Nautilus-like Jaw Elements of a Juvenile Ammonite

(*Nautilus*-artige Kiefer-Elemente in einem juvenilen Ammoniten)

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With 4 Text Figures

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Abstract: The jaw apparatus of a juvenile ammonite was investigated; the individual's shell is 0.96 mm in diameter and the jaw apparatus is composed of an upper and lower jaw. The upper jaw is calcified and does not differ from any known specimens. The lower jaw consists of two elements: an apical calcitic conchorhynch and a typical aptychus occupying the position of the external lamella. The concept of a lower jaw origin for the aptychi and a double function of the lower jaw in aptychi-bearing ammonites is confirmed.

Kurzfassung: Der Kieferapparat eines juvenilen Ammoniten, mit einem Gehäusedurchmesser von 0,96 mm, besteht aus Ober- und Unterkiefer. Der Oberkiefer ist verkalkt und wie bei anderen Ammoniten gebaut. Den Unterkiefer bilden zwei Elemente: ein apikal gelegener, kalzitischer Conchorhynchus und ein typisch gebauter Aptychus, der die Lage der Aussenlamelle einnimmt. Unbestritten ist, daß die Aptychen sich aus dem Unterkiefer entwickelt haben, und daß der Unterkiefer bei den meisten Ammoniten eine Doppelfunktion (Unterkiefer und Operkulum) hatte.

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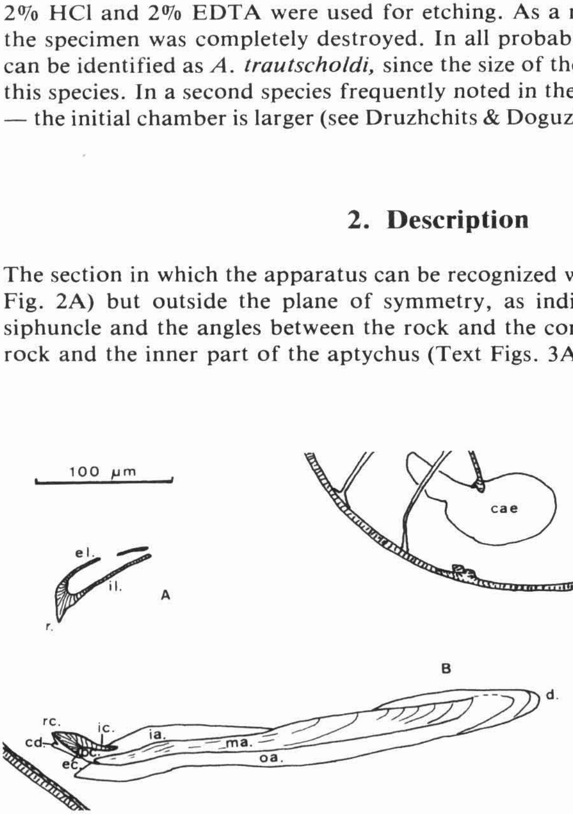
1. Introduction

The findings of ammonite jaw apparatuses are rare; the history of their study began in 1967 when two separate papers were published by Closs and Lehmann describing the jaw apparatuses inside the shells of adult specimens. Later, Lehmann (1970, 1972) suggested that the anaptychi and aptychi in ammonites are actually lower jaws and that they act both as lower jaws and opercula. According to Lehmann's concept, the anaptychi and aptychi are homologous to the external lamella of Recent cephalopods. Kulicki & Wierzbowski (1983) described a jaw apparatus from a juvenile ammonite characterized by the presence of a distinct calcified conchorhynch in addition to the internal and external lamellae; as this specimen was discovered in a thin section, detailed microstructural observations were impossible.

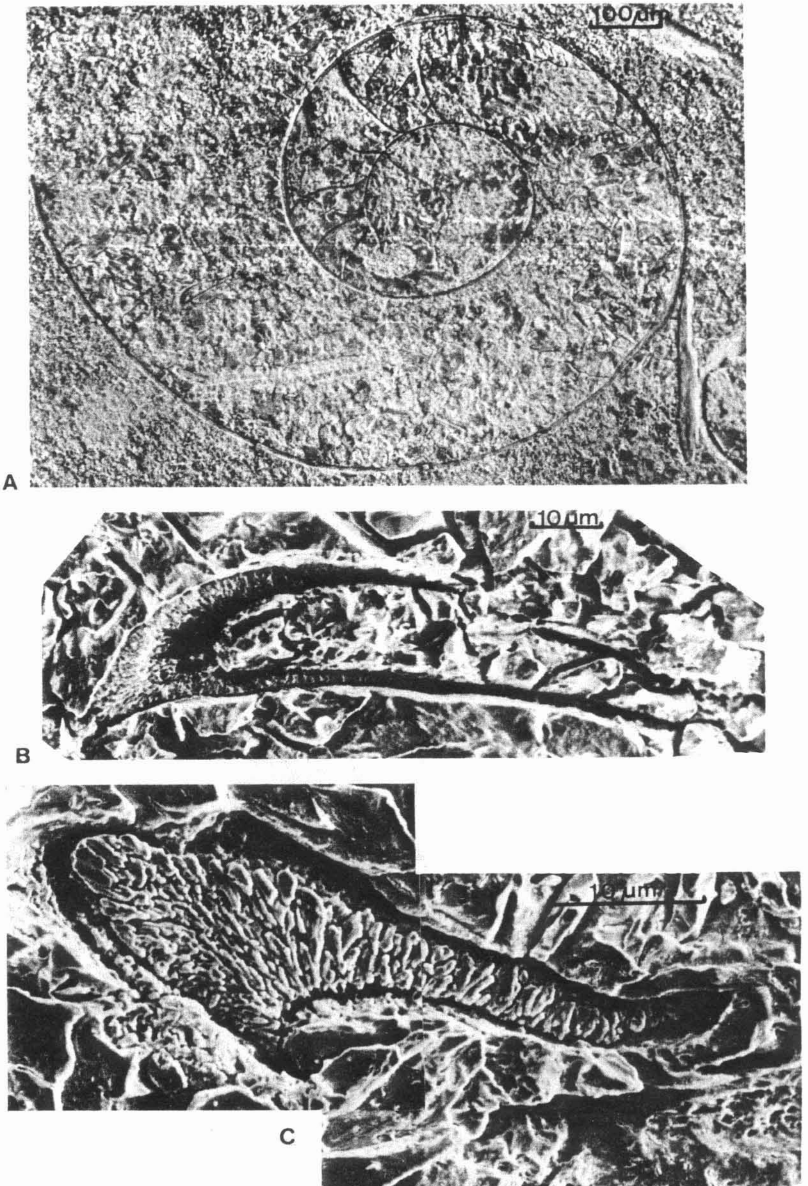
The present paper is based on one very well preserved specimen derived from a concretion in Lower Cretaceous (Aptian) clays found along the Volga River in the Ulianovsk area, central Russia, USSR. Concretions from this area abound in ammonites, such as *Aconeceras trautscholdi* Sinzov and *Deshayesites deshayesi* Leym. The concretion from which the described apparatus is derived is extremely rich in ammonitella stage ammonites. Small cubes cut from the concretion were serially sliced, polished, etched, coated with gold, and examined under the SEM. 2% HCl and 2% EDTA were used for etching. As a result of succesive sectioning the specimen was completely destroyed. In all probability, the specimen examined can be identified as *A. trautscholdi,* since the size of the initial chamber is typical of this species. In a second species frequently noted in the concretions — *D. deshayesi* — the initial chamber is larger (see Druzhchits & Doguzhaeva 1981: 109, 113).

2. Description

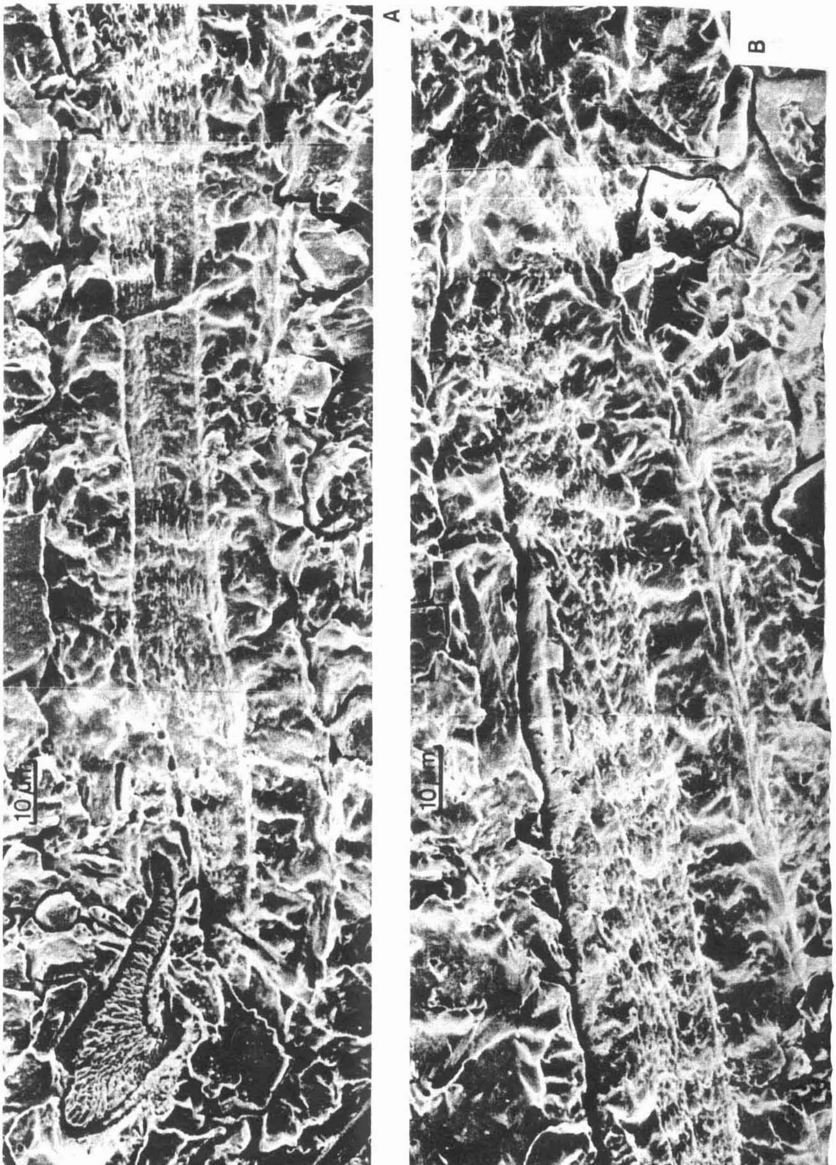
The section in which the apparatus can be recognized was close to the median (Text Fig. 2A) but outside the plane of symmetry, as indicated by the picture of the siphuncle and the angles between the rock and the conchorhynch and between the rock and the inner part of the aptychus (Text Figs. 3A, 3B). Because the specimen



Text Fig. 1. Schematic drawing of the sectioned jaw apparatus and nomenclature of its details. 200×. A - upper jaw; B - lower jaw; cae - caecum; cd - calcarous deposit on the external surface of the conchorhynch; d - distal part of the aptychus; ec - external lamella of the conchorhynch; el - external lamella of the upper jaw; ia - inner layer of the aptychus; ic - internal lamella of the conchorhynch; il - internal lamella of the upper jaw; ma - middle layer of the aptychus; oa - outer layer of the aptychus; pc - "pulp cavity"; r - rostrum of the upper jaw; rc - rostrum of the conchorhynch.



Text Fig. 2. A. General view of the sectioned juvenile shell, with jaw apparatus inside the body chamber; B. Upper jaw; C. Apical part of the lower jaw (or conchorhynch).



Text Fig. 3. General view of the lower jaw. A. Proximal part of the jaw; B. Distal part of the jaw.

was cut beneath its plane of symmetry, the real proportions of some elements as well as their sizes could be distorted.

The 0.96 mm specimen has seven septa. The length of the body chamber is 280° and its aperture is situated 145° behind the termination of the nepionic swelling. The height of the aperture is 0.36 mm. The jaw apparatus is situated in the body chamber at 1/3 of its length from the aperture and consists of an upper and a lower jaw. No radula has been found. The position of the jaw apparatus within the body chamber seems natural and unaffected by postmortem decay or burial (Text Fig. 2A).

In the section, the upper jaw has a typical shape, the internal and external lamellae being of equal length. The entire upper jaw is calcified. The separate prisms are arranged regularly, i.e., perpendicularly to the surface of both lamellae and radially in the rostral part. The length of the upper jaw from the apical part of the rostrum to the end of the external lamella is 88 μm (Text Figs. 1, 2B).

The lower jaw is built of two microstructurally different elements. The apical element is calcified in the same way as the upper jaw, consisting of a rostrum, an internal lamella, and a very narrow part corresponding to the external lamella. A shallow cavity in the basal part between the two lamellae resembles a "pulp cavity" (Text Figs. 1, 2C). The length of the apical element from the tip of the rostrum to the end of the internal lamella is 46 μm. The external surface of the rostrum and the external lamella has a calcareous coating, microstructurally slightly different from the remaining apical element.

The main part of the lower jaw is built of three layers: middle, outer and inner (Text Figs. 1, 3A, 3B). The middle layer has a fine laminar structure with individual laminae wedging out at its inner surface. The outer laminae are thus the longest, while the inner ones are shortest. In the distal part, the thickness of the individual laminae gradually increases. The outer layer is coarsely crystalline and grades into the coarsely crystalline material of the last distally deposited laminae.

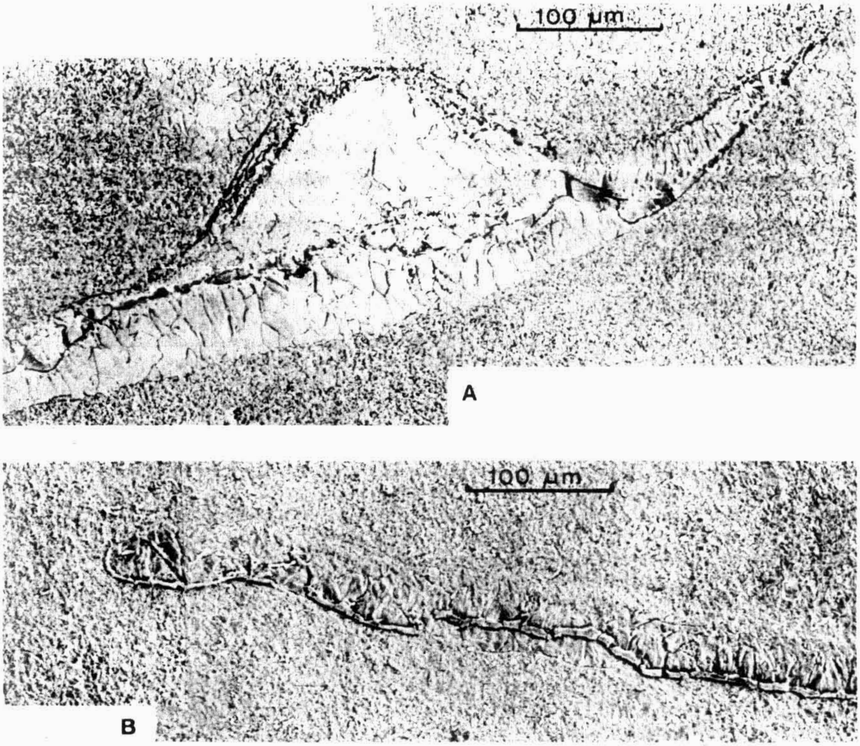
The inner layer is confined to the inner apical surface (Text Fig. 3A). The inner lamella of the apical element is partly incorporated in the coarsely crystalline material of the inner layer, which also fills the "pulp cavity (Text Fig. 3A).

3. Discussion and comparisons

The longitudinal section of the upper jaw of the juvenile specimen described here is fairly typical and comparable with sections of other ammonites, e.g., *Dactylioceras* (Lehmann 1979, pl. 27, fig. 1) and *Gaudryceras* (Tanabe, Fukuda, Kanie & Lehmann 1980, fig. 9D). In various ammonites observed in longitudinal sections, the ratios between the lengths of the external and internal lamellae vary and are therefore rather meaningless. The feature distinguishing the upper jaw of our specimen from other known findings is its complete mineralisation. The upper jaws of *Parkinsonia* and *Dactylioceras* described by Lehmann (1978, 1979) are built entirely of organic substance. Those of *Tetragonites* and *Neophylloceras* discussed by Tanabe, Fukuda, Kanie & Lehmann (1980) and *Scalarites* described by Tanabe, Hirano & Kanie (1980) are also built of organic matter, their rostral part, however has a calcareous covering similar to that in Recent *Nautilus* rhyncholite. The jaw apparatus of the juvenile perisphinctid described by Kulicki & Wierzbowski (1983) has a rhomboidal calcite element instead of a complete upper jaw. This element has been interpreted as a rhyncholite, but there is no absolute certainty whether it is a real rhyncholite, or whether both lamellae have perhaps been destroyed.

Lower jaw: In its shape and position, the apical element of the lower jaw described is comparable to the conchorhynch of the ammonite of the Jagua Formation (Kulicki & Wierzbowski 1983) and that of Recent *Nautilus*. The conchorhynch of the juvenile ammonite of the Jagua Formation is situated entirely on the external lamella of the lower jaw, whereas the conchorhynch described in the present paper is situated mainly on the inner surface of the jaw, as indicated by the strongly developed internal lamella and only slightly developed external one. Similarly situated on the inner surface of the lower jaw is the calcitic part of the conchorhynch in Recent *Nautilus* (see Lowenstam et al. 1984, fig. 4b).

The structure and growth lines of the elongated and largest element of the lower jaw described here are typical of aptychi (see Schindewolf 1958, Farinacci et al. 1976). Its position coincides with the position of the external lamella in Recent *Nautilus* and in ammonites. In the section shown in Text Figs. 2C & 3A, the connection between the rudimental external lamella of theconchorhynch and the middle layer of the aptychus is not preserved. Most probably this connection was not preserved because it was thin and fine like that observed in Recent *Nautilus* (Lowenstam et al. 1984, fig. 4b) and in the ammonite of the Jagua Formation (Kulicki & Wierzbowski 1983, fig. 3A). Also similar is the double bending of the external lamella of the lower jaw in the juvenile ammonite of the Jagua Formation and the laminae of the middle layer in the apical part of the aptychus presented here. Two mineral components — calcite and aragonite — are reported from jaws of Recent *Nautilus* by Lowenstam et al. (1984). The "ventral lamella" of Lowenstam et al. (1984, fig. 4b) is built solely of aragonite. The position of the "ventral lamella" is comparable to that of the aptychus described by the present authors, which differs in microstructure from the conchorhynch belonging to the same jaw, making our homology more probable. In Recent *Nautilus,* the space between the external and internal lamellae is filled with organic matter (the "protein-chitin complex" of Lowenstam et al.) left by soft tissue receding with growth. In our specimen this space is filled with calcite; in addition, the internal lamella of the conchorhynch is partly incorporated in the calcite of the inner layer. Such filling of the "pulp cavity" and the partial incorporation of the internal lamella of the conchorhynch into the calcite of the inner layer suggest that the soft tissue receded with growth from the "pulp cavity" and that the conchorhynch itself was either completely rejected (like milk teeth in mammals) or completely incorporated into the calcite of the inner layer. This conclusion is supported by the structure of the apical parts of the aptychi found in the same concretions in the Aptian of the Volga River area. The calcite building the body of the aptychus has the same microstructure as the outer layer and the distal part of our specimen. The aptychi have a distinct swelling on their inner side and are sharply pointed close to median plane (Text Fig. 4A). The sharpe edge is lacking in the lateral parts (Text Fig. 4B). This swelling can be compared only to the inner apical layer in a juvenile ammonite.



Text Fig. 4. Sections of the inner margin of the aptychus. A. close to median plane, the sharp edge and inner swelling are well developed; B. Lateral part.

4. Conclusions

1. In the very early postembrional stage, the lower jaw in ammonites consists of two microstructurally different parts: an apical conchorhynch and an aptychus situated behind it.

2. In ammonites, the conchorhynch is a rudiment inherited from ancestors and occurs only in juvenile stages. In other words, during their development ammonites recapitulate the stage of their ancestors with a jaw apparatus similar to Recent *Nautilus.*

3. The aptychi are elements comparable to the aragonite element in the external lamella of Recent *Nautilus*.

4. During later ontogenetic development, secretion in the apical part of the lower jaw is disorganised to such an extent that the formation of a primary (embryonal) conchorhynch is discontinued.

5. The above data clearly indicate that the lower jaw origin of the aptychi as well as their double function as a lower jaw and operculum are unquestionable.

6. Ammonites differ widely in the development of their lower jaw, from aptychi to *Nautilus*-type jaws as in *Gaudryceras* and *Scalarites*. Similar evolutionary trends resulted in the independent formation of "aptychi-type" jaw apparatuses in Nautiloids, as for example in *Aptychopsis* (see Turek 1977, Stridsberg 1983).

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