

## 10 | Ammonite Jaw Apparatus and Soft Parts

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**Abstract:** A short review is given of former interpretations of aptychi and anaptychi. The complete jaw apparati of 15 ammonoid genera (7 aptychi, 8 anaptychi) have been found within the living chamber of their ammonites. Ammonite jaws (aptychi and anaptychi) tend to become considerably longer than the corresponding upper jaws. Three types of jaw apparati in ammonoids are distinguished, the first resembling the jaw apparati of recent coleoids, the second characterized by lower jaws of the aptychus and anaptychus kind, the third equipped with calcareous beaks like those of recent *Nautilus*. The function of the jaw apparatus is discussed.

Short remarks on radulae, crop contents and ink sacs indicate the possibilities for further investigations of ammonoid living chambers.

Scientific progress in palaeontology depends largely on the availability of material, its preservation and on the research methods which can be applied to it. This can be exceptionally well demonstrated by the study of ammonite jaws and the theories developed about them, for three reasons:

- (1) The jaws of ammonites are not connected with the shells and will normally be separated from them after the animal has decayed.
- (2) The jaws consist of chitinous material or of a combination of chitinous and calcareous material, the preservation of which follows different lines.

- (3) Some lower jaws have developed in a strange way with the result that they do not look like jaws any more. They have been given special names: anaptychi are univalved chitinous plates; aptychi are bivalved calcareous plates. In many cases the outlines of both correspond roughly to the transverse section of the corresponding ammonite peristome.

The most thorough descriptions of anaptychi and aptychi were published by F. Trauth in a series of papers between 1927 and 1938. He mentioned the often bizarre ideas of earlier authors about what these structures might have been. At first they were not thought to be a part of ammonoids at all, but plates of cirrepedes inhabiting the living chamber in some kind of commensal relationship, or carapaces of predatory phyllocarids who had eaten the ammonoids, or, vice versa, the remnants of animals eaten by ammonoids, such as worms, bivalves, fish and even birds. Trauth himself and the majority of later authors definitely considered them to be part of the corresponding ammonoid, most probably protective opercula. Other interpretations were: calcifications of the stomach walls; protective organs for the gills or for the nidamental glands; inner shells of parasitic males living within the living chamber of the females; calcified rests of hood-like structures or even lower jaws (Meek and Hayden, 1864).

This last idea was discussed in detail by Trauth who admitted the correct interpretation of the upper jaw, but could not convince himself about that of the lower jaw, not having seen anything like the combination published by Meek and Hayden anywhere else. Trauth was an extremely scrupulous scientist, and I doubt if anyone in his situation would have acted otherwise. On the other hand, Meek and Hayden had worded their idea cautiously, it could indeed hardly be considered more than a working hypothesis, being founded on one specimen only.

I ran into these questions more or less incidentally, looking for radulae within the ammonite living chamber, and when I published the jaw interpretation of the anaptychus, I had gone through considerable doubt myself. So we built a model of the upper and lower jaws as we had found them within the living chamber of a specimen of *Arnioceras*. With this visual help, its jaw nature was almost immediately accepted.

To show the importance of the visual impression, I mention the paper by Dagys and Dagys (1975). They had more than 500 well

preserved though isolated anaptychi of Triassic and Jurassic age from north-east Siberia at their disposal and detected many hitherto unknown details about their intricate structure, but their material did not give any hints as to their function, so they remained sceptical even about the published evidence.

With aptychi, the situation was even more complicated. Most aptychi have been found in light-coloured limestones, in which organic components will normally not be preserved, therefore their most important functional part was missing. However, nobody questioned the completeness of their preservation, and so it was almost impossible for their true nature to be detected, until they were found under conditions which allowed calcareous as well as organic substances to be preserved. This situation happened to occur in our upper Liassic concretions in northern Germany. In them, two aptychi could be seen connected by a continuous inner chitinous layer resembling the anaptychi of other ammonites and enveloping a coleoid type of upper jaw. Regarding aptychi, even Schindewolf (1958) was misled by the unknown incompleteness of his material and believed that he had finally proved an operculum function for aptychi. He believed them to be parts of a hood-like structure resembling the hood of *Nautilus*, after proving that they could definitely not be extensions of a ventral mantle fold as Trauth had thought.

Once the jaw function of both anaptychi and aptychi was acknowledged and the method found to locate the corresponding upper jaw perfected (by serial sections through the living chamber), then additional conclusive arguments emerged. The first was the discovery of radular teeth between the upper and lower jaw, exactly at the place where they would be expected in the living animal. Even more conclusive was the recognition of a complete set, consisting of upper and lower jaw, radula, oesophagus and crop within the living chamber of a specimen of *Arnioceras* (Lehmann, 1971).

Most aptychi and anaptychi are found isolated, however, the only sure way to identify them as jaw elements is to find them together within the living chamber of an ammonite. In my experience, they are almost always in close proximity to each other, very similar to their supposed living position.

Until now, upper and lower jaws of the following ammonite genera have been found together within the living chamber:

"Anaptychi":	<i>Eoasianites</i>	(Closs, 1967)
	<i>Olenekites</i>	(Zakharov, 1974)
	<i>Ptychites</i>	(Lehmann, unpublished)
	<i>Psiloceras</i>	(Lehmann, 1970)
	<i>Arnioceras</i>	(Lehmann, 1970)
	<i>Pleuroceras</i>	(Lehmann, 1970)
	<i>Dactylioceras</i>	(Lehmann, 1979)
	<i>Gaudriceras</i>	(Kanie <i>et al.</i> , 1978)
"Aptychi":	<i>Eleganticeras</i>	(Lehmann, 1967, 1972)
	<i>Hildoceras</i>	(Lehmann, 1972)
	<i>Normannites</i>	(Lehmann, 1972)
	<i>Physodoceras</i>	(Lehmann, 1972)
	<i>Scaphites</i>	(Meek and Hayden, 1864; Lehmann, 1972)
	<i>Scalarites</i>	(Kanie <i>et al.</i> , 1978)
	<i>Parkinsonia</i>	(Lehmann, 1978)

In addition, Saunders and Spinoso (1974) mentioned having found mandibles in the living chamber of Mississippian, Pennsylvanian, and Permian ammonoids, but they gave no descriptions. According to these authors, they resemble more closely mandibles of modern dibranchiates than those of *Nautilus*. So they are, like those of *Eoasianites* and *Olenekites*, more or less normal cephalopod jaws. They show no calcareous deposits whatsoever.

The jaws of the Mesozoic ammonoids, however, developed in a very special way (Kaiser and Lehmann, 1971). Most characteristic is the difference in relative size of upper and lower jaws. In recent dibranchiates, the upper jaw tends to be longer than the lower jaw, whereas in the ammonites the lower jaw may be up to twice as long as the upper jaw. The relative length of the lower jaw in recent forms like *Loligo* is 50% that of the upper jaw, in *Nautilus* 100%, in ammonites with anaptychi like *Arnioceras* it is 150% and in *Eleganticeras* and other ammonites with aptychi it is 200%.

These ratios illustrate a peculiar morphological development. Whereas the upper jaws keep their shape and their size with regard to the body size, the lower jaws increase in relative size and at the same time they change their shape considerably. Most important seems to be the shortening of the inner lamella and the acquisition of calcareous coverings to the chitinous wings which develop into aptychi – but are ontogenetically later than their chitinous base. The beak region remains free of calcareous deposits and is thus quite different from that of *Nautilus* jaws.

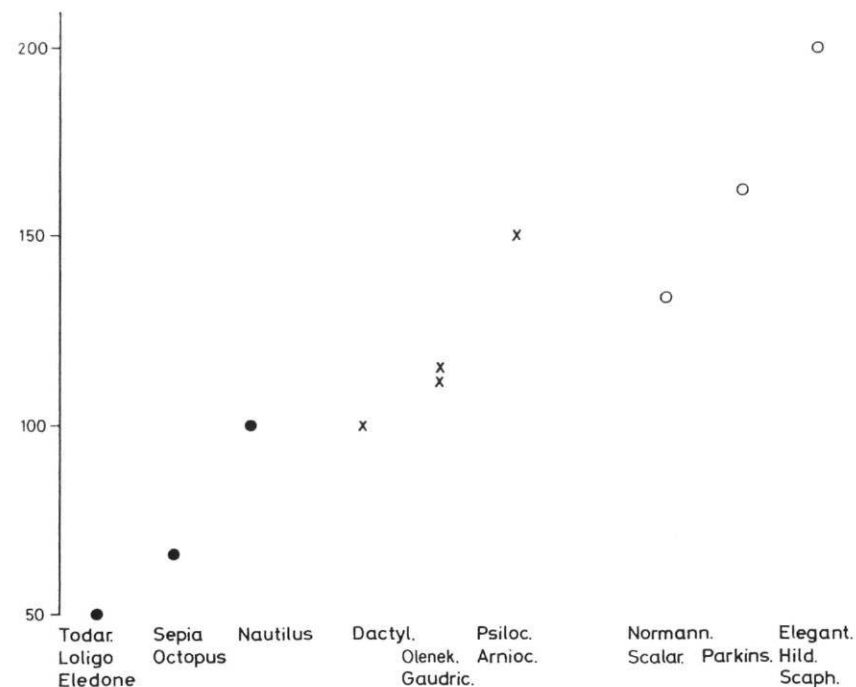


Fig. 1. Relative length of lower jaws (expressed as percentage of length of the corresponding upper jaw).

This general picture of Jurassic and Cretaceous ammonite jaws resulted mainly from an analysis of rather small ammonites only a few centimetres in diameter. Exceptions were larger macroconchs of *Eleganticeras* and *Hildoceras* with aptychi. The reasons for preferring smaller ammonites are that their living chambers are narrow, making it less probable that they have functioned as debris traps. Also, they are more frequently found in the type of nodule which originated diagenetically early and in relatively quiet waters, giving a better chance for parts of the body to be preserved within the living chamber.

However, only lately we noticed that we had disregarded one important group of jaws. Some anaptychi possess a distinct indentation in the centre of their frontal margin; in others, there is a horny or even in part calcareous thickening in the same place. One very large anaptychus from the Yorkshire coast (Fig. 3a) shows an unusually

thick calcareous central part in addition to an incision-like indenture. This anaptychus may belong to some large *Lytoceras*, other ammonites are too small to have possessed anaptychi of this size and Phylloceratida have different aptychi. We should even consider a nautiloid relationship. The main difference between nautiloid and ammonoid jaws so far seems to be that nautiloid jaws carry calcareous beaks known as rhyncholites (upper jaw) and conchorhynch (lower jaw). Saunders *et al.* (1978) showed that rhyncholites and conchorhynch range from Middle Triassic to recent, synchronous with the superfamily Nautilaceae. Without conclusive evidence, they have been considered to belong to nautiloids. Only recently, Schmidt-Effing (1972) found a conchorhynch within the living chamber of a *Ceratites* and considered it to be autochthonous, although the corresponding rhyncholite was not found. Mundlos (1973) rejected the idea, with good reason. Now, Japanese colleagues (Kanie *et al.*, 1978) find rather strange types of jaws which they attribute to Cretaceous ammonites. Most important seems to be an aptychus-type of jaw with rather nautiloid calcified beaks in the living chamber of *Gaudriceras*, a *Lytoceratacea*.

Besides the calcified beaks, nautiloid jaws show some other differences to those of ammonoids, as may be seen in Fig. 2. The upper jaw of *Nautilus* has one undivided inner lamella, as has that of typical recent dibranchiates. In ammonoids, the dorsal part of the inner lamella is missing, leaving two separate wings. The lower jaw in *Nautilus* has two separate wings of the outer lamella and a short inner lamella. In recent dibranchiates, both inner and outer lamella are rather long, the outer consisting of separate wings, the inner being undivided. However, in ammonoids, the inner lamella is short as in *Nautilus*, but the outer lamella has enormously widened to form an undivided, shovel-like structure.

The jaws of *Gaudriceras*, according to the interpretation of the Japanese authors, are unique. Both upper and lower jaws alike have a large, undivided outer lamella and a very short, brim-like inner lamella of organic material and a calcareous beak rather similar to that of *Nautilus*. The upper jaw is entirely covered by a thin calcitic layer. The calcareous beaks certainly remind us of *Nautilus*. It seems that here we have one possible bearer of Till's "nicht-Nautilus-Schnäbel" (1907), the rhyncholites in general, but this needs further confirmation.

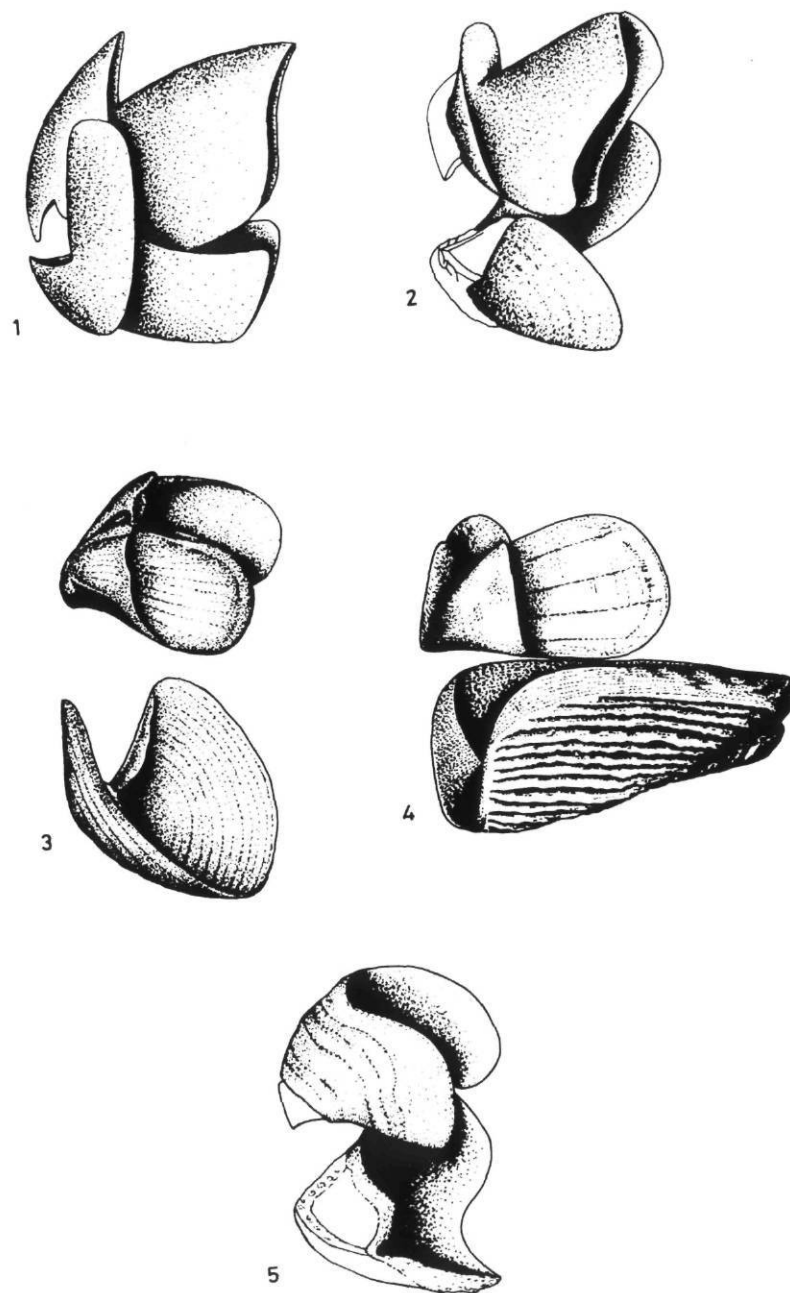


Fig. 2. Cephalopod jaw apparatus: 1, *Sepia* sp., Recent. 2, *Nautilus* sp., Recent. 3, *Psiloceras* sp., Hettangian (Lower Liassic). 4, *Hildoceras* sp., Toarcian (Upper Liassic). 5, *Gaudryceras* sp., Santonian (Upper Cretaceous).



If the *Gaudriceras* type is included, three types of ammonite jaws may thus be distinguished:

- (1) The type mentioned by Saunders *et al.* (1978) and exemplified by *Eoasianites* and *Olenekites*, which is rather similar to that of recent coleoids. It is the most primitive and most characteristically cephalopodian type of jaw. If we may judge from modern coleoids, bearers of these jaws may have tended to have a more or less carnivorous diet. These ammonoids seem to have disappeared during the Triassic. In them, the jaw material remained chitinous throughout.
- (2) The second type is that in which the lower jaw tends to widen and achieve the shape of anaptychi and aptychi. Although the outer lamella grows extremely large, the inner lamella is retained to some extent, giving space for the inner jaw muscles to attach. The outer muscles of the lower jaw seem to have been weakened and to have atrophied completely. Probably, these large lower jaws were rather passive in their function. I assume that they were used like shovels while the ammonites moved slowly close to the sea floor, stirring up epibenthic organisms. The contents of some fossil ammonoid crops suggest such a diet, for they contained foraminifera, ostracods, parts of crinoids, small broken aptychi and other parts of ammonite jaws. It is well known that recent coleoids may be voracious cannibals, and the ammonites may have had similar habits. These crop contents indicate part of the food eaten by ammonites; naturally, they cannot indicate anything about soft-bodied food or about food digested outside the body, not even about plankton. But the type of jaws and their limited speed of motion make it rather improbable that ammonites pursued large and highly mobile prey. Possibly they were omnivorous and scavenger-like. For the majority of ammonites, this seems to be the best supposition.
- (3) The third type is that represented by the jaws of *Gaudriceras* which seems to be characteristic of the *Lytocera* (excluding heteromorphs). The calcified beaks resemble the conchorhynchids and rhyncholites of *Nautilus*. Saunders *et al.* (1978) stress that the *Nautilus* jaw apparatus is capable of

very strong shearing action and that the calcified portions in some specimens show considerable wear which might result from a diet rich in hard or shelled food. According to an analysis by Tanabe *et al.* (1978), *Gaudriceras* lived in rather deep water, comparable to the depth preferred by recent *Nautilus*. It may be safe to assume a similar way of life for both. Possibly, nautiloids and the *Gaudriceras*-type ammonites were real ecological competitors.

Similar ways of life and similar shapes of *Gaudriceras* and *Nautilus* would make it interesting to know what type of radula *Gaudriceras* had. Since the first finds of ammonoid radulae in 1967, the search for more radulae has not been overwhelmingly successful. In the following five genera it was preserved well enough to reconstruct a characteristic scheme of tooth arrangement:

<i>Eoasianites</i>	(Closs, 1967)
<i>Arnioceras</i>	(Lehmann, 1971)
<i>Eleganticeras</i>	(Lehmann, 1967)
<i>Hildoceras</i>	(Lehmann, 1967)
<i>Dactylioceras</i>	(Lehmann, 1979)

Individual radular teeth have been observed in numerous other genera. The radula was always situated between the upper and lower jaw in the supposed life position. So far they have all been found to be arranged in rows of seven teeth each, just as in recent coleoids and differing from the thirteen teeth in *Nautilus*. The suggested differentiation between Late-Radulata and Anguste-Radulata still stands (Lehmann, 1967). The similarity of the radular apparatus in all recent coleoids and in fossil ammonoids as well, in contrast to its diversity in gastropods, indicates little selective importance of its shape and thus makes the radula a good means for phylogenetic studies. It seems to indicate a close relationship between ammonoids and coleoids.

The radulae can hardly be found anywhere else than between the jaws where they are well protected by the buccal mass. Since gastropods do not have structures of comparable type which so strongly enclose and protect the radula, I see no chance of ever finding fossil gastropod radulae at all.

The function of the radulae in recent cephalopods consists mainly in facilitating the swallowing process (Robson, 1929, 1930) which explains its rather uniform shape.

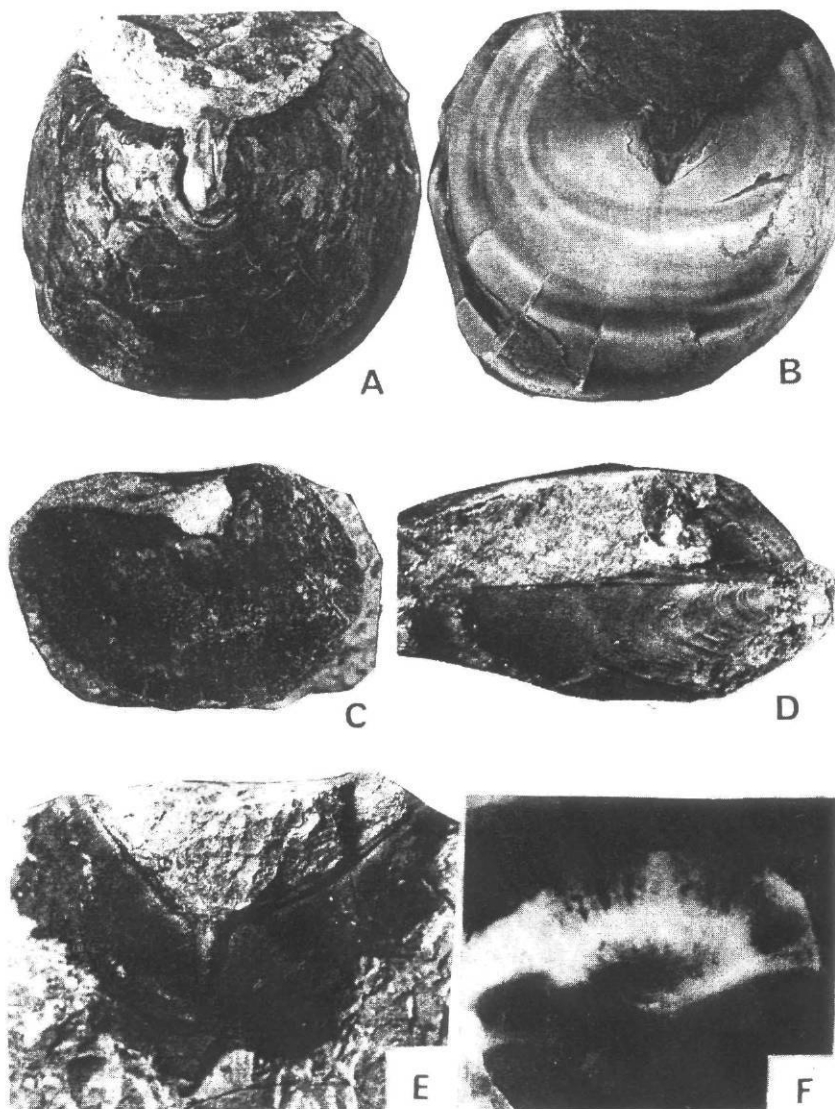


Fig. 3. Illustrations (from the sources indicated where new) of ammonoid jaw structures. A, Lytocerate *Anaptychus* (Lower Jaw). Found loose at Black Nab, Whitby, Yorkshire, England, Upper Jurassic.  $\times 2/3$ . (H. J. Lierl). B, Upper Jaw of *Gaudryceras* sp. Loc. K 79 c, Heiterozawa, Tombets, northern Hokkaido, Japan. Upper Campanian. Natural size. (T. Matsumoto). C, Lytocerate *Anaptychus* (? Upper Jaw). Rottorf am Kley. geol. sheet Süpplingen, North Germany. *Davoei* Zone, late-costa

The ink sac of ammonoids was first described in several specimens of *Eleganticeras* in 1967 (Lehmann), later by Wetzel (1968) in *Bochianites*, and in 1977 Mathur described the ink substance Melanin found in specimens of *Eopsiloceras* (Uppermost Triassic, Rhaetic). Investigations concerning the identification of the ink substance in *Eleganticeras* have not yet been finished. We did find several structures in specimens of *Ptychites* and *Dactylioceras* which morphologically and from the black appearance may correspond to ink sacs, but the substance has not yet been analysed. Such structures may not always have been ink sacs, but may have been light organs (Dilly and Herring, 1978), or glands secreting other substances. As with the jaws and the feeding habits, we must assume that ammonoids developed various different kinds of excretions.

I would like to draw attention to an observation which was already published in 1973 (Lehmann and Weitschat). In large specimens of *Hildoceras* we found jaws, radula and crop and a structure which can hardly be anything but gills (Fig. 3f). According to Dr A. Bidder (during discussion at the Symposium), the gills of coleoids contain a scaffold of connective tissue which has a fair chance of being fossilized under favourable conditions, in contrast to the soft tissue of most of the coleoid body. She accepted the evidence given as possible and even probable.

The picture (Fig. 3f) shows two of these gill-like structures in close contact. Although it cannot be excluded that another pair of gills was present in the living animal, it may well be that it actually had only two gills, judging from the excellent state of preservation of the present specimen. More specimens are needed to decide how many gills ammonoids had. The search will be most promising in larger specimens with more resistant connective tissue than small ones are likely to have had.

Finally, the most important progress concerning ecology as well as, possibly, taxonomy of ammonoids is the detection by Kanie,

subzone. Pliensbachium (Liase  $\gamma$ ).  $\times 4/5$ . (R. Jordan). D, Upper Jaw of *Parkinsonia* sp., seen from above. Middle Jurassic, Bethel/Bielefeld.  $\times 4$ . E, Lower Jaw of lytocerate type [*Lobolytoceras siemensii* (Denckmann)]. Lower Toarcian, Hoisdorf near Hamburg. Natural size. F, Structure interpreted as gills within the living chamber of *Hildoceras* (*Hildaites*) *levisoni* (Simpson). Lower Toarcian, Haverlahwiese, Lower Saxony.  $\times 2$ .

Tanabe and other Japanese colleagues, of a third type of jaw. These are peculiar and seem to me to be restricted to *Lytoceratida* in a strict sense, not including the heteromorphs. They possess calcareous beaks similar to rhyncholites. Jaws of this type have also been found in Europe, but in them, the calcareous beak element has not yet been recognized.

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