

Lower jaws of two species of *Menuites* (Pachydiscidae, Ammonoidea) from the middle Campanian (Upper Cretaceous) in the Soya area, northern Hokkaido, Japan

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Abstract The lower jaws of two pachydiscid ammonites *Menuites soyaensis* (Matsumoto and Miyachi) and *Menuites* sp. are described on the basis of two specimens from the middle Campanian (Upper Cretaceous) in the Soya area of northern Hokkaido, Japan. They are preserved *in situ* in the body chamber and characterized by a widely open outer lamella with a nearly flat rostral portion. The outer lamella consists of an inner “chitinous” layer sculptured by a median furrow in the anterior to mid-portions and an outer calcareous layer with prismatic microstructure. The lower jaw features of the two *Menuites* species are shared by other species of the Pachydiscidae described in previous works, indicating that they are diagnostic characters of this family. In view of the shovel-like shape without a pointed rostrum, the lower jaws of the two *Menuites* species were likely used as a scoop to feed on microorganisms.

Key words: pachydiscid ammonites, middle Campanian, lower jaw, Soya area (Hokkaido)

Introduction

Both modern and extinct cephalopod mollusks possess a well-developed jaw apparatus that consists of upper and lower elements (synonymous with beaks and mandibles; Clarke, 1962; Nixon, 1988, 2015; Tanabe and Fukuda, 1999). In modern cephalopods, the upper and lower jaws are contained in a globular organ, called the buccal mass, and have the special function of feeding on prey organisms using the surrounding jaw muscles (see Tanabe and Fukuda, 1987, fig. 1; Tanabe, 2012, fig. 1). The jaw apparatus of modern cephalopods is primarily composed of an organic hard substance that consists of a chitin-protein complex, in association with an anterior calcified tip in both the upper and lower jaws of the nautilids *Nautilus* and *Allonautilus* (Saunders *et al.*, 1978; Hunt and Nixon, 1981; Gupta *et al.*, 2008).

Fossilized jaw remains are sometimes preserved *in situ* within the body chambers of ammonoid conchs whose taxonomic relationships are known. In most cases, a single jaw element occurs in the body chamber, but upper and lower jaws are rarely

found together retaining their original life orientation. Based on such well-preserved specimens and their comparison with the jaws of modern cephalopods, previous authors (e.g. Nixon, 1988, 1996; Tanabe and Fukuda, 1999; Tanabe *et al.*, 2015a) provided criteria for distinguishing the upper and lower jaws of ammonoids. Namely, the larger form consisting of a wide, concave outer lamella and a shorter reduced inner lamella on the ventral side has been judged as a lower jaw. The smaller form consisting of paired wide inner lamellae and a short reduced outer one on the dorsal side is identified as an upper jaw. In the case of the *in situ* co-occurrence of these two forms, the smaller upper jaw is partly encircled by the concave outer lamella of the lower jaw, as in the jaw apparatuses of modern cephalopods (e.g. Tanabe, 2011; Tanabe *et al.*, 2015b, fig. 3).

We describe herein two pachydiscid ammonite specimens with a lower jaw preserved in their body chambers *in situ* that were recovered from the middle Campanian (Upper Cretaceous) strata in northern Hokkaido, Japan. We further discuss the taxonomic and paleoecological significance of the lower jaw features of the Pachydiscidae on the basis of a comparison with the lower jaws of other Cretaceous

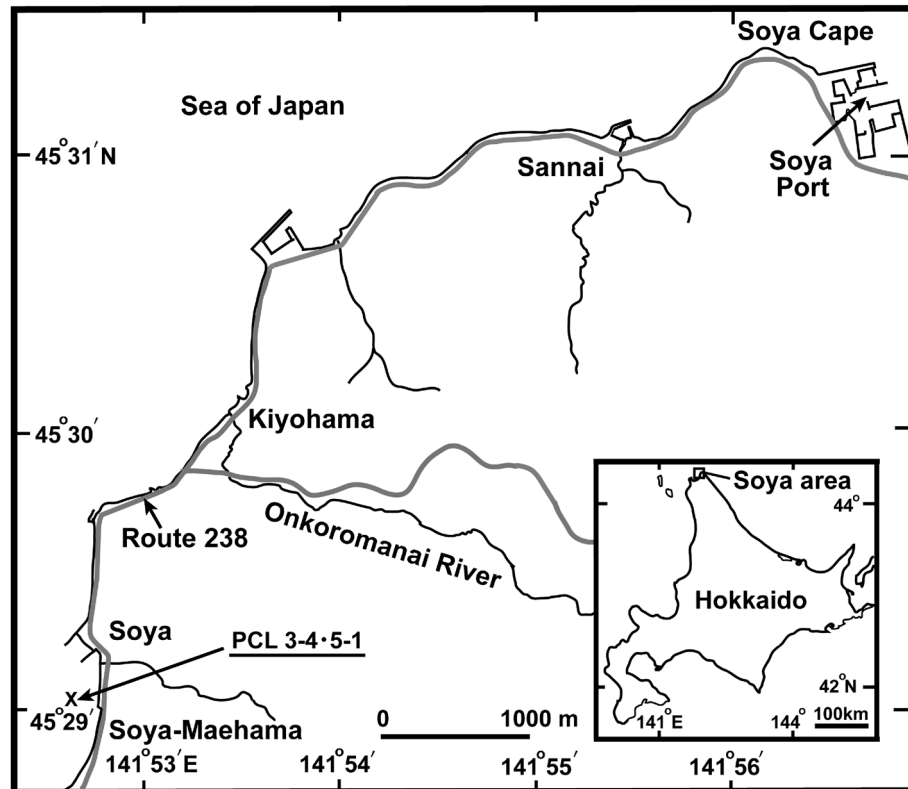


Fig. 1. Index map of the Soya area, northern Hokkaido, Japan, showing the locality (PCL 3-4-5-1) of the two pachydiscid ammonite specimens with a lower jaw preserved in the body chamber *in situ*.

ammonoids.

Institutional abbreviations: NMNS, National Museum of Nature and Science, Tsukuba; UMUT, University Museum, The University of Tokyo, Tokyo; GK, Kyushu University Museum, Fukuoka; UH, Hokkaido University Museum, Sapporo.

Material and geological settings

Two pachydiscid specimens, NMNS PM14316 and NMNS PM14321, were examined and both possess a lower jaw in the body chamber *in situ*. They are identified as *Menuites soyaensis* (Matsumoto and Miyauchi, 1984) and *Menuites* sp., respectively. These two species were described as *Pachydiscus soyaensis*, n. sp. and *Pseudomenuites* sp. by Matsumoto and Miyauchi (1984), then their generic positions were changed to *Menuites* by Shigeta and Izukura (2018). The two *Menuites* specimens were preserved individually in calcareous nodules that were recovered by the late Toshiya Miyauchi at the locality PCL 3-4-5-1 (45°29'01"N, 141°52'40"E), about 400 meters south of Soya Fishery Harbor in the Soya area of northernmost Hokkaido (Fig. 1). At this locality, greenish, silty, fine-

grained sandstone in the upper part of the Orannai Formation (= unit H of Matsumoto and Miyauchi, 1984) is sporadically exposed in the wave-cut bench. The strata that yielded the two *Menuites* specimens were biostratigraphically included in the *Schlueteria kawadai* Subzone of the *Metaplacenticeras subtilistriatum* Zone of the middle Campanian age (Shigeta *et al.*, 2016; Shigeta and Izukura, 2018).

Description

Terminology and measurements: We follow the terms and measurements of modern coleoid lower jaws proposed by Clarke (1962, 1986) and Clarke and Maddock (1988) in the description of the two lower jaws of the *Menuites* specimens examined. Basic morphology, descriptive terms, and the measurements of a pachydiscid lower jaw are shown in Fig. 2. The following abbreviations are used for measurements: *SD*, maximum shell diameter; *WH*, maximum whorl height; *WB*, maximum whorl breadth; *MW*, maximum length of wing; *WW*, width of paired wings; *HH*, height of hood; *OAW*, open angle of paired wings. The measurement data of

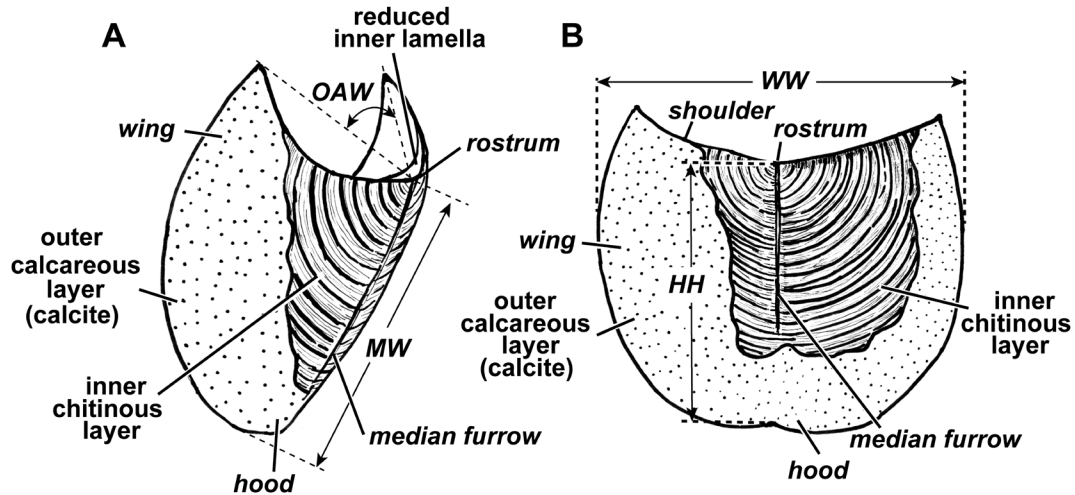


Fig. 2. Diagrammatic drawings of the intermediate type lower jaw in a Late Cretaceous pachydiscid ammonite. A, right anterolateral view. B, ventral view. The lower jaw is made of a large outer lamella consisting of inner chitinous and outer calcitic layers, and a shortly reduced inner lamella, both of which are jointed together in the anterior portion. After Clarke (1986) and Clarke and Maddock (1988) for descriptive terms of cephalopod jaw elements (shown in *italics*). Abbreviations for the measurements: *MW*, maximum length of wing; *HH*, height of hood; *WW*, width of paired wings.

Table 1. Measurements of Late Cretaceous pachydiscid specimens with a lower jaw preserved in the body chamber *in situ*. Abbreviations: *SD*, maximum shell diameter; *WH*, maximum whorl height; *WB*, maximum whorl breadth, *MW*, maximum length of wing; *WW*, width of wing; *HH*, height of hood; *OAW*, open angle of paired wings. *, secondarily deformed slightly.

Species	Specimen	<i>SD</i> (mm)	<i>WH</i> (mm)	<i>WB</i> (mm)	<i>WB/WH</i>	<i>MW</i> (mm)	<i>WW</i> (mm)	<i>HH</i> (mm)	<i>OAW</i> (deg.)	<i>WW/MW</i>	Sources
<i>Menuites</i> sp.	NMNS PM 14321	152.4	71.5*	86.9*	1.22	57.6	68.0	57.0	ca. 120	1.18	This study
<i>Menuites soyaensis</i> (Matsumoto and Miyauchi)	NMNS PM 14316	196.0	107.0	>71.0*	>0.66	79.3	91.4	72.8	ca. 140	1.15	This study
<i>Menuites naumanni</i> (Yokoyama)	UMUT MM 27835	131.2	61.6	103.2	1.68	49.0	77.6	46.0	ca. 110	1.58	Tanabe and Landman (2002); Tanabe <i>et al.</i> (2015a)
<i>Pachydiscus kamishakensis</i> Jones	UMUT MM 30876	305.0	175.7	93.8	0.53	102.9	58.8	111.2	ca. 60	0.57	Tanabe <i>et al.</i> (2012, 2015a)

conch and lower jaw elements in the two pachydiscid specimens are given in Table 1, together with the two other pachydiscid specimens described previously.

Menuites soyaensis (NMNS PM14316): This specimen measures 196 mm in diameter, but it lacks a part of the body chamber. The lower jaw is preserved on the right lateral side within the body chamber at about one-quarter whorl from its base (Fig. 3A). The mode of occurrence shows that the lower jaw has been moved and slightly tilted from its original position. The lower jaw appears to consist of widely open outer and reduced short inner lamellae, although the latter is coated with host rock and cannot be seen from the outside. The outer lamella is gently convex anteroventrally with an open angle of approximately 140 degrees (Fig. 3B). The paired wings are slightly elongated laterally ($WW/MW = 1.15$), and their anterior margin (shoulder) is weakly arched posteriorly without a sharply

pointed rostrum (r in Fig. 3B, C). The outer lamella is thickest in the anterior rostral portion (ca. 2 mm thick) and becomes thinner posteriorly. It is made of a black substance that might be primarily chitinous (chl in Fig. 3C), in association with a thin calcareous layer in the posterior portion (cl in Fig. 3C). The outer lamella lacks distinct concentric and radial ornamentation. Instead, it is sculptured by a median furrow, which divides the outer lamella into paired wings. The median furrow becomes weaker and disappears toward the posterior margin.

Menuites sp. (NMNS PM14321): This specimen measures 152.4 mm in diameter. Its body chamber is slightly deformed dorsoventrally, but the lower jaw is preserved on the ventral side within the body chamber at about one-quarter whorl from its base and it retains its original shape and orientation (Fig. 4A). It appears to consist of widely open outer and reduced short inner lamellae, although the latter is coated with host rock and cannot be seen from the

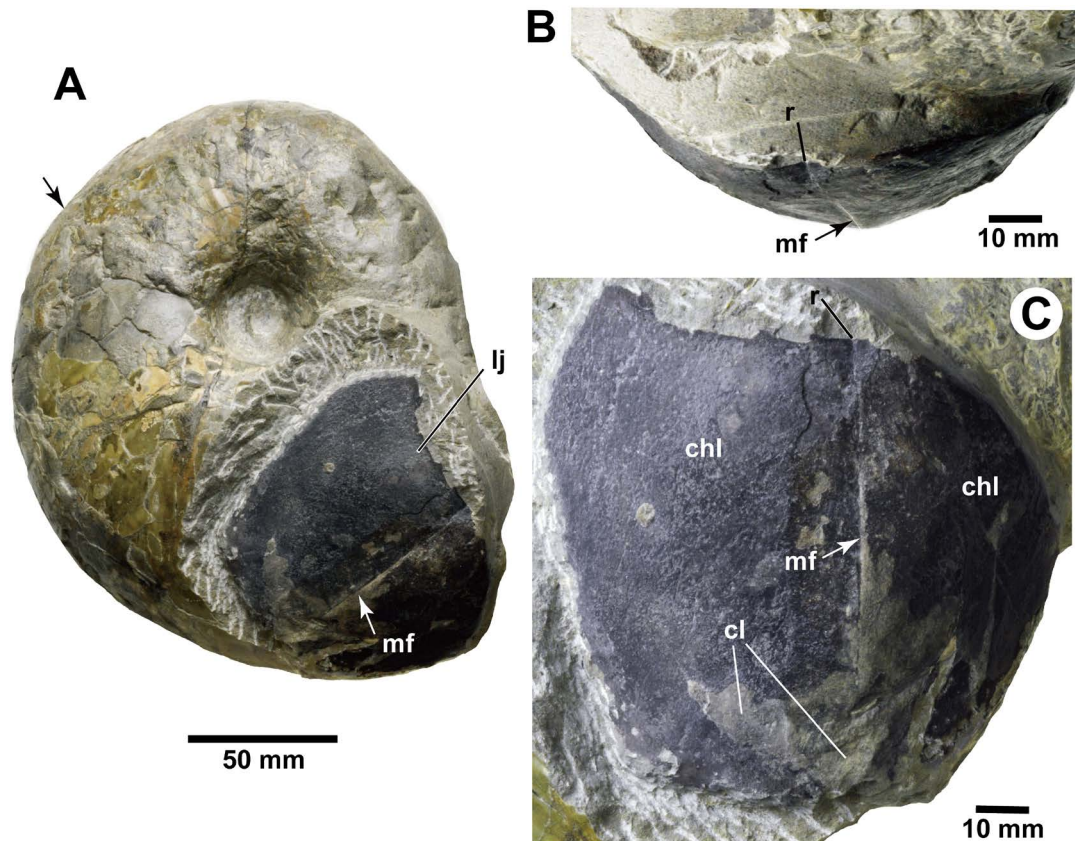


Fig. 3. *Menuites soyaensis* (Matsumoto and Miyauchi, 1984) with a lower jaw preserved in the body chamber *in situ*. NMNS PM14316 from the middle Campanian Orannai Formation at locality PCL 3-4-5-1 in the Soya area, northern Hokkaido (see Fig. 1). A, mode of occurrence of the lower jaw (lj) inside the body chamber. The arrow points to the base of body chamber. B, C, anterior (B) and ventral (C) views of the lower jaw. The outer lamella of the lower jaw consists of an inner “chitinous” layer (chl) and an outer calcareous layer (cl) with an almost flat rostrum (r). A shortly reduced inner lamella may present behind the outer lamella, but cannot be seen from the outside in the present specimen. A distinct median furrow (mf) is visible in the anterior to mid-portions of the black inner “chitinous” layer.

outside. The outer lamella is gently convex antero-ventrally with an open angle of approximately 120 degrees. The paired wings are slightly elongated laterally ($WW/MW = 1.18$), and their anterior margin (shoulder) is weakly arched posteriorly with a very weakly pointed rostrum (r in Fig. 4B). The outer lamella is thickest in the anterior rostral portion (ca. 1.0–1.5 mm thick) and becomes thinner toward the posterior margin. It is made of an inner black layer that may have been originally chitinous and an outer calcareous layer (chl and cl in Fig. 4B, C). The outer calcareous layer, about 0.5 mm thick, consists of polygonal prisms, each of which are 200 to 250 μm in diameter. The longer axes are arranged vertically to the outer surface (Fig. 4D, E). The inner black “chitinous” layer of the outer lamella is ornamented with several weak concentric undulations (Fig. 4B). Since the hood portion of the outer lamella is covered by a calcareous layer, we could

not ascertain the presence or absence of a median furrow in this specimen.

Discussion

Morphotype classification of lower jaws of Menuites: The jaw apparatuses of Cretaceous Ammonoidea have been classified into five morphotypes (normal, anaptychus, aptychus, rhynchaptychus, and intermediate types) on the basis of differences in the overall shape and lamellar structure and the presence or absence of calcareous elements in the lower jaws (see Tanabe *et al.*, 2015a for the definition and taxonomic distribution of each morphotype). *In situ* jaws of the superfamily Desmoceroidea (Ammonitina) were reported from *Damesites semicostatus* Matsumoto, 1955 (in Matsumoto and Obata, 1955); *Damesites* aff. *sugata* Forbes, 1846; *Damesites ainuanus* Matsumoto, 1957; *Tragodesmoceroidea sub-*

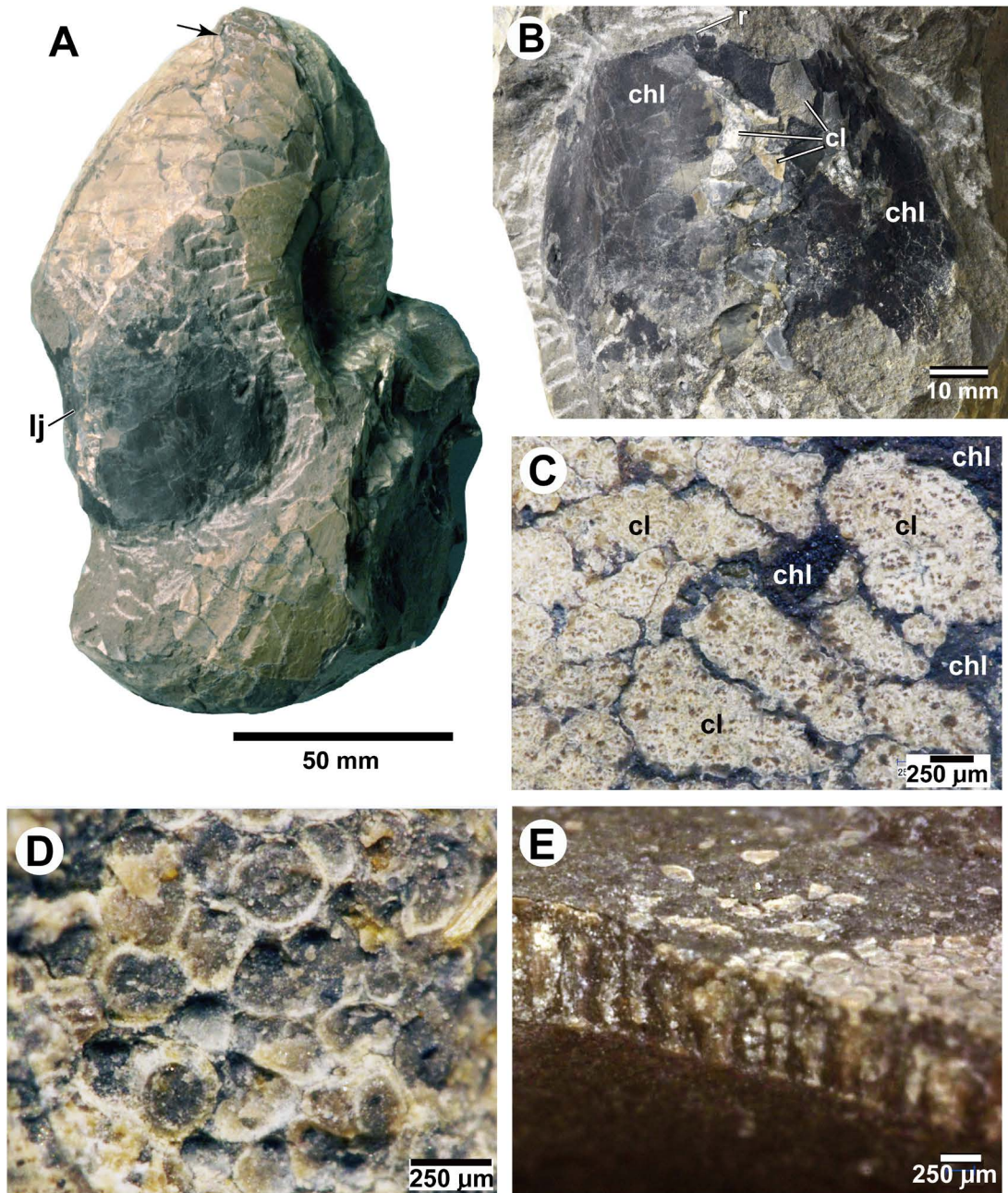


Fig. 4. *Menuites* sp. with an intermediate-type lower jaw preserved in the body chamber *in situ*. NMNS PM14321 from the same horizon and locality as those of NMNS PM14316 (*M. soyaensis*). A, mode of occurrence of the lower jaw (lj) inside the body chamber. The arrow points to the base of body chamber. B, C, ventral view (B) and close-up of the mid-hood portion (C) of the lower jaw. The outer lamella of the lower jaw consists of an inner “chitinous” layer (chl) and an outer calcareous layer (cl) with a weakly pointed rostrum (r). D, E, ventral (D) and cross sectional (E) views of the outer calcareous layer, showing prismatic microstructure.

costatus Matsumoto, 1954 of the family Desmoceratidae (Nagao, 1932; Tanabe, 1983; Tanabe and Landman, 2002; Tanabe *et al.*, 2012, 2015a); and *Menuites naumanni* (Yokoyama, 1890) and *Pachydiscus kamishakensis* Jones, 1963 of the family Pachydiscidae (Tanabe and Landman, 2002; Tanabe *et al.*, 2012, 2015a).

The lower jaws of these desmoceratoid species exhibit transitional features from the anaptychus-

type to the aptychus-type, such as the development of a distinct median groove or furrow on the outer “chitinous” lamella (Tanabe, 1983, pl. 71, figs. 1d, 3b; Tanabe and Landman, 2002, text-fig. 3.3; Tanabe *et al.*, 2015a, figs. 10.5f, 10.9.3b), and a thin “univalve” calcareous layer, which covers the “chitinous” lamella (Tanabe *et al.*, 2012, figs. 5, 6). Based on these features, the jaw apparatuses of the Desmoceratoidea were treated as the intermediate

type (Tanabe *et al.*, 2015a). As described earlier, the lower jaws of *Menuites soyaensis* and *M. sp.* examined also possess these characteristic features of the intermediate-type lower jaws; hence they are classified in this morphotype.

Lower jaw features of the Pachydiscidae: Beside the lower jaws of two *Menuites* species examined, *in situ* jaws were found in specimens of two other pachydiscid species: specimen UMUT MM 27835 of *Menuites naumanni* with upper and lower jaws preserved in the body chamber, from the middle Campanian in the Naiba area of south Sakhalin (Tanabe and Landman, 2002, text-fig. 1; Tanabe *et al.*, 2015a, fig. 10.5f), and specimen UMUT MM 30876 of *Pachydiscus kamishakensis* with a lower jaw preserved in the body chamber, from the lower Maastrichtian in the Alfred Creek, Talkeetna Mountains, southern Alaska (Tanabe *et al.*, 2012, figs. 4E, F, 6). Photographs and drawings of the two specimens viewed from the ventral side are shown in Fig. 5. The lower jaws of the two pachydiscid species share common features with those of the two *Menuites* species described herein, such as a widely open outer lamella consisting of inner “chitinous” and outer calcareous layers with a nearly flat rostral portion. There is also the development of a median furrow, which weakens posteriorly and disappears in the posterior margin. The outer calcareous layer in the lower jaw of the *P. kamishakensis* specimen consists of polygonal prisms (see Tanabe *et al.*, 2012, fig. 4E, F), like the lower jaw of NMNS PM14321 of *Menuites* sp. examined. These lines of evidence indicate that the aforementioned lower jaw features of the species of *Menuites* and *Pachydiscus* are regarded diagnostic of the Pachydiscidae.

Comparison with the lower jaws of the Desmocerotidae: Well-preserved lower jaws of the Desmocerotidae have been found *in situ* in the specimens of the following three species of two genera from the Upper Cretaceous of Hokkaido: two specimens UH 4545 and UMUT MM 30878 of *Damesites semicostatus* collected from the lower Santonian of the Mikasa area, central Hokkaido (Nagao, 1932; Tanabe, 1983, pl. 71, fig. 1a, d, text-fig. 3) and the Obira area, northwestern Hokkaido (Tanabe *et al.*, 2015a), specimen UMUT MM 27833 of *Damesites* aff. *sugata* from the Coniacian of the Haboro area, northwestern Hokkaido (Tanabe *et al.*, 2012, figs.

4C, D, 5A–C) and specimen GK H 8064 of *Tragodesmoceroides subcostatus* from the upper Turonian of the Nakagawa area, northern Hokkaido (Tanabe, 1983, pl. 71, fig. 3a–c, text-fig. 4). The lower jaws of these desmocerotids differ from those of the pachydiscids by having a more sharply pointed rostral tip and a distinct median depression on the entire hood portion of the “chitinous” outer lamella. Furthermore, a thin outer calcareous layer of the lower jaw is made of aragonite and has spherulitic prismatic microstructure in UMUT MM 27833 of *D. aff. sugata* (Tanabe *et al.*, 2012, fig. 4C, D). However, in UMUT MM 30876 of *Pachydiscus kamishakensis* retaining an aragonitic shell wall, it is calcitic. The microstructure of the outer calcareous layer is prismatic in this species and *Menuites* sp. These differences in the shape, microstructure, and mineralogy of the outer calcareous layer between the lower jaws of the Desmocerotidae and Pachydiscidae appear to be taxonomically important in distinguishing the two families.

Paleoecological significance of the pachydiscid lower jaw features: The lower jaws of Cretaceous ammonoids are known to exhibit remarkable taxonomic variation in their relative size to the co-occurred upper jaws, overall morphology, and the degree of development of the outer calcareous covering (Tanabe and Landman, 2002, text-fig. 2). The upper jaws, by contrast, are essentially similar in overall morphology, except for the development of a calcified tips in *Phyllopachyceras* and *Hypophylloceras* of the Phylloceratina (Tanabe *et al.*, 2013; Takeda *et al.*, 2016). Namely, the upper jaws of Cretaceous ammonoids all consist of “chitinous” reduced outer and large paired inner lamellae, both of which are jointed together in the anterior portion forming a sharply pointed rostrum.

Since the jaw apparatus is a primary feeding organ in both modern and extinct cephalopods, the wide morphological diversity observed in the lower jaws of Cretaceous ammonoids appear to reflect the feeding and dietary habits among them. In the overall shape of the large lower jaw without a pointed rostrum and small upper jaw (one-third the size of the lower jaw in specimen UMUT MM 27835 of *Menuites naumanni*; see Fig. 5A–B and Tanabe and Landman, 2002, text-fig. 1), the intermediate-type jaw apparatuses of the Pachydiscidae are similar to

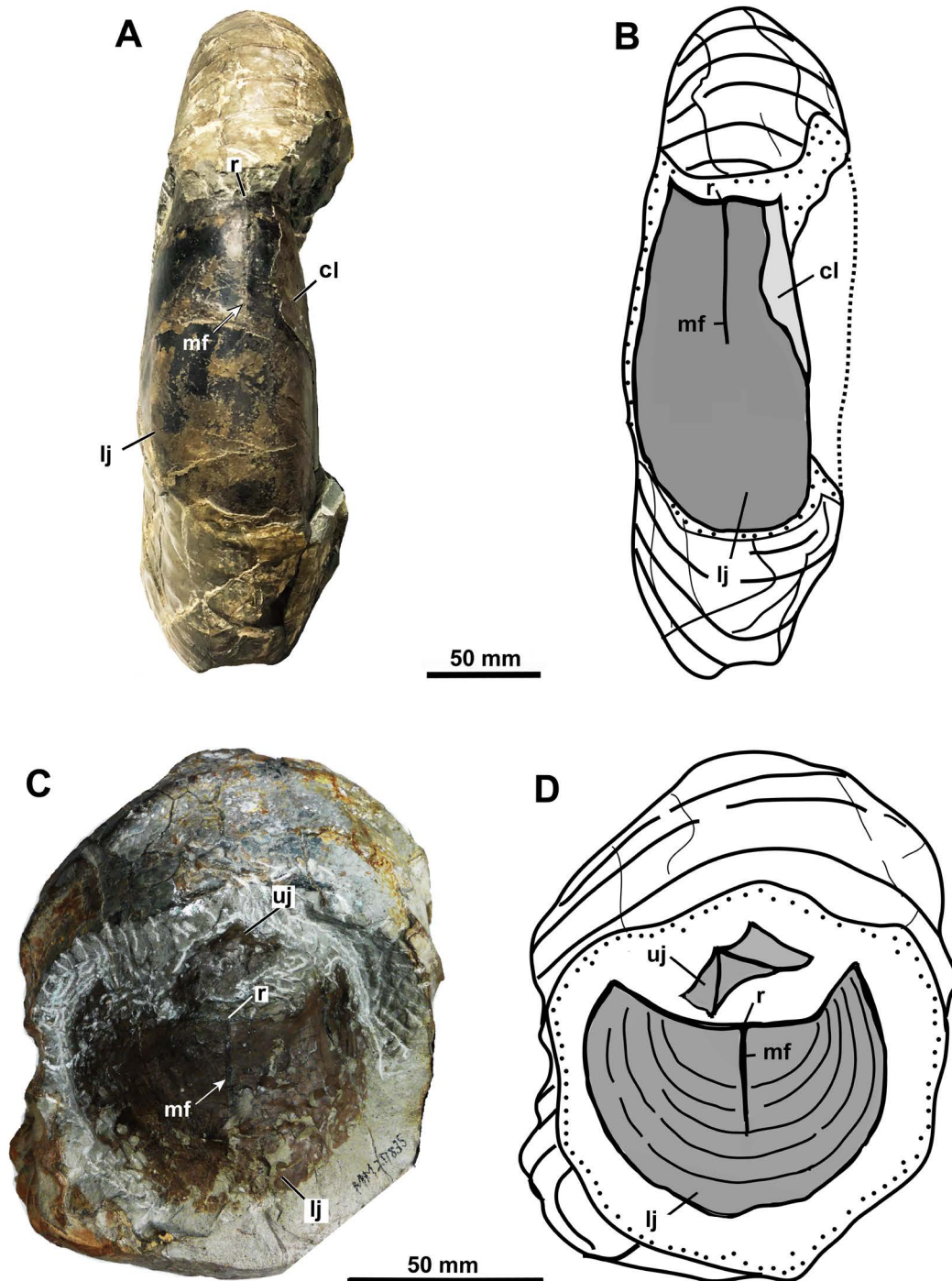


Fig. 5. Photographs (A, C) and drawings (B, D) of the jaw apparatus preserved *in situ* in the body chamber of two pachydiscid ammonites described previously (ventral view). “Chitinous” lamellae of upper and lower jaws are darkly colored. Abbreviations: lj, lower jaw; uj, upper jaw, mf, median furrow, r, rostrum, cl, calcitic layer which covers the underlying “chitinous” layer of the outer lamella of the lower jaw. A, B, *Pachydiscus kamishakensis* Jones, 1963. UMUT MM30876 from the lower Maastrichtian in the Alfred Creek, Talkeetna Mountains, southern Alaska. Same specimen as that figured by Tanabe *et al.* (2012, figs. 4E, F, 6A–C). C, D, *Menuites naumanni* (Yokoyama, 1890). UMUT MM 27835 from the Campanian of the Naiba area, south Sakhalin. Same specimen as that figured by Tanabe and Landman (2002, text-fig. 1) and Tanabe *et al.* (2015a, fig. 10.5f). The small upper jaw has been turned upside down during the biostratinomic process.

those of the aptychus-type, known in most Jurassic-Cretaceous Ammonitina and Cretaceous Ancyloceratina (Tanabe *et al.*, 2015a). In view of the shovel-like shape with a nearly flat rostral portion, the

lower jaws of the Pachydiscidae might not have the function to bite and cut prey. Instead, they were likely used as a scoop to feed on small organisms, as speculated by previous authors (e.g. Lehmann,

1971; Lehmann and Weitschat, 1983) for the aptychus-type lower jaws of some Jurassic Ammonitina, on the basis of their characteristic morphology and analysis of food remains preserved in the esophagus-stomach portions co-occurring with the jaws *in situ* within the body chambers.

In the Pachydiscidae, an anteroventrally elongated lower jaw is found in UMUT MM 30876 of *Pachydiscus kamishakensis* with a compressed body chamber (see Fig. 5A, B). However, a laterally expanded lower jaw occurs in NMNS PM 14316 of *Menuites soyaensis* and UMUT MM 27835 of *M. naumanni*, both with a depressed body chamber (see Figs. 3A–C, 5C, D). This fact may indirectly support the above-mentioned interpretation for the role of pachydiscid lower jaws in a passive microphagous feeding habit.

In contrast to those of the Pachydiscidae, the jaw apparatuses of the Desmoceratidae have a sharply pointed rostral tip on the equal-sized upper and lower jaws, as in modern coleoid cephalopods (Tanabe, 1983, text-figs. 2–4, pl. 71; Tanabe and Landman, 2002, text-figs. 2, 3). This suggests that their primary role was for a scavenging-predatory mode of feeding.

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