Paleontological
Research

Palaeontological
Society of Japan
日本古生物学会

Papers in Press

Humblet, M. and Iryu, Y. 2014: Pleistocene coral assemblages on Irabu-jima,
South Ryukyu Islands, Japan. *Paleontological Research*,
doi: 10.2517/2014PR020.

doi:10.2517/2018PR015

Taxonomic relationships and paleoecological significance of two exceptionally large lower jaws of Late Cretaceous ammonoids from Japan

KAZUSHIGE TANABE[1], AKIHIRO MISAKI[2], TETSUYA IKEDA[3], MASATAKA IZUKURA[4] AND KAZUYOSHI MORIYA[5]

[1] *University Museum, University of Tokyo, Hongo 7-3-1, Bunkyo-ku, Tokyo 113-0033, Japan. r (e-mail: tanabe@eps.s.u-tokyo.ac.jp)*

[2] *Kitakyushu Museum of Natural History and Human History, 2-4-1 Higashida, Yahatahigashi-ku, Kitakyushu, Fukuoka 805-0071, Japan*

[3] *Sanyo Techno Marine, Inc., 20-12 Enoki-cho, Suita, Osaka 564-0053, Japan*

[4] *N28 E21-1-3 Higashi-ku, Sapporo, Hokkaido 065-0028, Japan*

[5] *Department of Earth Sciences, Faculty of Education and Integrated Arts and Sciences, Waseda University, Nishiwaseda 1-6-1, Shinjyuku-ku, Tokyo 169-8050, Japan*

Abstract. Two exceptionally large cephalopod jaws collected from the Upper Cretaceous marine deposits of the Hidaka area, Hokkaido (Yezo Group), and Awaji Island, Southwest Japan (Izumi Group), respectively, are described. Further, their taxonomic relationships and functional morphologic aspect for feeding are discussed. Based on a comparison to counterparts of modern and extinct cephalopods, they were identified as the lower jaws of ammonoids. Owing to the development of a thick calcareous tip in the large outer chitinous lamella, the lower jaw from the Yezo Group is classified as a rhychaptychus-type known from the Cretaceous Lytoceratina and Phylloceratina. The lower jaw from the Izumi Group lacks a sharply pointed calcareous tip and is characterized by a posteriorly elongated outer chitinous lamella, whose outer surface is sculptured by a median furrow in the anterior portion. These features categorize it as an intermediate-type lower jaw shared by the Cretaceous Desmoceratoidea. As determined from the co-occurring ammonoids and the relationship between the dimensions of *in situ* lower jaws and conchs for ammonoids previously described, the two lower jaws from the Yezo and Izumi groups were, respectively, thought to belong to large gaudryceratid and pachydiscid specimens, both of which have shell diameters greater than 40 cm. The overall shape and structure of the two lower jaws suggest a scavenging-predatory feeding habit for the gaudryceratid and a passive microphagous habitat for the pachydiscid.

Key words: ammonoids, feeding habits, Japan, Late Cretaceous, lower jaws

Introduction

Virtually all modern cephalopod mollusks have a well-developed jaw apparatus consisting of upper and lower elements (synonymous with beaks and mandibles) and a radula as the primary feeding apparatuses. These apparatuses are housed in a globular-shaped muscular organ, termed the buccal mass, in the proximal portion of the digestive system, and the anterior portion of the upper jaw fits inside that of the lower jaw (Nixon 1988, 2015; Tanabe and Fukuda, 1999). Both upper and lower jaws have a special function to bite and cut prey by means of the surrounding jaw muscles and the chewed pieces of the prey are conveyed to the esophagus with the aid of the radula surrounded by the jaws (Nixon, 1988; Tanabe and Fukuda, 1999; Tanabe, 2012). In modern coleoids and nautilids, the jaw apparatus is darkly tinted, flexible during life, and composed of a chitin-protein complex (Saunders *et al*., 1978; Hunt and Nixon, 1981; Gupta *et al*., 2008), with a thick calcified rostral tip in both the upper and lower jaws of the nautilids (Saunders *et al*., 1978). The chitinous lamellae of cephalopod jaws have the potential to be preserved as fossils when they have been replaced by phosphoric minerals and pyrite during diagenesis (Kanie, 1982; Tanabe and Fukuda, 1983; Landman *et al*., 2006; Gupta *et al*., 2008; Tanabe *et al*., 2012).

Chitinous and calcareous remains of cephalopod jaws have been reported from Devonian to younger marine deposits (Tanabe and Fukuda, 1999; Tanabe *et al*., 2015; Nixon, 2015). They usually occur solitarily but are occasionally found *in situ* inside the body chambers of ammonoids (e.g. Meek and Hayden, 1864; Closs, 1967; Lehmann, 1967, 1971, 1976, 1980, 1990; Kruta *et al*., 2011) and nautilids (Dietl and Schweigert, 1999; Klug, 2001) and in the buccal mass portion of exceptionally well-preserved coleoid fossils retaining soft tissue remains (e.g. Nixon, 2015; Donovan and Fuchs, 2016). A comparison of these *in situ* fossil cephalopod jaws to those of modern cephalopod counterparts allows for the reconstruction of the morphological features of the upper and lower jaws of individual taxa in the life position and the realization of morphological and compositional differences of jaw apparatuses at a higher taxonomic level (Lehmann, 1976, 1980, 1990; Nixon, 1996; Tanabe and Fukuda, 1999; Tanabe *et al*., 2015). As a result of these previous studies, it is now possible to assign taxonomic positions of *ex situ* fossil cephalopod jaws via morphological comparison to those that are *in situ*.

We describe herein two exceptionally large cephalopod jaws exceeding 120 mm in maximal size that we refer to here as the lower jaws of ammonoids from the Upper Cretaceous marine strata of the Hidaka area, southern central Hokkaido and Awaji Island, Southwest Japan, and presume their holders' shell size, taxonomic relationships, and feeding habits.

Institutional abbreviations. – HMG, Hobetsu Museum, Mukawa Town, Hokkaido, Japan; KMNH, Kitakyushu Museum of Natural History and Human History, Kitakyushu City, Japan; UMUT, University Museum, The University of Tokyo, Tokyo, Japan.

Material

One of the two jaw specimens, HMG-1847, was collected by one of us (MI) as float at a locality in the Pankeushappu Creek, a tributary of the Saru River, Hidaka area, southern central Hokkaido (Figure 1A, B). In the Hidaka area, fossiliferous lower Albian to upper Campanian strata of the Yezo Group, deposited in the eastern offshore environments of the Yezo forearc marine basin, are exposed along the Saru River and its tributaries (Obata *et al*., 1973; Takahashi and Suzuki, 1986; Shigeta and Izukura, 2018a, b). HMG-1847 was preserved individually in a carbonate concretion, together with the shells of ammonoids *Tetragonites popetensis, Hauericeras angustum*, and an inoceramid bivalve *Sphenoceramus schmidti*. This faunal combination suggests that the concretion was derived from the *Sphenoceramus schmidti* Zone in the upper part of the Yezo Group (U3 to U4 units of the Upper Yezo Group of Obata *et al*., 1973; Hakobuchi Group of Takahashi and Suzuki, 1986) near the fossil locality. The *S. schmiditi* Zone in the Yezo Group is correlated to the lower part of the middle Campanian by Shigeta *et al.* (2016); hence, the age of HMG-1847 is regarded as middle Campanian.

The other jaw specimen, KMNH IvP 902012, was collected by one of us (TI) as float at a locality near Nadachino on the southwestern coast of Awaji Island, Southwest Japan (Figure 1C, D). It was found solitarily in a very fine-grained sandstone block that was presumably derived from a nearby outcrop of the Shimonada Formation, the upper unit of the Izumi Group of Awaji Island (Morozumi, 1985). The Izumi Group is distributed extensively on the northern side of the Median Tectonic Line (MTL) in Southwest Japan. The Shimonada Formation is narrowly distributed along MTL along the southwestern coast of Awaji Island (see Morozumi, 1985, fig. 1) and consists mainly of sandy mudstone with intercalations of sandstone near the jaw fossil locality. It is rich in macrofossils, and Morozumi (1985) reported specimens of seven ammonoid species including *Hypophylloceras hetonaiense*, *Gaudryceras izumiense*, *Anagaudryceras matsumotoi*, *Zelandites varuna*, and *Pachydiscus* aff. *subcompressus* from three localities 2–6 km northeast of the present cephalopod jaw locality, among which the specimen described as *G. izumiense* by Morozumi (1985, p. 24, pl. 8, fig. 2) was later referred to as *G. makarovense* by Maeda *et al*. (2005). Morozumi (1985) established the *Pachydiscus* aff. *subcompressus* Zone in the Shimonada Formation and correlated it to the lower Maastrichitian. This biozone was later dated to the middle to upper Maastrichtian by Shigeta *et al*. (2015) based on its faunal similarities to the Senpohshi Formation of the Nemuro Group in eastern Hokkaido, which was correlated magnetostratigraphically with polarity chrons C31n to C30n (Nifuku *et al*., 2009). In this study, we followed the opinion of Shigeta *et al*. (2015) and provisionally treated the age of KMNH IvP 902012 as middle to late Maastrichtian.

Recognition of jaw types and higher taxonomic relationships

We briefly summarize the major morphological differences of the jaw apparatuses among modern and fossil coleoids, nautilids, and ammonoids as a basis to determine the jaw type and higher taxonomic relationships of HMG-1847 and KMNH IvP 902012. Both the upper and lower jaws of modern and extinct cephalopods consist mainly of outer and inner chitinous lamellae that are joined together in the anterior portion (see Tanabe *et al*., 2015, fig. 10.4). The lower jaw is distinguishable from the upper jaw by a much wider and larger outer lamella. Because of the presence of a wide and large outer lamella, HMG-1847 and KMNH IvP 902012 are identified as lower jaws.

In ammonoids and nautilids, the inner lamella of the lower jaw is short and completely hidden by the outer lamella viewed from the lateral side, whereas in modern and fossil coleoids, it is much larger and elongated posteriorly (Clarke, 1962, 1986; Clarke and Maddock, 1988; Tanabe, 2012, figs. 3, 4; Tanabe *et al*., 2015, fig. 10.4e–h). KMNH IvP 902012 is comparable to the previously known lower jaws of Jurassic and Cretaceous Ammonitina and Cretaceous Ancyloceratina because of the presence of a large and posteriorly elongated outer lamella (Tanabe and Landman, 2002; Tanabe *et al*., 2015). Meanwhile, HGM-1847 has a thick calcified rostral tip like the lower jaws of modern and fossil nautilids (Saunders *et al*., 1978; Dietl and Schweigert, 1999, 2011; Klug, 2001) and some Cretaceous ammonoids belonging to suborders Phylloceratina and Lytoceratina (Tanabe *et al*., 1980, 2012, 2013; Kanie, 1982; Takeda *et al*., 2016). The arrowhead- and scallop-shaped calcified tips in the upper and lower jaws of modern and fossil nautilids and lytoceratid and phylloceratid ammonoids are currently termed rhyncholites and conchorhynchs, respectively (Teichert *et al*., 1964; Saunders *et al*., 1978; Tanabe *et al*., 1980). The lower jaws of modern and fossil nautilids are, however, much smaller (< 50 mm in maximal size even in the adult stage; Saunders *et al*., 1978; Tanabe *et al*., 1990; Dietl and Schweigert, 1999; Klug, 2001) than those of HMG-1847, and exceptionally large nautilid conchs that could accommodate a lower jaw similar in size to that of HMG-1847 have not yet been found from the Cretaceous of Japan or other regions. Based on the aforementioned characteristic features of HMG-1847 and KMNH IvP 902012, we assigned their higher taxonomic positions to the Ammonoidea.

Basic morphology, descriptive terms and measurements of the two types of lower jaws of the Late Cretaceous ammonoids, comparable to the two jaw specimens examined, are shown in Figure 2. The terms follow those of Clarke (1962, 1986) and Clarke and Maddock (1988) of modern coleoid lower jaws. The following abbreviations are used for measurements. *MW*: maximal length of wing, *DW*: dorsal width of wing, *HH*: height of hood, and *WW*: width of wing.

Method for identification of jaw and shell mineralogy

Raman spectroscopy is a useful method to identify polymorphs of materials even with a small amount of a sample. We applied this method to determine the mineralogy of the thick calcified rostral tip and black outer lamella of HGM-1847 and the shell wall of a co-occurred ammonoid T*etragonites popetensis*. For this purpose, small tips (*ca*. 200 mg in weight) were removed from these portions. They were soaked with approximately 5 wt% NaClO for overnight, and then analyzed by a Raman microbe in the Department of Earth Sciences, Waseda University. Raman spectra were obtained by Jobin Yvon LabRam300 (HORIBA), equipped with an optical microscope (Olympus, BX41) and Peltier-cooled CCD detector. For analyses, the excitation line of a 514.5 nm Ar^+ laser with a power of approximately 50 mW was employed. The laser spot size was approximately 3 µm. A grating with 1800 grooves/nm was used for all analyses. The diameter of the confocal hole and the width of the silt are 300 µm and 100 µm, respectively. The Raman shift was calibrated with a standard sample of Ne lump (918.322 cm^{-1}).

Description of jaws

HMG-1847

This specimen is an incomplete lower jaw, consisting of a posteriorly elongated larger outer lamella and a reduced short inner lamella, although the greater portion of the latter is coated in host rock (Figure 3). The posterior portion of the outer lamella was eroded away before recovery and is not preserved in the specimen (Figure 3A, C). The outer and inner lamellae are united in the anterior portion, forming a sharply pointed rostral tip (Figure 3A, B). Both lamellae are composed mainly of a black and homogeneous substance. The outer lamella is convex anteriorly with an open angle between the two wings of approximately 60°. It is thickest (*ca*. 1.8 mm) in the anterior rostral portion and becomes thinner posteroventrally. The left half of the outer black lamella in the anterior portion is secondarily exfoliated, in which a thick calcified rostral tip is exposed (Figure 3D, E). The calcified tip is triangular-shaped in frontal view, measuring 27 mm in height and more than 8 mm in thickness. It exhibits radially arranged fine crystals with indistinct concentric growth lines (Figure 3E). The outer lamellar surface is ornamented with more than 20 regularly spaced concentric undulations in the anterior portion that weaken toward the posteroventral margin. A conspicuous radial undulation is observed only on the left lateral side (Figure 3A); it was presumably formed secondarily during the taphonomic process.

Mineralogy of the black outer lamella and calcified tip. – The obtained Raman spectrum for the black outer lamella (Figure 4A) shows the presence of a characteristic peak for apatite at 964 cm^{-1}, indicating that it is composed of apatite, as those of the jaws of some Late Cretaceous ammonoids as determined using X-ray diffraction analysis (Kanie, 1982; Tanabe and Fukuda, 1983; Tanabe *et al*., 2012). The Raman spectrum for the calcified tip (Figure 4B) shows the presence of a peak for calcite at 281 cm^{-1}, but lacks a characteristic peak at 207^{-1} cm for aragonite, indicating that this portion is made of calcite.

Measurements. – MW = 116 mm, HH = 126 mm, WW = 86 mm, DW > 73 mm

KMNH IvP 902012

This specimen is a nearly complete lower jaw characterized by a posteriorly elongated large outer lamella (Figure 5). An inner lamella is not preserved in the specimen, but its coalesced attachment line is visible on the casted left and right lateral shoulder portions (pointed to by an arrow in Figure 5B, C). This fact indicates that the inner lamella was rudimentarily adhered to the overlying outer lamella along the shoulder. The outer lamella is thin (*ca*. 0.6 mm in thickness near the rostrum) and composed of a black homogeneous material without any trace of a calcified element. It is gently convex ventrally with a nearly flat rostrum, with an open angle between the two wings of approximately 70° and 130° at the anterior and posterior ends, respectively. The shoulder is gently arched posteriorly (Figure 5B). A median furrow is visible on the hood portion. It is deep and distinct in the anterior portion but weakens posteriorly and disappears near the posterior margin (Figure 5A). The outer lamella is partitioned into two symmetrical portions similar to a valve-open bivalve shell in ventral view. Its surface is smooth without any trace of ornamentation. Circular epizoan attachment scars (indicated by arrowheads in Figure 5) and two sharp cracks (Figure 5A, B) are visible on the outer lamellar surface. They presumably formed during the post-mortem biostratinomic process.

Measurements. – $MW = 125$ mm, $HH = 122$ mm, $WW = 78$ mm, $DW = 49$ mm

Estimation of shell size for the ammonoids containing the jaws

As of 2015 *in situ* jaw apparatuses of the Ammonoidea are known from 152 species of 109 genera distributed in 30 superfamilies of 8 suborders (Goniatitina, Gephuroceratina, Prolecanitina, Ceratitina, Phylloceratina, Lytoceratina, Ammonitina, and Ancyloceratina; see Tanabe *et al*., 2015, table 10.1 for a list of these species). HMG-1847 and KMNH IvP 902012 are larger than any of the *in situ* ammonoid jaws previously described.

To estimate the shell size of the ammonoids containing the two examined lower jaws, we used the measurement data of *in situ* jaws and conchs for 51 species of Mesozoic Ammonoidea listed in Tanabe *et al*. (2015, table 10.2 and references for the data sources) and those for five species of Paleozoic Ammonoidea previously described (Closs, 1967; Mapes, 1987; Doguzhaeva *et al*., 1997; Klug *et al*., 2016; reproduced in Table 1) and plot the maximal length of wing (*MW*) of the lower jaw versus shell diameter (*SD*) and whorl height (*WH*) of these species (Figure 6). There is a clear linear relationship between *MW* and *SD* and between *MW* and *WH* among these species, namely, $MW = 0.278SD + 2.844$ ($r = 0.9216$, $p < 0.0001$) and $MW = 0.599WH + 6.183$ ($r = 0.9374$, $p < 0.0001$), where r and p are the correlation coefficient and significance level, respectively. If we apply these equations to the two examined lower jaws, the holder ammonoids would have 407 mm in *SD* and 183 mm in *WH* for HMG-1847 and 439 mm in *SD* and 198 mm in *WH* for KMNH IvP 902012.

Discussion

Taxonomic relationships

The jaw apparatuses of the Ammonoidea currently known have been classified into five morphotypes (normal, anaptychus, aptychus, rhynchaptychus, and intermediate) on the basis of their overall morphology and composition, particularly the presence or absence of calcareous elements in the lower jaw (see Tanabe *et al*., 2015 for the definition and taxonomic distribution of these morphotypes). Of the five morphotypes, the normal type is distributed in four pre-Jurassic suborders (Goniatitina, Gephuroceratina, Prolecanitina, and Ceratitina), whereas the remaining four types are known from the order Ammonitida, consisting of the suborders Phylloceratina, Lytoceratina, Ammonitina, and Ancyloceratina from the Late Triassic to the Cretaceous (Tanabe *et al*., 2015, figs. 10.8.4, 10.8.5).

As determined from the overall shape with a thick anterior calcified tip, HMG-1847 is classified as a rhynchaptychus-type lower jaw, which occurs in some Cretaceous Phylloceratina (*Hypophylloceras subramosum* and *Phyllopachyceras ezoense*; Tanabe and Landman, 2002; Tanabe *et al*., 2013; Takeda *et al*., 2016) and Lytoceratina (*Anagaudryceras limatum*, *Gaudryceras denseplicatum*, *G. tenuiliratum*, and *Tetragonites glabrus*; Kanie *et al*., 1982; Tanabe *et al*., 2012, 2015). Isolated lower jaws with a scalloped-shaped calcareous tip (conchorhynch) have also been reported from the Middle Jurassic in the North Caucasus by Mironenko and Gulyaev (2018), who assigned their taxonomic relationships to the Phylloceratidae. Hence, this specimen can be identified as a species belonging to either Lytoceratina or Phylloceratina. Our Raman spectroscopic analysis shows that the primarily aragonitic shell wall of the *Tetragonites epigonus* specimen co-occurred with HMG-1847 has been changed into calcite during diagenesis (Figure 4C). Hence, we could not determine whether the original mineralogy of the calcified rostral tip of HMG-1847 was aragonite or calcite.

In the well-preserved lower jaws found *in situ* in the lytoceratid and phylloceratid conchs with a primary aragonitic shell wall, the black, possibly primarily chitinous outer lamella is wholly and/or partly covered with a thin aragonitic layer, in association with a thick calcitic rostral tip (Tanabe *et al*., 2011, figs. 3, 4A, B; Tanabe *et al*., 2013, fig. 2A–D). The thin outer aragonitic layer is, however, easily exfoliated from the underlying chitinous layer during its excavation from host rocks, such that it is usually unrecognizable in the jaw fossils collected from calcareous nodules if their external casts are unavailable (Kanie, 1982, pl. 40; Tanabe and Fukuda, 1983, fig. 1). We presume that the outer chitinous lamella of HMG-1847 was originally covered by a thin aragonitic layer, as in the well-preserved lower jaws of phylloceratids and lytoceratids as described by Tanabe *et al*. (2011, 2013).

The middle Campanian strata of the Hidaka area, from which HMG-1847 was recovered, yield abundant phylloceratid and lytoceratid ammonoids (Obata *et al*., 1973, table 2). One of us (MI) recently collected large shell fragments of *Gaudryceras,* probably *G. intermedium*, from the middle Campanian *Sphenoceramus schmidti* Zone near this area. This indirect evidence suggests that the specimen of this lower jaw would be a large *Gaudryceras* of approximately 400 mm in shell diameter.

In the presence of a median furrow that becomes indistinct near the posterior margin on the outer chitinous lamella, KMNH IvP 902012 can be classified as the lower jaw of an intermediate-type, which exhibits intermediate features between the lower jaws of the aptychus- and anaptychus-types. The lower jaws of this morphotype are known from some species of the Late Cretaceous superfamily Desmoceratoidea of the suborder Ammonitina, such as the pachydiscids *Menuites naumanni* (see Tanabe and Landman, 2002, text-fig. 1; Tanabe *et al*., 2015, fig. 10.5f) and *Pachydiscus kamishakensis* (see Tanabe *et al*., 2012, fig. 6), and desmoceratids *Tragodesmoceroides subcostatus* (see Tanabe, 1983, text-fig. 4, pl. 71, fig. 3), *Damesites semicostatus* (see Tanabe, 1983, text-fig. 3, pl. 71, fig. 1), and *D*. aff. *sugata* (see Tanabe *et al*., 2012, fig. 5). Among the lower jaws of these desmoceratoids, our specimen is most aligned in an overall shape with the nearly flat rostral portion and dimensions to the lower jaw of *P. kamishakensis* from the lower Maastrichtian (Member 3 of the Matanusuka Formation; Jones, 1963; Shigeta *et al*., 2010; Shigeta and Nishimura, 2013) in the Alfred Creek, Talkeetna

Mountains, southern Alaska. The lower jaw of *P. kamishakensis*, attaining 102.9 mm in *MW*, is preserved *in situ* inside the body chamber of a large specimen (UMUT MM 30876; 305 mm in maximal shell diameter) (Tanabe *et al*., 2012, fig. 6; here reproduced in Figure 7). The outer surface of the chitinous lamella in UMUT MM 30876 is wholly covered with a thin aragonitic layer, which is visible on the left lateral side of the jaw (Figure 7B). KMNH IvP 902012 is, therefore, distinguishable from the lower jaw of *P. kamishakensis* by the absence of a calcareous jaw element. We, however, suspect that KMNH IvP 902012 originally possessed a thin calcareous layer on the outer chitinous lamella, which might have been exfoliated and/or eroded away prior to recovery of the specimen. In summary, KMNH IvP 902012 can be identified as the lower jaw of an extremely large pachydiscid of approximately 40 cm or more in shell diameter.

Morozumi (1985, pl. 5, fig. 1, pl. 7, fig. 1) described a large specimen of *Pachydiscus* aff. *subcompressus* from the middle to upper Maastrichtian Shimonada Formation exposed on the southwestern coast of Awaji Island. The specimen, approximately 200 mm in diameter, consists of a phragmocone and a partial body chamber, and its reconstructed shell diameter was estimated to be more than 300 mm by Morozumi (1985). More recently, amateur collectors have obtained several very large pachydiscid specimens from the Shimonada Formation around the locality of KMNH IvP 902012, some of which were donated to the Osaka City Museum of Natural History. These lines of indirect evidence support our inference for the probable holder of KMNH IvP 902012.

Feeding habits of the jaw holders

Because the jaw apparatus is a primary feeding organ of modern and extinct cephalopods, its morphological and compositional features appear to reflect the feeding and dietary habits of living animals. Based on this, we considered the functional morphologic aspect of the two ammonoid lower jaws examined for feeding.

As previously described, the development of a thick, calcified rostral tip is the most characteristic feature of HMG-1847. This feature is commonly observed in rhynchaptychus-type upper and lower jaws of Cretaceous phylloceratid and lytoceratid ammonoids (Tanabe *et al*., 1980, 2012, 2013, 2015; Kanie, 1982; Tanabe and Landman, 2002; Takeda *et al*., 2016) and those of modern and fossil nautilids (Saunders *et al*., 1978; Dietl and Schweigert, 1999; Klug, 2001). Saunders *et al*. (1978) interpreted that in modern nautilids, the sharp, arrowhead-shaped calcareous tip of the upper jaw (rhyncholite) is used as an incisor, while the distinctly denticulated, scalloped-shaped calcareous tip of the lower jaw (conchorhynch) is used for grasping and shearing food.

This interpretation is justified by aquarium-based observations (Mikami *et al*., 1980) and the analysis of chewed pieces of prey (e.g. small fish, lobster, shrimp, nematodes, and smaller nautilus) in the esophagus and crop of wild-caught animals (Ward and Wicksten, 1980; Tanabe *et al*., 1980; Saisho and Tanabe, 1985). These available data suggest that similar to modern and fossil nautilids, the thick calcareous tip of HMG-1847 has been developed for grasping and shearing captured prey. In view of the unusually large jaw in association with a thick calcareous tip, the holder ammonoid might be a powerful predator and/or a scavenger in the marine ecosystem of Late Cretaceous Northwest Pacific region.

Unlike HMG-1847, KMNH IvP 902012 lacks a calcareous tip. The outer chitinous lamella with a nearly flat rostrum of the lower jaw is posteriorly elongated and is indistinctly partitioned into a pair of wings by a median furrow, which weakens posteriorly and disappears in the posterior margin. Because of the overall shape of the outer chitinous lamella without a pointed rostrum, KMNH IvP 902012 is seemingly similar to the aptychus-type lower jaws that are known from most Jurassic-Cretaceous Ammonitina and Cretaceous Ancyloceratina (Tanabe *et al*., 2015). The unusually large shovel-like lower jaw might not have an ability to bite and cut prey, and instead it was likely used as a scoop to feed on small organisms, as postulated by previous researchers (e.g. Lehmann, 1971, 1985; Lehmann and Weitschat, 1973) for the aptychus-type lower jaws of some Jurassic Ammonitina, relying on their overall morphology and analysis of diet preserved in the esophagus-stomach remains co-occurring with the jaws in situ within the body chambers.

The intermediate-type lower jaws shared by the holder of KMNH IvP 902012 and Late Cretaceous desmoceratoid ammonoids can be distinguished from the aptychus-type lower jaws by the less distinct median furrow in the outer chitinous lamella and the absence of paired calcitic plates (aptychus in *sensu stricto*; Arkell, 1957) on the chitinous lamella. In the well-preserved intermediate-type lower jaws of *Damesites* and *Pachydiscus*, the outer chitinous lamella is instead sealed by a single aragonitic layer (Tanabe *et al*., 2012). Hence, the development of a shovel-like outer lamella without a projected rostrum in the intermediate-type lower jaws of Desmoceratoidea and in the aptychus-types of Jurassic-Cretaceous Ammonitina and Cretaceous Ancyloceratina is interpreted as a convergence to specialize in a passive feeding style relying on small organisms. The wide variety of jaw morphologies in the Cretaceous Ammonoidea as shown in this and previous works (e.g. Tanabe and Landman, 2002; Landman *et al*., 2006; Kruta *et al*., 2011; Tanabe *et al*., 2012) may reflect the diversity of feeding and dietary habits among them.

The intermediate-type lower jaws of the Cretaceous Desmoceratoidea, including KMNH IvP 902012, presumably were mainly used for feeding, although an operculum-like secondary function proposed by Lehmann and Kulicki (1990) and Seilacher (1993) cannot be ruled out in view of their overall shape and the presence of a median furrow in the chitinous outer lamella that could allow opening to it.

Conclusions

Two exceptionally large cephalopod jaws, HMG-1847 and KMNH IvP 902012, were collected from the middle Campanian of the Hidaka area, Hokkaido, and the middle to upper Maastrichtian of Awaji Island, Southwest Japan, respectively. These were identified as the lower jaws of ammonoids based upon a comparison to the jaw apparatuses of previously known modern and extinct cephalopods. HMG-1847 is classified as a rhynchaptychus-type shared by the Cretaceous Lytoceratina and Phylloceratina because of the presence of a thick calcareous tip in the anterior portion of the outer chitinous lamella. KMNH IvP 902012 has diagnostic features of the intermediate-type of the Desmoceratoidea, such as the posteriorly elongated outer chitinous lamella without a pointed rostrum, whose outer surface is sculptured by a median furrow in the anterior portion.

Based on the co-occurring ammonoids and the relationship between the dimensions of the lower jaw and conch of the ammonoids previously described, the holders of HMG-1847 and KMNH IvP 902012 are thought to be large gaudryceratid and pachydiscid specimens, respectively, both attaining more than 40 cm in shell diameter. In view of the aforementioned characteristic lower jaw features, the gaudryceratid and pachydiscid ammonoids might have had scavenging-predatory and passive microphagous feeding habits, respectively.

Acknowledgments

We thank Yasunari Shigeta (National Museum of Nature and Science, Tsukuba) for his valuable comments on the biostratigraphic setting of the specimens examined, and Takenori Sasaki (University Museum, University of Tokyo) to access the UMUT specimen. We appreciate Isabelle Kruta (Sorbonne Universités, Paris) and Neil H. Landman (American Museum of Natural History, New York, NY) for critical comments to improve this manuscript.

References

Arkell, W. J., 1957: Aptychi. *In*, Moore, R. C. *ed.*, *Treatise on Invertebrate Paleontology, Part L, Mollusca 4, Cephalopoda, Ammonoidea*, p. L437–L441. Geological Society of America and University of Kansas Press, New York.

Clarke, M.R., 1962: The identification of cephalopod "beaks" and the relationship between beak size and total body weight. *Bulletin of the British Museum* (*Natural History*), *Zoology*, vol. 8, p.419–480.

Clarke, M.R. *ed*., 1986: *A Handbook for the Identification of Cephalopod Beaks*, 273 p. Clarendon Press, Oxford.

Clarke, M.R. and Maddock, L., 1988: Beaks of living coleoid Cephalopoda. *In*, Clarke, M.R. and Trueman, E.R. *eds*., *The Mollusca. Vol. 12. Paleontology and Neontology of Cephalopods*, p.121–131. Academic Press, San Diego.

Closs, D., 1967: Gonatiten mit Radula und Kieferapparat in der Itararé-Formation von Uruguay. *Paläontologische Zeitschrift*, vol. 41, p. 19–37.

Dietl, G. and Schweigert, G., 1999: Ein Nautilus mit in-situ liegendem, vollständigem Kieferapparat aus dem Nusplinger Plattenkalk (Oberjura, SW-Deutschland). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, Band 211, p. 75–87.

Doguzhaeva, L.A., Mapes, R.H. and Mutvei, H., 1997: Beaks and radulae of Early

Carboniferous goniatites. *Lethaia*, vol. 30, p. 305–313.

Donovan, D.T. and Fuchs, D., 2016: Part M, Chapter 13: Fossilized soft tissues in Coleoidea. *Treatise Online*, no. 73, p. 1–30. The University of Kansas and Paleontological Institution, Lawrence, Kansas.

Gupta, N.S., Briggs, D.E.G., Landman, N.H., Tanabe, K. and Summons, R.E., 2008: Molecular structure of organic components in cephalopods: Evidence for oxidative cross linking in fossil marine invertebrates. *Organic Geochemistry*, vol. 39, p. 1405–1414.

Hunt, S. and Nixon, M., 1981: A comparative study of protein composition in the chitin-protein complexes of the beak, pen, sucker disc, radula and oesophageal cuticle of cephalopods. *Comparative Biochemistry and Physiology*, vol. 68B, p. 535–546.

Jones, D., 1963: Upper Cretaceous (Campanian and Maastrichtian) ammonites from southern Alaska. *United States Geological Survey Professional Paper*, no. 432, p. 1–53.

Kanie, Y., 1982: Cretaceous tetragonitid ammonite jaws: a comparison with modern *Nautilus* jaws. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 125, p. 239–258.

Klug, C., 2001: Functional morphology and taphonomy of nautilid beaks from the Middle Triassic of southern Germany. *Acta Palaeontologica Polonica*, vol. 46, p. 43–68.

Klug, C., Frey, L., Korn, D., Jattiot, R. and Rücklin, M., 2016: The oldest Gondowanan cephalopod mandibles (Hangenberg black shale, Late Devonian) and the mid-Palaeozoic rise of jaws. *Palaeontology*, vol. 59, p. 611–629.

Kruta, I., Landman, N.H., Rouget, I., Cecca, F. and Tafforeau, P., 2011: The role of ammonites in the Mesozoic marine food web revealed by jaw preservation. *Science*, vol. 331, p. 70–72.

Landman, N.H., Tsujita, C.J., Cobban, W.A., Larson, N.H., Tanabe, K. and Flemming, R. L., 2006: Jaws of Late Cretaceous placenticeratid ammonites: how preservation affects the interpretation of morphology. *American Museum Novitates*, no. 3500, p. 1–48.

Lehmann, U., 1967: Ammoniten mit Kieferapparat und Radula aus Lias-Geschieben. *Paläontologische Zeitschrift*, vol. 41, p. 25–31.

Lehmann, U., 1971: Jaws, radula, and crop of *Arnioceras* (Ammonoidea). *Palaeontology*, vol. 14, p. 338–341.

Lehmann, U., 1976: *Ammoniten: ihr Leben und ihre Umwelt*, 171 p. Enke, Stuttgart.

Lehmann, U., 1985: Zur Anatomie der Ammoniten: Tintenbeutel, Kiemen, Augen. *Paläontologische Zeitschrift*, vol. 59, p. 99–108.

Lehmnn, U., 1980: Ammonite jaw apparatus and soft parts. *In*, House, M. R. and Senior, J. R. *eds*., *The Ammonoidea*, p. 275–287. Academic Press, London.

Lehmann, U., 1990: *Ammonoideen*, 257 p. Enke, Stuttgart.

Lehmann, U. and Kulicki, C., 1990: Double function of aptychi (Ammonoidea) as jaw elements and opercula. *Lethaia*, vol. 23, p. 325–331.

Lehmann, U. and Weitschat, W., 1973: Zur Anatomie und Ökologie von Ammoniten: Funde von Kropf und Kiemen. *Paläontologische Zeitschrift*, vol. 47, p. 69–76.

Maeda, H., Shigeta, Y., Fernando, A. G. S. and Okada, H., 2005: Stratigraphy and fossil assemblages of the Upper Cretaceous System in the Makarov area, southern Sakhalin, Russian Far East. *National Science Museum Monographs*, vol. 31, p. 25–120.

Mapes, R.H., 1987: Upper Paleozoic cephalopod mandibles: frequency of occurrence, modes of preservation, and paleoecological implications. *Journal of Paleontology*, vol. 61, p. 521–538.

Meek, F.B. and Hayden, F.V., 1864: Paleontology of the Upper Missouri. *Smithsonian Contribution of Knowledge*, vol. 172, p. 1–135.

Mikami, S., Okutani, T., Hirano, H., Kanie, Y. and Hamada, T., 1980: Behavior in captivity. *In*, Hamada, T., Obata, I. and Okutani, T. *eds*., Natutilus macromphalus *in Captivity*, p. 11–22. Tokai University Press, Tokyo.

Mironenko, A. and Gulyaev, D., 2016: Middle Jurassic ammonoid jaws (anaptychi and rhynchaptychi) from Dagestan, North Caucasus, Russia. *Palaeogeography*, *Palaeoclimatology, Palaeoecology*, vol. 489, p. 117–128.

Morozumi, Y., 1985: Late Cretaceous (Campanian and Maastrichtian) ammonites from Awaji Island, southwest Japan. *Bulletin of the Osaka Museum of Natural History*, no. 39, p.1–58.

Nifuku, K., Kodama, K., Shigeta, Y. and Naruse, H., 2009: Faunal turnover at the end of the Cretaceous in the North Pacific region: Implications from combined magnetostratigraphy and biostratigraphy of the Senpohshi Formation in the eastern Hokkaido Island, northern Japan. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 271, p. 84–95.

Nixon, M., 1988. The buccal mass of fossil and Recent Cephalopoda. *In*, M. R. Clarke and E. R. Trueman *eds*., *The Mollusca, Vol. 12, Paleontology and Neontology of Cephalopods*, p. 103–122. Academic Press, San Diego.

Nixon, M., 1996: Morphology of the jaws and radula in ammonoids. *In*, Landman, N.H., Tanabe, K. and Davis, R.A. *eds*., *Ammonoid Paleobiology*, p. 23–42. Plenum Press, New York.

Nixon, M., 2015: Prat M, Chapter 12: The buccal apparatus of Recent and fossil forms. *Treatise Online*, no. 69, p 1–29. The University of Kansas and Paleontological Institution, Lawrence, Kansas.

Obata, I., Maehara, T. and Tsuda, H., 1973: Cretaceous stratigraphy of the Hidaka area, Hokkaido. *Memoirs of the National Museum of Nature and Science*, vol. 6, p. 131–149.

Saisho, T. and Tanabe, K., 1985: Notes on the oesophagus and stomach-contents of *Nautilus pompilius* in Fiji. *Kagoshima University, Research Center for the South Pacific, Occasional Papers*, no. 4, p. 62–64.

Saunders, W.B., Spinosa, C., Teichert, C. and Banks, R.C., 1978: The jaw apparatus of Recent *Nautilus* and its palaeontological implications. *Palaeontology*, vol. 21, p. 129–141.

Seilacher, A., 1993: Ammonite aptychi: how to transform a jaw into an operculum? *American Journal of Science*, vol. 293A, p. 20–32.

Shigeta, Y. and Izukura, M., 2018a: Additional specimens of *Pravitoceras sigmoidale* Yabe from the upper Campanian (Upper Cretaceous) of Hokkaido, Japan. *Bulletin of the Hobetsu Museum*, no. 33, p. 1–10.

Shigeta, Y. and Izukura, M., 2018b: Discovery of the middle Campanian (Late Cretaceous) “Soya Fauna” ammonoids in the Hidaka area, Hokkaido, Japan. *Bulletin of the Hobetsu Museum*, no. 33, p. 11–26.

Shigeta, Y., Izukura, M., Nishimura, T. and Tsutsumi, Y., 2016: Middle and late Campanian (late Cretaceous) ammonoids from the Urakawa area, Hokkaido, northern Japan. *Paleontological Research*, vol. 20, p. 322–366.

Shigeta, Y. and Nishimura, T., 2013: A new species of *Gaudryceras* (Ammonoidea, Gaudryceratidae) from the lowest Maastrichtian of Hokkaido, Japan and its biostratigraphic implications. *Paleontological Research*, vol. 17, p. 47–57.

Shigeta, Y., Nishimura, T. and Nifuku, K., 2015: Middle and late Maastrichtian (latest Cretaceous) ammonoids from the Akkeshi Bay area, eastern Hokkaido, northern Japan and their biostratigraphic implications. *Paleontological Research*, vol. 19, p. 107–127.

Shigeta, Y., Tanabe, K. and Izukura, M., 2010: *Gaudryceras izumiense* Matsumoto and Morozumi, a Maastrichtian ammonoid from Hokkaido and Alaska and its biostratigraphic implications. *Paleontological Research*, vol. 14, p. 196–201.

Takahashi, K. and Suzuki, M., 1986: *Geological sheet map "Hidaka", scale 1:50,000 and its explanation text*, 44 p. Geological Survey of Hokkaido. (*in Japanese with English abstract*).

Takeda, Y., Tanabe, K., Sasaki, T., Uesugi, K. and Hoshino, M., 2016: Non-destructive analysis of in situ ammonoid jaws by synchrotron radiation X-ray micro-computed tomography. *Palaeontologia Electronica*, vol.19, article 45A, 13 p.

Tanabe, K., 1983: The jaw apparatuses of Cretaceous desmoceratid ammonites.

Palaeontology, vol. 26, p. 677–686.

Tanabe, K., 2012: Comparative morphology of modern and fossil coleoid cephalopod jaw apparatuses. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, Band 266, p. 9–18.

Tanabe, K. and Fukuda, Y., 1983: Buccal mass structure of the Cretaceous ammonite *Gaudryceras*. *Lethaia*, vol. 16, p. 249–256.

Tanabe, K. and Fukuda, Y., 1999: Morphology and function of cephalopod buccal mass. *In*, Savazzi, E. *ed*., *Functional Morphology of the Invertebrate Skeleton*, p. 245–262. John Wiley and Sons, London.

Tanabe, K., Fukuda, Y., Kanie, Y. and Lehmann, U., 1980. Rhyncholites and conchorhynchs as calcified jaw elements in some late Cretaceous ammonites. *Lethaia*, vol. 13, p.157–168.

Tanabe, K., Kruta, I. and Landman, N.H., 2015: Ammonoid buccal mass and jaw apparatus. *In*, Klug, K. *et al*. *eds*., *Ammonoid Paleobiology: From Anatomy to Ecology*, p. 429–484. Topics in Geobiology 43, Chapter 10. Springer.

Tanabe, K. and Landman, N.H., 2002: Morphological diversity of the jaws of Cretaceous Ammonoidea. *Abhandlungen der Geologischen Bundesanstalt*, Band 57, p.157–165.

Tanabe, K., Landman, N.H. and Kruta, I., 2012: Microstructure and mineralogy of the outer calcareous layer in the lower jaws of Cretaceous Tetragonitoidea and Desmoceratoidea (Ammonoidea). *Lethaia*, vol. 45, p.191–199.

Tanabe, K., Misaki, A., Lndman, N.H. and Kato, T., 2013: The jaw apparatuses of Cretaceous Phylloceratina (Ammonoidea). *Lethaia*, vol. 46, p. 399–408.

Tanabe, K., Tsukahara, J. and Hayasaka, S., 1990: Comparative morphology of living *Nautilus* (Cephalopoda) from the Philippines, Fiji and Palau. *Malacologia*, vol. 31, p. 297–312.

Teichert, C., Moore, R.C. and Nodine Zeller, D.E., 1964: Rhyncholites. *In*, Moore, R.C. *ed*., *Treatise on Invertebrate Paleontology, Part K, Mollusca 3*, p. K467-K484. Geological Society of America and University of Kansas Press, New York.

Ward, P. and Wicksten, M.K., 1980: Food sources and feeding-behavior of *Nautilus macromphalus*. *The Veliger*, vol. 23, p. 119–124.

Figure captions

Figure 1. Map of Japan and adjacent regions (**A**) showing the locations of Hidaka area, Hokkaido (**B**) and Awaji Island (**C**, **D**) from which the two examined cephalopod jaws were collected. Detailed fossil localities are shown in B and D.

Figure 2. Diagrammatic drawings of two Cretaceous ammonoid lower jaws of the rhynchaptychus-type (**A**) and intermediate-type (**B**). Abbreviations. *MW*: maximal length of wing, *DW*: dorsal width of wing, *HH*: height of hood, *WW*: width of wing. After Clarke (1962, 1986) and Clarke and Maddock (1988) for terms (shown in italics) and measurements.

Figure 3. Rhynchaptychus-type lower jaw, possibly attributed to a large *Gaudryceras* specimen. HMG-1847 from the middle Campanian unit of the Yezo Group in Hidaka area, southern central Hokkaido. Left lateral (**A**), dorsal (**B**), right lateral (**C**), and frontal (**D**) views of the entire jaw, and close-up view of the rostral portion (**E**). Abbreviations. ocl: outer chitinous lamella, icl: inner chitinous lamella, co: thick calcified tip (conchorhynch) in the anterior portion.

Figure 4. Raman spectra for the black outer lamella (**A**) and calcified rostral tip (**B**) of HGM-1847, and the shell wall of a co-occurred ammonoid T*etragonites popetensis* (**C**) compared with those of standard apatite, calcite and aragonite crystals.

Figure 5. Intermediate-type lower jaw, possibly attributed to a large pachydiscid specimen. KMNH IvP 902012 from the upper Maastrichitian Shimonada Formation near Nadachino, southwestern Awaji Island. Ventral (**A**), right lateral (**B**) and left lateral (**C**) views. Abbreviation. mf: median furrow. Epizoan attachment scars are pointed by arrowheads. Coalesced attachment line of a short inner lamella on the casted left and right lateral shoulder portions are shown by a white arrow in B and C.

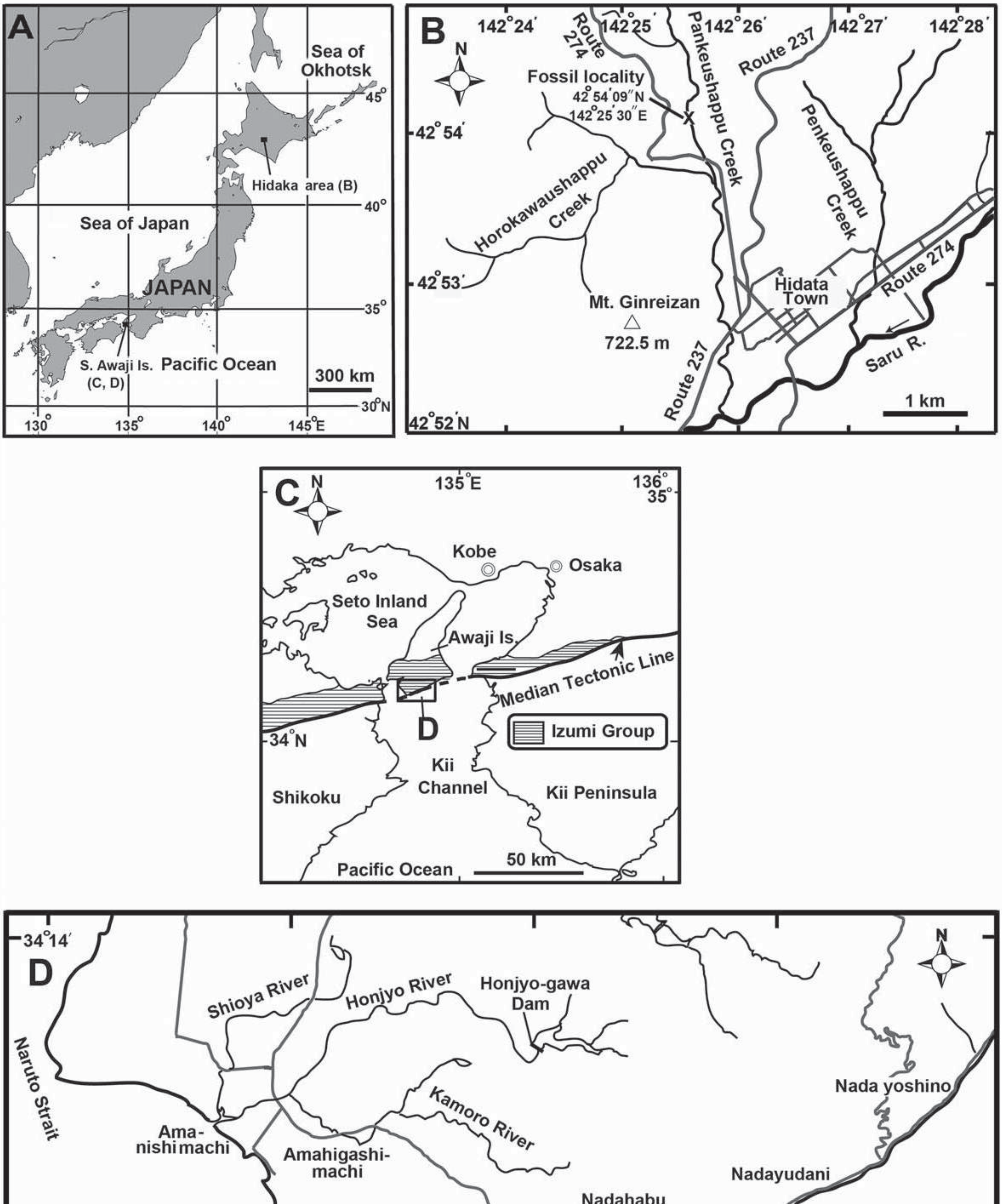
Figure 6. Scatter plots of maximum length of wing of *in situ* lower jaw (*MW*) versus shell diameter (*SD*) (**A**) and whorl height (*WH*) (**B**) for the 81 specimens of 56 species of Devonian to Cretaceous ammonoids described previously. Measurement data of 75 specimens of 51 Mesozoic species shown in Tanabe *et al*. (2015, table 10.2) and those of 6 specimens of 5 Paleozoic species (Table 1) are used in this figure. *: scaphitids. Regression lines in A and B by least squares fit. *r*: correlation coefficient, *N*: number of

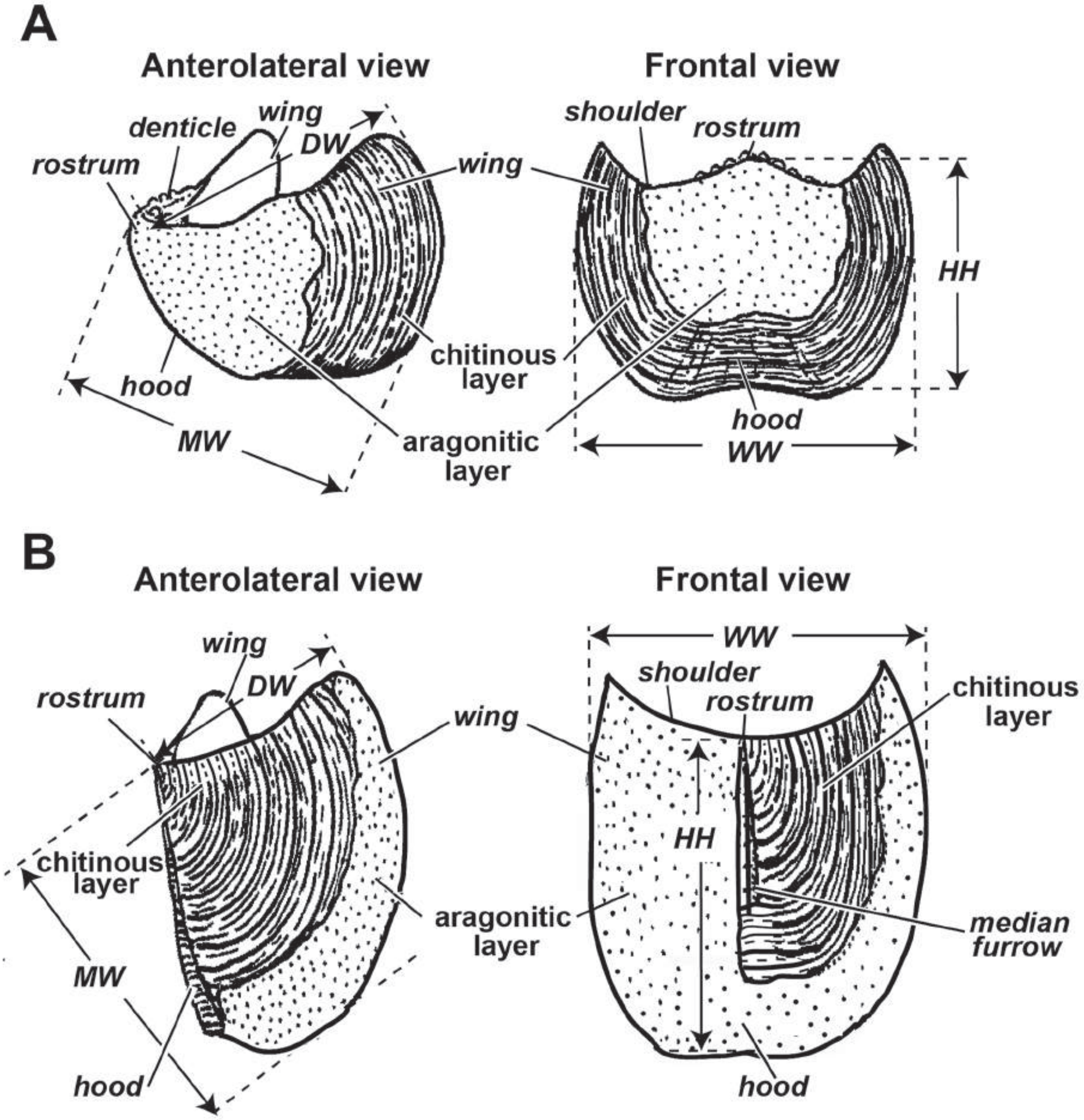
specimens. *MW* values of HMG-1847 and KMNH IvP 902012, and estimated *SD* and *WH* values of their holder ammonoids relying on the regression lines are also shown in this figure.

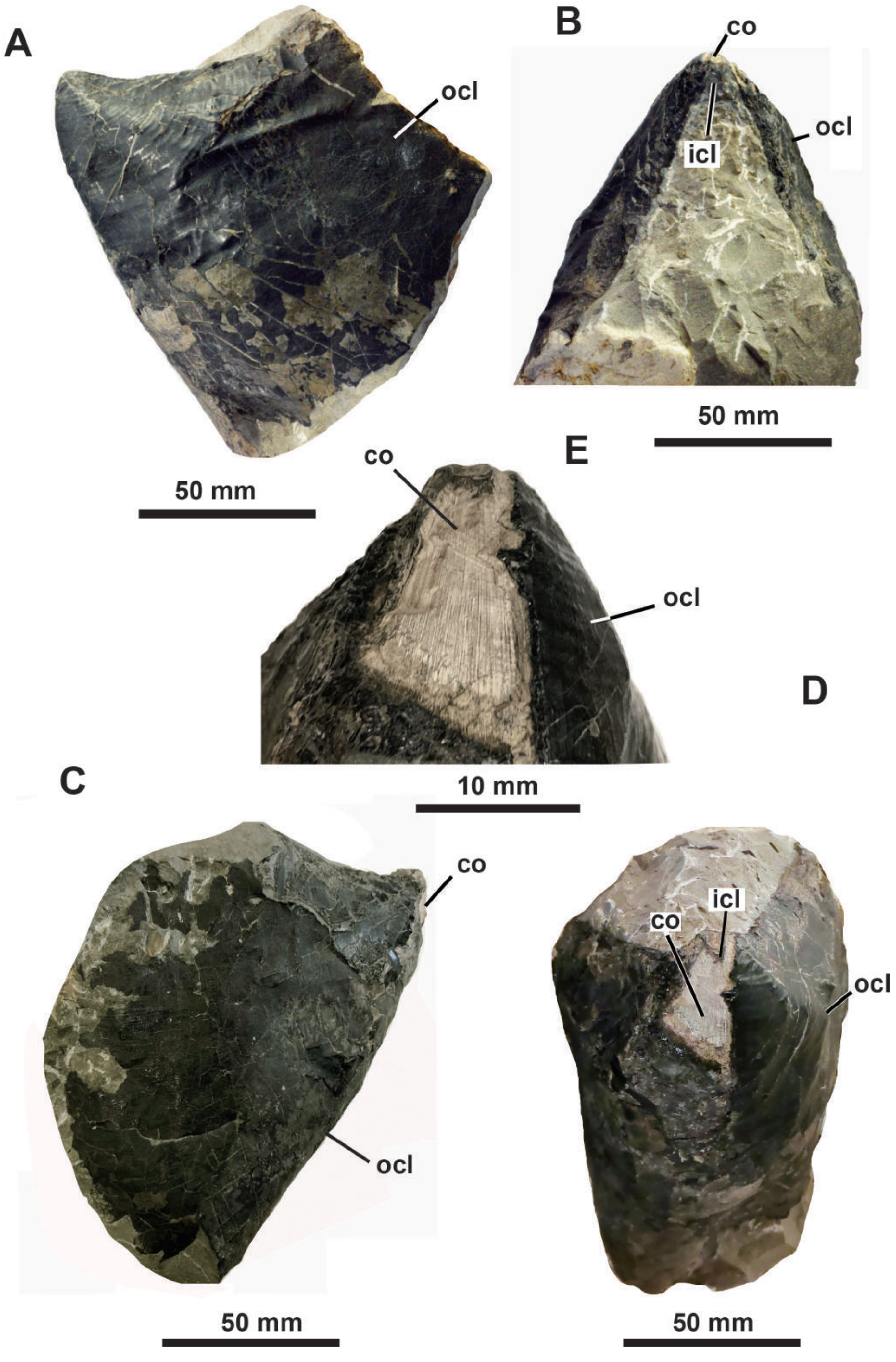
Figure 7. *Pachydiscus kamishakensis* with preserving an intermediate-type lower jaw *in situ* inside the body chamber (same specimen as that figured by Tanabe *et al*., 2012, fig. 6). UMUT MM 30876 from the lower Maastrichtian in southern Alaska. Mode of occurrence (**A**), and left lateral (**B**) and ventral (**C**) views of the lower jaw.

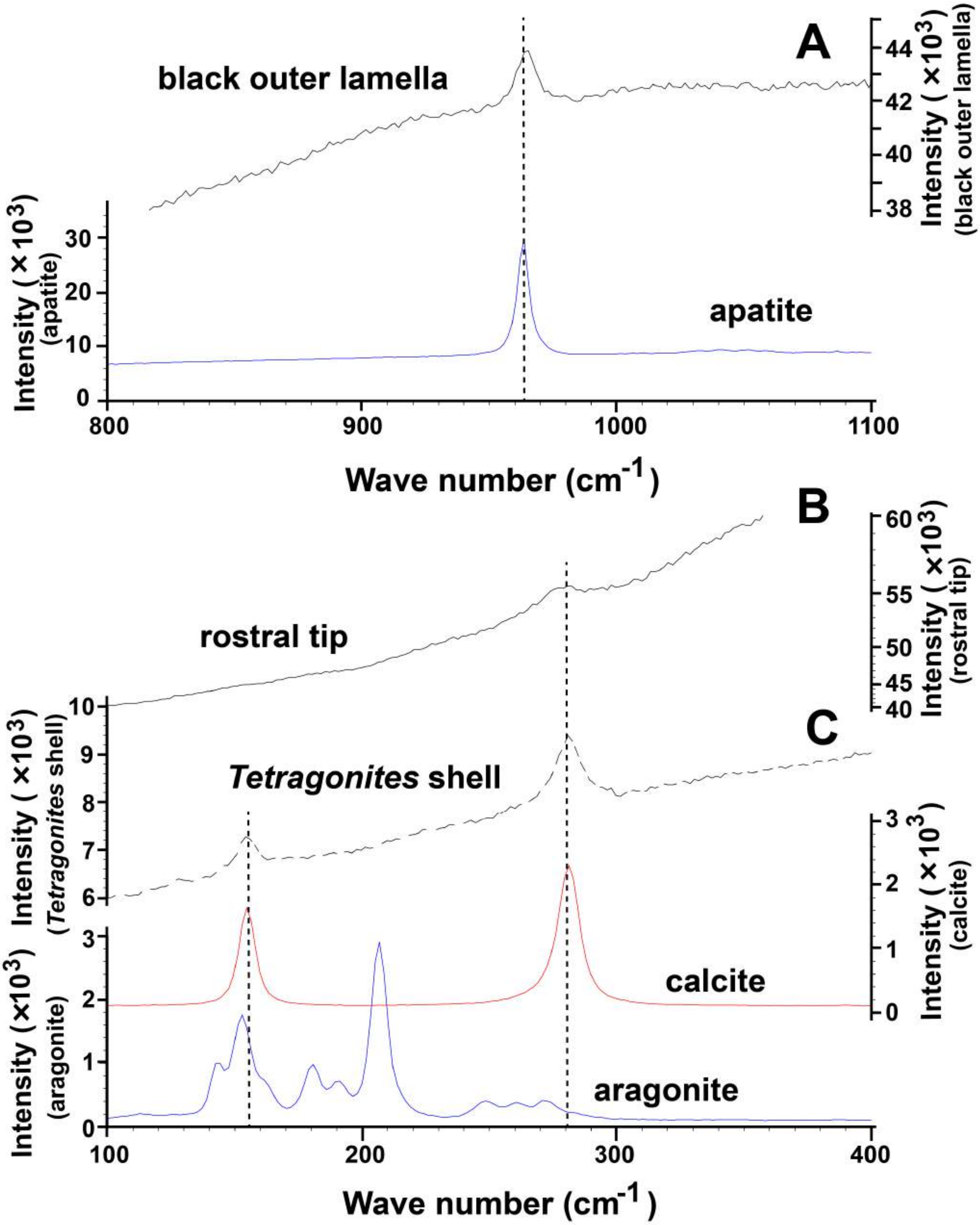
Table caption

Table 1. Measurement data of in situ jaw apparatuses of Paleozoic ammonoids. Abbreviations; *SD*: shell diameter, WH: whorl height, *MW*: maximal length of wing of lower jaw. Institutional abbreviations. PIMUZ: Paläontologische Institut und Museum, Universität Zurich, SUI: Department of Geology, University of Iowa, CMNH: Cinccinati Museum of Natural History.

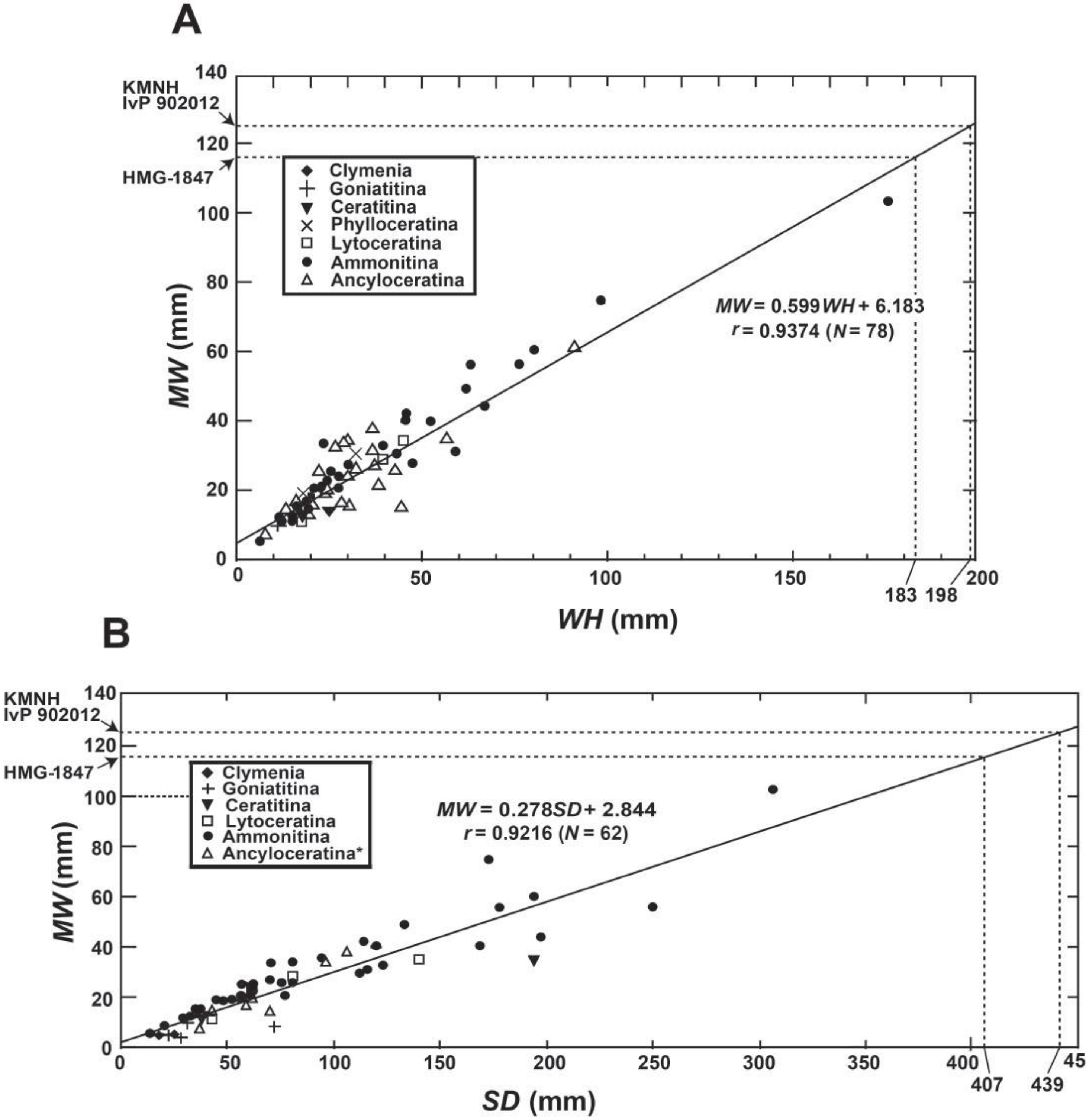

A
Sea of Okhotsk
45°
Hidaka area (B)
40°
Sea of Japan
JAPAN
35°
S. Awaji Is. (C, D)
Pacific Ocean
300 km
30°N
130°
135°
140°
145°E
B
142°24′
Route 274
142°25′
Pankeushappu Creek
142°26′
Route 237
142°27′
142°28′
N
Fossil locality
42°54′09″N
142°25′30″E
X
42°54′
Penkeushappu Creek
Horokawaushappu Creek
42°53′
Mt. Ginreizan
722.5 m
Hidata Town
Route 274
Saru R.
Route 237
1 km
42°52′N
C
N
135°E
136°
35°
Kobe
Osaka
Seto Inland Sea
Awaji Is.
Median Tectonic Line
D
34°N
Izumi Group
Shikoku
Kii Channel
Kii Peninsula
Pacific Ocean
50 km
D
34°14′
N
Shioya River
Honjyo River
Honjyo-gawa Dam
Naruto Strait
Kamoro River
Nada yoshino
Ama-nishimachi
Amahigashi-machi
Nadayudani
Nadahabu
34°12′N
Nadachino
Nada Fishery Port
Nadanigoro
X Fossil locality
(34°11′46.6″N,134°45′27.8″E)
134°42′E
Shiozaki Cape
134°44′
134°46′
134°48′
1 km


A
Anterolateral view
denticle
wing
DW
rostrum
wing
hood
MW
chitinous layer
aragonitic layer
Frontal view
shoulder
rostrum
HH
hood
WW
B
Anterolateral view
wing
DW
rostrum
wing
chitinous layer
MW
hood
aragonitic layer
Frontal view
WW
shoulder
rostrum
chitinous layer
HH
median furrow
hood


A
ocl
50 mm
B
co
icl
ocl
50 mm
co
E
ocl
D
10 mm
C
co
ocl
50 mm
icl
co
ocl
50 mm


A
black outer lamella
Intensity (×10^3)
(black outer lamella)
38
40
42
44
Intensity (×10^3)
(apatite)
0
10
20
30
apatite
800
900
1000
1100
Wave number (cm^{-1})
B
rostral tip
Intensity (×10^3)
(rostral tip)
40
45
50
55
60
C
Tetragonites shell
Intensity (×10^3)
(Tetragonites shell)
6
7
8
9
10
Intensity (×10^3)
(calcite)
0
1
2
3
calcite
Intensity (×10^3)
(aragonite)
0
1
2
3
aragonite
100
200
300
400
Wave number (cm^{-1})


A
B
mf
C
0
50 mm


A
KMNH
IvP 902012
HMG-1847
Clymenia
Goniatitina
Ceratitina
Phylloceratina
Lytoceratina
Ammonitina
Ancyloceratina
MW = 0.599WH + 6.183
r = 0.9374 (N = 78)
MW (mm)
0
20
40
60
80
100
120
140
0
50
100
150
200
183
198
WH (mm)
B
KMNH
IvP 902012
HMG-1847
Clymenia
Goniatitina
Ceratitina
Lytoceratina
Ammonitina
Ancyloceratina*
MW = 0.278SD + 2.844
r = 0.9216 (N = 62)
MW (mm)
0
20
40
60
80
100
120
140
0
50
100
150
200
250
300
350
400
450
407
439
SD (mm)

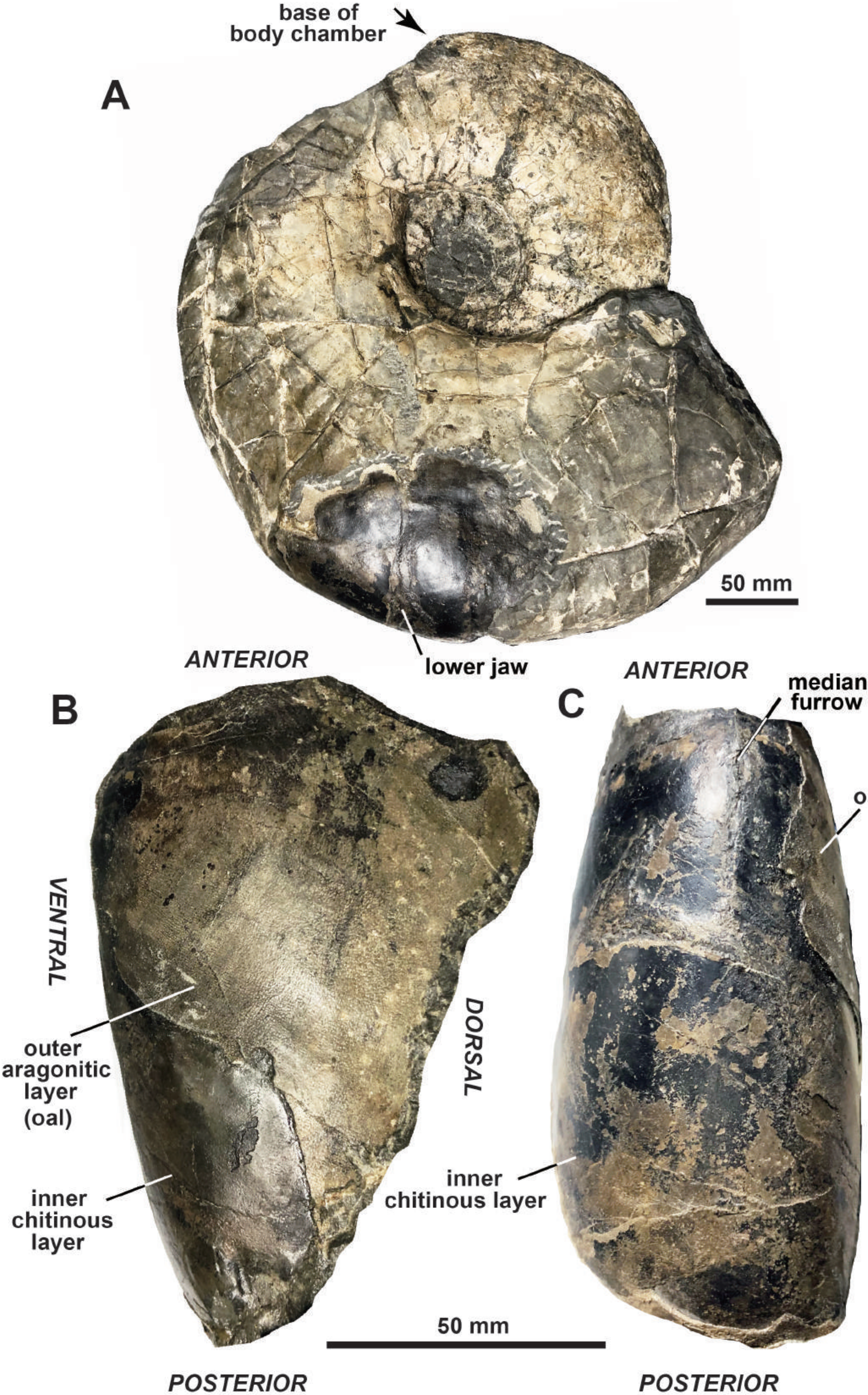

A
base of body chamber
50 mm
lower jaw
B
ANTERIOR
VENTRAL
DORSAL
outer aragonitic layer (oal)
inner chitinous layer
POSTERIOR
50 mm
C
ANTERIOR
median furrow
oal
inner chitinous layer
POSTERIOR

Table 1

Suborder	Superfamily	Species	Specimen and source	*SD* (mm)	*WH* (mm)	*MW* (mm)
Clymeniina	Clymenioidea	*Postclymenia calceola* Klein and Korn	PIMUZ 31557-1 (Klug *et al* , 2016)	*ca* . 19	?	*ca* . 5
			PIMUZ 31557-2 (Klug *et al* ., 2016)	*ca* . 24	?	*ca* . 5
Goniatitina	Goniatitoidea	*Girtyoceras limatum* (Miller and Faber)	Amer. Mus. unregistered sp. (Doguzhaeva *et al* ., 1997)	*ca* . 31	*ca* . 11	9.6
	Dimorphoceratoidea	*Anthracoceras* ? sp.	CMNH 34483 (Mapes, 1987)	22.3	?	*ca* . 4.6
	Neoglyphioceratoidea	*Cravenoceras feyettevillae* Gordon	SUI 51383 (Mapes, 1987)	28.3	?	3.9
	Gastrioceratoidea	*Glaphyrites* sp.	Univ. Tübingen collection (Closs, 1967)	*ca* . 70	?	8.2