

Microconchids of the species *Microconchus valvatus* (Münster in Goldfuss, 1831) from the Upper Muschelkalk (Middle Triassic) of Germany

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Abstract In the present paper, the commonly mentioned but poorly recognised microconchid species *Microconchus valvatus* (Münster in Goldfuss, 1831) is redescribed on the basis of material from the Upper Muschelkalk of Germany. ESEM studies of the microconchid tubes with clear morphological and microstructural characters were compared to the existing known Triassic species. *Microconchus valvatus* is characterised by fine growth lines and transverse riblets. ESEM analysis shows that tubes which appear smooth under the binocular microscope are in fact abraded. Thus, taphonomy must be taken into account and scanning microscopy must be used during studies of microconchid tubes. Quantitative ecology shows that particular microconchid populations developed various size ranges punctuated by some gaps, have non-normal distributions as expected in time-averaged assemblages, and suggests that differences among populations may reflect distinct hydrologic settings. This study provides a multidimensional investigation of microconchids and offers compelling evidence that microconchids were an important faunal group during the post-recovery Middle Triassic interval.

Keywords Microconchids · Taxonomy · Microstructure · Ecology · Triassic · Germany

Introduction

Microconchids, belonging to the Order Microconchida Weedon 1991 of the Class Tentaculita Bouček 1964, are small, tube-bearing encrusting organisms with a fossil record from the Late Ordovician until the Middle Jurassic (e.g. Taylor and Vinn 2006; Zatoń and Vinn 2011). Before the landmark papers of Weedon (1991, 1994) revising the biological affinities of microconchids, they were affiliated by various authors as either vermiform gastropods (e.g. Burchette and Riding 1977; Bełka and Skompski 1982) or, more commonly, as the sedentary, tube-bearing polychaete genus *Spirorbis*, with which they are morphologically and ecologically convergent. Unlike spirorbids, ubiquitous microconchids occurred in a variety of environments, being common in marine, brackish and freshwater settings (see Zatoń et al. 2012a for a review). The microlamellar tube microstructure penetrated by pseudopunctae, punctae or pores, and the ability for budding in some species (Wilson et al. 2011), make them closer to bryozoans or brachiopods than to tube-bearing polychaetes and molluscs. Currently, they are regarded to be more closely related to such lophophorates as phoronids (Taylor et al. 2010). However, whatever their relationship, soft-part anatomy is needed to firmly establish their true biological affinity.

Serious investigations of microconchids have only just started, so in fact very little is known about their taxonomic status and diversity, or ecology in particular periods. Although microconchids are commonly referred to as *Spirorbis*—a tube-dwelling polychaete worm—in palaeoecological literature, detailed data about their taxonomy and ecology are still very patchy. Our knowledge is mainly confined to the Paleozoic, especially the Ordovician–Silurian and Devonian (e.g. Vinn 2006; Zatoń and Krawczyński 2011a, b; Vinn and Wilson 2010, 2012; Caruso and Tomescu 2012; Zatoń et al. 2012b), and the Middle Jurassic (Zatoń and Taylor 2009; Vinn and Taylor 2007). Triassic microconchids, although very common in different palaeoenvironments (e.g. Wanner 1921;

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Brönnimann and Zaninetti 1972; Peryt 1974; Ball 1980; Kietzke 1989; Nützel and Schulbert 2005; McGowan et al. 2009; Hagdom 2010; Fraiser 2011; He et al. 2012), have rarely been investigated with respect to taxonomic affinity. They were either traditionally treated as *Spirorbis* or provisionally as the microconchid genus *Microconchus* (e.g. McGowan et al. 2009; Hagdom 2010). The only papers covering the taxonomic status of Triassic microconchids are Vinn (2010a) and Zatoń et al. (2013). Vinn (2010a) investigated the tube microstructure of the Middle Triassic helically coiled species *Microconchus aberrans* (Hohenstein), while the latter authors described small, spirally coiled tubes of a new Early Triassic microconchid from the Spathian of the USA (Zatoń et al. 2013).

According to Hagdom (2010), three species of microconchids occur in the Germanic Triassic: the previously mentioned Muschelkalk-Keuper *Microconchus aberrans* (Hohenstein), the Muschelkalk *Microconchus valvatus* (Münster in Goldfuss), and the Keuper *Microconchus germanicus* (Grupe). In this paper, we focus on *Microconchus valvatus* (Münster in Goldfuss), the species most commonly mentioned in the literature, but still insufficiently described. On the basis of detailed morphological and microstructural investigations of a number of specimens from different horizons, this species is here redescribed and its ecological population structure is reinterpreted.

Material and methods

Material and its provenance

The specimens examined in this paper have been collected from Upper Muschelkalk outcrops in southern and central Germany. For an overview of Upper Muschelkalk stratigraphy and facies in Germany, see Hagdom et al. (1998) or Hagdom and Simon (2005). The five microconchid samples were collected in different formations which were deposited in contrasting palaeogeographic positions within the lithostratigraphic column of the Upper Muschelkalk (Fig. 1). The youngest sample is approximately 2 Ma younger than the oldest samples. The samples and additional material are kept in the Muschelkalkmuseum Ingelfingen, Germany (abbreviated MHI).

Sample MHI 2080/1 This sample consists of more than 100 microconchids preserved on the internal mould of the nautilid *Germanonautilus* (Fig. 2). Originally, they encrusted the empty shell of this cephalopod.

Locality – Eiterfeld-Leibolds near Fulda (Hesse), Central Germany.

Lithostratigraphy and depositional environment – basal Meißner Formation. This unit is characterised by interbedding marlstones and limestones with infaunal bivalves and ceratites such as dominant elements; epibenthic bivalves and their encrusters are comparatively rare. The palaeoenvironment was

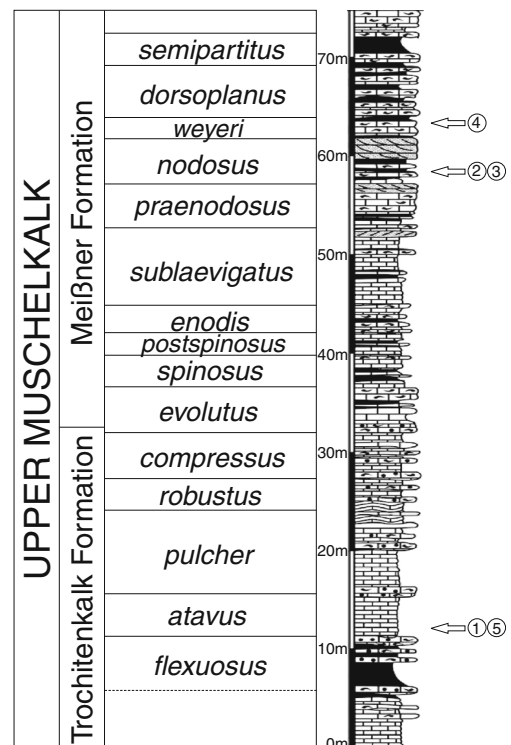


Fig. 1 Lithostratigraphic section of the Upper Muschelkalk for western Baden-Württemberg (Southwest Germany) with general positions of the studied samples indicated with arrows. Each sample number has prefix MHI 2080. Adapted from Hagdom (2004)

fully marine. The locality was situated in the Hesse Depression in a deep position of the Upper Muschelkalk carbonate ramp (Aigner 1985; Hagdom and Ockert 1993). It belongs to a Transgressive Systems Tract (Aigner and Bachmann 1992).

Biostratigraphy and age – atavus biozone of late Anisian (late Illyrian) age.

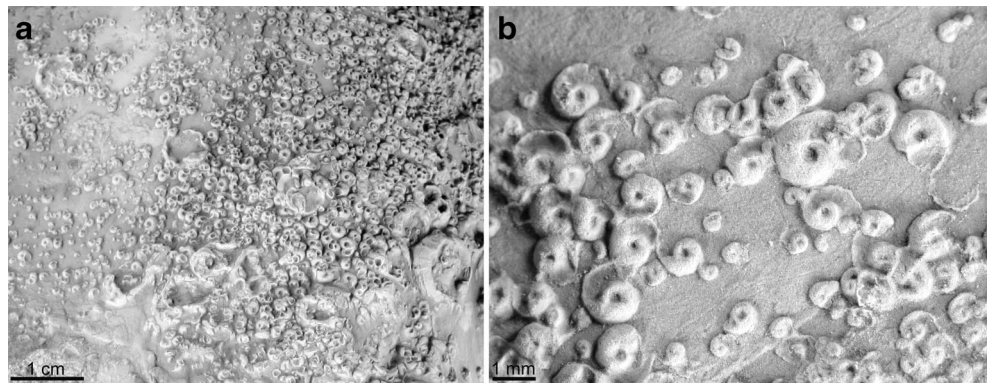
Samples MHI 2080/2–2080/3 These two samples comprise more than 100 microconchids each, encrusting shell fragments of the pectinacean *Pleuronectites laevigatus*. This bivalve had a calcitic outer shell layer that survived the diagenetic dissolution of the aragonitic inner shell layers. Thus, the microconchids are preserved immediately on their original attachment surface (Hagdom 2010).

Locality – Obersontheim-Ummenhofen near Schwäbisch Hall (Baden-Württemberg), southwest Germany.

Lithostratigraphy and depositional environment – upper part of Meißner Formation, Tonsteinhorizont 6 (former Tonhorizont zeta). The locality was situated on the shallow ramp (Aigner 1985) some tens of kilometers offshore of the Vindelician Bohemian Massif. Due to progressing brackish water influx from the north, in this part of the Muschelkalk, there are no stenohaline crinoids and echinoids. It belongs to the Highstand Systems Tract (Aigner and Bachmann 1992).

Biostratigraphy and age – nodosus biozone of early Ladinian (Fassanian) age.

Fig. 2 **a** A large number of specimens of *Microconchus valvatus* (Münster in Goldfuss, 1831) on internal mould (steinkern) of *Germanonautilus* (MHI 2080/1). **b** Close-up of some of the microconchids



Sample MHI 2080/4 The sample consists of two shell fragments of the bivalve *Pleuonectites laevigatus* encrusted by more than 100 microconchids. Many specimens are covered by secondary calcite crystals so that their tubes are not entirely visible.

Locality – Satteldorf-Neidenfels near Crailsheim (Baden-Württemberg), southwest Germany.

Lithostratigraphy and depositional environment – upper part of Meißner Formation, a few meters above MHI 2080/2. The influence of the nearby coastline is even more prominent than in deeper parts of the Meißner Formation. The thickly bedded shelly limestones contain mixed endobenthic and epibenthic faunal elements devoid of stenohaline crinoids and echinoids.

Biostratigraphy and age – *weyeri* to *dorsoplanus* biozones of early Ladinian (Fassanian) age.

Sample MHI 2080/5 This sample consists of ca. 70 microconchids attached to a shell fragment of *Myalina blezingeri*. This bivalve had an extremely thick prismatic and calcitic outer shell. It was commonly encrusted by crinoids, bivalves, and microconchids (Hagdorn 1978; Hagdorn and Ockert 1993). Most of the microconchids are poorly preserved as attachment bases and abraded tubes.

Locality – Mistlau near Kirchberg an der Jagst (Baden-Württemberg), Southwest Germany.

Lithostratigraphy and depositional environment – Crailsheim Member (contemporaneous with the Hassmersheim Member of the more westerly Baden-Württemberg area) of Trochitenkalk Formation. This unit of extremely thick-bedded crinoidal limestones was deposited under fully marine conditions on top of a regional shoal in shallow water some tens of kilometers offshore of the Vindelician Bohemian Massif. This shoal represents the shallow part of the lower Upper Muschelkalk carbonate ramp (Aigner 1985). On the seaward side towards the deeper water, crinoids and other epibenthic faunal elements settled on small biohermal structures that allowed the abundant microconchids to encrust bivalves, crinoids and other anchoring grounds (Hagdorn and Ockert 1993). Towards the north and west, water deepened and the crinoidal limestones become thinner with thick marlstone

layers intercalated (Hassmersheim Member) and finally disappeared (transition to the base of the Meißner Formation).

Biostratigraphy and age – *atavus* biozone of late Anisian (late Illyrian) age. Thus, sample MHI 2080/5 has approximately the same age as sample MHI 2080/1; however, the latter microconchids lived in deeper water.

Methods

For morphological and microstructural features, the specimens from all samples were investigated using a Philips XL 30 environmental scanning electron microscope (ESEM) in uncoated state using backscattered imaging. Due to the large size of samples MHI 2080/1 and 2080/2, some of the well-preserved specimens were removed from the substrate for ESEM study. All specimens preserved on small bivalve shells (MHI 2080/4 and 2080/5) were investigated using the ESEM; however, only the best preserved tubes were photographed. Many microconchids with eroded upper parts of their tubes provided good opportunities for microstructural observations.

For statistical analyses of microconchid populations, the two samples (MHI 2080/1 and 2080/2) from different stratigraphic horizons and palaeoenvironments (*atavus* Zone: normal marine vs. *nodosus* Zone: marine but with no stenohaline crinoids or echinoids) containing the most specimens free of matrix have been quantified in order to find out whether there are differences in size or morphology. For this purpose, the diameters of 100 specimens from each sample were measured under the binocular microscope with a graduated ocular. Several standard statistical tests were used in order to check whether both microconchid populations have the same size distribution. At first, using histograms and probability Q-Q plots, the populations investigated were visually checked with respect to their normal distribution. Next, in order to verify the normal distribution, a non-parametric Kolmogorov–Smirnov test (one-sample K–S test) with a modification (Liliefors test), and additionally the Shapiro–Wilk test (S–W test), were used. Here, populations do not have a normal distribution if $p < 0.05$.

In order to check the distribution asymmetry, a measure of skewness was used. Skewnesses equal to 0 indicate an ideally

symmetric distribution, and skewnesses with positive and negative values indicate right-sided and left-sided asymmetry, respectively. The analysis of kurtosis was used as a measure of flattenedness of distribution. Populations characterised by normal distribution have kurtosis of 0 and in those characterised by non-normal distributions have kurtosis values different from 0. The Wilcoxon and Mann–Whitney U tests, which are non-parametric alternatives for the t test, were used in order to check the differences between the two microconchid populations (result is significant if $p < 0.05$). The Levene test (based on means) and Brown–Forsythe test (based on medians) were used in order to check whether the populations investigated have homogeneous variance. In contrast to the Levene test, the latter is better here as it does not need an assumption of normal distribution of variables. The statistically significant (at $p < 0.05$) result of the test indicates that the variances are different and thus that the populations investigated differ from each other.

The analyses and figures have been performed using the PAST (Hammer et al. 2001), STATISTICA v.7 and R (R Development Core Team 2011) software. The dataset used in this study are accessible from the first author upon request.

Systematic palaeontology

Class Tentaculita Bouček, 1964

Order Microconchida Weedon, 1991

Genus *Microconchus* Murchison, 1839

Type species: *Microconchus carbonarius* Murchison, 1839

Diagnosis: Tube planispirally coiled with a tendency for helical uncoiling in later stages of ontogeny. Exterior tube surface covered by variously developed growth lines, perpendicular ridges and longitudinal striae. Tube microstructure lamellar, penetrated by minute punctae.

Microconchus valvatus (Münster in Goldfuss, 1831)

Figures 3 and 4

Material: A few hundreds of specimens encrusting shelly substrates as outlined above, of which 42 were selected for ESEM study.

Diagnosis: Tube planispirally coiled, dextral. Exterior ornamented with closely-spaced growth lines and transverse riblets. Tube microstructure lamellar, penetrated by tiny punctae.

Description: Tube small (up to 2.3 mm in diameter), dextral, planispirally coiled throughout ontogeny (Fig. 3), attached by almost its entire length except for the most terminal part of the

tube which may be directed upward (Fig. 3c, h–k). Tube section semi-circular to elliptical in outline, although at the aperture it may be slightly triangular in some specimens (Fig. 3j, l). Umbilicus usually opened, varying in width in some specimens (Fig. 3a–g); in others slightly covered by the terminal aperture (Fig. 3h, i). Tube exterior ornamented with fine growth lines and variously thick, closely spaced transverse riblets starting at the umbilical slope and running down to the base (Fig. 3c–e, g–l). Thin longitudinal striae present in some well-preserved specimens, gently cross the transverse ornamentation without formation of any thickening structures (Fig. 3c, d). Tube ultrastructure microlamellar, with microlaminae bent towards the tube exterior by distinct, cement-filled punctae (Fig. 4a, c). Punctae visible on the exfoliated tube exterior as distinct, closely spaced pits differing in diameter depending on the depth and angle of tube exfoliation (Fig. 4b).

Discussion: The presence of a microlamellar tube ultrastructure penetrated by distinct punctae gives evidence for assignment of the specimens studied to *Microconchus*. The present species was described and illustrated by Goldfuss (1831) as *Serpula valvata* and was later mentioned by many authors under the generic name *Spirorbis* in the Triassic literature. However, Goldfuss's diagnosis is not only very short but also imprecise, stating that the species has a planispirally coiled tube with a smooth exterior. The illustrations, however, show two specimens encrusting the same substrate, one smooth and the other ornamented with thin ribs or growth lines. Thus, based on the original description and illustration, there is uncertainty whether there are one or two species, one with ribs and one with a smooth exterior. Microconchids with a smooth exterior were previously referred to *Serpula omphalodes* (see Goldfuss 1831). Later, Schmidt (1928) showed two forms of his *Spirorbis valvata*, one slightly ribbed and the other smooth. This study helps clarify the diagnostic characters of *Microconchus valvatus*.

The two morphotypes illustrated by Goldfuss (1831) represent the same species. In the material examined here, the smooth and the ornamented form have been encountered on the same substrate. However, what has been unclear under the binocular microscope is obvious when using the ESEM. The smooth morphotypes are poorly preserved specimens with abraded surfaces and thus devoid of ornamentation (Fig. 3a, b, f). This is well shown by specimens with their exteriormost part of the tubes partly worn, showing the smooth surface beneath (Fig. 3c, e). The co-occurrence of variously preserved specimens on the same substrate may simply result from time-averaging, a phenomenon that often affected hard substrate communities. Thus the scanning electron microscopy is crucial for detecting the true state of preservation of these tiny fossils and has a profound effect on taxonomic identity and differentiation.

The morphological variability of well-preserved specimens is mainly confined to tube coiling and ornamentation pattern. This variability has previously been detected among other microconchid species (e.g. Zatoń and Krawczyński 2011b). With respect to coiling, the specimens consist of those with wider, open umbilicus and those with nearly occluded umbilicus. The occluded umbilici have been mainly encountered among specimens settling close to each other and crowded on the substrate. The differences in ornamentation mainly

concern the density and thickness of transverse riblets. They may be more or less fine or coarse in particular individuals.

As the morphological and ultrastructural characters of Triassic microconchid tubes are poorly known, a comparison of *Microconchus valvatus* to other Triassic species is now very limited. The only detailed description has been provided for *Microconchus aberrans* (Hohenstein) by Vinn (2010a). This species differs from *M. valvatus* in its helical coiling and the lack of punctae-deflecting microlaminae. The only tube

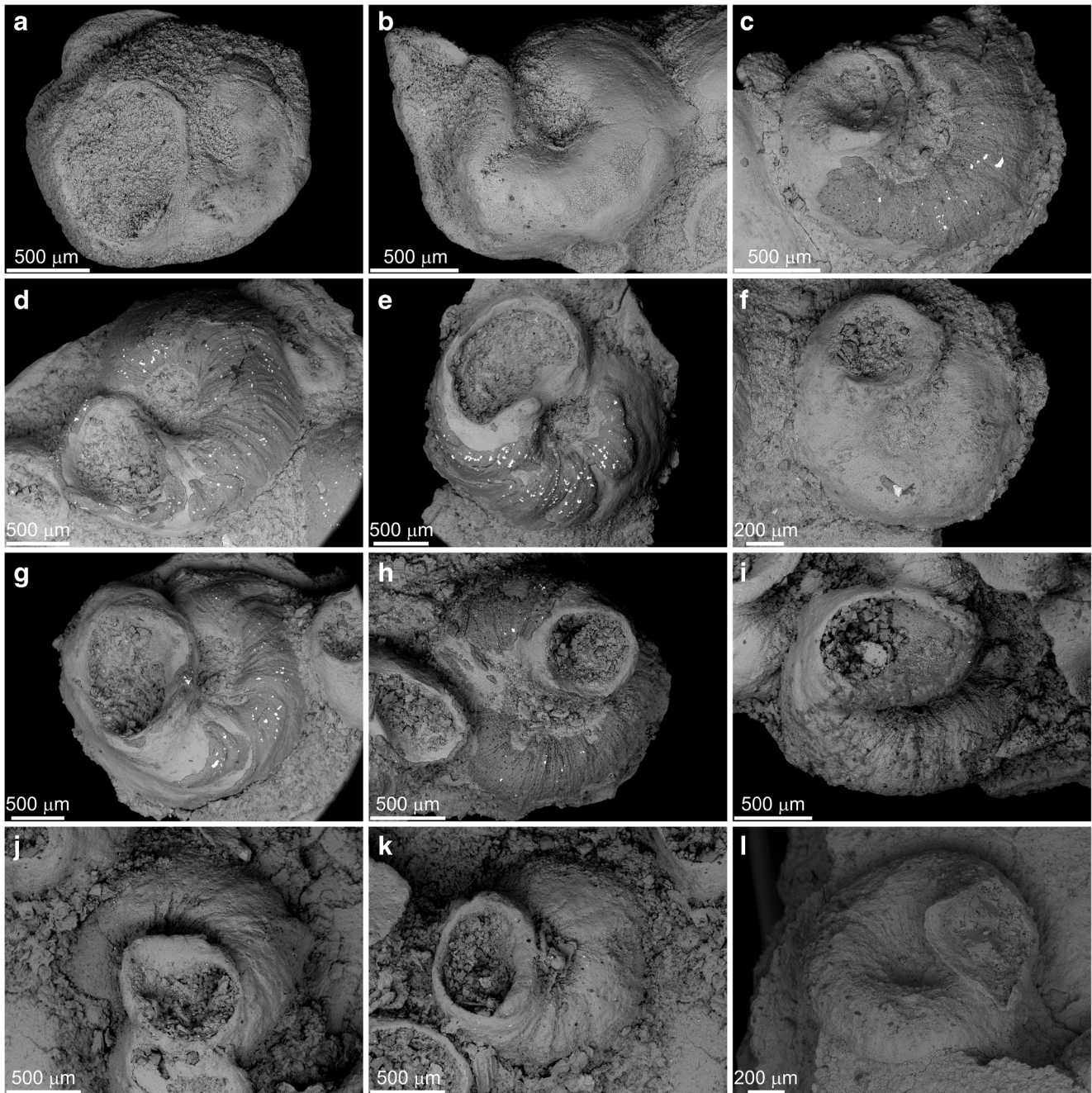


Fig. 3 ESEM photomicrographs of *Microconchus valvatus* (Münster in Goldfuss, 1831) from the Upper Muschelkalk of Germany. **a, b** MHI 2080/1, **c–h** MHI 2080/2, **i–k** MHI 2080/4, **l** MHI 2080/5

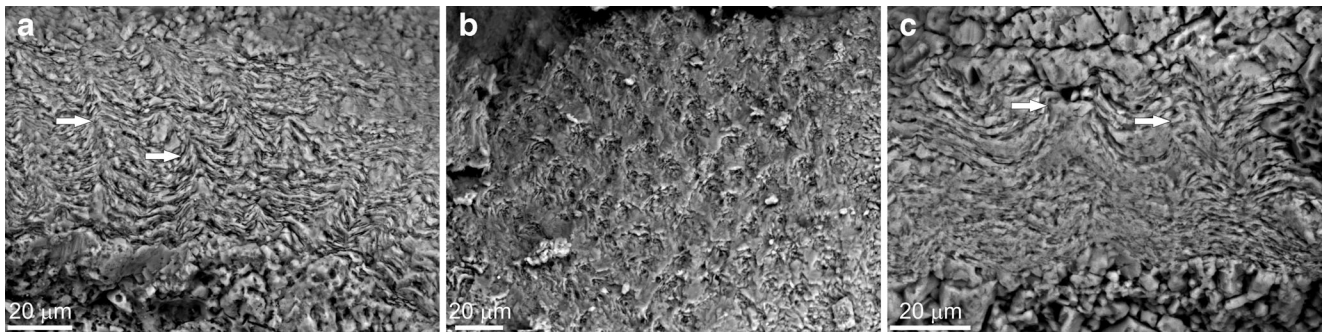


Fig. 4 ESEM photomicrographs of tube microstructure of *Microconchus valvatus* (Münster in Goldfuss, 1831) from the Upper Muschelkalk of Germany. **a–b** MHI 2080/1, **c** MHI 2080/2

structures it possesses are indistinct pseudopunctae which are characteristic of such Palaeozoic genera as *Palaeoconchus* Vinn, 2006. In our opinion, *M. aberrans* needs additional investigation. ‘*Spirorbis*’ cf. *valvata* as reported from the Early Triassic (Smithian) Sinbad Formation by Nützel and Schulbert (2005) is closer to *Microconchus valvatus* in its fine ornamentation but differs in having a helically coiled portion of the tube. Its tube microstructure is also unknown. The Early Triassic (Spathian) *Microconchus utahensis* Zatoń, Taylor and Vinn (2013) is a small species with a nearly occluded umbilicus and thicker and straight transverse ridges and tiny punctae. *Spirorbis phlyctaena* described by Brönnimann and Zaninetti (1972) from the Early Triassic of northern Italy, Iran and possibly from the Middle Triassic of France may belong to the genus *Microconchus* because its tubes have punctae-like ‘minute pits’ (see Brönnimann and Zaninetti 1972). However, this species is known only from thin-sections, which do not allow a direct comparison with *Microconchus valvatus*. However, the more evolute coiling and the presence of both dextral (clockwise) and sinistral (anti-clockwise) coiling in *S. phlyctaena* are striking features that differentiate it from *Microconchus valvatus*. ‘*Spirorbis*’ from the Triassic of New Mexico illustrated by Kietzke (1989) has a similar ‘ribbing’ pattern but differs in its more evolute coiling and

large ‘protoconch’. It occurs in non-marine deposits as evidenced from its association with ostracodes and charophyte gyrogonites. The Late Triassic (Keuper) microconchid from Germany, provisionally known as *Microconchus germanicus* (Grupe) (see Hagdom 2010), may be much more evolute and has prominent transverse ridges (Schmidt 1928). However, details of its tube microstructure are unknown, precluding closer comparisons. The Late Triassic ‘*Spirorbis*’ *inexpectatus* described by Wanner (1921) from non-marine deposits in Pennsylvania has thicker transverse ridges, that are slightly bent backward, and is thus clearly different from *M. valvatus*.

Occurrence According to the current knowledge, microconchids with the above-described characters are limited to the Middle Triassic Upper Muschelkalk of Germany. It is probable that *Microconchus valvatus* also occurs in neighbouring regions, but this must be confirmed by further studies.

Results of population structure analysis

Despite the similar mode of encrustation, the microconchid populations from the *atavus* and *nodosus* zones are different from a statistical point of view. The population from the

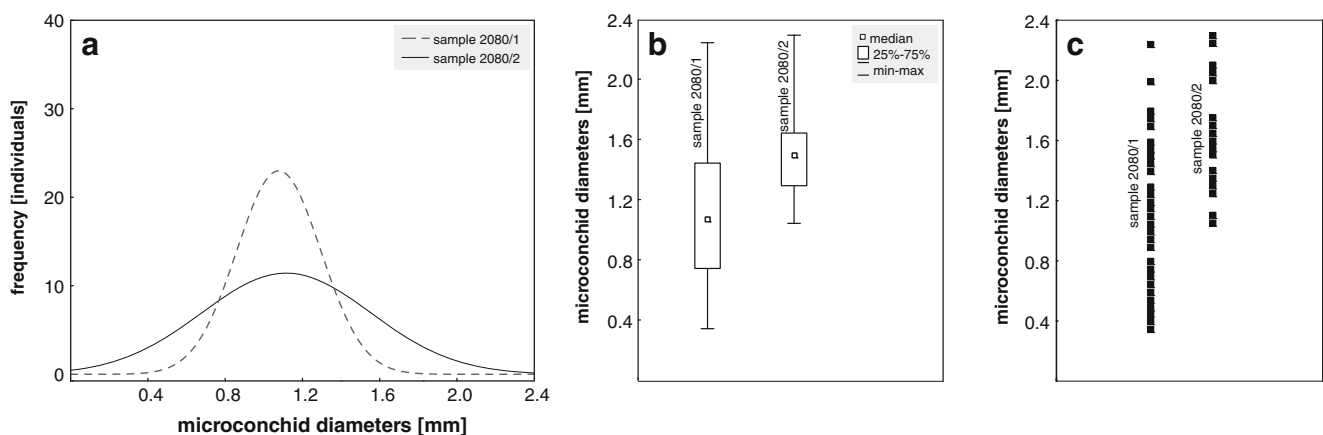
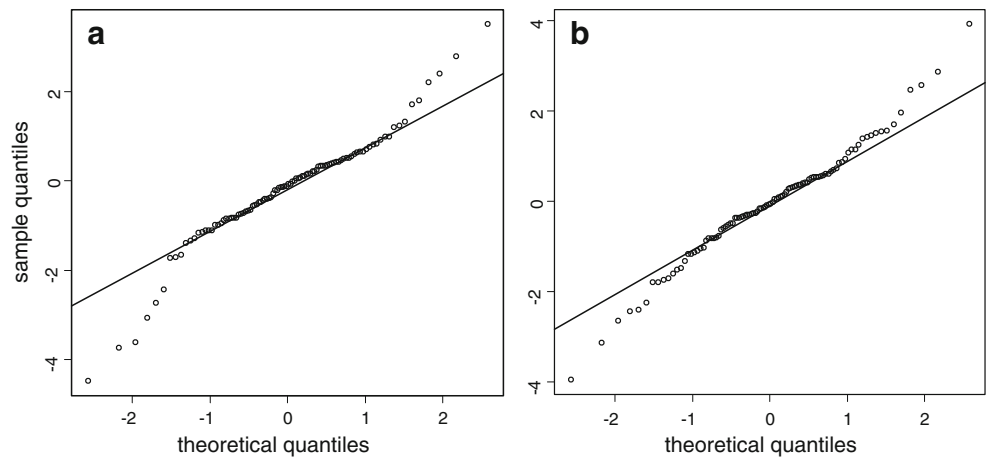


Fig. 5 Basic plots for two investigated microconchid populations from Germany. **a** normal fits, **b** box plots with whiskers, **c** graph showing size gaps within populations size ranges

Fig. 6 Probability Q-Q plots for both investigated populations, **a** sample MHI 2080/1, **b** sample MHI 2080/2



atavus Zone (MHI 2080/1) is characterised by specimens with a diameter ranging from 0.35 to 2.25 mm, with a mean diameter of 1.11 mm (SD=0.44). The stratigraphically younger population from the *nodosus* Zone (MHI 2080/2) comprises specimens with tube diameters ranging from 1.05 to 2.3 mm, with a mean diameter of 1.52 mm (SD=0.26). The population from the *nodosus* Zone is characterised by specimens having a larger average tube diameter than those from the *atavus* Zone (Figs. 5 and 7).

However, according to the K–S test of population MHI 2080/1 from the *atavus* Zone ($d=0.09163$, $p>0.2$; Lilliefors $p<0.05$) and population MHI 2080/2 from the *nodosus* Zone ($d=0.21715$, $p<0.01$; Lilliefors $p<0.01$), neither populations has a normal distribution (Figs. 5a, 6, 7). This is confirmed by an independent S–W test, which for both populations has $p<0.05$. Each of the populations is also characterised by some distribution asymmetry. The population MHI 2080/1 has skewness 0.32 and kurtosis -0.48 (platokurtic distribution), and population MHI 2080/2 has skewness 1.08 and kurtosis 1.05 (leptokurtic distribution).

The population from the *nodosus* Zone (MHI 2080/2) is characterised by the presence of the largest individuals. The population from the *atavus* Zone (MHI 2080/1) contains a

majority of small specimens (Fig. 7a). Each of the populations is also characterised by some discontinuity in the presence of some sizes between the smallest and largest specimens (Fig. 5c).

The test between these two populations indicates that they differ from each other (Levene: $F(1,df)=31.62$, $df=198$, $p<0.001$; the Brown-Forsythe test gave the same result what the Levene test). It is also confirmed by Wilcoxon test ($W=3737$, $p<<0.001$) as well as by Mann–Whitney U test ($Z=6,384$, $p<<0.001$).

Discussion

As encrusting organisms, microconchid tubes are usually found cemented to organic and lithic hard substrates, (e.g. Vinn and Taylor 2007; Zatoń and Taylor 2009; Vinn and Wilson 2010, 2012; Caruso and Tomescu 2012; He et al. 2012). Therefore, they are most commonly found in situ attached to substrates which makes them valuable objects in palaeoecological investigations (Taylor and Wilson 2003). Microconchid tubes found loose and detached from their substrate may have settled on substrates with low fossilisation potential, e.g. on aragonitic shells or algae (e.g. Vinn and

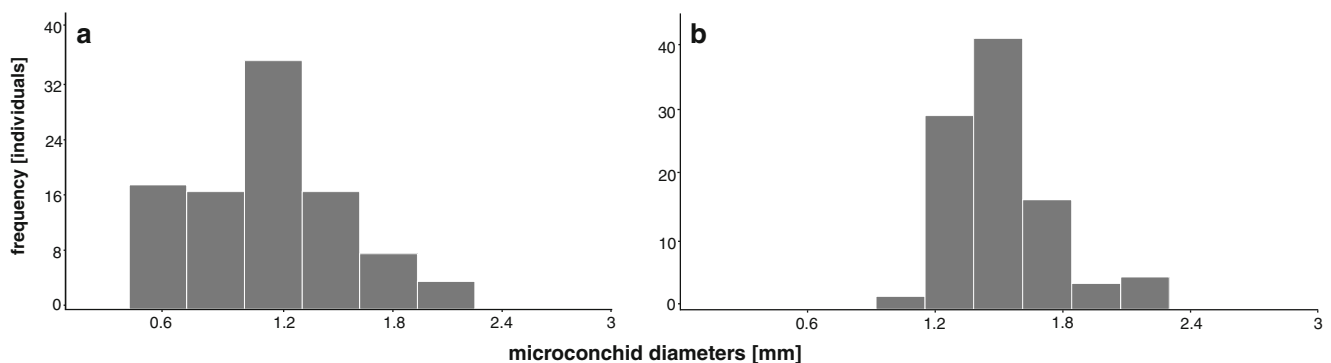


Fig. 7 Histograms showing size-distribution of individuals in particular populations of studied microconchids. **a** sample MHI 2080/1, **b** sample MHI 2080/2. $N=100$ individuals from each population

Taylor 2007; Zatoń and Krawczyński 2011a) that dissolved and decomposed.

The Upper Muschelkalk microconchids under study here encrusted bivalve or cephalopod shells. The particular assemblages consist of individuals of different tube diameter, from tiny juveniles up to three-whorl tubes presumably belonging to fully mature adults. The specimens are usually found associated close to each other, which often makes the tubes of adjacent individuals tightly coiled, presumably a response against crowding.

The analysis of two microconchid populations by independent tests showed their non-normal and different size distributions. The stratigraphically older population (MHI 2080/1) from the *atavus* Zone is characterised by a predominance of significantly smaller individuals than the younger population (MHI 2080/2) from the *nodosus* Zone. Unlike the microconchids from the *atavus* Zone, those from the *nodosus* Zone lived in a slightly different water environment with respect to salinity, as based on the lack of such stenohaline taxa as crinoids and echinoids. Interestingly, the microconchids from the *nodosus* Zone also attained larger tube sizes than those from normal marine settings of the *atavus* Zone. It is known (e.g. Taylor and Vinn 2006; Zatoń et al. 2012a) that microconchids developed well in restricted environments; however, as we compare only two samples, it would be speculative to state that those from the more restricted environment developed better than those from normal marine habitats. Therefore, the most parsimonious explanation is that size differences simply resulted from specific population structures.

Which factors were responsible for a higher mortality of smaller (juvenile) microconchids in the population living during the *atavus* Zone and longer growth of the more successful individuals during the *nodosus* Zone? Encrusters, as organisms permanently cemented to the substrate, are vulnerable to various lethal factors, both biotic and abiotic (see Taylor and Wilson 2003). Biotic factors may include encrustation by larger metazoans or algae occupying the same substrate, and abiotic factors include a wide array of environmental perturbations as, e.g. oxygen deficiency or higher sedimentation rate/resuspension. The only other encrusters present on the samples studied here are the oyster-like bivalves *Placunopsis*, the shells of which are also observed to encrust some of the microconchids. However, the size of the encrusted microconchids is similar to those unaffected by the bivalves. Therefore, in this case, the encrustation by bivalves seems to be irrelevant. The encrustation by algae may also be excluded, as in this case we would expect the microconchids to have highly elevated terminal portions of their tubes—a well-known response against progressive covering (Vinn 2010b; Zatoń and Krawczyński 2011a). Instead, the microconchid tubes are planispirally coiled throughout their ontogeny. The same tube response would be seen when slow but continuous sedimentation appeared. Thus, the latter factor may also be excluded, especially that these microconchids colonised a highly convex cephalopod shell forming an

elevation on which the sediment particles would be easily winnowed even by weak bottom currents (e.g. Massel 1999). The gaps in tube size structure (Fig. 5c) is most easily explained by a second generation of microconchids that settled next to the parent generation and was finally smothered by sediment during a storm event.

In the case of the microconchids from the *nodosus* Zone, the population consists of larger individuals having clearly directed terminal portions of their tubes upward. That means the individuals grew undisturbed on the substrate after the larvae settled on the substrate for a longer time span, but later may have witnessed at least periodical higher sedimentation rates. It cannot be excluded that sediment completely covered some individuals inhibiting their later growth, which may also be supported by the presence of gaps in size distribution of some of the microconchids (Fig. 5c). Thus, the microconchid size differences in the two populations resulted from different timing of external disturbance affecting the populations.

Although also present in settings slightly differing in salinity (e.g. *nodosus* Zone), it may be concluded that *M. valvatus* inhabited marine environments during the Lower and Upper Muschelkalk, and, unlike the species *M. aberrans* and *M. germanicus*, was intolerant of both hypersaline and brackish-water influxes (Hagdom 2010). The two latter species are also not associated with *M. valvatus* in the same deposits, indicating that they were intolerant of normal marine environments. There is a growing evidence (Fraiser 2011; He et al. 2012), that microconchids were the only encrusters inhabiting the harsh, post-extinction hard and firm substrate environments during the earliest Triassic and, along with the bivalve *Placunopsis* (see Pruss et al. 2007), were dominant hard substrate organisms later on in the Spathian (Zatoń et al. 2013). Even in the Middle Triassic, when environments and biotas had fully recovered to pre-extinction conditions, microconchids, along with *Placunopsis* bivalves, were still important encrusters, as demonstrated here.

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