

First three-dimensionally preserved *in situ* record of an aptychophoran ammonite jaw apparatus in the Jurassic and discussion of the function of aptychi

Günter Schweigert

Abstract: A unique specimen of the microconch ammonite *Lingulaticeras planulatum* Berckhemer in Ziegler, 1958 comes from a tempestite bed within the Upper Jurassic lithographic limestones of Schamhaupten in Franconia (Painten Formation, uppermost Kimmeridgian). The shell is unique because it retains the complete jaw apparatus in the body chamber. The articulation of the Lamellaptychus and the corresponding upper beak are well preserved. The function of the aptychus is discussed in general, and an operculum function is thought to be unlikely. The formation of strongly calcified aptychi in aspidoceratids and some oppeliid ammonoids is interpreted as an added ballast weight to stabilize the conch for swimming in the water column.

Keywords: Ammonites, aptychus, preservation, functional morphology, Upper Jurassic, lithographic limestones, Franconia, Germany

Zusammenfassung: Ein einzigartig erhaltenes Exemplar des mikroconchen Ammoniten *Lingulaticeras planulatum* Berckhemer in Ziegler, 1958 aus einer Tempestitlage des oberjurassischen Plattenkalks von Schamhaupten in Franken (Painten-Formation, oberstes Kimmeridgium) enthält noch den vollständigen Kieferapparat in seiner Wohnkammer. Es zeigt die perfekte Artikulation des Lamellaptychus mit dem dazugehörigen Oberkiefer. Die Funktion des Aptychus wird allgemein diskutiert und eine Deckelfunktion für unwahrscheinlich gehalten. Die Ausbildung stark verkalkter Aptychen wie in Aspidoceraten und manchen Oppeliiden wird als zusätzliches Tariergewicht gedeutet, um das Gehäuse in starker bewegtem Wasser zu stabilisieren.

Schlüsselwörter: Ammoniten, Aptychus, Erhaltung, Plattenkalke, Funktionsmorphologie, Oberjura, Franken, Deutschland

Address of the author: Dr. Günter Schweigert, Staatliches Museum für Naturkunde, Rosenstein 1, D-70191 Stuttgart. E-mail: schweigert.smns@naturkundemuseum-bw.de

Exceptional preservation of ammonites in Upper Jurassic plattenkalks

Ammonites are one of the most common invertebrate fossils in many of the famous fossil *Lagerstätten* of the "Solnhofen type" in the Upper Jurassic of southern Germany (Fig. 1). Due to their mostly compressed preservation, which makes them less attractive for many researchers, they have contributed little to ammonite research. However, as recently stated by Keupp (2007), they have an enormous potential for increasing our understanding of ammonite palaeobiology and even anatomy. And, because the ammonites evolved rapidly in the Jurassic, they provide a mechanism for precise age determinations for the various ammonite-bearing plattenkalk sites (Schweigert 2007).

The preservation potential of ammonite shells and other ammonite remains depend on early diagenetic processes. These diagenetic processes differ within the various laminated limestones often summarized as the "Solnhofen-type". In some localities the shells are barely discernible or even are completely dissolved (Zandt, Ettlting). In contrast, the classic plattenkalks or lithographic limestones of Solnhofen and Eichstätt show a typical diagenetic history which was studied in detail by Seilacher et al. (1976). *In situ* finds of shells with the corresponding aptychus occur frequently (e.g. Oppel 1863, Quenstedt 1887-1888, Rothpletz 1909, Schweigert 1998, Schweigert & Dietl 1999, 2001). The coupling of ammonite genera with the corresponding aptychus type provides important data for systematic placement in addition to important details of the shell form, ornamentation, suture line, ontogeny, growth parameters, and sexual dimorphism (e.g. Engeser & Keupp 2002, Parent et al. 2008, Schweigert & Dietl 2008).

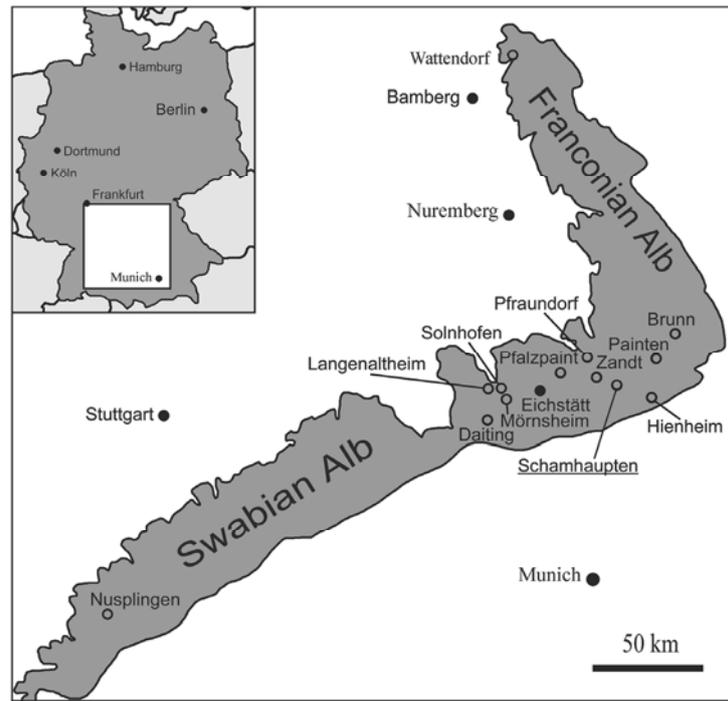


Fig. 1: Location of Schamhaupten, the finding site of the studied ammonite and other important plattenkalk localities in S Germany (modified from Fürsich et al. 2007).

Moreover, stomach or crop contents within the body chambers of ammonites allow interesting insights to their lifestyles (e.g. Schweigert & Dietl 1999, 2001, Keupp 2000, 2007). Further information comes from various invertebrates that incrust some ammonite shells. A well-documented example is the polyphasic overgrowth of barnacles on small aspidoceratids in the upper Kimmeridgian plattenkalks of Brunn in eastern Bavaria, which happened during the lifetime of the ammonites (Keupp et al. 1999). The Brunn locality is also the only one where small phosphatic granules occur in the body chamber; these granules were interpreted as nephroliths (Keupp et al. 1999). Much more common in many lithographic limestones and plattenkalks are small oysters of the genus *Liostrea*, which encrusted shells of living and dead ammonites (Scholz et al. 2008).

In the Late Jurassic fossil *Lagerstätten*, there are only a few examples of preservation of the originally organic, uncalcified upper jaws are known (Keupp 2007). Radulae have not yet been discovered in ammonites from the Solnhofen-type plattenkalks, but they are known from other localities and ages (Nixon in Landman et al. 1996, Kennedy et al. 2002). In general, complete beak apparatuses have been recorded rarely in ammonites (e.g. Tanabe & Fukuda 1987, Riegraf & Schmitt-Riegraf 1995, Nixon 1996, Tanabe & Landman 2002: table 1 and references therein). In the bituminous upper Kimmeridgian plattenkalks of Nusplingen, Germany, isolated upper jaws occur frequently. In several cases the upper jaws were found in close context to the ammonite shells or even within the body chamber. In this latter situation the jaws were not in life position due to the rapid onset of decay of the soft body prior to burial of the ammonite shell. A similar example is recorded from the lower Tithonian plattenkalks of Daiting in Franconia (Germany): The latter occurrence is a strongly compressed *Fontannesella prolithographica* (Fontannes), which shows not only its Lamellaptychus, but also an imprint of the corresponding upper jaw (Fig. 2). The upper jaw of this specimen preserves no organic matter because of the oxidization of the rock by weathering processes. Interestingly, the upper jaw appears to be much shorter than the neighbouring Lamellaptychus, but the possibility cannot be excluded that distal parts of the upper jaw remained on the counterpart, which is not available for study. The same observation was made in a *Metahaploceras* sp. from Nusplingen (Fig. 3) where both part and counterpart were recovered. The two finds together suggest that a relatively short upper jaw is indeed characteristic for at least some macroconch oppeliids.

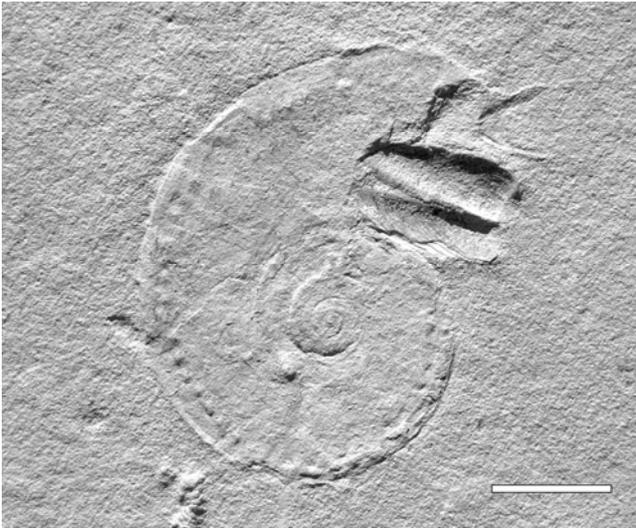


Fig. 2: *Fontannesella prolithographica* (Fontannes), a strongly compressed specimen with its corresponding Lamellaptychus and upper jaw in close context. Daiting, Franconia, S Germany. Upper Jurassic, Mörnsheim Formation, lower Tithonian, Hybonotum Zone, Moernsheimensis Subzone, *moernsheimensis* horizon. SMNS 66067. - Scale equals 2 cm.

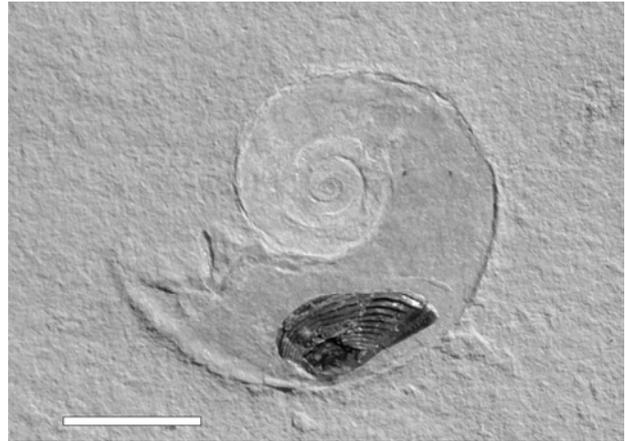


Fig. 3: *Metahaploceras* sp., with phragmocone in whitish phosphatic periostracum preservation, Lamellaptychus in "normal position" and upper jaw in front of the aperture. Nusplingen, Swabia, SW Germany. Upper Jurassic, Nusplingen Lithographic Limestones (bed C in section of Dietl et al. 1998), upper Kimmeridgian, Beckeri Zone, Ulmense Subzone, *hoelderi* horizon. SMNS 63998. - Scale equals 2 cm.

An outstanding locality: Schamhaupten

Besides the long-known site Nusplingen in Swabia, Germany (Dietl & Schweigert 2001, 2004) and the classical outcrops in the vicinity of Solnhofen and Eichstätt in Germany (Barthel 1978; Barthel et al. 1999; Frickhinger 1994, 1999), two new localities were recently opened and excavated scientifically at Brunn (Röper et al. 1996) and Schamhaupten (Viohl & Zapp 2006, 2007, Wattendorf: Fürsich et al. 2007); some excavations are still ongoing. Recently, the site of Schamhaupten (Fig. 1) has become famous for the finding of the unique theropod dinosaur *Juravenator starki* (Göhlich & Chiappe 2006, Göhlich et al. 2006). The stratigraphic age of this site is situated around the preliminary Kimmeridgian/Tithonian boundary, which has not been formally ratified by international agreement (Zeiss et al. 2005). Even though the ammonite fauna from Schamhaupten has not yet been described in detail, typical elements of the uppermost Kimmeridgian *rebouletianum* faunal horizon are known to occur, including *Neochetoceras rebouletianum* (Fontannes), *Sutneria bracheri* Berckhemer, *Hybonotoceras kamicense* (Schopen), and *Lingulaticeras planulatum* Berckhemer in Ziegler. Other taxa are mentioned in a preliminary faunal list (Viohl & Zapp 2006). The *rebouletianum* horizon is also recorded from Swabia and from south-eastern France (Schweigert 2007).

The material from the excavations in Schamhaupten is stored in the collections of the Jura-Museum in Eichstätt. The specimen of the microconch of the ammonite *Lingulaticeras planulatum*, which is the focus of this study, is part of those collections.

Institutional acronyms: JME = Jura-Museum Eichstätt, Germany; SMNS = Staatliches Museum für Naturkunde Stuttgart, Germany.

Systematic palaeontology

Superfamily Haploceratoidea Zittel, 1884

Family Oppeliidae Douvillé, 1890

Subfamily Taramelliceratinae Spath, 1928

Genus *Lingulaticeras* Ziegler, 1958

Type species: *Ammonites nudatus* Oppel, 1858.

Remarks: The genus *Lingulaticeras* was originally erected by Ziegler (1958) as a subgenus of *Glochiceras* Hyatt. The genus *Glochiceras* in this broad sense contains various microconch oppeliids which correspond to rather different macroconch partners. Since the genus *Glochiceras* s.str. (Type species: *Ammonites nimbatus* Oppel) corresponds to *Ochetoceras* as its macroconch (female) partner, it belongs to a different subfamily than *Lingulaticeras*. *Lingulaticeras* corresponds to *Taramelliceras* and closely allied genera (*Metahaploceras*, *Neocheotoceras*). Due to this polyphyletic content of *Glochiceras* sensu Hyatt and Ziegler, it is no longer possible to treat these taxa as subgenera of a single genus, and *Lingulaticeras* is thus raised to full generic rank (see also Schweigert & Callomon 1997, Schweigert 1998).

Lingulaticeras planulatum Berckhemer in Ziegler, 1958

Fig. 4A

- 1958 *Glochiceras* (*Lingulaticeras*) *planulatum* Berckhemer n. sp. - Ziegler: 146, pl. 15, fig. 10.
 1959 *Glochiceras* (*Lingulaticeras*) *planulatum* Berckhemer. - Berckhemer & Hölder: 110, pl. 26, figs. 137–138.
 1977 *Gl. planulatum* Berckhemer. - Barthel & Schairer: 105.
 1994 *Glochiceras* (*Lingulaticeras*) *planulatum* Berckhemer, em. Ziegler 1958. - Schlegelmilch: pl. 16, fig. 22.
 1996 *Glochiceras planulatum* (Berckhemer). - Schweigert et al.: 195.
 1998 *Glochiceras planulatum* (Berckhemer). - Schweigert: 303.
 2005 *Gl. planulatum*. - Zeiss et al.: 29.
 2006 *Glochiceras* (*Lingulaticeras*) *planulatum* Berckhemer in Ziegler, 1958. - Viohl & Zapp: 73.

Holotype: Specimen illustrated by Ziegler 1958, pl. 15, fig. 10, re-figured in Schlegelmilch 1994, pl. 16, fig. 22; SMNS no. 19400.

Type locality: “Heilandkapelle” (Heiland Chapel), west of Fridingen an der Donau, south-western part of Swabian Alb, south-western Germany.

Type horizon and age: Zementmergel Formation, uppermost Kimmeridgian, Beckeri Zone, Ulmense Subzone, *rebouletianum* horizon (for biostratigraphy see Schweigert 2007, table 1). The stratigraphic position indicated by Ziegler (1958) as “Weißjura zeta 1” (=Liegende Bankkalke Formation) is incorrect, in fact the type series comes from higher in the section. At the type locality, the younger beds are separated from the “Weißjura zeta 1” by a fault. The same locality and horizon also yielded the type series of *Sutneria bracheri* Berckhemer and *Taramelliceras rebouletianum fridingense* Berckhemer & Hölder; the latter is probably conspecific with *Oppelia rebouletiana* Fontannes and represents the macroconch partner of *L. planulatum*.

Studied material: Holotype and 4 topotypes in the collection of the SMNS (nos. 19400–19404) and one specimen from Franconia in the collection of the JME, with its beak apparatus *in situ* (Fig. 4A-C).

Occurrence: Upper Jurassic of South Germany (Mergelstetten Formation of eastern Swabia, Zementmergel Formation of south-western Swabia, Painten Formation of Franconia).

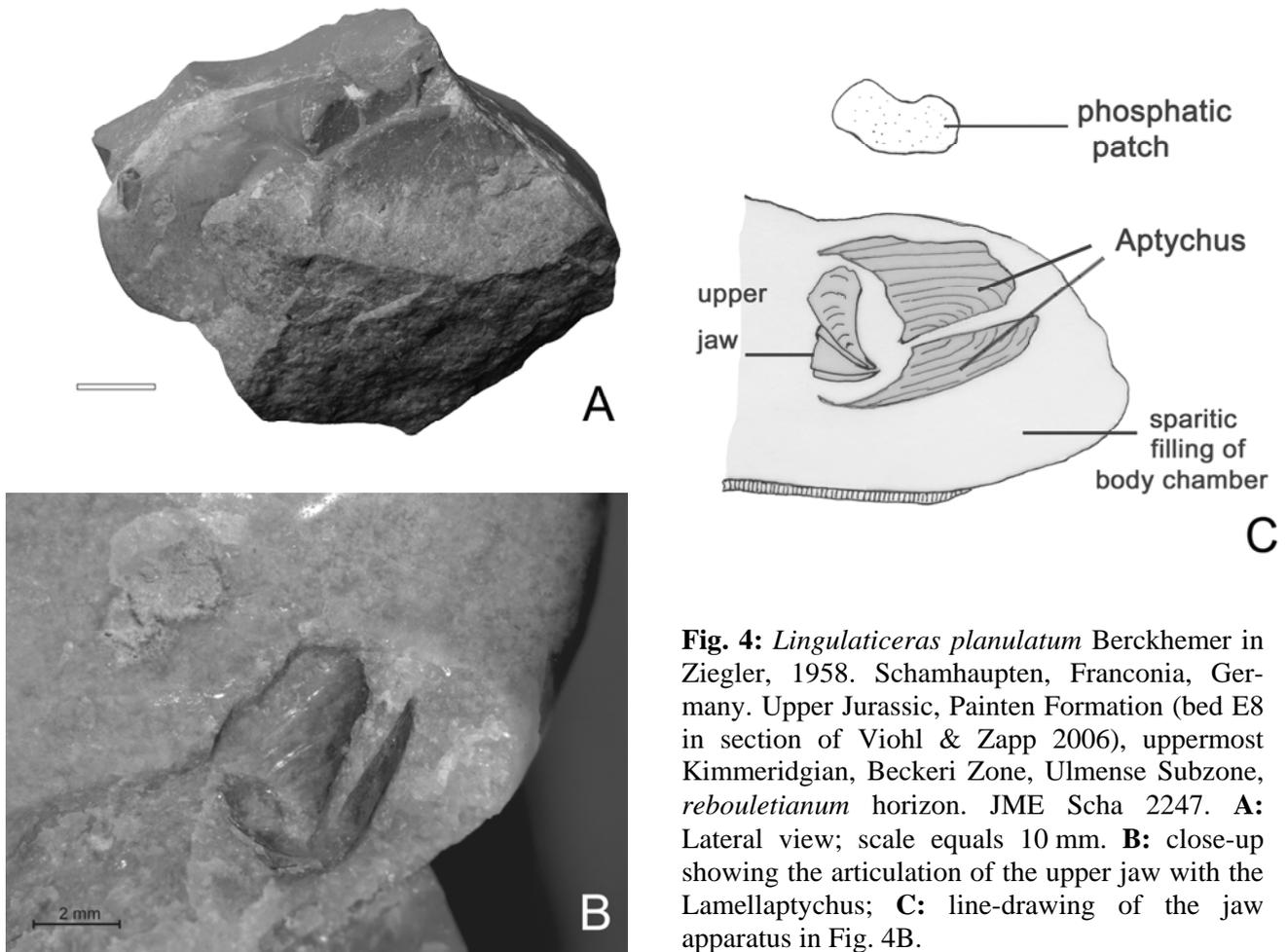


Fig. 4: *Lingulaticeras planulatum* Berckheimer in Ziegler, 1958. Schamhaupten, Franconia, Germany. Upper Jurassic, Painten Formation (bed E8 in section of Viohl & Zapp 2006), uppermost Kimmeridgian, Beckeri Zone, Ulmense Subzone, *rebouletianum* horizon. JME Scha 2247. **A:** Lateral view; scale equals 10 mm. **B:** close-up showing the articulation of the upper jaw with the Lamellaptychus; **C:** line-drawing of the jaw apparatus in Fig. 4B.

Description: The ammonites from bed E8 in the section of Schamhaupten (Viohl & Zapp 2006: fig. 5) all represent three-dimensionally preserved steinkerns with shell replaced by calcite. When breaking the ammonite-bearing rock into smaller pieces, the ammonite test mostly remains on the negative part, so that the ammonites only exhibit the steinkern. The specimen of *Lingulaticeras planulatum* (Fig. 4A) is almost complete, showing its terminal lappet. A small part of the body chamber was lost in the field when splitting the rock. However, this loss allows a view into the body chamber, which is partly filled with micritic calcareous sediment. The remaining space in the body chamber is a geopetal filling that consists of calcite spar. In the micritic calcareous sediment in the body chamber, a double-valved Lamellaptychus occurs in the so-called 'Normalstellung' (= normal position) sensu Trauth (1927). The Lamellaptychus lies rather deep within the body chamber of the ammonite, ca. at the beginning of the last third of the body chamber. Dorsally from the Lamellaptychus an upper jaw is discernible (Fig. 4B-C). It consists of two wing-like lobes which join at their anterior end in the symmetry plane. The tip of the upper jaw fits perfectly with the dorsal-anterior notch of the Lamellaptychus. As in other oppeliid upper jaws, the tip lacks a cutting edge and is rounded and not calcified (Schweigert & Dietl 2001). The upper jaw is preserved as coalified matter which is the usual preservation for former organic proteins in the Nusplingen Lithographic Limestones (Klug et al. 2005). The posterior part of the lobes of the upper jaw are paper thin and fragile so that it was impossible to prepare them completely from the surrounding spar. A short distance dorsal from the jaw apparatus, at mid-height of the whorl section, a small phosphatic spot lies directly on the surface of the steinkern. The phosphatic composition is determined from its characteristic luminescence using ultraviolet illumination. This phosphatic replacement area could represent either a stomach or crop content, or the remains of a muscle.

Remarks: The three-dimensional preservation of the *Lingulaticeras* and its geopetal filling points to a rapid burial, which is also indicated from other taphonomic and sedimentological features of bed E8. It is possible the ammonite died during the deposition of this bed, which is interpreted as a tempestite mainly because of its characteristic sedimentological features (Viohl & Zapp 2006, 2007). The preservation of the beaks shows that diagenesis must have been relatively rapid. This interpretation is supported by the fact that parts of the beaks with the upper jaw were cemented with blocky spar before the decay of the organic matter had finished. The deep position of the beaks within the body chamber did not allow a later dislocation, and the early diagenesis hampered further decay or bioturbation by which the original position could have been otherwise disturbed.

Discussion of the aptychus function

Since the recognition of the aptychus as part of the ammonite there has been a long and controversial debate whether this organ had the function of a jaw, an operculum, or both (e.g. Schindewolf 1958, Kaiser & Lehmann 1971, Lehmann 1972, Lehmann & Kulicki 1990, Seilacher 1993, Morton 1981, Schweigert & Dietl 1999, 2001, Keupp 2000, 2003, 2007). However, in the most recent compendium of ammonoid palaeobiology (Landman et al. 1996), this important aspect was not discussed.

The outlines of aptychi often fit quite well with the ammonites' apertures. In some findings, namely in aspidoceratids and oppeliids, the aptychus lies in a position resembling a "closing position". Morton (1981) argued that this position was not the original life position but occurred after the decay of vertically embedded specimens. The published examples of aptychi showing this "closing position" are all macroconchs. However, aptychi occur in both sexes. The *in situ* find from Schamhaupten is a microconch with long, well-developed lappets. In microconchs the lappets presumably functioned as a defense to preserve the body tissue at the aperture from attacks of predators. If this was the case, then it is difficult to explain why lappets should have developed in addition to an already present operculum, which would have served the same function.

Many specimens including the specimen of *Lingulaticeras planulatum* described herein indicate directly or indirectly that the beaks could be withdrawn deeply into the body chamber. This withdrawal into the body chamber was enabled by the development of a ligament in the symmetry plane of the aptychus. The ligament was not used for an up-and-down-movement in place, but for withdrawal of the body into the body chamber. Thus, the main function of this ligament - a question which was not reliably resolved by Seilacher (1993) - is supposed to be the necessity of a reduction of the width of the jaw apparatus during withdrawal deep into the body chamber.

Ammonites with sublethally injured shells show that they could survive severe loss of their body chamber shell and could regrow the lost shell, therefore, the damage was not lethal (e.g. Schweigert 1997, Kröger 2000, Keupp 2006). If the hypothesis is put forward that the aptychus had a dual function as both an operculum and a jaw, the predator would just have to destroy the aptychus at the aperture of the conch to gain access to the soft body tissue. And, it seems impossible that an ammonite could then survive the loss of its aptychus since it was part of its beak apparatus responsible for feeding. Healed shells indicate that one of the ammonites' major escape strategies was to withdraw deep into the body chamber when attacked by predators. Additional support for this conclusion is provided by some Jurassic ammonites (e.g. Schweigert 1997, Keupp 2000, Kröger 2000) Lethal injuries are those that are without shell repairs (excluding such phenomena as diagenetic crushing, implosion etc.). On some Jurassic ammonites this type of injury is located in the last third of the body chamber, which seems to have been a preferred place for successful attacks by some predators such as sharks and other fish (personal observations).

Additional reports of a possible operculum function besides that of the general outline that resembles the apertural shape include possible colour patterns and injuries. Keupp (2000) interpreted a Lamellaptychus from the Lower Tithonian of Daiting (Franconia, Germany) as having a colour pattern, which was used as camouflage. Indeed, a colour pattern on the visible outer surface of the aptychus would support such a function. However, during life of the ammonite the convex surface of the aptychus was obviously covered with an organic tissue of the buccal mass. This is deduced from the porous surface of the aptychus. A colour pattern within this outer organic layer would be enough for a camouflage. The specimen in question is an isolated Lamellaptychus broken into several fragments, most likely as the result of predation. In my opinion this "colour pattern" represents an inorganic manganese mineralization deposit, which occurs at the pressure points of lamellae of the superimposed fragments. Thus, if this opinion is correct, then the only known use of colour patterns for camouflage on the external shells of cephalopods is exclusively limited to the shell (see

Mapes & Davies 1996). The other argument that has been used to support an operculum function of the aptychus is injuries of the aptychus itself. These injuries resemble the '*forma aegra verticata*' pathology in ammonite shells which is caused by puncture injuries of the epithelia (Keupp 1992). Attacks on the apertural edge of ammonite shells were probably produced by decapod lobsters (Kröger 2000). The '*forma aegra verticata*' pathology occurs only on the concave side of the aptychus, where growth lines are developed. Pathologies on the convex side of the aptychus are extremely rare (Keupp 2000, fig. on p. 114 top right). However, if there are several pathologies of the '*aegra verticata*' type in the same aptychus, they are not symmetrically arranged and do not show an apparent orientation preference (e.g. Schweigert & Dietl 2001). Therefore, this pathology was more likely caused by parasites living inside the ammonite rather than by predators attacking the tissue at the apertural edge of the shell.

One of the main reasons why ammonite aptychi were often interpreted as operculi, apart from their big size and outline that resembles the aperture, is the strong calcification, especially in aspidoceratids and in oppeliids. In contrast to the calcitic caps developed on the tips of nautiloid jaws, the calcification of the aptychus is ventral from the horny layer (= inner lamella) lying on the concave side of the aptychus (Seilacher 1993). In some bituminous plattenkalks it is evident that the horny layer sometimes disintegrated from the aptychus during decay and was separately buried (Schweigert & Dietl 2001). Seilacher (1993) suggested that the antagonist for the horny upper jaw is completely lost and functionally replaced by the radula. However, the antagonist still exists; it is the lateral border of the horny layer inside the aptychus, and not the underlying calcitic aptychus. Therefore, it seems reasonable that the calcified part of the aptychus must have had an additional function other than that of feeding. This additional function is directly related to the extensive calcification of the aptychus, which added the weight of the aptychus to that of the shell, and this ballast was used to stabilize the shell in life position by lowering the centre of gravity. This aspect has never been calculated in ammonite modelling (e.g., Raup 1967, Reyment 1980, Jacobs & Landman 1993, see Westermann 1996 for a critical review) – even by those who erroneously concluded some ammonites had negative buoyancy (Ebel 1983, Shigeta 1993). It may be argued that in the Jurassic the strongly calcified aptychi are restricted to aspidoceratids and some oppeliids, whereas, they are only weakly calcified in stephanoceratids and perisphinctids despite the fact that in the serpenticone shells of the latter groups a stabilization would be even more effective than in those of aspidoceratids. Possibly aspidoceratids and some oppeliids lived closer to the water surface - at least partially, like the Recent *Nautilus* at night (cf. Saunders & Ward 1987) - whereas the serpenticone forms were perhaps restricted to deeper habitats, and were therefore more removed from surface water energy. Indeed, aspidoceratids often occur in rather shallow water deposits in the Kimmeridgian of Northern Switzerland, the Paris and Aquitaine basins, or north-western Germany (these areas forming the "biome franco-germanique" of Hantzpergue 1989). In these areas ammonites with serpenticone shells are extremely rare (?drifted empty conchs only) or are completely missing. Moreover, aspidoceratids were able to tolerate significant amounts of additional weight as proved by the numerous calcareous shelled invertebrates that used the ammonite shell as a substrate while the ammonite was alive (Keupp et al. 1999, Scholz et al. 2008).

In summary, it is reasonable to conclude that an operculum function of double-valved aptychi appears unlikely. The primary and only function for this structure was that of a beak primarily used to gather food. The lack of a calcified tip or similar structures in the upper jaw (in contrast to nautiloids, phylloceratids, and some Cretaceous ammonoids!) implies that there was probably no true biting function in the Jurassic Aptychophora, and these ammonites were probably microphagous, although the exact way of feeding is still speculative (Schweigert & Dietl 2001, Keupp 2007, Keupp & Riedel 2009, in press).

Acknowledgements

Martina Kölbl-Ebert, director of the Jura-Museum Eichstätt, is thanked for loaning this interesting specimen for study. Martin Ebert separated the specimen from the bulk of the excavation material from Schamhaupten and thus brought it to our attention. Royal Mapes and his wife is heartily thanked for several suggestions and linguistic improvement. For numerous fruitful discussions we are grateful to Gerd Dietl (Stuttgart). Karin Wolf-Schwenninger (SMNS) helped with the preparation of the microphotograph.

References

- Barthel, K.W. (1978): Solnhofen. Ein Blick in die Erdgeschichte.- 393 p., Thun (Ott).
- Barthel, K.W. & Schairer, G. (1977): Die Cephalopoden des Korallenkalks von Laisacker bei Neuburg a. d. Donau, II. *Glochiceras*, *Taramelliceras*, *Neochetoceras*.- Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie, **17**: 103-113.
- Barthel, K.W., Swinburne, N.H.M. & Conway Morris, S. (1990): Solnhofen: A study in Mesozoic palaeontology.- IX+236 p., Cambridge (Cambridge University Press).
- Dietl, G. & Schweigert, G. (2001): Im Reich der Meerengel – Fossilien aus dem Nusplinger Plattenkalk.- 144 p., München (F. Pfeil).
- Dietl, G. & Schweigert, G. (2004): The Nusplingen Lithographic Limestone - a “fossil lagerstaette” of Late Kimmeridgian age from the Swabian Alb (Germany).- *Rivista Italiana di Paleontologia e Stratigrafia*, **110**: 303-309.
- Dietl, G., Schweigert, G., Franz, M. & Geyer, M. (1998): Profile des Nusplinger Plattenkalks (Oberjura, Schwäbische Alb).- *Stuttgarter Beiträge zur Naturkunde (B)*, **265**: 1-37.
- Ebel, K. (1983): Calculations on the buoyancy of ammonites.- *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1983**: 614-640.
- Engeser, T. & Keupp, H. (2002): Phylogeny of the aptychi-possessing Neoammonoidea (Aptychophora nov., Cephalopoda).- *Lethaia*, **34**: 79-96.
- Frickhinger, K.A. (1994): Die Fossilien von Solnhofen.- 336 p., Korb (Goldschneck).
- Frickhinger, K.A. (1999): Die Fossilien von Solnhofen, vol. 2.- 190 p., Korb (Goldschneck).
- Fürsich, F.T., Mäuser, M., Schneider, S. & Werner, W. (2007): The Wattendorf Plattenkalk (Upper Kimmeridgian) - a new conservation lagerstätte from the northern Franconian Alb, southern Germany.- *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **245**: 45-58.
- Göhlich, U. & Chiappe, L. (2006): A new carnivorous dinosaur from the Late Jurassic Solnhofen archipelago.- *Nature*, **440**: 329-332.
- Göhlich, U., Tischlinger, H. & Chiappe, L. (2006): *Juravenator starki* (Reptilia, Theropoda), ein neuer Raubdinosaurier aus dem Oberjura der südlichen Frankenalb (Süddeutschland): Skelettanatomie und Weichteilbefunde.- *Archaeopteryx*, **24**: 1-16.
- Hantzpergue, P. (1989): Les Ammonites Kimméridgiennes du haut-fond d'Europe occidentale. Biochronologie, Systematique, Évolution, Paléobiogéographie.- *Cahiers de Paléontologie*, 428 p., Paris.
- Jacobs, D.K. & Landman, N.H. (1993): *Nautilus* - a poor model for the function and behaviour of ammonoids?- *Lethaia*, **26**: 101-112.
- Kaiser, P. & Lehmann, U. (1971): Vergleichende Studien zur Evolution des Kieferapparates rezenter und fossiler Cephalopoden.- *Paläontologische Zeitschrift*, **45**: 18-32.
- Kennedy, W.J., Landman, N.H., Cobban, W.A. & Larson, N.L. (2002): Jaws and radulae in *Rhaeboceras*, a Late Cretaceous ammonite.- *Abhandlungen der Geologischen Bundesanstalt*, **57**: 113-132.
- Keupp, H. (1992): Rippenscheitel bei Ammoniten-Gehäusen.- *Fossilien*, **1992(5)**: 283-290.
- Keupp, H. (2000): Ammoniten. Paläobiologische Erfolgsspiralen.- 160 p., Stuttgart (Thorbecke).
- Keupp, H. (2003): Aptychen: Kiefer, Deckel oder beides?- *Fossilien*, **2003(2)**: 104-110.
- Keupp, H. (2006): Sublethal punctures in body chambers of Mesozoic ammonites (forma aegra fenestra n.f.), a tool to interpret synecological relationships, particularly predator-prey interactions.- *Paläontologische Zeitschrift*, **80**: 112-123.
- Keupp, H. (2007): Complete ammonoid jaw apparatuses from the Solnhofen plattenkalks: implications for aptychi function and microphagous feeding of ammonoids.- *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **245**: 93-101.
- Keupp, H. & Riedel, F. (2009): Remarks on the possible function of the apophyses of the Middle Jurassic microconch ammonite *Ebrayiceras sulcatum* (Zieten, 1830), with a discussion on the palaeobiology of Aptychophora in general.- *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* [in press].

- Keupp, H., Röper, M. & Seilacher, A. (1999): Paläobiologische Aspekte von *syn-vivo*-besiedelten Ammonoiten im Plattenkalk des Ober-Kimmeridgiums von Brunn in Ostbayern.- Berliner geowissenschaftliche Abhandlungen, **E30**: 121-145.
- Klug, C., Brühwiler, T., Korn, D., Schweigert, G., Brayard, A. & Tilsley, J. (2007): Ammonoid shell structures of primary organic composition.- *Palaeontology*, **50**: 1463-1478.
- Klug, C., Schweigert, G., Dietl, G. & Fuchs, D. (2005): Coleoid beaks from the Nusplingen Lithographic Limestone (Late Kimmeridgian, SW Germany).- *Lethaia*, **38**: 1-20.
- Kröger, B. (2000): Schalenverletzungen an jurassischen Ammoniten - ihre paläobiologische und paläoökologische Aussagefähigkeit.- Berliner geowissenschaftliche Abhandlungen, **E33**: 1-97.
- Landman, N.H., Tanabe, K. & Davies, R.A. (1996): Ammonoid paleobiology.- XXIV + 857 p., New York, London (Plenum Press).
- Lehmann, U. (1972): Aptychen als Kieferelemente der Ammoniten.- *Paläontologische Zeitschrift*, **46**: 34-48
- Lehmann, U. & Kulicki, C. (1990): Double function of aptychi (Ammonoidea) as jaw elements and opercula.- *Lethaia*, **23**: 325-331.
- Mapes, R. H. & Davies, R. A. (1996): Color patterns in ammonoids.- In: Landman, N.H. et al. (eds.): Ammonoid palaeobiology.- *Topics in Geobiology*, **13**: 103-127, New York (Plenum Press).
- Morton, N. (1981): Aptychi: the myth of the ammonite operculum.- *Lethaia*, **14**: 57-61.
- Nixon, M. (1996): Morphology of the jaws and radula in ammonoids.- In: Landman, N.H. et al. (eds.): Ammonoid palaeobiology.- *Topics in Geobiology*, **13**: 23-42, New York (Plenum Press).
- Oppel, A. (1863): Palaeontologische Mitteilungen. III. Ueber jurassische Cephalopoden.- *Palaeontologische Mitteilungen aus dem Museum des koeniglich Bayerischen Staates*, **1**: 163-266.
- Parent, H., Scherzinger, A. & Schweigert, G. (2008): Sexual phenomena in Late Jurassic Aspidoceratidae. Dimorphic correspondence between *Physodoceras hermanni* (Berckhemer) and *Sutneria subeumela* Schindewolf, and first record of possible hermaphroditism.- *Palaeodiversity*, **1**: 181-187.
- Quenstedt, F.A. (1887-1888): Die Ammoniten des Schwäbischen Jura, 3. Der Weiße Jura, 817-1140, Stuttgart (Schweizerbart).
- Raup, D.M. (1967): Geometric analysis of shell coiling: Coiling in ammonoids.- *Journal of Paleontology*, **41**: 43-65.
- Reyment, R.A. (1980): Floating orientations of cephalopod shell models.- *Palaeontology*, **23**: 931-936.
- Riegraf, W. & Schmitt-Riegraf, C. (1995): Mandibula fossiles ammonitorum et nautilorum (Rhyncholithi et rhynchoteuthes, excl. aptychi et anaptychi.- In: Westphal, F. (ed.): *Fossilium Catalogus. I. Animalia*, **134**, 219 p., Amsterdam & New York (Kugler).
- Röper, M., Rothgaenger, M. & Rothgaenger, K. (1996.): Die Plattenkalke von Brunn (Landkreis Regensburg).- 102 p., Eichendorf (Eichendorf Verlag).
- Rothpletz, A. (1909): Ueber die Einbettung der Ammoniten in die Solnhofener Schichten.- *Abhandlungen der königlich Bayerischen Akademie der Wissenschaften*, 2. Klasse, 2. Abteilung, **24**: 313-337.
- Saunders, W.B. & Ward, P.D. (1987): Ecology, distribution and population characteristics of Nautilus.- In: Saunders, W.B. & Landman, N.H. (eds.): *Nautilus: The Biology and Paleobiology of a Living Fossil*, 137-162, New York (Plenum Press).
- Schindewolf, O.H. (1958): Über Aptychen (Ammonoidea).- *Palaeontographica (A)*, **111**: 1-46.
- Schlegelmilch, R. (1994): Die Ammoniten des süddeutschen Malms.- VII + 297 p., Stuttgart, Jena, New York (G. Fischer).
- Scholz, A., Schweigert, G. & Dietl, G. (2008): Bivalves from the Nusplingen Lithographic Limestone (Jurassic, Upper Kimmeridgian, Southern Germany).- *Palaeodiversity*, **1**: 111-131.
- Schweigert, G. (1996): Die Hangende Bankkalk-Formation im schwäbischen Oberjura.- *Jahresberichte und Mitteilungen des Oberrheinischen geologischen Vereines*, Neue Folge, **78**: 281-308.
- Schweigert, G. (1997): Erstaunliches Regenerationsvermögen bei Ammoniten.- *Fossilien*, **1997(1)**: 36-40.
- Schweigert, G. (1998): Die Ammonitenfauna des Nusplinger Plattenkalks (Ober-Kimmeridgium, Beckeri-Zone, Ulmense-Subzone, Baden Württemberg).- *Stuttgarter Beiträge zur Naturkunde (B)*, **267**: 1-61.

- Schweigert, G. (2007): Ammonite biostratigraphy as a tool for dating Upper Jurassic lithographic limestones from South Germany - first results and open questions.- *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **245**: 117-125.
- Schweigert, G. & Dietl, G. (1999.): Zur Erhaltung und Einbettung von Ammoniten im Nusplinger Plattenkalk (Oberjura, Südwestdeutschland).- *Stuttgarter Beiträge zur Naturkunde, (B)* **272**: 1-31.
- Schweigert, G. & Dietl, G. (2001): Die Kieferelemente von *Physodoceras* (Ammonitina, Aspidoceratidae) im Nusplinger Plattenkalk (Oberjura, Schwäbische Alb).- *Berliner geowissenschaftliche Abhandlungen*, **E36**: 131-143.
- Schweigert, G. & Callomon, J.H. (1997): Der *bauhini*-Faunenhorizont und seine Bedeutung für die Korrelation zwischen tethyalem und subborealem Oberjura.- *Stuttgarter Beiträge zur Naturkunde, (B)* **247**: 1-69.
- Schweigert, G., Krishna, J., Pandey, B. & Pathak, D.B. (1996): A new approach to the correlation of the Upper Kimmeridgian Beckeri Zone across the Tethyan Sea.- *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **202**: 345-373.
- Seilacher, A. (1993): Ammonite aptychi: how to transform a jaw into an operculum.- *American Journal of Science*, **293A**: 20-32.
- Seilacher, A., Andalib, F., Dietl, G. & Gocht, H. (1976): Preservational history of compressed Jurassic ammonites from Southern Germany.- *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **152**: 307-356.
- Shigeta, Y. (1993): Post-hatching early life history of Cretaceous Ammonoidea.- *Lethaia*, **26**: 23-46.
- Tanabe, K. & Fukuda, Y. (1987): The jaw apparatus of the Cretaceous ammonite *Reesidites*.- *Lethaia*, **20**: 41-48.
- Tanabe, K. & Landman, N.H. (2002): Morphological diversity of the jaws of Cretaceous Ammonoidea.- *Abhandlungen der Geologischen Bundesanstalt*, **57**: 157-165.
- Trauth, F. (1927): Aptychenstudien. I. Über die Aptychen im Allgemeinen.- *Annalen des naturhistorischen Museums in Wien*, **41**: 171-259.
- Viohl, G. & Zapp, M. (2006): Die Fossil-Lagerstätte Schamhaupten (oberstes Kimmeridgium, Südliche Frankenalb, Bayern).- *Archaeopteryx*, **24**: 27-78.
- Viohl, G. & Zapp, M. (2007): Schamhaupten, an outstanding Fossil-Lagerstätte in a silicified Plattenkalk around the Kimmeridgian-Tithonian boundary (Southern Franconian Alb, Bavaria).- *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **245**: 127-142.
- Westermann, G.E.G. (1996): Ammonoid life and habitat.- In: Landman, N.H. et al. (eds.): *Ammonoid paleobiology*: 607-707, New York, London (Plenum Press).
- Zeiss, A., Schulbert, C. & Viohl, G. (2005): The ammonites from Schamhaupten (Southern Franconian Alb, Bavaria) - an interesting faunal association at the boundary Upper Kimmeridgian/Lower Tithonian.- *Zitteliana (B)*, **26**: 29.