

THE JAW APPARATUSES OF CRETACEOUS DESMOCERATID AMMONITES

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ABSTRACT. The jaw apparatuses of three late Cretaceous desmoceratines (*Tragodesmocerooides subcostatus*, *Damesites ainuanus*, and *D. semicostatus*) are described and compared with those of other ammonites and modern cephalopods. The jaws of the three species morphologically resemble one another, and belong to the anaptychus-type jaws of Lehmann (1981), because of the fundamental jaw structures and the absence of a calcareous element. Based on comparison of jaw structures with modern cephalopods and the jaw-muscle relations in modern *Nautilus*, a possible buccal structure of the Desmoceratinae is proposed.

JAWS and a radula have been regarded as primary feeding apparatuses in modern and extinct Cephalopoda. Recently, comparative morphological studies on the jaws of the Ammonoidea have been made successfully in some genera on the basis of well-preserved *in situ* materials (e.g. Closs 1967; Lehmann 1967, 1970, 1971*a, b*, 1972, 1976, 1979, 1981; Zakharov 1974; Kanie 1982; Kanie *et al.* 1978; Tanabe *et al.* 1980*a, b*). As a result, it has become clear that the jaw morphology of the Mesozoic Ammonoidea known to us is markedly variable in internal structures, mineralogy, and relative size versus shell size (Kaiser and Lehmann 1971; Lehmann 1976, 1981). Further work on various Mesozoic taxa is, however, required in order to obtain a general idea of the taxonomic and palaeoecological value of ammonite jaws. Most previous work on ammonite jaws dealt with Jurassic material, and little is known on the Cretaceous Ammonoidea other than *Scaphites* (Meek and Hayden 1864), *Scalarites* (Tanabe *et al.* 1980*a*), *Gaudryceras* and *Tetragonites* (Kanie *et al.* 1978; Kanie 1982; Tanabe *et al.* 1980*b*).

This paper gives a description of the jaws of three late Cretaceous desmoceratid ammonites on the basis of well-preserved *in situ* specimens from Hokkaido, Japan. A possible buccal structure of the Desmoceratinae is also proposed, relying on comparison with modern *Nautilus*.

MATERIALS

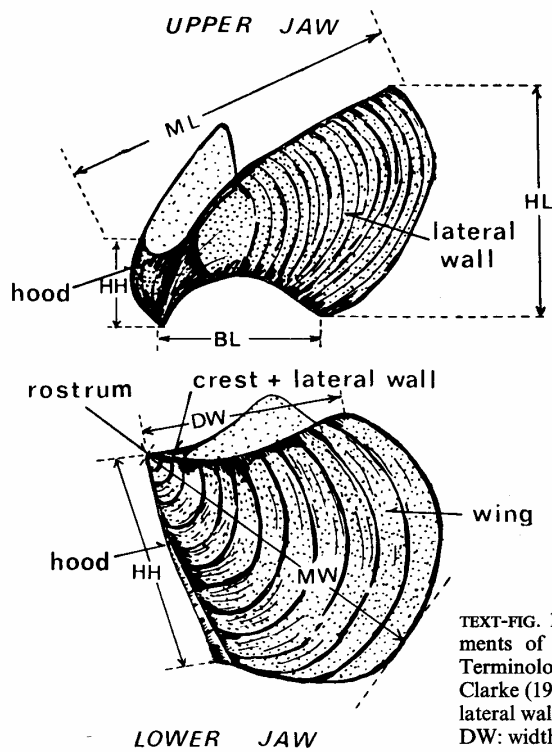
The jaw specimens utilized are: one lower jaw of *Tragodesmocerooides subcostatus* Matsumoto (GK. H 8064) from the upper Turonian in the lower course of the Abeshinai river, Saku area, northern Hokkaido (lat. 44° 44' N, long. 142° 3' E) (K. Tanabe coll.); one upper jaw of *Damesites ainuanus* Matsumoto (GK. H 8065) in a rolled nodule derived from the middle Turonian in the Gakkonosawa, Saku area (lat. 44° 44' N, long. 142° 1' 30" E) (T. Matsumoto coll.); and a complete jaw apparatus (upper and lower jaws) of *D. semicostatus* Matsumoto (UH. 4545) from the upper Santonian in the Kikumenzawa, a tributary of the Ikushumbets river, Ikushumbets area, central Hokkaido (lat. 43° 12' N, long. 142° 1' 30" E) (R. Saito coll.). Specimens with prefixes GK and UH are stored in Kyushu University and Hokkaido University respectively.

A 70% alcohol-preserved buccal mass of a male *Nautilus pompilius* Linnaeus, captured off Bindoy, Negros Oriental, the Philippines, was also studied for comparison. The specimen is kept at Ehime University without registered number.

DESCRIPTION

The ammonite jaws examined were found *in situ* within the body chambers, although they have been slightly removed from their original position during fossilization (Pl. 71). As they are all preserved in calcareous nodules, a three-dimensional reconstruction of jaw morphology is possible on the basis of comparison with modern cephalopod jaws.

Concerning recognition of upper and lower jaws, I follow Lehmann's (1970) definition, relying on the mode of occurrence of jaws and radula within the body chamber in life position. The morphotype with a wide, concave outer lamella in the jaw specimens examined is regarded as comprising lower jaws, because of the essential similarity in gross morphology to Lehmann's (1970) anaptychus-type lower jaws. The morphotype consisting of a pair of wide inner lamellae and a short reduced outer one, is compared with the upper jaws of most previously known ammonites (Meek and Hayden 1864; Lehmann 1970, 1971a, 1972, 1975, 1976, 1981). Text-fig. 1 shows the basic morphology and measurements of the reconstructed desmoceratid ammonite jaws.



TEXT-FIG. 1. Basic morphology, terminology, and measurements of desmoceratine ammonite jaws (lateral views). Terminology is that applied to modern coleoid jaws by Clarke (1962). BL: length of base, ML: maximum length of lateral wall, HH: height of hood, HL: height of lateral wall, DW: width of wing, MW: maximum length of wing.

Suborder AMMONITINA Hyatt, 1889
 Superfamily DESMOCERATACEAE Zittel, 1895
 Family DESMOCERATIDAE Zittel, 1895
 Subfamily DESMOCERATINAE Zittel, 1895
 Genus DAMESITES Matsumoto, 1942
 Upper jaw of *Damesites ainuanus* Matsumoto

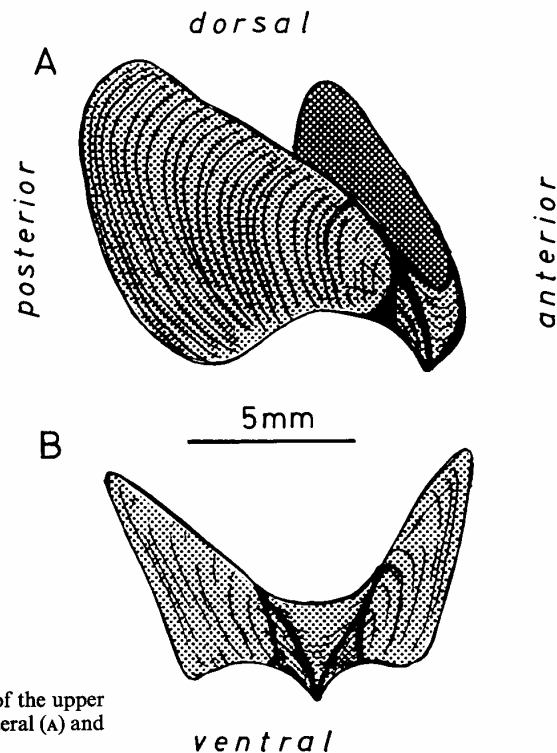
Plate 71, fig. 2a-c; text-fig. 2

The upper jaw bearing shell of *D. ainuanus* attains 30 mm in diameter, although it lacks the majority of the body chamber. The upper jaw is preserved near the base of the body chamber (Pl. 71, fig. 2a). It is made up of a pair of wide inner lamellae (lateral wall without crest region) and a reduced short inner lamella (hood). These lamellae are combined one with another in the anterior rostral region. The jaw lamellae are composed of dark-coloured homogenous material only. They are thickest in the anterior portion, and become thinner toward the

posterodorsal margin. The rostrum projects strongly ventrally, like a parrot's beak. A V-shaped depression is present along the median line of the outer lamella. The open angle between the paired inner lamellae is about 30°. The inner and outer lamellar surfaces are sculptured with regularly spaced, concentric undulations (numbering more than twenty) and fine striae respectively.

Measurements (cf. text-fig. 1)

ML	HL	HH	BL	HL/ML
13.75 mm	10.02 mm	3.45 mm	10.02 mm	0.73



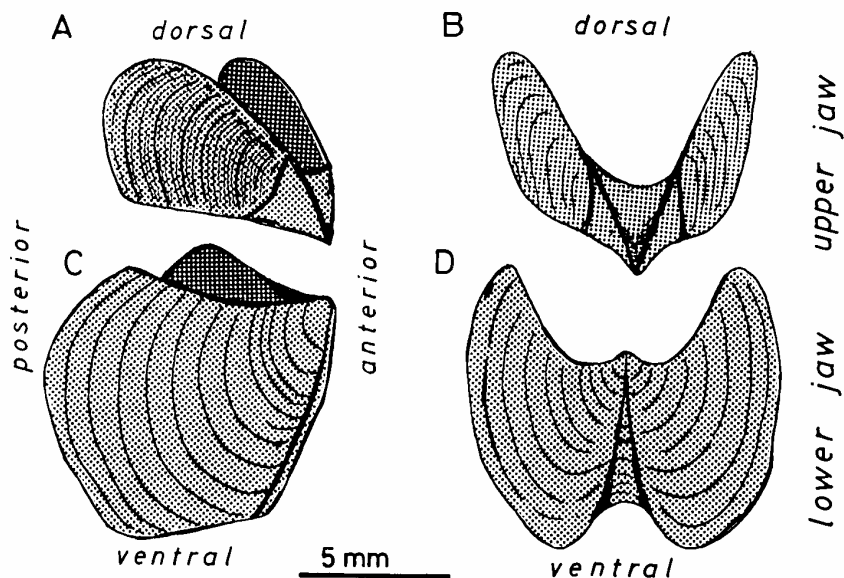
TEXT-FIG. 2. Three-dimensional reconstruction of the upper jaw of *Damesites ainuanus*. GK. H 8065. Left lateral (A) and anterior (B) views.

Jaw apparatus of *Damesites semicostatus* Matsumoto

Plate 71, fig. 1a-d; text-fig. 3

Complete upper and lower jaws are preserved in the middle part of the body chamber of an immature *D. semicostatus* (29.65 mm in maximum shell diameter with an almost perfect body chamber). The lower jaw was formerly interpreted by Nagao (1932) as an operculum, but I have recently found an upper jaw on the posteroventral side of the lower (Pl. 71, fig. 1a). The mode of occurrence shows that both jaws have been moved slightly from their original position.

Upper jaw. The upper jaw is similar in fundamental morphology to that of *D. ainuanus*. It differs, however, from the latter in having a less projected rostrum, smaller lateral wall height in relation to maximum lateral wall size (see LH/ML in the measurements), and more widely spaced, less numerous concentric undulations on the inner lamellar surface. Furthermore, unlike *D. ainuanus*, the paired inner lamellae possess more than ten radial striae on the posterodorsal margin. The open angle formed by the paired lateral walls is acute (c. 40°) as in *D. ainuanus*.



TEXT-FIG. 3. Three-dimensional reconstruction of the jaw apparatus of *Damesites semicostatus*. UH. 4545. Left lateral (A, C) and anterior (B, D) views of the upper (A, B) and lower (C, D) jaws.

Lower jaw. The lower jaw may consist of widely developed outer and reduced short inner lamellae, although the greater part of the latter are coated with host rock. In all probability the two lamellae are united in the anterior rostral region. The outer lamella is gently convex anteriorly, and there is a prominent radial groove along the hood, dividing the outer lamella into two wing areas. The open angle between the two wings is about 50°. The outer lamellar surface is ornamented with more than twenty regularly spaced concentric undulations.

The upper and lower jaws are not much different in size, as shown by the following measurements.

Measurements (cf. text-fig. 1)

	ML	HL	BL	HH	HL/ML	ML/shell diam.
Upper jaw	11.00 mm	6.15 mm	9.30 mm	2.65 mm	0.56	0.37
	MW	DW	HH	HH/DW	MW/shell diam.	
Lower jaw	11.15 mm	9.35 mm	10.85 mm	1.16	0.38	

Genus TRAGODESMOCEROIDES Matsumoto, 1942
Lower jaw of *Tragodesmoceroides subcostatus* Matsumoto

Plate 71, fig. 3a-c; text-fig. 4

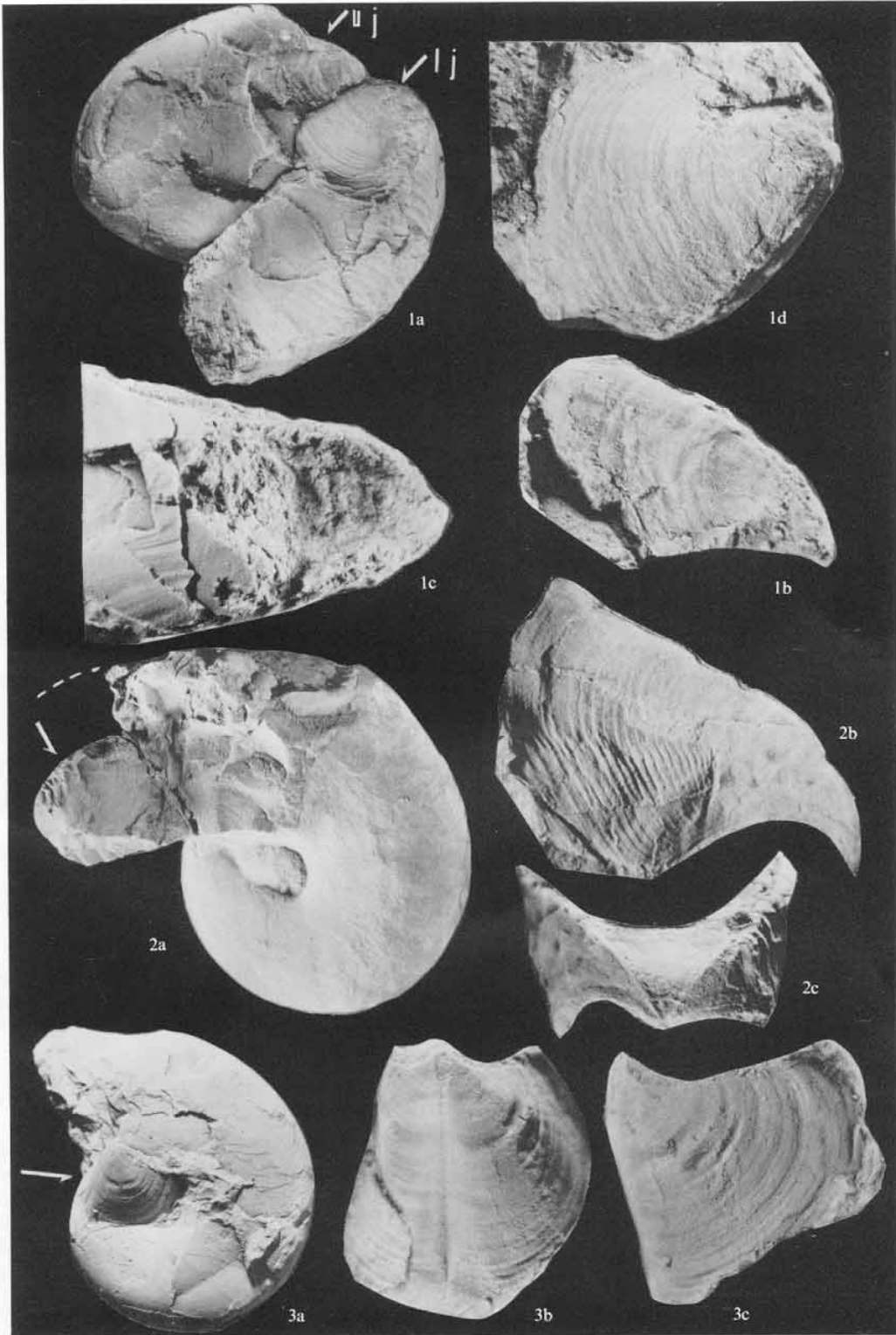
EXPLANATION OF PLATE 71

Fig. 1. Jaw apparatus of *Damesites semicostatus* Matsumoto. UH. 4545. 1a, mode of occurrence of upper (uj) and lower (lj) jaws within the body chamber, $\times 1$. 1b, c, right lateral (b) and dorsal (c) views of the upper jaw, $\times 2$. 1d, right lateral view of the lower jaw, $\times 1$.

Fig. 2. Upper jaw of *Damesites ainuanus* Matsumoto. GK. H 8065. 2a, mode of occurrence within the incomplete body chamber, $\times 1$. 2b, c, right lateral (b) and anterior (c) views, $\times 2$.

Fig. 3. Lower jaw of *Tragodesmoceroides subcostatus* Matsumoto. GK. H 8064. 3a, mode of occurrence near the aperture, $\times 1$. 3b, c, anterior (b) and left lateral (c) views, $\times 1.7$.

All specimens whitened.

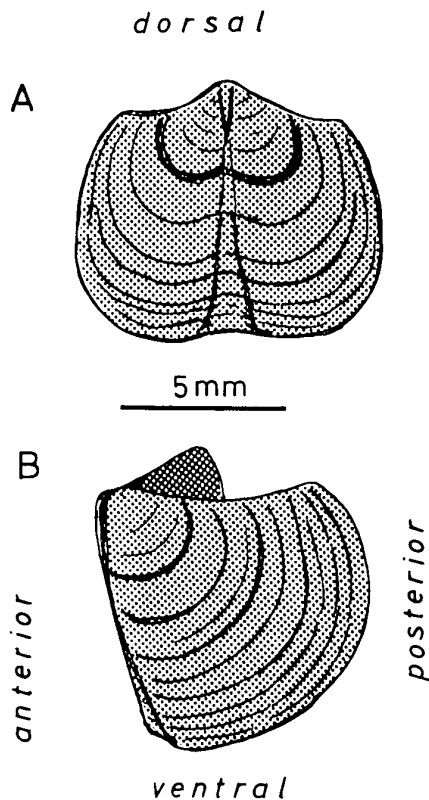


TANABE, Cretaceous ammonite jaws

A lower jaw was found near the aperture of an immature shell 26.9 mm in maximum shell diameter. It is characterized by the gently convex, wide outer lamella. An inner lamella is not well exposed in the present specimen, but it may be reduced, as in *D. semicostatus*. The outer lamella is divided into two wing areas by a prominent groove running along the hood. The surface of the lamella is sculptured with many regular-spaced, concentric undulations. The gross morphology and surface ornament of the lower jaw of the present species are, therefore, essentially similar to those of *D. semicostatus*, but it is distinguished by the more strongly projected rostral edge. Furthermore, the lower jaw in relation to the shell diameter of this species is smaller than that of *semicostatus*.

Measurements (cf. text-fig. 1)

MW	DW	HH	HH/DW	MW/shell diam.
8.60 mm	7.60 mm	7.75 mm	1.02	0.25



TEXT-FIG. 4. Three-dimensional reconstruction of the lower jaw of *Tragodesmocerooides subcostatus*. GK. H 8064. Anterior (A) and right lateral (B) views.

COMPARATIVE MORPHOLOGY

On the basis of differences in the internal structures and mineralogy, Lehmann (1981) classified the complete jaw apparatuses of fifteen ammonite genera known to us into the following three morphotypes: (1) anaptychus (= normal) type, represented by such Palaeozoic and Mesozoic genera as *Eoasianites*, *Olenekites*, *Psiloceras*, and *Dactylioceras*; (2) aptychus type, which is characterized by some Jurassic and Cretaceous genera (e.g. *Eleganticeras*, *Hildoceras*, *Scaphites*, and *Scalarites*); and (3) calcified anaptychus type (= rhynchaptychus type of Lehmann *et al.* 1980), which is probably restricted to Mesozoic Lytocerataceae and Phylloceratina (Tanabe *et al.* 1980b).

As described above, the jaw apparatuses of the three desmoceratines examined resemble one another in basic morphology and surface ornament. This fact suggests to us that jaw morphology is taxonomically stable in the Desmoceratinae. Judging from the fundamental jaw structures and the absence of a calcified element, the jaws of the three species apparently belong to the anptychus-type of Lehmann (1981). They are, however, slightly different from the typical anptychus-type jaws of Jurassic *Psiloceras*, *Arnioceras*, and *Pleuroceras* (Lehmann 1970) in the larger upper jaws in relation to the lower ones and the presence of a distinct median depression in the lower jaws. As such a median depression is also observed on the inner chitinous layer of all aptychus-type lower jaws (Lehmann 1972, 1976, 1981), the lower jaws of the Desmoceratinae correspond to an intermediate form between the typical anptychus-type jaws and the aptychus-type jaws.

The fossil record of aptychi and anptychi (Trauth 1927-1936) suggests that most Palaeozoic and Triassic Ammonoidea possessed an anptychus-type jaw apparatus (Lehmann 1976, 1981). In the early Jurassic aptychus-type jaws first appear in some genera of the Ammonitina, and throughout the Jurassic and Cretaceous they have been specially adapted in many groups of the Ammonitina and Ancyloceratina (Lehmann 1976, 1981). In contrast to this, anptychus-type jaws are rare in occurrence in the middle Jurassic to Cretaceous. This paper is the first reliable record of Cretaceous ammonites with anptychus-type jaws. Moreover, the lower jaws of the early Cretaceous Haplocerataceae, a possible ancestor of the Cretaceous Desmocerataceae (Wright 1981), are represented by the form genera lamellaptychi and laevilamellaptychi (Trauth 1927-1936), both of which are included in the aptychus-type lower jaws of Lehmann (1976, 1981). From these lines of evidence, it is probable that the jaws of the Desmoceratinae evolved in a different way from the anptychus-type jaws of the early Jurassic Ammonitina.

Comparison with modern cephalopod jaws shows that the upper jaws of *Damesites semicostatus* and *D. ainuanus* somewhat resemble those of modern coleoids (especially of octopods) in having a beak-like rostral edge and a reduced short outer lamella (hood). They are, however, clearly distinguished from all modern cephalopod upper jaws, because the inner lamella is distinctly divided into two lateral walls.

The lower jaws of *D. semicostatus* and *Tragodesmocerooides subcostatus* are more similar to those of modern *Nautilus* than coleoids in the presence of a widely developed, convex outer lamella (wing and hood) and a short reduced inner lamella (crest and lateral wall). But they do not possess an anterior calcified element (conchorhynch), which is present in the Nautilida and in lytoceratid and phylloceratid ammonite lower jaws (Müller 1974; Saunders *et al.* 1978; Tanabe *et al.* 1980b). The surface ornament pattern on the upper and lower jaws of the desmoceratines examined is essentially like those of modern cephalopods.

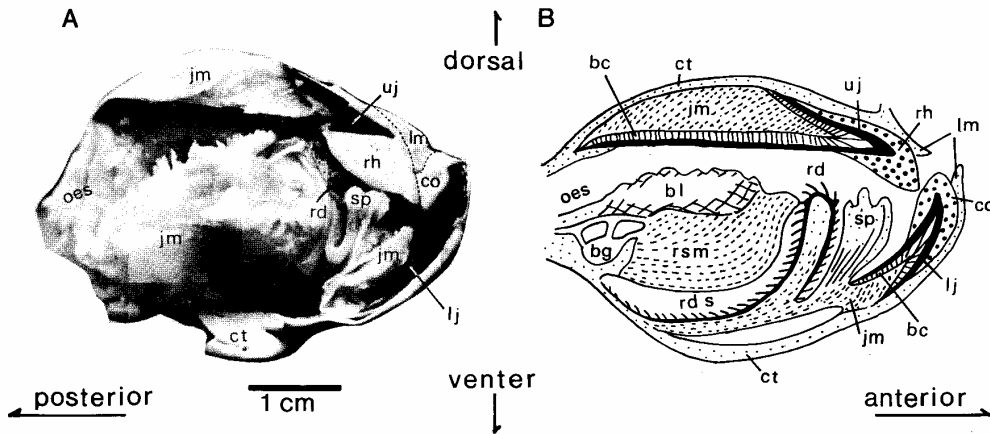
RESTORATION OF BUCCAL STRUCTURE

It is well known that in the modern Cephalopoda the jaw apparatus is present within a buccal mass. The buccal mass of cephalopods includes jaw plates, radula, jaw and radular support muscles, buccal palp, salivary papilla and oesophagus (Young 1977). Both upper and lower jaws are connected with strong jaw muscles for biting or cutting up food.

The mode of occurrence of the upper and lower jaws-radula association within the body chambers of some Jurassic ammonites (Lehmann 1967, 1971a, 1972, 1979) strongly suggests that the jaws and radula in the Ammonoidea were present within a buccal mass, as in all modern cephalopods. Details of the buccal structures in the Ammonoidea, however, have long been uncertain. The reason for this owes much to the lack of knowledge about the structural relationship between jaw plates and muscles. Kanie (1982) recently speculated on possible jaw-muscle relations in the Cretaceous tetragonitid ammonites, relying on comparison with the muscular system of modern *Nautilus*. However, he showed no concrete evidence of the muscles of either ammonites or *Nautilus*.

More recently, Tanabe and Fukuda (1983) proposed detailed buccal structures in a late Cretaceous *Gaudryceras* (Lytoceratina) on the basis of the comparative histological observations of the chitin-secreting cell impressions on the jaw surface of the ammonite and modern cephalopods. As Dilly and

Nixon (1976) have already realized, in modern Cephalopoda a layer of chitin-secreting cells (beccublast cells) is intercalated between the hard tissue of the jaws and jaw muscles. Tanabe and Fukuda (1983) made clear that the beccublast cells and jaw muscles are only present in the outer side of the upper jaw and/or the inner side of the lower jaw in *Sepia* and *Nautilus*. The other sides of the jaws are, therefore, free from muscles and are directly covered with a connecting tissue. Text-fig. 5 shows such jaw-muscle relations in modern *Nautilus*.



TEXT-FIG. 5. Buccal structure of *Nautilus pompilius*. A, photograph of the median-sectioned buccal mass. Ehime University specimen from off Bindoy, Negros Oriental, the Philippines. B, Diagram showing the internal organs of a buccal mass. uj, upper jaw; lj, lower jaw; rh, rhyncholite, co, conchorhynch; jm, jaw muscles; bc, beccublast cells; rd, radula; rds, radular sac; rsm, radular support muscles; bl, lateral buccal palp; sp, salivary papilla; bg, inferior buccal ganglion; lm, labial margin; oes, oesophagus, ct, connecting tissue. Terminology from Young (1965, 1977).

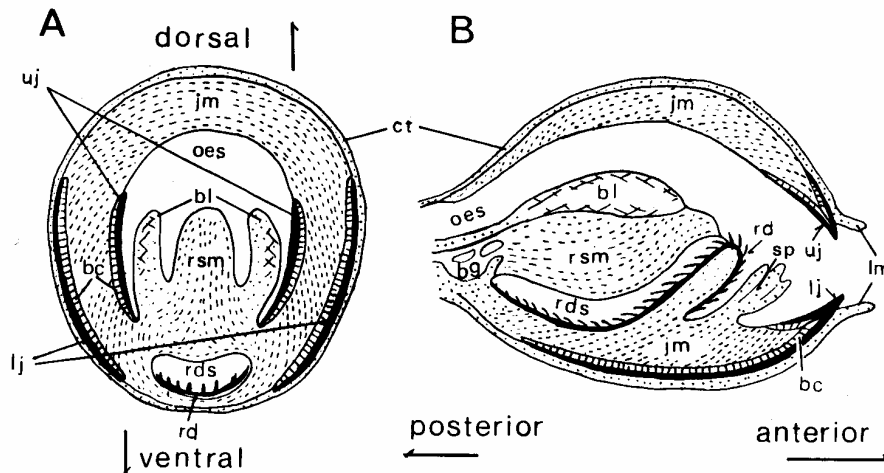
Tanabe and Fukuda (1983) reconstructed a modern *Nautilus*-like jaw muscular system in *Gaudryceras*, on the basis of the restriction of beccublast cell imprints to the inner side of the lower jaw.

As already described, the lower jaws of *D. semicostatus* and *T. subcostatus* examined are essentially similar to those of *Nautilus* and *Gaudryceras*, except for the absence of an anterior calcified element, the conchorhynch. Furthermore, the outer side of the lower jaws of the two desmoceratines is ornamented with numerous concentric growth rings, as in *Nautilus*. From this indirect evidence, it is postulated that in the Desmoceratinae the jaw muscles and beccublast cells were connected with the inner side of the lower jaw.

In all modern cephalopods the inner lamella of the upper jaw is formed of a strongly convex, single chitinous layer, unlike that of the desmoceratines (Clarke 1962). The outer side of the upper jaws of modern cephalopods are wholly covered with fairly thick jaw muscles with intercalated beccublast cells (Young 1965, 1977; Tanabe and Fukuda 1983). Although there is no concrete evidence for the upper jaw-muscle relations in the Desmoceratinae, the outer surface of the paired inner lamellae was probably covered with jaw muscles, as in all modern cephalopods. In the desmoceratines examined the inner lamella of the upper jaws is distinctly divided into two separated lateral wall areas in the posterior region. This fact means a reduction of muscle attachment area on the upper jaws. It is therefore reasonable to deduce that in the Desmoceratinae the mechanical properties of jaw muscles in the side of the upper jaw might be weaker than those of the lower jaw. In connection with this problem, Lehmann (1981) pointed out that in most Mesozoic ammonites the upper jaws are more or less smaller than the lower ones. In all probability in the Mesozoic Ammonoidea which possessed

aptychus- or anaptychus-type jaws, the lower jaws might have functioned more actively for feeding than the upper jaws.

In conclusion, a buccal structure of the Desmocerotinae is proposed in text-fig. 6.



TEXT-FIG. 6. Diagram showing presumed buccal structure of a desmoceratine ammonite, based on comparison with the buccal structure of modern *Nautilus*. Cross (A) and median (B) sections. For abbreviations see explanation of text-fig. 5.

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