Early Jurassic anoxia triggered the evolution of the oldest holoplanktonic gastropod *Coelodiscus minutus* by means of heterochrony

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The tiny gastropod *Coelodiscus minutus* is superabundant in concretions of the Early Jurassic *Posidonia* Shale of South Germany which were formed under anoxic or extremely dysoxic conditions. Previous suggestions that *C. minutus* was a holoplanktonic organism are corroborated based on new evidence from exceptionally well-preserved specimens. The measurements of shell thickness show that the shell of *Coelodiscus* is very thin (mean 11 μm). In contrast to previous suggestions, the shell of *Coelodiscus* was not formed in three ontogenetic phases (embryonic, larval and adult shell) but in two phases comprising an embryonic and a secondary shell, the latter forming during an extended larval phase. Hostile conditions on the sea floor, absence or extreme scarcity of epibenthic animals as well as the small size also argue against a benthic life style of this gastropod. *Coelodiscus minutus* is the oldest known holoplanktonic gastropod. We speculate that *Coelodiscus* evolved during the Early Jurassic from a benthic precursor, which had a planktotrophic larval development. Probably under the influence of increasing frequency of dysoxic episodes along with hostile benthic conditions, the larval phase was extended neotenously and eventually, a holoplanktonic species evolved. During the Early Toarcian anoxic event, *C. minutus* was highly abundant in the plankton and dead shells rained down to the anoxic or dysoxic sea bottom. These thin and fragile shells formed an ooze similar to the pteropod ooze in the modern deep sea. The shells were preserved due to the absence or low level of deposit feeding and bioturbation as well as the formation of early diagenetic concretions.

Key words: Gastropoda, *Coelodiscus minutus*, holoplanktonic gastropods, anoxia, heterochrony, neoteny, Jurassic, Toarcian.

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Introduction

The tiny Early–Middle Jurassic (Pliensbachian–Aalenian) gastropod *Coelodiscus minutus* (Schübler in Zieten, 1833; family Coelodiscidae Gründel and Nützel in Schulbert and Nützel, 2013) is superabundant in some strata exposed in Central Europe and England. The small (max. diameter ca. 3 mm), low-spired to planispiral specimens are especially abundant and even rock forming in the Early Toarcian oxygen deficient facies of the *Posidonia* Shale Formation from Germany. There is an ongoing controversy whether *C. minu-tus* had an epibenthic (e.g., Etter 1996) or a holoplanktonic mode of life (e.g., Jefferies and Minton 1965; Bandel and Hemleben 1987). The Jurassic genera *Coelodiscus* Brösamlen, 1909 and *Tatediscus* Gründel, 2001 form the family Coelodiscidae which ranges from the Early Pliensbachian to the Early Aalenian (Todd and Munt 2010; Schulbert and Nützel 2013). If *C. minutus* was indeed holoplanktonic, this would represent the earliest example for this mode of life in the class Gastropoda.

In modern oceans, holoplanktonic gastropods, such as pteropods and heteropods, form an important part of the zoo-

plankton and their shells contribute to oceanic sedimentation to a considerable amount in areas with bottom depths above the aragonite compensation depth (i.e., pteropod ooze; Lalli and Gilmer 1989). Holoplanktonic means that an organism has a planktonic mode of life throughout its entire lifetime. Many modern holoplanktonic shelled pteropods or heteropods have highly derived shells with a tendency to evolve bilateral symmetrical shells as an adaption to active swimming (e.g., Richter 1973). The Recent holoplanktonic gastropods are of low diversity comprising about 140 species but not all of them have shells in the adult stage (Lalli and Gilmer 1989). In these gastropods, the holoplanktonic mode of life is polyphyletic, i.e., it evolved independently in the superorders Caenogastropoda Cox, 1960 (families Janthinidae Lamarck, 1822, Atlantidae Rang, 1829, Carinariidae Blainville, 1818a) and Heterobranchia Burmeister, 1837 (pteropods: Thecosomata and Gymnosomata). The fossil record of these gastropod groups is not older than Late Cretaceous or Cenozoic (the report of Jurassic Carinariidae by Bandel and Hemleben [1987] is refuted here, see below), with the first occurrences in the Eocene (Atlantidae), the Rupelian (Carinariidae), and the Messinian (Janthinidae) (Tracey et al. 1993; Paleobiology Database http://paleobiodb.org). Some of the Paleocene and Eocene forms previously assigned to Atlantidae have been recently transferred to the benthic family Hipponicidae (Lozouet 2012; Schnetler 2013). The Early Cretaceous genus *Bellerophina* d'Orbigny, 1843 (family Bellerophinidae Destombes, 1984) was interpreted as an extinct example of the holoplanktonic heteropods (Tracey 2010). Thecosomata originated in the Late Paleocene (Janssen 2003) and Gymnosomata in the late Oligocene (Janssen 2012). Thus, if *C. minutus* was indeed holoplanktonic, Coelodiscidae would be the oldest example for this mode of life in the class Gastropoda (Bandel and Hemleben 1987).

Besides holoplanktonic gastropods, many marine gastropod species have free-swimming planktonic veliger larvae that metamorphose to benthic adult forms (e.g., Jablonski and Lutz 1983; Nützel 2014).

Based on very well preserved material from the Early Toarcian of Southern Germany, we present new evidence that *C. minutus* was in fact a holoplanktonic snail. Furthermore, we present evidence that it is not a member of a living heteropod family and propose a hypothesis on the evolution of *C. minutus*.

Institutional abbreviations.—BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany.

Other abbreviations.—TOC, total organic carbon.

Material and methods

The studied material comes from a layer with calcareous concretions of the *Posidonia* Shale Formation (Lower Toarcian), collected from a temporary outcrop in the city of Altdorf near Nuremberg (Northern Bavaria, Southern Germany). This level of concretions is called informally "Zweier-Laibsteine" (*Harpoceras falcifer* Ammonite Zone, *Harpoceras elegans* Subzone). Generally, several limestone horizons occur throughout the *Posidonia* Shale Formation (e.g., Röhl et al. 2001) and long-distance correlation of the horizon in Northern Bavaria that yielded the studied material is difficult. However, it is most likely that it can be assigned to the so-called "Oberer Stein" in the profile discussed by Röhl et al. (2001). The studied limestone is dark and highly fossiliferous, containing abundant ammonites, superabundant shells of *C. minutus* as well as bivalves and vertebrate remains.

For the preparation of fossils, the material was coarsely fractured using a jaw crusher. In a second step, it was alternately stored in water for 12 h, removed, frozen and submerged in hot water. This procedure was repeated 10 times to enhance the break-off of fossils in a second, finer fracturing with the jaw crusher. The resulting rock debris was washed, sieved (2 mm, 0.5 mm, and 0.125 mm mesh size), the residues were picked for fossils and well-preserved specimens were studied with a CamScan SEM. In addition, fractured rock surfaces were covered with ammonium chloride and studied with a Leica M420 macroscope equipped with a DFC 320 camera. Several thin sections were prepared in order to gain information on lithology and microfacies using a Zeiss Axiophot equipped with a MRc5 camera. Thin sections were also used to measure the thickness of the shell wall in in relation to specimen size. Measurements were taken from sections approximately perpendicular to the shell surface from calibrated images of the thin sections using the software Zeiss AxioVision 4.8. The linear increase of the shell thickness with body size was indicated by linear bivariate modelling with Ordinary Least Squares Regression in PAST3 (Hammer et al. 2001), once using the original measurement data and once using the log-transformed data. To measure the total organic carbon (TOC) of the rocks, samples were decarbonized using hydrochloric acid (10%) and analysis of organic carbon was performed with an elemental analyser (CE 1110) connected online to a ThermoFinnigan Delta V Plus mass spectrometer. Accuracy and reproducibility of the analyses was checked by replicate analyses of jon1 standard. Reproducibility was better than ±0.03% (1σ). The apatite-preserved vertebrate fauna was gained by dissolving 0.7 kg rock material in acetic acid (10%) and the residue was studied with the SEM.

Results

The limestone concretions yield two lithologies. The main facies is an ammonite floatstone with a grain-supported matrix of highly abundant *C. minutus* shells and fecal pellets (*Coelodiscus*/fecal pellet grainstone). This grainstone is cemented by a sparry calcite that fills also the ammonites (Fig. 1A). This dominant grainstone facies alternates with layers that are mud-supported (mud- and wackestone). The second and sub-
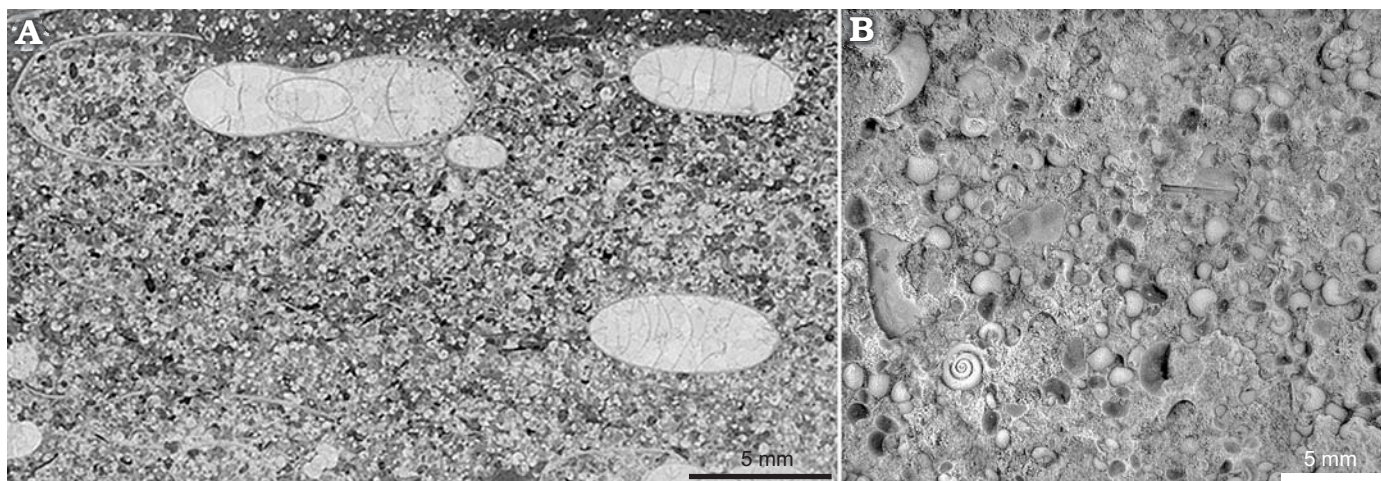
Fig. 1. The lithology of the limestone concretion, *Posidonia* Shale Formation, Lower Toarcian; Altdorf near Nuremberg, Northern Bavaria, Southern Germany. **A**. BSPG 2008 XXIX 11a, ammonite floatstone with grain-supported matrix consisting of the holoplanktonic gastropod *Coelodiscus minutus* (Schübler in Zieten, 1833) and fecal pellets, cemented by sparry calcite. Each of the small bright dots represents a juvenile specimen of *C. minutus*. **B**. BSPG 2008 XXIX 5a, surface of the ammonite floatstone with superabundant specimens of *C. minutus*.

ordinate facies type in the concretions is a distinctly laminated mudstone with bivalve filaments and abundant fish remains. The ammonite floatstone has a TOC of 0.30–0.36% (n = 5). The laminated mudstone has a TOC of 2.30–2.82% (n = 5).

Coelodiscus minutus is superabundant in the limestone concretions (Figs. 1A, B, 2A). The originally aragonitic shells of all molluscs, including *C. minutus*, are replaced by calcite. The preservation of *C. minutus* is excellent including preservation of the protoconch (embryonic shell) and fine ornamental details. *Coelodiscus minutus* is as wide as ca. 3 mm (ca. 5 whorls) but most specimens are much smaller (less than 0.5 mm). The shells are low-spired to almost planispiral and wider than high. The spire is usually elevated but specimens with plane or somewhat depressed spire are also known (Fig. 2B, C). The protoconch (embryonic shell) consists of somewhat less than one whorl and has a diameter of 175 μm ±2.2 μm SE (n = 13). It is largely smooth with a faint pitted ornament on its initial part and the transition to the teleoconch is abrupt (Fig. 2D). The teleoconch whorls are ornamented with fine spiral lirae separated by wide interspaces (Fig. 2E). The growth lines are opisthocyrt with the backmost point situated in an adapical direction (Fig. 2F). Some of the specimens show growth abnormalities (Fig. 2G, H). The teleoconch whorls are convex as is the base of the whorls. The base is deeply umbilicated. The shell sculpture is also visible with the very small specimens, thus ensuring an attribution to *C. minutus* (Fig. 2I). The shell thickness inferred from thin sections ranges 2–41 μm (mean = 11.3 μm ±0.5 μm SE, n = 132) and shows a statistically significant correlation ($p_{perm.}$ = 0.001) with the diameter of the shells: the larger the specimen, the thicker the shell (Fig. 3A, B).

The ammonites represent specimens of the genus *Harpoceras* Waagen, 1869. In addition, numerous bivalve prodissoconchs (planktonic larval shells) are present. They are always articulated and represent pteriomorphs (Fig. 4A). The limestone concretions contain also few larger bivalves (*Me-*

leagrinella substriata [Münster in Goldfuss, 1831] [Fig. 4B] and specimens representing the genus *Oxytoma* Meek, 1864 [Fig. 4C], both superorder Pteriomorphia). The acetic acid dissolved sample of 0.7 kg rock yielded ca. 300 g vertebrate remains (fish remains, teeth, bones, etc.) representing mainly the fish *Lepidotes elvensis* Blainville, 1818b.

Discussion

Three Early Jurassic gastropod taxa have been identified as being probably holoplanktonic: *Coelodiscus minutus*, the species of *Tatediscus* (both family Coelodiscidae), and *Pterotrachea liassica* Bandel and Hemleben, 1987 (probably a junior synonym of *Ammonites ceratophagus* Quenstedt, 1858). The latter taxon represents a larval shell whose modern counterpart is present in the living heteropod genus *Pterotrachea* Forsskål in Niebuhr, 1775 (Bandel and Hemleben 1987). Among these Jurassic holoplanktonic gastropods, *C. minutus* is best known and most abundant, especially in the Early Toarcian *Posidonia* Shale deposited under oxygen depleted conditions.

Since it is thin-shelled, small and primarily aragonitic, it is preferably preserved in early diagenetic limestone concretions (Bandel and Knitter 1983; Röhl 1998). However, it was probably present throughout the entire deposition of the *Posidonia* Shale as is indicated by the presence of pyritic internal moulds from shells of this species (Riegraf et al. 1984). Etter (1996) and Schulbert and Nützel (2013) showed that *C. minutus* ranges to the Aalenian (early Middle Jurassic) in Switzerland and Northern Bavaria. Extensive sampling of Late Pliensbachian grey shale (Amaltheenton Formation) of Northern Bavaria showed that *C. minutus* is absent until the Early Toarcian onset of oxygen depleted sediments of the *Posidonia* Shale Formation (AN personal observation). *Coelodiscus minutus* has also been reported
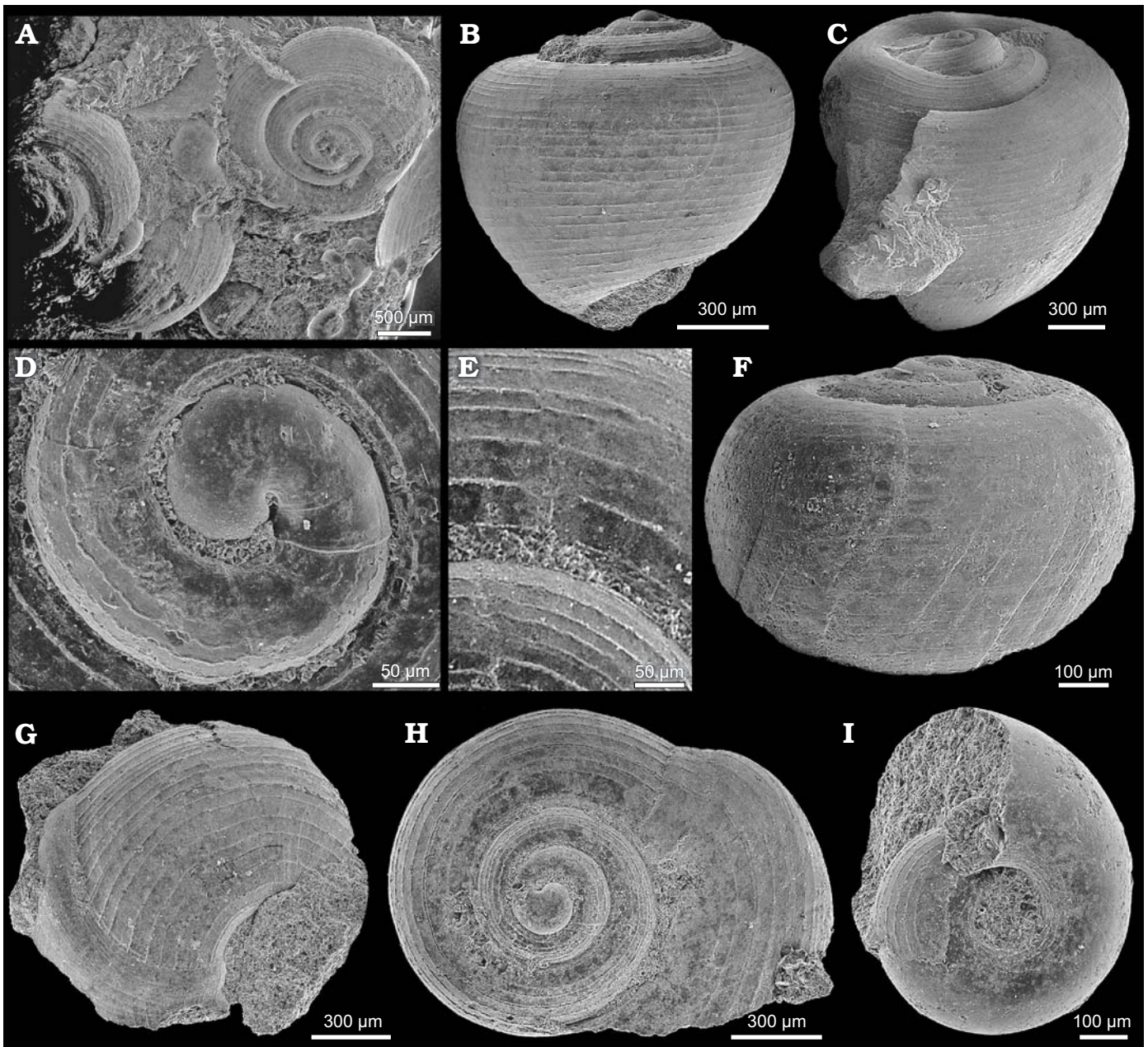
Fig. 2. Occurrence and morphology of the holoplanktonic gastropod *Coelodiscus minutus* (Schübler in Zieten, 1833), *Posidonia* Shale Formation, Lower Toarcian; Altdorf near Nuremberg, Northern Bavaria, Southern Germany. **A**. BSPG 2008 XXIX 36a, superabundance in the limestone concretions. **B**. BSPG 2008 XXIX 56f, lowspired shell, wider than high. **C**. BSPG 2008 XXIX 42a, elevated but somewhat depressed spire. **D**. BSPG 2008 XXIX 26a, abrupt transition from protoconch to teleoconch. **E**. BSPG 2008 XXIX 56c, fine spiral lirae separated by wide interspaces. **F**. BSPG 2008 XXIX 56a, opisthocyrt growth lines with the backmost point situated in adapical direction. **G**. BSPG 2008 XXIX 24a, growth abnormality represented by loss of ornamentation. **H**. BSPG 2008 XXIX 42c, growth abnormality represented by a swell of the shell. **I**. BSPG 2008 XXIX 62c, small specimen with well-preserved sculpture ensuring an attribution to *C. minutus*.

from Northern and Southern Germany (Röhl 1998) and from the bituminous Lower Toarcian shales of England (Hallam 1967; Morris 1979). Another species of the genus *Coelodiscus*, *Coelodiscus wrightianus* Tate in Tate and Blake, 1876, has been reported from the Early Pliensbachian (*Prodactylioceras davoei* Ammonite Zone) of England together with the species of *Tatediscus* which represent another possible example of planktonic gastropods (Todd and Munt 2010). An unidentified species representing *Coelodiscus* or *Tatediscus*

has also been reported from the Early Pliensbachian of Argentina (Gründel 2001). However, the preservation quality of these specimens is not sufficient to make a statement of their potential mode of life. Though a holoplanktonic mode of life cannot be excluded, it would also be possible that those organisms represent benthic precursors, which had a planktotrophic larval development. The holoplanktonic mode of life could have evolved in response to local hostile bottom conditions and proliferation of holoplanktonic gastropods
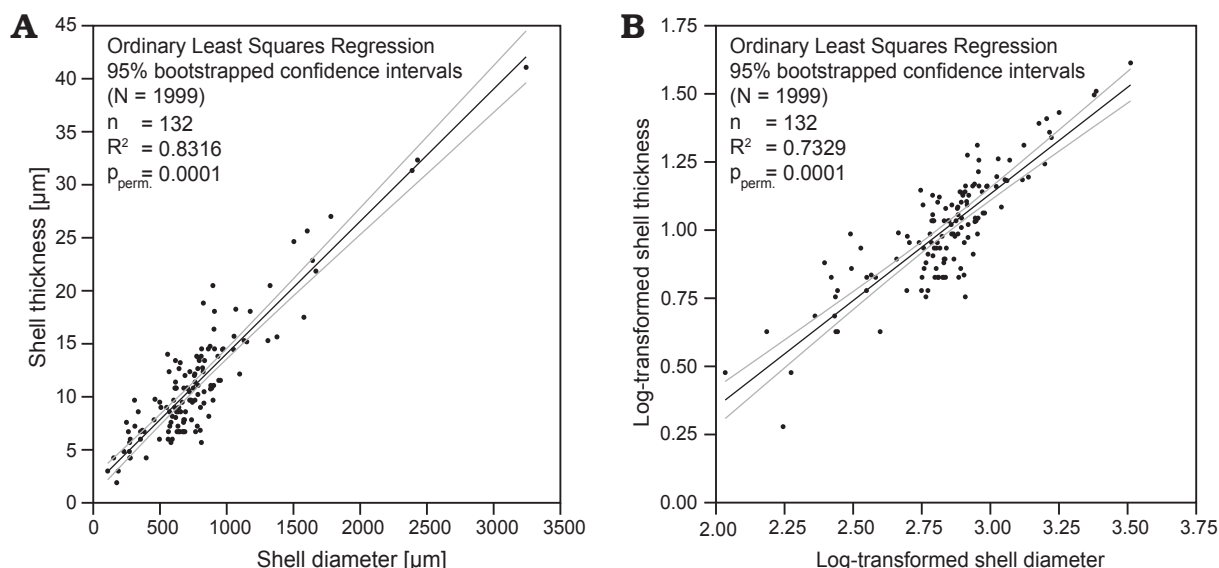
Fig. 3. Correlation between the shell thickness and shell diameter; by linear bivariate modelling using Ordinary Least Squares Regression in PAST3 (Hammer et al. 2001). **A**. The data show that the shell of *Coelodiscus minutus* is generally very thin and shows a linear increase with shell diameter; this linear increase is generally typical of shelled molluscs and is also present in modern holoplanktonic gastropods. **B**. The log-transformed data of the original measurements confirm the linear increase with shell diameter. Abbreviations: N, number of bootstrap replicates; n, number of measured specimens; R^2, coefficient of correlation; p_{perm}, permutation test on correlation (R^2), using 9999 replicates.

was eventually enhanced by widespread anoxia in the Early Toarcian. The youngest species assigned to *Coelodiscus* is *Coelodiscus sadharaensis* Szabo and Jaitly, 2004 from the Callovian–Oxfordian of Western India (Szabo and Jaitly 2004). However, this species is very large (diameter 10 mm) compared with *C. minutus* and the attribution to the genus *Coelodiscus* needs corroboration.

The mode of life of *Coelodiscus*.—Several authors advocated a holoplanktonic mode of life for *C. minutus* mainly because it occurs predominantly in sediments which formed under anoxic or heavily oxygen depleted conditions (Jefferies and Minton 1965; Bandel and Knitter 1983; 1986; Bandel and Hemleben 1987; Röhl 1998). Others assumed that it had a benthic life style (Quenstedt 1858; Einsele and Moosebach 1955; Kauffman 1981; Urlichs et al. 1994; Etter 1996). Traditionally, the *Posidonia* Shale Formation has been interpreted as a stagnant, anoxic basin sediment and there can be still little doubt that oxygen availability in bottom waters was generally low as is indicated by various sedimentological and palaeontological criteria (black-shale facies, high TOC and pyrite content, lamination, low levels of bioturbation, absence or low diversity of benthic macro fauna, etc. [Röhl and Schmid-Röhl 2005]). However, fluctuations in oxygen concentration are now considered to have played a pivotal role during deposition (Röhl et al. 2001). Although the environmental conditions during the Early Toarcian of Southern Germany were generally oxygen depleted, episodes with somewhat higher oxygen concentrations facilitated the establishment of specialized benthic communities. Therefore, a benthic mode of life was principally possible for *C. minutus*. Etter (1996) argued that the frequency of *C. minutus* shells in the Opalinus Clay (Aalenian) of Switzer-

land is associated with benthic conditions and that this would imply a benthic mode of life for *C. minutus*. Accordingly, *C. minutus* was adapted to extremely dysoxic conditions. Similarly, Schulbert and Nützel (2013) showed that *C. minutus* was still highly abundant (preserved as pyritic steinkerns) in the Late Toarcian of Northern Bavaria just above the *Posidonia* Shale and subsequently decreased in abundance until the Early Aalenian while diversity of the benthos increased at the same time. However, this does not necessarily imply that *C. minutus* was benthic. An alternative explanation would be that specimens of *C. minutus* fell down from the plankton but were preferably preserved when bioturbation and deposit feeding were reduced due to oxygen deficiency. *Coelodiscus minutus* ooze as present in the concretions studied herein could only form under anoxic or extremely dysaerobic conditions. The calcareous concretion horizons Unterer Stein and Oberer Stein (Lower and Upper Stone) of the Early Toarcian *Harpoceras falciferum* Ammonite Zone, which commonly consist of superabundant *C. minutus* shells are considered to represent the episodes with the worst benthic living conditions of the *Posidonia* Shale (Röhl 1998). The shells of *C. minutus* are very thin (mean = 11.3 µm ±0.5 µm SE, n = 132) and thus vulnerable to bioturbation, deposit feeding or transport. The mass accumulation and the excellent preservation are easiest to explain by plankton rain and lack of deposit feeding and bioturbation. The relatively low TOC values of 0.30–0.36% can be explained by diagenesis as it is also evident by the calcitic cementation of the *Coelodiscus minutus*/ fecal pellet grainstone.

Besides the superabundant *C. minutus*, the studied fossil assemblage consists overwhelmingly of nektonic organisms (ammonites, fishes) and planktonic larval shells of bivalves (prodissoconchs) which are clearly pre-metamorphic and
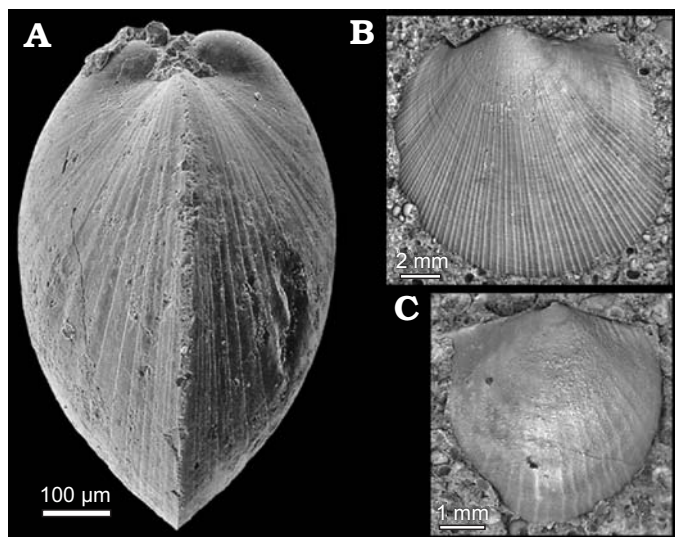
Fig. 4. Fossil content beside the *Coelodiscus minutus* shells, *Posidonia* Shale Formation, Lower Toarcian; Altdorf near Nuremberg, Northern Bavaria, Southern Germany. **A**. BSPG 2008 XXIX 69h, articulated bivalve prodissoconchs of the order Pterioida. **B**. BSPG 2008 XXIX 1d, valve of the epifaunal bivalve *Meleagrinella substriata* (Münster in Goldfuss, 1831). **C**. BSPG 2008 XXIX 2b, valve of the epifaunal bivalve *Oxytoma* sp.

have always articulated valves. They represent undoubtedly larval fall. The highly abundant fecal pellets probably derive from nektonic and planktonic organisms. The bivalves *Oxytoma* sp. and *Meleagrinella substriata* are rare in the studied assemblage and their concomitant appearance with ammonites could point to a pseudoplanktonic mode of life (Röhl 1998). Röhl (1998) interpreted the life habit of *M. substriata* as epibenthic or facultative pseudoplanktonic (see also Duff 1975; 1978; Kaim 2001).

The fact that *C. minutus* is small and very thin-shelled supports the assumption of a planktonic mode of life. The assumption that *C. minutus* might have a very thin shell has been remarked before but lacked corroboration with quantitative measurements (Kauffman 1981; Riegraf et al. 1984). The continuous thickening during growth (Fig. 3) is generally typical for molluscs and has also been shown for modern holoplanktonic gastropods (Lalli and Gillmer 1989). We also showed that *C. minutus* did not have three ontogenetic stages (embryonic, larval, adult), but two, being an embryonic and a holoplanktonic adult stage, as it also holds for the modern counterparts.

In conclusion, the following arguments account for a planktonic mode of life of *C. minutus*: (i) the high abundance in anoxic to dysoxic facies, (ii) the presence in fossil assemblages entirely or largely lacking benthic organisms due to unfavourable benthic conditions, (iii) the small size, and (iv) the very thin shell.

Is *Coelodiscus* a member of the modern holoplanktonic heteropods?—Bandel and Knitter (1983) and Bandel and Hemleben (1987) correctly pointed out that *C. minutus* (and its junior synonym *C. fluegeli*) resembles the larval shells of some extant holoplanktonic heteropods and placed *C. minutus*

in the extant family Carinariidae. Spirally ornamented larval shells of some species of the genus *Atlanta* Lesueur, 1817 (family Atlantidae) are also quite similar. However, the heteropod families Atlantidae and Carinariidae have shells representing three ontogenetic stages: embryonic (protoconch 1), larval (protoconch 2), and adult (teleoconch) shell portions, as it is typical for caenogastropods with planktonic larval development (Nützel 2014). The adult shells (teleoconchs) of shell bearing extant heteropods are disc- or limpet-like (Lalli and Gilmer 1989; Newman 1998). However, *Atlanta* has a real teleoconch following the larval shell, being planispiral with a prominent keel. This type of tertiary shell is clearly lacking in *C. minutus* and thus, the shells of modern heteropods as a whole are definitely unlike the shell of *C. minutus*. Only the larval shell of some modern heteropods resembles *C. minutus*. By contrast, the shell of *C. minutus* consists only of two ontogenetic shell portions: a smooth embryonic shell of somewhat less than one whorl and a spirally ornamented shell consisting of several whorls. The size of this shell (up to 3 mm, according to Bandel and Hemleben [1987] even 5 mm) suggests that it is not an isolated larval shell (see Nützel 2014). Fossil larval shells of gastropods older than Cretaceous are usually smaller than 1 mm (Mapes and Nützel 2009; Nützel 2014) and are thus distinctly smaller than fully-grown members of the Coelodiscidae. A tertiary shell portion could not be found in the studied material. However, Bandel and Hemleben (1987: fig. 8) illustrated an alleged transition from a spirally striated larval shell to a smooth teleoconch. This shell is 1.3 mm wide and shows a suture in its terminal part; the shell is largely smooth after this suture. If the spirally ornamented part of this shell was a larval shell it would have a width of 1.2 mm. However, we studied numerous *C. minutus* shells which are entirely ornamented at a width of 2–3 mm. Therefore the spirally ornamented shell of *C. minutus* is not a larval shell because it is too large. The *C. minutus* specimens illustrated by Bandel and Hemleben (1987: figs. 7, 8) which allegedly have post-larval adult shell portions most probably show healed shell fractures with a disturbed morphology of the terminal portion of the shell. Shell anomalies as response to healed fractures were also frequently observed in our samples (Fig. 2G, H). We agree with Bandel and Hemleben (1987) that *C. minutus* could be related to modern heteropods. However, this genus is not a member of any of the modern heteropod families but represents its own family, Coelodiscidae, as suggested in Schulbert and Nützel (2013). The assignment of Coelodiscidae to a superfamily remains unresolved at this point.

Conclusions

There are three possibilities to interpret the identity of *Coelodiscus minutus*:
- *Coelodiscus minutus* is a vetigastropod, a group of basal gastropods with a shell that consists of the protoconch 1 (embryonic shell of about one whorl) and a teleoconch

and which principally lacks a larval shell (protoconch 2) (e.g., Nützel 2014). If *C. minutus* was holoplanktonic, this seems unlikely because vetigastropods are benthic and never produced holoplanktonic forms although some tiny Recent representatives are able to swim temporarily (Hickman and Porter 2007).

- *Coelodiscus minutus* represents an isolated larval shell of an unknown larger caenogastropod. This is unlikely because despite good knowledge of Early Jurassic gastropods of Europe, a teleoconch with a *C. minutus* larval shell was never found. Additionally, with up to 3 mm or even 5 mm diameter, it is too large for a larval shell of the planktotrophic type.

- *Coelodiscus minutus* can be derived from a plankton feeding caenogastropod veliger larva and changed the larval stage into a holoplanktonic adult stage. This heterochronic, neotenous process represents the most likely hypothesis for the evolution of *C. minutus*. The same extension of the larval phase has been convincingly proposed for the evolution of the extant holoplanktonic pteropods (Lemche 1948; Bandel and Hemleben 1987), which are not related to heteropods including *C. minutus*.

We conclude that *C. minutus* is indeed the oldest known holoplanktonic gastropod. Since gastropods are principally a benthic group, *Coelodiscus* must have evolved from a benthic precursor, probably during the Early Jurassic. We speculate that this precursor had a planktotrophic larval development and that probably under the influence of increasing frequency of dysoxic episodes along with hostile benthic conditions, the larval phase was extended and eventually a holoplanktonic species evolved. This speculation is based on that the first appearance of holoplanktonic gastropods is associated with wide-spread anoxia. Being holoplanktonic or benthic is a zero-one issue and the evolutionary transition must have been fast. Thus, it cannot be expected that the evolution from a benthic precursor to a holoplanktonic species can be studied in the fossil record. It is also questionable whether the benthic precursors can ever be identified. Based on an alleged similarity of their larval shells, Bandel (2007: 172, fig. 23) assumed that the holoplanktonic Heteropoda including *Coelodiscus* form the sister group of Stromboidea with a hypothetical Triassic stem species. However, as stated by Gründel et al. (2009), there are no convincing arguments for this phylogenetic scenario; the secondary shell of *Coelodiscus* and spirally ornamented larval shells present in the heteropod genus *Atlanta* are unlike larval shells of Stromboidea, especially those of Jurassic heteropods. Based on the similarity of the larval shell of some species representing the genus *Atlanta* to the secondary shell of *Coelodiscus*, an assignment of Coelodiscidae to heteropods as suggested by Bandel and Hemleben (1987) is justified according to the current state of knowledge although the teleoconch morphology of the modern *Atlanta* and other heteropods is unknown in Jurassic or older gastropods.

During the Early Toarcian anoxic event, *C. minutus* was highly abundant in the plankton and dead shells rained down to the anoxic or dysoxic bottom. These thin and fragile shells formed an ooze similar to the pteropod ooze in the modern deep sea. The shells were exceptionally well preserved due to the absence or low level of deposit feeding and bioturbation as well as the formation of early diagenetic concretions.

Acknowledgements

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