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Uncalcified cephalopod jaws from the Middle Jurassic of Poland

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With 3 figures in the text

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Abstract: In a sample of 11 three-dimensionally preserved jaws from Łuków concretions a single unmineralized aptychus with very narrow inner lamella, an upper jaw of unknown affinities, and two types of coleoid upper jaws, probably belonging to belemnites, were identified. The coleoid jaws differ from jaws of Recent squids in having a rounded, instead of an acute, incision below the rostrum and from each other in the depth of this incision. Possible associations of the jaws with phragmocones and arm hooks occurring in the Łuków concretions, as well as phylogenetic implications, are discussed.

Key words: Cephalopoda, Coleoidea, Jurassic, belemnites, jaws, aptychi, evolution; Poland.

Zusammenfassung: Kalkkonkretionen aus der Callovium-Tongletscherscholle von Łuków, Polen, enthalten dreidimensional erhaltene Cephalopoden-Kiefer mit karbonisierter organischer Substanz. Unter 11 Kiefern sind: ein einzelner unmineralisierter Aptychus mit sehr enger Innenlamelle, ein oberer Kiefer unbekannter Stellung und zwei Typen der Coleoidea-Oberkiefer (einer mit einem Unterkiefer assoziiert), die wahrscheinlich zu Belemniten gehören. Diese Coleoidea-Kiefer unterscheiden sich von den Kiefern rezenter Kalmaren durch runden statt scharfem Einschnitt unterhalb des Rostrums und untereinander durch die Tiefe dieses Einschnitts. Beziehungen der Kiefer zu den Phragmokonen und Armhaken aus den Łuków-Konkretionen wie auch phylogenetische Folgerungen werden diskutiert.

Introduction

A lot of important information can be derived from the morphology of cephalopod jaws. The regression for relationships between the body weight and particular dimensions of the beak, calculated by CLARKE (1962) allows studies on the population dynamics based on isolated jaws (CLARKE 1977). Growth rings in the beaks can be used to study cephalopod ontogeny (CLARKE 1965). There is enough reason to expect that knowledge of the jaw morphology of extinct cephalopods could be of crucial importance in understanding their biology.

Beaks of Recent coleoid cephalopods, although unmineralized, are rather resistant to decomposition in marine sediments. They occur abundantly on the ocean bottom, in concentrations reaching 15.000 specimens per square meter

(BELYAEV 1962). Somewhat surprisingly, they appear to be extremely rare in fossil assemblages and reports on isolated coleoid jaws are virtually lacking. A relatively common occurrence of such jaws in a Callovian locality near Łuków Podlaski, Poland, is thus of special interest. A few large blocks of black Jurassic clays were deposited in the vicinity of Łuków during the Vistulian ice epoch (JAHN 1949, KOSMULSKA 1973). Their source area is most probably the bottom of the Baltic sea. The clays contain sideritic and limestone concretions, the latter extremely fossiliferous, with excellently preserved fossils. The fossil assemblage is dominated by aragonitic ammonite shells (with empty phragmocone chambers), with a subordinate contribution of benthic molluscs. The belemnites and belemnite rostra are not uncommon, with aragonitic parts of their shells unusually well preserved. Rare specimens of a single species of the nautilids have also been reported (i. a. MAKOWSKI 1952, 1962; DZIK 1984).

The cephalopod jaws occurring in the Łuków concretions are preserved as empty cavities in the limestone matrix, partially filled up with a black carbonized organic matter. Only the thickest rostral parts of the beaks are completely preserved, while the thin proximal parts are more or less fragmentary. Their remains are usually shrunken or folded.

Specimens described here are housed in the collection of the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw (abbreviated ZPAL).

The problem of taxonomic identifications

Jaw apparatuses of four kinds are represented among specimens collected in Łuków. Only in one case do both the upper and the lower jaws match. Even the most similar among these types are still quite distinct morphologically from each other. In fossil assemblages from the Łuków clays virtually all cephalopod genera (with the possible exception of *Quenstedticeras*, which still awaits biometrical population studies) are represented by a single species. It seems neither necessary nor sensible to create new Linnean names for the beak types particularly as there is reason to doubt whether allopatric species of the same genus differ enough in morphology of their jaws to be recognizable on this basis. According to CLARKE (1962: 442) »it is probably impossible to identify the species from a beak (unless some chemical means is found), but familiés may be identified by reference to quite distinct characters« (but see also CLARKE & KRISTENSEN 1980). Presumably the shell morphology will remain the best basis for recognition of fossil cephalopods.

Dealing with structures as poorly known and uncharacteristic as jaws of extinct cephalopod groups there is always risk of misinterpretation. There are many fossils which are superficially similar to jaws and have been attributed to cephalopods. In some cases, like the polyplacophoran plate described as a nautiloid jaw, it was already possible to identify true relationships (YOCHELSON

1971). Many doubtful findings still await proper identification (i. a. CLOSS et al. 1964). Three recent descriptions may be briefly commented on here. RENZ (1978) erected a new genus and species *Rhynchocameratus jonicus*, which was based in fact on radial plates (interpreted as a lower jaw) and winged brachials (supposed to be an upper jaw) of a planktic crinoid *Saccocoma*, the name of which is consequently its senior synonym (see PISERA & DZIK 1979). Supposed aptychi of a nautilid *Liroceras* are bivalve shells, as evidenced by the mode of increment (THOMPSON et al. 1980: Pl. 1: 7) which is in the opposite direction to that of the real calcitic aptychus. ZAKHAROV & LOMINADZE (1983) have published description of a Permian fossil named by them *Permiorhynchus dentatus*, which was interpreted as a lower coleoid jaw. Both the general shape and the microstructure suggest vertebrate affinities. Histologically, it is like a phosphatic bone and may represent a jaw of a *Dorypterus*-like fish.

The jaws described here do not exhibit any jaw angle, which demarcates rostral parts in Recent coleoid beaks. The terminology proposed by CLARKE (1962) for the squid jaws thus cannot be adequately applied to these fossil jaws. Nevertheless, I do not introduce any new terms, preferring rather to use neutral terms (like »outer and inner lamellae« of LEHMANN (1972)), that are understandable without special explanation.

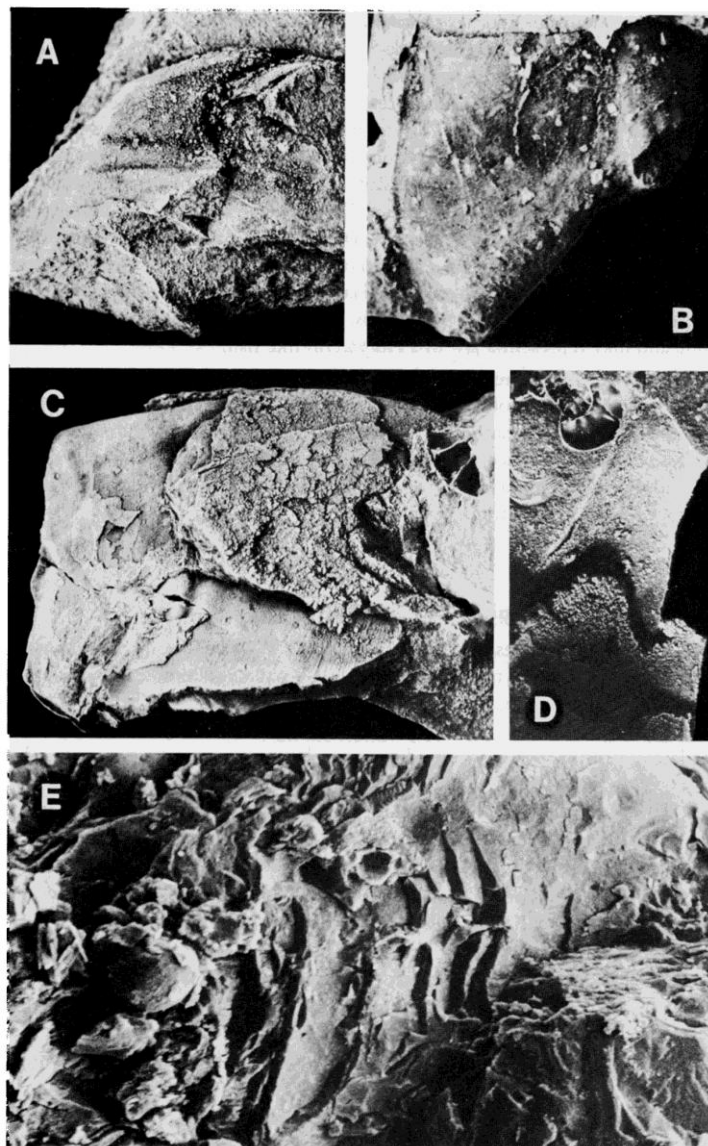
Descriptions

A jaw of unknown affinities (Figs. 1C–E, 3F–G)

A single but well preserved upper jaw (ZPAL V.XVI/6) represents the most enigmatic jaw apparatus type in the collection. What makes this beak quite different from all other cephalopod beaks from Łuków is its unusually thin cutting (»inner«) edge. Owing to its thinness and consequent incomplete preservation the lateral profile of the cutting edge cannot be reconstructed completely reliably but it was probably almost straight, without any significant incisions (Fig. 3G). The inner lamella reaches its greatest thickness in the midlength, where it is significantly (secondarily?) mineralized. Macroscopically, the wall shows lamellar texture and exfoliates easily. Scanning electron micrographs show it to have an almost amorphous microstructure (Fig. 1E), presumably composed of sparitic calcite.

Although the dorso-proximal margin of the inner lamella and ventral parts of the outer lamella are broken away, their outlines can be safely reconstructed. Delicate concentric growth lines are recognizable in the marginal parts of the outer lamella indicating the original shape of this part of the beak. An outline of the inner lamella can be inferred from the course of concentric, somewhat irregular wrinkles (Fig. 1C), which probably follow growth increments.

I was not able to find descriptions of any morphologically similar jaws in the literature. They probably do not belong to ammonites because of the well deve-



oped dorsal wall of the outer lamella, which is reduced in known upper ammonite jaws (LEHMANN 1972, 1980; TANABE 1983). The acute appearance of the dorsal part of the inner lamella (crest) in its cross section makes it rather dissimilar to other coleoid upper jaws from Łuków although such an appearance is not uncommon among Recent squids. There is some similarity between the outline of the studied specimen and that of the upper jaw of Recent *Nautilus* (see GASIOŁOWSKI 1973, SAUNDERS et al. 1978). Nautilids are known to occur in the Callovian of Łuków, namely *Cenoceras calloviense* (OPPEL, 1867). Adult specimens of this species are less than 10 cm in shell diameter (DZIK 1984) – it seems unlikely for an animal of this size to have an upper jaw length of 13 mm. Members of the order Nautilida are believed to possess calcified rostra of their jaws since Triassic times. To interpret this jaw as a nautilid would require secondary exfoliation of a calcareous rhyncholite from the organic jaw rostrum, which can be easily made artificially (SAUNDERS et al. 1978) in Recent *Nautilus*. The shape of the rostrum and rather low angle between the outer and inner lamella makes it unlikely that a rhyncholite was present originally.

An ammonite jaw (Fig. 1B)

Only the left half of a lower jaw (aptychus) is present in the collection. The wall of the outer lamella is very thin and completely organic, without any signs of mineralization. Low, indistinct wrinkles run concentrically, probably parallel to the outer margin of the aptychus. A gentle bending of the outer lamella indicates that it had considerable elasticity prior to the fossilization. The inner lamella is very narrow and forms only a sharp ridge along the cutting edge of the aptychus.

LEHMANN (1972: 40, Pl. 10: 3) illustrated a complete aptychus of the same type from Łuków and identified it as belonging to a species of *Quenstedticeras*. Ammonites of this genus are the most common in the Łuków concretions but it is possible that this type of aptychus may represent a species of *Kosmoceras*, which is another common, though subordinate, member of the fauna. Other ammonite genera (see MAKOWSKI 1952, 1962) are very rare in Łuków and therefore unlikely to belong to the discussed aptychus.

Fig. 1. A: Coleoid type B, upper jaw ZPAL V.XVI/1, lateral view. Note wrinkles in the proximal part of the outer lamella. – B: Left valve of the aptychus of ?*Quenstedticeras* sp. ZPAL V.XVI/3. C–E: Upper jaw of undetermined affinities ZPAL V.XVI/6. C: Lateral view of the inner lamella; note its considerable thickness in the centre. D: Ventral view of the counterpart; note outline of the rostrum and relationship between the outer and inner lamellae. E: Breakage of mineralized wall of the inner lamella under SEM. Except of E, which is $\times 1200$, all remaining pictures $\times 5$.

Coleoid jaws

Type A (Figs. 2A–E, 3C–E). – Both the upper and lower jaw of this type were found in a single piece of the rock (Fig. 2D). They are almost in contact although displaced in such a way that their rostra are oriented outwards. Despite this displacement it seems almost certain that they are parts of the same beak apparatus.

Five other upper jaws have been found. The cutting edge has a characteristic profile, with a rather shallow and widely gaping notch (Figs. 2A, 3E). With the possible exception of specimen ZPAL V.XVI/9 (Fig. 2B), which is rather tentatively attributed to this type, both the outer and inner lamellae are only fragmentarily preserved. Most probably the margin of the shoulder was nearly parallel to the dorsal wall of the inner lamella (Fig. 3E). A line of contact between the lamellae approaches the shoulder almost perpendicularly.

The lower jaw was rather robust, with very thick organic outer lamella in its rostral parts (Fig. 2E) and very thin and only partially preserved (Fig. 2D) inner lamella. The cutting edge of the rostrum is bordered by triangular thickened areas. Here the wall is at its thickest. Free margins of both inner and outer lamellae are trapezoidal in cross section, with the crest and corresponding parts of the rostrum flattened (Fig. 2E, 3D).

Type B (Fig. 1A, 3A–B). – A single upper jaw, which is otherwise similar to jaws of type A, shows a very distinct lateral profile of the rostral parts. It differs from the jaws described above in a much deeper, parabolic notch below the rostrum. Accordingly, the shoulder area is transformed in such a way that the margin of the shoulder is almost perpendicular to the rostrum. A few wrinkles visible on the outer lamella of the specimen suggest that there was a rather elongated outer lamella («hood»). The inner lamella is preserved very fragmentarily.

These two types of coleoid jaws are so similar to each other that they doubtlessly belong to closely related species. They may be derived from a hypothetical common ancestor by a simple transformation of shapes. In the Callovian age the Coleoidea were represented by the belemnites, squids and sepiids (DONOVAN 1977). Members of each of these groups can be considered as potential possessors of these jaws.

Jaws of Late Jurassic vampyroteuthid (?) squids from the Solnhofener Plattenkalk have not yet been described in detail. Judging from published illustra-

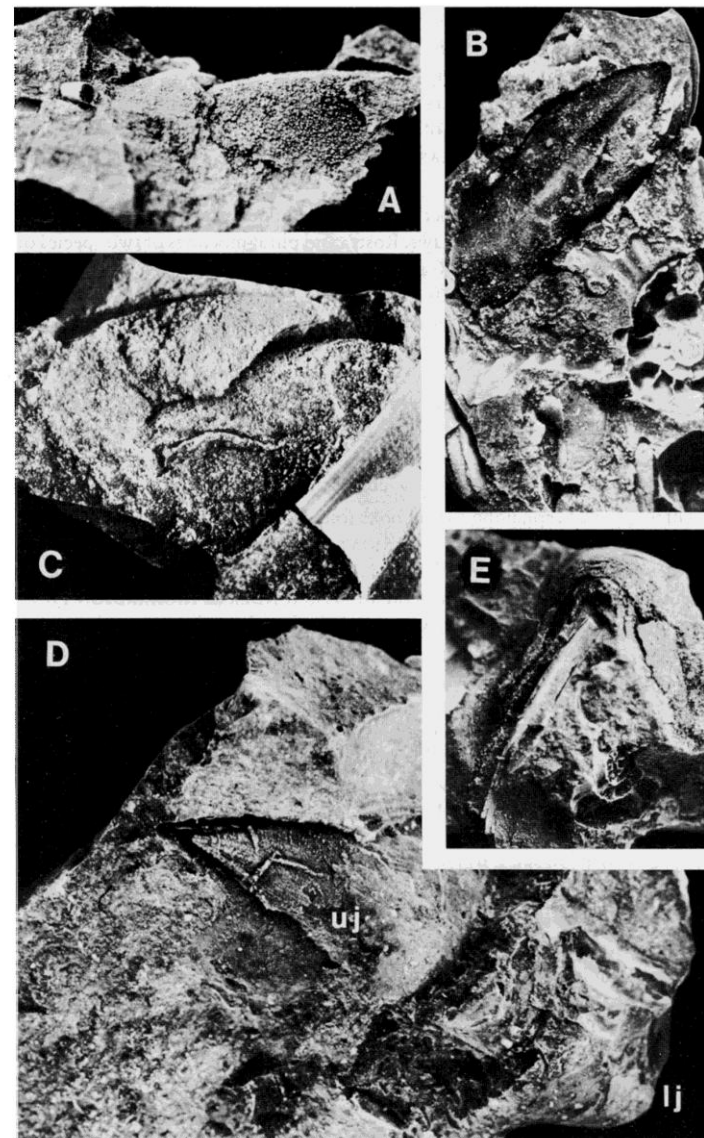


Fig. 2. Coleoid type A jaws. A: Lateral view of the upper jaw ZPAL V.XVI/2. B: Dorsal view of the upper jaw ZPAL V.XVI/9. C: Lateral view of a very large upper jaw ZPAL V.XVI/8; note the shape of the basal cavity. D–E: Displaced lower and upper jaws probably representing the same apparatus ZPAL V.XVI/7; D: Lateral view of the upper jaw (uj) and a dorsal view of the lower jaw (lj); note partially exposed inner lamella. E: Occlusal view of the rostrum of the lower jaw. All $\times 5$.

tions (NAEF 1922: Fig. 42f) their rostral angle is like that of all Recent squids which would argue against the jaws from Łuków belonging to the Teuthida or Vampyroteuthida.

The lower jaw of type A bears some similarity to corresponding jaws of Recent sepiids; but the upper jaw of *Rossia* has an angle below the rostrum quite similar to that in squid jaws (CLARKE 1962), which argues against a relationship with the sepiids.

Three species of Coleoidea occur in Łuków abundantly enough to be considered as possible owners of the jaws. Rostra and phragmocones of two species of belemnites are known from the Callovian of Łuków. *Aulacoteuthis* cf. *altdorfensis* (BLAINVILLE) (see RIEGRAF 1980) is the most numerous one, with 16 specimens in the collection. *Cylindroteuthis* sp. (3 specimens) is also not rare. Nothing is known of the morphology of jaws in the Belemnitida, so no direct comparison is possible. In their Triassic relative *Phragmoteuthis*? *ticinensis* RIEBER jaws are known that do not have a squid-type rostral angle (see RIEBER 1970) although the specimen preservation is too poor for jaw structures to be reliably characterized. Phragmocones of a belemnite *Belemniteuthis polonica* MAKOWSKI are relatively common in the Łuków concretions (6 specimens collected).

Three types of cephalopod arm hooks (onychites) are known to occur in the Callovian of Łuków (KULICKI & SZANIAWSKI 1972). The onychites (see also WIND et al. 1976 for additional data on morphology) are associated with phragmoteuthids (DONOVAN 1977), aulacoteuthids (SAUNDERS & RICHARDSON 1979), and also with belemnites (RIEGRAF 1980). Whether these three named types of onychites from Łuków really represent distinct species and which of them eventually corresponds to particular phragmocone species and jaw type is not yet certain. Nevertheless, it may be worth noting that a form of arm hooks named *Deinuncus brevirostris*, which is closely related to one of the Łuków onychite types (to *D. longirostris*) occurs in the Volgian of Poland (KULICKI & SZANIAWSKI 1972) where belemnites are totally lacking. Onychites of this type (without spur) must thus belong to the belemniteuthids or another unknown group of Jurassic cephalopods which lack a calcitic rostrum but possess arm hooks (see RIEGRAF & REITNER 1979; ENGESER & REITNER 1981). There is thus a possibility that *D. longirostris* KULICKI & SZANIAWSKI is a younger synonym of *Belemniteuthis polonica*. *Arcuncus makowskii* KULICKI & SZANIAWSKI and *Paraglycerites* sp. A may turn out to correspond to the two species of the Łuków belemnites. Perhaps at least the type A jaw is a belemnite one.

Evolution of cephalopod jaws

It has been experimentally shown that in Recent dibranchiate cephalopods the jaw apparatus is involved in biting the food, which is afterwards transported to the oesophagus owing to an action of the radula and the dorsally located buc-

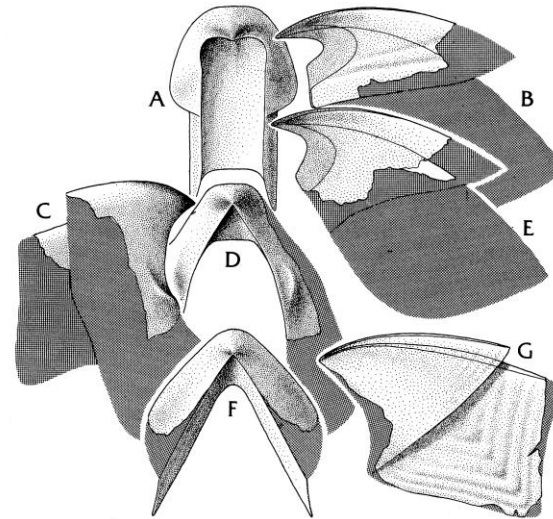


Fig. 3. Reconstructions of coleoid jaws from Łuków. A–B: Coleoid type B, upper jaw in occlusal and lateral views. C–E: Coleoid type A, lower jaw in lateral and occlusal views and upper jaw in lateral view. F–G: Upper jaw of undetermined affinity in occlusal and lateral views. The shaded parts are hypothetical. Approximately $\times 3$.

cal palps. The lower and upper jaws evidently perform different functions. The lower jaw does not move during feeding. It functions mainly as a support for the muscles, which are attached to its wings. Contracting, they move the upper jaw, which acts by lowering and raising its rostrum. The role of the lower jaw, which is located slightly in front of the upper jaw in the oral area, is more important than that of the upper jaw in fragmentation of the food (ALTMAN & NIXON 1970).

The upper and lower jaws may also be different in their origins. The lower jaw, which in ammonites and some orthoconic nautiloids performed the function of an operculum, was proposed to be a homologue of the operculum of the gastropods (DZIK 1982). The aptychi and anaptychi are, according to this interpretation, the most ancient and primitive types of cephalopod lower jaw. Their inner lamellae developed phylogenetically late in order to strengthen the cutting edge of the jaw and to permit an effective cutting action. Along with the development of the buccal cavity and the buccal musculature, the inner lamella ex-

panded in width to provide a lining of the cavity and to prevent its collapsing as a result of muscle contraction.

Data on the morphology of unmineralized lower jaws from the Jurassic, presented above, fit the proposed interpretation of their phylogeny. The inner lamella in the aptychus from Łuków is very narrow, which may be a primitive feature. In calcified aptychi the original organic linings are usually not preserved and even if their remnants can be recognized one cannot be certain of the original relationship between the outer and inner lamellae. In the case of the Łuków material, with the outer and inner lamellae preserved in the same way, there is little doubt that the record is reliable. The inner lamella in the lower jaw of Recent *Nautilus* is much wider than in Jurassic aptychi but still not as wide as the outer lamella. The inner lamella expands beyond the margin of the outer lamella in the coleoid lower jaw. The Jurassic coleoid jaw probably had a wider inner lamella than outer one, but still very thin, and the outer lamella contributed much more to the mechanical function of the jaw. The jaw from Łuków shows strengthened elevated areas on its shoulders to support the working part of the jaw apparatus. Thus, also in Jurassic times the lower jaw was mechanically the basic part of the apparatus. Later, in the myopsid and oegopsid squids, a sharp incision (angle) developed, which separated the rostrum from the shoulders. Originally, presumably, the cutting edge of the coleoid jaw was almost straight similar to the condition in the jaws of Nautiloidea and Ammonoidea.

The origin of the upper cephalopod jaw is even more enigmatic. I proposed that the triangular element complementing the aptychus of some Silurian ariococeratid nautiloids represents an initial upper jaw (DZIK 1982), but this was opposed by TUREK (1983) and STRIDSBERG (1984). It should be noted that objections raised against this interpretation, on the supposed grounds of spatial constraints on the action of the jaw apparatus in my model (STRIDSBERG 1984), are not valid. When not arranged into an oval defensive structure but acting as a jaw, the triangular element had to be oriented perpendicularly to the hinge of the aptychus and a lot of free space was then left allowing sufficient bending of the aptychus. Nevertheless, the internal structure of this element is not known, which leaves room for much speculation. It is obvious that relationships between the two valves of the aptychus and the triangular median element were of different nature. This element was not firmly attached to the rest of the opercular apparatus (TUREK 1983).

The upper jaw of the ammonites had its inner lamella much wider than the outer one – opposite to the relationships in the lower jaw (LEHMANN 1972, 1980). Usually the dorsal surface of the beak is concave and the respective part of the inner lamella is missing, perhaps to accommodate the shape of the body chamber in involute shells. The upper jaw of the nautilids developed a calcitic rhyncholite (LOWENSTAM et al. 1984), which, at least since the Triassic, covers the rostrum

but otherwise the organic part does not differ from upper jaws of the coleoid cephalopods.

New data on the morphology of Jurassic cephalopod jaws provide additional evidence that in ancient cephalopods upper and lower jaws were quite dissimilar to each other and that apparent structural similarity between the respective parts of the jaw apparatus of Recent squids developed late in their phylogeny. Features that could be expected in any primitive cephalopod jaw apparatus are shown by the single upper jaw of unknown affinities from Łuków. The two types of coleoid jaw from Łuków, having rather uniform design, differ only in their more (type B) or less (type A) deeply incised rounded notch between the rostrum and the shoulders. This recalls conditions in sepiid jaws. This may mean that upper jaws with a well developed sharp jaw angle, typical for Recent vampyroteuthid, myopsid, and oegopsid squids, developed after separation of their clade from that leading to the sepiids.

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