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# The jaw apparati of ectocochleate cephalopods

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With 9 figures

Kurzfassung: Der gegenwärtige Stand der Diskussion um Anaptychen, Aptychen und Opercula von Ammonoideen wird dargelegt. Die von KANIE et al. (1978) und TANABE et al. (1980) beschriebenen Kieferapparate der lytoceraten Gattungen *Gaudryceras* und *Tetragonites* wurden von LEHMANN (1981) als besonderer Rhynchaptychus-Typ herausgestellt. Nach erneuter Analyse erwiesen sie sich als den Kieferapparaten des rezenten *Nautilus* so ähnlich, daß sie als eingeschwemmte Nautiliden-Kiefer angesehen werden können. Dagegen erhält TANABE aufrecht, daß an ihnen entdeckte Beccublasten-Eindrücke sich von entsprechenden Eindrücken des *Nautilus* deutlich unterscheiden.

Die Autoren halten Untersuchungen zu den folgenden Punkten für wünschenswert:

a) in wieweit es sich bei paläozoischen Anaptychen-Ansammlungen um solche von Deckeln (Opercula) oder von Kiefer-Elementen handelt;
b) die Funktion der Laevaptychen, deren Kiefer-Funktion noch angezweifelt werden kann;
c) die Autochthonie der Kieferelemente vom Rhynchaptychus-Typ in der japanischen Oberkreide.

Abstract: The present state of knowledge concerning the function of anaptychi, aptychi, and opercula of ammonoids is reviewed. The jaw apparati found associated with the lytoceratid genera *Gaudryceras* and *Tetragonites* by KANIE et al. (1978) and TANABE et al. (1980) and classified as rhynchaptychus type of ammonoid jaws by LEHMANN (1981) are re-interpreted. Morphologically, they are very similar to *Nautilus* jaws. Their interpretation as allochthonous nautiloid jaws is discussed and considered probable. However, beccublast cell impressions in *Gaudryceras* and recent *Nautilus* differ considerably.

Further investigations are deemed necessary concerning

a) the nature of the anaptychi in Palaeozoic anaptychus assemblages, whether they are opercula or jaw elements;
b) the function of the laevaptychi. Their jaw nature is still open to doubt;
c) the autochthony of the rhynchaptychus-type lower jaws found in lytoceratid Upper Cretaceous ammonites in Japan.

## Introduction

The delicate, complicated organic jaws of recent dibranchiate cephalopods are easily isolated postmortally. Their chances to become fossilized in an identifiable state are minimal. If the jaw apparati of ectocochleate cephalopods remained enclosed in the living chamber and thus associated with their bearer, their chances to become fossilized were better. Even so, most of them are found isolated. It requires unusually well preserved specimens, consisting of upper and lower jaw with the radula still in situ between them within the living chamber, to recognize the true nature of these structures, and to make this knowledge convincing even to the sceptic.

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What is here considered as the jaw elements had been known for a long time as anaptychi and aptychi; their most popular interpretation (SCHINDEWOLF 1958, MILLER et al. 1957, ARKELL et al. 1957) was as protective opercula similar to the hood of recent *Nautilus*. We believe, however, against SCHINDEWOLF (1958) and with DZIK (1981), that jaw elements of the anaptychus and especially of the aptychus type may also, in double function, have served as protective opercula. If ammonoids did have opercula of the hood-type they must have had it in addition to the jaws. The co-existence of jaws with a hood-like operculum (CLOSS 1967, BANDEL 1988) was observed in a specimen of *Eoasianites* and *Gyroceratites*. According to reinvestigation by DAGYS and WEITSCHAT, those parts in *Eoasianites* interpreted as opercula show typical growth lines and are in reality shell fragments. In *Gyroceratites* X-ray analysis leaves some doubt. Although it seems quite possible that at least some ammonoids may have had such an operculum, it would usually not be possible to prove that a certain operculum belongs to a distinct specimen. A hood-type operculum would probably be the first part of the animal to become disintegrated and swept away postmortally. Specimens from the Middle Devonian *Gyroceratites* from Wissenbach, if studied in great detail, may possibly provide such rare instances of jaw-operculum co-existence. In very rare instances, however, the operculum of fossil gastropods such as Triassic neritaceans and Devonian euomphalids was preserved.

In their basic plan, anaptychus- and aptychus-type jaws are similar. A different type of jaw apparatus was found associated with the Cretaceous lytocerate genera *Gaudryceras* and *Tetragonites*. It is characterized by calcareous coverings of the rhyncholite and conchorhynch type on the beaks (KANIE et al. 1978, TANABE et al. 1980).

This discovery prompted recognition of a third type of ammonoid jaw apparatus ascribed to the Lytocerata and named the rhynchaptychus type (LEHMANN 1981). Its similarity to nautiloid jaws was evident and even lead to the assumption that in Cretaceous seas nautiloids and Lytocerata may have been ecological competitors. TANABE still thinks that the *Nautilus*-like tetragonitid lower jaws were specially adapted for carnivorous feeding habits, suggesting a convergence between the Nautilida and the Lytocerataceae.

Detailed discussions and investigations during a stay of A. S. DAGYS in Hamburg resulted in the conclusions outlined in this paper. We recognize only two types of ammonoid and one type of nautiloid jaw apparatus; the former rhynchaptychus type of ammonoid jaw apparatus is ascribed to nautiloids.

These conclusions are not shared by TANABE for reasons given below.

## Morphology of the anaptychus type of jaw apparatus

LEHMANN (1970) was the first to interprete an anaptychus as a lower jaw after investigating material found in the body chamber of the genus *Psiloceras*. We believe the model of the jaws of *Psiloceras* proposed by LEHMANN to be correct, but some details of the morphology of this type of jaw apparatus can be added, following investigations of phosphatic early Mesozoic anaptychi by serial sectioning and preparation of artificial casts (DAGYS & DAGYS 1975).

The morphology of this type of ammonoid jaw is very stable and specific. The lower jaw or anaptychus consists of two plates. The outer plate is more or less cap-shaped; it always has concentric growth lines on the outer surface and varies considerably in outline and general form. The inner plate is invariably smaller and has a more complex morphology than the outer one. Near the rostrum there is always a fairly deep, more or less triangular pit (Fig. 1a, 2a–c) which was not well preserved in the material described by LEHMANN (1970). Posterior to the pit the inner plate forms an elevated and flattened central platform, suboval in outline. This platform is connected with the margins of the outer plate by depressed lateral platforms, which are narrower and shorter than the central platform. The length of the inner plate in

Triassic and Liassic lower jaws is 1/3 to 1/2 that of the outer plate. A more or less differentiated rostrum is absent in lower jaws of this type.

The upper jaw also consists of two plates (Fig. 1b; 2d–f), which differ in shape and relative length from those of the lower jaw. The outer plate is always smaller; its flattened median part strongly bends downward to the lateral parts. Concentric sculpture is almost absent in the median part and only feebly developed laterally. The outer plates and especially their median parts are very thin and therefore usually not completely preserved. The inner plate of the upper jaw of early Mesozoic ammonoids consists of two lamellae, connected only in their rostral part. The lateral parts of both lamellae are subvertical (dorso-ventral), and the median ones are usually very narrow. Usually every lamella bears feeble concentric growth lines. Invariably the upper jaw has a distinct, more or less sharp rostrum.

Both jaws of this type consist of organic material ("chitin") only, and mineralisation, if observed, is always secondary (diagenetic).

Upper and lower jaws of this type have been found in living chambers of several Triassic and Liassic ammonoids (LEHMANN 1981, 1988). The lower jaw of this type described as anaptychus by TANABE (1983) from the Upper Cretaceous possesses a distinct median groove; therefore DAGYS thinks that more likely it is the inner organic layer of an aptychus-type lower jaw. In his opinion the last anaptychus is known from the Toarcian; all younger forms are aptychi or neoanaptychi (= nautiloid jaws). The morphology described here is also characteristic of Upper Paleozoic ammonoid jaws. Reinvestigation of CLOSS' (1967) collection in Tübingen showed that all jaws are compressed and partly crushed; a reconstruction derived from them was presented by BANDEL (1988). The lower jaw is similar to Mesozoic anaptychi and differs mainly in its unusually big inner plate which attains at least 2/3 the length of the outer plate. A pit is present (see CLOSS 1967: pl. 3, fig. 4), but not as deep as in Mesozoic forms. The main part of the inner plate is occupied by the central platform, whereas the lateral platforms are very narrow. The morphology of the upper jaw is not recognizable in detail. If BANDEL's (1988) reconstruction is correct, the outer plate in *Eoasianites* is larger than in other ammonoids. However, most of us have a different opinion as to the reconstruction of the upper jaw and the relative length of its outer plate, and previous reconstructions (CLOSS 1967, BANDEL 1988) must be reconsidered. From the specimens of the CLOSS collection it may be concluded that the inner plate of the upper jaw is divided and rather similar to the inner plate of Triassic and Liassic forms.

The mandibles described by BANDEL (1988) from the Middle Carboniferous of Wuppertal (Nordrhein-Westfalen) are similar to what we know of ammonoids in general. Among numerous oblique sections of juvenile specimens of the genera *Reticuloceras* and *Vallites* there are some cross-sections of jaws which are similar to those of Triassic and Liassic ones. BANDEL's text fig. 15 seems to be a section of a lower jaw showing differentiated central and lateral platforms of the inner plate. His text fig. 17 shows a cross-section near the rostrum again of a lower jaw with distinct inner pit.

The anaptychi described by CLAUSEN (1968) from the Upper Devonian of the Rheinisches Schiefergebirge apparently do not show indications of duplication or marginal fissures and thus may well have been opercula. One of several thousand specimens was observed in the aperture of a *Manticoceras.*

Despite the lack of conclusive information about the inner plate of Devonian ammonoids it seems that jaws of Palaeozoic and Early Mesozoic (up to Toarcian) and even Upper Cretaceous (TANABE 1983) ammonoids had one general Bauplan. The lower jaw is represented, quite unlike the jaw of Recent cephalopods, by what was usually called the anaptychus; the upper jaw is represented by structures which were also at first described as anaptychus – *Anaptychus sellaeformis* var. *bicarinata* (TRAUTH 1934), *Anaptychus* B (DAGYS & DAGYS 1975) – the morphology of which is more similar to that of upper jaws of Recent cephalopods.

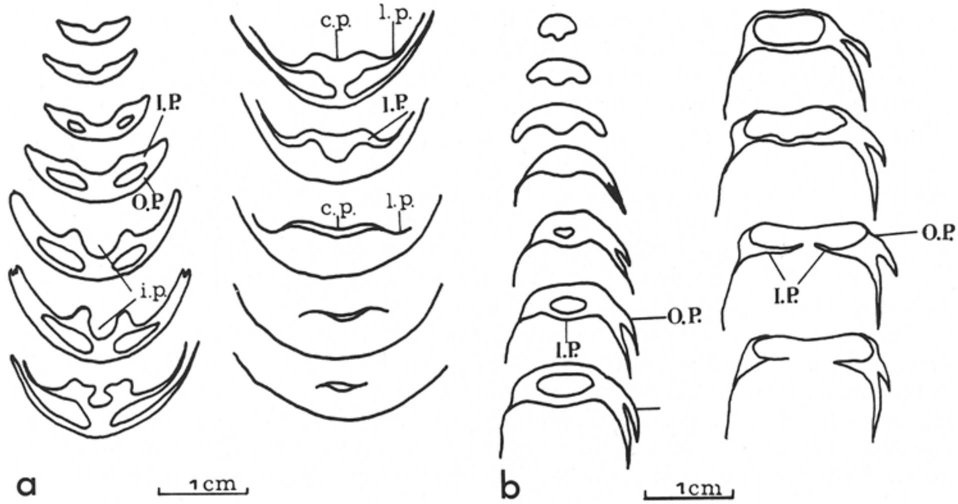


Fig. 1. Serial transverse sections through lower (a) and upper (b) jaw of Middle Triassic ammonoids. Upper Anisian, North-Eastern USSR, Russkaya river, Omolon-Basin. – I. P.- inner plate; O. P.- outer plate, c. p.- central platform, i. p.- inner pit, l. p.- lateral platform.

Abb. 1. Serienschliffe durch Unter- (a) und Ober (b)-Kiefer mitteltriassischer Ammonoideen. Ober-Anis, NE-UdSSR, Russkaya-Fluß, Omolon-Becken. – I. P.- Innenlamelle, O. P.- Außenlamelle, c. p.- zentrale Plattform, i. p.- innere Grube, l. p.- laterale Fläche.

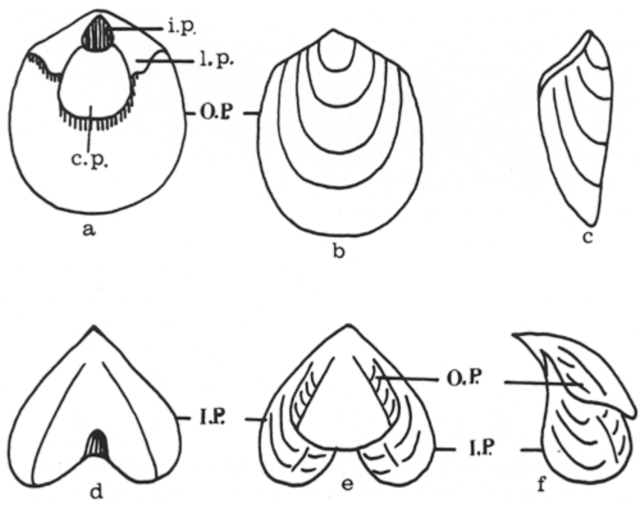


Fig. 2. Morphology of the lower (a, b, c) and upper (d, e, f) jaws of Middle Triassic ammonoids, Abbreviations as in Fig. 1.

Abb. 2. Morphologie von Unterkiefer (a, b, c) und Oberkiefer (d, e, f) mitteltriassischer Ammonoideen, Abkürzungen wie in Fig. 1.

Further investigation may well prove that some of the anaptychi found in the Wissenbacher Schiefer of Lower Middle Devonian age (BANDEL 1988) and other Palaeozoic strata (Büdesheim, CLAUSEN 1968) are opercula.

Finally, is it actually quite impossible that the thick laevaptychi, by some parallelism, are modified opercula? Their jaw nature has not been established beyond doubt.

## Morphology of the aptychus-type of jaw apparatus

From the lower jaw of this mandible type usually only two calcitic plates are preserved – the aptychi. Their interpretation as lower jaw of ammonites (LEHMANN 1972) now seems to have been widely accepted by palaeontologists.

The organic ("chitinous") parts of the lower jaw of this type are only very rarely preserved. The first reconstruction of the organic parts of the lower jaw was made from serial cross-sections of *Hildaites levisoni,* some of which are shown in Fig. 3. It appears from these sections that the lower jaw, as in other cephalopods, consists of two plates. The outer plate is undivided and shows two distinct layers, an outer, smaller calcitic layer (the aptychus) and an inner organic layer (Fig. 3). In the sections, the organic layer of the outer plate is usually wrinkled and in some parts separated from the calcitic aptychus. This is caused by post mortem processes. Both the calcitic and the organic layer extend forward up to the cutting edge, but posteriorly the length of the calcitic layer is only about $^{2}/_{3}$ of that of the organic layer. Thus the aptychus covers only half the area of the organic layer (i. e. of the outer plate of the lower jaw).

The inner plate of the lower jaw is difficult to analyse, but evidently structures like the inner pit and differentiated platforms are absent (Figs. 3, 4). The inner plate of the aptychus-type lower jaw appears to be a simple plate with a groove-like depression in the median part. It was always considerably smaller than the outer plate and hardly exceeded half of its length. The inner plate is always organic and shows no signs of mineralisation.

The upper jaw of the aptychus-type jaw apparatus is very similar to those associated with the anaptychus-type of jaw apparatus. It consists of two plates, an outer, small one, which, owing to rather poor conservation, can only be reconstructed in general (Fig. 4), and an inner plate, which is much longer and consists of two subparallel lamellae connected in the rostral part of the jaw. Both plates of the upper jaw are built of organic material only.

Aptychi are known from the Upper Liassic (Lower Toarcian) to the Upper Cretaceous, but organic parts of aptychus-like jaws have only very rarely been observed. LEHMANN (1972: pl. 9, fig. 1) described and figured sections through a well preserved and complete jaw apparatus of *Eleganticeras elegantulum* (YOUNG & BIRD) with both aptychus and organic layers preserved, and (pl. 10, fig. 3) a lower jaw (aptychus) of *Quenstedtoceras* from the Callovian of Lukóv which distinctly shows the inner plate in the rostral region. The character of the organic parts of jaws associated with different kinds of aptychus and the evolution of this structure among Jurassic and Cretaceous ammonoids needs further investigation. Possibly this type of jaw is also stable like the anaptychus type and did not undergo essential changes in time.

## Morphology of the neoanaptychus- or rhynchaptychus-type of jaw apparatus

This type of jaw was originally established as anaptychus-like operculum of Upper Cretaceous ammonites by NAGAO (1931) and named *Neoanaptychus.* It is distinguished from older anaptychi by the presence of a calcareous layer in the apical part or rostrum. Recently Cretaceous anaptychus-like structures were reinterpreted as jaws of ammonites (KANIE et al. 1978, 1980; LEHMANN et al. 1980; TANABE et al. 1980; KANIE 1982), and a new Rhynchaptychus type of jaw apparatus was proposed.

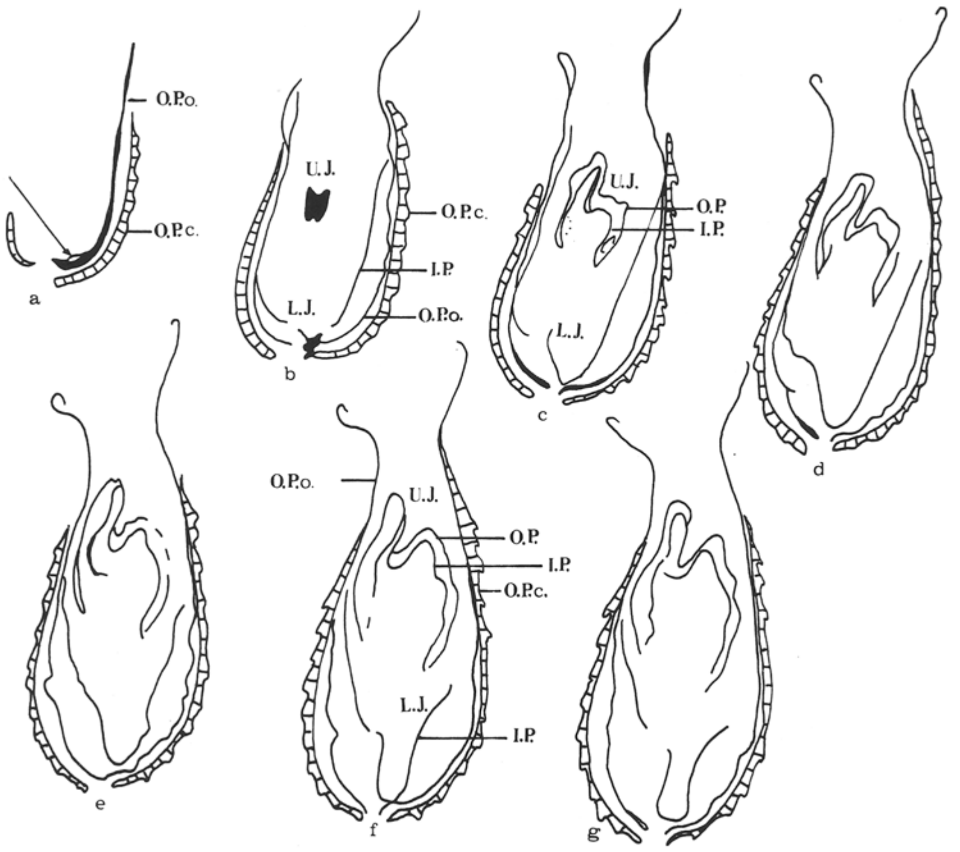


Fig. 3. Section through the jaw apparatus of *Hildaites levisoni*, Lower Toarcian of Haverlahwiese, North Germany (7/1), U. J.- upper jaw, O. P.- outer plate of upper jaw. I. P.- inner plate of upper jaw, L. J.- lower jaw, O. p. o.- outer plate of lower jaw, organic layer, O. p. c.- outer plate of lower jaw, calcitic layer (aptychus).

Abb. 3. Serienschnitte durch den Kieferapparat von *Hildaites levisoni*, Unteres Toarcium von Haverlahwiese, Norddeutschland (7/1). U. J.- Oberkiefer, O. P.- Außenlamelle des Oberkiefers, I. P.- Innenlamelle des Oberkiefers, L. J.- Unterkiefer, O. p. o.- Außenlamelle des Unterkiefers, organische Schicht, O. p. c. – Außenlamelle des Unterkiefers, kalkige Schicht (Aptychus).

The morphology of the neoanaptychus, which is undoubtedly the lower jaw of a cephalopod, is now rather well known. This jaw is always more or less wide, the width surpassing the length, and consists of two organic plates. The outer plate is bigger and shows strong concentric growth lines on the outer surface (Fig. 5). The inner plate is smaller, its length is about half that of the outer plate. In the medial part of the inner plate there is a more or less distinct groove (Figs. 5, 6). An inner pit and differentiation of the inner plate into separated platforms are not observable.

In the frontal part of the lower jaw there are calcareous deposits which cover the rostral part of the outer plate and partly fill up the medial groove of the inner plate. In extremely well

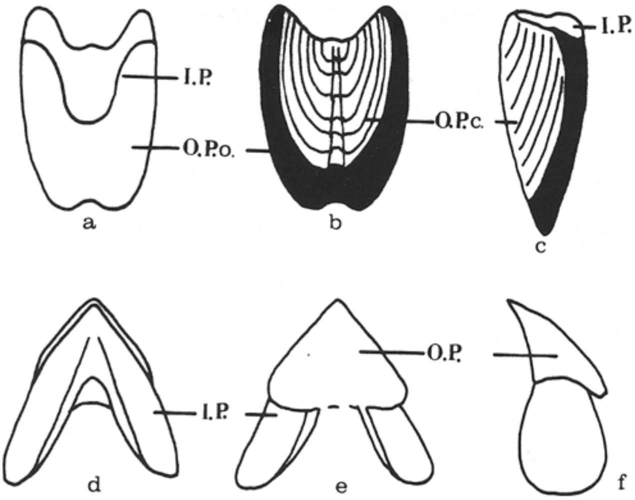


Fig. 4. Morphology of the lower (a, b, c) and upper (c, d, e) jaw of the Jurassic ammonite *Hildaites levisoni*. Schematic reconstruction after Fig. 3. I. P.- inner plate, O. P.- outer plate, O. P. c.- outer plate calcitic layer, O. P. o.- outer plate organic layer.

Abb. 4. Morphologie des Unterkiefers (a, c, c) und des Oberkiefers (c, d, e) des jurassischen Ammoniten *Hildaites levisoni*. Schematische Rekonstruktion gemäß Fig. 3. I. P.- Innenlamelle, O. P.- Außenlamelle, O. P. c.- kalzitische Schicht der Außenlamelle, O. P. o.- organische Schicht der Außenlamelle.

preserved specimens denticulation is present on the rostrum of the jaw (KANIE 1982). Calcareous deposits are known only in some specimens which are sufficiently well preserved.

The upper jaw of this kind of jaw apparatus is rather doubtful. The neoanaptychi designed as upper jaws are not essentially different from lower jaws (KANIE et al. 1978, TANABE et al. 1980, KANIE 1982). According to the opinion of TANABE et al. (1980: 158), "the upper jaws are easily distinguished from the lower ones by their smaller size, more strongly convex outer lamella, presence of strong radial sculpture in the anterior region of outer lamella, and absence of denticulation of a calcareous covering". All these differences concern either variable morphological features of neoanaptychi or the degree of their preservation (absence of denticulation). In general the upper jaw in this interpretation is indistinguishable from the lower one. Some of the illustrations show clear resemblance of "upper jaws" to lower jaws (TANABE et al. 1980: fig. 2c is a cast of the groove in the inner plate of a lower jaw). The main objection against the reconstruction of the upper jaw of the neoanaptychus type is based on the unusual proportions of their inner and outer plate. According to the interpretation of KANIE et al. (1978), TANABE et al. (1980), KANIE (1982) and LEHMANN et al. (1980), the inner plate of the upper jaw is shorter than the outer. This feature is unusual not only for ammonoids, but for all recent and fossil cephalopods. In all of them the upper jaw is characterized by a short outer and a long inner plate.

The close similarity of neoanaptychus to the jaw of *Nautilus* was noted by NAGAO (1931), but he considered this resemblance as superficial only. This similarity was also underlined in recent papers but, prompted by the co-occurrence of neoanaptychus with ammonites and some findings of neoanaptychus in body chambers of the genera *Gaudryceras* and *Tetragonites*, it was supposed that some Cretaceous ammonites had jaw apparati similar to those of Recent

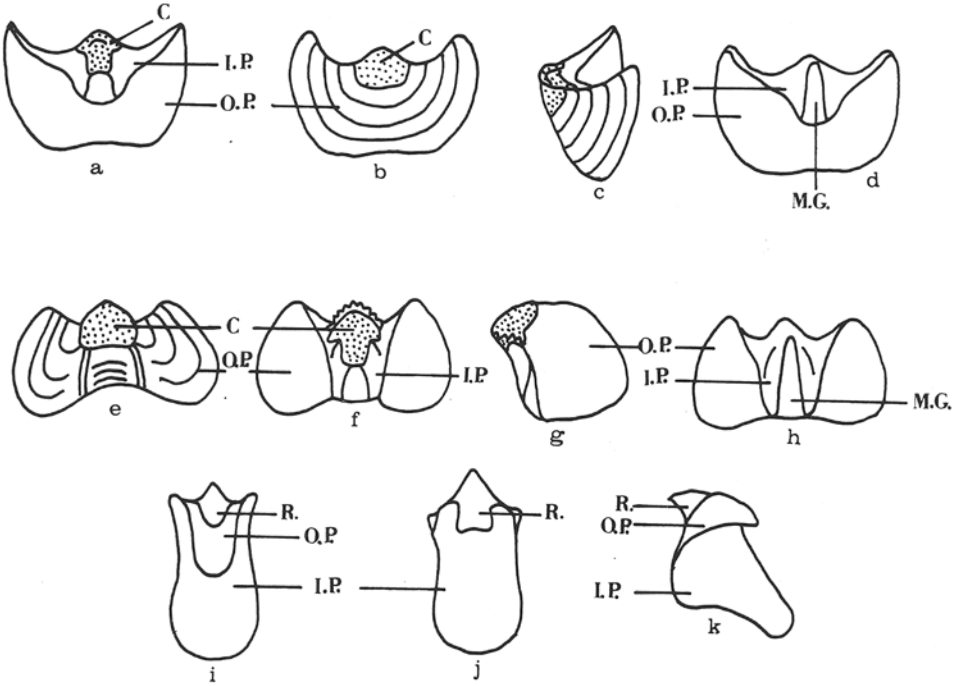


Fig. 5. Morphology of a neoanaptychus-type jaw apparatus (lower jaw) and of lower and upper jaw of recent *Nautilus*. – a–d: Lower jaw of neoanaptychus, described as *Anaptychus wereschagini* (ZAKHAROV, 1973). a: internal, b: external, c: lateral views, d: internal view (without conchorhynch), e–h: lower jaw of recent *Nautilus*, e: external, f: internal, g: lateral views, h: internal view (without conchorhynch). i–k: upper jaw of recent *Nautilus*, i: external, j: internal, k: lateral view. C.- conchorhynch, I. P.- inner plate, M. G.- medial groove, O. P.- outer plate, R.- rhyncholite.

Abb. 5. Morphologie eines Unterkiefers vom Neoanaptychus-Typ und von Unter- und Oberkiefer des rezenten *Nautilus*. a–d: Unterkiefer vom Neoanaptychus-Typ, von ZAKHAROV (1973) als *Anaptychus wereschagini* beschrieben. a: Innen-, b: Außen-, c: Lateral-, d: Innen- (ohne Conchorhynchus)Ansicht, e–h: Unterkiefer des rezenten *Nautilus*, e: Außen-, f: Innen-, g: Lateral-Ansicht, h: Innen-Ansicht ohne Conchorhynchus. i–k: Oberkiefer des rezenten *Nautilus*. i- Innen-, j- Außen-, k- Lateral-Ansicht, C- Conchorhynchus; I. P.- Innenlamelle; M. G.- mediane Furche; O. P.- Außenlamelle; R.- Rhyncholithus.

*Nautilus*. However, all indications of in situ position of Cretaceous jaws from Japan (TANABE et al. 1980, KANIE 1982 and others) are doubtful. They mean only that some jaws were found in living chambers, but they were never associated with the radula and never show a natural assemblage of lower and upper jaw as in the anaptychus and aptychus types of jaw apparatus (LEHMANN 1970, 1972 and others). TANABE now thinks that there is a possibility that he and his co-outhors (1980) mistakenly identified the isolated lower jaws of *Gaudryceras* and *Tetragonites* as upper jaws. The mode of occurrence of neoanaptychus (rhynchaptychus) within the body chamber of *Gaudryceras* and *Tetragonites* is indeed not autochthonous in a strict sense. To clarify this problem, "true" upper jaw-rhynchaptychus association within the body chamber of the Cretaceous lytoceratids should be searched for.

TANABE et al. (1982) noted that nautilids are rare in Cretaceous deposits and considered this condition as an additional proof for the ammonoid nature of the Cretaceous neoanaptychus. TANABE now adds that the rhynchaptychus-type jaws occur very abundantly in the off-

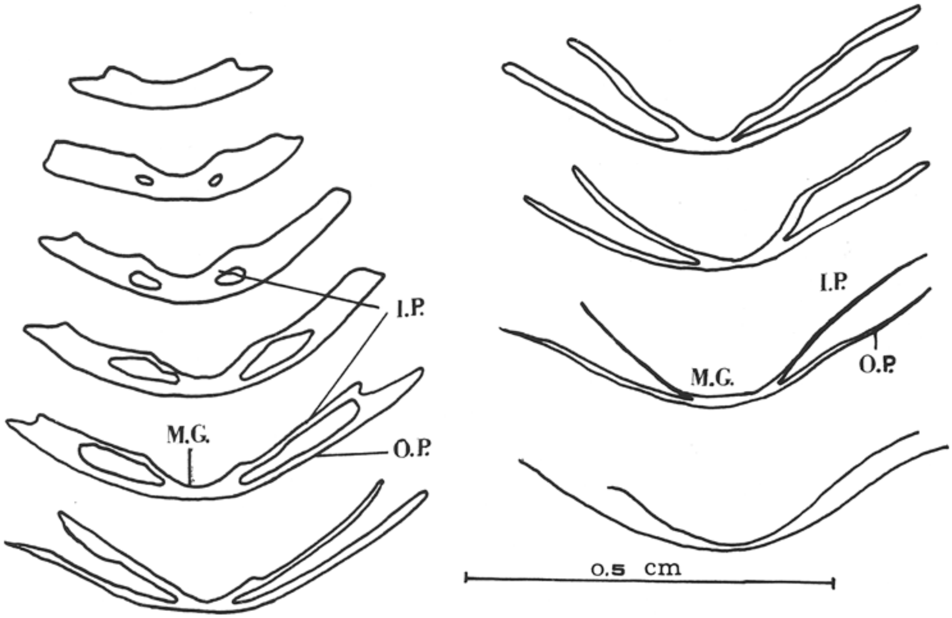


Fig. 6. Sections of lower jaw from the Upper Cretaceous (Turonian-Coniacian) of Sakhalin Island, described by ZAKHAROV (1979) as *Anaptychus wereschagini*, I. P.- inner plate; M. G.- medial groove; O. P.- outer plate.

Abb. 6. Unterkiefer-Querschnitte aus der Oberkreide (Turonium bis Coniacium) von Sachalin, von ZAKHAROV (1979) als *Anaptychus wereschagini* beschrieben. I. P.- Innenlamelle; M. G.- mediane Furche; O. P.- Außenlamelle.

shore muddy facies of the Hokkaido Cretaceous, in which lytoceratids are found, but shell remains of nautiloids are extremely rare.

A second point in favour of TANABE's opinion is the difference in beccublast cell impressions between *Nautilus* jaws and rhynchaptychus (TANABE 1982). The anchored type of impressions in *Gaudryceras* is more similar to those in modern coleoid jaws than to the impressions in *Nautilus* jaws with numerous micropores. This point needs further investigation.

Neoanaptychus is known not only from the Cretaceous of the Far East, but also from the Lower Cretaceous of Silesia (TILL 1906, reinvestigated by BANDEL 1988). A typical neoanaptychus or lower jaw of nautilids was figured by LEHMANN (1981: fig. 3c) as lytocerate anaptychus from the Lower Pliensbachian of Rottorf am Kley (North Germany). Perhaps the anaptychus with calcareous covering described by HÖLDER (1958: fig. 1) from the Lower Liassic of Tübingen (South Germany), must be interpreted as a lower jaw of a nautilid.

## Functional analysis and evolution of the jaw apparatus in ectocochleate cephalopods

The main distinguishing feature of the anaptychus-type lower jaw is absence of calcareous coverings and presence of a more or less marked pit in the rostral part of the inner lamella. It is likely that the upper jaw was overlapped by the lower jaw, as in recent cephalopods, and that the pit represents the place of insertion of the rostrum of the upper jaw. If this reconstruction

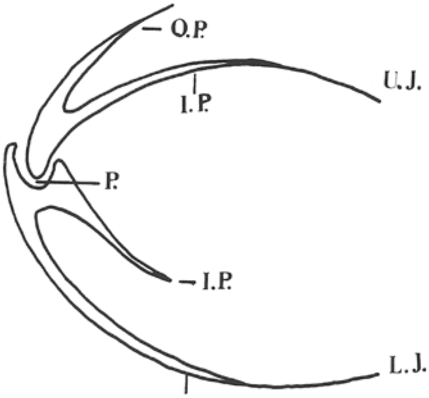


Fig. 7. Schematic longitudinal section of an anaptychus-type jaw apparatus, L. J.- lower jaw, U. J.- upper jaw, I. P.- inner plate, O. P.- outer plate, P.- inner pit.

Abb. 7. Schematischer Längsschnitt durch einen Kieferapparat vom Anaptychus-Typ, L. J.- Unterkiefer, U. J.- Oberkiefer, I. P.- Innenlamelle; O. P.- Außenlamelle, P.- innere Grube.

is correct, it may be supposed that the main action of this type of jaw apparatus was crushing (Fig. 7). In this case the older ammonoids may have preferred rather coarse food and animals with fairly hard shells.

This specialisation was absent in the aptychus-type of jaw apparatus, which is characterized by the presence of calcareous plates covering the flanks of the lower jaw. Their front edges may have supported a cutting function of the jaw, at least more so than in the anaptychus type. But the earlier suggestion of a shovel-like function (LEHMANN 1972, 1975, 1981) without too much crushing or cutting still has its merits. MORTON & NIXON (1987) suggested that the shovel-like lower jaws may have expelled water while retaining captured small prey.

The function of the nautiloid jaw apparatus is rather well known (WARD 1987). This type seems to be quite old, but well preserved fossil jaws are extremely rare, apart from the specimens described from the Cretaceous of the Far East.

In order to reach final results, future work ought to concentrate on three main intriguing topics:

a) The main morphological differences between hood-type opercula, which are one-layered simple plates, and jaw elements, in which two lamellae unite to form a beak-like structure in front, seem to render it easy to tell one from the other. The Devonian Wissenbacher and Büdesheimer Schiefer contain pertinent and promising material.

b) Several types of aptychi have been demonstrated to occur together with jaw apparati and form part of them. The thick laevaptychi, which are associated with ammonites of the family Aspidoceratidae, may be an exception. No well preserved upper jaws have been found associated with them yet. So they are an enigma which can only be solved by unusual material containing organic and inorganic components together.

c) The Upper Cretaceous genera *Gaudryceras* and *Tetragonites* need further investigation with special reference to the question whether the jaws found with them are actually autochthonous. Complete jaw apparati, possibly together with radular elements, would be convincing. But again, the calcareous matrix in which they were found is not favourable for their preservation and for an answer to the main question of this paper.

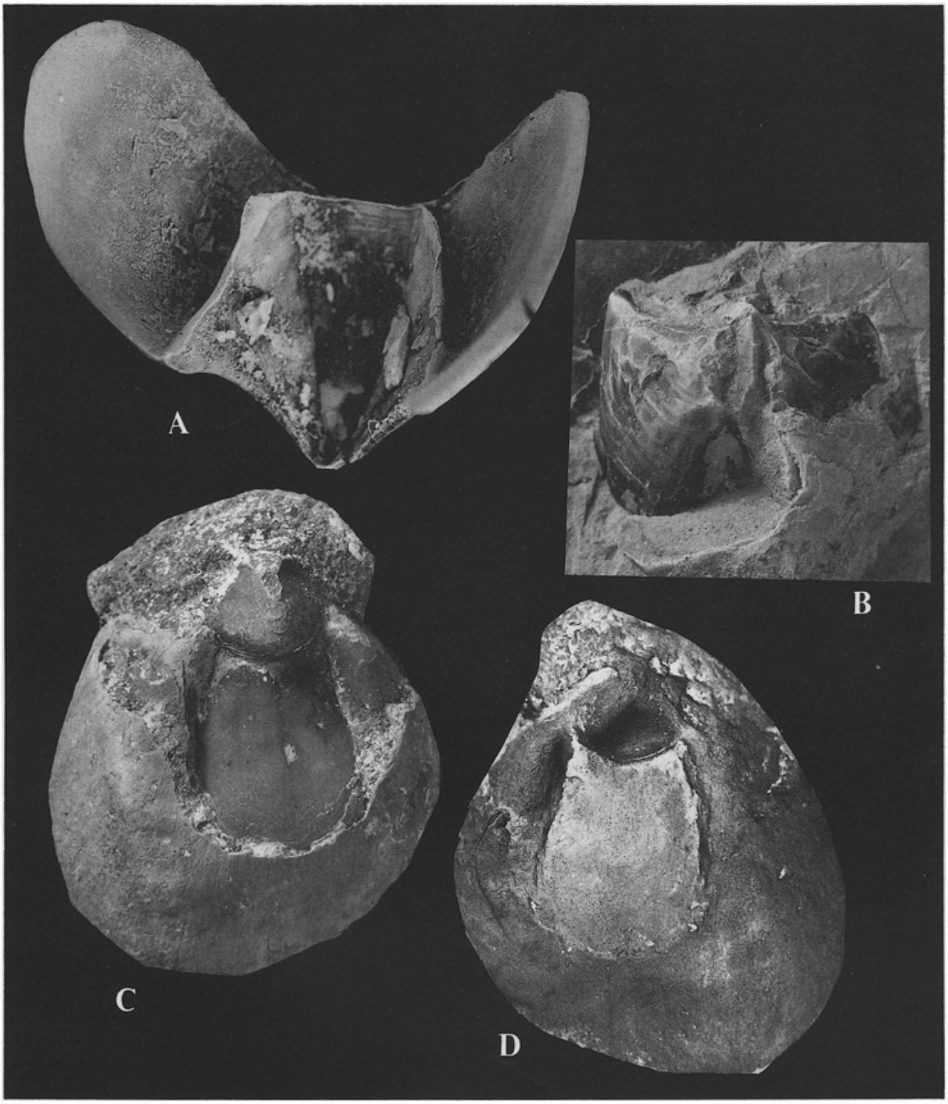


Fig. 8
A: Dorsal view of decalcified lower jaw of recent *Nautilus,* showing outer and inner lamella; 5/2 nat. size.
B: Lower jaw, described as *Anaptychus wereschagini* by ZAKHAROV (1979), Upper Cretaceous, Sakhalin Island, Naiba River; 4/1 nat, size.
C: Natural cast of central part of *anaptychus*-type lower jaw, showing central platform and inner pit. Middle Anisian, Torellneset, W-Spitsbergen; 2,5/1 nat. size.
D: Artificial positive of the natural cast of Fig. C; 2,5/1 nat. size.

Abb. 8
A: Dorsal-Ansicht des entkalkten Unterkiefers des rezenten *Nautilus* mit Außen- und Innenlamelle; 5/2 nat. Gr.
B: Von ZAKHAROV (1979) als *Anaptychus wereschagini* beschriebener Unterkiefer, Oberkreide, Sachalin, Naiba-Fluß; 4/1 nat. Gr.
C: Natürlicher Abdruck des mittleren Teils eines Unterkiefers vom *Anaptychus*-Typ mit zentraler Plattform und innerer Grube, Mittel-Anis, Torellneset, W-Spitzbergen; 2,5/1 nat. Gr.
D: Positiv-Abdruck des in Fig. C gezeigten natürlichen Abdrucks: 2,5/1 nat. Gr.

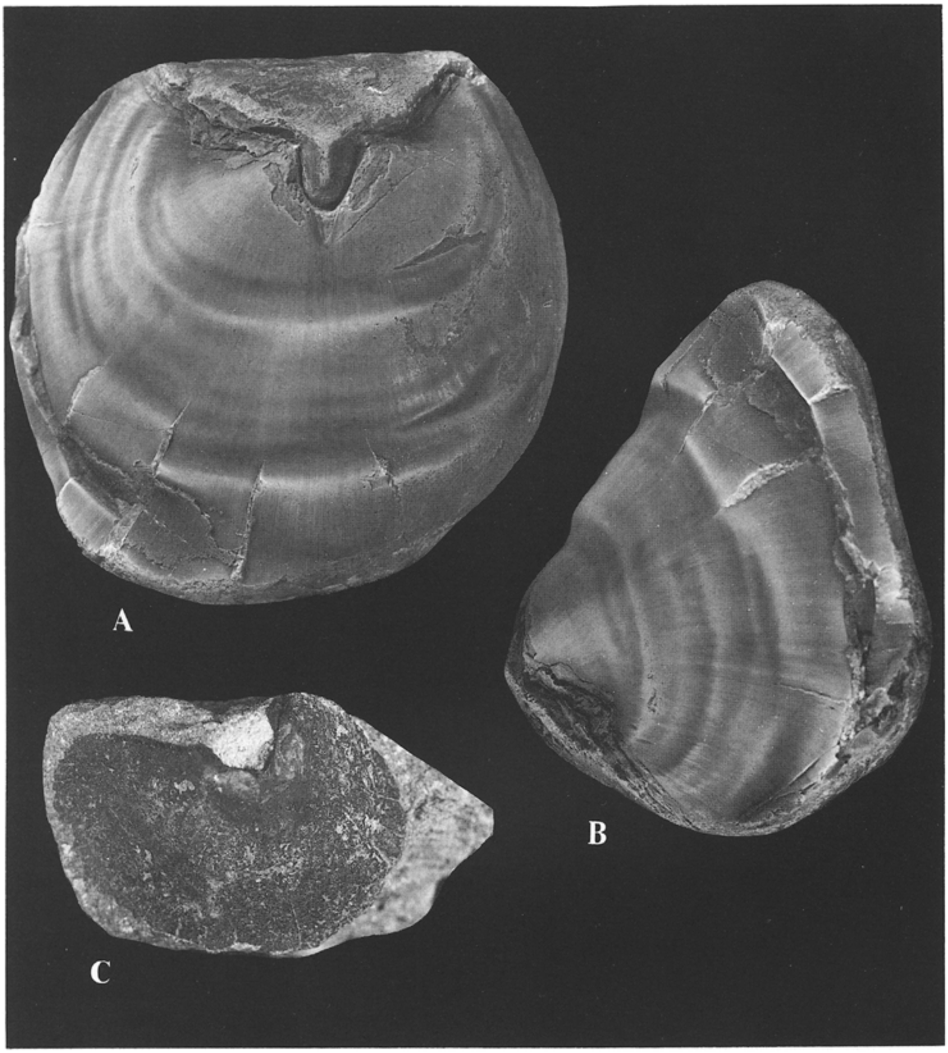


Fig. 9
A–B: Natural cast of a huge anaptychus-type lower jaw, showing inner pit. Toarcian, Yorkshire, 1/1 nat. size. A: Frontal view, B: lateral view.
C: Nautiloid lower jaw (interpreted as lytoceratid anaptychus in LEHMANN 1980: fig. 3). Pliensbachian, davoei Zone, Rottorf am Kley; 2/1 nat. size.

Abb. 9
A–B: Steinkern eines riesigen Unterkiefers vom Anaptychus-Typ mit der inneren Grube. A: Vorderansicht; B: Lateralansicht. Toarcium, Yorkshire; 1/1 nat. Gr.
C: Nautiloider Unterkiefer (von LEHMANN 1980: fig. 3 als lytoceratid angesehen), Pliensbachium, davoei-Zone, Rottorf am Kley; 2/1 nat. Gr.

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