

Soft-tissue attachment structures and taphonomy of the Middle Triassic nautiloid *Germanonautilus*

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New examinations of numerous steinkerns of the Middle Triassic nautiloid *Germanonautilus* from southern Germany revealed new anatomic, ecologic, and taphonomic details, which are compared with Recent *Nautilus*. The attachment structures of the cephalic retractor muscle (large scar) and of the dorsal (black layer) and the posterior mantle (posterior narrow scar, anterior band scar of the mantle and septal myoadhesive bands), some with tracking bands (recording the anteriorward movement of the soft body during ontogeny), were seen in several specimens. The shape and proportions of these soft-tissue attachment structures resemble those of Recent *Nautilus macromphalus* and indicate a similar soft part anatomy. Based on their conch geometry, the mode of locomotion of *Germanonautilus* is reconstructed. Owing to the wide whorl cross section and the high whorl expansion rate, drag of the conchs was high, the aperture was oriented at an oblique angle which made *Germanonautilus* a rather slow horizontal swimmer. Because of their large sizes and widths, conchs of *Germanonautilus* were often deposited on their broad venters, forming elevated “benthic islands” (secondary hardgrounds). A broad range of animals (fish, decapods, ophiurans, crinoids, brachiopods, bryozoans, bivalves, *Spirorbis*, foraminiferans) lived in and on these comparatively large secondary hardgrounds.

Key words: Nautiloidea, *Germanonautilus*, soft-tissue attachment, taphonomy, palaeoecology, epifauna, Triassic, Germany.

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Introduction

Conchs and mandibles of *Germanonautilus* are moderately common in the marls and limestones of the German Muschelkalk (Anisian, Ladinian). Although usually preserved as steinkerns, cephalopods from the German Muschelkalk sometimes display exceptionally well preserved delicate morphological details such as the black layer (Klug et al. in press), siphuncular membranes (Hagdorn and Mundlos 1983; Wang and Westermann 1993; Rein 1995), three-dimensionally preserved nautiloid mandibles with their originally chitinous wings (Müller 1963, 1969, 1974; Klug 2001), three-dimensionally preserved *Ceratites* mandibles that lack extensive calcified components (Lehmann 1985; Rein 1993) and moulds of the buccal mass of *Germanonautilus* (Müller 1969; Klug 2001).

Germanonautilus conchs exceed diameters of 300 mm and were thus recognised by early natural scientists. Specimens of *Germanonautilus* were figured at least eight times in the 18th century (Fritsch 1906). What might be the first figure was printed in Büttner (1710: 270, pl. 20: 1–4) where he showed the conch and the siphuncle. Mojsisovics (1873: pl. 4: 3; 1882: pl. 83: 4, pl. 91: 3) was perhaps the first to figure and discuss the attachment area of the cephalic retractor in Triassic nautiloids. Fritsch (1906) gave a detailed review of the older publications on *Germanonautilus*, whereas Mundlos

and Urlichs (1984) discussed the younger literature (1906 to 1984). In the latter article and also in Urlichs (2000a, b), comprehensive revisions of some species belonging to this genus can be found.

Soft-tissue attachment structures in nautiloids have been described by several authors (e.g., Ward 1987; Isaji et al. 2002). In most cases, the functional interpretation of these structures was that they were for muscle attachment and fixation of the posterior mantle (e.g., Griffin 1900; Doguzhaeva and Mutvei 1991; Mutvei 1957, 1964; Mutvei et al. 1993). Isaji et al. (2002) emphasised the essential constructional differences in the muscle-shell attachment in Recent *Nautilus* compared with benthic molluscs. According to them, the “myoadhesive epithelium-semi-transparent membrane junction in *Nautilus pompilius* seems to be physically weak against tensile stress caused by muscle movement”. They interpreted this phenomenon as being an effect of adaptation to the nektonic mode of life in combination with the mode of shell growth.

The aim of this study is to describe and figure traces of soft-tissue attachment and arguable soft part remains in *Germanonautilus*, with remarks on manoeuvrability, the epifauna encountered on the conchs, and the taphonomy.

Abbreviations.—BCL, body chamber length; WER = $[(dm-ah)]^2$, whorl expansion rate; dm, diameter; ww, whorl

width; wh, whorl height (from umbilical seam to venter); ah, apertural height (from venter of the previous whorl/ dorsum to venter of the last whorl); uw, umbilical width.

Methods

The whorl expansion rate (WER) is considered to be one of the most significant conch parameters of ammonoids (and other ectocochliate cephalopods with more or less logarithmically coiled shells), reflecting body chamber length and the orientation of the living animal in the water column (e.g., Raup 1967; Saunders and Shapiro 1986).

WER is here not computed using Raup's equation (1967). We prefer the method below, because it does not refer to the embryonic shell (Korn and Klug 2002). Instead, it uses diameters which can be measured easily even in fragments or poorly preserved specimens:

$$\text{WER} = [\text{dm}/(\text{dm} - \text{ah})]^2 = [\text{dm}_1/\text{dm}_2]^2$$

where $\text{dm}_2 = \text{dm} - \text{ah}$.

The body chamber length is measured in degrees from the last formed septum (anterior part of the external lobe) to the aperture. Saunders and Shapiro (1986) measured this parameter at the hyponomic sinus, which is not very deep neither in most Carboniferous ammonoids nor in Recent *Nautilus*. In some specimens of *Germanonutilus* (e.g., MHI 919), however, the hyponomic sinus covers about an eighth of the length of the body chamber and would thus alter this value significantly. It appears more reasonable therefore to use the ocular sinus instead. The body chamber length depends mainly on the whorl expansion rate, degree of whorl overlap, shape of whorls, and shell thickness (Raup 1967; Saunders and Shapiro 1986). This parameter also correlates with the orientation of the aperture, which is measured in degrees from the vertical direction. The orientation of the aperture can be altered during life by epizoa or other irregularities such as injuries, diseases, or environmental stress.

Material and institutional abbreviations

All Recent (*Nautilus pompilius*, *N. macromphalus*) and fossil steinkern specimens (*Germanonutilus dolomiticus*, *G. bidorsatus*, *G. tridorsatus*, *G. suevicus*), presented and discussed in this study are stored in the Staatliches Museum für Naturkunde in Stuttgart (SMNS), the Museum für Natur-

kunde der Humboldt Universität zu Berlin (MB), the Muschelkalkmuseum Hagdorn, Ingelfingen (MHI), and the Geologische Bundesanstalt Wien (GBAW). The material is listed in Appendix 1, and measurements and ratios are given in Appendix 2.

Attachment of the cephalic retractor

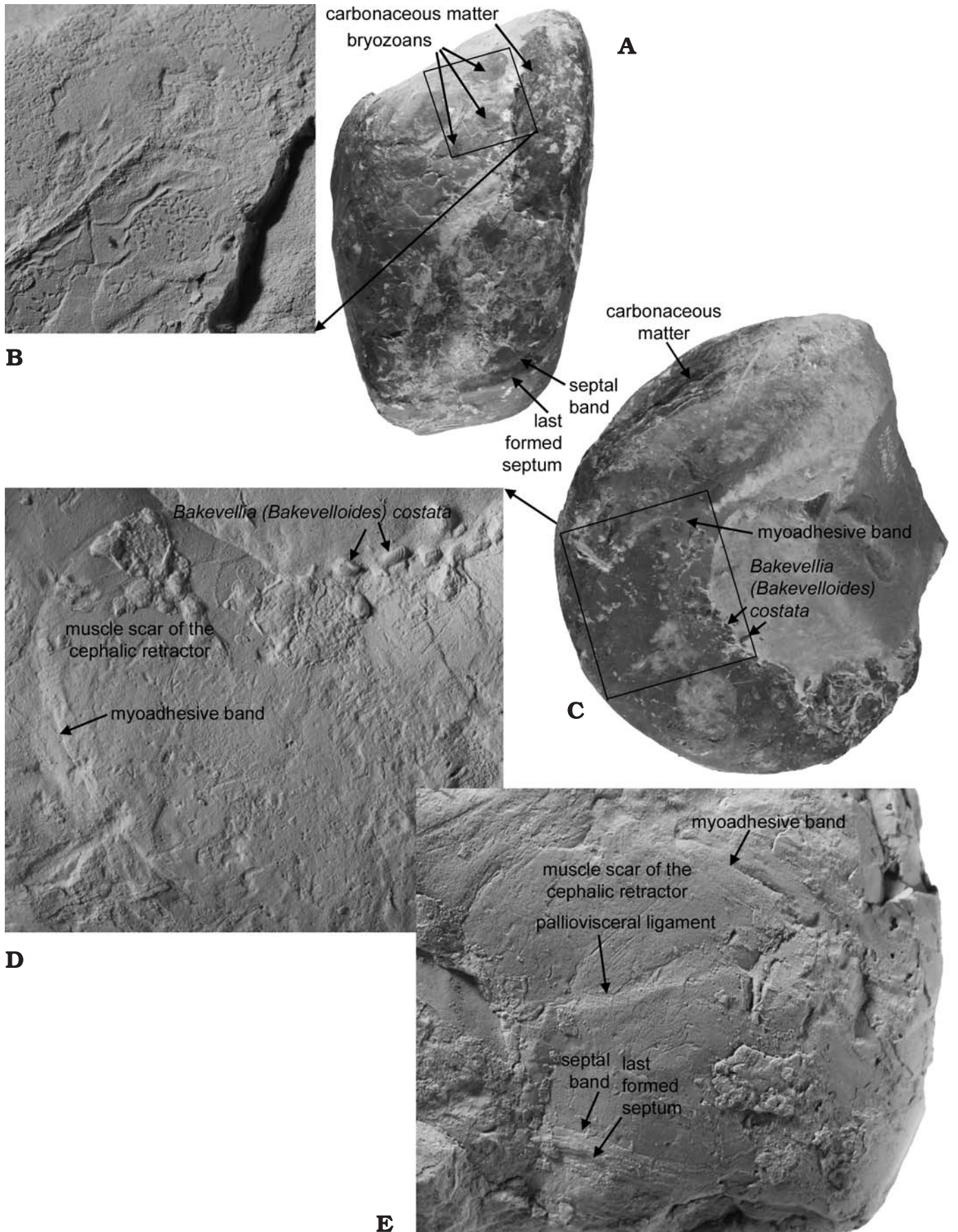
The cephalic retractor muscles represent the most massive muscles in *Nautilus* and probably also in *Germanonutilus*. In *Nautilus*, they serve to retract the soft body and also play an important role in locomotion. These muscles insert in the capito-pedal cartilage and form a roof above the mantle cavity (Doguzhaeva and Mutvei 1991). By contraction of its longitudinal muscle fibres, the head is withdrawn into the shell, exerting pressure on the mantle cavity and thus pressing water out of the pallial cavity.

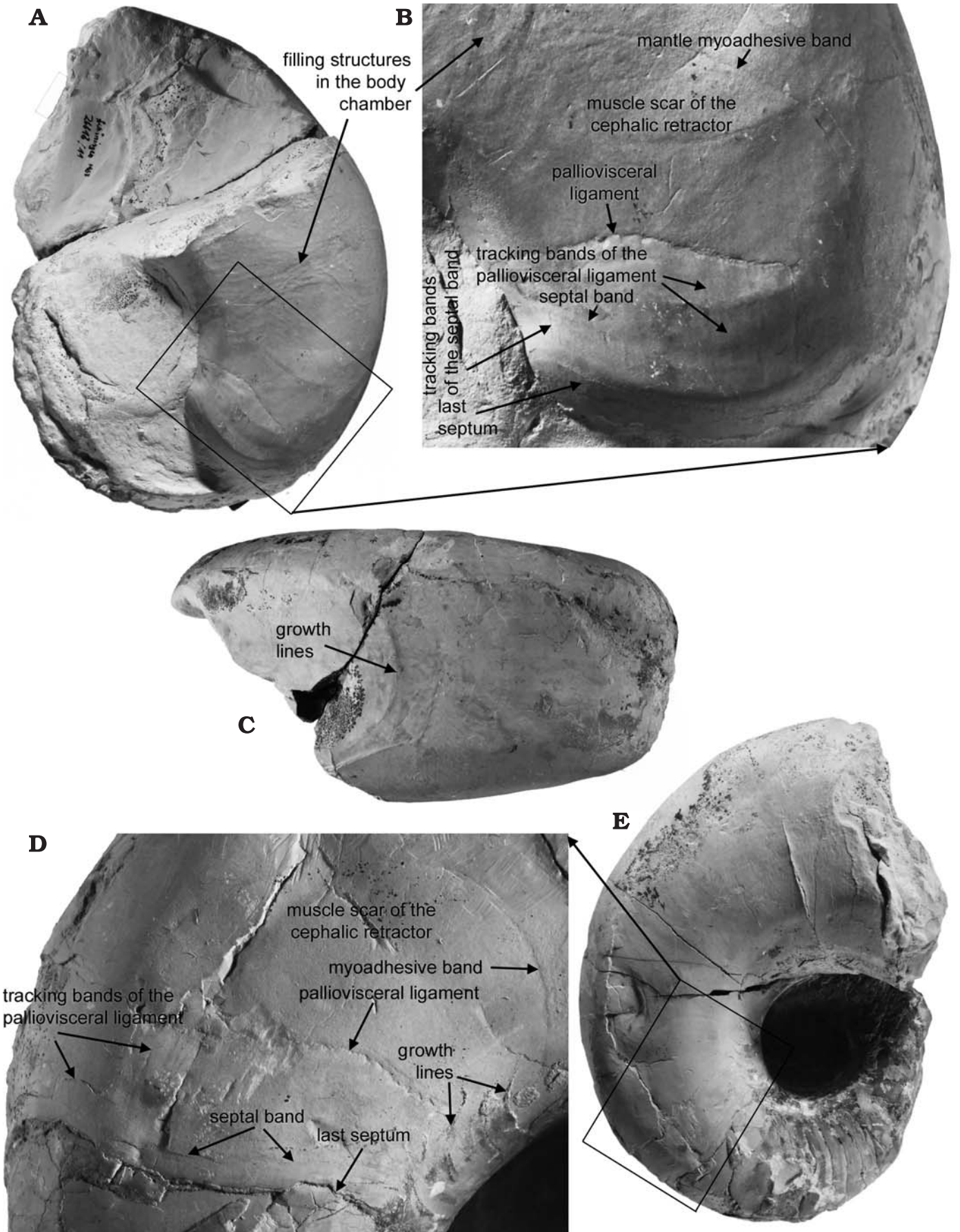
Specimen SMNS 64881 is a *Germanonutilus bidorsatus* (von Schlotheim, 1820), with a diameter of 123 mm (Fig. 1). It shows the well-preserved attachment of the mantle myoadhesive band (= "anterior band scar" in Isaji et al. 2002), the anterior edge of the bean-shaped to semicircular attachment area of the cephalic retractor on both sides. This structure was called "functional area of origin of retractor muscles (conchial zone I)" by Mutvei (1957: 225, fig. 3; = "large scar" in Isaji et al. 2002). This line is represented by a shallow furrow with a parabolic course in the surface of the steinkern. From the umbilical shoulder, it gently sweeps anteriorly, and 14 mm further ventrad, it turns in a postero-ventral direction. The irregularly undulating posterior edge (attachment of the palliovisceral ligament) is visible on the left flank only.

Six to 16 mm anterior of the septal myoadhesive band of one specimen (*G. bidorsatus*; SMNS 26618/11), the attachment scar of the palliovisceral ligament is preserved as an irregular furrow of varying depth on both flanks (at 193 mm diameter; Figs. 2, 3). From the deeper parts of this line, and from the septal myoadhesive band, thin lines run posteriorly in a spiral direction. These lines are interpreted to be tracking bands, recording the ontogenic translocation of the cephalic retractor muscle and the attachment of the posterior mantle.

Similar to the individual described above, SMNS 75229-1 shows the almost complete outline of what is here interpreted as the attachment area of the cephalic retractor, which is surrounded partially by the attachment areas of the palliovisceral ligament as well as the mantle myoadhesive

Fig. 1. *Germanonutilus bidorsatus* (von Schlotheim, 1820); SMNS 64881, coll. H.E. Meuret, Upper Muschelkalk, Nussloch/ Heidelberg (southern Germany). **A.** Ventral view; $\times 0.75$. **B.** Detail of the venter (rectangle in A), showing epifauna consisting of the oyster *Placunopsis ostracina* (von Schlotheim, 1820) which bioimmured arachnidid bryozoans (specimen coated with ammonium chloride); $\times 2$. **C.** Left lateral view with carbonaceous matter; $\times 0.75$. **D.** Detail of the left flank (rectangle in C, specimen coated with ammonium chloride), showing juvenile specimens of the byssate bivalve *Bakevelliella (Bakevellioides) costata* (Schlotheim, 1820) and the large scar of the cephalic retractor; $\times 2$. **E.** Detail of the right flank showing the large scar of the cephalic retractor with the mantle and septal myoadhesive bands, as well as the attachment scar of the palliovisceral ligament (specimen coated with ammonium chloride); $\times 2$.





band (at 214 mm diameter; Figs. 3, 4). The attachment line of the palliovisceral ligament is curved rursiradiately, giving off clear tracking bands, especially in its ventral portion. Surprisingly, the tracking bands have two divergent directions (Fig. 4B): the majority runs spirally, while a few deeper lines in a ventrolateral position cross the former at an angle of ~15° in a posteroventral direction. The reason for this divergence is unclear. During ontogeny, all organs are usually translocated in a spiral path.

As mentioned before, three specimens that display at least parts of what is probably the outline of the attachment area of the cephalic retractor were figured by Mundlos and Urlichs (1984: pl. 2: 1; pl. 3: 4b; pl. 5: 1). The lectotype of *G. bidorsatus* (von Schlotheim, 1820) partially shows the anterior as well as the complete irregular posterior margin (attachment of the mantle myoadhesive band and the palliovisceral ligament) of the probable cephalic retractor attachment area at a diameter of 197 mm (MB C625). Only the attachment point of the mantle myoadhesive band is preserved in the specimen of *G. salinarius* (Mojsisovics, 1882: pl. 83: 4, pl. 91: 3) from Austria at a size of 87 mm (GBAW 4124). Similarly, a specimen of *G. tridorsatus* (Böttcher, 1938) from southern Germany (SMNS 26824) displays this soft-tissue attachment structure at a diameter of 180 mm.

Outlines of the large scar of the cephalic retractor are partially visible in the specimens SMNS 75424/1, 75245/4, and MHI 919. They can be referred to *G. bidorsatus* (von Schlotheim, 1820).

Rein (2002: 36, fig. 3) figured a specimen that displays dark areas on its flanks. On the one hand, he interpreted these structures as scars of the cephalic retractor muscle. On the other hand, we are convinced that these represent traces of a shell repair structure with two layers of conchiolin.

The attachment structure of the retractor muscle has a convex posterior edge with a smooth course and thus a subcircular outline in *Nautilus pompilius* Linnaeus, 1758 (SMNS ZI 9615; Figs. 3, 4). In *N. macromphalus* Sowerby, 1849 (SMNS ZI 9614; Fig. 4), the attachment area of the cephalic retractor has a bean-shaped outline and thus resembles *Germanonautilus* in this respect (in this Triassic nautilid, the palliovisceral line had an irregularly undulating course). At the attachment area of the septal myoadhesive band of *N. macromphalus*, the shell is slightly thickened, which might have been the case in its Triassic counterparts too (there is no shell preserved, but a subtle elevation is present along this line). Within the attachment structure of the retractor muscle of *N. pompilius*, a kind of fine “growth lines” is visible (Fig. 3A). These “growth lines” are parallel to the anterior margin but cross the external shell growth lines of the aperture. In the attachment areas, the septal

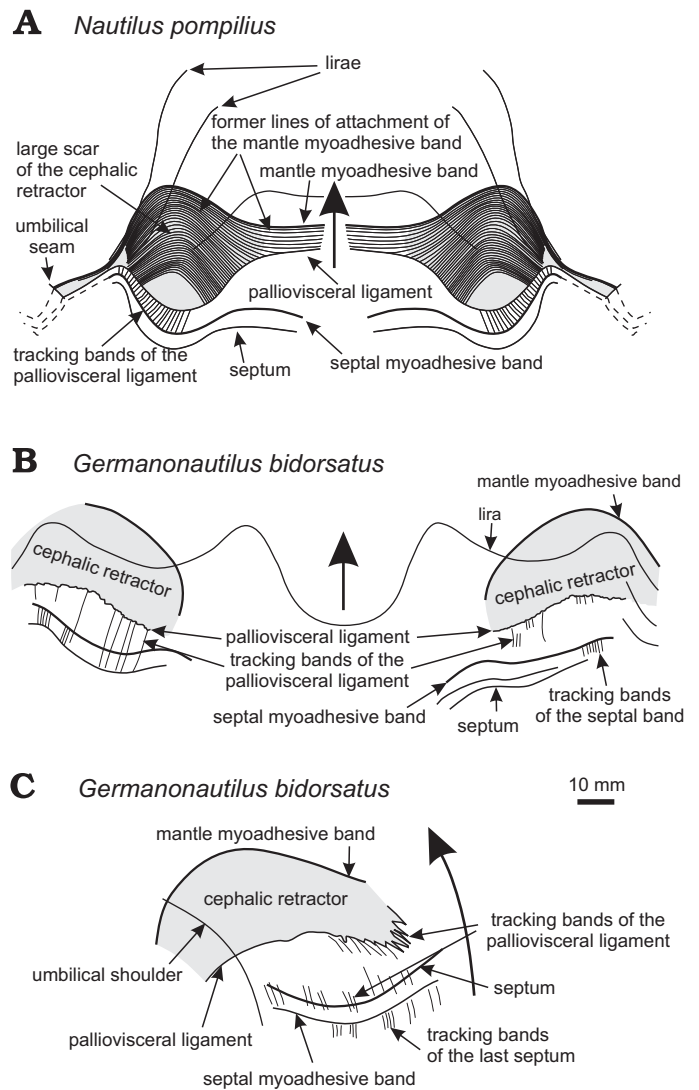


Fig. 3. Outline of soft-tissue attachment structures in Triassic and Recent Nautiloidea; the large scar of the cephalic retractor is in light grey. **A.** *Nautilus pompilius* Linnaeus, 1758, Recent, locality unknown, SMNS ZI 9615. **B.** *Germanonautilus bidorsatus* (von Schlotheim, 1820); SMNS 26618/11, coll. R. Mundlos, Upper Muschelkalk (Anisian, Triassic), Schöningen/Elm (central Germany); the growth lines are partially reconstructed. **C.** The same species, right flank; SMNS 75229-1, coll. M. Warth, Haßmersheimer Marls 3, *atavus* Zone, Upper Muschelkalk (Anisian, Triassic), Weiler zum Stein (southern Germany). Note the larger distance between the attachment areas of the cephalic retractor due to the broader venter of *G. bidorsatus* (**B**) and the different course of the attachment of the palliovisceral ligament.

myoadhesive band, the palliovisceral ligament, and the mantle myoadhesive band left a thin layer of shell behind. Consequently, shell thickness increases in at least three steps in the

← Fig. 2. *Germanonautilus bidorsatus* (von Schlotheim, 1820); SMNS 26618/11, coll. R. Mundlos, Upper Muschelkalk (Anisian, Triassic), Schöningen/Elm (central Germany). **A.** Right flank with the large scar of the cephalic retractor and filling structures; × 0.5. **B.** Detail of the right flank (rectangle in A) with the large scar, the attachment areas of the mantle and septal myoadhesive bands and the palliovisceral ligament with tracking bands; × 1.5. **C.** Ventral view, note the varying strength of the growth lines; × 0.5. **D.** Detail of the left flank (rectangle in E) with the large scar, the attachment areas of the mantle and septal myoadhesive bands, and the palliovisceral ligament with tracking bands; × 1.5. **E.** Left flank with the large scar of the cephalic retractor; × 0.5. Photographs by W. Gerber (Tübingen).

posterior body chamber, corresponding to Mutvei's "annular elevation" (1957: 225, fig. 3).

The lines that are parallel to the attachment site of the mantle myoadhesive band in *N. pompilius* (Figs. 3, 4) document the permanently repeated shift of the retractor muscle throughout ontogeny. This shift apparently happens synchronously with apertural shell growth (Isaji et al. 2002). The absence of such lines behind the septal myoadhesive band indicates a shift of this soft-tissue attachment site corresponding to the formation of new chambers (Isaji et al. 2002).

The specimen of *N. macromphalus* Sowerby, 1849 (SMNS ZI 9614; Fig. 3) shows a slightly different situation to *N. pompilius* Linnaeus, 1758. No lines other than those parallel to the aperture are visible within the area of the cephalic retractor. Additionally, the palliovisceral line is clearly visible and gives a bean-shaped outline to this soft-tissue attachment structure, just as in *Germanonautilus*. Also, there is a thin ventral and a dorsal connecting band between the two lateral attachment areas ("intermediate areas" between the palliovisceral ligament and the mantle myoadhesive band; Mutvei 1957: 225, fig. 3). Whether this arrangement of soft-tissue attachment structures is the plesiomorphic state or whether it simply depends on an open umbilicus is unclear. Of course, numerous other Mesozoic Nautiloidea display these soft-tissue attachment structures [e.g., *Cenoceras striatum* (Sowerby, 1820) from the Early Jurassic (Sinemurian) Arietenkalk of southern Germany; SMNS 60995].

Septal myoadhesive band

The muscles of the septal portion of the body wall originate at the posterior end of the body chamber ("posterior narrow scar" in Isaji et al. 2002). A 3 to 5 mm wide, finely striated band is visible on the left flank and the venter of specimen SMNS 64881 (*Germanonautilus bidorsatus*, at 123 mm diameter), which is filled by carbonaceous matter on the venter (Fig. 1). According to its position, dimension, course, and preservation, it is putatively homologised with the scar of the septal myoadhesive band. Mutvei (1957: 225, fig. 3) called this band the "origin of subepithelial musculature of dorsal portion of body proper (conchial zone II)".

In front of the last septum of specimen SMNS 26618/11 (*G. bidorsatus*, at 193 mm in diameter), a 5 mm wide band is visible on both flanks (not on the venter) which is slightly darker than the rest of the steinkern (Figs. 2, 3). It is separated from the adjacent area by a faint line. This band is considered here to mark the attachment area of the septal myoadhesive band.

The septal myoadhesive band is clearly visible in SMNS 75229-1 (*G. bidorsatus*) on the right side and the venter at a diameter of 214 mm (Figs. 3, 4). On the flank, it lies 3.4 mm in front of the last formed septum whereas on the venter, the space between these two lines measures 11 mm. In this specimen of *G. bidorsatus* (von Schlotheim, 1820), the septal myoadhesive band consists of two parallel lines lying 1 mm

apart from each other. Very fine tracking bands are visible posterior of the septal band, but also behind the last septum near the end of the phragmocone. In both occasions, these are irregularly spaced but apparently do not get closer than one millimetre in that specimen.

Among the specimens figured by Mundlos and Urlichs (1984), only the specimen of *G. tridorsatus* (Böttcher, 1938) from southern Germany (SMNS 26824) displays traces of the attachment structure of the mantle myoadhesive band and the growth lines (at a diameter of 180 mm).

The specimens of *Nautilus macromphalus* Sowerby, 1849 (SMNS ZI 9614) and *N. pompilius* Linnaeus, 1758 (SMNS ZI 9615) both show the attachment structure of the septal myoadhesive band (Figs. 3, 4). These species differ in the extent of the intermediate area between the septal myoadhesive band and the palliovisceral ligament, which is broader in *N. macromphalus*.

Black layer

The black layer represents the attachment structure of the dorsal mantle in Recent *Nautilus* (Ward 1987). In this genus, the hood is directly connected with the dorsal mantle and therefore, the presence of the black layer is here considered to be an indication for the presence of a non-mineralised hood. In contrast to representatives of the ammonoids *Paraceratites* and *Ceratites* from the Upper Muschelkalk (Middle Triassic), remains of *Germanonautilus* only rarely show remains of the black layer (i.e., the attachment structure of the dorsal mantle). Specimen SMNS 64961 (*Germanonautilus suevicus* Philippi, 1898; Fig. 5), a slightly deformed body chamber which was deposited in a vertical position, displays a black band spanning its imprint zone that was interpreted as the remains of the black layer by Klug et al. (in press).

One of the best specimens (MHI 72; Fig. 5E) to display the black layer is a juvenile representative of *G. suevicus* Philippi, 1898 measuring less than 40 mm in diameter. The body chamber is broken off, but the internal (first) whorl is well preserved and perfectly displays the characteristic pattern of intersecting growth lines and spiral lines on the replacement shell. On top of the replacement shell, thick remains of the black layer are visible.

The third *Germanonautilus* example showing the black layer is a large specimen of *G. bidorsatus* (von Schlotheim, 1820) that was deposited on its venter (MHI 919; dm ~207 mm; Fig. 5B–D). It has faint remains of the black layer on the dorsum anterior to the aperture, but the outline of the black layer is not visible. Much of the surface of this internal mould has an unusual brownish colour, perhaps representing remains of the periostracum. Additionally, a feature rarely visible in Recent *Nautilus* can be seen in this specimen, the black layer continues along a growth line as a fine line marking an abandoned aperture. Consequently, the lateral portion and the ventral portion of the growth lines can be correlated, which is usually difficult because of the narrow spacing at

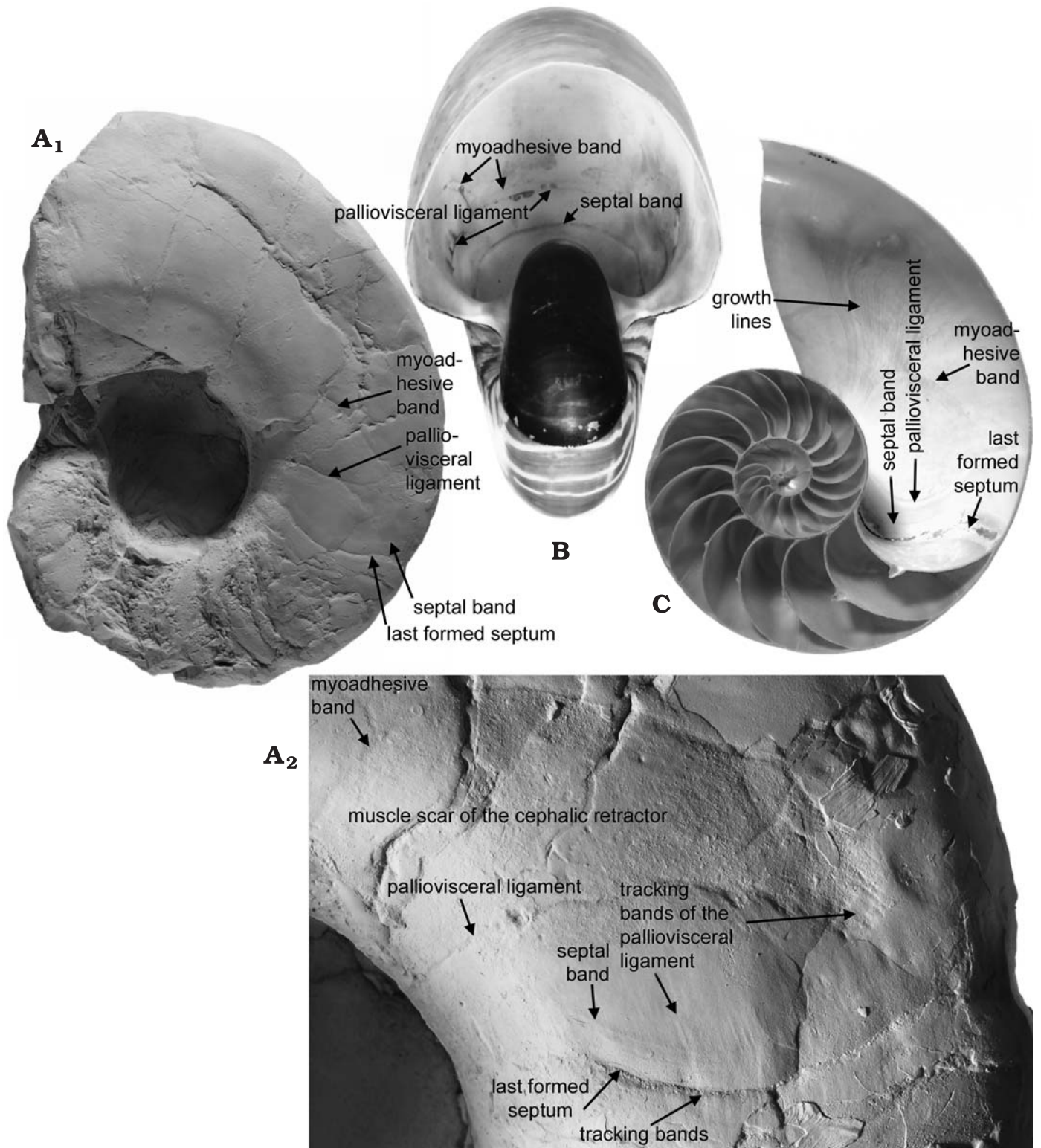


Fig. 4. *Germanonautilus bidorsatus* (von Schlotheim, 1820) from the German Muschelkalk and Recent *Nautilus* from the Indopacific. **A.** *Germanonautilus bidorsatus* (von Schlotheim, 1820), right lateral view; SMNS 75229-1, coll. M. Warth, Haßmersheimer Marls 3, *atavus* Zone, Upper Muschelkalk (Anisian, Triassic), Weiler zum Stein (southern Germany); coated with ammonium chloride in right lateral view (A₁); × 0.5. Detail of flank of the same (A₂); note the attachment area of the cephalic retractor, the mantle myoadhesive band, the palliovisceral ligament, and the septal myoadhesive band with tracking bands (also behind the last formed septum); coated with ammonium chloride; × 2. **B.** Apertural view of *Nautilus macromphalus* Sowerby, 1849 (SMNS ZI 9614, Recent, New Caledonia, coll. Wessel 1860, displaying the attachment areas of the cephalic retractors, the mantle myoadhesive band and the dorsal mantle (black layer); × 0.5. **C.** Internal view of *Nautilus pompilius* Linnaeus, 1758; SMNS ZI 9615, Recent, locality unknown, with attachment areas of the cephalic retractors, the mantle and septal myoadhesive bands; × 0.75.

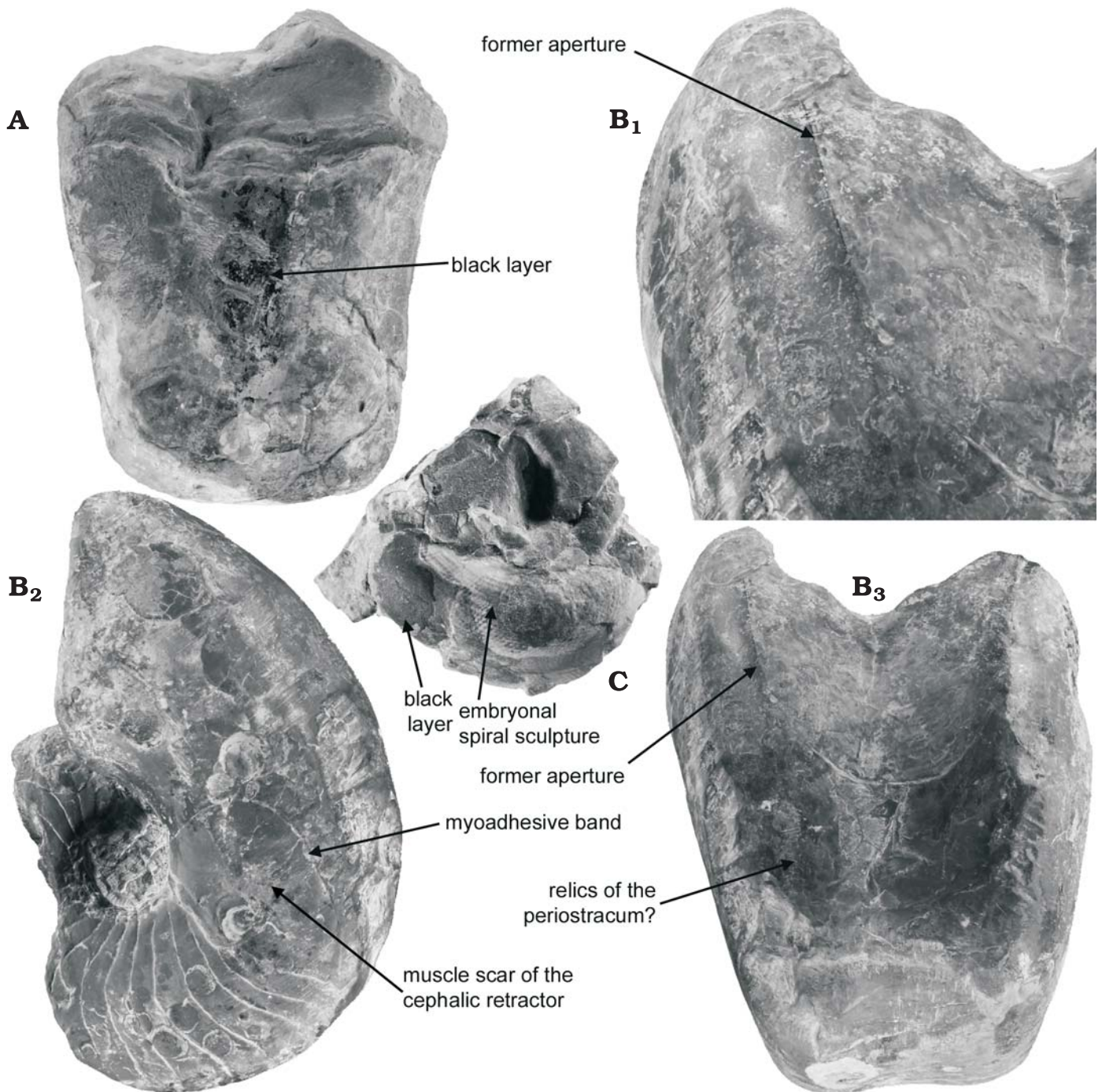


Fig. 5. *Germanonutilus* with remains of the black layer from the German Muschelkalk (Anisian, Ladinian, Middle Triassic). **A.** *G. bidorsatus* (von Schlotheim, 1820), MHI 919, *compressus* Zone, Upper Muschelkalk, Middle Triassic, Garnberg near Künzelsau; this specimen shows the attachment structures of the cephalic retractors, mantle myoadhesive band, palliovisceral ligament, septal myoadhesive band, dorsal mantle, and the aperture; $\times 0.5$. **B.** *G. suevicus* Philippi 1898, SMNS 64961, Upper Muschelkalk, Middle Triassic, Kupferzell-Rüblingen (Kleinknecht quarry). Note the black layer in the concave whorl zone and the epifauna consisting of the oyster *Placunopsis* and the inarticulate brachiopod *Disciniscia*; B₁ ventral view, showing a detail of B₃ with a thin line of the black substance extending along a growth line, $\times 1$; B₂ lateral view, with the attachment structures of the mantle myoadhesive band and the cephalic retractor, $\times 0.5$; B₃ ventral view, complete specimen with a thin line of the black substance extending along a growth line; the dark colour of the venter might be caused by remains of the periostracum, $\times 0.5$. **C.** Juvenile specimen of *G. suevicus* Philippi 1898, MHI 72, Tonhorizont ζ , *nodosus* Zone, Upper Muschelkalk, Middle Triassic, Heimbacher Steige, Schwäbisch Hall; this specimen is preserved with the embryonal spiral sculpture and the black layer; $\times 0.5$.

the ventrolateral edge. In this specimen, the hyponomic sinus swept apically over almost 70° (~ 106 mm). This provided extensive space for turning the hyponome and implies good

manoeuvrability for this individual (Klug et al., in press). This extreme depth of the hyponomic sinus is either at the margin of the variability of *G. bidorsatus* (von Schlotheim,

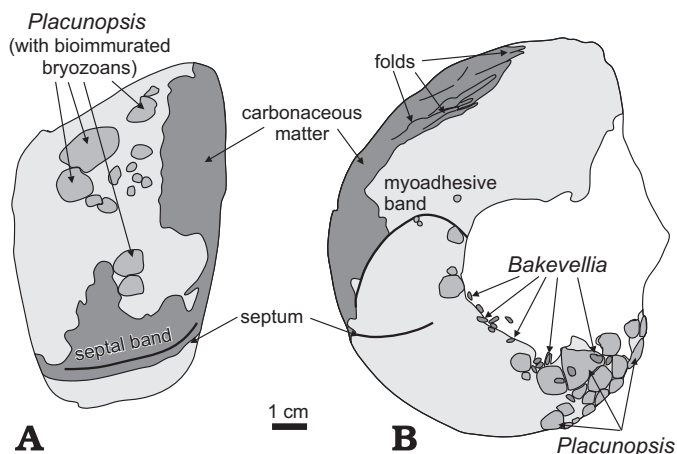


Fig. 6. Outline in venter (A) and left flank (B) of the folded carbonaceous layer (remains of the soft parts?), the attachment area of the cephalic retractor and the posterior mantle (mantle myoadhesive band) of *Germanonutilus bidorsatus* (von Schlotheim, 1820), SMNS 64881, coll. H.E. Meuret (1959), Upper Muschelkalk, Nussloch/ Heidelberg (southern Germany).

1820) or it might be a pathologic specimen, because in other individuals the hyponomic sinus turns adapically over approximately 20°, which is significantly less. Nevertheless, the hyponomic sinus in *Germanonutilus* is always broad and deep yielding space for extensive hyponome movements.

Soft-tissue?

A significant portion of the venter of the *G. bidorsatus* specimen SMNS 64881 (dm = 123 mm), perhaps the entire venter, and the right flank display a carbonaceous (?) layer at and near the surface of the steinkern (partially freed from matrix), and thus the carbonaceous layer follows the internal surface of the shell (Figs. 1, 6). Close to the aperture, this black layer shows irregular wrinkles 1–4 mm in width and up to 30 mm long. This entire structure might be interpreted as an organic filling of the space between the primary and the repaired shell formed after an injury (“*forma conclusa*”; e.g., Müller 1978; Rein 1988, 1989, 1990, 1993, 2002). Alternatively, it can be interpreted as remains of the soft body still attached to the shell at the ventral portion of the mantle myoadhesive band or as other organic material of unknown origin.

The conch was inhabited by a variety of organisms (post mortem): Several specimens of the fixosessile oyster *Placunopsis ostracina* (von Schlotheim, 1820), some with both valves, settled on the flanks and venter of the outside, and on the venter inside the body chamber. Some of the specimens within the body chamber must have lived in the narrow space between the carbonaceous layer and the shell (1–2 mm high). This contradicts the hypothesis that it is a *forma conclusa*, because it is unlikely that *Placunopsis* (diameter of the valves up to 13 mm) could survive in such a narrow space surrounded by shell. This is corroborated by the fact that in

cephalopods with a *forma conclusa*-type shell repair, usually this shell void is completely closed (Rein 2002). Otherwise, the organic matter in this void might have provided a fertile substrate for microorganisms and these could have represented the nutrition of these oysters. In the latter case, the area with shell duplicature must have had an opening where *Placunopsis*-larvae could have entered.

The carbonaceous matter covers most of the venter of the body chamber and its posterior end on the venter and also ventrolaterally, terminating with the last formed septum. Consequently, it appears more likely that remains of the cephalopod soft body remained attached with the septal myoadhesive band to the shell (in contrast to the *forma conclusa* hypothesis), and speculatively, the soft tissues shrunk during necrolysis, losing contact with some parts of the lateral shell wall and providing space for the *Placunopsis* inside the venter of the shell.

Taphonomy

The taphonomy of *Germanonutilus* conchs from the Muschelkalk has been discussed by several investigators (Böttcher 1938; Geisler 1939; Mundlos 1971; Voigt 1975; Hagdorn and Mundlos 1983; Mundlos and Urlichs 1984). Other researchers attempted to reconstruct these taphonomic processes in *Paraceratites* and *Ceratites*, which are certainly comparable to *Germanonutilus* conchs in many respects (e.g., Kumm 1927; Seilacher 1963, 1966, 1968, 1971; Mayer 1968; Mundlos 1970; Aigner 1975, 1985; Düringer 1982; Mundlos and Urlichs 1990; Singer 1991; Rein 1997, 1998; Zeeh and Hagdorn 2002).

Hagdorn and Mundlos (1983) discussed the filling mechanisms, destruction of siphuncle (decoupling of siphonal elements) and septa, destruction of the shell by boring organisms (e.g., phoronids; Voigt 1975; Mundlos and Urlichs 1984), and the formation of siphuncle-steinkerns of *Germanonutilus*. They were able to distinguish four different stages in the destruction of internal shell features of *Germanonutilus*: 1. Siphuncle intact, filling of body chamber and siphuncle; 2. Apical decoupling of siphuncle and partial filling of phragmocone; 3. Complete decoupling of siphuncle; 4. Dissolution of septa, complete filling of phragmocone.

Because of their broad whorls with a flat venter, many specimens of *Germanonutilus* were deposited more or less in life position, i.e. with the venter resting in the sediment and the aperture opening obliquely upwards (Hagdorn and Mundlos 1983). This is probably one reason why remains of the black layer (covered by the inner whorls) and the attachment structures of the cephalic retractors and the posterior mantle (diagenetic and compactional processes) have so far been discovered in only a few specimens (e.g., SMNS 64961; Fig. 5).

Nevertheless, the question remains why are these delicate soft-tissue attachment structures preserved in some specimens? Apparently, specimens from more clayey layers

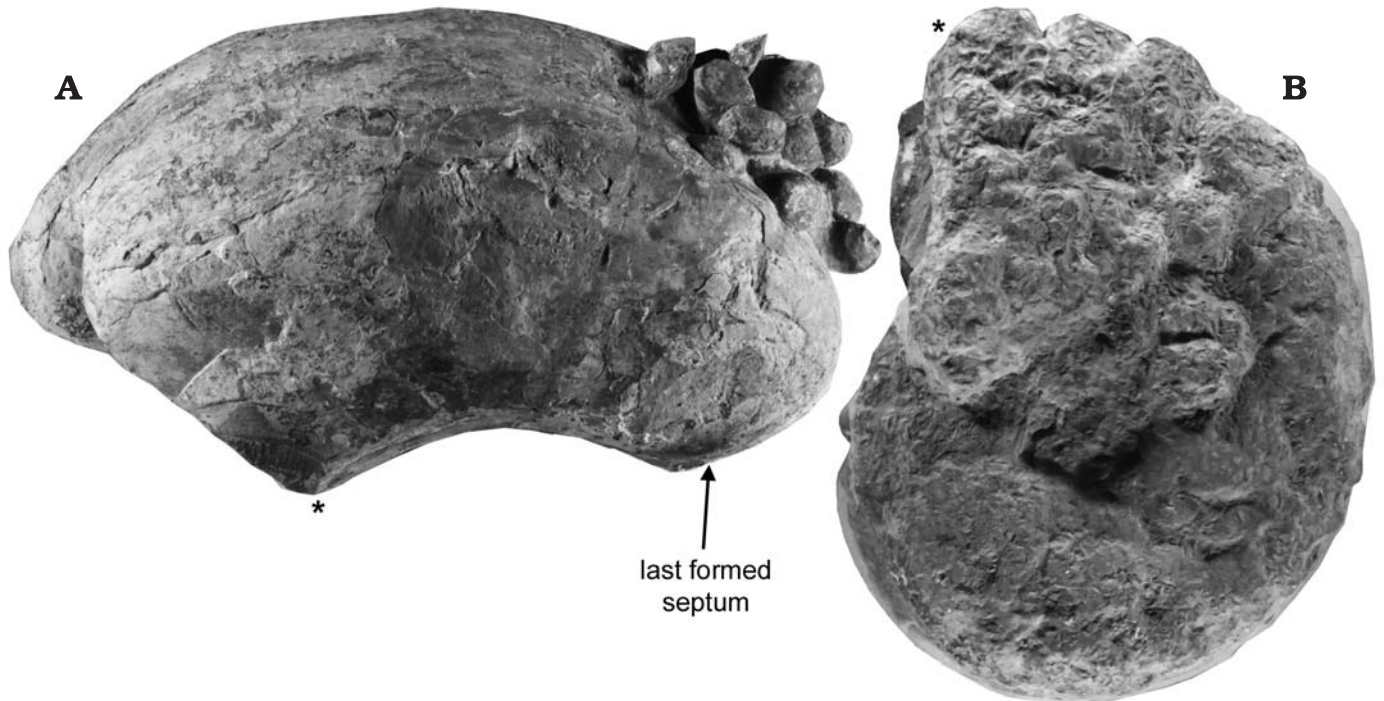


Fig. 7. Epifauna on *Germanonautilus* conchs. **A.** A cluster of 14 specimens of the brachiopod *Coenothyris vulgaris* (Schlotheim, 1820) on the venter of a large body chamber of *Germanonautilus bidorsatus* (von Schlotheim, 1820), SMNS 26679 (wh = 108 mm), Haßmersheimer Mergel, Upper Muschelkalk, Middle Triassic, Helmhof near Untergimpfern (cf. Aigner et al. 1978); $\times 0.5$. **B.** *Germanonautilus suevicus* Philippi, 1898, SMNS 24999/2 (dm = 298 mm), *dorsoplanus* Zone, Upper Muschelkalk, Middle Triassic, Kupferzell-Rüblingen (Kleinknecht quarry); $\times 0.3$. Note the thick bulbous crust consisting of the oyster *Placunopsis ostracina* (von Schlotheim, 1820). Asterisk denotes the approximate position of aperture in incomplete specimens.

within the Muschelkalk more often show these features, including the black layer. Therefore, it is probably the grain-size that facilitates the host rock to form moulds of these subtle shell elevations and which prevents the organic matter from vanishing through pores in the sediment.

Epifauna

The large conch size in *Germanonautilus* (diameters up to 310 mm; Mundlos and Urlichs 1984) and the fact that the shells often settled on the sediment surface in life position, probably explain why the empty conchs often served as secondary hardgrounds ("benthic islands"; Seilacher 1981) in a softground environment (compare Aigner 1985).

Most specimens are encrusted by the common oyster *Placunopsis ostracina* (von Schlotheim, 1820), and sometimes they even represent the nucleus of a *Placunopsis*-bioherm (Fig. 7B; Bachmann 1979).

Rein (1997, 1998, 1999, 2000) interpreted the mode of life of *Germanonautilus* based on the epifauna. Based on the orientation and position of the *Placunopsis* valves on the nautiloid conchs, he tried to determine whether these oysters had settled on the *Germanonautilus* conch *syn vivo* (epizoa) or *post mortem* (epicole). He stated that *Placunopsis*, which lived as true epizoans (see Davis et al. 1999) did not reach the same size on conchs of *Germanonautilus* (<27 mm) as those

living on the ammonoid *Ceratites* (>50 mm) because of a difference in the ecology of these two nautiloids (compare also e.g., Meischner 1968). Rein hypothesised a benthic mode of life in *Ceratites* and a nekto-benthic mode of life in *Germanonautilus*, because, in his opinion, the load of *Placunopsis* shells was in many cases too heavy for the nautiloid to maintain neutral buoyancy. In contrast, we prefer the hypothesis that the maximum size of *Placunopsis*-shells reflects differences in living conditions (e.g., nutrient availability), which was possibly caused by a discrepancy in the swimming activities of *Germanonautilus* on the one hand and *Ceratites* on the other hand (Max Urlichs, personal communication 2002). Because of their slender conchs and their horizontal apertures, the representatives of *Ceratites* probably were more active swimmers than *Germanonautilus* with their wide conchs and thick shells. Tentatively, especially the larger and oxyconic representatives of *Ceratites* were able to provide *Placunopsis* with an enhanced nutrient stream, allowing them to grow to a larger maximum size as for instance in bioherms close to the sea-floor.

Consistent with Hans Hagdorn (personal communication, Ingelfingen 2002), the oyster *Enantiostreon difforme* (Schlotheim, 1820) also rarely lived on *Germanonautilus* conchs. Occasionally, the bivalves *Plagiostoma striata* (Schlotheim, 1820), *Pleuronectites laevigatus* (Schlotheim, 1820), and *Bakevella* (*Bakevellioides*) *costata* (Schlotheim, 1820) were attached to nautiloid conchs by their byssus (own material and

Hans Hagdorn, personal communication, Ingelfingen 2002). These species apparently preferred to settle in the umbilicus. Seventeen juvenile specimens (mostly 2–3 mm long) of the byssate bivalve *B. (Bak.) costata* (Schlotheim, 1820) are preserved on specimen SMNS 64881, most near the umbilical shoulder and some on the flank. Because of their small size, the reduced size range, and their common habitat, it appears reasonable to assume that these bivalves represent a single generation of larvae that settled on this shell.

Interestingly, the internal side of the body chamber (SMNS 64881), in the area with the carbonaceous layer, was first encrusted by bryozoans (Ctenostomata; Fig. 1B) which are preserved by bioimmuration of 14 *Placunopsis* valves (Todd and Hagdorn 1993). Todd and Hagdorn (1993) referred these remains to the family Arachnidiidae. Phoronid borings in *Germanonutilus* shells have been reported by Mundlos and Urlichs (1984; cf. Voigt 1975; Schmidt 1993). The articulate brachiopod *Coenothyris vulgaris* (Schlotheim, 1820) was shown to have lived on *Germanonutilus* conchs, because specimen SMNS 26679 (Fig. 7A), a large body chamber, shows a cluster of 14 specimens on its venter (Aigner et al. 1978). *Spirorbis valvata* Berger, 1859 is also a common fixosessile epibiont on *Germanonutilus* conchs (e.g., Rein 1998). Moreover, Hagdorn found encrusting Foraminifera on these cephalopod shells (personal communication, Ingelfingen 2002).

In addition to the epifauna, several organisms obviously used the empty conchs for shelter, including coelacanth (Martin and Wenz 1984), crustaceans (own material), and ophiurans (personal communication from Hans Hagdorn, Ingelfingen 2002). It is likely that additional organisms used these empty shells as cover.

Mode of life of *Germanonutilus*

Measurements of 30 specimens of *Germanonutilus* (*G. bidorsatus*, *G. tridorsatus*, and *G. suevicus*) yielded values of the whorl expansion rate mostly between 2.3 and 3.0. In Recent *Nautilus* (*N. macromphalus* and *N. pompilius*), this ratio is approximately 2.8 to 3.2. Preadult specimens of the Recent nautiloids have lower whorl expansion rates (Saunders and Shapiro 1986).

Because of incomplete preservation, the precise body chamber length is difficult to determine in most specimens of *Germanonutilus*. Nevertheless, some specimens (e.g., SMNS 26824) display remains of the densely spaced growth lines near the aperture, indicating a terminal aperture. Additionally, the morphometric values taken from less complete specimens reveal at least the minimum body chamber length. Because of the strongly varying depth of the hyponomic sinus, the ocular sinus and the external lobe are used as reference points. According to these measurements, *Germanonutilus* had a body chamber length of about 150 to 190°, which is slightly more than in Recent *Nautilus* (124 to 167° according to Saunders and Shapiro 1986).

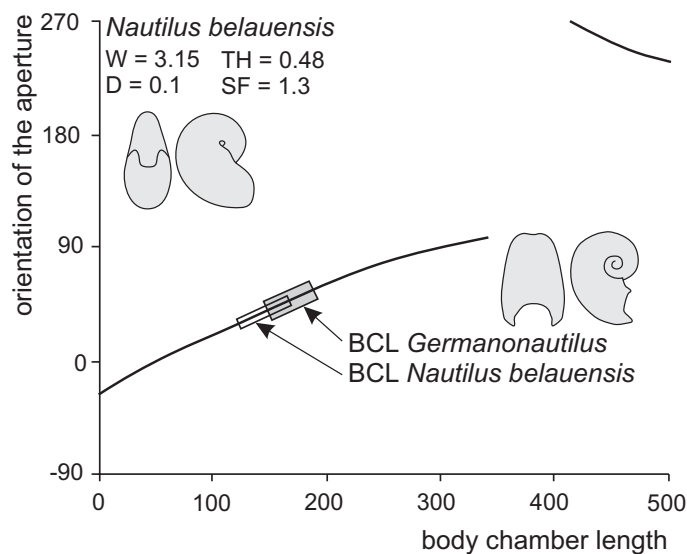


Fig. 8. Orientation of the aperture and body chamber length of *Germanonutilus bidorsatus* (von Schlotheim, 1820) from the German Muschelkalk and of Recent *Nautilus* (modified after Saunders and Shapiro 1986).

Based on the relation between body chamber length and orientation of the conch (Saunders and Shapiro 1986), the aperture of most adult specimens of *Germanonutilus* was probably oriented obliquely upwards at an angle of 40 to 60° from vertical (Fig. 8; compare also Raup 1967).

Because of its deep hyponomic sinus and the usually rursiradial course of the growth lines and thus the aperture, the hyponome of *Germanonutilus* was probably easily directed backwards for forward locomotion as in *Nautilus* (compare Packard et al. 1980). Speculatively, the deep and wide hyponomic sinus facilitated the oscillation of the wings of the funnel and might have extended the range of swimming velocities that could be achieved by this mode of locomotion (see Packard et al. 1980; Jacobs and Chamberlain 1996). Presumably, the stability within the water column (defined by the distance between the centres of gravity and buoyancy) was rather high, as in Recent *Nautilus* (for a review on static stability see Jacobs and Chamberlain 1996).

The most significant differences between the conch morphologies of *Germanonutilus* and *Nautilus* are the umbilical width ($uw/dm \sim 0.2$ to 0.3 in *Germanonutilus*, umbilicus closed or narrow in Recent *Nautilus*: $uw/dm \sim 0$ to 0.1), the dorsoventral compression of the whorls ($wh/dm \sim 0.45$ to 0.52 in *Germanonutilus*, $wh/dm = 0.58$ in Recent *Nautilus macromphalus*), and the whorl width ($ww/dm \sim 0.6$ to 0.8 in *Germanonutilus*, $ww/dm = 0.45$ in Recent *N. macromphalus*). These factors most likely affected the hydrodynamic properties of the conch (Chamberlain 1976; Jacobs and Chamberlain 1996), which are poorer in *Germanonutilus* than in Recent *N. macromphalus*. The moderate manoeuvrability of *Germanonutilus*, suggested by the orientation and shape of the aperture and the deep hyponomic sinus, is supported by the smaller size of *syn vivo* encrustations of the

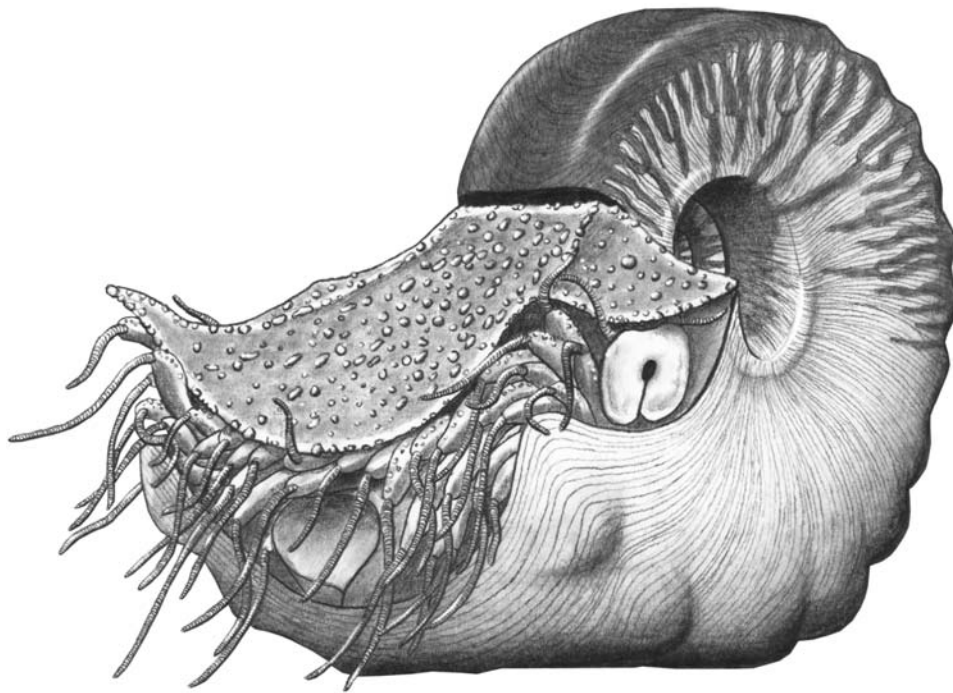


Fig. 9. Reconstruction of the conch and the soft parts of *Germanonautilus tridorsatus* (Böttcher, 1938); oblique view; $\times 0.3$.

oyster *Placunopsis* (see discussion above; compare Rein 1997, 1998, 1999, 2000).

In summary, the orientation of the aperture of Triassic nautiloids is slightly higher than among their Recent counterparts. This indicates a moderate manoeuvrability in all directions similar to the Recent nautiloids, whereas the overall conch geometry—especially the clearly less stream-lined morphology—indicates high drag. High drag would have caused high energetic costs for horizontal swimming motions and thus, *Germanonautilus* most probably did not swim fast. Its mode of life was perhaps nekto-benthic as in Recent *Nautilus* but with pronounced forward and vertical components to their movements (Fig. 9).

Conclusions

Specimens of various species of *Germanonautilus* from the German Muschelkalk preserve correlates of the attachment areas of the cephalic retractor, the mantle myoadhesive band, the palliovisceral ligament, and the septal myoadhesive band with tracking bands. These features appear to have been developed to a similar extent in all species of this genus. The overall morphology of these soft-tissue-attachment structures closely resembles that of Recent *Nautilus* and thus, the soft part morphology of the Triassic forms was probably similar. As in Recent *Nautilus*, the two different modes of growth (that of the septa and that of the aperture) affect the soft-tissue attachment structures in different ways: The mantle myoadhesive band and the cephalic retractor appear to move forward simultaneously with aper-

tural growth, whereas the palliovisceral ligament and the septal myoadhesive band were probably shifted anteriorly with the construction of new septa. The faintness of the traces of these soft-tissue attachment structures suggests that the shell to soft-tissue connection was probably weak, as in Recent *Nautilus*.

Although the orientation of the aperture was similar in Recent representatives of the Nautilioidea and their Triassic counterparts, there are differences in conch geometry (whorl expansion rate, body chamber length, whorl width, and depth of the hyponomic sinus). The extremely broad and dorsoventrally compressed whorls of the less stream-lined conch of *Germanonautilus*, and the slightly smaller attachment area of the cephalic retractor muscles combined with the large whorl cross section reflect differences in locomotory ability.

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Appendix 1

Mesozoic and Recent Nautiloidea with soft-tissue attachment structures stored in the Staatliche Museum für Naturkunde, Stuttgart. Measurements in mm.

species	stratigraphy, locality	leg.	No.	attachment structures	dm	WER
<i>Germanonutilus bidorsatus</i>	Upper Muschelkalk, Nussloch near Heidelberg	Meuret	64881	cephalic retractor, mantle myoadhesive band, palliovisceral ligament, septal myoadhesive band, tracking bands	123	
<i>Germanonutilus bidorsatus</i>	lower Upper Muschelkalk, Schöningen	Mundlos	26618/11	cephalic retractor, mantle myoadhesive band, palliovisceral ligament, septal myoadhesive band	193	3.19
<i>Germanonutilus bidorsatus</i>	Haßmersheimer Marls 3, Weiler zum Stein	Warth	75229-1	cephalic retractor, mantle myoadhesive band, palliovisceral ligament, septal myoadhesive band, tracking bands	214	2.70
<i>Germanonutilus bidorsatus</i>	0.4 m above "Spiriferina"-horizon, Neudenau		75242/1	cephalic retractor, mantle myoadhesive band	225	
<i>Germanonutilus bidorsatus</i>	<i>compressus</i> Zone, Garnberg	Hagdorn	MHI 919	cephalic retractor, mantle myoadhesive band, palliovisceral ligament, septal myoadhesive band, dorsal mantle, hood, aperture, periostracum?	?207	
<i>Germanonutilus bidorsatus</i>	Tonhorizont β2, Gundelsheim	Kurzweil	75245/4	cephalic retractor, mantle myoadhesive band	244	
<i>Germanonutilus suevicus</i>	Upper Muschelkalk, Rüblingen	Wegele	64961	dorsal mantle, hood	? 140	
<i>Germanonutilus suevicus</i>	Tonhorizont ζ, Heimbacher Steige	Hagdorn	MHI 72	dorsal mantle, hood	<40	
<i>Cenoceras striatum</i>	early Sinemurian, Engstlatt/ Balingen	Dopatka	60995	cephalic retractor, mantle myoadhesive band, septal myoadhesive band, tracking bands	? 290	
<i>Nautilus macromphalus</i>	Recent, New Caledonia	Wessel	ZI 9614	cephalic retractor, mantle myoadhesive band, palliovisceral ligament, septal myoadhesive band, tracking bands	160	2.88
<i>Nautilus pompilius</i>	Recent, locality unknown		ZI 9615	cephalic retractor, mantle myoadhesive band, palliovisceral ligament, septal myoadhesive band, tracking bands	134	2.88

Abbreviations: dm, maximum diameter; WER, whorl expansion rate.

Appendix 2

Measurements (in mm) and ratios of Triassic and Recent Nautiloidea stored in the Staatliche Museum für Naturkunde, Stuttgart.

species of <i>Germanon.</i>	stratigraphy	leg.	locality	No.	dm	ww	uw	WER	ww/dm	uw/dm
<i>dolomiticus</i>	mu	M, U	Leimen		53	37.7	14	3.03	0.71	0.26
<i>dolomiticus</i>	mu2	Ü	Dornstetten		66.3		11.5	2.81		0.17
<i>dolomiticus</i>	mu1	M	Dornstetten	7516/1	28.5		7.5	2.50		0.26
<i>dolomiticus</i>	mu2	M, U	Lauerbach/Sulzb.	26672	230	165	87	1.72	0.72	0.37
<i>bidorsatus</i>	Tonhorizont β	A	Zimmern	4462/2	24.5	17.1		2.34	0.70	
<i>bidorsatus</i>	mo		?		222	140	54	2.51	0.63	0.24
<i>bidorsatus</i>	Haßmersh. Sch. 9	M, U	Neckarrens	26670/32	70.5	42	16.9	2.80	0.60	0.24
<i>bidorsatus</i>	Haßmersh. Sch. 9	M, U	Neckarrens	26670/30	88		22.3	3.30		0.25
<i>bidorsatus</i>	Haßmersh. Sch. 9	M, U	Neckarrens	26670/28	215		64.3	2.54		0.30
<i>bidorsatus</i>	Haßmersh. Sch. 9	M, U	Neckarrens	26670/1	117.7	80.8	30.3	2.86	0.69	0.26
<i>bidorsatus</i>	Haßmersh. Sch. 9	M	Gundelsheim	75228/1	228	149	70	2.28	0.65	0.31
<i>bidorsatus</i>	Haßmersh. Sch. 9	M	Gundelsheim	75228/1	151	99	38	3.08	0.66	0.25
<i>bidorsatus</i>	Haßmersh. Sch. 9	M	Gundelsheim	75228/1	86	67	23	3.50	0.78	0.27
<i>bidorsatus</i>	<i>cycloides</i> -Bk. -9 m	M	Neudenu		29.6	22.6	6.7	2.59	0.76	0.23
<i>bidorsatus</i>	Trochitenb.1 -0.5 m	M	Neidenfels		38	20	8.3	2.31	0.53	0.22
<i>bidorsatus</i>	above Trochitenb.6	W	Neidenfels		86.1	56.1	21.8	3.01	0.66	0.25
<i>bidorsatus</i>	mo2	Do	Markgröningen	75238/1	192		54.7	2.42		0.28
<i>bidorsatus</i>	mo2	Do	Markgröningen	75238/2	171	118	51.2	2.084	0.69	0.30
<i>bidorsatus</i>	<i>robustus</i> -Zone	U	Bechstetd/Wagel	75235	175	98	52.6	2.00	0.56	0.30
<i>tridorsatus</i>	Tonhorizont β 1	H	Rielinghausen	75244	144	101	35.5	2.87	0.70	0.25
<i>tridorsatus</i>	mo2	D	Kirchberg	26667	191	116	54.3	2.23	0.61	0.28
<i>tridorsatus</i>	<i>spinusus</i> -Zone	M	Neudenu	26831/1	151		36.8	2.51		0.24
<i>tridorsatus</i>	<i>spinusus</i> -Zone	Ü	Hoheneck	23106	143	81	27.7	2.59	0.57	0.19
<i>tridorsatus</i>	mo2	M	Neudenu	26831/10	64.9	50.5	12.8	2.33	0.78	0.20
<i>tridorsatus</i>	mo2	Do	Markgröningen.	250		120	2.16		0.48	
<i>tridorsatus</i>	mo2	D	Neustadt/ Waibl.	75282	199	116	50.6	1.40	0.58	0.25
<i>suevicus</i>	mo3	S	Heldenmühle	18043	313	205	86	2.08	0.65	0.28
<i>suevicus</i>	mo3		Maubach	26814	148	105.1	45.9	2.83	0.71	0.31
<i>suevicus</i>	<i>cycloides</i> -B. +0.6 m	M	Gundelsheim	26822	118.2		26	2.93		0.22
<i>suevicus</i>	mo3, bed 5	S	Heldenmühle	18308	203	147	52.3	2.26	0.72	0.26
<i>suevicus</i>	mo3	Ü	Zuffenhausen	26815	217	150	57.5	3.01	0.69	0.27
<i>suevicus</i>	mo3		Braunsbach	26811	98.6	78.7	22.6	2.61	0.80	0.23
<i>suevicus</i>	mo3	W	Hegnabrunn	75248/2	242		76.7	2.86		0.32

Abbreviations: A, F. v. Alberti; D, W. Diem; Do, H. Doná; H, K. Hofsäß; M, R. Mundlos; S, A. Schweizer; U, M. Urlichs; Ü, G.N. Übele; Wa, R. Walter; W, M. Wild; dm, maximum diameter; ww, whorl width; uw, umbilical width; WER, whorl expansion rate; ww/dm, whorl width / diameter ratio; uw/dm, umbilical width / diameter ratio.