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# Microstructure of some Jurassic Ammonoid (Hildoceratid) Jaw Plates†

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Three kinds of the lower jaw plates; one is close by the shell of *Harpoceras* (s.s) *chrysanthemum* (Yokoyama), a second is on the body chamber of *Harpocaras* (s.s) *inouyei* (Yokoyama), and a third is morphologically identified as *Harpocaras* (s.l.) sp.; from the Nishinakayama Formation of the Jurassic Toyora Group, can be differentiated into two layers, inner and outer. The external surfaces of the inner layers show general resemblance to a phylogenetically older anaptychus and a cornaptychus-type morphology which characterizes the hildoceratid lower jaw plates, while the internal surfaces of the outer layers show a lamellaptychus-type morphology which characterizes the oppeliid lower jaw plates. The inner layer is chitinous and secreted by the beccublast cells. The outer layer is calcareous and secreted by the labial region cells. Thus the structural differences between the outer and inner layers are derived from the different secretory tissue. The structure of the two layers is described in detail. Previous works have stated that hildoceratid lower jaws are cornaptychi, but the external surface of the lower jaw of *H.* (*H.*) *chrysanthemum* shows the characteristics of lamellaptychus.

**Key words:** Jurassic, *Harpoceras*, lower jaw plate, cornaptychus, lamellaptychus, layered structure

## 1. Introduction

Aptychi and anaptychi occur fairly commonly, either within the body chambers of ammonoids or separated from their shells. Their affiliation had long been a riddle, until they were demonstrated as being the jaw apparatus of ammnoids, based on the in situ association of an aptychus with radulae within a body chamber and comparison of aptychi and anaptychi with the jaw apparatus of modern Cephalopods, including living *Nautilus* (e.g. Lehmann, 1971[1)], 1972[2)], 1976[3)], 1981[4)]). In these years, the restoration of the buccal mass structure was attempted for the Cretaceous taxa *Gaudryceras*, *Desmoceras* and *Tragodesmoceroides*, as well as recognition of chitin secreting cell imprints in some jaw plates based on histological research (Tanabe & Fukuda, 1983[5)]; Tanabe, 1983[6)]). Thus, although histological research and systematics of jaw plates have been much advanced, nonetheless, the details of the inner structure of jaw plates have not been researched since the description by Schindewolf (1958)[7)] and Lehmann (e.g., 1972[2)], 1976[3)], 1981[4)]).

The new findings show that: (1) the morphologies of the external surface of the inner layer and the internal surface of the outer layer are completely different, (2) in different species the morphology of the external surface of the inner layer is similar, (3) the morphology of the internal surface of the outer layer varies from species to species, (4) the morphology of the external surface of the outer layer of *H.* (*H.*) *chrysanthemum* is not identified with cornaptychus but with lamellap-

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tychus, and thereby further research is necessary to define cornaptychus and lamellaptychus, and (5) the honeycomb structure of the inner sublayer of the outer layer may be undeveloped in the early ontogenetic stage.

## 2. Materials and methods

The materials which were studied comprise the following three specimens, A, B and C: Specimen A- one aptychus which is close to but physically separated from the shell of *Harpoceras* (s.s.) *chrysanthemum* (Yokoyama) and lying on the same bedding plane. Specimen B- one aptychus lying on the apertural area of the body chamber of *Harpoceras* (s.s.) *inouyei* (Yokoyama). Specimen C- one small aptychus which is identified as *Harpoceras* (s.l.) sp.

These specimens were obtained from the Nm Member of the Nishinakayama Formation, Toyora Group (Hirano, 1971[8)]), Yamaguchi Prefecture, southwest Japan. The Nm Member is composed of black shale which judging from lithology and mode of fossil-preservation is very similar to the Posidonienschiefer of Holzmaden, Southern Germany. It is dominantly platy due to fissility and is termed paper-shale (Shikama and Hirano, 1970[9)]; Hirano, 1971[8)]; Tanabe, 1983[10)]; Tanabe et al., 1984[11)]). Bacause of the fissility of the shale ammonites are preserved as internal and external moulds, and aptychi also are separated into an inner and an outer layer. For comparison with these specimens, we used one lamellaptychus obtained from an exposure of the Aptychenschichten in the Kalkalpine Zone, about 25 km west of the Kochel See lying about 55 km SSW of München.

Specimens -A and -B are observed by an optical microscope and used for the illustration to show the general morphology and the mode of occurrence. Specimen- C was viewed by SEM (Hitachi H–450) on both its separated surfaces of inner and outer layers after having been coated with gold. The cross section of Specimen-C was also observed by SEM. Main element compositions of the inner and the outer layers, and for comparison the rock matrix were analyzed by EDA. The lamellaptychus from the Aptychenschichten was serially observed with SEM by etching with 5 % HCl from the outer surface to the inner end.

## 3. Description of lower jaw plates

Although they exist very close to or on ammonite shells, affiliation of these aptychi may be inconclusive by the reason that they are not preserved strictly within their body chambers. Ammonoids which can contain an aptychus as large as Specimen-A, however, are limited only to *H.* (*H.*) *chrysanthemum* at the locality and in the equivalent stratigraphic level. The locality of Specimen-B yields only *H.* (*H.*) *inouyei*. Specimen-C is reasonably affiliated to *H.* (s.l.) sp. because of the morphological resemblance to the other specimens as will be discussed later. On the basis of these facts and discussion, we may be able to deal with these jaw plates as *H.* (*H.*) chrysanthemum, *H.* (*H.*) *inouyei* and *H.* (s.l.) sp. respectively. The affiliation is not conclusive, however, from the mode of occurrence, and the taxonomy of the Jurassic ammonoid jaws has not yet been established. Thus, we describe them as *Harpoceras* (*H.*) sp. A, *H.* (*H.*) sp. B and *H.* (s.l.) sp. C below.

Superfamily Hildocerataceae Hyatt, 1867

Family Hildoceratidae Hyatt, 1867

Subfamily Harpoceratinae Neumayr, 1875

Genus *Harpoceras* Waagen, 1869

*Type-species.* - *Ammonites falcifer* Sowerby, 1820 (designated by Arkell, 1951, I. C. Z. N. Opinion 363,

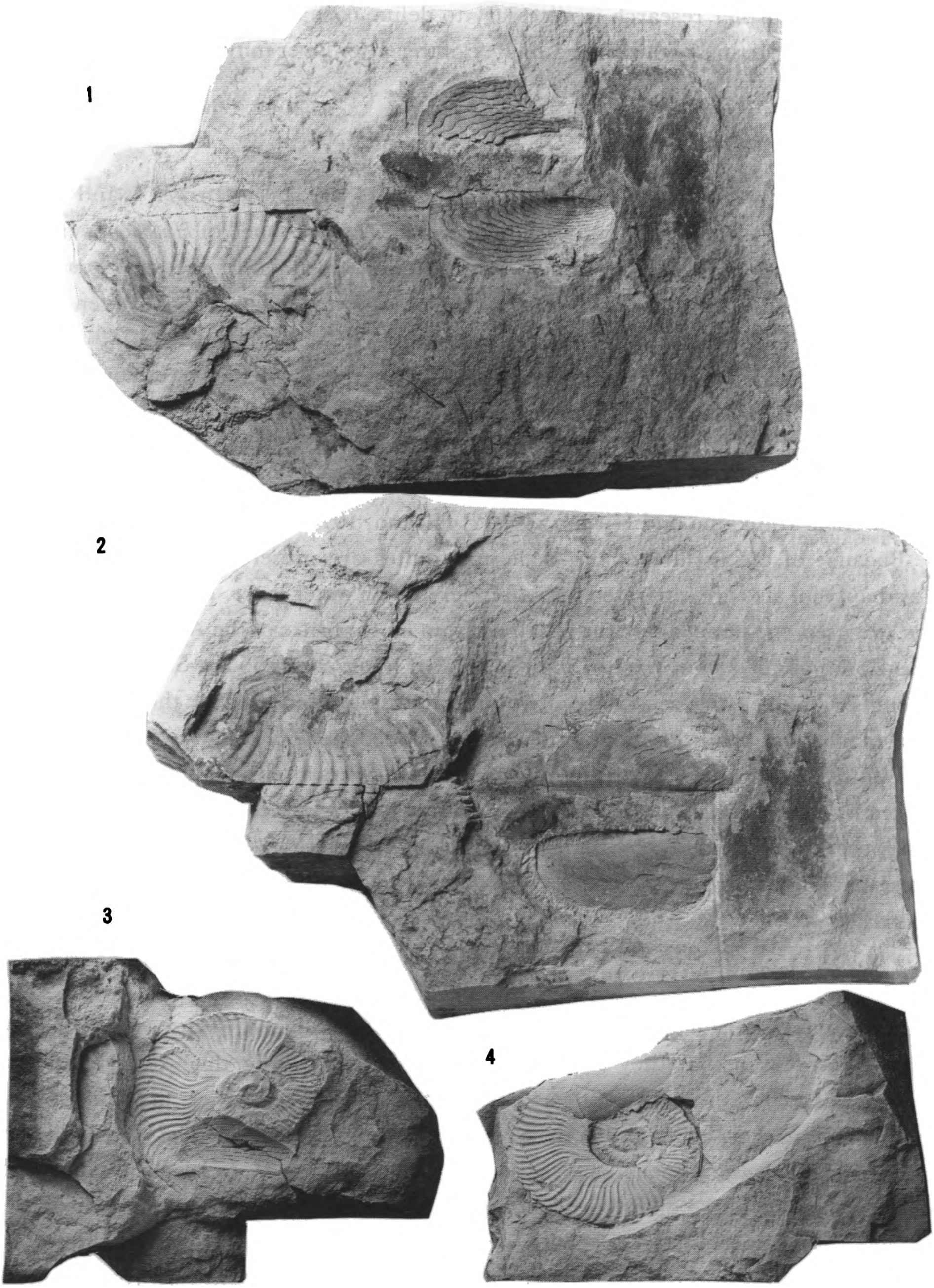


Fig. 1. Lower jaw plates of *H.* (*H.*) sp. A(1–2) and *H.* (*H.*) sp. B(3–4).

1. An internal surface of the outer layer of the lower jaw plate and *Harpoceras* (s.s.) *chrysanthemum* (Yokoyama).

2. An external surface of the inner layer of the lower jaw plate and an external mould of *Harpoceras* (s.s.) *chrysanthemum* (Yokoyama) of the Fig. 1: 1.

3. An internal surface of the outer layer of the lower jaw plate and an external mould of *Harpoceras* (s.s.) *inouyei* (Yokoyama).

4. An external surface of the inner layer of the lower jaw plate and *Harpoceras* (s.s.) *inouyei* (Yokoyama). All shown natural size.

1954).

Subgenus *Harpoceras* Waagen, 1869

Lower jaw plate of *Harpoceras* (*Harpoceras*) sp. A

Fig. 1: 1–2

*Materials*.- Specimen-A, mentioned above. Both left and right lobes of the lower jaw plate are separated from, but close to the shell of *H.* (*H.*) *chrysanthemum* and lie on the same bedding plane. Both lobes are separated into outer and inner layers. An internal surface of the outer layer and an external surface of the inner layer are exposed on the rock matrix. The specimen is in the collection of Ryuzo Sekiya.

*External view of the inner layer*: The general outline is nearly rectangular, of which the corners are rounded. A median depression provides a divisions into left and right lobes (Fig. 1: 2). The median depression becomes wider posteriorly and the central part swells to form the posterior ridge, although its crest is not preserved in the present specimen. The width of the median ridge in the posterior area of one lobe is at least 1.4 mm, and it is estimated that it would be about 2.8 mm if restored. The width of one lobe is 12.6 mm. Therefore the width of the completely restored inner layer would be about 28 mm. The maximum length is 28.9 mm. There are eleven to twelve undulations (or ribs) which are parallel to the outline on each lobe. The undulations are somewhat stronger in the anterior area than in the posterior area. There are more than 150 striae which are parallel to the outline, and therefore they are also parallel to the undulations on each lobe. These undulations and striae were originally concentric when both lobes were articulated. On the median depression of one lobe also there are about twenty to thirty longitudinal striae.

*Internal view of the outer layer*: General outline (Fig. 1: 1) is mostly same as the inner layer and the maximum length is 28.5 mm. The width of one lobe is 13.2 mm. The anterior median depression is not discernible, and the posterior median ridge is flattened. There are seventeen narrow and deep grooves which are parallel to the outline of the layer. These grooves from a concentric pattern when the two lobes are articulated, and are fairly flexuous with a minute zig-zag pattern. They neither converge nor run strictly parallel to each other. No undulations are discernible on the surface.

*Comparison*.- The morphology of the external surface of the inner layer of the present species resembles that of *Hildoceras* (*Hildaites*) *levisoni* (Simpson) (Lehmann, 1972[2] Taf. 9, fig. 4), altough it has only been partially illustrated. The main criteria for the classification of Jurassic aptychi by Trauth (1927)[12] and Lehmann (1976)[3] are the general shape and ornamentation of the external surface of the outer layer. Therefore, their classification cannot be applied to the external surface of the inner layer. However if their classification terms are used for the sake of convenience, the external surface of the inner layer of the present species can be identified as a typical cornaptychus of Lehmann (1976, p. 94, Abb. 73–a)[3], described from hildoceratid ammonites.

The ornamentation of the internal surface of the outer layer differs completely from the external surface of the inner layer. The morphology of the former shows that it belongs to lamellaptychus (Trauth, 1927[12]; Lehmann, 1976[3]). As mentioned later in this paper, the grooves of the internal surface of the outer layer of *Harpoceras* (s.l.) sp. C correspond to the ribs of the external surface of the outer layer. However the situation seen in *Harpoceras* (s.l.) sp. C is not applicable in the present instance because of differences in the ontogenetic stage and/or species between these two examples. Also, the morphology of the external surface of the lower jaw of *H.* (*H.*) *chrysanthemum* as illustrated by Yokoyama (1904, pl. 2, fig. 1)[13] and Hirano (1973, pl. 2, fig. 2)[14] shows that the ribs of the external surface do not show the zig-zag pattern of the grooves of the internal surface. The external surface of the outer layer of *H.* (*H.*) *chrysanthemum* has clearer and stronger ribs, which are similar to those of *H.* (*H.*) *levisoni* (Lehmann, 1972[2], Taf. 9, fig. 4), than with the typical cornaptychus of Lehmann (1976, p. 94, Abb. 73–a)[3]. Trauth (1927)[12] and Lehmann (1976)[3] stated that hildoceratid jaws are cornaptychi, and Lehmann (1976)[3] stated that geologically younger cornaptychi are smooth. The stratigraphical range of *H.* (*H.*) *chrysanthemum* is from the Falcifer to the Bifrons Zone (Hirano, 1973[15]), and the present specimen was obtained from a level of the *Protogrammoceras nipponicum* Zone which is correlated with the Lower Flacifer Zone. It is therefore probably not geologically young in terms of the evolution of hildoceratid ammonoids. The features are, however, not those of cornapthchus.

*Measurements.*- The size of the jaw plate and its size relationship to the shell of *H.* (*H.*) *chrysanthemum* are as follows (in mm):

| Shell | | Jaw plate | | | |
|---|---|---|---|---|---|
| Whorl diameter | Whorl height | Inner layer width | Inner layer length | Outer layer width | Outer layer length |
| 51.6+ | 20.0 | 28± | 28.9 | 26.4 | 28.5 |

The inner layer is somewhat larger than the outer layer, in agreement with the restoration by Lehmann (1972, Taf. 10, fig. 6)[2].

*Remarks.*- As has already been demonstrated by the illustrations of Yokoyama (1904, pl. 2, fig. 4)[13] and Hirano (1973, pl. 2, fig. 2)[14] and is apparent in the lower jaw plate of *H.* (*H.*) sp. B described below, the lower jaw of the present species is also fairly large by comparison with the shell.

*Locality.*- A stream a little lower than the loc. 6 of Hirano (1971, p. 98, fig. 3)[8]. *H.* (*H.*) *inouyei* (Yokoyama), juvenile *Fuciniceras nakayamense* (Matsumoto) and numerous *Parainoceramus matsumotoi* Hayami were obtained in addition to the above described specimen, from the same locality in this time by the third author. The level is correlated with the Lower Whitbian *Protogrammoceras nipponicum* Zone of the Nm Member, Nishinakayama Formation, Toyora Group.

Lower jaw plate of *Harpoceras* (*Harpoceras*) sp. B
Fig. 1: 3–4

*Materials.*- Specimen-B, mentioned above. A right lobe of the lower jaw plate is preserved on the body chamber of *H.* (*H.*) *inouyei*. Both an external surface of the inner layer and an internal surface of the outer layer can be observed. The specimen is in the palaentological collection of Waseda University.

*External view of the inner layer*: The outline of the right lobe of the inner layer is triangular (Fig. 1: 4). The length between the anterior and posterior ends is 19.8 mm, the width is 7.8 mm, and the preserved width of the posterior median ridge is 0.8 mm, although the crest is incomplete. There are weak concentric undulations which center on the anterior end of the median depression. Undulations are somewhat stronger in the anterior area than in the posterior, and there are about six striae on one undulation. Striae are also concentric, whose center is also the anterior end of the median depression, and are parallel to undulations, existing regularly both on and interspaces of undulations. There are more than 200 and less than 250 striae.

*Internal view of the outer layer*: The outline is same as that of the inner layer (Fig. 1: 3). The length is 17.6 mm, width is 7.6 mm, and the median depression does not take up any space. There are fourteen, narrow, deep and radial grooves which originate from the anterior end of the median depression. They are not flexuous, but are weakly arcuate.

*Measurements*.- in mm.

| Shell | | Jaw plate | | | |
|---|---|---|---|---|---|
| Whorl | Whorl | Inner layer | | Outer layer | |
| diameter | height | width | length | width | length |
| 30.8 | 13.7 | 16(+)* | 19.8 | 15.2* | 17.6 |

* Restored approximate size, calculated from one lobe.

The present specimen has also a larger inner layer than an outer layer as restored by Lehmann (1972, Taf. 10, fig. 6)[2].

*Comparison*.- The morphology differs considerably between the external surface of the inner layer and the internal surface of the outer layer. The external surface of the inner layer is similar to that of cornaptychus (Trauth, 1927[12], 1930[16], pl. III, figs. 4–16; Lehmann, 1976[3], p. 94, Abb. 73–a), whereas that of the internal surface of the outer layer is similar to that of the lamellaptychus. The grooves on the internal surface of the outer layer run radially from the anterior end of the median depression and they terminate in the posterior or postero-leteral area. They do not terminate in the area of the median depression as shown in lamellaptychus (Lehmann, 1976[3], p. 94, Abb. 73–b).

The outline of the lower jaw plate of *H.* (*H.*) sp. A is nearly rectangular, and the undulations, striae, and grooves bend with a large angle. On the other hand, the outline is triangular, and the undulations, striae, and grooves draw weak arcs in the present species. The grooves of the present species are different from those of *H.* (*H.*) sp. A in that the present species does not show a zig-zag pattern.

*Remarks*.- The present species also has a large lower jaw plate compared with the whorl-height as in the case of *H.* (*H.*) sp. A and/or *H.* (*H.*) *chrysanthemum*.The ratio of the width of the lower jaw plate of *H.* (*H.*) sp. A to the whorl-height of *H.* (*H.*) *chrysanthemum* is about 1.4 and that in the present species is about 1.2, although the process of fossilization have rendered the lower jaw plate nearly flat, originally it was curved as shown by Lehmann (1976, p. 98, Abb. 78)[3].

*Locality*.- Specimen-B was obtained by Mr. H. Hayakawa at loc. 47 of Hirano (1971, p. 98, fig. 3)[8]. This locality is an old type-exposure of the Nishinakayama Formation and belongs to the *Dactylioceras helianthoides* Zone (Hirano, 1973)[14].

## Lower jaw plate of *Harpoceras* (s. l.) sp. C

Figs. 2–5

*Materials*.-Specimen-C, comprising an outer and an inner layer of a small lower jaw plate. The present specimen is preserved separately from the shell. Because of its good preservation, the specimen is described by the aid of SEM. It is curated at Chiba Prefectural Institute of Public Health.

*External view of the inner layer* : Only an external view (Fig. 2) and a cross section (Fig. 3: 5–6) are visible for the inner layer. The length between the anterior and the posterior margin of the lower jaw plate is about 4.5 mm. The plate is composed of left and right lobes, bordered by an anterior me-

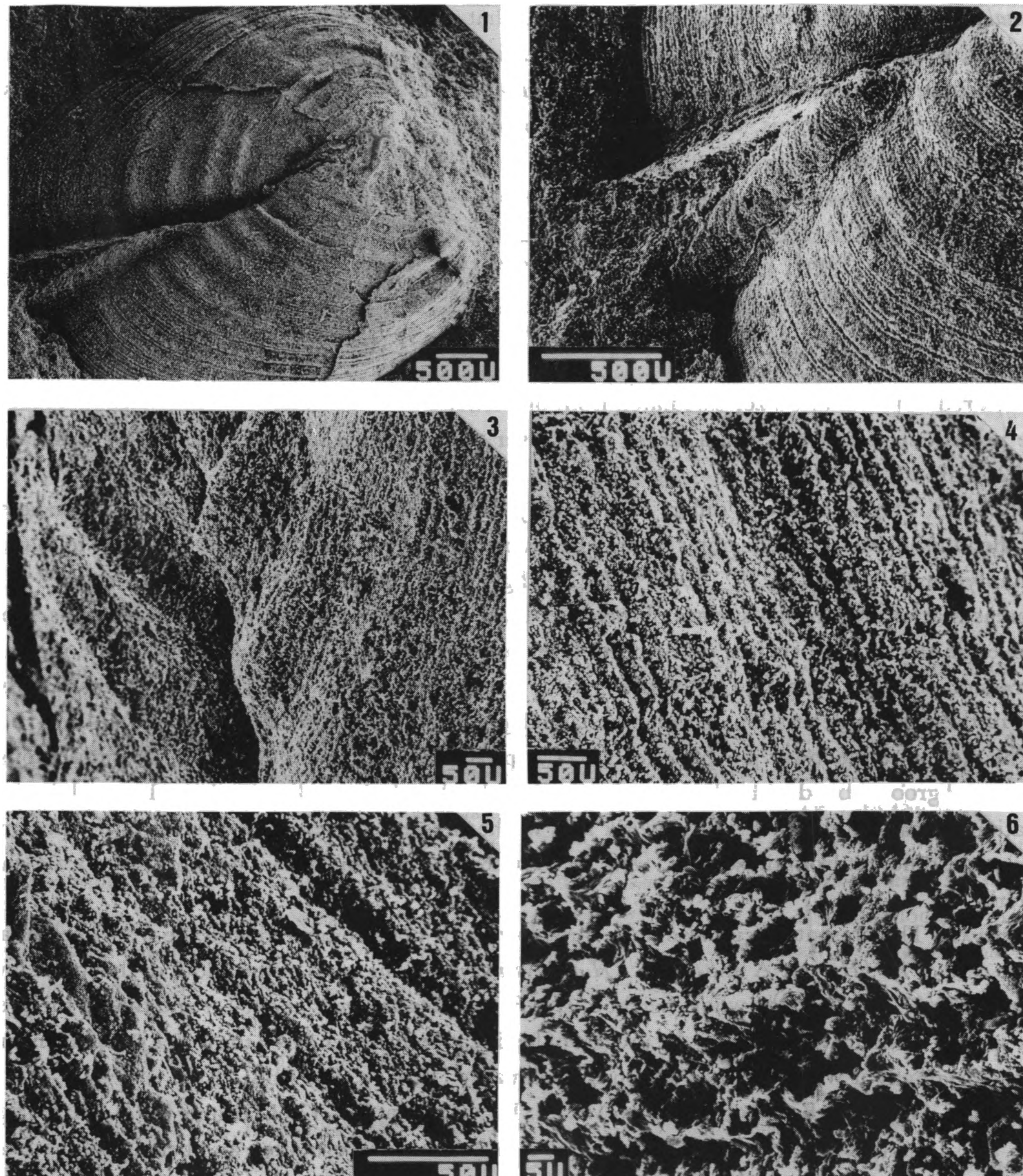


Fig. 2. Electron micrographs of the external surface of the inner layer of the lower jaw plate of *Harpoceras* (s.l.) sp. C, from the Toyora Group.

1. General outline, with morphology suggestive of cornaptychus. The anterior margin is upper right.
2. Median ridge.
3. Median depression, and right and left lobes.
4. Concentric striation.
5. Concentric striation.
6. Microstructure suggestive of original lamellar structure.

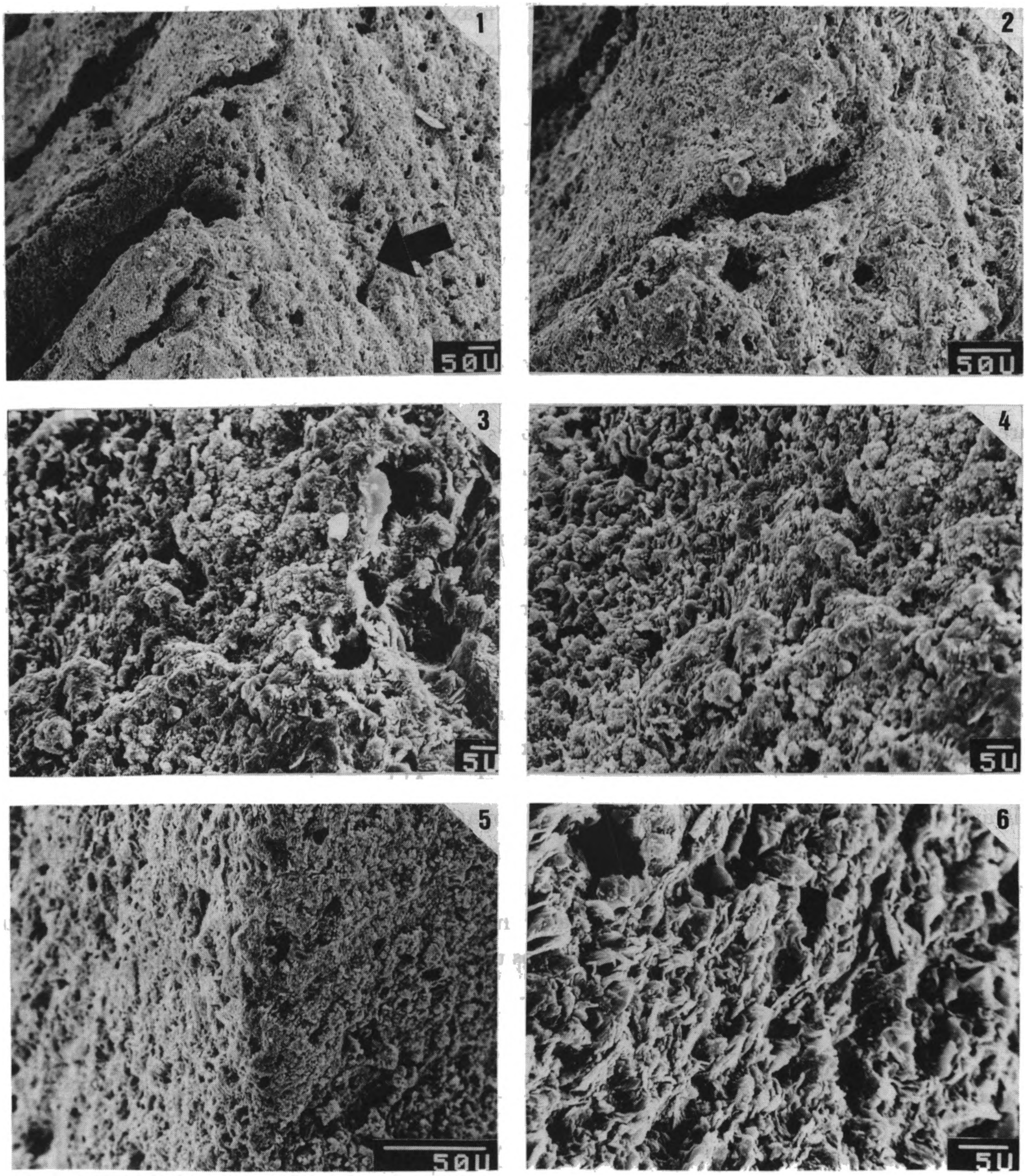


Fig. 3. Electron micrographs of the cross section of the lower jaw plate of *Harpoceras* (s.l.) sp. C, from the Toyora Group.

1. An internal surface of the outer layer showing some grooves (left half) and the cross section [about 200 to 300 μm thick] (Right). Arrow indicates the boundary between the aptychus and sediments.
2. An internal surface and the cross section of the outer layer, showing a groove about 150 μm deep.
3. Microstructure of the cross-section of the outer layer.
4. Same as 3. Barely discernible is some suggestion of the presence of regular prismatic structure in the direction from the left-lower to the right-upper.
5. An external surface of the inner layer (left half) and the cross section [ca. 60 μm in thickness] (Right half).
6. Microstructure of the cross section of the inner layer suggesting that a chitinous lamellar structure was the original microstructure.

dian depression and a posterior median ridge. The maximum width of the inner layer is about 4 mm. There are numerous concentric striae on the surface of the right and the left lobes. There are about ten concentric undulations, with individual wave lengths of about 250 $\mu$m and amplitude about 40 $\mu$m. Each undulation carries about fifteen concentric striae on one wave length. The thickness of the inner layer is about 60 $\mu$m (Fig. 3: 5–6). Although the original microstructure is not always well preserved, there are indications of a lamellar structure (Fig. 2: 6).

The element composition indicates that Si is dominant with Al also abundant. In decreasing order of abundance K, Fe, P and S are detected (Fig. 4: 1) (cf. Tanabe et al., 1980[17], p. 165, fig. 10). Although chitin was probably the original material (Lehmann, 1976[3]), it is not preserved, because of elemental substitution through diagenetic processes.

*Internal view of the outer layer* : The morphology of the internal surface of the outer layer (Fig. 5) differs considerably from that of the external surface of the inner layer, and the right and left lobes are sculptured by narrow, deep and radial grooves. The depth of each groove is about 150 $\mu$m and the width is about 20 to 50 $\mu$m as measured from the cross section (Fig. 3: 1–4). Fifteen grooves are present. In contrast to Lehamann's illustration (1976, p. 94, Abb. 73), these grooves are not parallel with each other from the anterior to the posterior margin but appear to be radial. Concentric undulations on the inner layer are also present on this outer layer, crossing radial grooves mentioned above. However, the numerous concentric striae that exist on the inner layer are not present on the outer layer.

The thickness of the outer layer is about 200 to 300 $\mu$m as measured from the cross section (Fig. 3: 1–2). The morphology of the border between the outer layer and the rock matrix shows that radial grooves influence the sculpture of the external surface, and grooves on the internal surface convert into fine ridges (or ribs) on the external surface. Although the original microstructure is not always well preserved, a prismatic structure is apparent (Fig. 3: 3–4).

The elemental composition does not differ much from that of the inner layer, being dominant in Si, which is the main element of the rock matrix, and Al is the second dominant (Fig. 4: 2). However P is more abundant in the outer layer than in the inner layer. Elemental substitution due to diagenesis has completely altered the composition of the original calcareous layer.

*Measurements*.- in mm.

| Jaw plate | | | |
|---|---|---|---|
| Inner layer | | Outer layer | |
| width | length | width | length |
| 4(+) | 4.5 | 3.5 | 3.5 |

As described by Lehmann (1972)[2] and as present in *H.* (*H.*) sp. A, and *H.* (*H.*) sp. B, the inner layer is larger than the outer layer.

*Comparison*.- The morphology of the external surface of the inner layer is similar to cornaptychus (Trauth, 1927[12], 1930[16], pl. III, figs. 4–16; Lehmann, 1976[3], p. 94, Abb. 73–a, 1972[2], Taf. 9, fig. 4) and that of the internal surface of the outer layer is similar to lamellaptychus (Trauth, 1927[12], 1930[16], pl. III, figs. 17–28; Lehmann, 1976[3], Abb. 73–b). The outline of the present species being rectangular, is similar to that of *H.* (*H.*) sp. A described above, but is

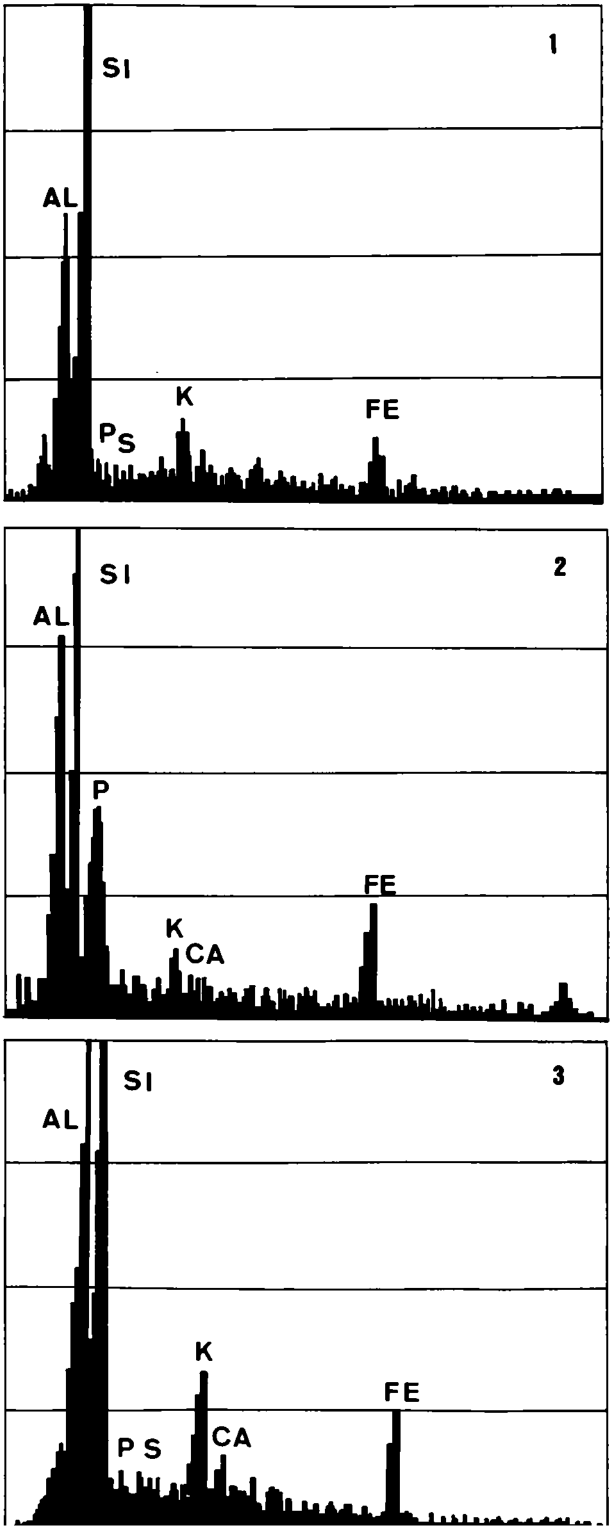


Fig. 4. Energy dispersion X-ray spectra for the inner layer (1), the outer layer (2) and rock matrix (3) of the lower jaw plate of *Harpoceras* (s.l.) sp. C. The procedure was performed under the conditions of 10 KeV for an accelerate voltage and 60 seconds for an integral time.

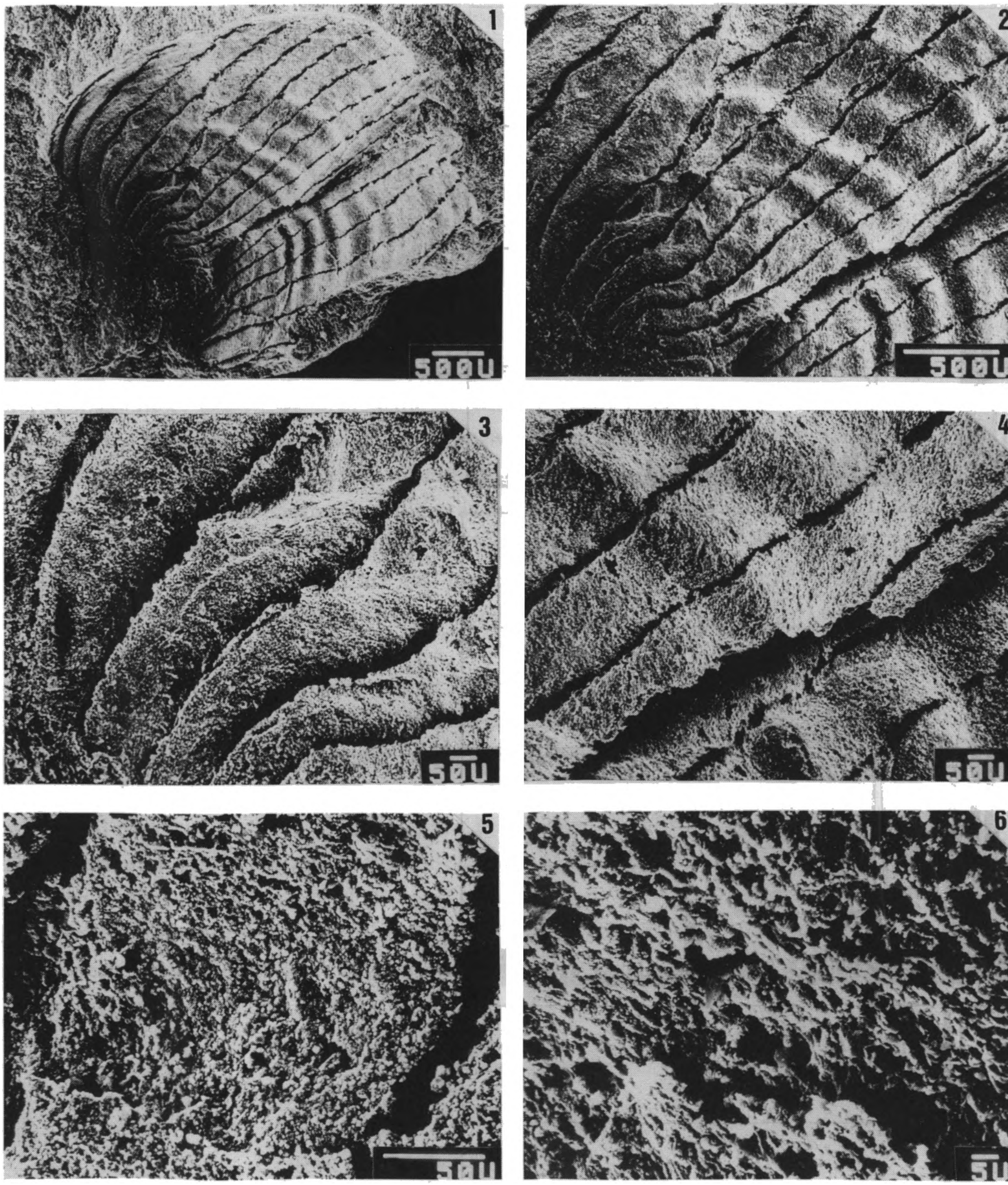

Fig. 5. Electron micrographs of the internal surface of the outer layer of the lower jaw plate of *Harpoceras* (s.l.) sp. C, from the Toyora Group.

1. General outline, with morphology suggestive of lamellaptychus. The anterior margin is lower left. This outer layer originally covered the inner layer shown in Fig. 2.
2. Anterior area.
3. Grooves of the anterior area.
4. Grooves and the impression of the concentric undulation in the anterior area.
5. Surface microstructure.
6. Microstructure suggestive of an original prismatic structure.

different from that of *H.* (*H.*) sp. B.

The external surface of the inner layer of the present species is similar to that of *H.* (*H.*) sp. A. However, concerning the internal surface of the outer layer, the grooves of *H.* (*H.*) sp. A bend toward the median depression and those of the present species run radially, terminating at the posterior end.

Thus although the present species differs from the two species of *Harpoceras* (*Harpoceras*) described above, it would nonetheless be affiliated to *Harpoceras* (s.l.) sp., judging from its general resemblance and the fauna of the locality.

The outer layer has been described as being composed of two sublayers, of which an inner sublayer consists of honeycomb structure. However observation of cross sections of the present species shows that the grooves of the internal surface of the outer layer convert into the ribs of the external surface of the layer. This fact indicates either that the honeycomb structure does not exist in the present species or that the structure is still undeveloped in this individual due to its early stage in growth. Morphological relations between the external surface and the internal surface require further study.

*Remarks.* -Due to the small size of the specimen, some of the original convexity is preserved.

*Locality.* -Same as the specimen-A with the shell of *H.* (*H.*) *chrysanthemum* described above.

## 4. Discussion

Cornaptychus (Trauth, 1927[12)]), the lower jaw plate of Jurassic Hildoceratidae, of which inner layer is thin and composed of chitin, has a configuration similar to that of an anaptychus of the older ammonites. Out of this chitinous inner layer, there are two thin calcareous layers, forming concentric ribbing (Lehmann, 1976[3)]).

On the other hand, the Late Jurassic Oppeliidae, which derived from the Liassic Hildoceratidae via the Middle Jurassic Hammatoceratidae (Moore ed., 1957[18)]; Donovan, Callomon and Howarth, 1981[19)]), has a somewhat thick, prismatic calcareous outer layer in a lower jaw plate, and the external surface has stronger concentric ribbing than cornaptychus, being named by Trauth (1927)[12)] as lamellaptychus.

Unfortunately, most of the hildoceratid jaws that have been collected, including those of *Harpoceras* (*Harpoceras*) have not yet fully been illustrated, although the general principles of jaw classification have been proposed. As a result, the distinction between cornaptychus and lamellaptychus is not clear. For instance, Lehmann (1972, Taf. 9, fig. 4)[2)] shows the external surfaces of the inner and the outer layers of the lower jaw of *Hildoceras* (*Hildaites*) *levisoni*. The outer layer of this specimen is identified with lamellaptychus (Lehmann, 1976[3)], p. 94, Abb. 73–b) using surface morphology, rather than with cornaptychus of Lehmann (1976, p. 94, Abb. 73–a)[3)]. The external surface of the lower jaw of *Harpoceras* (*H.*) *chrysanthemum* (Yokoyama, 1904[13)], pl. 2, fig. 1; Hirano, 1973[14)], pl. 2, fig. 2) is, as mentioned above, very similar to that of *H.* (*H.*) *levisoni*.

The structure of the outer layer is also problematical. The grooves of the internal surface of the outer layer of the lower jaw of *Harpoceras* (s.l.) sp. seem to correspond to the ribs of the external surface. But this relationship does not appear to hold in *H.* (*H.*) *chrysanthemum*. Also, according to Lehmann (1976)[3)] the outer layer is composed of two calcareous sublayers and the inner sublayer has a honeycomb structure. However, honeycomb structure is not observed in the present study.

If the structures of the external and internal surfaces of the outer layer are in fact corresponding

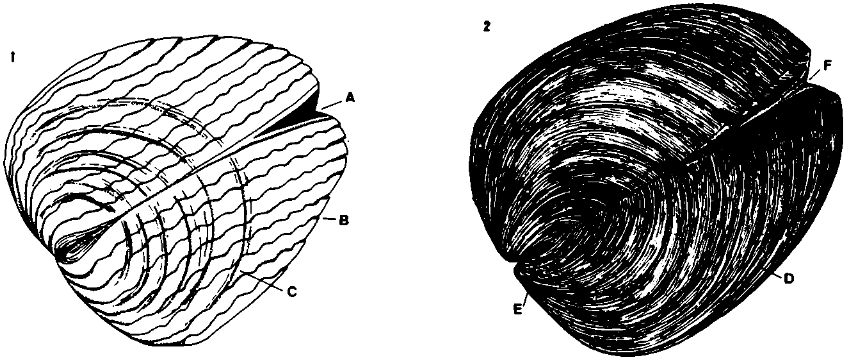


Fig. 6. Diagrammatic illustrations of the lower jaw plate of *Harpoceras* (s.l.) sp. C.
1. An internal view of the outer layer.
2. An external view of the inner layer.
A: Posterior median ridge, B: Groove, C: Impression of concentric undulation, D: Concentric striation, E: Median depression, F: Median ridge.

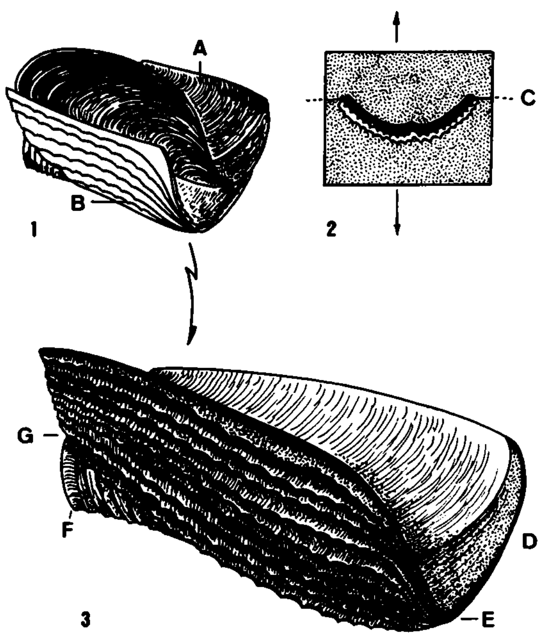


Fig. 7 Schematic restoration and the mode of occurrence of the lower jaw plate of *Harpoceras* sp. C.
1. Separation of the outer and inner layers.
2. Mode of preservation in the rock matrix.
3. Restored lower jaw plate.
A: Internal surface of the inner layer (Invisible in Specimen-C). B: External surface of the outer layer (Invisible in Specimen-C). C: Exfoliated surface. D: Anterior margin. E: Anterior. F: Posterior median ridge. G: Posterior.

to each other, there is the possibility that in at least some species honeycomb structure is undeveloped either in the early growth stage or all through the life. Thus, our study reveals that such a study of the inner structure of jaws is too scarce to generalize the existence of the honeycomb structure.

Although Lehmann (e.g., 1976)[3] showed that some lower jaws were bent inwards, this is not confirmed in our specimens.

We diagrammatically restore the morphology (Fig. 6) and the mode of occurrence of the lower jaw plate (Fig. 7) mostly based on Specimen-C and the discussion above.

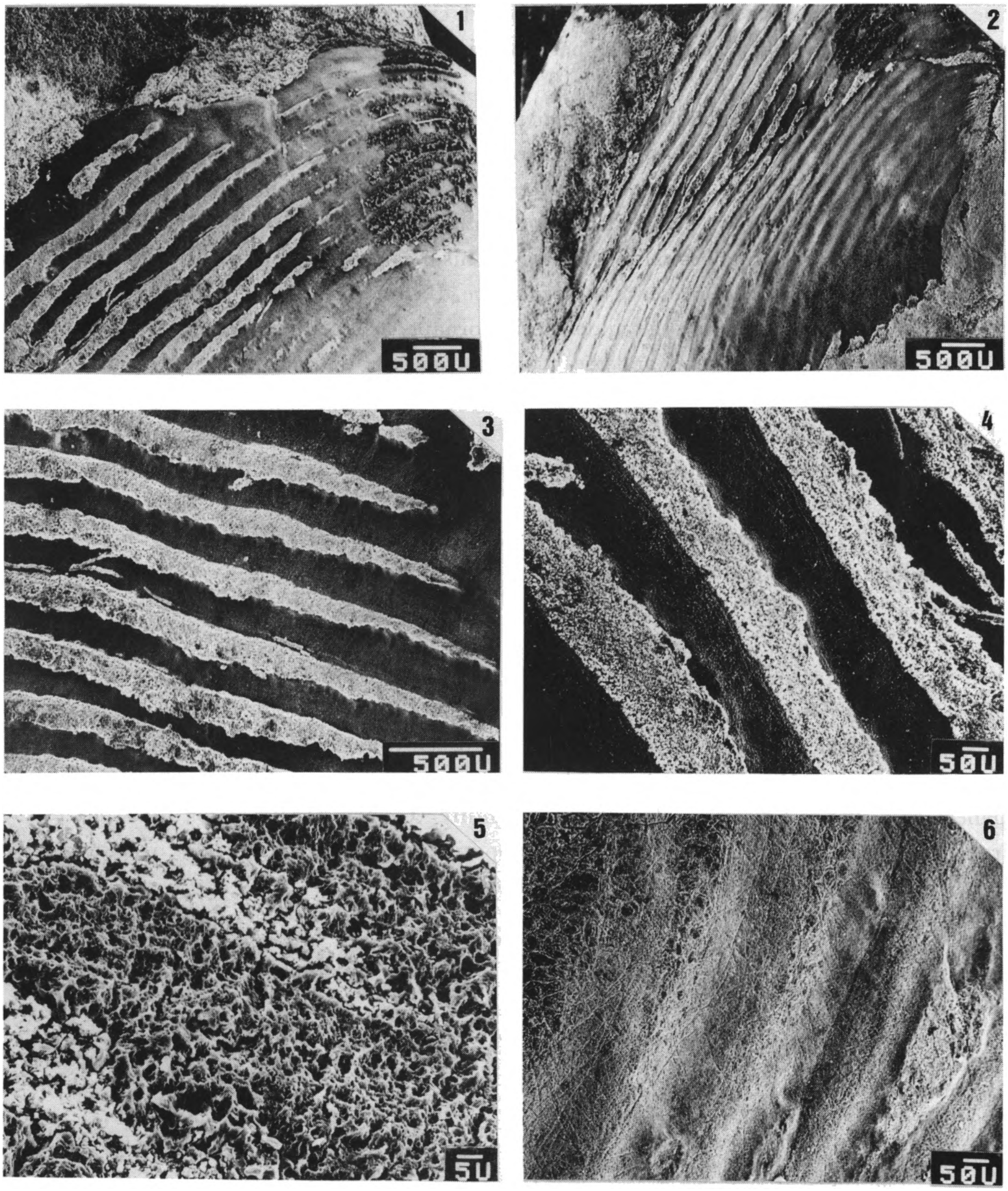


Fig. 8. Electron micrographs of an aptychus from the Aptychenschichten in Kalkalpine Zone.
1–4. An external surface of the right lobe. Concentric ribs shown as white lines. The concentric striation of the inner layer is shown as an impression on the right area of Fig. 8: 2.
5. An etched external surface of the aptychus. No biogenic microstructure is preserved.
6. External surface of aptychus, after additional etching to that of 5. Diagenesis has decomposed the original structure.

For purposes of comparison, serial observation from the external surface to the internal surface was carried out on a lamellaptychus from the Aptychenshiefer by etching with 5 % HCl and recorded by SEM (Fig. 8). The electron micrographs obtained show the presence of numerous concentric striae on the external surface of the inner layer, which cross the radial ribs of the external surface of the outer layer (Fig. 8: 2). Thus, the Upper Jurassic lamellaptychus also has a cornaptychus-type inner layer.

Judging from the restored buccal mass structure (Tanabe & Fukuda, 1983[5]; Tanabe, 1983[6]), and the structure of the lower jaw plate (Lehmann, 1976[3]), the chitinous inner layer of the lower jaw plate is most likely secreted by the beccublast cells and the calcareous outer layer by the labial region cells. Lehmann (1976)[3] described that the inner layer of the cornaptychus retains an anaptychus-type form, i. e., an ancestral morphology. This means that the inner layer of the lower jaw plate would in all probability preserve the prototype. If this is valid, the aptychi of *Harpoceras* from the Toyora group preserve the hildoceratid cornaptychi in the inner layer as the prototype. Although the systematic position and the geological age are different from each other, Tanabe (1983)[6] described a similar phenomenon in some Cretaceous desmoceratids. Together with those of Tanabe, our results support the description of Lehmann on this point as a general rule.

However, the structural transition of jaw plates from the Hildoceratidae to the Oppeliidae requires to be researched.

Ammonoid phylogeny would be confirmed by the studies of the structural evolution of the jaw plates in addition to the conventional studies on shell morphology.

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