Functional morphology and taphonomy of nautiloid beaks from the Middle Triassic of southern Germany

CHRISTIAN KLUG

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New records of nautiloid beak elements conventionally classified as '*Rhyncholithes hirundo* (Biguet, 1819)' and '*Conchorhynchus avirostris* (von Schlotheim, 1820)' with carbonised (originally chitinous) three-dimensionally preserved appendages from the Upper Muschelkalk (Middle Triassic) of northern Württemberg (Southwest Germany) enable restoration of the complete beak of *Germanonautilus*. In three specimens, the lower mandible is embedded within the living chamber of *Germanonautilus* conchs. Beak elements of *Germanonautilus* differ from those of Recent *Nautilus* in the more elongate appendages of the fossil lower mandibles and the weaker sculpture on the originally chitinous parts. Furthermore, the dorsal sculpture of the fossil conchorhynchs consists of ridges rather than denticles and the ventral sculpture of the fossil rhyncoliths displays ridges in places where the Recent rhyncoliths have a smooth surface. Additionally, the fossil beak elements attained a larger size than their Recent counterparts. During transport of '*Rhyncholithes hirundo*', the light chitinous parts served as a sail and the heavier conchorhynch anchored in the sediment causing alignment. In contrast to the irregularly embedded isolated rhyncoliths, the conchorhynchs usually settled with their ventral side up. From the study of 407 fossil nautiloid beak-elements, a significant variability of the hard parts is evident. Consequently, the assignment of specific morphologies to the species of *Germanonautilus* is impossible.

Key words: Conchorhynch, rhyncolith, functional morphology, taphonomy, Muschelkalk, Triassic, Germany.

Christian Klug [christian.klug@uni-tuebingen.de], Institut und Museum für Geologie und Paläontologie, Sigwartstraße 10, D-72076 Tübingen, Germany.

Introduction

Calcitic parts of nautiloid beaks are common in the Muschelkalk deposits of the South-German basin, and their remains have been known since the end of the 18th cen-

tury (Knorr 1768; Biguet 1819; von Schlotheim 1820; Quenstedt 1849). Some of the early authors who worked on fossil nautiloid beak elements, struggled with the interpretation of these remains and concluded that they belonged to ectocochleate cephalopods. It was Owen (1832) who discovered indications for their affiliation to cochleate cephalopods, in contrast to his contemporaries who often misinterpreted these fossils as birds' beaks (d'Orbigny 1825), cirripeds (von Schlotheim 1820), or belemnoid or sepiid beaks (Biguet 1819; Gaillardot 1824). Later, they were regarded as beaks of *Ceratites* (Schmidt-Effing 1972; Mayer 1974). Rutte (1962) interpreted an unusually shaped specimen of '*Conchorhynchus*' as the only complete specimen of a *Germanonautilus* conchorhynch (actually, Rutte's specimen falls within the broad variability of '*Conchorhynchus avirostris*'). Mundlos (1973) investigated the size correlations of conchorhynchs versus *Ceratites* and *Germanonautilus* species through time. As a consequence, he questioned Schmidt-Effing's (1972) conclusion and suggested the conchorhynchs belonged to *Germanonautilus* or other coiled nautiloids. Mayer (1974) responded that neither rhyncholiths nor conchorhynchs were found in the Lower Muschelkalk, in contrast to the locally abundant *Germanonautilus* (this objection is now removed by the discovery of a conchorhynch from the lower Muschelkalk in a member that yielded also *Germanonautilus dolomiticus*).

Since 1960, only a few investigators focused their attention on the morphology of '*Conchorhynchus*' and '*Rhyncholithes*'. Müller (1963a, b, 1969) and Mundlos (1971, 1973) contributed studies on biometric aspects, microstructure, systematics and taphonomy. Taphonomic aspects and discoveries of non-calcitic parts of the beak apparatuses were published by Müller (1963a, 1969) and Mundlos (1973). Saunders *et al.* (1978) compiled a detailed study on the morphology and function of Recent nautiloid beaks and compared them with their fossil counterparts. Recently, Rein (1998) reviewed the beak and conch remains of Upper Muschelkalk nautiloids.

This study on the functional morphology and taphonomy of the Triassic nautiloid mandibles is based mainly on previously undescribed specimens, some of these specimens display three-dimensionally preserved remains of the originally chitinous inner and outer lamellae.

Taxonomic considerations

There are some inconsistencies in spelling of the form-taxonomy names of nautiloid beaks. '*Rhyncolites* Biguet, 1819' is probably among the most discussed generic names in palaeontological literature (Riegraf & Schmitt-Riegraf 1995, 1998). Max Urlichs (personal communication 2000) proposes to use the younger synonym '*Rhyncholithes* Blainville, 1827' instead of Biguet's (1819) '*Rhyncolithes*' (which is a homonym) because it is older than '*Scaptorrhynchus*'. This contradicts Riegraf & Schmitt-Riegraf (1998) who preferred the younger synonym '*Scaptorrhynchus*'. The assignment of both '*Rhyncholithes hirundo*' and '*Conchorhynchus avirostris*' to the genus *Germanonautilus* does not appear to be in doubt, although the variability of these beak-elements prohibits a determination which type of rhyncholiths and conchorhynchs belonged to which species of *Germanonautilus*. Consequently, '*Rhyncholithes hirundo*' and '*Conchorhynchus avirostris*' can be considered as collective groups

(International Commission on Zoological Nomenclature 1999, Article 13.3) and hence, they do not have priority over the younger genus *Germanonautilus*. Therefore, these binomens will be listed in inverted commas. Additionally, rhyncholiths and concho- rhynchs are understood to be only the calcitic parts of the beaks. The term mandible re- fers to the unit of both the calcitic and the chitinous part of either part of the beak.

Material

Most of the material under study was collected by H. Hagdorn (Ingelfingen, Ger- many). It is deposited in the Muschelkalkmuseum Ingelfingen (MHI). Some additional specimens examined for this study are stored in the Staatliches Museum für Natur- kunde, Stuttgart (SMNS, Germany). From a total of 407 specimens in these two collec- tions, 31 of the best preserved were selected. Almost all of the specimens are from the Upper Muschelkalk of Germany. The material contains only one conchorhynch (MHI 1707) from the lower Muschelkalk (*Beneckeia buchi*-Mergel, Pelson, Anisian, Middle Triassic). The specimen in Fig. 11 is housed at the private collection of Hubert Donà, Schaeferweg 7, 71706 Markgröningen, Germany. For information about stratigraphy, localities, detailed descriptions, and some measurements of the calcitic parts of the ma- terial see appendices 1 to 3. The terminology of the hard parts is shown in Fig. 1.

Comparison of Middle Triassic and Recent nautiloid lower mandibles

Non-mineralised parts. — Because of their primary flexibility, the chitinous append- ages of the fossil lower mandibles are usually distorted during fossilisation. Conse- quently, their outlines display a marked variability (Müller 1974). However, the com- parison of the outlines of the lower mandibles of the new exceptionally well preserved specimens from the Middle Triassic and of Recent nautiloids reveals some differences (Figs. 2, 3). The wings of the lower mandible of *Nautilus pompilius* display wide and suboval outlines, whereas those same appendages of the three '*Conchorhynchus*' specimens MHI 1516 (1A), MHI 876 (1B), and SMNS 1380/1 appear to be more elon- gate. In contrast to the Recent lower mandibles, the outer lamellae of the fossil lower mandibles were not calcified. Additionally, only very weak traces of the concentric growth lines on the appendages were found in one fossil specimen (MHI 309); it shows some wrinkles on the anterior portion of the appendages which are arranged in a simi- lar way as in Recent lower mandibles. Thus, the lower mandible of *Germanonautilus* differs from *Nautilus* by having a slightly more elongate outline, lacking any distinct sculpture, and an uncalcified outer lamella.

Mineralised parts. — In many cases, the variability of the conchorhynchs from the Muschelkalk (Middle Triassic) can be explained by various alterations produced by mechanical abrasion, transport, and dissolution at various stages of diagenesis. How- ever, there is a significant primary variability (Fig. 4), and Saunders *et al.* (1978) de- scribed a comparable variability in conchorhynchs of Recent *Nautilus*. In particular, the dorsal side of the conchorhynch and its anterior fold display varying shapes in both

Recent and fossil conchorhynchs (MHI 856 and 1686 to 1688; Figs. 1, 4, 5). The conchorhynchs of *Nautilus* have a distinct furrow between the shearing edge and the denticles. Furthermore, the sculpture on the dorsum of the more massive '*Conchorhynchus avirostris*' consists of ridges (MHI 1687), whereas *Nautilus pompilius* conchorhynchs have denticles.

In cross-sections of the fossil conchorhynchs published by Müller (1963a), the dorsal portion is darker in colour and a distinct boundary separates this part from the light-coloured calcitic lamellae of the hood. Additionally, the relative position of the conchorhynch hood versus the unit of the anterior fold and the dorsal lamella is not uniform. In some specimens, the apex of the hood reaches anteriorly to the fold (MHI 1688, Figs. 1, 4). In other specimens, there is a distance of about two millimetres between fold and apex (MHI 1686 and 1687). Furthermore, the anterior wall of the fold is inclined anteriorly in some specimens (MHI 856), posteriorly in others (MHI 1686 and 1688), and a few conchorhynchs entirely lack this fold. This allows the interpretation that the tissues secreting these calcitic parts operated independently. From the comparison of the fossil conchorhynchs with those of Recent *Nautilus*, the anterior fold in *Germanonautilus* conchorhynchs is interpreted as a part of the ventral duplicature of the appendages which is calcified to a varying extent.

As a consequence, the conchorhynch published by Rutte (1962) has to be interpreted as falling within the extreme variability of '*Conchorhynchus avirostris*'. In this specimen, the anterior fold is massive and very high (ca. 10 mm), a character interpreted by Rutte as diagnostic for complete specimens. However, newly discovered specimens show transitions between this extreme shape (MHI 856; Fig. 4) and the characteristic shape of conchorhynchs.

Thus, the fossil conchorhynchs display a significant variability similar to that observed in conchorhynchs of Recent *Nautilus*. This is caused by the independent growth of the hood and the fold-dorsal surface-unit at least to some extent. Otherwise, the larger size and the dorsal sculpture of the fossil conchorhynchs represent the only differences to the Recent conchorhynchs.

Comparison of Middle Triassic and Recent nautiloid upper mandibles

Non-mineralised parts. — Both proportions and shapes of the upper mandibles of Recent *Nautilus* and of Triassic *Germanonautilus* were compared as a contribution to the discussion on the systematic affiliation of this beak element. The ratio of the length of the calcitic part to the length of the carbonised appendage (the inner lamella) appears to be similar in *Nautilus* beaks (ca. 0.80) and in the rhyncholiths of *Germanonautilus* (ca. 0.83 in MHI 1517; ca. 0.92 in SMNS 75226; Fig. 6). Because of the deformation of the fossil specimens, these ratios are only approximations. The maximum ventrolateral extension of the appendages in relation to the height of the calcitic part of MHI 1672 (ca. 1.00) is smaller than the same ratio in the upper mandible of a *Nautilus* (1.38). In specimen MHI 1517, the major part of the posterior portion with the left duplicature of the non-mineralised parts is preserved. The carbonised parts of MHI 1672 probably represent the flattened anterior duplicature of the chitinous appendage.
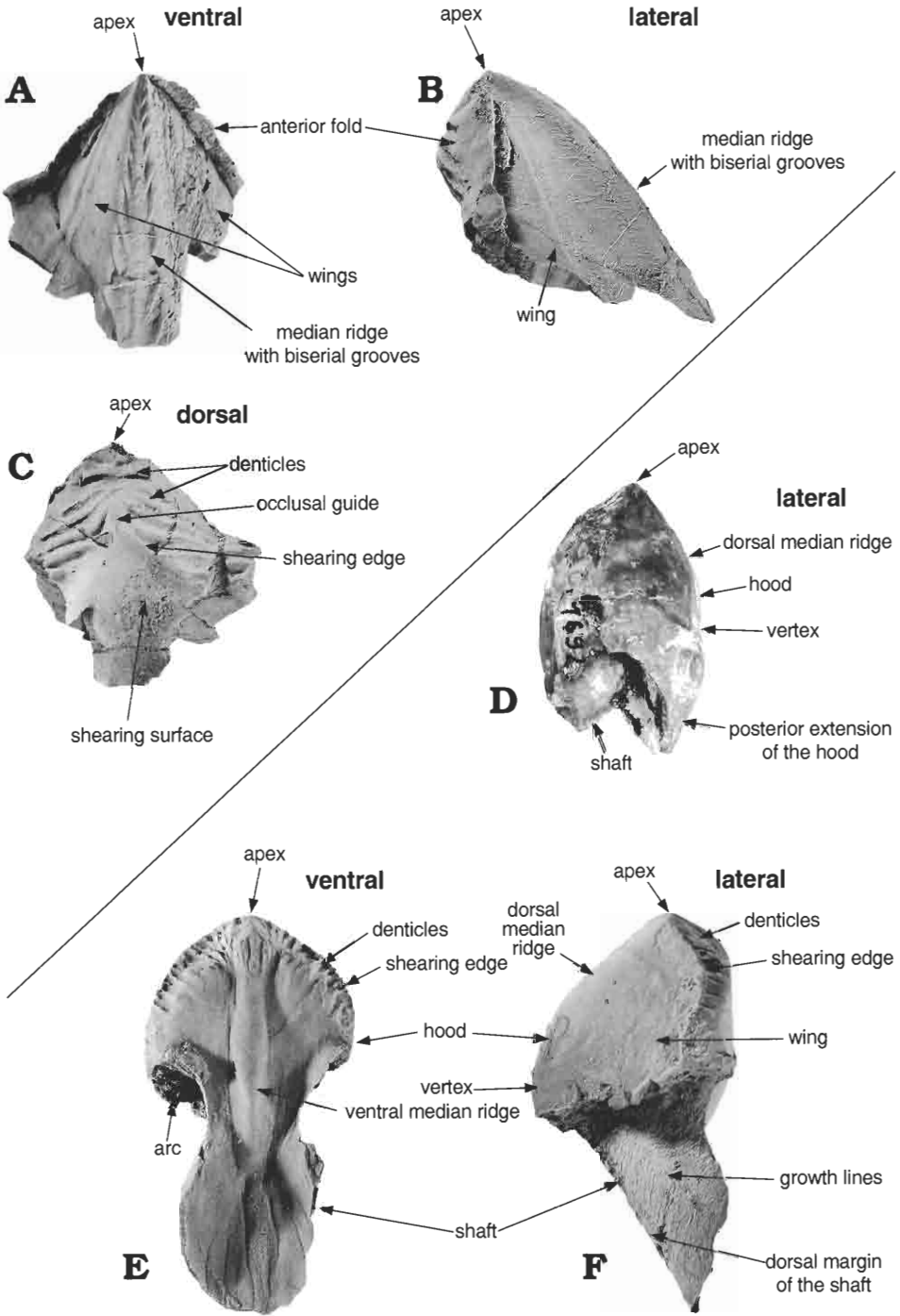
Fig. 1. Terminology of conchorhynchs (**A–C**) and rhyncholiths (**D–F**), partially after Saunders *et al.* (1978), Riegraf & Schmitt-Riegraf (1995), and Rein (1998). All figures twice natural size.

In both fossil specimens, the non-mineralised parts can be interpreted as being homologous with the chitinous parts of the upper mandible of *Nautilus*, based on their dimensions, position, material, and outline (Saunders *et al.* 1978: pl. 1: 1).

From the comparison of complete Middle Triassic upper mandibles with Recent nautiloid mandibles, no significant differences were found besides the larger dimensions of the fossil specimens (Figs. 6, 7). However, the distorted carbonised parts of the inner lamellae did not allow a complete comparison with the same parts of the Recent *Nautilus*.

Mineralised parts. — Rhyncholiths of Recent *Nautilus* have a sharp anterior apex which is usually less rounded than in its fossil counterparts. In living nautiloids, the sculpture on the rhyncholith venter is smoother and lacks denticles or ridges. However, most specimens of fossil rhyncholiths display subparallel, radially arranged ridges on the venter of the hood (Figs. 6, 8).

As Rein (1998) pointed out, many of the rhyncholith specimens are incomplete. This conclusion is justified after studying the posterior edges of the hood of the upper mandibles. In most cases, the posterior margins of the wings of the hood terminate in fractures. Similar to the specimen figured by Rein (1998), some rhyncholiths with complete hoods were discovered (Fig. 8). In these complete specimens, the posterior extension of the hood reaches a length similar to the shaft. It is thin-walled and strongly curved both laterally and sagitally. This extension of the hood certainly served for muscle attachment and it probably had a chitinous continuation of varying length similar to the upper mandible of *Nautilus*. Some specimens display thin carbonised walls between the shaft and the posterior extension of the hood. These walls are interpreted as remains of the chitin which fills this interspace entirely in Recent rhyncholiths (Saunders *et al.* 1978). In the specimens of '*Rhyncholithes*' with complete hoods (MHI 731, 1040, 1096, 1689, 1690, 1691, 1692, 1693), a strong resemblance to the hood in rhyncholiths of *Nautilus pompilius* can be seen. In some specimens (MHI 1690 and 1692; Fig. 8) of Triassic rhyncholiths, the hood extends even further posteriorly than in the Recent rhyncholiths, and the angle between this extension and the shaft is less. This posterior extension of the hood was probably not uniformly calcified in the upper mandible of *Germanonautilus*. Recent rhyncholiths grew to a maximum length of about 17 mm (Saunders *et al.* 1978) whereas the rhyncholiths of *Germanonautilus* reached a length of 29 mm.

In summary, the main differences between the Triassic and the Recent rhyncholiths are the larger size, the stronger ventral sculpture, and the longer extension of the hood of the fossil specimens.

Variability of the rhyncholiths and species distinction. — Similar to the rhyncholiths of *Nautilus*, the fossil specimens display a striking variability (Figs. 1, 6, 8). Addi-

Fig. 2. The beak of a preadult *Nautilus pompilius* Linné, 1758 and the lower mandible of *Germanonautilus*, '*Conchorhynchus avirostris* (von Schlotheim, 1820)', from the Upper Muschelkalk of Baden-Württemberg with carbonised appendages. **A**. The beak of *N. pompilius* (SMNS Zla 30494), × 2. A_1. Lateral view of the lower mandible. A_2. Anterior view of the beak with the buccal mass. A_3. Ventral view of the lower mandible. A_4. Dorsal view of the lower mandible (the arrows point to the joint). A_5. Dorsal view of the beak with the buccal mass. **B**. Oblique ventrolateral view of a complete and only slightly deformed lower mandible (SMNS 1380/1), × 1. **C**. Ventral view of a complete and only slightly deformed lower mandible (MHI 1516), × 1.
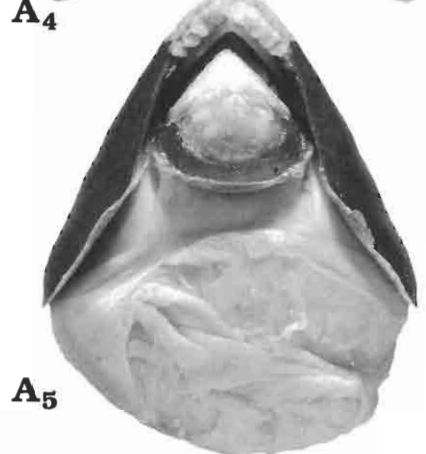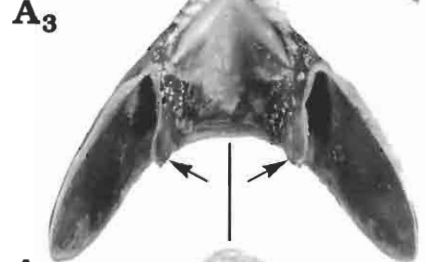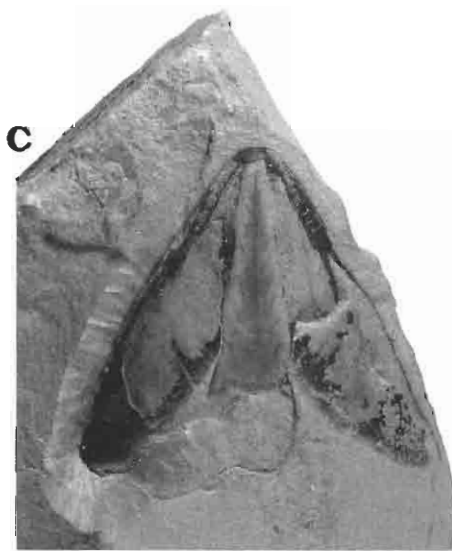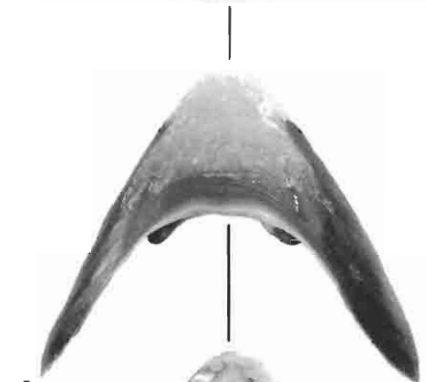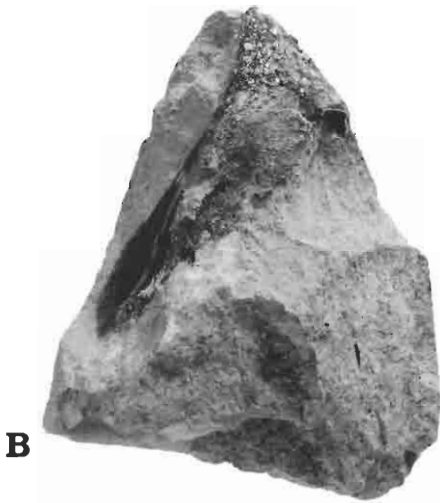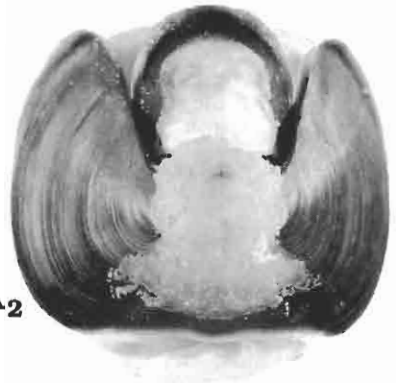
tionally, various degrees of abrasion, corrosion, distortion, and fragmentation make it impossible to assign distinct rhyncholith morphologies to the five species of *Germanonautilus* which are known from the middle European Muschelkalk. The entire morphology of the rhyncholith is affected by these variables.

The rhyncholiths can be described as follows: The apex may be sharp (MHI 1695, 1696; Fig. 8) or smoothly rounded (MHI 1699); the dorsal median ridge of the hood can be straight (MHI 1699) or strongly curved (MHI 1698); the posterior arcs of the hood may or may not extend ventrally (MHI 1698); the shaft is narrow and long in some specimens (MHI 1694, 1695, and 1698) and broad and short in others (MHI 1699); the angle between the crest of the hood and the ventral side varies considerably ($< 45°$ in MHI 1697; $> 100°$ in MHI 1694), similar to the angle between the shaft and the ventral side, etc. Each of these characters occurs in all possible combinations (Fig. 8). Hence, the subdivision in '*Recti*' and '*Curvati*' suggested by Till (1906) is not very useful. The anterior 'cutting' edge of the hood probably experienced strong shearing forces during food ingestion and therefore, variation in the shapes of both apex and hood can be interpreted as being caused by wear (Urlichs 1998: fig. 3.16). In combination with the primary variability, there are sometimes superimposed secondary alterations produced during transport.

Function of the *Germanonautilus* beak

According to the reconstructions by Rutte (1962) and Müller (1963a), the *Germanonautilus* rhyncholith and conchorhynch did not interact in the same manner as the beak-elements in Recent *Nautilus*. Instead, the mandibles rather worked like jaws, with the venter of the rhyncholith and the dorsum of the conchorhynch acting as crushing surfaces. Because of the sculptured dorsal morphology of the conchorhynch and of the venter of the rhyncholith, these elements were not suitable for occlusion: the grooves and ridges in the surfaces of conchorhynch and rhyncholith display a completely different and variable orientation (Figs. 5, 7). Additionally, both the very shallow elongate pits behind the strongly sculptured dorsum of the conchorhynch (MHI 1686 and 1687) and the variation in the shapes of both apex and hood of the rhyncholith are interpreted as traces of wear. This happened while the nautiloid was cutting its prey by shearing conchorhynch and rhyncholith against each other (Fig. 9). The ridges on the dorsal side of the conchorhynchs probably helped hold the prey in place so that it was cut instead of slipping in the interspace between conchorhynch and rhyncholith. Additionally, Recent *Nautilus* beaks show that the anterodorsal side of the rhyncholith interacts with the posterodorsal side of the conchorhynch (Saunders *et al.* 1978). However, the fossil beak elements have a massive calcitic part and in some specimens, the traces of wear are extensive. Apparently, *Germanonautilus* was able to crush rather thick shells and to easily cut the soft parts of its prey. Urlichs (1998: fig. 3.16) figured a rhyncholith where the anterior half of the hood was abraded. He in-

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Fig. 3. The beak and soft body of a preadult *Nautilus pompilius* Linné, 1758 and the lower mandible of *Germanonautilus* '*Conchorhynchus avirostris* (von Schlotheim, 1820)' from the Upper Muschelkalk of Baden-Württemberg with carbonised appendages. **A.** Anterior (**A₁**) and oblique lateral view (**A₂**) of a
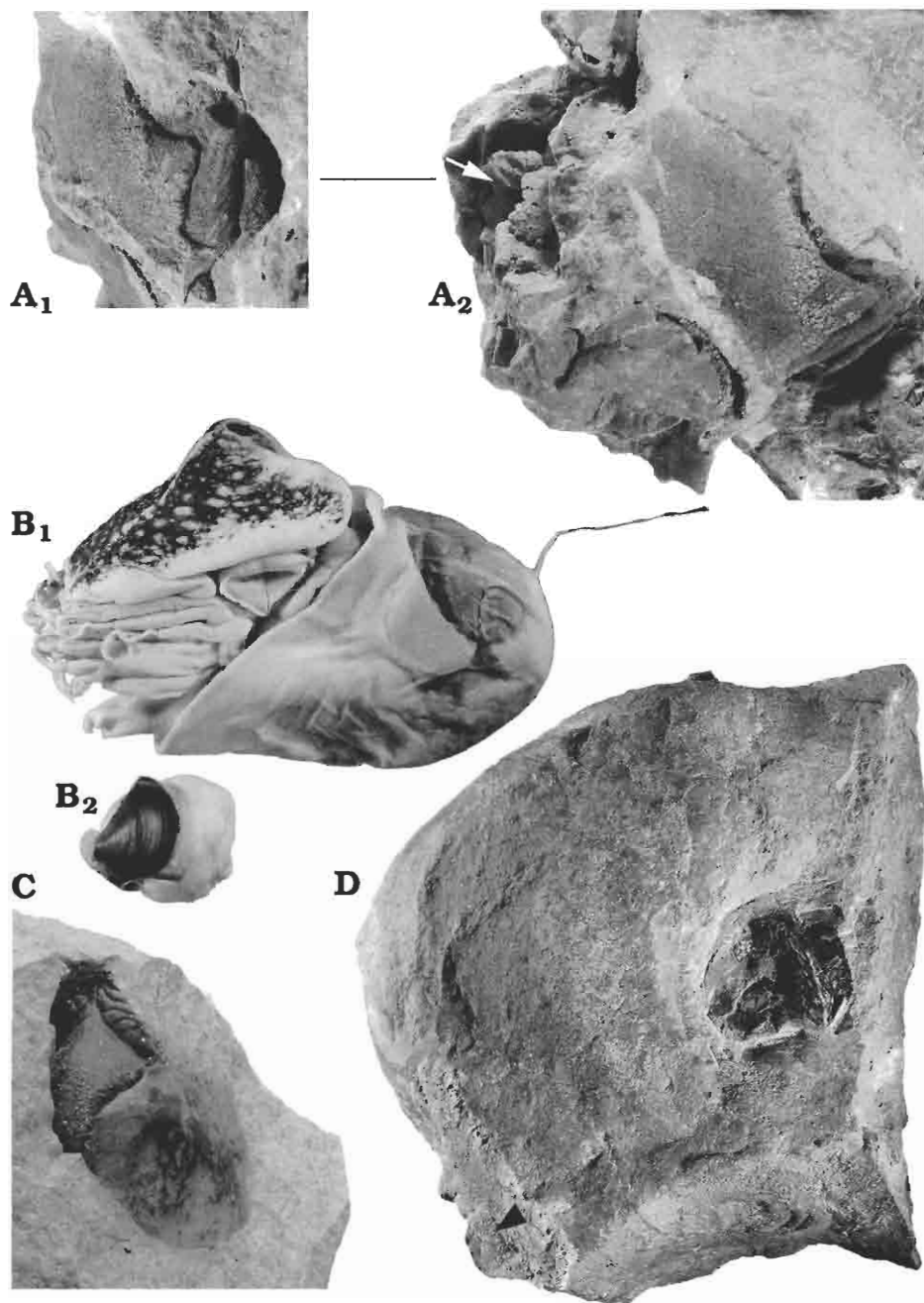
conchorhynch in the living chamber of *Germanonautilus* sp. (MHI 876); the arrow points to remains of the siphuncle, × 1; **B**. Soft parts of a preadult *N. pompilius* (SMNS Zla 30494), × 2. **B₁**. Lateral view of body. **B₂**. Lateral view of the beak with the buccal mass of the same specimen. **C**. Ventral view of an undistorted *C. avirostris* (SMNS 18113); note the sculptured mould of the calcitic part, × 1. **D**. Living chamber of *Germanonautilus* sp. with lower mandible (MHI 461); the arrow points to remains of the siphuncle. According to the proportions, the lower mandible probably belonged to a second animal, × 1.
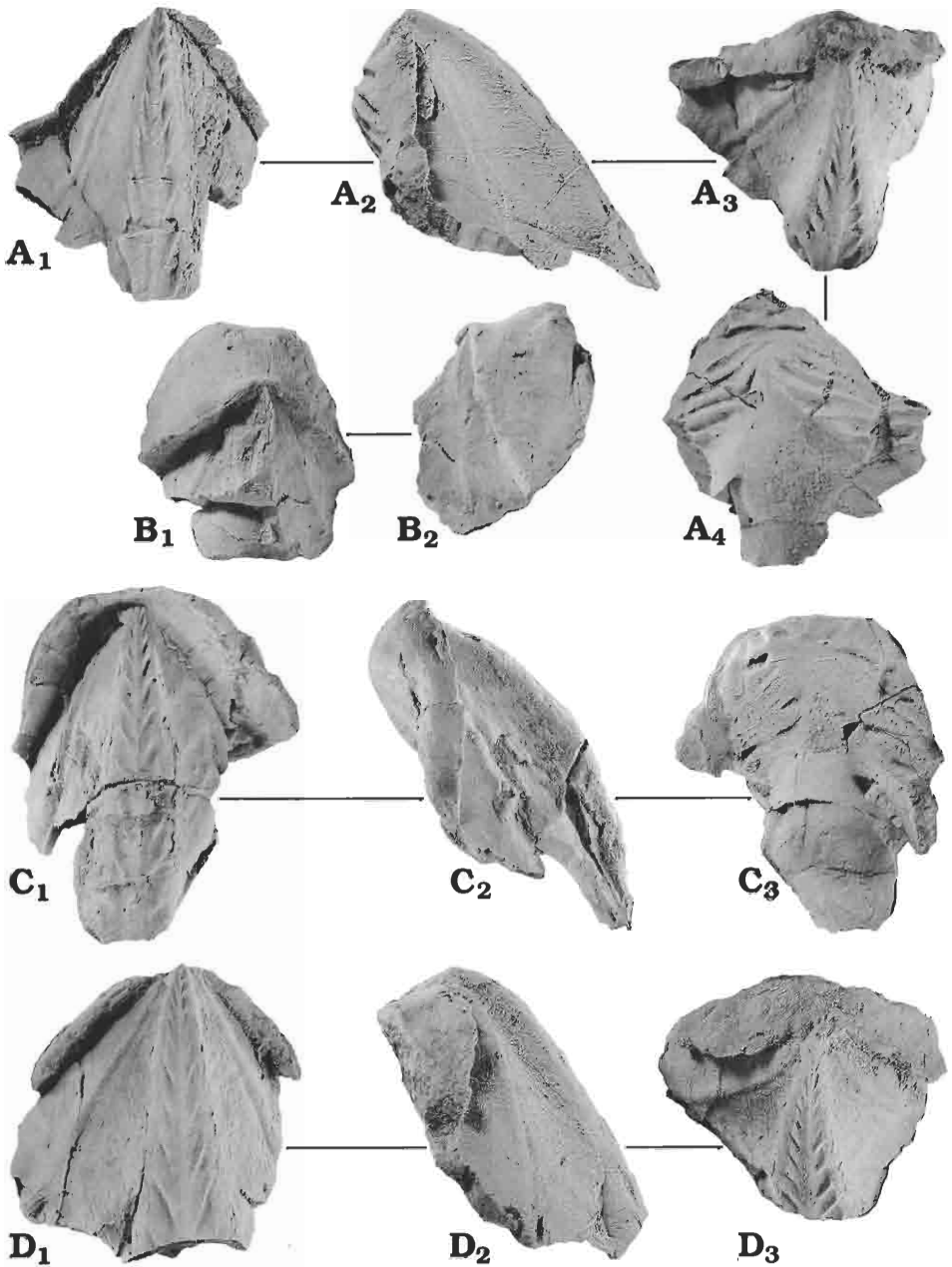
Fig. 4. Variability of conchorhynchs from the Upper Muschelkalk of Baden-Württemberg. **A**. MHI 1687 with the 'normal' conchorhynch morphology in ventral (A_1), lateral (A_2), anterior (A_3), and dorsal view (A_4). **B**. MHI 856 with unusually broad anterior fold in ventral (B_1) and lateral view (B_2). **C**. MHI 1686 with broad shape of the occlusal face and the fold in ventral (C_1), lateral (C_2), and dorsal view (C_3). **D**. MHI 1688 with broad anterior fold in ventral (D_1), lateral (D_2), and anterior view (D_3). All figures × 2.

Germanonautilus   *Nautilus pompilius*
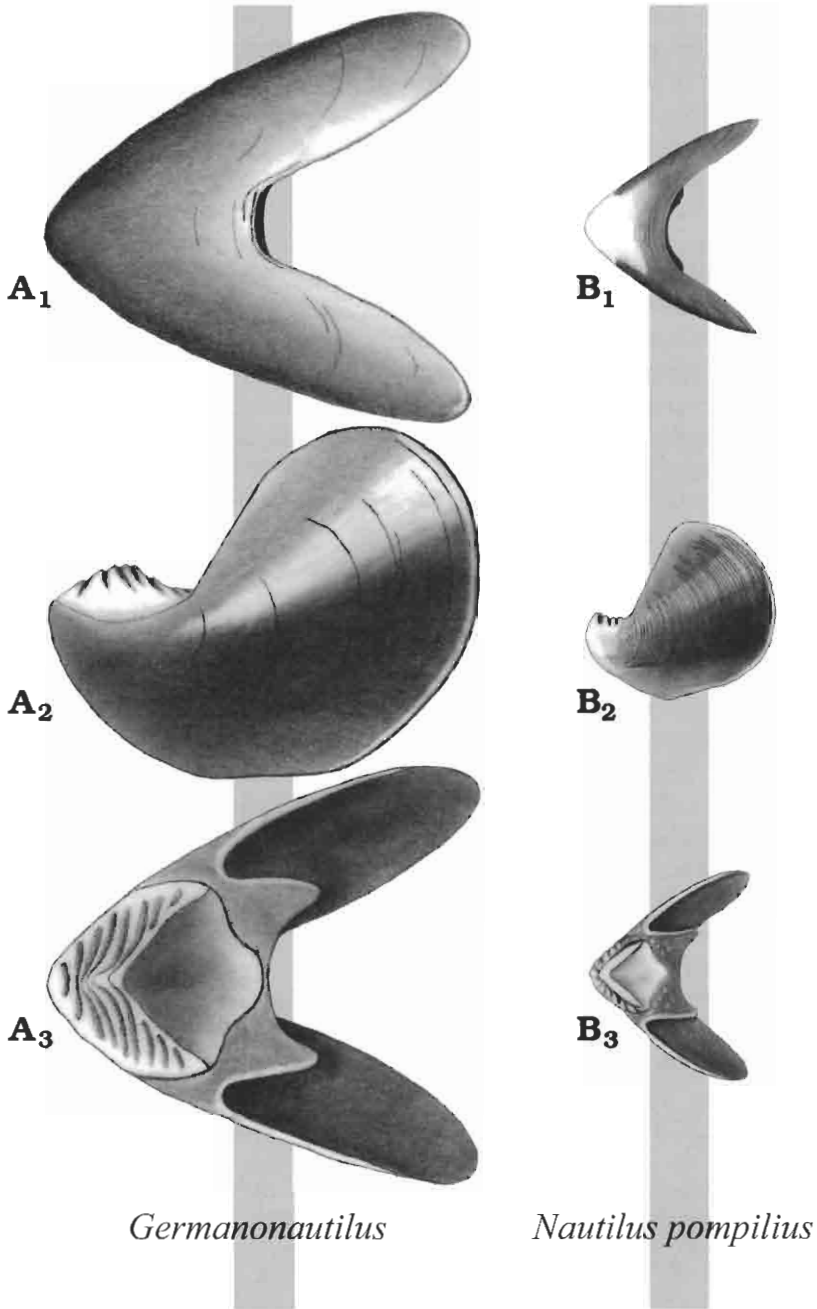
Fig. 5. Comparison of the lower mandibles of preadult *Nautilus pompilius* Linné, 1758 and the fossil *Germanonautilus* sp. The reconstruction of the lower mandible of *Germanonautilus* is based on the fossil specimens MHI 1516 and MHI 876 in combination with the Recent lower mandible of *N. pompilius*. All drawings display the lower mandibles in natural size. **A**. Ventral (A_1), lateral (A_2), and dorsal (A_3) views of the complete lower mandible of *Germanonautilus*. **B**. Ventral (B_1), lateral (B_2), and dorsal (B_3) views of the complete lower mandible of a preadult *N. pompilius*.

terpreted this specimen as an extreme example of wear caused by crushing the shells of prey animals. In this rhyncholith, weathering during transport can be excluded because the posterior end of the shaft is well preserved.

In *Nautilus pompilius*, a joint-like structure exists between the lower and the upper mandible (Fig. 2A$_3$, A$_4$). In the lower mandible, shallow furrows are located on the posterior labial surface of the inner lamella. This furrow carries the anterior edge of the strengthened connection between the inner and the outer lamella of the upper mandible. In the fossil material, only the latter structure can be seen. Nothing can be said about the strength nor about the function with certainty due to the lack of articulated material. Because of the other overall morphological similarities, the same kind of articulation of the *Germanonautilus* mandibles appears to be likely.

An identical function for the interaction of the lower and the upper mandibles of Triassic and Recent nautiloid beaks can be deduced from the morphology, the proportions, and from traces of wear. Even the mode of articulation was probably the same. In the Triassic material, the anterior ventral edge of the chitinous part of the upper mandible was probably carried by a furrow which was positioned at the posterior dorsal edge of the inner lamella of the lower mandible.

Taphonomy of the *Germanonautilus* mandibles

A comparison with the better known lower mandibles of *Germanonautilus* is helpful to understand the taphonomy of the fossil upper mandibles. Mundlos (1973) discussed the taphonomic constraints and possible modes of transport of the chitinous appendages of the Muschelkalk conchorhynchs. From the orientation of Triassic lower mandibles on the bedding planes (occlusal face down) he concluded that the appendages were flexible and behaved like a sail while being transported, and stabilised its position on the sea-floor. This conclusion is supported by specimen MHI 876, where one of the carbonised appendages is bent over the dorsal side of the calcitic part of the conchorhynch. In contrast, the more massive and dense calcitic portion acted as an anchor in the sediment. Because of this anchoring, each lower mandible was aligned on the sediment surface with its apex facing the current. Specimen MHI 1672 (Fig. 6) provides indications for a similar mode of transport and embedding of the upper mandible of *Germanonautilus*. The rhyncholith is embedded with its venter on the surface of a marly limestone in a small subcircular depression. The bedding planes in the depres-

Fig. 6. The beak of a preadult *Nautilus pompilius* Linné, 1758 (**A**) and the upper mandible of *Germanonautilus* '*Rhyncholithes hirundo* (Biguet, 1819)' (**B–E**) from the Upper Muschelkalk of Baden-Württemberg. All figures natural size, except **A** (× 2). **A**. The beak of *N. pompilius* (SMNS Zla 30494). **A$_1$**. Dorsal view of the upper mandible. **A$_2$**. Lateral view of the upper mandible. **A$_3$**. Ventral view of the upper mandible. **A$_4$**. Posterior view of the beak with the articulated mandibles (the arrows point at the joint). **B**. MHI 1517 in dorsal view with black carbonised parts; note the tongue-shaped appendage extending to the posterior side and the remains of the left duplicature directed anterolaterally. **C**. Ventral view of specimen SMNS 75226 preserved in claystone with the flattened posterior appendage. **D**. Dorsal view of SMNS 3173/11, figured by Quenstedt (1849: pl. 34: 15); note the remains of the posterior carbonised appendage which is encrusted by three specimens of *Placunopsis*. **E**. Specimen MHI 1672 in posterior (**E$_1$**) and dorsal (**E$_2$**) views; both anterior duplicatures of the carbonised appendages are preserved; the rhyncholith is positioned in a pot cast.
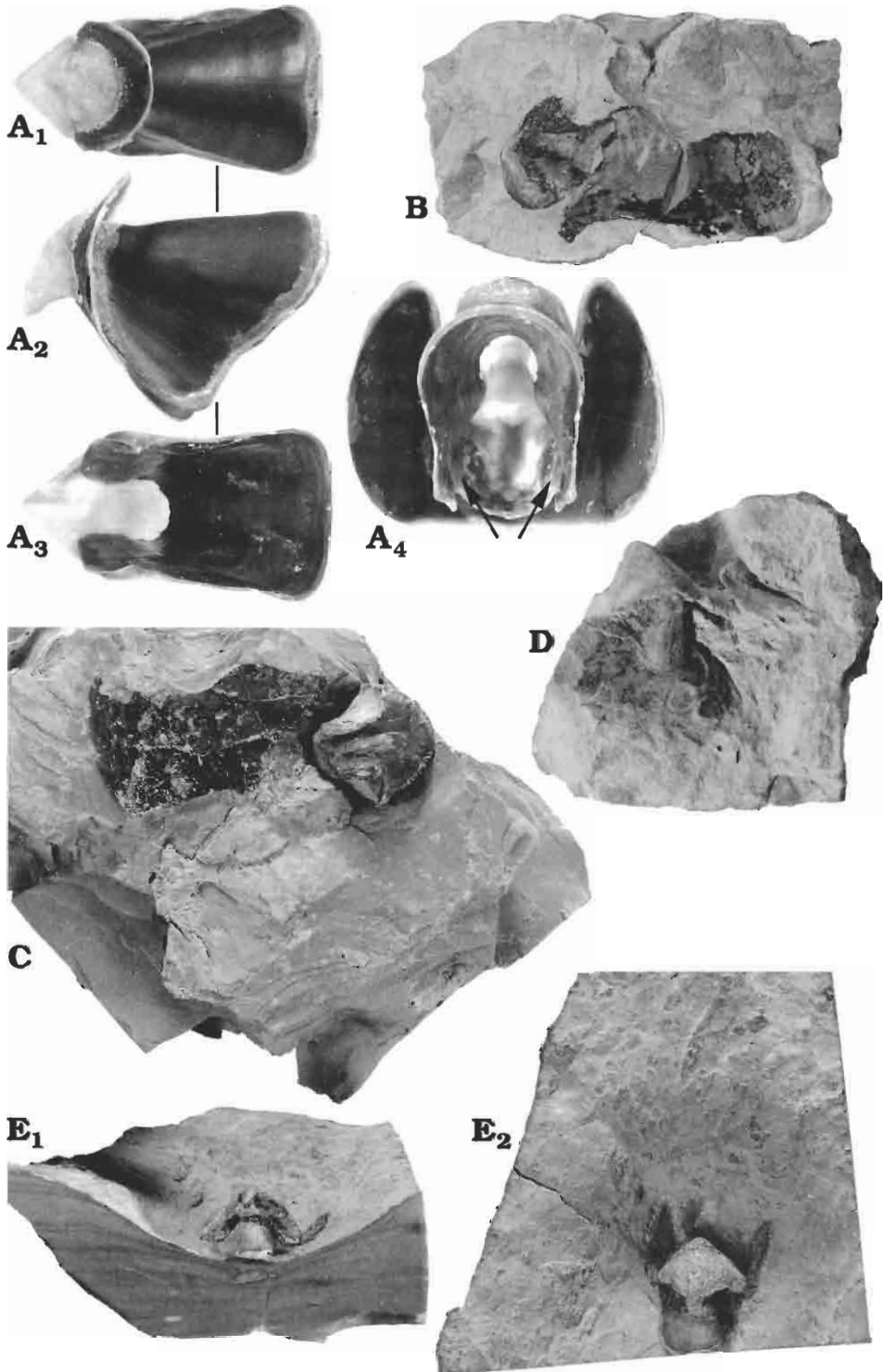
sion are bent downwards, wedging or thinning out towards the centre of the depression (Fig. 6). These facts and the presence of an obstacle in the centre (the upper mandible, creating eddies in a current and thus scouring) are indicators for a fossil scour mark or pot cast (compare Aigner 1978), probably created by a storm-induced current (Aigner 1985). However, the orientation of the carbonised parts in relation to the rhyncholith does not correspond with the position of the originally chitinous appendages during the nautiloid's life. It is likely that the distortion of the flexible chitinous parts began directly after settling on the sediment surface, before the rhyncholith was buried under the sediment (Fig. 10). This is supported by the fact that all rhyncholiths preserved with carbonised appendages are positioned with the ventral side resting on the bedding plane. In contrast, the isolated rhyncholiths were found in various positions, which is reflected in the distribution of encrustations.

As long as the chitinous lamellae of the fossil beak-elements were preserved, the mode of transport was uniform. In both cases, the heavier calcitic part 'anchored' in the sediment and the chitinous appendages were aligned subsequently. This way, the lower mandible usually came to rest on its dorsum whereas the upper mandible often landed on the venter. After the disintegration of the soft parts, the conchorhynch usually came to rest on its dorsum. The encrustations of rhyncholiths vary considerably and hence, no uniform orientation settling on the sea-floor occurred. This might be explained by re-working or by the lack of a stable position of the isolated calcitic part in a current.

Not only were the flexible appendages affected by taphonomic processes. From the numerous modes of preservation, alterations that occurred during transport can be in-ferred. In particular, the fragile posterior margin of the conchorhynchs easily broke off. During transport, the anterior margin was also worn. This wear pattern can be ex-plained by the fact that the anterior margin has a higher density/surface ratio and there-fore, it was more likely to hit the substrate first.

In 1845, Gottlieb Weissmann (a fossil collector from Stuttgart) was probably the first to collect a conchorhynch with three-dimensionally preserved carbonised append-ages (SMNS 1380/1, Fig. 2B; Max Urlichs personal communication 2000). Addi-tionally, this lower mandible displays a small specimen of the common Triassic en-crusting bivalve *Placunopsis ostracina* (von Schlotheim, 1820) attached to its right wing. Later, Müller (1963a) figured a lower mandible in which the organic appendages were populated by several specimens of the tube worm '*Spirorbis*' *valvata* Berger, 1859. Additionally, both '*Spirorbis*' and *Placunopsis* settled on the calcitic parts. In contrast to the rhyncholiths, the conchorhynchs had a more stable position with the dorsum facing the sediment surface. Consequently, the encrusting organisms mostly settled on the ventral side of the conchorhynchs.

Similarly, some Muschelkalk rhyncholiths are encrusted by either the tube worm '*Spirorbis*' *valvata* or juvenile *Placunopsis ostracina* (maximum 10 mm in diameter). Quenstedt (1849) was the first to illustrate a rhyncholith with remains of the carbo-nised appendages encrusted by *Placunopsis*. These epizoans were found both on the venter (MHI 1700 and 1053) and on the wings of the hood (MHI 1701) of the rhyncho-liths (Fig. 7).

Many specimens display traces of transport. Often, the thin posterior calcitic parts of the hood or of the shaft are missing and many specimens are rounded by abrasion caused by rolling or tumbling on the substrate. A striking phenomenon is the abun-
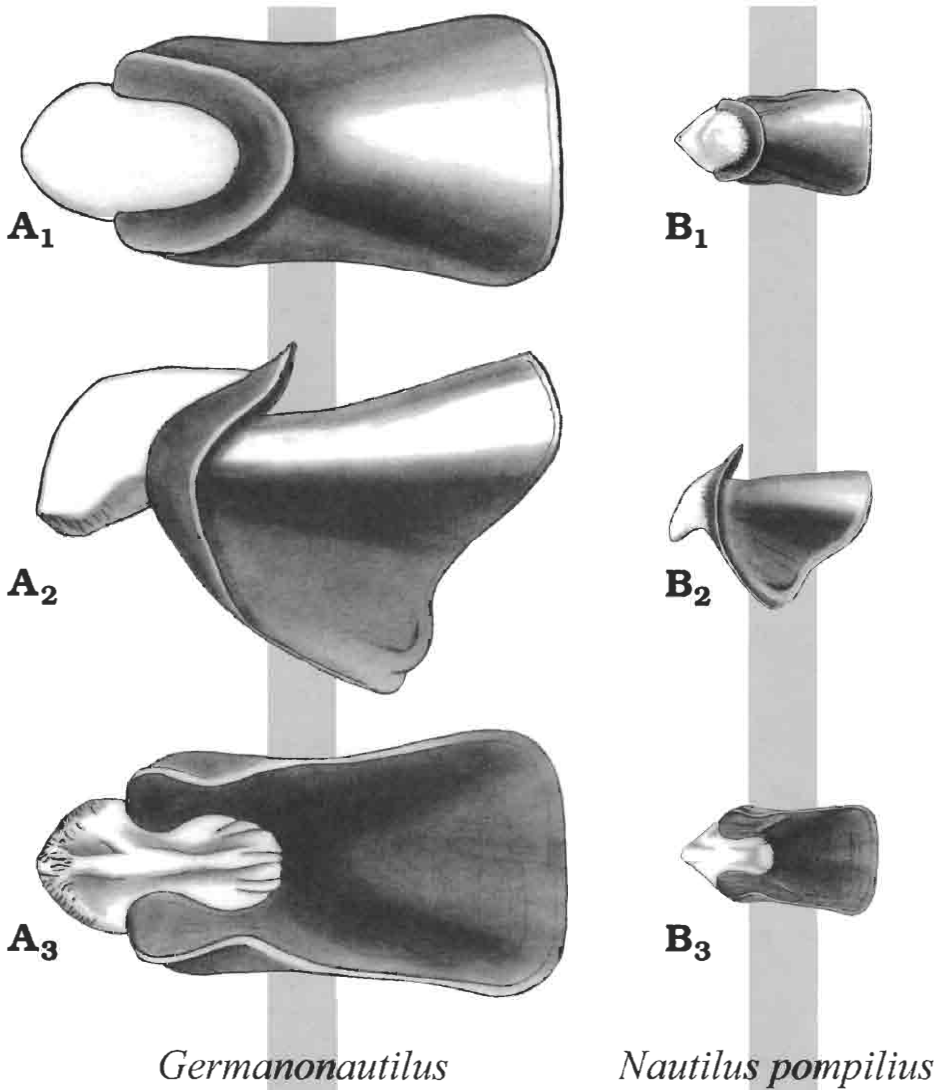
Fig. 7. Comparison of the upper mandibles of a preadult *Nautilus pompilius* Linné, 1758 and the Triassic *Germanonautilus* sp. The reconstruction of the upper mandible of *Germanonautilus* is based on the fossil rhyncholith specimens MHI 1517 and MHI 1672 in combination with the upper mandible of *N. pompilius*. All drawings display the mandibles in natural size. **A**. Complete mandible of *Germanonautilus* in dorsal (A_1), lateral (A_2), and ventral (A_3) views. **B**. Complete mandible of *N. pompilius* in dorsal (B_1), lateral (B_2), and ventral (B_3) views.

dance of rhyncholiths in a bonebed near the *Ceratites robustus / C. compressus* Zones boundary of the river Jagst valley near Crailsheim (Baden Württemberg, Germany). In this horizon, objects with a certain density, size, and high fossilisation potential caused by diagenetic resistance (rhyncholiths, reworked vertebrate and invertebrate remains, calcitic shell fragments) were concentrated forming this 'lag deposit' as a result of
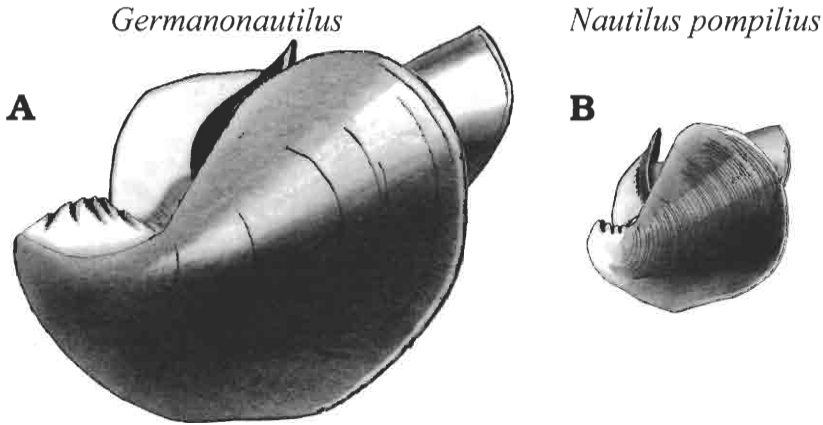
Germanonautilus   Nautilus pompilius
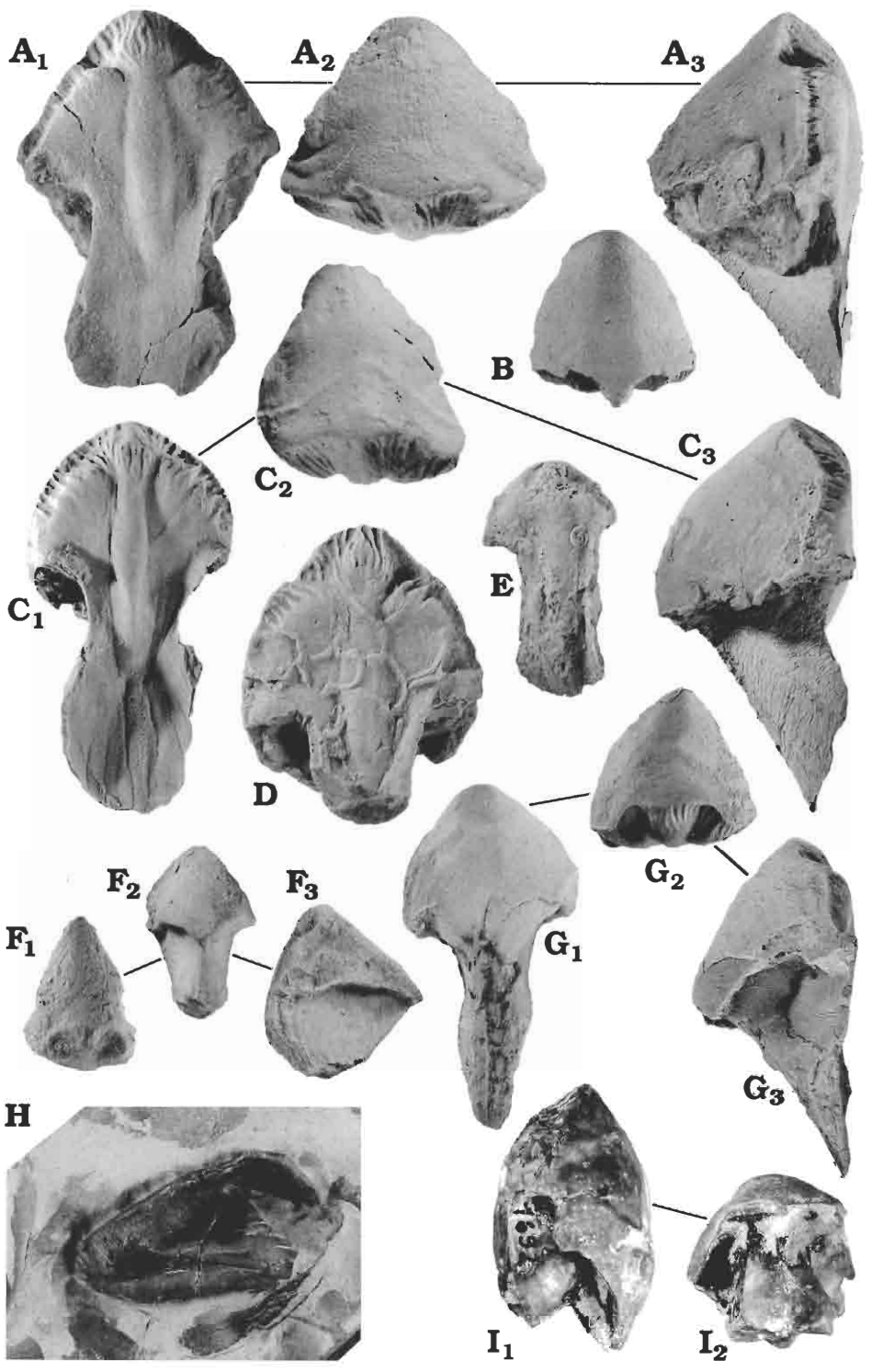
Fig. 9. Reconstruction of the beak apparatus (lateral view) of *Germanonautilus* (**A**) and the complete beak (lateral view) of a preadult *Nautilus pompilius* (**B**). All drawings display the mandibles in natural size.

winnowing. Remarkably, most of the rhyncholith specimens and the ceratite fragments which were found in this layer are worn.

In some rare cases, lower mandibles have been found within *Germanonautilus* conchs. In these cases, two interpretations are possible. Either both belonged to the same individual or the mandible belonged to a second animal and was washed into an empty conch. Only one of the specimens available for this study fulfils several criteria (listed below) which indicate that the conchorhynch and the *Germanonautilus* conch belonged to the same individual (Fig. 11). In this specimen, (1) the conchorhynch is preserved with the complete outer lamella, (2) it is similarly oriented within the living chamber as it was during the animal's lifetime, (3) the pit around it in combination with the pyrite and the wrinkles on the surface of the steinkern can be interpreted as traces of the buccal mass and possibly other soft tissue, and (4) the proportion of the conchorhynch in relation to the *Germanonautilus* conch (length of lower mandible/whorl height = 0.35) is similar to that in Recent *Nautilus* (length of lower mandible/whorl height = 0.34). In the other two specimens, the conchorhynch is also well preserved. However, in specimen MHI 876 the preservation of the conchorhynch is excellent and the alteration of the surrounding sediment might be caused by remains of soft tissue but the conch remains are insufficient to obtain reliable measurements. In specimen

Fig. 8. Variability of rhyncholiths from the Upper Muschelkalk of northern Baden Württemberg and some taphonomic features. All figures twice natural size. **A**. MHI 1699, a large and broad specimen in ventral (A_1), anterior (A_2), and lateral (A_3) views. **B**. MHI 1695 with sharp apex, anterior view. **C**. MHI 1698, large specimen with strong ventral median ridge and curved wings of the hood; ventral (C_1), anterior (C_2), and lateral (C_3) views. **D**. MHI 1053b with remains of at least 16 individuals of the encrusting bivalve *Placunopsis ostracina* (von Schlotheim, 1920) on the ventral side; ventral view. **E**. MHI 1700, with a '*Spirorbis*' specimen on the occlusal face at the transition from the hood to the shaft; ventral view. **F**. MHI 1697, a high and slender rhyncholith with a small angle between shaft and hood; in anterior (F_1), dorsal (F_2), and lateral (F_3) views. **G**. MHI 1694, a slender specimen with narrow shaft and a strongly curved shearing edge, in dorsal (G_1), anterior (G_2), and lateral (G_3) views. **H**. MHI 1690 in oblique ventrolateral view; note the posterior extension which is longer than the shaft. **I**. MHI 1692 in lateral (I_1) and posterior view (I_2) with carbonised remains between hood-extension and shaft.
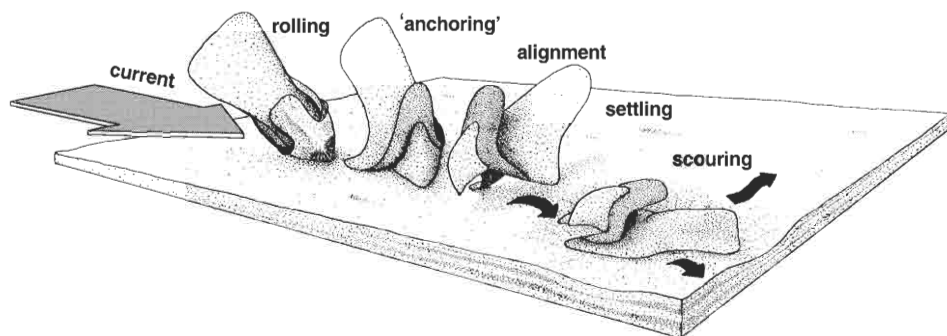
Fig. 10. Rolling upper mandible of *Germanonautilus* with chitinous 'wings' and subsequent alignment with the wings pointing in current direction after settling on the sediment surface. After the object came to a rest, eddies developed and scouring began. The gray arrow on the left indicates the current direction. Reconstruction according to Fig. 4 in Mundlos (1973) and specimen MHI 1672 (Fig. 4.).

MHI 461, the conchorhynch is complete but slightly distorted. Additionally, the proportions are different than those of *Nautilus* and the other specimens (length of lower mandible/ whorl height = 0.22). Hence, the conchorhynch probably belonged to a different animal and was transported into this living chamber.

Several processes probably caused the disintegration of the soft body and of the originally chitinous parts of the *Germanonautilus* mandibles. Microbes feeding on the organic matter and selective mechanical abrasion of the unmineralised chitinous appendages certainly played a role. There are no indications yet for digestion of the chitinous appendages while the mandibles of *Germanonautilus* were inside the digestive system of a hypothetical predator or scavenger because indications for predation on this nautiloid are lacking. Comparatively rapid embedding of some of the complete nautiloid mandibles (e.g., specimen MHI 876, Fig. 3A, appendix 2-1C) in the course of the deposition of a tempestitic layer probably accounts for their excellent preservation. Specimens of *Placunopsis* and '*Spirorbis*' encrusting on the originally chitinous appendages of the mandibles show that these parts remained intact for a certain time prior to embedding or disintegration. However, these *Placunopsis* valves do not exceed 10 mm in diameter which is significantly smaller than the largest specimens (ca. 40 mm in diameter). Hence, these specimens might have been killed at a juvenile stage when the *Germanonautilus* mandibles were covered by sediment.

Conclusions

Three-dimensionally preserved lower and upper mandibels of *Germanonautilus* enable the restoration of the beak of this coiled nautiloid. Differences in morphology between the fossil and the Recent lower mandible are the more elongate appendages and the absent or weaker sculpture on the wings of the lower mandible and the dorsal sculpture of its calcitic part. Furthermore, the conchs of *Germanonautilus* and the associated nautiloid beak-elements attained larger sizes than their Recent relatives. However, the originally chitinous appendages of the fossil upper mandible do not dis-
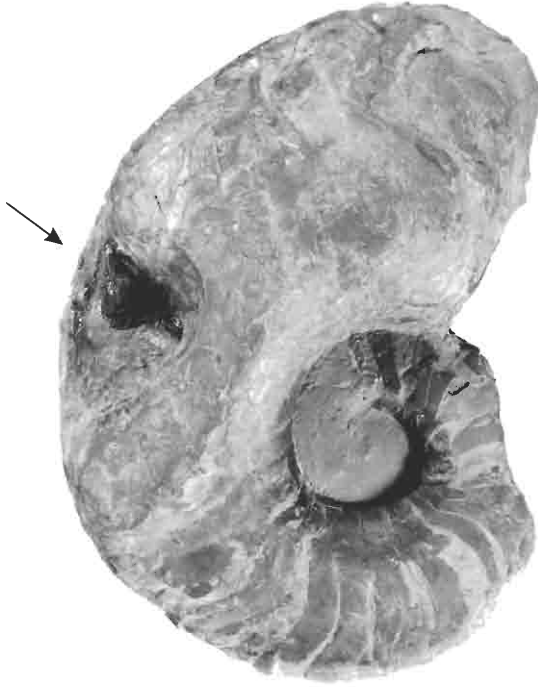
Fig. 11. Conch of *Germanonautilus bidorsatus* (von Schlotheim, 1820) with the complete lower mandible *in situ* (arrow) and with traces of soft tissue (coll. H. Donà, Markgröningen, Germany) from the Upper Muschelkalk of Baden-Württemberg. Half natural size.

play any significant differences to their Recent counterparts, although the rhyncoliths display a slightly more complicated sculpture. The association of '*Rhyncholithes hirundo*' and '*Conchorhynchus avirostris*' with the most common Muschelkalk-nautiloid, *Germanonautilus* is corroborated by discoveries of well-preserved lower mandibles inside *Germanonautilus* conchs. As a result of the study of 407 fossil nautiloid beak elements, a significant variability of the hard parts is evident. Consequently, the assignment of distinct mandible morphologies to the conch-based species of *Germanonautilus* is impossible.

The mode of transport of the complete upper mandible of *Germanonautilus* probably corresponds with the reconstruction suggested by Mundlos (1973) for its lower mandible. The light chitinous parts served as a sail and the heavier rhyncolith acted as an anchor in the sediment, causing alignment in a current. After disintegration of the appendages, the conchorhynchs usually settled with the ventral side up, whereas the isolated rhyncoliths can be found in various orientations.

Acknowledgements

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Morfologia funkcjonalna oraz tafonomia aparatów szczękowych środkowo-triasowych łodzików z południowych Niemiec

CHRISTIAN KLUG

Streszczenie

Zrekonstruowano aparat szczękowy łodzika z rodzaju *Germanonautilus* wykorzystując nowe materiały z górnego wapienia muszlowego (środkowy trias) północnej Wirtembergii (południowo-zachodnie Niemcy). Opisane elementy aparatu szczękowego *Germanonautilus*, tradycyjnie klasyfikowane jako „*Rhyncholites hirundo* (Biguet, 1819)" oraz „*Conchorhynchus avirostris* (von Schlotheim, 1820)", są dobrze zachowane, niekiedy ze zwęglonymi, pierwotnie chitynowymi wyrostkami. Trzy okazy dolnej szczęki znaleziono w komorze mieszkalnej *Germanonautilus*, co potwierdza powiązanie opisanych elementów aparatu szczękowego z tym rodzajem łodzika. W porównaniu ze współcześnie żyjącym łodzikiem z rodzaju *Nautilus*, elementy dolnej szczęki *Germanonautilus* mają bardziej wydłużone wyrostki i mniej wydatne urzeźbienie części pierwotnie organicznych, oraz urzeźbienie grzbietowej części elementów zmineralizowanych (konchorynchów) w postaci grzbiecików, a nie ząbków jak u *Nautilus*. Pierwotnie organiczne elementy górnej szczęki u *Germanonautilus* oraz współczesnego łodzika są bardzo podobne, natomiast części zmineralizowane górnych szczęk (ryncholity) *Germanonautilus* różnią się bardziej rozciągniętą pokrywą oraz wydatną rzeźbą części brzusznej w postaci grzbiecików (u *Nautilus* element ten jest gładki). W czasie pośmiertnego transportu pierwotnie organiczne i lżejsze elementy górnej szczęki *Germanonautilus* działały zapewne jak żagiel, natomiast cięższe elementy szczęki dolnej kotwiczyły się w osadzie, powodując doprądową orientacje skamieniałości. Po rozkładzie części organicznych, elementy aparatu ulegały rozproszeniu, jednak o ile ryncholity znajdowane są w osadzie w rozmaitym położeniu, to konchorynchy położone są najczęściej stroną brzuszną do góry.

Appendix 1

List of the localities and the stratigraphy of the studied *Conchorhynchus* and *Rhyncho-lithes* specimens. If not mentioned otherwise, the specimens derive from the Upper Muschelkalk.

Specimen	Ceratite zonation, lithological units	Quarry	Locality
Conchorhynchus			
MHI 309	Dolomitische Mergel γ	Dölker	Gottwollshausen/Schwäbisch Hall
MHI 461	*postspinosus,* Tonhorizont β	Hirsch	Schwäbisch Hall-Steinbach
MHI 856	*pulcher*	Neumayer	Mistlau/Kirchberg/Jagst
MHI 876	*nodosus-weyeri,* Seestern-Bank	Leyh	Bölgental/Crailsheim
MHI 943	*robustus,* Astarte-Bank		Altenheerse/Willebadessen
MHI 1516	*atavus,* Trochitenbank 3		Wollmershausen/Crailsheim
MHI 1686	*semipartitus*	Schneider	Ummenhofen
MHI 1687	*weyeri-semipartitus*	Trender	Nitzenhausen
MHI 1688	*weyeri-semipartitus*	Trender	Nitzenhausen
MHI 1707	*buchi*-Schichten, layer 1; lower Muschelkalk	Ferenc	Schneidemühle; Bödigheim/Buchen
SMNS 1380/1	Hohenlohe-Fm.		Crailsheim
SMNS 18113	*dorsoplanus,* Trigonodus-Dolomit		Stuttgart-Münster
coll. Doná	*atavus,* Haßmersheimer M. 3	Zimmermann	Roßwag, Vaihingen/Enz
Rhyncholithes			
MHI 731	*Encrinus*-Platten	Leyh	Wollmershausen/Crailsheim
MHI 1040	*weyeri-semipartitus*	Schumann	Eschenau/Vellberg
MHI 1096	*nodosus,* Bank d. kleinen Terebrateln	Schneider	Ummenhofen
MHI 1517	*robustus-compressus*	Schön & Hippelein	Satteldorf-Neidenfels/Crailsheim
MHI 1672	*postspinosus* Tonhorizont b	Feldner	Barenhaldenmühle/Satteldorf
MHI 1689	?	Kleinknecht	Rüblingen
MHI 1690	*enodis/laevigatus*	Trender	Nitzenhausen
MHI 1691	*nodosus*	Manger	Baldersheim/Aub
MHI 1692	*nodosus,* Tonhorizont ζ		road Eltershofen-Gelbingen, Schwäbisch Hall
MHI 1693	*nodosus,* Tonhorizont ζ	SHB	Berlichingen
MHI 1694	*nodosus*	Feldner	Barenhaldenmühle/Satteldorf
MHI 1695	*weyeri-semipartitus*	Schön & Hippelein	Satteldorf-Neidenfels/Crailsheim
MHI 1696	*nodosus*	Feldner	Barenhaldenmühle/Satteldorf
MHI 1697	*dorsoplanus-semipart.*	Schneider	Ummenhofen
SMNS 3173/11	Hohenlohe-Fm.		Crailsheim
SMNS 75226	*atavus,* Haßmersheimer M. 3	Ehrmann	Remseck-Neckarrems
SMNS 75227	? Hohenlohe-Fm.	Kleinknecht	Rüblingen

Appendix 2

Descriptions of the specimens.

1. Lower mandible with with soft parts:

1A. Specimen MHI 1516 (collected and identified. by S. Düll, Ilshofen-Buch, Fig. 2C) is a lower mandible of a rather large animal, it is positioned on its occlusal face and its conchorhynch measures 33 mm in length; the carbonised wings are 44 mm long and 48 mm wide. The complete and uncrushed conchorhynch is largely covered by the coalified parts, except for the ventral median ridge and adjacent anterior areas. As in all conchorhynch specimens, the characteristic chevron pattern of biserial grooves on the median ridge and the anterior fold of the occlusal surface are exposed. Remarkably, the carbonic appendages are almost only dorsoventrally compressed. Small fissures in their posterior margin are traces of this deformation. Their outline resembles an arrowhead, with a shallow posterior depression which reaches the posterior end of the median ridge of the conchorhynch. Between the rounded posterior tips of the wings and the median ridge, the posterior margin is gently curved. The interspace between the calcitic and the coalified part is filled with sediment, except for the area ventral to the median ridge. Most other 'Conchorhynchus avirostris' specimens published previously do not display such a well preserved outline of the appendages (e.g. Müller 1963a). However, the shape is still altered, probably by predepositional deformation and during compaction of the sediment and hence, *Nautilus*-beaks had additionally to be used for the reconstruction (Fig. 9).

1B. In 1845, Weissmann discovered the complete specimen SMNS 1380/1 (Fig. 2B). It is three-dimensionally preserved and only slightly dorsoventrally compressed by compaction. Both of the carbonised wings display wrinkles which run parallel to the bedding-plane and therefore, they were probably formed during this deformation. Because of dolomitisation, the calcitic part is poorly preserved. However, the outline and arrangement of the appendages can be studied. They are tongue-shaped and the posterior edge reaches the posterior end of the median ridge of the conchorhynch. The conchorhynch is 18 mm long and the entire specimen with the appendages measures 38 mm. Remarkably, a *Placunopsis* specimen with a diameter of 10 mm grew on the right appendage.

1C. Similar to the first two specimens (MHI 1516, SMNS 1380/1), the lower mandible SMNS 18113 (Fig. 3C) is preserved with an insignificantly deformed carbonised appendage. It is slightly dolomitised and the calcitic part is preserved as a mould. The appendage displays a tongue-shaped outline with a more strongly curved posterior edge. It is 29 mm high and displays an irregular surface. Both of the sediment-filled pockets (the interspace between the two parts of the duplicature) are preserved.

1D. The specimen MHI 876 (Fig. 3A) is especially remarkable in two respects: Firstly, the carbonised appendages are three-dimensionally preserved (but only the right part is undeformed) and secondly, the specimen lies in the living chamber of a *Germanonautilus* conch. It was discovered in the 'Seesternbank' (= starfish-bed, *nodosus*- to *weyeri* Zone). This coarse bioclastic limestone was probably deposited during several storm-events, the last of which quickly covered all fossils with sediments. This is corroborated by the presence of articulated *Trichasteropsis weissmanni* (Münster 1843) skeletons, and can be used as an explanation for the unusual preservation of the conchorhynch *in situ*.

Sagitally, the conchorhynch measures 29 mm but the apex is slightly damaged. It is 16 mm wide and 12 mm high. Only the right wing of the two carbonised appendages is completely visible. In its maximal dorsolateral extension it measures 33 mm and is 17 mm wide. The appendage extends only 3 mm behind the posterior margin of the calcitic part. Anteriorly, the margin of the right wing is gently curved backwards whereas the posterior margin displays an irregular outline. A triangular sediment-filled pocket in between the carbonic and the calcitic parts is preserved on both sides of the median ridge. In contrast to the right part, only this triangular pocket of the left appendage can be seen. Directly dorsal to the conchorhynch, a second carbonic layer can be seen in the broken specimen. It is connected anteriorly with the triangular pocket and thus, it is interpreted as the left appendage which was dorsally bent over the conchorhynch towards the right wing. Again, this indicates the original flexibility of these organic parts (compare with 1A., MHI 1672). Only parts of the umbilical wall, the siphuncle and some septa are preserved of the *Germanonautilus* conch. However, the minimum apertural height of this specimen measured more than 60 mm. Around the beak element, the sediment is ochre coloured, possibly a result of dolomitisation.

1E. A well preserved conch of *Germanonautilus bidorsatus* (von Schlotheim, 1820) with the complete lower mandible *in situ* (coll. H. Donà, Markgröningen; Fig. 11) displays several remarkable features: The conchorhynch is obliquely oriented with the median ventral ridge directed to the left ventrolateral edge of the conch. It is positioned in a deep pit on the left ventrolateral edge, 35 mm in front of the last septum and approximately 95 mm behind the aperture. This pit has an irregular outline and is about 20 mm deep. On the margins of the pit, traces of pressure solution and thin layers of pyrite can be seen. Additionally, the surface of the steinkern displays small wrinkles anterior to the pit.

1F. A large conchorhynch preserved as a mould with incomplete remains of the outer lamella (MHI 943).

1G. On both sides of the well preserved conchorhynch of the lower mandible MHI 309, the sediment filled pockets of the lateral appendages are visible. Because of the fine grained marly matrix, details of the surface structure of the appendages can be seen. They are finely wrinkled parallel to the median ridge. Towards the anterolateral folds, these wrinkles turn towards the anterolateral edges of the calcitic part. There, the wrinkles run parallel to these edges.

1H. A small lower mandible in a large fragment of a *Germanonautilus* living chamber (MHI 461, Fig. 3D).

1J. Specimen MHI 1707 is the only record of a conchorhynch from the lower Muschelkalk available for this study. It is only moderately well preserved with carbonised remains of the outer lamella covering the hard parts. There is no evidence of a significant morphological difference to the younger conchorhynchs.

2. New records of '*Conchorhynchus avirostris*' which display the variable morphology of the mineralised parts (Fig. 4): MHI 856; MHI 1686; MHI 1687; MHI 1688:

The medium-sized conchorhynch MHI 856 (Fig. 4B) shows the same shape as the specimen figured by Rutte (1962). The marginal fold of the conchorhynch is seven millimetres thick at the apex and it wedges out posteriorly. Anterolaterally, the fold is gently concave with an irregular pattern of faint dorsoventral ridges.

3. Four specimens of '*Rhyncholithes hirundo*' with carbonised parts preserved *in situ* are available for this study (Fig. 6):

3A. Specimen MHI 1672 (Fig. 6E) was found by the author. It was cut and polished at the posterior end of the rhyncholith to clarify sedimentological aspects. The carbonised parts are partially preserved. Two carbonised 'processes' are symmetrically arranged anterior to the rhyncholith. They have an elongate subtriangular outline (length: ca. 12 mm) and the posterior part appears to be attached to the shaft, directly posterior to the hood.

3B. With its carbonised appendage, specimen MHI 1517 (Fig. 6B) measures 65 mm in length. It is laterally distorted and slightly longitudinally compressed. The originally chitinous appendage is flattened and measures about 30 mm from the posterior end of the rhyncholith. It covers the major part of the rhyncholith shaft. The right side of this appendage is incomplete but its overall outline is subrectangular. An incomplete projection of carbonised matter is directed anteriorly.

3C. SMNS 75226 was collected by Warth in 1979 (Fig. 6C). As with specimen MHI 1517, this upper mandible displays most of the posterior appendage. From the rhyncholith itself, the posterior part of the shaft is missing. However, the length of the calcitic part can be deduced from the mould. It probably measured 23 mm. With the appendage, this upper mandible is 48 mm long.

3D. Remarkably, specimen SMNS 3173/11 (Fig. 6D) was illustrated by Quenstedt (1849). It displays incomplete and flattened remains of the left carbonised wing and the posterior appendage. To my knowledge, this specimen represents the first record of a upper mandible with remains of the carbonised parts. Additionally, four incomplete valves of *Placunopsis* encrusted the posterior appendage.

4. Eight specimens of '*Rhyncholithes hirundo*' with remains of the posterior process of the hood were available for this study (Fig. 7): MHI 731; MHI 1040; MHI 1096; MHI 1689; MHI 1690; MHI 1691; MHI 1692; MHI 1693:

The rhyncholith MHI 1690 (Fig. 7H) rests on the right anterodorsal side of the hood on a slab of bivalve coquina. In contrast to the other specimens, the exposed flank displays an almost complete posterolateral margin of the posterior process of the hood. This process is a little longer than the shaft and runs subparallel to the occlusal face of the rhyncholith. Its posterior ventrolateral margin is slightly dorsally curved. Beginning at the posteroventral corner of the hood, it runs posterodorsally at an angle of approximately 40° to the ventral side of the rhyncholith.

5. Seven specimens of '*Rhyncholithes hirundo*' which display the variable morphology of the mineralised parts (Fig. 8): MHI 73; MHI 1694; MHI 1695; MHI 1696; MHI 1697; MHI 1698; MHI 1699.

6. Three specimens of '*Rhyncholithes hirundo*' with special taphonomical features (Fig. 7):

Two specimens display both traces of transport and are encrusted by the annelid worm tubes '*Spirorbis*' *valvata*. In the rhyncholith MHI 1700 (Fig. 7E), the '*Spirorbis*' tube is attached to the occlusal face at the transition from the hood to the shaft. In specimen MHI 1701 the '*Spirorbis*' animals lived near the mid of the right posterior margin of the hood. In both rhyncholiths, the anterior edge of the hood is rounded by transport, in contrast to the posterior margin of the shaft, which is largely intact. On the occlusal face of the rhyncholith

MHI 1053b, remains of at least 16 individuals of *Placunopsis ostracina* (von Schlotheim, 1920) are visible (Fig. 7D).

Appendix 3

Measurements of the calcitic parts in mm.

Nr.	length	width	height
conchorhynchs			
MHI 1516	33		
SMNS 1380/1	18	? 19	? 11
SMNS 18113	22		16
MHI 876	29	? 16	12
MHI 943	? 12	? 11	? 10
MHI 309	13	**12**	? 8
rhyncholiths			
MHI 1672	19	14	12
MHI 1517	ca. 17	ca. 16	
SMNS 75226	? 23	? 17	? 13
SMNS 3173/11	20	? 12	? 11
MHI 731		**13**	14
MHI 1689	**22**	**? 12**	14
MHI 1690	**18**		
MHI 1691	**26**	**14**	17
MHI 1692	20	13	13
MHI 1693	19	10	11
MHI 1096		**13**	**14**
MHI 1040	14	**9**	**11**
MHI 1694	26	13	13
MHI 1695	21	11	11
MHI 1696	? 20	13	12
MHI 1697	? 17	9	12
MHI 1698	29	16	14
MHI 1699	29	20	16
MHI 73	4.7	2.7	2.2
MHI 1700	19	11	10
MHI 1701	24	12	11
MHI 1053b	? 25	18	14