ratio and H_2S content, are related to different ecological environments and gastropod habitats.

Aragonitic cement often covers the shells (Pl. 7, fig. 2). In most specimens the aperture is broken off. Sometimes this seemed to have happened during the life time of the snails and many shells thus show healed fractures. Most of the planorbids of Steinheim lake did not stabilise their aperture with an inner collar, neither when fully grown nor during growth.

As already mentioned, there is evidence for transport and parauthochtony of the snails and this has to be taken into consideration. This transport did not disturb the zonation of the gastropods. The predominantly good preservation makes it unlikely that transport was really important.

The early lake and *Gyraulus kleini*

We have not been able to assemble own data on the very early lake, because all historic outcrops of the oldest beds have disappeared. Because of the importance of the pioneer fauna we try to present a brief overview of the available literature data.

The oldest sediments (*kleini*-beds or 'Sylvana Kalke') were known only from the western edge of the basin at the 'Vordere Grot' and from the northern edge (Hilgendorf, 1867; Gottschick, 1911, 1920; Gottschick & Wenz, 1919-1922). Additionally, Mensink (1984) reported the *kleini*-beds from boreholes also in the deeper parts of the basin.

According to Mensink (1984) the *kleini* beds are not very fossiliferous and the fauna is not diverse. In contrast Gottschick (1920) and Gottschick & Wenz (1919-20) reported a diverse fauna with abundant specimens. They noted 16 species of fresh water gastropods and amongst them 4 planorbids: *Planorbis cornu* (Brongniart, 1810), *P. (Gyrorbis) hilgendorfi* Fraas, 1868, *P. (Gyrorbis) septemgyratiformis* Gottschick, 1911 and *Gyraulus trochiformis* (Stahl, 1824), for which the junior synonym *Planorbis multiformis* (von Zieten, 1830) has commonly been used and has been taken into synonymy by Wenz (1923). All endemic and non endemic taxa of *Gyraulus* that occur in Steinheim were commonly designated as "varieties" of *G. trochiformis*. Each variety had three and in some cases four infraspecific names (Hilgendorf, 1867; Hyatt 1880; Gottschick, 1911, 1920; Gottschick & Wenz, 1920; Wenz, 1923).

According to Gottschick & Wenz (1916, 1920) and Gottschick (1920) *G. trochiformis* contains three non endemic taxa, which grade into each other morphologically: *G. trochiformis applanatus* (Thomae, 1845), *G. trochiformis dealbatus* (Braun, 1851) and *G. trochiformis kleini* (Gottschick & Wenz, 1916). They were reported from the lowermost beds of Steinheim, as well as from other Miocene deposits in Germany. They differ from each other in the number and shape of the whorls (Fig. 5). In contrast, Mensink (1984), who used binominal names, noticed that the planorbids from the *kleini* beds show little variability.

G. trochiformis kleini (Gottschick & Wenz, 1916) seems to be identical with Hilgendorf's ancestral taxon *Planorbis multiformis* (?) *aequeumbilicatus* (Hilgendorf, 1867). Gottschick (1920) proposed that the three different non endemic taxa of *G. trochiformis* gave rise to the different branches of the phylogenetic tree. In his opinion the

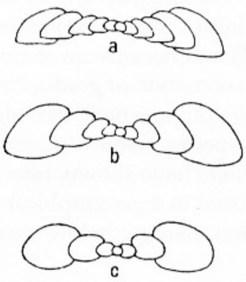

Fig. 5. Sections through the three non endemic morphs of *Gyraulus trochiformis* (Stahl, 1824); a: *applanatus* (Thomae, 1845); b: *dealbatus* (Braun, 1851); c: *kleini* (Gottschick & Wenz, 1916) (after Gottschick, 1920).

endemic *G. steinheimensis* (Hilgendorf, 1867) contains some infraspecific taxa, each of which is related to one of the three non endemic taxa of *G. trochiformis*. Hilgendorf (1867) already had subdivided *G. steinheimensis*.

We can summarise that several planorbid infraspecific taxa were reported from the *kleini* beds as well as from the following *steinheimensis* beds. These taxa designate planispiral, smooth shells with attached whorls, which we call 'normal planorbid pattern' in this paper. Those taxa differ from each other in size, in the number of whorls and in the depth of the umbilici. In addition, our own data have shown that amongst shells from the *steinheimensis* beds, which display normal planorbid pattern, different types of protoconch microsculptures occur.

Classification and species problems

Nowadays seven species of the genus *Gyraulus* coexist in Central Europe and (according to Meier-Brook, 1983) two or three species commonly are found together within one body of water). This author suggested that within the Planorbidae the Planorbinae represent a monophyletic taxon which can be described by features of the anatomy, especially the morphology of the penis. Since all features regard the anatomy of the soft body a safe identification of the genus *Gyraulus* in fossil samples seems to be very difficult. Meier-Brook (1983) is of the opinion that all Mesozoic references to the *Gyraulus-Planorbis* tribe are in error and that the earliest ancestors of *Gyraulus* lived in Europe and North America in the Eocene.

Gyraulus loryi (Coquand, 1855) from the European Wealden (earliest Cretaceous) is similar to Recent species of the genus *Gyraulus*, regarding dimensions, shell shape, and protoconch microsculpture (Bandel, 1991). It resembles Steinheim forms as well as modern species. Since the main difference between *Planorbis* and *Gyraulus* is anatomical and shells are not diagnostic with regard to the generic assignment, it will never be possible to classify the Jurassic-Cretaceous planorbids with certainty according to genus.

As mentioned three or four names were commonly used to assign the so called varieties of *Gyraulus trochiformis* (Stahl, 1824), respectively its junior synonym *Planorbis multiformis* (von Zieten, 1830). Each variety was defined by a set of characters. The category 'variety' itself was not defined by any of these authors for the Steinheim context. Multinominal nomenclature was chosen because the heritability of the characters was doubtful (Reif, 1984) and because an exclusively typological species concept was difficult to apply to a succession of gradually changing morphs.

Although Hilgendorf's (1867) phylogenetic tree shows bifurcations and trifurcations, he did not change the species name *Planorbis multiformis*. As Gittenberger (1972), Willmann (1985) and others have shown, taxa below species level have different meanings, when they are used in a geographical (subspecies) or a chronological context. In the Steinheim context, naming below species level resulted in extensive synonymy lists (Wenz, 1923).

Mensink (1984) found statistical evidence for bifurcations in the main-branch and consequently chose binominal names. In the present paper morpho-groups of similar shells are defined by morphological characters in relation to other morpho-groups, especially to their assumed stem group. Although the traditional typological method, combined with bed to bed comparison seems more arbitrary than statistical methods, it is suitable to demonstrate bifurcations, which possibly reflect speciations. A bifurcation is indicated by an increasing variability within a morpho-group and shells with characters of the stem group as well as of the newly forming group appear (transitional morphs).

In Steinheim a new morpho-group normally occurs together with transitional morphs to the assumed stem group (often within one sample). Going upward in the stratigraphic section transitional morphs disappear and the new morpho-group continues to exist. In some cases the stem group continues to exist as well, in other cases it vanishes. After a species had evolved, it did not hybridise with others (transitional morphs do not reappear), as it is the case for some Neogene gastropods of Greece (Willmann, 1981).

The lack of transitional morphs after a new morpho-group has come into existence and the fact that there is no Recent example for an intraspecific variability in fresh water snails that can be compared to what is known from Steinheim, suggests that we are dealing at least with some gone biospecies. Thus, it seems justified to designate the morpho-groups as species.

The transition from *G. minutus* (Hilgendorf, 1867) to *G. costatus* (von Klein, 1847) may serve as an example for a bifurcation or a possible speciation: *G. minutus* is a small, smooth planorbid with fine growth lines. In the *sulcatus* beds smooth shells, shells with stronger growth lines and specimens with ribs occur. In this period a definition between growth lines and distinct ribs would be most arbitrary, because morphological transitions are present. Subsequently, in the uppermost *sulcatus* beds, specimens with stronger growth lines, which may be designated as transitional morphs, are not present any longer. The smooth *G. minutus* and the ribbed *G. costatus* coexist and can easily be distinguished from each other. So the ancestral species continues to exist. This possibility is rejected by many authors, e.g. Hennig (1982) and Willmann (1985), because reproductive isolation as diagnostic feature for a biospecies is only applicable to synchrone populations.

We are aware of the fact that a mixture of the typological method and a biospecies concept basing on speciation events is problematical. In Steinheim, where numerous shells can be compared from bed to bed, it seems suitable to demonstrate the probable phylogenetic relations.

The absolute speed of the speciations in Lake Steinheim is unknown. The time it took to establish a new species seems to be short compared with the time span of its existence. This punctualism is confirmed by the cluster analysis of the main-branch (Povel, 1993). Statistical data of Povel (1993) and Mensink (1984) confirm that real speciations happened.

As far as possible the old names of von Klein (1847), Hilgendorf (1867) and Hyatt (1880) are used and raised to species level. Only two new species are proposed. This paper is no revision of the Steinheim planorbids and thus no type material, if there is any, has been examined.

For a revision especially the planorbids of the early Steinheim lake as well as the other planorbids of the Miocene of southern Germany should be studied in detail. This revision should include SEM-micrographs of the teleoconchs as well as of the protoconchs. The original material of Hilgendorf and Gottschick has to be examined as well. New excavation in the *kleini* beds would also be necessary.

Characters

Teleoconch characters

Shape: the shells are planispiral or trochospiral and whorls may be detached. The grade of involution, depth and width of the upper and lower umbilicus are diagnostic features. The shells are considered to be pseudodextral (hyperstrophic) because Recent representatives of *Gyraulus* are organised sinistrally regarding their anatomy, even when their shells are dextral (Meier-Brook, 1983).

Shape of the whorls: the height/width-ratio and the outline of the whorls in transverse section (round, circular, oval, rounded subrectangular or triangular) are used as diagnostic features. The whorls may have collars (carinae) and may be angular.

Number of whorls: depends on the ontogeny and is thus only suitable for fully grown or nearly fullgrown specimens.

Diameter: depends on the number of whorls, the increase of the whorls, the grade of involution, and the outline.

Height: in planispiral shells identical with the height of the aperture, in helical forms dependent on spire height.

Aperture: the outline is mostly identical with that of transverse whorl section; the aperture sometimes bears an inner collar, but in most cases the shell is just getting thinner and is fractured. It thus is difficult to distinguish a fullgrown specimen from a juvenile one. The aperture and the last part of the body whorl are often deflected downward, in a few cases upward.

Teleoconch sculpture: growth lines may be weak or strong; the presence of ribs, their density (related to 0.5 whorls) and their height are diagnostically relevant. Spiral furrows are common amongst main-branch and side-branch 1 snails. Microsculptures of spirally arranged, often crescentic nodules and of straight or meandering cords represent probably a continuation of the protoconch microsculpture and can be interpreted as a neotenous effect.

Shell thickness: was not used, but seems to be of some diagnostic significance (main-branch morphs generally have thicker shells than side-branch morphs).

Protoconch characters

Protoconch size and shape of the planorbids of the Steinheim Basin are quite uniform. It is planispiral and has 1.2 to 1.4 whorls. The diameter of the protoconch is 0.3-0.4 mm. The initial cup of the first whorl is 0.08-0.12 mm wide and commonly covered with irregular folds. Even in trochiform morphs the first whorl is planispiral and in morphs with detached whorls the uncoiling never reaches the first whorl. Hatching from the egg can be recognised by the onset of strong growth lines, the cessation of microsculpture of the embryonic shell and sometimes by a ledge. In most cases the transition from the protoconch to the teleoconch is difficult to locate because protoconch microsculpture ceases earlier or continues onto the teleoconch. The growth lines are commonly already visible on the embryonic shell and may appear right beyond the initial cup. This reflects the direct development of the planorbids.

Gottschick (1920) first mentioned the spiral striation on the protoconchs of the Steinheim planorbids; he noted that this striation is typical for planorbids. Gorthner (1984a, 1992) and Riedel (1990) examined protoconchs and confirmed that the species of Steinheim actually belong to the Planorbidae and may represent the genus *Gyraulus*.

The oldest known planorbids (Late Jurassic) already have a spiral striation of the same type on their protoconchs (Bandel, 1991). Meier-Brook (1983) noticed a spiral striation in every Recent species of the genus *Gyraulus* that he had studied. Furthermore he suggested that the microsculpture of the protoconch is of some taxonomical significance within the Planorbidae. This was confirmed by Gorthner (1992).

Nearly all planorbids of the Steinheim Basin show a spiral striation on their protoconchs, but there are a lot of different patterns to be distinguished. In some cases the correlation between protoconch microsculpture and teleoconch morphology is good [e.g. *G. crescens* (Hilgendorf, 1867)]. Here the shape of the teleoconch is bound to a particular type of protoconch microsculpture. In other cases shells with similar teleoconchs have different protoconch sculptures (e.g. *G. costatus* and its descendants). The variability of this character is thus different in different morphospecies. Recent species differ in the number of spiral striae (Gorthner, 1992) and he also noted that in the main-branch planorbids of Steinheim the number of striae increases with time.

Description of the species

Here groups are defined and based on microsculpture of the protoconch as well as on teleoconch shape. The groups are named according to typical members:

G. steinheimensis/*G. pseudotenuis* group

G. crescens group

G. minutus group.

All measurements are based on at least three typical mature specimens, which were studied by SEM.

A) The *G. steinheimensis*/*G. pseudotenuis* group

Species:

Gyraulus steinheimensis, including *G. kraussii* (von Klein, 1847)

Gyraulus pseudotenuis.

The members of this group are planispiral and their protoconch microsculpture consists of indistinct spiral striae, which differ markedly from that of *G. kleini*. The striae are commonly interconnected with each other by little bows. The uniform microsculpture pattern confirms Hilgendorf's (1867) opinion that *G. steinheimensis* is the ancestor of *G. pseudotenuis*. In addition both species have spiral furrows on the teleoconch.

Gyraulus steinheimensis (Hilgendorf, 1867)

Pl. 1, figs. 1-2; Pl. 2, figs. 1-3.

Material — Numerous specimens studied; 8 specimens studied by SEM.

Description — Shape: planispiral, moderately involute, upper side moderately deepened, lower side with a deep narrow umbilicus. Shape of the whorls: round, rapidly increasing. Aperture: approximately as high as wide (1.8-1.9 mm); rounded subquadrangular. Number of whorls: 4.0-4.5, smaller *G. steinheimensis* were called *G. kraussii* von Klein, 1847. Diameter: 4.5-6.8 mm. Height: see height of the aperture. Teleoconch sculpture: fine growth lines, one or few spiral furrows. Protoconch sculpture: indistinct spiral pattern, spirals are connected with little bows (Pl. 1, figs. 1, 2).

Stratigraphic range — *steinheimensis* to *sulcatus* beds; smaller *steinheimensis* type snails (*G. kraussii*) range into the *sulcatus* beds.

Phylogenetic relationships — *G. steinheimensis* is the first main-branch morph and the ancestor of the rest of the main-branch. It also is the ancestor of *G. pseudotenuis* (side-branch 1). The origin of *G. steinheimensis* is unclear.

Remarks — *G. steinheimensis* is a relatively big, normal looking planorbid. Specimens with the typical protoconch microsculpture occur in the lowermost sample (B 31.8-32.0). This sculpture is very different from distinct spiral striation as it was reported by Gorthner (1992) from *G. kleini*. The teleoconch shape and the size of *G.*

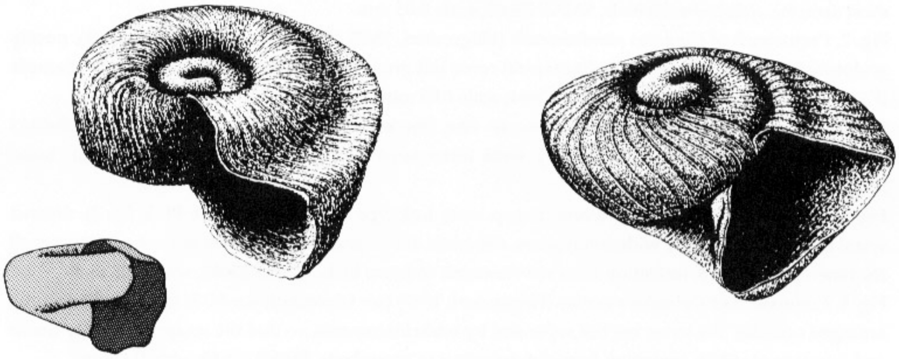

Fig. 6. Juvenile or incomplete specimens of *Gyraulus sulcatus* (Hilgendorf, 1867) (left) and *G. trochiformis* (Stahl, 1824) (right). Most main-branch morphs can easily be distinguished from side-branch morphs, even when the shells are not complete. The very rapid increase of teleoconch whorls is the most characteristic feature of the main-branch morphs. Drawn by Mrs Lewandowski.

steinheimensis are variable. Hilgendorf (1867) distinguished the varieties *G. multiformis steinheimensis typus*, *G. multiformis steinheimensis involutus* and *G. multiformis kraussii*. Gottschick (1920) reported three varieties each of them related to one of the three morphs of *G. multiformis*.

In the early beds small *G. steinheimensis*-like snails occur, which have a protoconch microsculpture of distinct spiral cords. Those morphs are named *G. protocrescens* herein. There is obviously no close relationship to *G. steinheimensis*.

The *G. steinheimensis* specimen figured in Pl. 2, fig. 3 has more relatively slowly increasing whorls than typical *G. steinheimensis*. Its shape is similar to *G. kleini* but it is much bigger.

The polymorphic *G. steinheimensis* 'sensu previous authors possibly is a polyphyletic species, containing some cryptic species, and thus the deviation of the main-branch from *G. kleini* is doubtful.

Gyraulus pseudotenuis (Hilgendorf, 1867)
Pl. 2, fig. 4.

Material — C. 20 specimens studied; 4 specimens studied by SEM.

Description — Shape: planispiral, rather evolute; upper side flat, lower side with an umbilicus. Shape of the whorls: subrectangular with an external angle at the base, slowly increasing, sometimes with an inner collar at the upper side. Aperture: subrectangular; wider than high (height 0.4 mm, width 0.5-0.6 mm); sometimes with an inner collar; deflected somewhat downward. Number of whorls: 2.4-2.8. Diameter:

Plate 1. Different types of protoconch microsculptures

Fig. 1. Protoconch microsculpture of *Gyraulus steinheimensis* (Hilgendorf, 1867) (for teleoconch see Pl. 2, fig.1), indistinct spiral cords are connected with small transverse bows. Sample B 31.8-32.0 (lowermost sample), *steinheimensis* beds, SMNS 25663, scale 0.03 mm.

Fig. 2. Protoconch of *Gyraulus steinheimensis* (Hilgendorf, 1867) (for teleoconch see Pl. 2, fig. 2), poorly sculptured, almost smooth, no distinct spiral cords but growth increments starting very early. Sample B 30.0-30.5, *steinheimensis* beds, SMNS 25664, scale 0.03 mm.

Fig. 3. Protoconch of *Gyraulus protocrescens* sp. nov. (for teleoconch see Pl. 3, fig. 2), relatively distinct and straight spiral striae, separated by wide interspaces. Sample B 29.2-29.4, *steinheimensis* beds, SMNS 25668, scale 0.1 mm.

Fig. 4. Protoconch of *Gyraulus protocrescens* sp. nov., holotype (for teleoconch see Pl. 3, fig. 3), distinct spiral cords, separated by wide interspaces, the cords are meandering and they are not continuous all the time. Sample SF18, transition from *steinheimensis* to *tenuis* beds, SMNS 25669, scale 0.03 mm.

Fig. 5. Protoconch of *Gyraulus minutus* (Hilgendorf, 1867) (for teleoconch see Pl. 5, fig. 5), with spirally arranged nodules, the striae are not separated by wide interspaces, so that the sculpture is very dense and fine. Sample SF18, transition from *steinheimensis* to *tenuis* beds, SMNS 25682, scale 0.1 mm.

Fig. 6. Protoconch of *Gyraulus platystomus* (Hilgendorf, 1867) (for teleoconch see Pl. 7, fig. 7), showing labyrinthic pattern, spiral elements are lacking totally, morphs with ribs and rapidly increasing whorls tend to reduce the spiral pattern of the protoconch (see also Pl. 8). Sample S32, upper *trochiformis* beds, SMNS 25697, scale 0.03 mm.

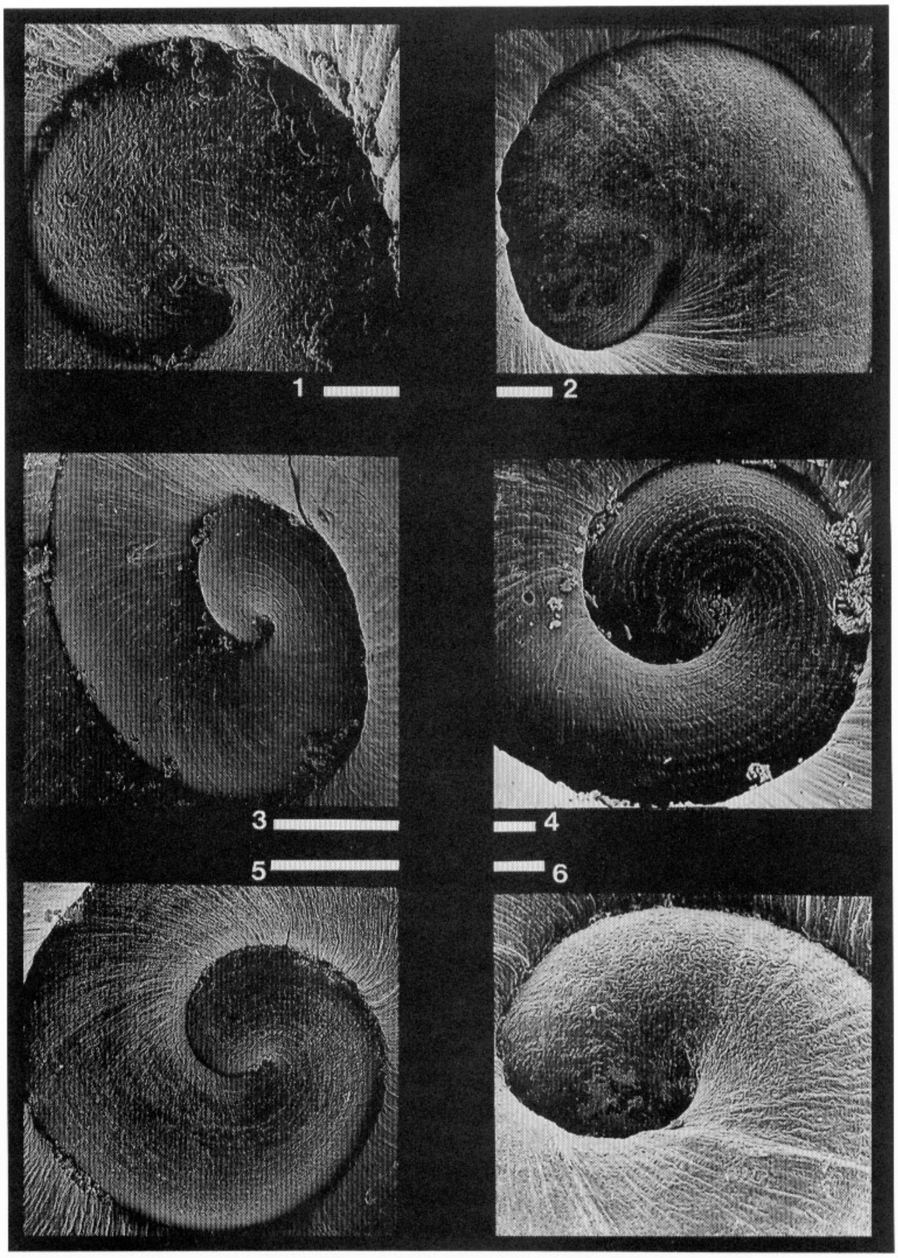

Plate 1

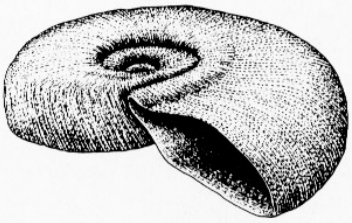

Fig. 7. *Gyraulus pseudotenuis* (Hilgendorf, 1867) collar and a furrow at the upper side. Drawn by Mrs Lewandowski.

1.3-1.6 mm. Height: see height of the aperture. Teleoconch sculpture: strong growth lines and spiral furrows; spiral microsculpture. Protoconch sculpture: similar to that of *G. steinheimensis*.

Stratigraphic range — Uppermost *sulcatus* beds to *trochiformis* beds.

Phylogenetic relationships — There is no doubt that *G. pseudotenuis* is related to the main-branch. Shape and sculpture of the protoconch and the teleoconch is very similar to that of *G. steinheimensis* or small individuals of *G. steinheimensis* which were formally called *G. kraussii*. There is a significant stratigraphic gap between *G. steinheimensis* and the first *G. pseudotenuis* but Hilgendorf (1867) reported some transitional morphs in the uppermost *sulcatus* beds.

Generally *G. pseudotenuis* is only common in the upper *trochiformis* beds.

Remarks — Early *G. tenuis* show a habitus similar to *G. pseudotenuis* (see Pl. 3, fig. 1), but the stratigraphical gap between both is even bigger than that between *G. pseu-*

Plate 2

Fig. 1. *Gyraulus steinheimensis* (Hilgendorf, 1867), sample B 31.8-32.0, *steinheimensis* beds, SMNS 25663. Smooth, rapidly increasing whorls, showing only growth lines; upper umbilicus flat, lower one deep and narrow, shell is thick, whorls as high as wide; a: scale 1 mm, b: scale 0.3 mm, c-d: scale 0.03 mm, c: protoconch, d: protoconch detail (see Pl. 1, fig. 1).

Fig. 2. *Gyraulus steinheimensis* (Hilgendorf, 1867), sample B 30.0-30.5, *steinheimensis* beds, SMNS 25664. Smooth, rapidly increasing whorls, showing only growth lines and one spiral furrow on the last whorl, upper umbilicus flat, lower one deep, whorls as high as wide; a-b: scale 1 mm, c: scale 0.03 mm, protoconch (see Pl. 1, fig. 2), d: scale 0.1 mm, protoconch detail (see Pl. 1, fig. 2).

Fig. 3. *Gyraulus steinheimensis* (Hilgendorf, 1867), sample B 29.2- 29.4, *steinheimensis* beds, SMNS 25665. Smooth, slowly increasing whorls, showing only growth lines, upper umbilicus as deep as lower one (like *G. kleini*, but the number of whorls of this specimen is higher and the diameter is greater), whorls as high as wide, aperture deflected upward, protoconch corroded; a-c: scale 1 mm.

Fig. 4. *Gyraulus pseudotenuis* (Hilgendorf, 1867), sample S36, upper *trochiformis* beds, SMNS 25666. Small, distinct angle at the base, rapidly increasing whorls, strong growth lines, spiral furrows on the teleoconch, upper side flat, lower with a deep umbilicus, shell is thick, whorls wider than high, aperture deflected downward, protoconch of *steinheimensis* type; a-b: scale 0.3 mm, c: scale 0.03 mm (compare Pl. 1, fig. 1).

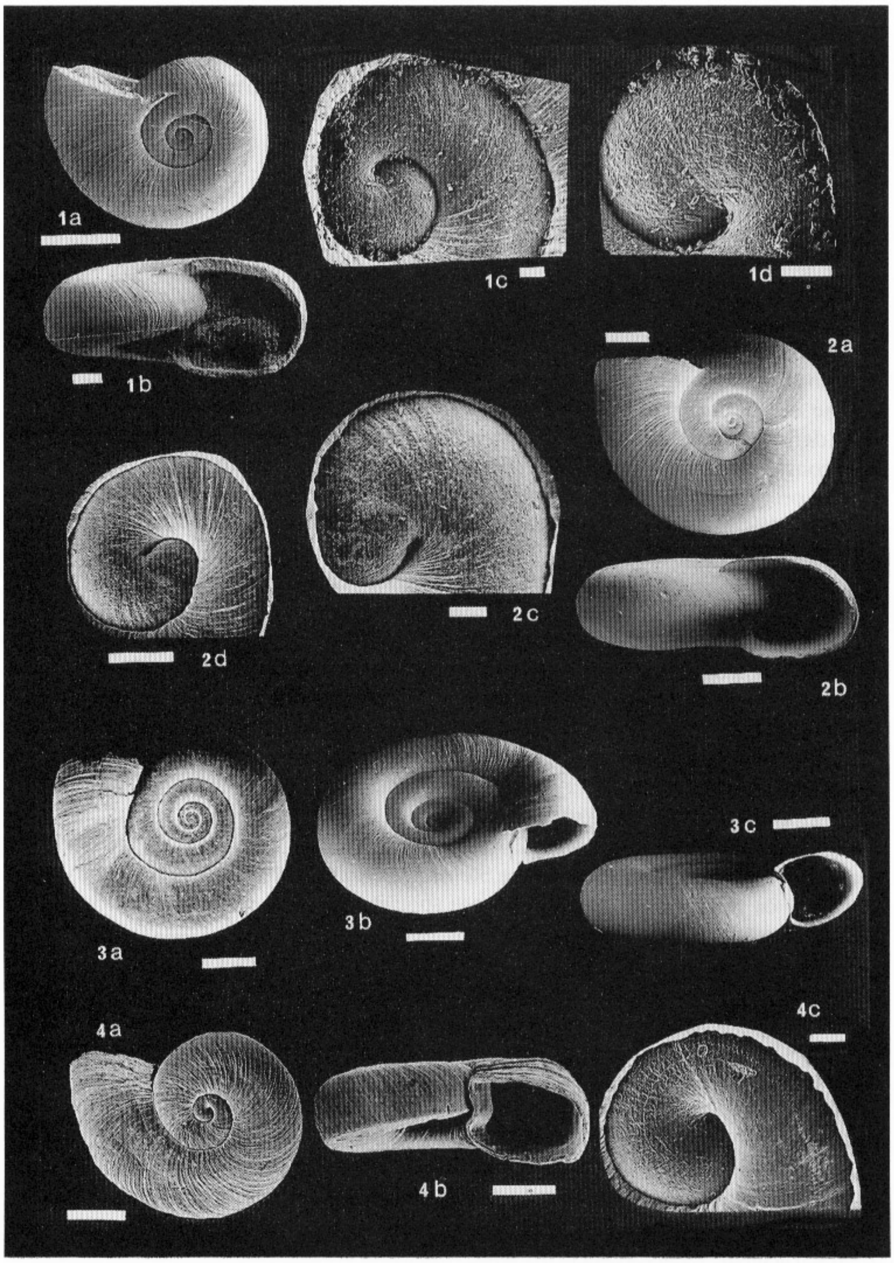

Plate 2

dotenuis and *G. steinheimensis*. Additionally *G. tenuis* has a protoconch microsculpture with many spiral cords, which is typical for higher main-branch morphs.

G. pseudotenuis is a characteristic species with little variability and a short range.

B) The *G. crescens* group

Species:
Gyraulus kleini
Gyraulus protocrescens
Gyraulus triquetrus
Gyraulus crescens.

The members of this group are tiny and planispiral. They differ from each other only in shape and number of whorls.

The key character of this group is the protoconch microsculpture: it shows 7 to 15 well defined spiral cords (*crescens* type, see Pl.1, figs. 3, 4). The *crescens* group is rather conservative in terms of shell shape and protoconch sculpture.

The proposed ancestor species *G. kleini* has the type of protoconch redescribed by Gorthner (1992). It seems to represent the ancestor species of the *crescens* group.

Gyraulus kleini (Gottschick & Wenz, 1916)

Description [after Hilgendorf (1867) and Gorthner (1992)] — Shape: planispiral, upper umbilicus as wide and deep as the lower one. Shape of the whorls: round, evolute, slowly increasing. Aperture: approximately as high as wide. Number of whorls: 3.3-3.8. Diameter: 3.3-4.0 mm. Teleoconch sculpture: smooth with fine growth lines. Protoconch sculpture: *crescens* type; according to Gorthner (1992) 7-11 well defined spiral cords.

Stratigraphic range — *kleini* to *steinheimensis* beds.

Phylogenetic relationships — *G. kleini* is the proposed non-endemic founder species of all endemic planorbids of the Steinheim Basin. Herein it is assumed to represent at least the founder species of those species that have a similar microsculpture on their protoconchs (*crescens* type).

Gyraulus protocrescens sp. nov.
Pl. 1, figs. 3-4; Pl. 3, figs. 2-3.

Material — Numerous specimens studied; 15 specimens studied by SEM.

Holotype — Pl. 1, fig. 4; Pl. 3, fig. 3, SMNS 25669.

Paratypes — Pl. 1, fig. 3; Pl. 3, fig. 2, SMNS 25668 and SMNS 25711.

Type locality — Steinheim Basin, Steinheim am Albuch, Baden-Württemberg, Germany.

Type horizon — Middle Miocene, vertebrate zone MN 7, transition from the *steinheimensis* to the *tenuis* beds, sample SF18.

Derivatio nominis — The ancestor of *G. crescens* Hilgendorf, 1867.

Diagnosis — A small planorbid with a *crescens* type microsculpture of the protoconch and round slowly increasing whorls.

Differential diagnosis — *G. protocrescens* is similar to *G. minutus* but it is a bit larger and differs in the microsculpture of the protoconch. *G. protocrescens* is also similar to *G. kleini* but it is much smaller. *G. protocrescens* is similar to *G. crescens* but it is smaller and has no strong growth lines.

Description — Shape: planispiral, rather evolute, upper side nearly flat, lower side moderately concave. Shape of the whorls: round, oval, slowly increasing. Aperture: round, oval, a bit wider than high (height 0.5 mm, width 0.6 mm). Number of whorls: 2.6-3.1. Diameter: 1.4-1.7 mm. Height: like height of the aperture. Teleoconch sculpture: smooth, fine growth lines.

Protoconch sculpture: 10-15 well defined, often meandering spiral cords with relatively wide interspaces (*crescens* type, Pl. 1, figs. 3, 4).

Stratigraphic range — *steinheimensis* to *trochiformis* beds.

Phylogenetic relationships — Teleoconch shape and protoconch sculpture are similar to those of *G. kleini* (Gorthner, 1992), but *G. protocrescens* is smaller and has a lower number of whorls. It seems very likely that *G. kleini* is the ancestor of *G. protocrescens*.

G. protocrescens is the ancestor of *G. triquetrus* (*sulcatus* beds) and *G. crescens* (upper *trochiformis* beds). With the occurrence of *G. crescens G. protocrescens* vanishes.

Remarks — *G. protocrescens* can hardly be distinguished from *G. minutus* without looking at the protoconch microsculpture. In average it has a slightly higher number of whorls and thus is larger than *G. minutus*. So in the past *G. protocrescens* was not distinguished from *G. minutus*.

In the lowermost samples specimens occur that have a relatively deep and narrow lower umbilicus, so that they look like small *G. steinheimensis* (Pl. 3, fig. 2). But the microsculpture of the protoconch differentiates them.

Gyraulus triquetrus (Hilgendorf, 1867)

Pl. 3, figs. 4-5; Pl. 4, figs. 3-4.

Material — C. 20 specimens studied; 9 specimens studied by SEM.

Description — Shape: planispiral, upper side nearly as deep as lower side; moderately involute. Shape of the whorls: rounded triangular, with internal collars on the upper and the lower side (the latter is sometimes lacking). Aperture: rounded triangular, a little wider than high (width 0.5 mm, height 0.4-0.5 mm). Number of whorls: 3.0-3.3. Diameter: 1.5-2.0 mm. Height: same as aperture. Teleoconch sculpture: smooth with fine growth lines; sometimes a fine spiral microsculpture is visible. Protoconch sculpture: *crescens* type (10-14 well defined spiral cords, Pl. 3, fig. 4c).

Stratigraphic range — *sulcatus* beds.

Phylogenetic relationships — *G. triquetrus* is a descendant of *G. protocrescens*.

Remarks — *G. triquetrus* is quite common in the middle *sulcatus* beds. Most of the specimens were corroded, only two were preserved well enough to examine the microsculpture of the protoconch which is clearly of the *crescens* type.

Restriction in time of occurrence (Willmann, 1985) and typical shape of the whorls establish this species well.

Gyraulus crescens (Hilgendorf, 1867)
Pl. 4, figs. 3-6.

Material — Numerous specimens studied and 21 specimens studied by SEM

Description — Shape: flat; planispiral; upper side nearly flat, lower side moderately deep. Shape of the whorls: round, sometimes rounded triangular (Pl. 4, figs. 4b, 5c) with round angle at the periphery or an angle at the base (Pl. 4, fig. 6); slowly increasing. Aperture: round, little wider than high, sometimes rounded triangular. Number of whorls: 3.5-3.8. Diameter: 2.6-3.0 mm. Height: same as aperture. Teleoconch sculpture: strong growth lines. Protoconch sculpture: *crescens* type (Pl. 4, figs. 3a, d).

Stratigraphic range — Uppermost *trochiformis*- to *revertens* beds.

Phylogenetic relationships — *G. crescens* is a descendant of the smaller *G. protocrescens*.

Remarks — *G. crescens* occurs frequently in the *oxystoma* beds. It is quite variable in number and shape of the whorls. In average the number of whorls is significantly higher than that of its ancestor *G. protocrescens*. Some specimens of *G. revertens* are similar to *G. crescens*. Gorthner (1992) figured a specimen which seems to be *G. crescens* and designated it as *G. revertens*. Its size lies in the range of *G. crescens* and its protoconch sculpture is of the *crescens* type and thus atypical for main-branch morphs. *G. oxystoma*, the proposed stem morph of *G. revertens*, still has a main-branch protoconch

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Plate 3

Fig. 1. *Gyraulus tenuis* (Hilgendorf, 1867), sample B 22.5-22.6, *tenuis* beds, SMNS 25667. Main-branch morph, angle at the base, rapidly increasing whorls, strong, padded growth lines, spiral furrows at the teleoconch, upper side flat, lower side deeply and narrowly umbilicated, shell is thick, aperture wider as high and subrectangular, protoconch with many distinct spiral cords; a-c: scale 0.3 mm, d: scale 0.1 mm.

Fig. 2. *Gyraulus protocrescens* sp. nov., sample B 29.2-29.4, *steinheimensis* beds, SMNS 25668. Possibly juvenile specimen, with smooth round whorls, showing fine growth lines, upper umbilicus flat, lower one deep, shell is thin, whorls wider than high, protoconch with few, well separated spiral cords (*crescens* type); a-b: scale 0.3 mm; c: scale 0.1 mm, protoconch (see Pl. 1, fig. 3).

Fig. 3. *Gyraulus protocrescens* sp. nov., holotype, SF18, transition from *steinheimensis* to *tenuis* beds, SMNS 25669. Smooth, round whorls, showing fine growth lines, upper umbilicus flat, lower one deep, shell is thin, whorls wider than high, protoconch with few, well separated and meandering spiral cords (*crescens* type); a: scale 0.3 mm; b: scale 0.03 mm (see Pl. 1, fig. 4); c: scale 0.3 mm.

Fig. 4. *Gyraulus triquetrus* (Hilgendorf, 1867) (transitional from *G. protocrescens*), sample SF10, *sulcatus* beds, SMNS 25670. Smooth, evolute, slowly increasing whorls, showing fine growth lines, upper umbilicus flat, lower one deep, shell is thin, whorls wider than high, the inner half of the whorls is 'blown up' on the upper side (inner collar). The whorls of the typical *G. triquetrus* are blown up on the upper as well as on the lower side so that the whorls and the aperture are rounded triangular (see Pl. 4, fig. 1-2), protoconch with few, well separated spiral cords (*crescens* type); a-b: scale 0.3 mm; c: scale 0.03 mm (see Pl. 1, fig. 3).

Fig. 5. *Gyraulus triquetrus* (Hilgendorf, 1867), sample SF3, *sulcatus* beds, SMNS 25671. Similar to Pl. 3, fig. 4, but the irregularity of this specimen is somewhat different, protoconch corroded; a-b: scale 0.3 mm.

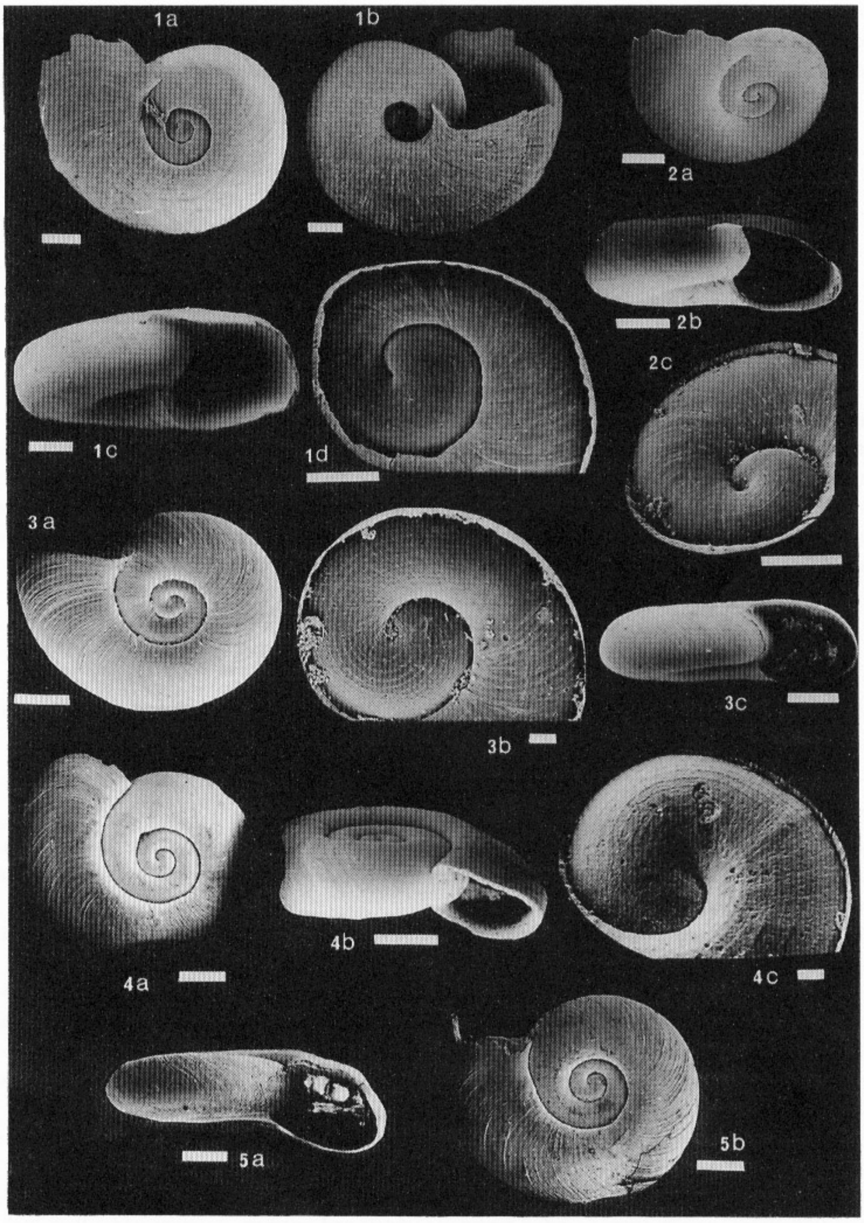

Plate 3

sculpture, similar to that of *G. sulcatus* and *G. trochiformis*, with up to 32 distinct spiral cords, whereas Gorthner's specimen has less than 10 cords. A possible phylogenetic relationship between *G. crescens* and *G. revertens* should be investigated.

C) The *G. minutus* group

Species:
Gyraulus minutus
Gyraulus costatus
Gyraulus distortus
Gyraulus denudatus
Gyraulus platystomus
Gyraulus rotundostomus.

This group contains morphs that deviate strongly from the normal planorbid pattern and shows a high variability of shape and sculpture. Its members are tiny. Uncoiling and ribs are important morphological features. The protoconch sculpture is primarily fine and dense but shows a wide range of variability. Spirally arranged nodules occur as well as spiral cords, which are not separated by distinct interspaces as is the case in the *crescens* group. Ribbed forms with a big aperture (*G. platystomus* and *G. rotundostomus*) tend to reduce spiral elements of the protoconch microsculpture.

Gyraulus minutus (Hilgendorf, 1867)
Pl. 1, fig. 5; Pl. 5, figs. 5-6; Pl. 6, figs. 1-5.

Material — Numerous specimens studied; 20 specimens with attached whorls and 29 uncoiled specimens were studied by SEM.

Plate 4

Fig. 1. *Gyraulus triquetrus* (Hilgendorf, 1867) (typical), sample SF9, *sulcatus* beds, SMNS 25672. Similar to Pl. 3, figs. 4-5, but with the typical rounded triangular aperture, upper umbilicus as deep as the lower one, protoconch corroded; a-b: scale 0.3 mm.

Fig. 2. *Gyraulus triquetrus* (Hilgendorf, 1867), sample SF3, *sulcatus* beds, SMNS 25673. Similar to Pl. 4, fig. 1, but not so strongly involute; a-b: scale 0.3 mm.

Fig. 3. *Gyraulus crescens* (Hilgendorf, 1867), sample S37, lowest *oxystoma* beds, SMNS 25674. Flat, evolute, slowly increasing, round whorls, showing distinct growth lines, upper umbilicus flat, lower one deeper, aperture as high as wide, higher number of whorls and thus a greater diameter than *G. protocrescens*, protoconch with few, well separated spiral cords (*crescens* type); a: scale 0.03 mm; b-c: scale 0.3 mm; d: scale 0.1 mm.

Fig. 4. *Gyraulus crescens* (Hilgendorf, 1867), sample K7, *oxystoma* beds, SMNS 25675. Flat variety with a rounded angle at the periphery; a-b: scale 0.3 mm.

Fig. 5. *Gyraulus crescens* (Hilgendorf, 1867), sample K2, *oxystoma* beds, SMNS 25676. Very flat specimen with strong growth lines, rounded triangular whorls and aperture, aperture wider than high, protoconch with few, well separated spiral cords (*crescens* type), the shape of the protoconch is abnormal: it increases very fast within the first whorl; a and c: scale 0.3 mm; b: scale 0.1 mm.

Fig. 6. *Gyraulus crescens* (Hilgendorf, 1867), sample Ph19, *oxystoma* beds, SMNS 25677. Specimen with an angle at its base; a-b: scale 0.3 mm.

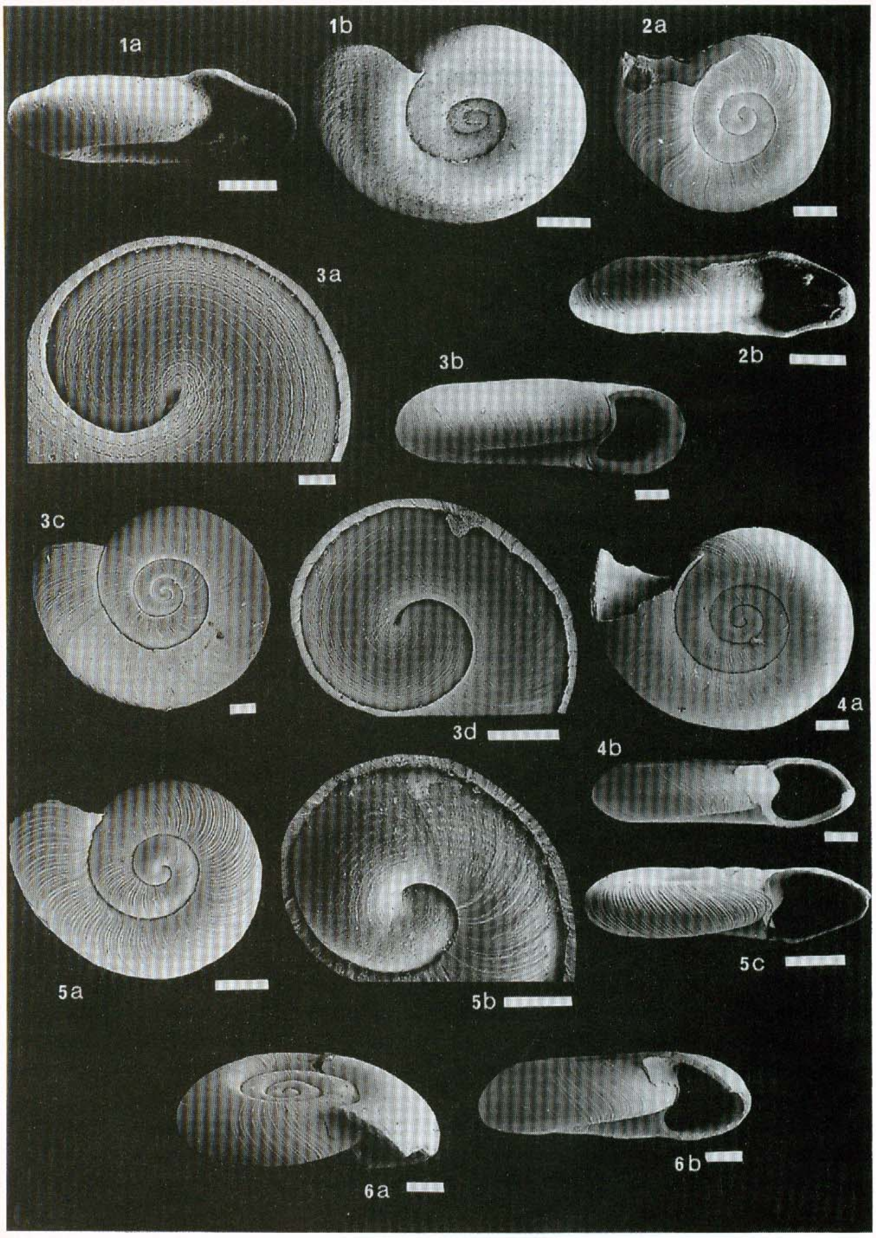

Plate 4

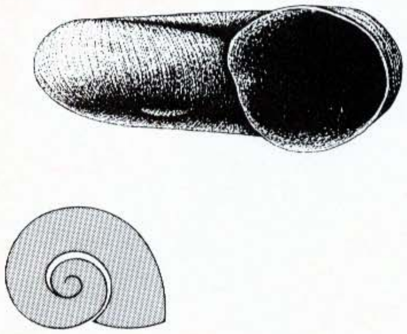

Fig. 8. Planispiral *Gyraulus minutus* (Hilgendorf, 1867) with detached whorls. Drawn by Mrs Lewandowski.

Description — Shape: planispiral, often uncoiled, rather evolute, upper side nearly flat, lower side weakly concave. Shape of the whorls: round, oval, slowly increasing in diameter. Aperture: round, oval, little wider than high, sometimes with an inner collar (Pl. 5, fig. 6b). Number of whorls: 2.5-3.0. Diameter: 1.4-1.7 mm; height:

Plate 5

Fig. 1. aff. *Gyraulus parvus* (Hilgendorf, 1867), sample B 30.9-31.8, *steinheimensis* beds, SMNS 25678. Small, flat planorbid with round whorls, aperture wider than high, shell smooth, showing only fine growth lines, upper umbilicus flat, lower one a little deeper; a-b: scale 0.3 mm.

Fig. 2. *Gyraulus* sp., sample B 27.6-27.8, transition from *steinheimensis*- to *tenuis* beds, SMNS 25679. Flat planorbid, width of the whorls is rapidly increasing, originally more than three whorls (preserved inner lip) and a diameter of at least 2.7 mm, shell smooth with fine growth lines, protoconch of *minutus* type, sculpture very dense, little interspace between the striae (cords and spirally arranged nodules), after the first whorl more and more transverse elements are occurring. Possibly a *minutus* ancestor; a-b: scale 0.3 mm; c: scale 0.03 mm; d: scale 0.1 mm.

Fig. 3. *Gyraulus* sp., sample B 22.5-22.6, *sulcatus* beds, SMNS 25680. Similar to Pl. 5, fig. 2 but with an angle at the periphery, protoconch corroded; a: scale 1 mm; b: scale 0.3 mm.

Fig. 4. *Gyraulus* sp., sample B 22.2-22.3, *sulcatus* beds, SMNS 25681. Similar to Pl. 5, figs. 1-3, aperture much wider than high, protoconch is somewhat corroded, but seems to be of the *minutus* type; a-b: scale 0.3 mm; c: scale 0.1 mm.

Fig. 5. *Gyraulus minutus* (Hilgendorf, 1867), sample SF18, transition from *steinheimensis* to *tenuis* beds, SMNS 25682. Small planispiral shell, smooth with fine growth lines, whorls nearly as wide as high, slowly increasing, round whorls, protoconch with fine and dense sculpture (*minutus* type); a-b: scale 0.3 mm; c: scale 0.03 mm; d: scale 0.1 mm.

Fig. 6. *Gyraulus minutus* (Hilgendorf, 1867), sample S17, transition from *sulcatus*- to *trochiformis* beds, SMNS 25683. Similar to Pl. 5, fig. 5, complete aperture with an inner collar, upper side flat, lower with a relatively deep umbilicus, protoconch with fine and dense sculpture (*minutus* type); a-b: scale 0.3 mm; c: scale 0.1 mm.

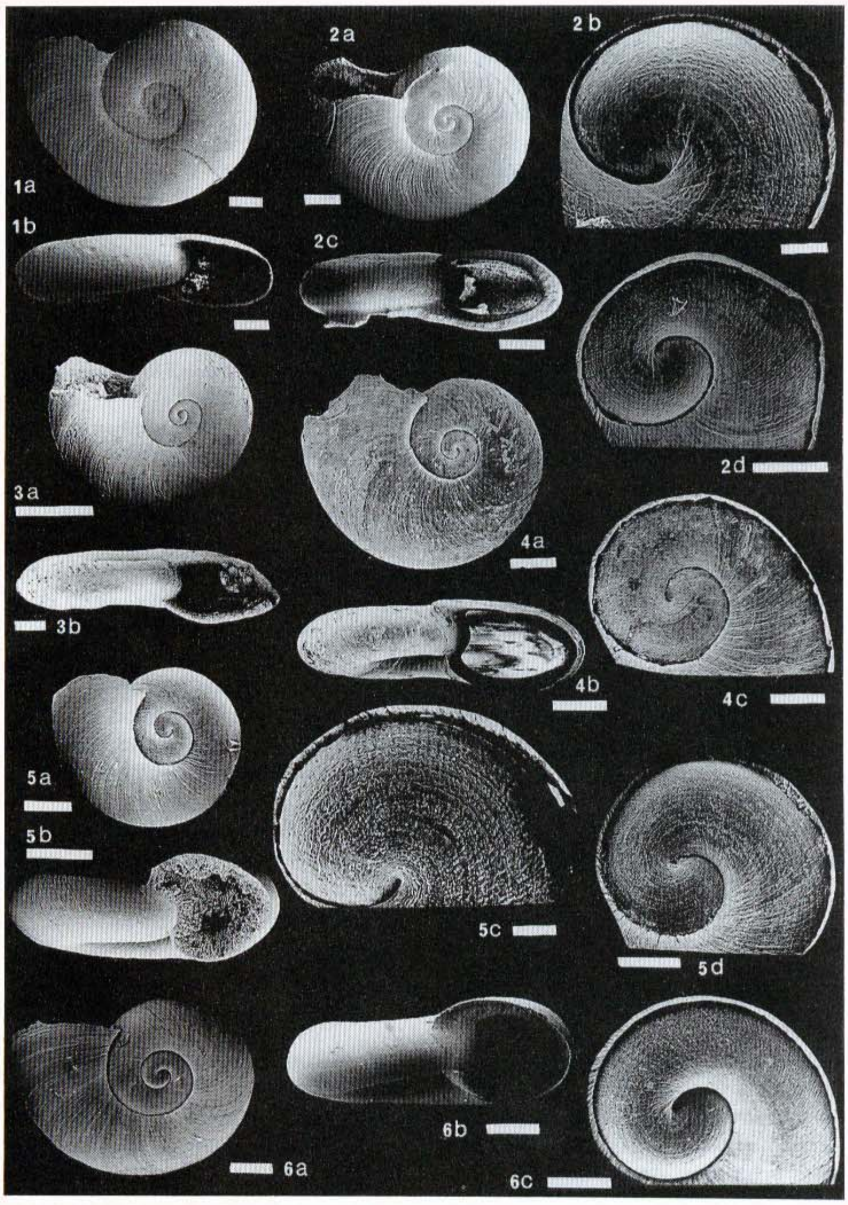

Plate 5

0.6-0.8 mm. Teleoconch sculpture: smooth, fine growth lines. Protoconch sculpture: fine and dense; cords or/and spirally arranged little nodules; many spiral striae with small interspaces (*minutus* type, Pl. 1, fig. 5).

Stratigraphic range — *steinheimensis*- to *trochiformis* beds.

Phylogenetic relationships — Possibly derived from flat planorbids with a wide aperture (Pl. 5, figs. 1-4). Some of these flat planorbids show a rounded marginal angle and a *minutus*-type protoconch. They occur rarely in the *steinheimensis*- to lower *sulcatus* beds. Some of them are similar to the poorly defined *Planorbis multiformis* var. *parvus* (Hilgendorf, 1867), which in Hilgendorf's (1867) phylogenetic tree was placed between *G. kleini* and *G. minutus*.

G. minutus is considered to be the ancestor of *G. costatus* and its descendants.

Remarks — This tiny planorbid represents the stem species of side-branch 2. Its relation to *G. kleini* is uncertain. There are no intermediate morphs and both differ from each other markedly in size and protoconch microsculpture.

G. minutus has a strong tendency to uncoil (Pl. 6, figs. 1-4). The number of uncoiled specimens as well as the grade of uncoiling reaches a maximum in between the uppermost *steinheimensis* bed and the *tenuis* bed. *G. minutus* with detached whorls occurs up to the uppermost *sulcatus* beds. Uncoiling never involves the first whorl. In uncoiled planispiral morphs the whorls are often nearly in touch with each other or they loose contact in the early whorls but later come to touch each other again. *G. minutus* usually uncoils in a dextral trochospira and whorls may be close to or distant from each other. Although the whorls are not in contact, their internal side is flat or concave.

Uncoiled *G. minutus* are not considered to have species rank, because the feature 'free whorls' is not connected with any other new character. In addition, intermediate morphs between normally coiled and uncoiled morphs are present throughout the time of occurrence of this species. Nevertheless uncoiling is an interesting feature and for its restriction in time there must be a reason.

The fact that all uncoiled *G. minutus* have a *minutus* type protoconch is a good argument to separate it from the similar *G. protocrescens* which never uncoils.

Gyraulus costatus (von Klein, 1847)

Pl. 6, figs. 6-7; Pl. 7, figs. 1-8.

Material — Numerous specimens studied; 34 specimens studied by SEM.

Description — Shape: planispiral, rather evolute (sometimes uncoiled), upper side moderately concave, lower side a little more concave. Shape of the whorls: round, slowly increasing in diameter. Aperture: approximately as high as wide (0.4-0.5 mm). Number of whorls: 2.0-2.6. Diameter: 1.0-1.6 mm. Height: same as aperture. Teleoconch sculpture: strong or fine ribs (between 1.5 and 2.0 whorls 10 to 40 ribs); between the ribs often remains of calcified periostracum are found. Protoconch sculpture: *minutus* type, but quite variable - relatively well defined spiral cords are found (Pl. 7, fig. 1b). Ribs mostly start within the first whorl and the protoconch microsculpture ceases when the first ribs appear.

Stratigraphic range — Upper *sulcatus* beds to lower *revertens* beds.

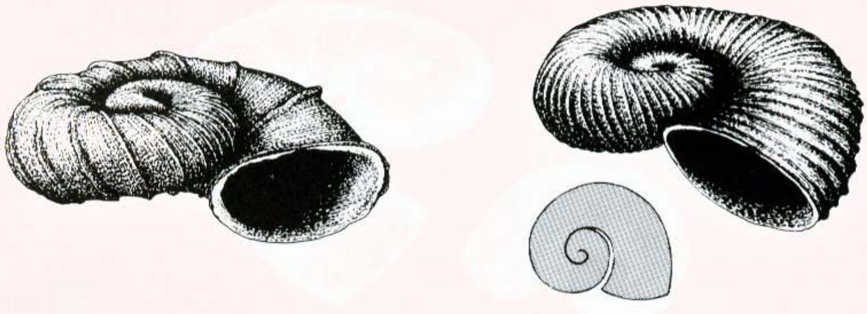

Fig. 9. *Gyraulus costatus* (von Klein, 1847) with few ribs (left) and with many ribs and last part of the last whorl detached (right). Drawn by Mrs Lewandowski.

Phylogenetic relationships — The tiny *G. costatus* is clearly a descendant of *G. minutus*. They are similar in size, shape and protoconch microsculpture. The ribs can be derived from strong growth lines and in the *sulcatus* beds transitional morphs can be found (Pl. 6, figs. 6-7).

G. costatus is the ancestor of *G. distortus* and *G. platystomus*.

Remarks — *G. costatus* is the most frequent side-branch planorbid of the Steinheim Basin. It is very abundant and variable in the *trochiformis* beds. *G. costatus* has a strong tendency to uncoil, especially the last whorl and to deflect it downward. Uncoiled *G. costatus* have more rapidly increasing whorls than *G. distortus* and its ribs are not as distant from each other (Pl. 7, fig. 8).

Gyraulus distortus (Hyatt, 1880)

Pl. 8, figs. 2-5.

Material — Numerous specimens studied; 24 specimens studied by SEM.

Description — Shape: uncoiled, dextrally trochospiral or planispiral; uncoiling starts after 1.0 to 1.5 whorls and never involves the first whorl. Shape of the whorls: round, almost circular, slowly increasing in diameter. Aperture: approximately as high as wide (0.4 mm). Number of whorls: not counted because detached irregularly. Diameter: 1.5-2.0 mm. Teleoconch sculpture: strong or fine ribs, the distance between the ribs is much larger than in *G. costatus*, the tendency to become cork screw like, the number and strength of ribs is reduced, often the shell is polygonal with angles at the ribs. Protoconch sculpture: *minutus* type.

Stratigraphic range — *trochiformis* to *oxystoma* beds.

Phylogenetic relationships — *G. distortus* is an uncoiled descendant of *G. costatus*. *G. distortus* is the ancestor of *G. denudatus*.

Remarks — It is not easy to explain why *G. distortus* is seen as a species of its own and not just as an uncoiled *G. costatus*. The real *G. distortus* has an almost circular aperture whereas uncoiled *G. costatus* are more or less internally flat or concave. The

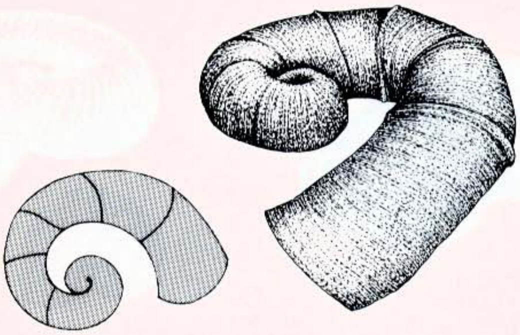

Fig. 10. *Gyraulus distortus* (Hyatt, 1880). Number of ribs strongly reduced, whorls very slowly increasing in diameter and slightly angular at the places of the ribs. Drawn by Mrs Lewandowski.

whorls of *G. distortus* increase more slowly than those of uncoiled *G. costatus*. At least the number of ribs is more reduced in *G. distortus*. This reduction leads to the smooth *G. denudatus*.

Plate 6

Fig. 1. Uncoiled *Gyraulus minutus* (Hilgendorf, 1867), sample SF18, transition from *steinheimensis* to *tenuis* beds, SMNS 25684. Uncoiling starts after the first whorl, detached whorls coil in a flat dextral trochospira, although the whorls are not in touch with each other their inner side is flattened or concave, protoconch with fine and dense sculpture (*minutus* type); a-b: scale 0.3 mm; c: scale 0.1 mm.

Fig. 2. Uncoiled *Gyraulus minutus* (Hilgendorf, 1867), sample SF18, transition from *steinheimensis* to *tenuis* beds, SMNS 25685. Small planispiral shell, uncoiling starts after the first whorl and ends after 1.7 whorls, then the whorls are again in touch with each other; scale 0.3 mm.

Fig. 3. Uncoiled *Gyraulus minutus* (Hilgendorf, 1867), sample SF18, transition from *steinheimensis* to *tenuis* beds, SMNS 25686; similar to Pl. 6, fig. 1; scale 0.3 mm.

Fig. 4. Uncoiled *Gyraulus minutus* (Hilgendorf, 1867), sample SF13, *sulcatus* beds, SMNS 25687. Small planispiral shell, uncoiling starts after the first whorl and continues, but the whorls are very close to each other; a-b: scale 0.3 mm.

Fig. 5. Uncoiled *Gyraulus minutus* (Hilgendorf, 1867), sample SF14, *sulcatus* beds, SMNS 25688. Uncoiled trochospirally, whorls are close to each other; scale 0.3 mm.

Fig. 6. *Gyraulus minutus* (Hilgendorf, 1867) (transitional to *G. costatus*) with strong growth lines, sample SF9, *sulcatus* beds, SMNS 25689. Small planispiral shell, whorls nearly as wide as high, slowly increasing round whorls, very strong growth lines, nearly ribs and thus a transition to *G. costatus*, protoconch with fine and dense sculpture (*minutus* type); a: scale 0.03 mm; b-c: scale 0.3 mm; d: scale 0.1.

Fig. 7. *Gyraulus costatus* (von Klein, 1847), sample S1, *sulcatus* beds, SMNS 25690. Small planispiral shell, whorls nearly as wide as high, slowly increasing round whorls, relatively weak ribs and thus still near to *G. minutus*, first rib at 1.0 whorls, ribs not dense, protoconch with fine and dense sculpture (*minutus* type); a: scale 0.1 mm; b: scale 0.03 mm; c: scale 0.1 mm.

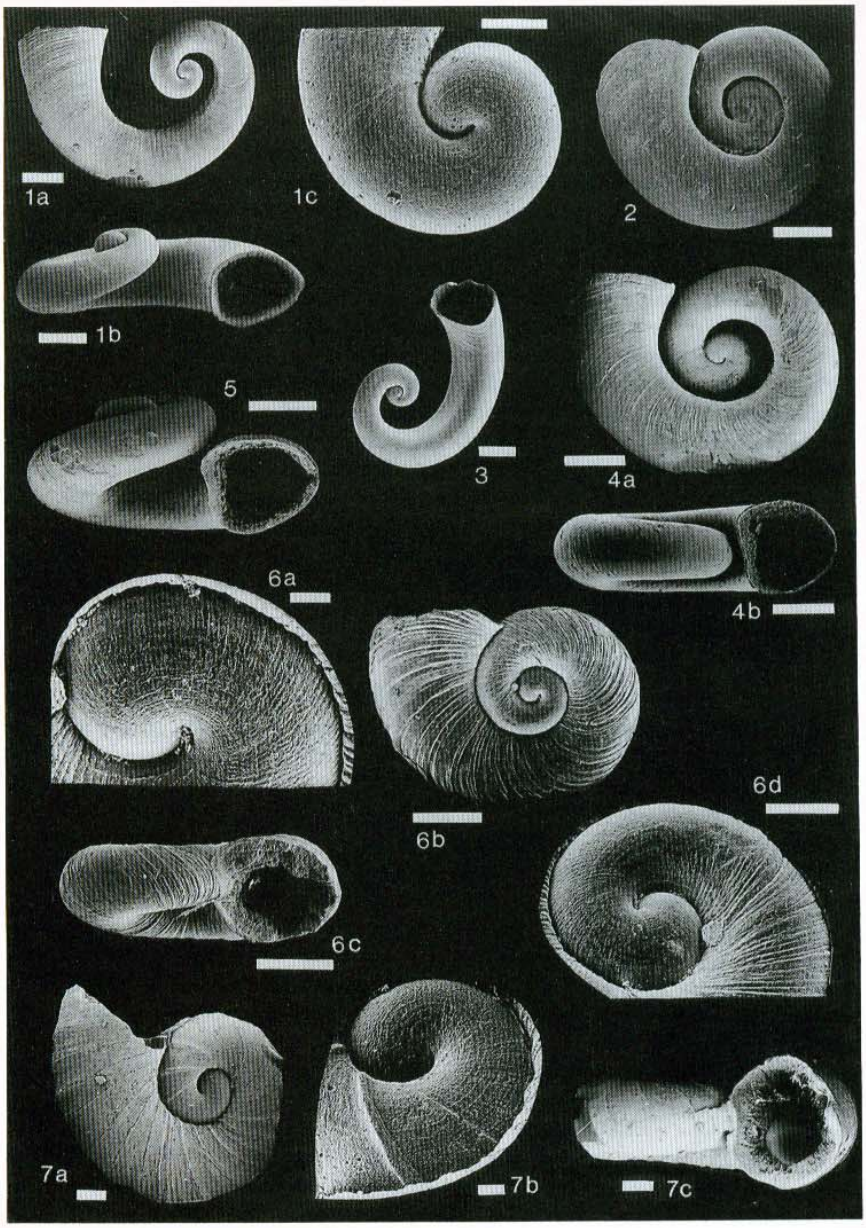

Plate 6

Gyraulus denudatus (Hilgendorf, 1867)
Pl. 7, fig. 6.

Material — 15 specimens studied; 6 specimens studied by SEM.

Description — Shape: the first whorl is planispiral, the following whorls are uncoiled cork-screw like. Shape of the whorls: round, almost circular. Aperture: almost circular; as high as wide (0.3 mm). Number of whorls: up to 4.2. Diameter: up to 0.9 mm. Height: up to 1.7 mm. Teleoconch sculpture: smooth with fine growth lines and a microsculpture of small spirally arranged, sometimes crescentic nodules. Protoconch sculpture: *minutus* type (Pl. 7, fig. 6c).

Stratigraphic range — Upper *trochiformis* beds.

Phylogenetic relationships — *G. denudatus* is clearly a descendant of *G. distortus*. Specimens of *G. distortus* that are uncoiled in a cork-screw like way tend to reduce the number and the strength of ribs. *G. denudatus* is not an uncoiled variety of *G. minutus* as Hyatt (1880) and Miller (1900) supposed. Uncoiled *G. minutus* are common in the *steinheimensis* and *tenuis* beds and do not appear before the typical *G. denudatus* is present. Although some uncoiled *G. minutus* are trochiform, no specimen has the strict cork-screw pattern of *G. denudatus*.

Remarks — The amazing and rare morpho-species *G. denudatus* is restricted to the

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Plate 7

Fig. 1. *Gyraulus costatus* (von Klein, 1847), sample S32, *trochiformis* beds, SMNS 25691. Typical *Gyraulus costatus*, small planispiral, upper side as deep as lower one, relatively dense ribs, starting within the first whorl, protoconch with distinct spiral striation but still very dense (*minutus* type); a: scale 0.3 mm; b: scale 0.03 mm.

Fig. 2. *Gyraulus distortus* (Hyatt, 1880), sample S34, *trochiformis* beds, SMNS 25692. Uncoiling starts after the first whorl, whorls circular, ribs are long and distant from each other, protoconch sculpture of *minutus* type continues onto the teleoconch; a: scale 0.3 mm; b: scale 0.1 mm.

Fig. 3. *Gyraulus distortus* (Hyatt, 1880), sample S33, *trochiformis* beds, SMNS 25693; scale 0.3 mm.

Fig. 4. *Gyraulus distortus* (Hyatt, 1880), sample S26, *trochiformis* beds, SMNS 25694. Wide trochospirally uncoiled, ribs are weak and distant from each other; scale 0.3 mm.

Fig. 5. *Gyraulus distortus* (Hyatt, 1880), transitional to *G. denudatus* (Hilgendorf, 1867), sample S26, *trochiformis* beds, SMNS 25695. Uncoiling in a narrow, regular trochospira, ribs are weak and very distant from each other; a-b: 0.3 mm.

Fig. 6. *Gyraulus denudatus* (Hilgendorf, 1867), sample S33, *trochiformis* beds, SMNS 25696. Typical form, first whorl planispiral, than uncoiling in a narrow trochospira, no ribs are developed, protoconch of *minutus* type; a: scale 0.3 mm; b-c: scale 0.1 mm.

Fig. 7. *Gyraulus platystomus* (Hilgendorf, 1867), sample S32, *trochiformis* beds, SMNS 25697. Incomplete specimen, whorls are increasing rapidly, protoconch does not show spiral pattern, but a labyrinthic microsculpture; a: scale 0.3 mm; b: scale 0.03 mm, protoconch with labyrinthic pattern (see Pl. 1, fig. 6).

Fig. 8. *Gyraulus costatus* (von Klein, 1847), uncoiled, sample S25, *trochiformis* beds, SMNS 25698. Whorls are increasing more rapidly than in *G. distortus* and ribs are not so distant from each other; scale 0.3 mm.

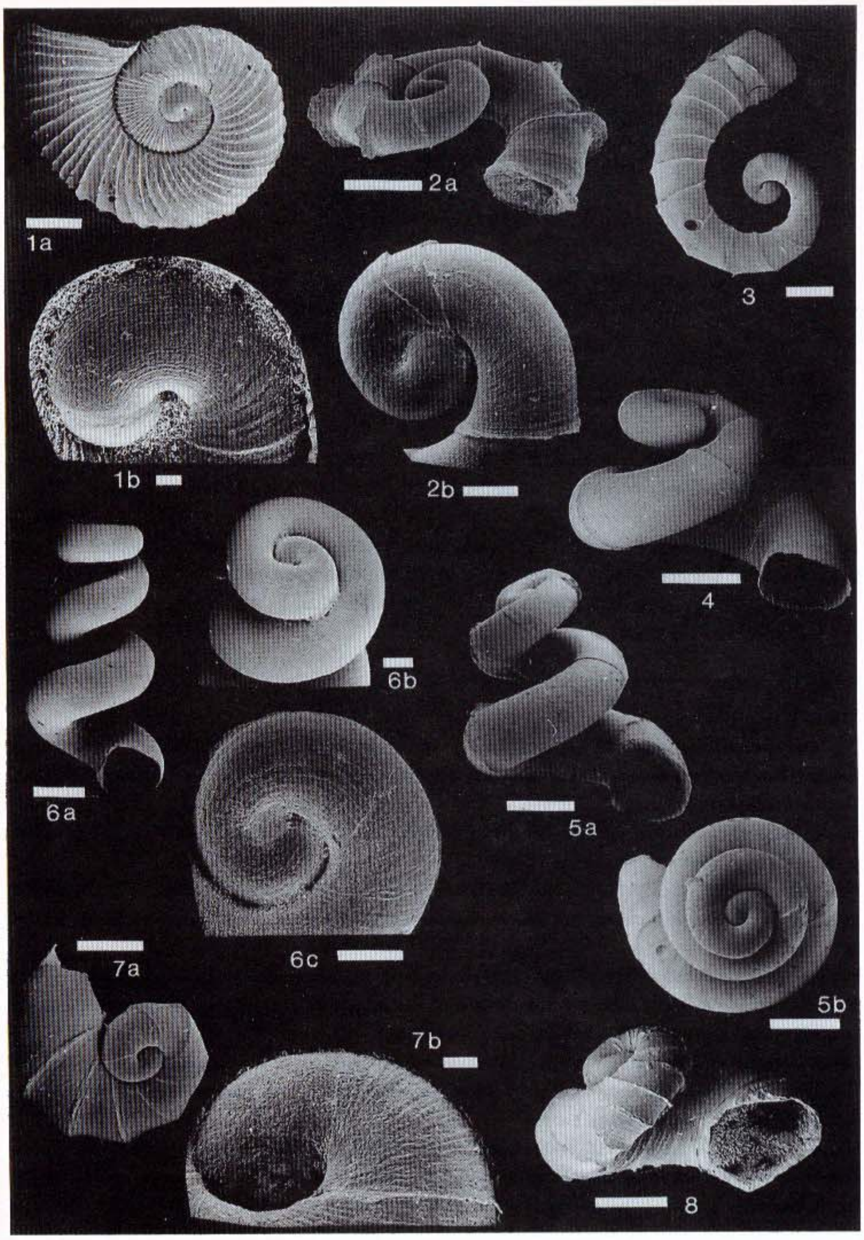

Plate 7

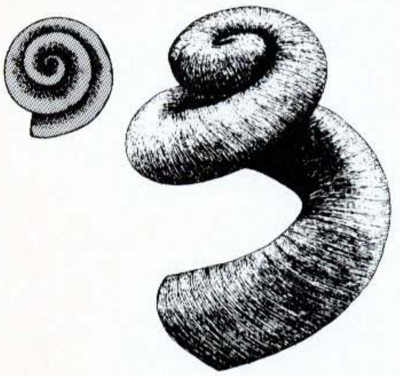

Fig. 11. *Gyraulus denudatus* (Hilgendorf, 1867). Cork-screw-like detached smooth whorls. The top view illustrates a regular mode of trochospiral uncoiling. Drawn by Mrs Lewandowski.

uppermost *trochiformis* beds. The restriction in time and the very characteristic pattern of uncoiling are good arguments to establish this species.

An adaptive process leading to this species is difficult to imagine.

Plate 8

Fig. 1. *Gyraulus platystomus* (Hilgendorf, 1867), sample S36, *trochiformis* beds, SMNS 25699. Typical specimen, no spiral pattern on the protoconch; a-b: scale 0.3 mm; c: scale 0.03 mm, protoconch, spiral elements are reduced.

Fig. 2. *Gyraulus platystomus* (Hilgendorf, 1867), sample S33, *trochiformis* beds, SMNS 25700. Specimen with extremely developed ribs; scale 0.3 mm.

Fig. 3. *Gyraulus platystomus* (Hilgendorf, 1867), sample S27, *trochiformis* beds, SMNS 25701. Incomplete specimen with relatively strong ribs and remains of calcified periostracum; a: scale 0.1 mm; b: scale 0.03.

Fig. 4. *Gyraulus platystomus* (Hilgendorf, 1867) transitional to *G. rotundostomus*, sample S32, *trochiformis* beds, SMNS 25702. The aperture is relatively big and still wider than high. It is distintively higher than the aperture of a typical *G. platystomus*; scale 0.3 mm.

Fig. 5. *Gyraulus rotundostomus* sp. nov., paratype, sample S36, upper *trochiformis* beds, SMNS 25703. The aperture is approximately as high as wide, the whorls are rapidly increasing, the last whorl is deflected downward; a-b: scale 0.3 mm.

Fig. 6. *Gyraulus platystomus* (Hilgendorf, 1867), sample S33, *trochiformis* beds, SMNS 25704. Distinct growth increments cover the protoconch; a: scale 0.3 mm; b: scale 0.1 mm.

Fig. 7. *Gyraulus rotundostomus* sp. nov., holotype, sample K2, *oxystoma* beds, SMNS 25705. The aperture is circular and bears an inner collar, last whorl strongly deflected downward and thus an overall trochoid shape, whorls are rapidly increasing, lower umbilicus deep and narrow, dense sculpture on the protoconch shows only indistinct spiral elements; a-c: scale 0.3 mm; d: scale 0.03 mm.

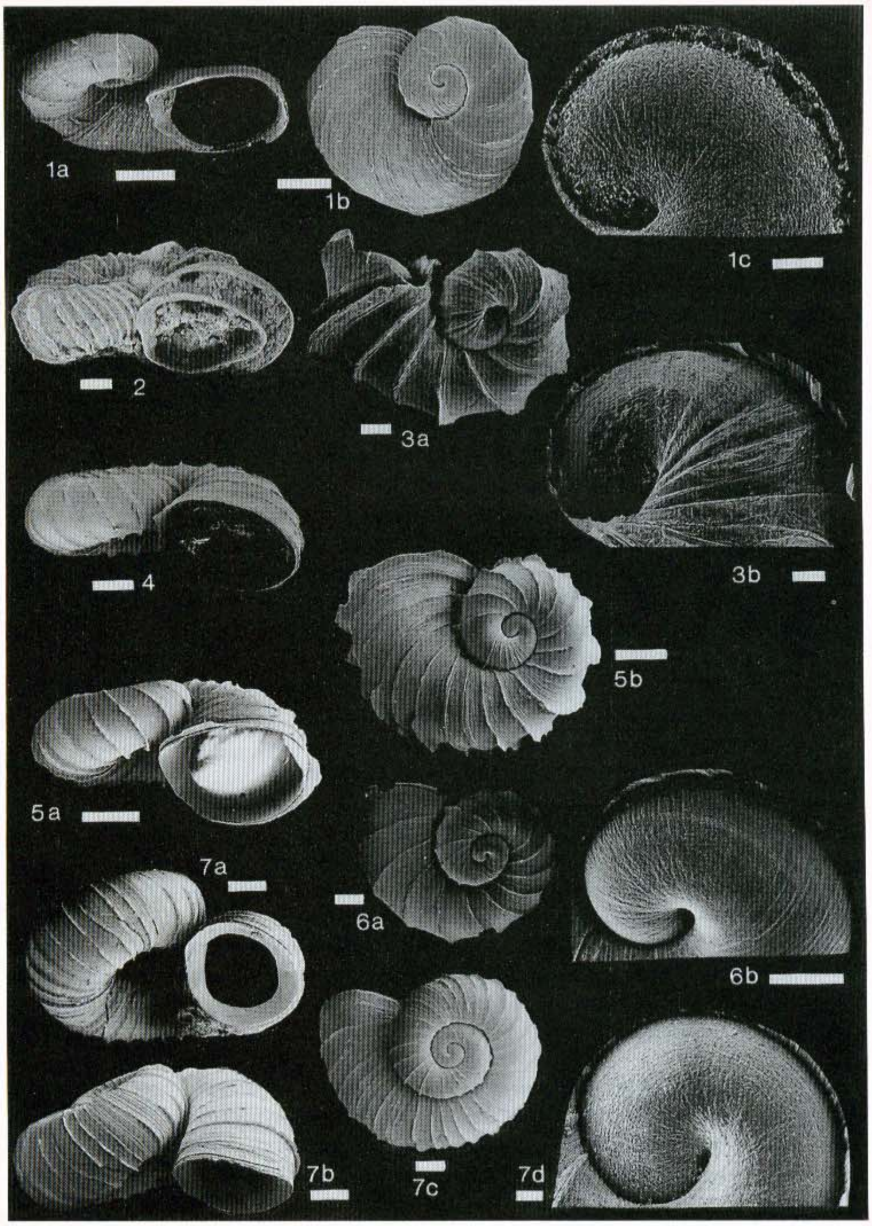

Plate 8

Stratigraphic range — Upper *trochiformis* to *oxystoma* beds.

Phylogenetic relationships — *G. rotundostomus* is a descendant of *G. platystomus*, which occurs a little earlier.

Remarks (including differential diagnosis) — *G. rotundostomus* is quite common in the *oxystoma* beds. It is much bigger than *G. costatus* and has more rapidly increasing whorls. It also is bigger than *G. platystomus* and its aperture is not flat but almost circular.

G. rotundostomus seems not to be identical with *Planorbis multiformis* var. *costatus* var. *major* Hilgendorf, 1867, which was reported from the *oxystoma* and *revertens* beds, but could not be re-identified from our material. After Hilgendorf's (1867) description var. *major* reaches a diameter of 3 mm and its ribs do not continue around the whorls. However, *G. rotundostomus* is smaller and has continuous ribs. Further Hilgendorf (1867) did not mention the flat trochiform shape and the deep lower umbilicus for var. *major*, which are typical characters for *G. rotundostomus*.

Additional to the already described morphospecies some problematical planorbid specimens have been examined (Pl. 8, figs. 1-4). Their relation to other species is unclear and they are therefore designated *Gyraulus* sp.

Gyraulus sp. 1
Pl. 9, fig. 1.

One single specimen from the *sulcatus* beds with a remarkable protoconch. The first whorl has an open umbilicus and is swollen at the beginning. The shell is planispiral and a little over two whorls are preserved (diameter 1.4 mm). The microsculpture of the protoconch is rather indistinct with relatively wide spiral striae. This specimen possibly represents a pathological *G. minutus*.

Gyraulus sp. 2
Pl. 9, fig. 2.

This morph from the *oxystoma* beds has extremely slowly increasing circular whorls and deep sutures. With nearly three evolute whorls it has a diameter of only 1.2 mm. The last half whorl is deflected downward, so that the specimen seems to be nearly mature. The protoconch microsculpture is somewhat similar to the *minutus* type, but much denser, and spiral elements are hardly visible.

Gyraulus sp. 2 is clearly not related to any of the other Steinheim planorbids and was possibly an unsuccessful invader.

Gyraulus sp. 3
Pl. 9, fig. 3.

Gyraulus sp. 3 is another type of an evolute planorbid with a very finely sculptured protoconch. It appears rarely in the *trochiformis* beds and its relation to other morphotypes is unclear.

Gyraulus sp. 4
Pl. 9, fig. 4.

This morphotype occurs occasionally in the *trochiformis* beds. It is flat, has c. three evolute round whorls and reaches a diameter of c. 1.8 mm. On the protoconch a microsculpture of spirally arranged and transversely orientated crescentic nodules is visible. Growth lines start very early on the embryonic shell.

Gyraulus sp. 3 is maybe a descendant of *G. protocrescens* or *G. minutus*. Shape and size are similar whereas the protoconch microsculpture differs from both.

Conclusions

Three morphogroups, each of which is based on a particular type of protoconch microsculpture, were evolving in Lake Steinheim. The character of the protoconch ornamentation also changed with time. At least it seems to be clear that they were evolving independently from each other since the *steinheimensis*-period. Although there is an information deficit about the *kleini* beds one can state that polyphyly of the Steinheim planorbids is as likely as their monophyly.

The three groups are showing different patterns of evolution.

1. The main-branch and side-branch 1 group (including the *G. steinheimensis*/*G. pseudotenuis* group) has a strong tendency to increase in size and to modify the normal planorbid pattern in developing trochoid shape, collars and angles.

2. The *G. crescens* group remains conservative. The shell shape is always planispiral. No ribs are observed and neither trochiform nor uncoiled morphs occur. Only slight differences in size and shape of the whorls differentiate these species.

3. The *G. minutus* group contains very small shells and includes morphs which deviate strongly from the normal planorbid morphology. Morphs showing ribs and uncoiling are restricted to this group. Trochiform shells are common. The protoconch microsculpture is extraordinarily variable and the object of evolution. At the same time the *minutus* group contains morphs displaying a normal planorbid pattern throughout the stratigraphic section. Angles and collars, common amongst the other two groups, are not present in the *minutus* group, in which the whorls are always round.

So each group is characterised by its own morphological plasticity and its specific

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Plate 9

Fig. 1. *Gyraulus* sp. 1, sample SF13, *sulcatus* beds, SMNS 25706. Planorbid with abnormously swollen protoconch; a-b: scale 0.3 mm; c: scale 0.1 mm.

Fig. 2. *Gyraulus* sp. 2, sample Ph17, *oxystoma* beds, SMNS 25707. Very evolute planorbid with slowly increasing whorls and special protoconch microsculpture; a-b: scale 0.3 mm; c: scale 0.1 mm.

Fig. 3. *Gyraulus* sp. 3, sample S25, *trochiformis* beds, SMNS 25708. Problematical, evolute planorbid, with specimen of *Pseudamnicola pseudoglobulus* (d'Orbigny, 1852) in aperture; a-b: scale 0.3 mm; c: scale 0.1 mm.

Fig. 4. *Gyraulus* sp. 4, sample, S28, *trochiformis* beds, SMNS 25709. Problematical evolute planorbid; a-b: scale 0.3 mm; c: scale 0.1 mm, protoconch with spirally arranged, tranverse crescentic nodules.

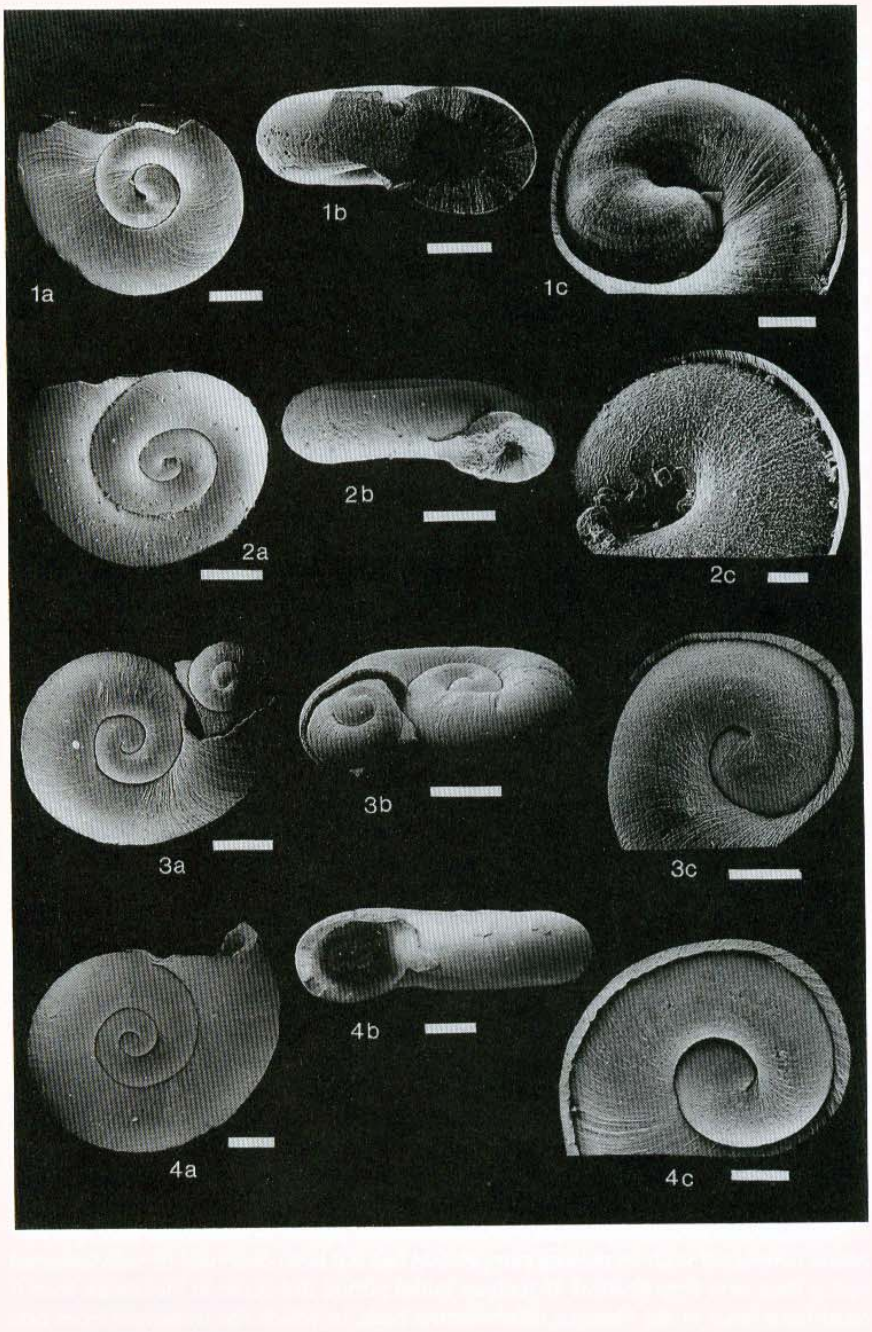

Plate 9

variability. All planorbids of Steinheim have a high ability of changing shell shape compared to the lymnaeid *Lymnaea dilatata* and the hydrobiid *Pseudamnicola pseudoglobulus*. So one can state that morphological plasticity is a diagnostic feature, both for the stem species and for their descendants.

Remarks on the reasons for the local radiation

Gottschick (1920) and Gottschick & Wenz (1919-22) supposed that all described morphs are ecophenotypes of the same species and that hot springs were the motor for change in shell shape. Indeed there is a rough correlation between the grade of deviation from normal planorbid pattern and some geochemical parameters like enrichment in O^{18}, a low Ca/Mg-ratio and aragonitic cementation (Bajor, 1965; Wolff & Füchtbauer, 1976; Mensink, 1984). These features implicate an unusual water chemistry which was not originated by hot springs but to a high degree of evaporation. This hypothesis of a radiation would explain why the lake was not colonised repeatedly by non endemic planorbids during its history. On the other hand the changes of the shell shapes are too specific and obviously related to species, to represent exclusively the result of the changing of a single or a few abiotic factors.

Gorthner (1984a) and Gorthner & Meier-Brook (1985) suggested that lake Steinheim existed for a very long time and that its highly endemic fauna is the result of intralacustrine speciation of generalists, normally living in ephemeric habitats. The species had become specialists (adapted to microenvironments) in a stable habitat. These forms remained endemic, because they had become too specialised for the surrounding ephemeric habitats. On the other hand generalists from the outside could not immigrate, because all niches were occupied.

This hypothesis is based on an actualistic comparison with the Recent long lasting Lake Ochrid (Yugoslavia) that displays a normal water chemistry. Lake Ochrid is populated by a highly endemic gastropod fauna and some of its planorbid species are convergent to species of the Steinheim Basin. But it was neither satisfactorily shown that the endemic species of Lake Ochrid are adapted to narrow niches nor could the proposed coevolutionary effects be demonstrated.

Gorthner (1992) modified this hypothesis in proposing that the changes in shell shapes of the planorbids in Recent long lasting lakes as well as in the ancient lake Steinheim are non adaptive and non functional. He suggested that an initial period of intralacustrine speciation pushed by competition results in more effective utilization of habitats. As a consequence competition and selective pressure is reduced in the endemic and specialised fauna. Thus modifications and mutations, which are neither useful nor harmful, are resulting in a high degree of variability and in speciations. The morphological deviations are restricted by an inherent range of the bauplan. As a quintessence he stated that high selective pressure, common in ephemeric environments, stabilises morphology whereas low selective pressure, characteristic for long-lasting environments, destabilises morphology.

An objection to this explanation is that an initial period of speciation and specialization connected with increasing competition has not been observed or substantiated and is thus very hypothetical. If such an initial period did occur in Steinheim than it must have been in the *kleini* to *steinheimensis* beds, in which the transition from non

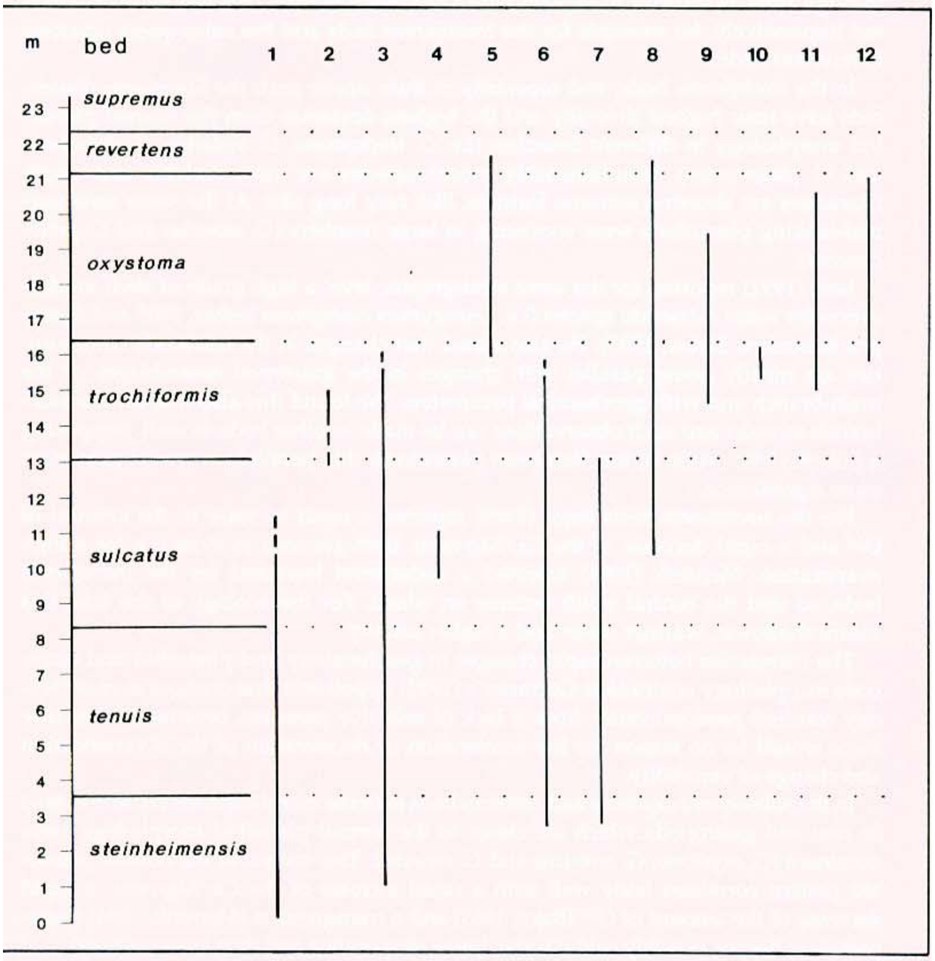

Fig. 12. Stratigraphic range of the species; 1: *Gyraulus steinheimensis*; 2: *G. pseudotenuis*; 3: *G. protocrescens*; 4: *G. triquetrus*; 5: *G. crescens*; 6: *G. minutus*; 7: *G. minutus*, uncoiled; 8: *G. costatus*; 9: *G. distortus*; 10: *G. denudatus*; 11: *G. platystomus*; 12: *G. rotundostomus*.

endemic to endemic faunas took place. This initial period was proposed by Gorthner (1992) to explain why the populations in ancient lakes remain endemic.

For Steinheim another objection has to be made. There is a fairly good correlation between geochemical parameters on the one hand and diversity and variability of the planorbids on the other. Especially the fact that an accelerating change of geochemical parameters goes parallel with an acceleration of diversification and variability through time, is difficult to explain with Gorthner's model. This can be demonstrated impressively, for example for the *trochiformis* beds and the subsequent *oxystoma* to *revertens* beds:

In the *trochiformis* beds, and especially in their upper part, the Steinheim planorbids have their highest diversity and the highest deviation from the normal planorbid morphology in different branches (i.e. *G. trochiformis*, *G. distortus*, *G. denudatus* and *G. platystomus*). Simultaneously morphospecies are most variable and single characters are showing extreme features, like very long ribs. At the same time normal-looking planorbids were coexisting in large numbers (*G. minutus* and *G. protocrescens*).

Janz (1992) reported for the same stratigraphic level a high grade of shell modification for some ostracode species (i.e. *Leucocythere esphigmena* Sieber, 1905 and *Ilyocypris binocularis* Sieber, 1905). He also stated that changes in the ostracode communities are mostly going parallel with changes in the gastropod assemblages of the main-branch and with geochemical parameters. We found this also true for the side-branch morphs and such observations can be made in other beds as well. Supposing a polyphyletic origin of the Steinheim planorbids, this parallelism would gain even more significance.

For the *trochiformis* beds Bajor (1965) reported a rapid increase in the amount of O^{18} and a rapid decrease of the Ca/Mg-ratio. Both are seen as evidence for a high evaporation. Mensink (1984) reported a water-level lowstand for the *trochiformis* beds, so that the central uplift became an island. For the ecology of the lake this meant shallower, warmer water and a higher salinity.

The correlation between rapid changes in geochemistry and planorbid and ostracode morphology contradicts Gorthner's (1992) hypothesis that changes in morphology resulted predominantly from a lack of selective pressure, because in this case there would be no reason for the acceleration or deceleration of the diversification and change of variability.

In the subsequent *oxystoma* and *revertens* beds extreme morphospecies became extinct or rare and gastropods which are closer to the normal planorbid morphology were dominant (*G. oxystoma*, *G. revertens* and *G. crescens*). This revival of the normal planorbid pattern correlates fairly well with a rapid increase of the Ca/Mg-ratio, a rapid decrease of the amount of O^{18} (Bajor, 1965) and a transgression (Mensink, 1984) (interpretation: deeper, possibly colder water, lower evaporation and thus lower salinity).

The fact that extreme morpho-species became extinct and did obviously not hybridise with their more conservative stem species suggests species rank of the extremists as well as ecological and external control of their occurrence. This non-hybridisation was demonstrated by Mensink (1984) for *G. trochiformis* and it is also true for side-branch morphs, e.g. for *G. denudatus*. Furthermore it is remarkable that the normal looking planorbids of the *oxystoma* to *revertens* beds are similar but not morphologically identical to the planorbids of the older beds (see also Mensink, 1984).

The evolution in the *oxystoma*/*revertens* beds could be explained by external influences as well as by Gorthner's (1992) hypothesis. Selective pressure increases when a stable habitat becomes instable (more similar to ephemeric environments) and as a consequence variability decreases. From the subsequent *supremus* beds again changes to abnormal shell shapes are reported (Hilgendorf, 1867; Mensink, 1984). Our

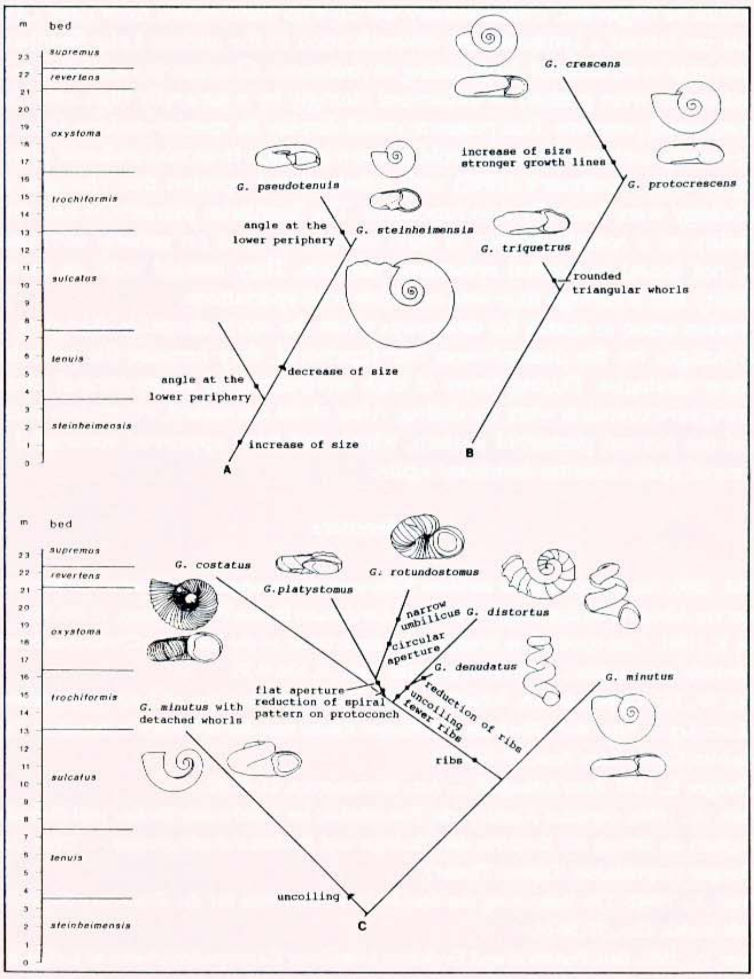

Fig. 13. Phylogenetic trees of the three *Gyraulus* groups which were evolving independently at least since the *steinheimensis*-period. Possibly they do not derive from one common ancestor. The trees are not cladograms because the deviation rule is not followed. Every straight line represents the stratigraphic range of a morphospecies. Quadrangles represent the occurrence of important new characters. Triangles represent the occurrence of characters within one morphospecies. A: *Gyraulus steinheimensis*/*G. pseudotenuis* group; B: *Gyraulus crescens* group; C: *Gyraulus minutus* group.

material provides only few data about these beds.

Concluding we agree with Janz (1992) that external factors were influencing the evolution in the Steinheim Basin. On the other hand the convergence to endemic gastropods in other, still extant ancient lakes, which have a fairly normal water chemistry, cannot be neglected. Unfortunately we have no fossil record from Lake Ochrid.

Thus we favour a synthesis: the diversification in the ancient Lake Steinheim was only possible in an isolated, long-lasting environment. Changes in variability as well as diversification were pushed or influenced strongly by a generally high and changing environmental pressure. This pressure could display its species-making force only in a long-lasting environment and would prevent invasion from non-endemic planorbids. We agree with Gorthner's (1992) well substantiated opinion that changes in shell morphology were basically non-functional. The Steinheim planorbids had an inherent ability, to a specific degree in each branch, to react on general environmental stress, not found in normal ephemeric habitats. They reacted with an increase of variability and if enough time was available with speciations.

It makes sense to search for new ways when the environment is changing, even if these changes for the present seem non-functional, they increase the probability to find new strategies. During times of high environmental stress normal planorbids and morpho-extremists were coexisting. After stress decreased, extremism was rejected and the normal planorbid pattern, which had been approved successful during millions of years, became dominant again.

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