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Morphological Diversity of the Jaws of Cretaceous Ammonoidea

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3 Text-Figures, 1 Table and 1 Plate

Cretaceous
Ammonoidea
Taxonomy
Functional Morphology

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Kiefermorphologische Diversität kretazischer Ammonoidea

Zusammenfassung

Die Kiefermorphologie von 19 Kreideammoniten der Phylloceratina, Lytoceratina, Ammonitina und Ancyloceratina wurde verglichen. Die von sieben Gattungen bekannten Oberkiefer der Ammonitina und Ancyloceratina sind im Wesentlichen ähnlich mit reduzierten hornigen äußeren und großen paarigen inneren Lamellae, beide im vorderen Teil miteinander zu einer scharfen rostralen Spitze verwachsen. Diese Merkmale wurden auch bei den Oberkiefern der Goniatitina und Ceratitina beobachtet, was auf morphologischen Konservativismus des Oberkiefers bei Ammoniten schließen lässt. Im Gegensatz dazu zeigen die Unterkiefer bei Kreideammoniten eine bemerkenswerte taxonomische Variationsbreite in ihrer relativen Größe zum Oberkiefer, ihrer gesamten Morphologie und dem Entwicklungsgrad der äußeren Calcitlage. Sie können Rhynchaptychus-, Anaptychus- oder Lamellaptychus-Typen zugeordnet werden, doch gibt es auch Zwischenformen. Der Anaptychus-Typus mit großer, horniger Lamella, einer medianen „Symphyse" und paarigen Calcitplatten könnte eine sekundäre Funktion als Operculum übernommen haben.

Abstract

Jaw morphologies of 19 Cretaceous ammonoid genera that are distributed in the suborders Phylloceratina, Lytoceratina, Ammonitina, and Ancyloceratina were compared. The upper jaws known from seven genera of the Ammonitina and Ancyloceratina are essentially similar in having horny reduced outer and large paired inner lamellae, both of which are united in the anterior portion forming a sharp rostral tip. These features have also been recognized in the upper jaws of Goniatitina and Ceratitina, suggesting the morphological conservatism of the upper jaws in the Ammonoidea. The lower jaws of Cretaceous ammonoids, by contrast, exhibit remarkable taxonomic variation in their relative size to the upper jaws, overall morphology, and the degree of development of the outer calcitic covering. They may fall into either rhynchaptychus- or anaptychus- or aptychus-types, but intermediate forms are present among them. The anaptychus-type lower jaw in some Ammonitina and Ancyloceratina with a large outer horny lamella with a median "hinge" and paired calcite plates may have acquired a secondary function as an operculum.

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1. Introduction

Jaw remains are occasionally preserved within the body chambers of ammonoids whose taxonomic relationships are known. Based on such in situ material, the three-dimensional structure of the jaw apparatus in Cretaceous ammonoids has been reconstructed in such genera as *Gaudryceras, Tetragonites, Damesites, Reesidites, Scalarites, Jeletzkytes*, and *Rhaeboceras* by previous authors (MEEK & HAYDEN, 1864; TANABE et al., 1980a, b; KANIE, 1982; TANABE, 1983; TANABE & FUKUDA, 1987a; LANDMAN & WAAGE, 1993; KENNEDY et al., in press; see Table 1). As a result, it is clear that the jaw apparatuses of Cretaceous ammonoids exhibit taxonomic variation in their overall morphology, structure, and mineralogical composition, allowing us to classify them into anaptychus, aptychus, and rhynchaptychus types (LEHMANN, 1990; TANABE & FUKUDA, 1999). However, a question still remains with respect to the recognition of these morphotypes because of the presence of an intermediate form among them. We have reexamined some of the previously published jaw material, together with newly collected material of other taxa.

This article presents an overview of the morphological variation of the jaws of Cretaceous Ammonoidea and evaluates the significance of their variation with respect to taxonomy and functional morphology.

2. Data Sources

Our knowledge of the jaw apparatuses of Cretaceous ammonoids is based on material from 25 species of 20 genera, which belong to the suborders Phylloceratina, Lytoceratina, Ammonitina, and Ancyloceratina (see Table 1). In every case, the jaw remains were preserved within the body chambers in situ as complete upper and lower elements or either as an incomplete upper or a lower element. In most species, excluding *Aconeceras trautscholdi* (Psilocerataceae; Ammonitina; DOGUZHAEVA & MUTVEI, 1992), *Texanites soutoni* (Acanthocerataceae; Ammonitina; KENNEDY & KLINGER, 1972) and an unknown species of the Placenticeratidae (SUMMESBERGER et al., 1996, 1999), specimens with preserved remains of jaws have been dis-

Table 1.
List of Cretaceous ammonites whose jaw apparatuses have been described.

Suborder	Superfamily	Species	Jaws	Sources
Phylloceratina	Phyllocerataceae	*Phyllopachyceras ezoense* (Yokoyama)	Lj	This study
Lytoceratina	Tetragonitaceae	*Gaudryceras denseplicatum* (Jimbo)	Lj	Tanabe et al. (1980a), Kanie (1982)
		Gaudryceras tenuiliratum Yabe	Lj	Tanabe et al. (1980a), Kanie (1982)
		Tetragonites glabrus (Jimbo)	Lj	Tanabe et al. (1980a), Kanie (1982)
Ammonitina	Psilocerataceae	*Aconeceras trautscholdi* Sinzow	Uj+Lj	Doguzhaeva and Mutvei (1992)
	Desmocerataceae	*Tragodesmoceroides subcostatus* Matsumoto	Lj	Tanabe (1983)
		Damesites semicostatus Matsumoto	Uj+Lj	Nagao (1932), Tanabe (1983)
		Damesites ainuanus Matsumoto	Uj	Tanabe (1983)
		Damesites sugata Forbes	Lj	This study
		Menuites naumanni (Yokoyama)	Uj+Lj	This study
	Hoplitaceae	Placenticeratidae, gen. et sp. indet.	Uj(?)+Lj	Summesberger et al. (1996, 1999)
	Acanthocerataceae	*Reesidites minimus* Hayasaka and Fukada	Uj+Lj	Tanabe and Fukuda (1987a)
		Texanites soutoni (Baily)	Lj	Kennedy and Klinger (1972)
Ancyloceratina	Turrilitaceae	*Scalarites mihoensis* Wright and Matsumoto	Uj+Lj	Tanabe et al. (1980b)
		Polyptychoceras cf. *pseudogaultinum* (Yokoyama)	Lj	Nagao (1931b, c), this study
		Subptychoceras sp.	Uj+Lj	This study
		Sciponoceras kossmati (Nowak)	Lj	This study
		Baculites cf. *princeps* Matsumoto	Lj	This study
	Scaphitaceae	*Scaphites cobbani* Birkelund	Lj	Birkelund (1965)
		Yezoites puerculus (Jimbo)	Lj	Nagao (1931c), this study
		Hoploscaphites nicolletii (Morton)	Lj	This study
		Discoscaphites gulsous (Morton)	Lj	Landman and Waage (1993)
		Jeletzkytes nebrascensis (Owen)	Uj+Lj	Meek and Hayden (1864)
		Jeletzkytes spedeni Landman and Waage	Uj+Lj	Landman and Waage (1993)
		Jeletzkytes dorfi Landman and Waage	Uj+Lj	Landman and Waage (1993)
		Rhaeboceras halli (Meek and Hayden)	Uj+Lj	Kennedy et al. (2002)

covered from the Upper Cretaceous of the northwestern Pacific region (Hokkaido and Sakhalin) and the U.S. Western Interior Province (MEEK & HAYDEN 1864; TANABE et al., 1980a, b; LEHMANN et al., 1980; KANIE, 1982; TANABE, 1983; TANABE & FUKUDA, 1983, 1987a, 1999; LANDMAN & WAAGE, 1993; KENNEDY et al., 2002). Aptychi and anaptychi preserved within the body chambers of several genera have been mistakenly described as opercula by NAGAO (1931a–c, 1932), but they have been reinterpreted as lower jaws by TANABE et al. (1980b) and TANABE (1983). The jaws of these specimens were reexamined by ourselves on this occasion, together with newly discovered jaws belonging to six other genera (*Phyllopachyceras, Menuites, Subptychoceras, Sciponoceras, Baculites*, and *Hoploscaphites*) from Hokkaido, Sakhalin, and South Dakota.

The figured specimens are housed in the Department of Earth and Planetary Sciences, Kyushu University (GK), the Department of Earth and Planetary Sciences, Hokkaido University (HK), the University Museum, University of Tokyo (UMUT), the Black Hills Museum of Natural History (BHMNH), and the American Museum of Natural History (AMNH).

3. Desription of the Jaws of Cretaceous Ammonoids

3.1. Recognition of Upper and Lower Jaw

As in extant cephalopods, the jaw apparatus of ammonoids consists of upper and lower jaws. The upper and lower jaws occasionally co-occur within the ammonoid body chambers approximately retaining their normal orientation in life (see TANABE & FUKUDA, 1987a, Fig. 5A and LANDMAN & WAAGE, 1993, Fig. 39 for *Reesidites minimus* and *Jeletzkytes dorfi*). The morphological criteria to distinguish upper and lower jaws were first established from careful observations of such specimens; namely, the larger jaw element with a widely open outer lamella on the ventral side is identified as a lower jaw, while the smaller element partly enclosed by the lower jaw on the dorsal side is regarded as an upper jaw.

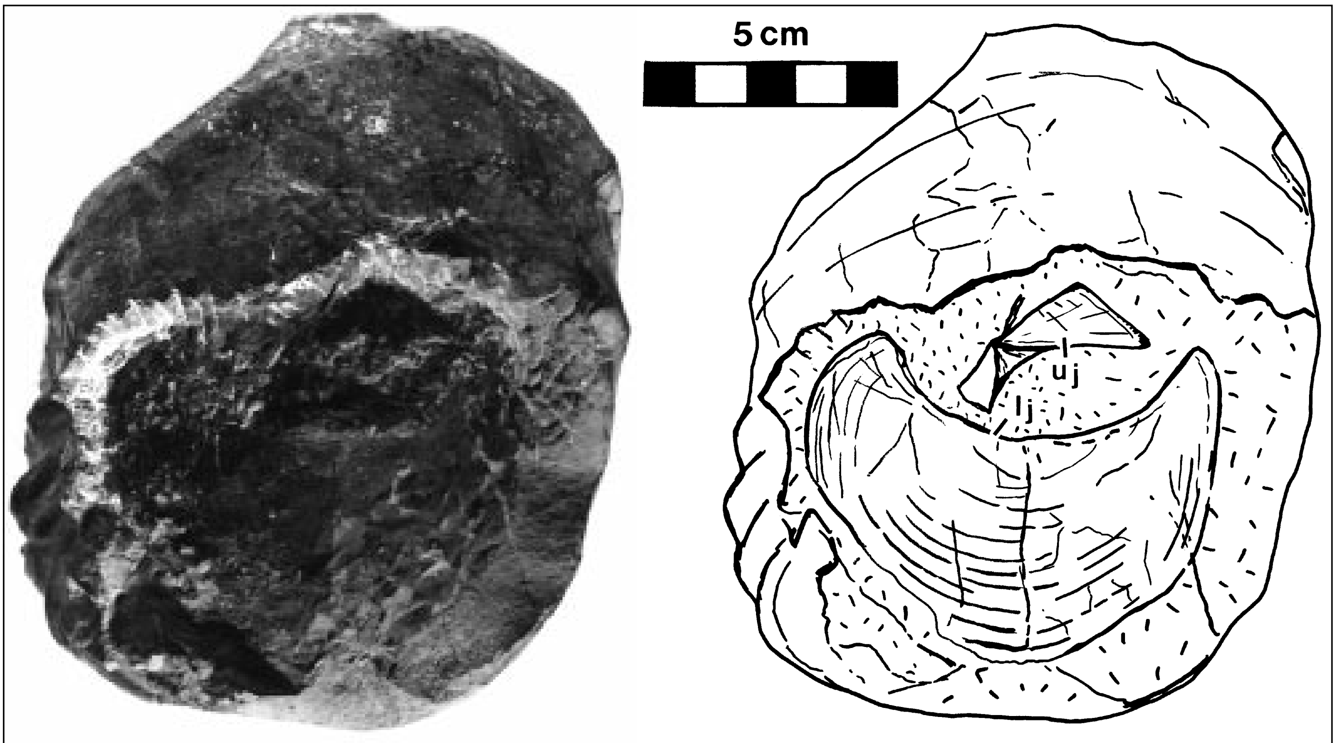
More frequently, a single jaw element is found within the ammonoid body chamber, in which case, recognition of upper and lower jaws relies upon morphological comparison with co-occurring upper and lower jaws. Although the lower jaw morphology of the Mesozoic Ammonoidea known to us is fairly variable in overall shape and degree of development of an outer calcareous covering, we follow the previous interpretation that jaw elements known as aptychi and anaptychi are ammonoid lower jaws (LEHMANN, 1970, 1972, 1976; see also TANABE & FUKUDA, 1999, for review). Problems about the recognition of the "upper jaws" in the Lytocerataceae will be discussed later.

3.2. Phylloceratina

Jaws of Phylloceratina are scarce, since only a lower jaw is known from *Phyllopachyceras ezoense* (Pl. 1, Fig. 1a, b). The lower jaw is preserved in the middle portion of the body chamber and appears to retain its original orientation and is fairly large, its length being approximately 40 % of the shell diameter. It consists of a widely open, black horny lamella and a short reduced inner lamella. A conspicuous calcareous covering is observable in the anterior portion.

3.3. Lytoceratina

Jaws have been described from *Gaudryceras* and *Tetragonites* (KANIE et al., 1978; TANABE et al., 1980b; KANIE, 1982; TANABE & FUKUDA, 1983). In both genera, only a single jaw element is preserved within the body chamber. According to previous descriptions (TANABE et al., 1980b, Fig. 9C, D;



Text-Fig. 1.
Photograph and drawing of immature specimen of *Menuites naumanni* (YOKOYAMA), with upper and lower jaws preserved in body chamber.
Frontal views of upper jaw (uj) and lower jaw (lj) are visible in the specimen. The posterior portion of the upper jaw is not completely excavated.
UMUT MM 27835, from the Campanian of Naiba area, south Sakhalin.

KANIE, 1982, Text-Figs. 4, 7), the "upper" and lower jaws of both genera are similar in overall morphology and mineralogical composition, consisting of widely open outer and short reduced inner horny black lamellae with a conspicuous anterior calcareous covering (see Text-Fig. 3.1 for generalized drawing); the upper jaw is distinguishable from the lower jaw by a more strongly convex outer lamella and strong radial sculpture. Curiously, the "upper" jaws of *Gaudryceras* and *Tetragonites* show no morphological resemblance to the upper jaws of any other known ammonoid genus.

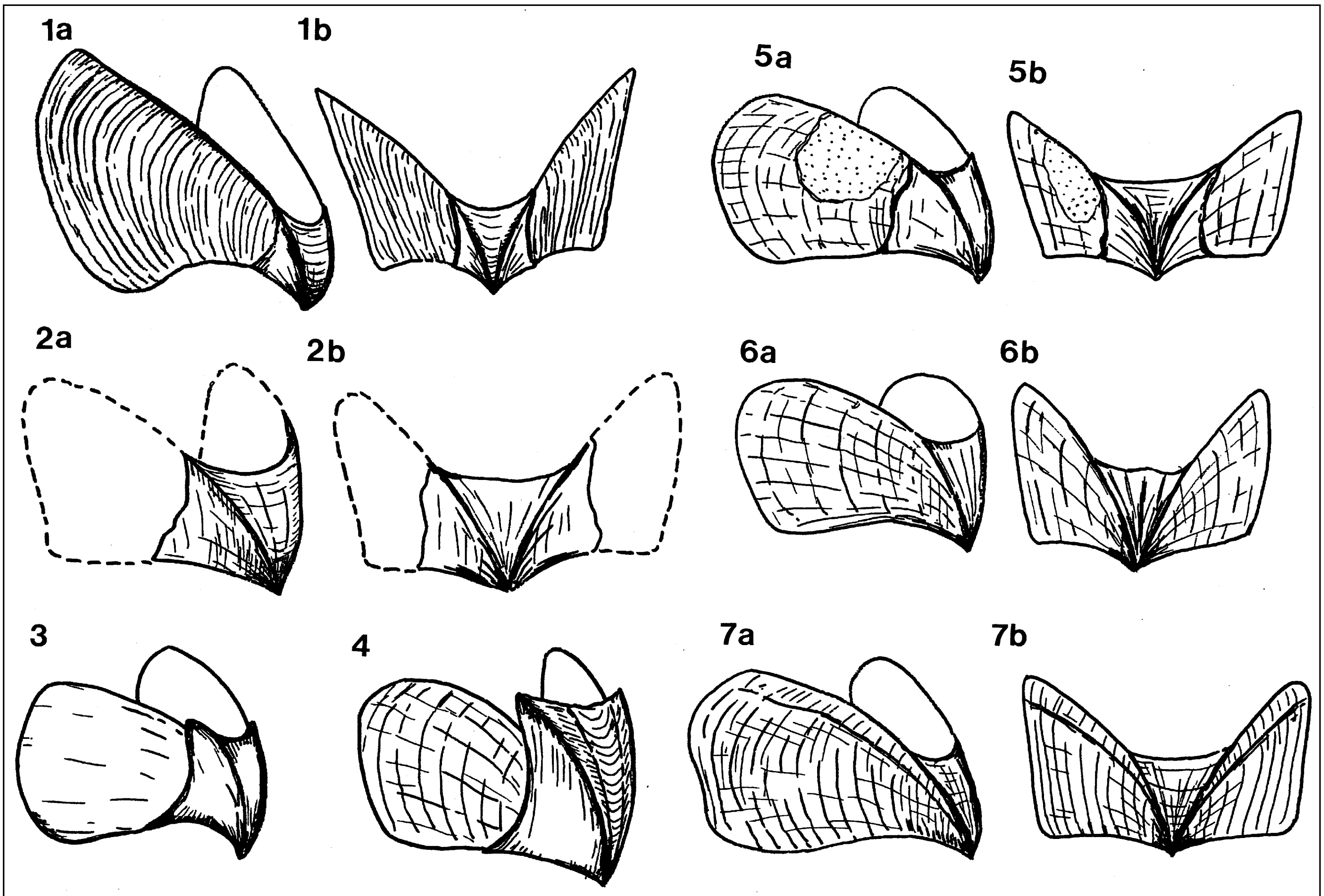
These observations strongly suggest that the "upper" jaws of *Gaudryceras* and *Tetragonites* described by KANIE et al. (1978), TANABE et al. (1980b) and KANIE (1982) actually represent deformed lower jaws. The upper jaws of the Lytoceratina are, therefore, still unknown. An isolated upper jaw co-occurring with isolated rhynchaptychus-type lower jaws and many shells of *Gaudryceras* from the Coniacian of Hokkaido (Pl. 1, Fig. 2a, b) may be attributed to the Lytocerataceae, but this identification should be verified with in situ material.

3.4. Ammonitina

Remains of the jaw apparatus have been found from six genera of the Psiloceratidae (*Aconeceras*; DOGUZHAEVA & MUTVEI, 1992), Desmocerataceae (*Tragodesmoceroides* and *Damesites*; TANABE, 1983; *Menuites*; this study) and Acanthocerataceae (*Texanites*; KENNEDY & KLINGER, 1972; *Reesidites*; TANABE & FUKUDA, 1987a). Also, SUMMESBERGER et al. (1996, 1999) described lower jaws preserved in the body chambers of ammonites attributed to the Placenticeratidae, together with two isolated upper jaws from the Campanian of Slovenia.

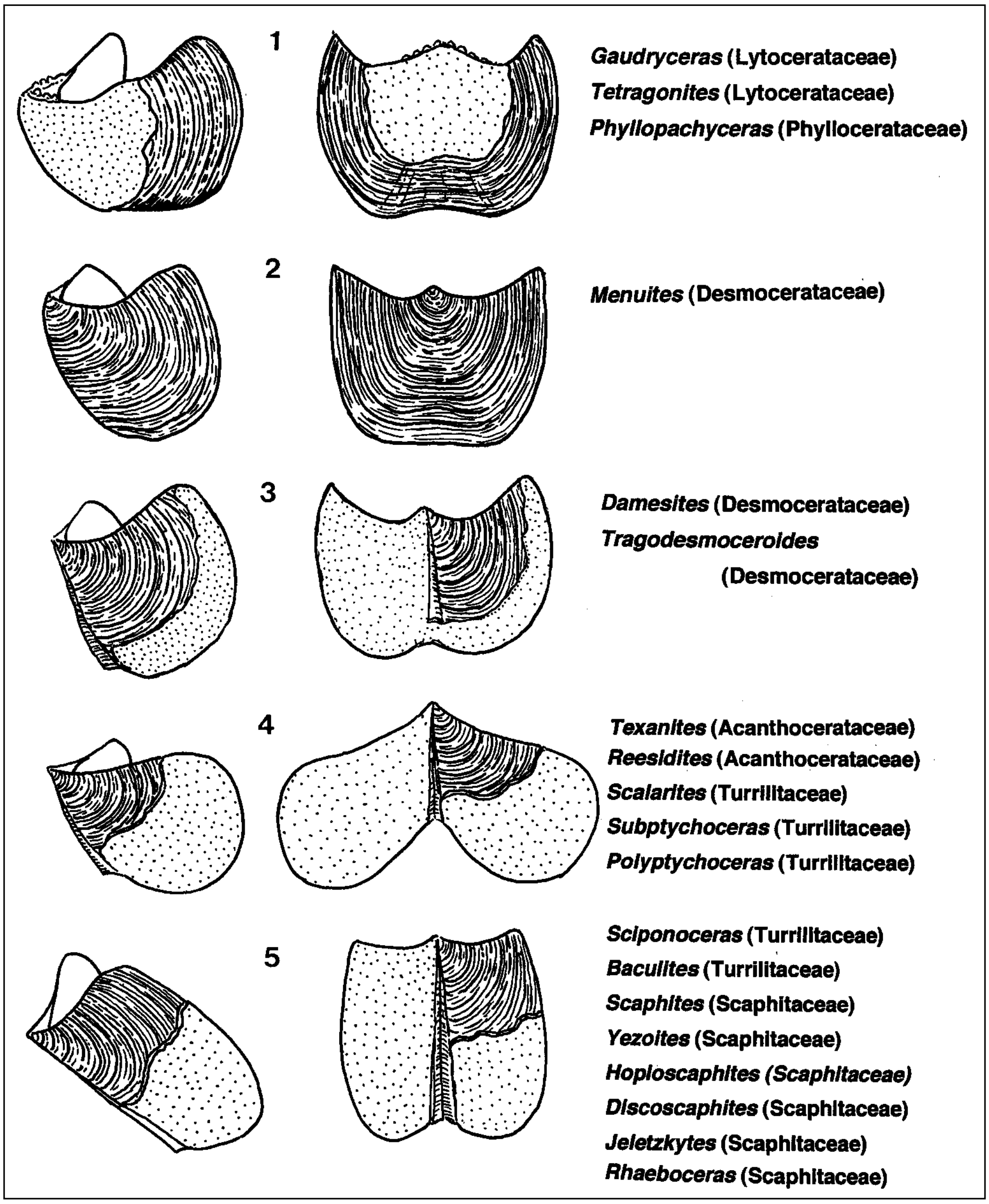
The upper jaws of *Menuites* (Text-Figs. 1, 2.2), *Damesites* (Text-Fig. 2.1; TANABE, 1983, Pl. 71, Figs. 1a–c, 2a–c), and *Reesidites* (Text-Fig. 2.3; TANABE & FUKUDA, 1987a, Fig. 3) share a similar overall morphology and horny wall structure, each consisting of a pair of widely open inner lamellae and a short reduced outer lamella. DOGUZHAEVA & MUTVEI (1992, Pls. 4–5) described medially sectioned upper jaws of *Aconeceras*, which are made of inner horny and outer calcareous lamellae. The two isolated upper jaws interpreted as belonging to the Placenticeratidae by SUMMESBERGER et al. (1999, Text-Figs. 1, 2), though secondarily flattened on the bedding plane, are similar in overall morphology to those of the six genera mentioned above.

The lower jaws of Cretaceous Ammonitina exhibit marked taxonomic variation in their relative size, sculpture, and the degree of development of an outer calcareous element, when compared with upper jaws. The lower



Text-Fig. 2.
Drawings of upper jaws of selected Cretaceous ammonoids.
Antero-lateral (a = left) and frontal (b = right) views are indicated for 1–2 and 5–7. Antero-lateral view for 3 and 4.
1) *Damesites ainuanus* MATSUMOTO (Desmocerataceae, Ammonitina). Modified from TANABE (1983, Text-Fig. 2).
2) *Menuites naumanni* (YOKOYAMA) (Desmocerataceae, Ammonitina).
3) *Reesidites minimus* HAYASAKA and FUKADA (Acanthocerataceae, Ammonitina). Modified from TANABE & FUKUDA (1987a, Fig. 3).
4) Isolated upper jaw, possibly attributed to the Lytocerataceae.
5) *Scalarites mihoensis* WRIGHT and MATSUMOTO (Turrilitaceae, Ammonitina). A thin calcareous covering is dotted.
6) *Subptychoceras* sp. (Turrilitaceae, Ammonitina).
7) *Jeletzkytes spedeni* LANDMAN & WAAGE. Calcareous covering is exfoliated.
Drawings based on photographs shown by LANDMAN & WAAGE (1993, Fig. 41B, D).

Text-Fig. 3.
Diagrammatic drawings showing the remarkable morphotypic variation of the lower jaws in Cretaceous ammonoids.
Anterolateral (left) and frontal (right) views are shown in each morphotype. Remnants of calcareous coverings are dotted.
1) Rhynchaptychus-type characterized by a widely open, univalved outer horny lamella with a thick anterior calcareous covering.
2) Anaptychus-type, with a widely open, univalved horny lamella.
3) Transitional form from anaptychus-type to aptychus-type. The univalved outer horny lamella is covered with a very thin calcareous layer and is marked by a distinct median depression.
4) Aptychus-type, with a short median "hinge" and an anterior projection.
5) Typical aptychus-type, with a long commissure and gently arched anterior margin.



jaws of the three desmoceratacean genera (*Tragodesmoceroides, Damesites*, and *Menuites*) share a well-developed, gently convex outer horny lamella with a sharply pointed anterior portion (see Text-Fig. 3.2, 3.3 for generalized drawings). Furthermore, there is a shallow median groove on the outer lamella of the lower jaws of *Tragodesmoceroides* and *Damesites* (Text-Fig. 3.3; TANABE, 1983, Pl. 71, Figs. 1d,3b, Text-Figs. 3.4), but is absent from the lower jaw of *Menuites* (Text-Figs. 1, 3.2). In the well-preserved lower jaw of *Damesites sugata*, the outer horny lamella is covered with a very thin (less than 0.1 mm thick) calcareous layer. The lower jaws of the unknown species of the Placenticeratidae (SUMMESBERGER et al., 1996, Pl. 5, Figs. 1, 2) resemble those of *Tragodesmoceroides* and *Damesites* in having a gently convex outer horny lamella with a distinct median groove. The lower jaws of *Reesidites* (TANABE & FUKUDA, 1987a, Fig. 1A–B, 4C–D, 5A, D) and *Aconeceras* (DOGUZHAEVA & MUTVEI, 1992, Pls. 4, 8) both consist of inner horny and outer calcareous elements. Their horny lamella is markedly elongated anteroposteriorly and is marked by a prominent median depression ("hinge"), but the anterior portion is still sharply pointed, with rows of serrated ridges and grooves in *Reesidites*. The lower jaw of *Texanites* (KENNEDY & KLINGER, 1972, Pl. 73) is similar to the lower jaws of *Reesidites* and *Aconeceras*, but the outer paired calcareous plates with tuberculate ornamentation ("spinaptychus") are much thicker than those of the former.

3.5. Ancyloceratina

Remains of the jaw apparatus have been found from 11 genera of the Turrilitaceae (*Scalarites*, Text-Fig. 2.5; KANIE et al., 1978, Pl. 1, Fig. 1; TANABE et al., 1980b, Text-Fig. 1, Pl. 20, Figs. A–F; *Polptychoceras*, Pl. 1, Fig. 6; NAGAO, 1931b, Figs. 1–2; 1931c, Pl. 15, Fig. 8a–c; *Subptychoceras*, Pl. 1, Fig. 7a–c; *Sciponoceras*, Pl. 1, Fig. 9; *Baculites*, Pl. 1, Fig. 8) and Scaphitaceae (*Scaphites*; BIRKELUND, 1965, Fig. 87; *Yezoites*, Pl. 1, Fig. 4; NAGAO, 1931b, Fig. 2; 1931c, Pl. 15, Figs. 9, 9a; *Discoscaphites*; BIRKELUND 1965, Fig. 109; LANDMAN & WAAGE, 1993, Fig. 167E, G; *Hoploscaphites*, Pl. 1, Fig. 5; BIRKELUND, 1965, Fig. 97; *Jeletzkytes*; MEEK & HAYDEN 1864; LANDMAN & WAAGE, 1993, Figs. 37–39, 41, 42; *Rhaeboceras*; KENNEDY et al., 2002, Pl. 3, Figs. 1–4; Pls. 4–6). Most of them are represented by lower jaws, but complete jaw apparatuses have been found from limited specimens of *Jeletzkytes* (LANDMAN & WAAGE, 1993, Figs. 37, 39), *Rhaeboceras* (KENNEDY et al. 2002, Pls. 4–6), *Scalarites* (TANABE et al., 1980b, Pl. 20, Fig. A), and *Subptychoceras* (Pl. 1, Fig. 7a).

The upper jaws of these four genera are similar in overall morphology and consist of a shorter outer lamella and a pair of larger, wing-like lateral parts (= inner lamellae) that become narrower and join to form a sharply pointed tip on the anterior side. The short reduced outer lamella is clearly visible in *Scalarites* (Text-Fig. 2.5a, b), but it may be joined together to the paired inner lamellae in *Subpty-*

choceras (Text-Fig. 2.6a,b), *Jeletzkytes* (Text-Fig. 2.7a,b) and *Rhaeboceras* (KENNEDY et al., 2002, Pls. 4, 5). The paired lateral parts of the upper jaws of the three genera are ornamented by a combination of concentric ribs or striae (growth lines) and fewer weak radial undulations, with a distinct indentation on the posterior margin in *Jeletzkytes* (Text-Fig. 2.7a,b; LANDMAN & WAAGE, 1993, Figs. 40B, 41B). The anterodorsal portion of the upper jaws of the four genera lack a concentric ornament, and instead, it is either smooth for *Jeletzkytes* (LANDMAN & WAAGE, 1993, Fig. 41D) and *Rhaeboceras* (KENNEDY et al. 2002, Pl. 5, Fig. 2) or sculptured by weak radial striations for *Scalarites* (Text-Fig. 2.5; TANABE et al., 1980b) and *Subptychoceras* (Text-Fig. 2.6b). The upper jaw lamellae of *Jeletzkytes, Rhaeboceras, and Scalarites* all exhibit a thin calcareous covering.

The lower jaws of the 11 genera listed above consist mainly of widely open outer and short inner horny lamellae. The outer horny lamella is divided into two lateral areas by a prominent radial furrow (commissure). The lateral sides of the furrow are markedly elevated ventrally, forming two radial ridge-like flanges (see LANDMAN & WAAGE, 1993, Fig. 42). The horny outer lamella is covered with a pair of thin calcitic plates. In the Scaphitidae and Baculitidae, the outer lamella of the lower jaw is markedly elongated antero-posteriorly, with a long commissure, and its anterior end is gently arched without a beak-like projection (Text-Fig. 3,5). The lower jaws of the three diplomoceratid genera (*Scalarites, Subptychoceras*, and *Polyptychoceras*) are less specialized, with a pointed anterior tip (Pl. 1, Figs. 6, 7a,c; Text-Fig. 3.4).

4. Discussion

Our extensive survey of the jaw apparatuses of Cretaceous Ammonoidea has revealed that the upper jaws of the 7 genera belonging to the Ammonitina (*Damesites, Menuites*, and *Reesidites*) and Ancyloceratina (*Scalarites, Subptychoceras, Jeletzkytes*, and *Rhaeboceras*) are similar in their three-dimensional architecture; they consist of horny reduced outer and large paired inner lamellae, both of which are united in the anterior portion forming a sharp rostral tip (Text-Fig. 2). These features of the upper jaws are also shared by Upper Paleozoic Goniatitina (SAUNDERS & RICHARDSON, 1979; MAPES, 1987; BANDEL, 1988), Triassic Ceratitina (ZAKHAROV, 1974; LEHMANN, 1985, 1988), and Jurassic Ammonitina (LEHMANN, 1967, 1970, 1972, 1978, 1979). Although the upper jaws of the Lytoceratina and Phylloceratina are still unknown, available data strongly suggest that in the Ammonoidea, the morphology of the upper jaws remained little changed throughout their long evolutionary history. Interestingly, the upper jaws of ammonoids are easily distinguished from those of extant coleoids and *Nautilus*, both of which have a continuous inner lamella (SAUNDERS et al., 1978; CLARKE, 1986; TANABE & FUKUDA, 1987b, 1999; NIXON, 1988).

In contrast to the morphological conservatism of the upper jaws, the lower jaws of Cretaceous ammonoids exhibit remarkable taxonomic variation in their relative size, overall morphology, and the degree of development of the outer calcitic layer (Text-Fig. 3). The lower jaws of the Phylloceratina and Lytoceratina are characterized by a well-developed univalved outer chitinous lamella with an anterior calcified rostral tip (Text-Fig. 3.1) bearing teeth as in living *Nautilus* (OKUTANI & MIKAMI, 1977; SAUNDERS et al., 1978), which appears to be effective for a scavenging-predatory mode of feeding in deeper marine environments, as in the jaws of *Nautilus*. This lower jaw morphotype was called rhynchaptychus-type (LEHMANN et al., 1980; LEHMANN, 1988, 1990) or neoanaptychus-type (DAGYS et al., 1989).

The lower jaws of the other 16 genera may fall into either aptychus- or anaptychus-types of LEHMANN (1990), but this classification has no biological meaning because of the presence of an intermediate form between them. For example, the lower jaws of *Damesites* and *Tragodesmoceroides* exhibit transitional features from the anaptychus-type to the aptychus-type, by the presence of a distinct median depression on the outer horny lamella (Text-Fig. 3.3) and a very thin calcareous layer which covers the horny lamella. The functional morphology of the aptychus-type lower jaws has been discussed by LEHMANN & KULICKI (1990), SEILACHER (1993), and TANABE & FUKUDA (1999). According to the model of LEHMANN & KULICKI (1990), the semi-flexible outer horny lamella of the lower jaw was presumably connected with jaw muscles via beccublasts on the dorsal side, and the living ammonite could fold it during foraging activity. This interpretation is strengthened by the discovery of the imprints of the beccublasts on the inside surface of the horny lamella of an aspidoceratid lower jaw (TANABE & FUKUDA, 1999, Fig. 19.5D). LEHMANN & KULICKI (1990) also argued that when the head was drawn back by means of the head retractor muscles, the lower jaw could tilt upwards to seal the aperture. This action would lead to the backward retraction of the outermost buccal membrane and exposure of the paired thick calcareous outer plates which served as a protective shield against predators. The lower jaws of the Acanthocerataceae, Hoplitaceae, Scaphitaceae, and Turrilitaceae lack a sharply pointed anterior tip and instead, they are all characterized by a widely open, large outer horny lamella with a median depression ("hinge") covered by a thin bivalved calcitic plate (Text-Fig. 3.4, 3.5). These ammonoids might have lived in shallower water environments (WESTERMANN, 1996). The lower jaws of these ammonoids may have been specialized for feeding on various kinds of microorganisms. The lower jaws of *Damesites* and *Tragodesmoceroides*, both with a distinct median "hinge" on the outer horny lamella, could be accommodated within a buccal mass by bending the flexible chitinous outer lamella. They presumably served for feeding, though an operculum-like secondary function is also possible (TANABE & FUKUDA, 1999).

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Plate 1

Jaws of selected Cretaceous ammonoids.

Fig. 1: ***Phyllopachyceras ezoense* (YOKOYAMA).**
Juvenile specimen with lower jaw preserved in body chamber.
Fig. 1a: Lateral view.
Fig. 1b: Frontal view.
UMUT MM 27831, from the Turonian in the Nakakinenbetsu River, Obira area, northwestern Hokkaido.
×2.

Fig. 2: **Isolated upper jaw, possibly attributed to Lytocerataceae.**
Fig. 2a: Lateral view.
Fig. 2b: Frontal view.
UMUT MM 27832, from the Coniacian in the Pankezawa Creek, Obira area, northwestern Hokkaido.
×1.5.

Fig. 3: ***Damesites sugata* FORBES.**
Ventral view of lower jaw preserved in body chamber of adult specimen.
A thin calcareous layer was exfoliated during preparation (visible on the inner surface of the removed slab).
UMUT MM 27833, from the Coniacian in the Sakasagawa River, Haboro area, northwestern Hokkaido.
×1.

Fig. 4: ***Yezoites puerculus* (JIMBO).**
Oblique view of microconch, with lower jaw (arrow) preserved in body chamber.
HK 3198, from the Turonian of the Oyubari area, central Hokkaido.
×5.

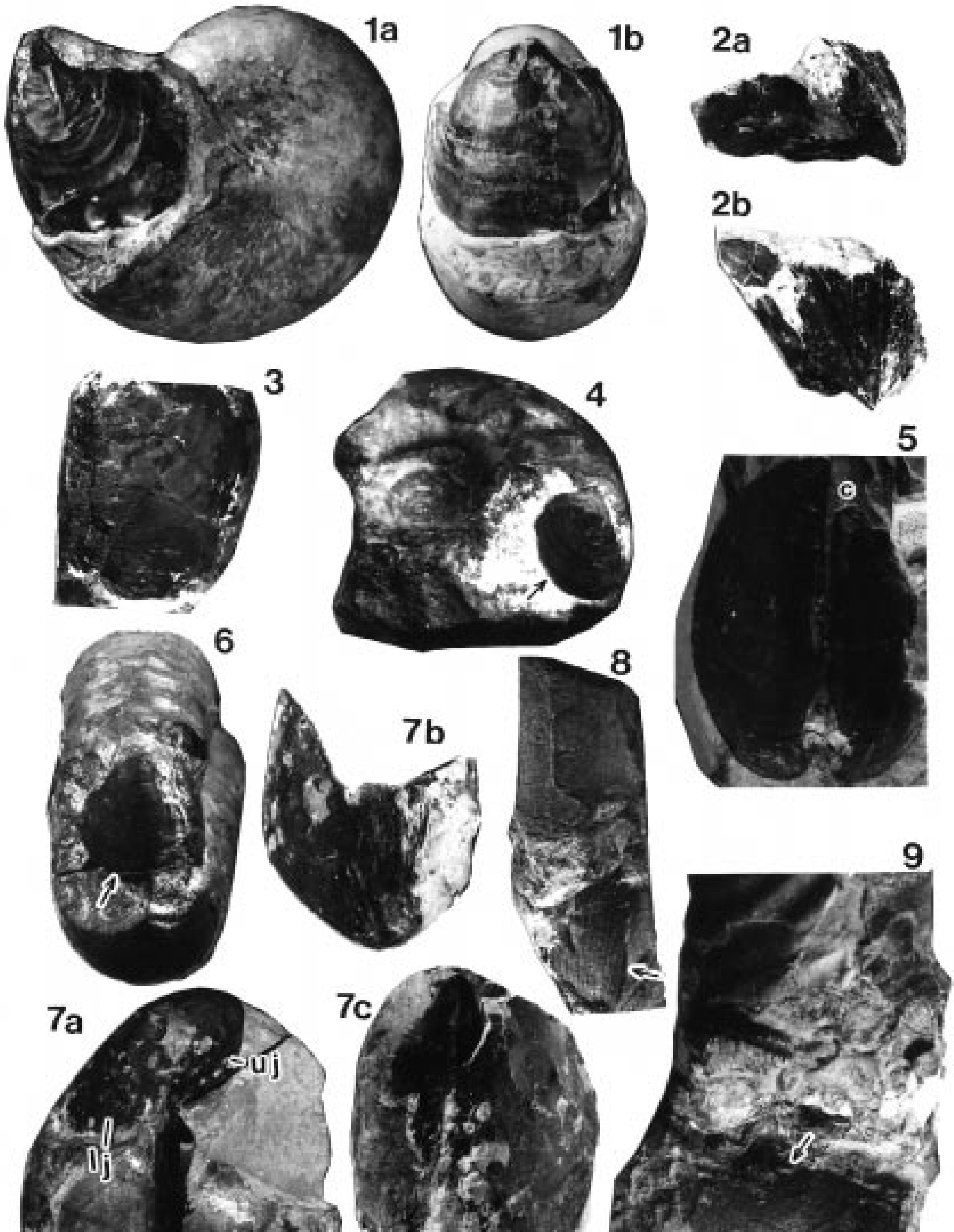
Fig. 5: ***Hoploscaphites nicolletii* (MORTON).**
Ventral view of lower jaw, preserved in body chamber of adult macroconch.
A thin calcareous layer (c) covering the outer horny lamella is visible in the anterior portion.
BHMNH 3007, from the lower part of the Fox Hills Formation (upper Maastrichtian), north-central South Dakota.
×2.

Fig. 6: ***Polyptychoceras* cf. *pseudogualtinum* (YOKOYAMA).**
Ventral view of lower jaw (arrow) preserved in broken adult body chamber.
HK 4592, from the Santonian of the Panke-Oshokenai rivulet, Hetonai area, southern central Hokkaido.
×1.2.

Fig. 7: ***Subptychoceras* sp.**
Fig. 7a: Mode of occurrence of upper and lower jaws within body chamber of adult specimen.
lj: lower jaw, uj: upper jaw.
×1.
Fig. 7b: Frontal view of upper jaw.
×2.
Fig. 7c: Ventral view of lower jaw.
×2.
UMUT MM 27834, from the Santonian of the Oyubari area, central Hokkaido.

Fig. 8: ***Baculites* cf. *princeps* MATSUMOTO & OBATA.**
Fragment of adult specimen with lower jaw (arrow) in body chamber.
GK.H 4908, from the Campanian at Gyoshamatsu, Arita area, Wakayama Pref., west Japan.
×3.

Fig. 9: ***Sciponoceras kossmati* (NOWAK).**
Ventral view of part of the lower jaw preserved in adult body chamber (arrow).
GK.H 4335, from the lower Turonian in the Ikusyunbetsu River, Mikasa area, central Hokkaido.
×2.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