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A Turonian polycotyloid plesiosaur (Reptilia; Sauropterygia) from Obira Town, Hokkaido, and its biostratigraphic and paleoecological significance

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Abstract. The Polycotylidae are short-necked plesiosaurs known from the Cretaceous in various parts of the world, but only a few occurrences have been documented in Japan where elasmosaurid remains are much more common. An indeterminate polycotyloid specimen from the Upper Cretaceous in Obira Town, Hokkaido, is described. Characteristics of the vertebrae and clavicular arch support its taxonomic affinity. The Turonian occurrence of the specimen indicates the continuous presence of the Polycotylidae across the Cenomanian-Turonian boundary in the northwestern Pacific. Macroscopic osteological features of the vertebrae and clavicular arch indicate an advanced stage of ossification, and there are histological characteristics suggesting slowed growth. The osteoporotic-like condition implies a high degree of aquatic adaption.

Key words: Plesiosauria, Polycotylidae, Cenomanian-Turonian boundary, ontogeny, histology

Introduction

The Yezo Group in Japan and Sakhalin is so far the only place in the northern Pacific where a continuous stratigraphic sequence of mid to uppermost Cretaceous is available with a reasonable number of reptilian fossils and good stratigraphic controls (Sato *et al.*, 2012; Takashima *et al.*, 2004; Konishi *et al.*, 2016). Basic taxonomic studies of Yezo fauna are therefore crucial to understand the temporal and geographic distributions of various Cretaceous marine reptiles. Remains of the Plesiosauria (Reptilia: Sauropterygia) are fairly common in the Japanese Upper Cretaceous (Sato *et al.*, 2012), and the long-necked Elasmosauridae numerically dominate the record, represented by several incomplete but articulated skeletons (e.g., Nakaya 1989; Ogawa and Nakaya, 1998; Sato *et al.*, 2006). In contrast, non-elasmosaurid specimens, such as those of the Polycotylidae and Pliosauroidae, are much fewer in number and represented by more fragmentary remains. However, reports of their occurrences have doubled in the last decade or so (e.g., Sato *et al.*, 2012), suggesting their taxonomic and/or morphological diversity is higher than perceived.

In this study, we describe a polycotylid specimen from the Turonian of the Yezo Group in Hokkaido. This specimen is important because 1) it includes the first reasonably complete clavicular arch of the Polycotylidae from Japan, 2) its Turonian

occurrence demonstrates the survival of Polycotylidae across the Cenomanian-Turonian boundary in northwest Pacific, and 3) it provides the first histological data of definite Polycotylidae using CT-scanning and thin-sectioning.

Much of the Yezo plesiosaurian specimens were collected as isolated floats in a riverbed. Even the preserved bones tend to be incomplete due to their large size and weathering of the float, and their stratigraphic origins are often given as a range of the horizons exposed in the area. For example, Echizenya and Minoura (2005) reported the occurrence of two damaged vertebrae and the anterior tip of the interclavicle from the upper Cenomanian to lower Turonian of the Yezo Group, but the fragmentary nature of the specimen and lack of co-occurring age-indicative fossils did not allow in-depth investigation on the morphology and stratigraphic significance of their specimen.

Previous studies on plesiosaurian bone histology are limited in their taxonomic, geographic, and stratigraphic coverage. Indeterminate elasmosaurids of southern high latitudes in the latest Cretaceous (Campanian – Maastrichtian) are the most common material (e.g., Wiffen *et al.*, 1995; Fostowicz-Frelik and Gaździcki, 2001; Talevi and Fernández, 2014), whereas Cruickshank *et al.* (1996) and Street and O’Keefe (2010) studied a pliosaurid and a cryptoclidid of the Jurassic, respectively. To our knowledge, there are no previous studies on the histology of definite polycotylid

specimens. Wiffen *et al.* (1995) examined skeletal histological features of two “pliosaurid” vertebrae from the Campanian-Maastrichtian of New Zealand. The classification back then was the one proposed by Brown (1981) in which the Polycotylidae was not recognized as a discrete taxon, and it is quite possible that Wiffen’s “pliosaurid” specimens may actually represent or include polycotylid material, but it is difficult to prove it.

Material and Methods

The specimen described here, HMG-357 of Hobetsu Museum in Mukawa Town, Hokkaido, came from the Upper Cretaceous Yezo Group in Obira Town, Hokkaido; see Figure 1 and “Remarks on stratigraphy” in Systematic Paleontology for details on its geology. Sato and Nishimura (2012) and Sato *et al.* (2012) briefly reported/mentioned its occurrence.

Two antermost dorsal ribs, #7 and #15 (see Systematic Paleontology below) are used for our histological study. CT scanning was performed using Tesco Microfocus CT TXS320-ACTIS (0.2 mm resolution, 260kV, 200 μ A) at the National Museum of Nature and Science, Tokyo, Japan, and image segmentation and visualization were performed using VG Studio Max 2.0.5 (Volume Graphics GmbH, Heidelberg,

Germany). The thin sectioning procedure generally follows Chinsamy and Raath (1992). The rib #15 was sectioned at six points, and prepared sections were numbered #15-I to #15-VI from the proximal to distal end. Thin sections were observed in transmitted light using a Leica Z6 APO microscope at Tokyo Gakugei University and Leica M125 microscope at the University of Tokyo, and photographed using Leica DFC290 HD digital sight camera and Canon EOS Kiss X6i digital single-lens camera, respectively. Because of the large size of the samples, multiple photographs were integrated into a single image showing the entire section. The polarizing microscope Olympus BX41 at the University of Tokyo was also used in observation of thin sections, using Canon EOS Kiss X6i digital camera. Original CT images were processed on the software (Photoshop Creative Cloud) to emphasize the contrast.

Nomenclature and definitions of technical terms in bone histology are based on Francillon-Vieillot *et al.* (1990).

SYSTEMATIC PALEONTOLOGY

Sauroptrygia Owen, 1860

Plesiosauria de Blainville, 1835

Polycotyliidae Cope, 1869

Polycotyliidae gen. et sp. indet.

Referred specimen.--HMG-357, a partial skeleton consisting of five articulated vertebrae at the base of the neck, eight ribs, clavicular arch, and a scapular dorsal blade.

Locality.--Collected as a float in the Obirashibe River in the Lake Obirashibe area, Obira Town, Hokkaido, Japan.

Horizon.--Estimated to be in an upper part of the Saku Formation (Mm-o unit) of the Yezo Group, upper middle to lower upper Turonian.

Remarks on the stratigraphy.--HMG-357 was collected in 1986 as a float in the Obirashibe River by Ken-ichi Chiyokawa and donated to the Hobetsu Museum. A reservoir (Lake Obirashibe) was constructed in 1992 and the locality has been submerged.

The nodule containing HMG-357 was prepared sometime before our research,

but the remaining matrix consists of bioturbated mudstone and includes very fine sands and abundant wood particles. Judging from matrix, the nodule came from Mm-o stratigraphic unit, i.e., the uppermost geological unit of Saku Formation. Mm-o unit correlates to the upper part of *Inoceramus hobetsensis* Zone and the lower part of *Inoceramus teshioensis* Zone (Tanabe *et al.*, 1977; Funaki and Hirano, 2004). In addition, the ammonoid *Scalarites* sp. co-occurred in the nodule; this genus is known from the Turonian to the Coniacian in the Yezo Group (Matsumoto, 1977; Toshimitsu and Hirano, 2000). Based on these evidence, the stratigraphic origin of the plesiosaur specimen is confidently estimated to be in an upper part of the Saku Formation (Mm-o unit) of the Yezo Group, representing the upper middle Turonian to the lower upper Turonian.

Osteological description:

HMG-357 includes five vertebrae, eight ribs, a part of the left scapula and a clavicular arch. Judging from the anatomical positions and size of individual elements, it is safely assumed that this specimen originated from the pectoral region of a single individual. The neurocentral suture is completely closed in all vertebrae, indicating this individual was an “adult” or “old adult” *sensu* Brown (1981; also see Discussion). An

Arabic numeral is painted on each element (but it does not match the anatomical order), and in the following description this number is employed to distinguish ribs, e.g., #15 for the rib with the painted number of “HMG 357-15”.

The articulated vertebrae (Figure 2A, B) represent the transition from the cervical to dorsal vertebrae, and the rib facets gradually shift from the centrum in cervicals to the tip of the transverse process in dorsals. The centra are amphicoelous (Figure 2C, D), and wider than tall and taller than long (Table 1), and there is no ventral notch on the ventral edge of the intervertebral facet. The foramina subcentralia are located in the shallow depressions on the ventral surface separated by a longitudinal ridge (Figure 2E). The neural spine slightly narrows dorsally in lateral view, and lacks the thickening at the anterior and posterior corners seen in the “pectoral” vertebrae of elasmosaurids (e.g., Sato *et al.*, 2006).

All of the eight ribs (#7, 8, 10 to 15: Figure 3) are more or less damaged, but most of them can be matched with the corresponding vertebrae with reasonable confidence based on the fit of the head and rib facet, as well as the symmetry. We consider #11 as the antermost right rib in the preserved series because of the shortness and the presence of the anterior process. #10 is slightly longer than #11, and likely represents the next right rib, because the partly damaged distal end retains the base of

the anterior process. The articular facet is elongate and seems to match the facet on the second antermost vertebra, although it may have been compressed slightly. #12 is longer than #10, and has an elongate articular facet which corresponds to the rib facets of the 3rd anterior vertebra, and paired with #14 based on the characteristics of the constriction near the head, as well as the thickness of the shaft.

#15 and #7 are used for the histological study and described in detail. #7 is the best preserved rib in this specimen, although the distal end and the rim of the articular facet are slightly damaged. It is about 13 cm long from the rib facet to the broken distal end, and the longitudinal diameter of the damaged proximal end is about 25 mm. The shaft is gently curved, and the articulation facet is deeply concave to fit the convex facet on the transverse process, and there are ridges and gentle grooves on the surface near the head. #15 is heavily abraded and missing the rim of the head, the dorsal surface and the distal part, but paired with #7 based on the similarity of the ridge and groove near the ventral edge, as well as the concavity and inferred size of the articular facet. It is about 75 mm long, and the longitudinal diameter of the damaged proximal end is about 20 mm. #8 and #13 represent the postermost pair belonging to the postermost vertebra in the preserved series. The rib head is more massive than #7, the articular facet is deeply concave with a well-defined rim, and the shaft is thicker.

In plesiosaurs, the transition from the cervical to dorsal vertebrae is gradual and they are conventionally distinguished based on the location of the rib facet relative to the neurocentral suture (e.g., Welles, 1943; Carpenter, 1999). The neurocentral suture is completely closed in HMG-357 and cannot be traced in the vertebra bearing #7 and #15 ribs, but the rib facet on the short transverse process is convex without any trace of suture, suggesting it is a dorsal vertebra. In addition, the damaged shaft of #7 indicates that it was much longer than more anterior ribs. Therefore, we interpret #7 and #15 as the first dorsal ribs of this plesiosaur.

The preserved portion of the clavicular arch is missing much of the original edge of the bone (Figure 4). It is fairly thick in the anteromedial portion near the large interclavicular foramen, but the element thins posterolaterally, and it is only 1 mm thick or so at the broken edge of the interclavicle and clavicles. The three bones are fused, but the suture is partially traceable. There are longitudinal sharp ridges on the interclavicle lateral to the interclavicular foramen. This portion of the arch is slightly asymmetrical.

Judging from the thickness of the anterior edge and concavity on the medial side, the preserved dorsal blade came from the left scapula (Figure 5). The distal end of the blade is damaged but indicates that the tip of the blade widens and did not simply taper.

Microanatomical and histological descriptions

CT images of HMG-357 rib #7.—The CT value (X-ray transmissivity) of the matrix and bone did not differ considerably, and the contrast of the image was enhanced in Figure 6. The comparison with the structures observed in thin sections supports our interpretation of these images. The brightness of the bone is reversed in some places within the same image, i.e., the trabeculae appear brighter than the matrix in the anterior half of the rib but darker in the posterior half, likely reflecting the subtle difference in the relative transmissivity between the matrix and bone. The bright spots in spongiosa likely represent pyrite crystals (see “microscopic description” below).

The inner rib structure exhibits osteoporotic-like condition at the sectioned two points (i.e., rib head and mid-shaft). The medullary cavity is surrounded by extensive spongiosa, and a thin layer of compact cortical bone forms the solid surface.

Microscopic description.--The longitudinal section of a rib head (HMG-357 #15-1, Figure 7A) displays loose spongiosa, consisting of thin trabeculae (about 0.2 mm) oriented longitudinally to the articular facet. The outermost cortex at the ventral side of the rib exhibits nearly avascular primary bone with few secondary osteons. There is a

mass of tissue at the ventral corner of the articular facet, which appears homogeneous and contains numerous fiber bundles, possibly related with tendon insertions (Figure 7D; Haines and Mohuiddin, 1968; Petermann and Sander, 2013). Bands of alternating light and dark tissue are present in the fiber bundles showing possible tempo and mode of calcification of existing soft tissue (see also Main *et al.* 2005). In the medullary region, the trabecular tissue is mostly secondary remodeled.

In the shaft sections, there is a large open medullary cavity surrounded by spongiosa with numerous erosion lacunae throughout the preserved portion (Figure 7B, C). Most parts of the cortex are heavily remodeled; especially, the ventral region is completely remodeled by dense Haversian tissue (Figure 7E).

A thin layer of primary bone tissue consisting of parallel-fibered bone is present in the outermost cortex of the posterior side (Figure 7G). A part of the peripheral bone tissue comprises mostly avascular tissue including possible lines of arrested growth (LAG) (Figure 7I), which resembles an external fundamental system (EFS) (e.g., Sander *et al.*, 2006). The outermost edge of ventral side includes numerous fiber bundles running toward periphery between secondary osteons (Figure 7D). There are numerous erosion cavities in the deeper cortex; they are irregularly shaped and larger in deeper area. Howship's lacunae are occasionally present in the wall of the erosion cavity,

indicating active resorption by osteoclasts (Figure 7F). The trabeculae are about 0.1-0.3 mm thick and form a coarse network and are composed of secondary lamellar bone tissue (Figure 7H).

The marrow spaces of HMG-357-#15 are filled with minerals. Dark irregular spots are observed on the trabecular surfaces and form thick black layers in places (e.g., Figure 7F). They are opaque in transmitted light, but exhibit metallic luster in reflected light, likely representing pyrite crystals commonly occurring in fossilized bones from Yezo Group (e.g., Kaim *et al.*, 2008).

DISCUSSION

Justification of taxonomic identification

HMG-357 is identified as a polycotyloid based on the morphology of the vertebrae and clavicular arch. Preserved bones of HMG-357 are comparable in size to the previously described Yezo polycotyloid specimens which represent relatively small adult individuals (e.g., Sato and Storrs, 2000; Echizenya and Minoura, 2005).

The vertebrae of HMG-357 shows typical features of polycotyloid “pectorals”, such as the short centrum with oval articular faces without a ventral notch, a pair of

foramina subcentralia separated by a ridge, large zygapophyses, and the neural spine which narrows dorsally (e.g., Williston, 1903; Adams, 1997; Frey *et al.*, 2017). In contrast, more common elasmosaurid “pectoral” vertebrae are characterized by the square neural spine in which the anterior and posterior corners are thickened and the intervertebral facet bears a ventral notch, and they lack the sharp ridge on the ventral surface of the centrum separating the paired depressions hosting the foramina subcentralia (e.g., Sato *et al.*, 2006). Morphology of the clavicular arch is quite variable among the elasmosaurids (e.g., Welles 1962), but an elongate interclavicular foramen between the sharp longitudinal ridges as in the HMG specimen has not been reported in any known elasmosaurid taxa. Much less information is available for the Cretaceous pliosauroids because of the paucity of the postcranial materials, but HMG-357 can be distinguished from the two genera with comparable specimens: *Brachauchenius* which lacks foramina subcentralia (e.g., Williston, 1903; Albright *et al.*, 2006a), and *Kronosaurus* whose cervical and anterior dorsal centra are taller than wide (Romer and Lewis, 1959). The clavicular arch has been described only in a few pliosauroids (e.g., *Peloneustes* in Andrews, 1913), but we are not aware of any with an interclavicular foramen and surrounding ridge.

Characteristics of the interclavicular arch of HMG-357 distinguish it from

non-polycotylics, but they are fairly common among polycotylics for which detailed comparison is available. HMG-357 shares the presence of a large interclavicular foramen with ridges on the sides with *Dolichorhynchops osborni*, *D. bonneri*, *Eopolycotylus rankini*, and *Trinacromerum bentonianum* (Williston 1903, 1908; Adams, 1997; Albright *et al.*, 2007b; O’Keefe, 2008); the taxa with the large foramen range from the Cenomanian to Santonian or Campanian. In the Campanian-Maastichtian *D. herschelensis* Sato 2005, however, the area for the interclavicular foramen is mostly ossified, leaving very small openings and weak lateral ridges. The interclavicle is poorly preserved or unknown in many polycotylic taxa and it is hard to assess the effect of ontogenetic variability, but the presence of well-defined foramen in the adult individual HMG-357 and other early polycotylics suggests that the closure of this foramen in *D. herschelensis* likely represents an autapomorphic condition.

Significance of the occurrence of Turonian polycotylics in Japan

Early polycotylic remains have been reported from the upper Lower Cretaceous of North America and Australia (Druckenmiller and Russell, 2009), although phylogenetic relationships within the group and referral of certain genera at higher taxonomic level conflict in recent studies (e.g., Albright *et al.*, 2007b;

Druckenmiller and Russell, 2008; Ketchum and Benson, 2010). Diverse polycotyliids are known from the Cenomanian to Campanian, mostly from the Western Interior Seaway (WIS) of North America but also from Asia and northern Africa, with the latest ones from the Campanian-Maastrichtian of the North America and the southern hemisphere (summarized in Druckenmiller and Russell, 2009; Schmeisser McKean and Gillette, 2012).

The fossil record of Late Cretaceous polycotyliids is geographically and stratigraphically sparse and uneven outside the WIS, and the polycotyliid remains from Japanese Cretaceous are important to understand the global distribution of the group. For example, the Cenomanian occurrence of an indeterminate polycotyliid (Sato and Storrs, 2000) and the Turonian age of HMG-357 indicate that polycotyliids crossed the Cenomanian-Turonian (CT) boundary in the northwestern Pacific as they did in the Western Interior Seaway, indicating the survival was not a local phenomenon restricted to the latter. No other Late Cretaceous polycotyliid localities in the Pacific have a stratigraphic range across the boundary.

In the Yezo Group of Japan and Russian Far East, CT boundary events such as faunal turnover among shelled molluscs (ammonoids, inoceramids) and some microfossils, as well as the excursion of carbon isotope ratio, are recognized, and their

causal relationship with an oceanic anoxic event (OAE2) has been debated (e.g., Toshimitsu *et al.*, 2003; Takashima *et al.*, 2004; Yazykova *et al.*, 2004; Takahashi, 2005; Kurihara *et al.*, 2012). Meanwhile, some groups appear to have been less affected. There are no marked extinction events among radiolarians and dinoflagellate cysts (Yazykova *et al.*, 2004; Kaneko and Hirano, 2005), and the coleoid cephalopods *Longibelus matsumotoi* and *Conotheuthis hayakawai* occur in Cenomanian and Turonian strata (Tanabe *et al.*, 2017). Sato and Tanabe (1998) reported the occurrence of a Cenomanian polycotyloid skeleton which contains many jaw apparatus of ammonoids as its stomach contents. Most ammonoid species went extinct at the CT boundary just to be replaced with other new species in the Turonian (Toshimitsu *et al.*, 2003). Although the number and quality of Yezo plesiosaur specimens are not sufficient to analyze changes at lower taxonomic levels as in these invertebrates, they do demonstrate the survival of the clade across the C/T boundary, thanks to the continuous stratigraphic sequence with fine biostratigraphic resolution.

Ontogenetic stages and aquatic adaptation inferred from bone histology

Ontogeny affects morphology and various other aspects of an animal, and the importance of assessing the growth stage of studied specimen(s) cannot be

over-emphasized. However, growth stages are only roughly estimated for large fossil vertebrates, because their remains are often fragmentary and/or rare, and it is hard to document an ontogenetic sequence. Here we assess the growth stage of HMG-357 based on the osteological and histological features.

Unlike dinosaurs for which various criteria to distinguish ontogenetic stages have been proposed (summarized in Hone *et al.*, 2016), there are very few previous studies for plesiosaurs. Brown (1981: 255) distinguished “juvenile”, “adult”, and “old adult” individuals of plesiosaurs based on osteological characters. An individual is “juvenile” if the neural arches and centra are not fused; it is “adult” if they are fused, and “old adult” if the individual exhibits additional characters indicative of advanced ossification. As Brown himself clearly indicated, these terms should be always used with quotation marks to indicate their special meanings which do not necessary correspond to the biological age or maturity. Unfortunately this practice is not strictly followed, and it is sometimes unclear whether the distinction of juvenile and adult is based on the criterion set by Brown or not (e.g., Wiffen *et al.*, 1995; Liebe and Hurum, 2012).

Brown’s criterion has been widely used in the description of plesiosaurian specimens, probably because it is so practical; vertebrae are commonly found and easily

identified as plesiosaurian. At the same time, it is quite approximate, in particular for the distinction of “adult” and “old adult” specimens. Ontogenetic sequence of ossification remains unknown for plesiosaurs, and it is hard to judge if a particular character of ossification appears earlier or later than other features. In the first place, the sequence of the closure of neurocentral sutures within the vertebral column (e.g., Brochu, 1996; Hone *et al.*, 2016) has not been established to show if there is a consistent pattern within the Plesiosauria or subgroups, so even the distinction of “juvenile” and “adult” is challenged if the suture is partially closed within an individual. It is practically impossible to distinguish “adult” and “old adult” individuals for the fragmentary specimens in which additional characters indicative of advanced ossification cannot be confirmed.

In the case of HMG-357, the closure and complete obliteration of the neurocentral suture indicates it does not represent a “juvenile” *sensu* Brown. The interclavicle and clavicles are fused, leaving partially obliterated sutures, and this may be taken as an evidence of advanced ossification at “old adult” level. These bones are fused but sutures are clearly visible at least in one “juvenile” *Trinacromerum* specimen (the holotype of *T. “willistoni”* Riggs 1944; *T. bentonianum* in Carpenter 1996), and they are at least partially visible in several polycotyloid specimens in which neurocentral

sutures are closed (e.g., Sato, 2005; Albright *et al.*, 2007b).

The parallel-fibered avascular bone observed in HMG-357 (Figure 7G) can be interpreted as a sign of slow periosteal growth immediately before death. Woven-fibered tissue with plexiform or radial vascular canals have been observed in the juvenile and subadult individuals of various non-polycotyloid plesiosaurs and “plesosaurid” (see Introduction) plesiosaurs (Wiffen *et al.*, 1995; Fostowicz-Frelik and Gaździcki, 2001; Liebe and Hurum, 2012), suggesting relatively rapid bone deposition (Huttenlocker *et al.*, 2013). Assuming that rapid deposition of bone tissue also occurred in an early ontogenetic stage of polycotyloid plesiosaurs, the peripheral bone tissue in HMG-357 may indicate slowed deposition at a late ontogenetic stage of the individual.

Given that the degree of remodeling is mostly related with skeletal maturity in tetrapods such as dinosaurs, marine reptiles, and terrestrial mammals (Zug *et al.*, 1986; Wiffen *et al.*, 1995; Klein and Sander, 2008; Mitchell *et al.*, 2017), the extensive remodeling of the rib may suggest that HMG-357 have reached skeletal maturity. In addition, although obscured by the extensive remodeling, the presence of the peripheral bone tissue which resembles an EFS implies an effective cessation of any significant periosteal growth of the bone in HMG-357 (e.g., Erickson, 2005; Woodward *et al.*, 2011).

The extensive spongiosa and thin compacta in the studied HMG ribs represents an osteoporotic-like condition (Ricqlès and Buffrénil, 2001), which has been reported in highly aquatic amniotes including extinct taxa such as ichthyosaurs (Houssaye *et al.*, 2014; Houssaye *et al.*, 2016; Nakajima *et al.*, 2014) and mosasaurs (Houssaye *et al.*, 2013). Prominence of the erosion spaces including the Howship's lacunae, suggests ongoing osteoclast activity and intense resorption activity. In extant taxa, active swimmers such as cetacean and pinnipeds displays a similar microanatomical features (notably the spongy inner organization) requiring efficient swimming abilities (e.g. manoeuvrability, speed) and relying on a hydrodynamic buoyancy and body trim control (Ricqlès and Buffrénil, 2001; Houssaye, 2009). Therefore, these results on HMG-357 suggest that this polycotyloid plesiosaur has acquired highly aquatic adaptation in bone microstructure.

In summary, osteological features indicate that HMG-357 represents an “old adult” *sensu* Brown (1981), in which the periosteal deposition of bone tissue was probably slowed by maturity at least in this part of the skeleton. The microscopic features also exhibit an osteoporotic-like condition, suggesting that polycotyloid plesiosaurs were highly aquatic animals.

Conclusions

HMG-357 represents an indeterminate polycotyloid plesiosaur from the Upper Cretaceous Yezo Group in Hokkaido, Japan. Its stratigraphic origin is estimated to be the upper middle to lower upper Turonian, and the Turonian occurrence demonstrates the survival of the polycotyloids across the Cenomanian-Turonian boundary in northwestern Pacific. The specimen consists of five vertebrae and ribs at the base of the neck, clavicular arch, and a scapular blade, and the ribs were subjected to the first detailed histological study of the Polycotyloidae. The complete closure of the neurocentral suture and partial obliteration of the clavicular sutures indicates that the individual reached an advanced stage of ossification. Parallel-fibered tissue and a possible EFS in the rib are signs of slowed growth, and osteoporotic-like condition suggests that this polycotyloid was highly adapted to life in water.

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Figure and Table captions

Figure 1. Locality map and stratigraphy of HMG-357. **A**, map of Hokkaido with a star indicating the fossil locality and grey areas the distribution of the Yezo Group; **B**, details of the now-submerged locality area: Mm-o refers to local stratigraphic units, Ng to Neogene, Pg to Paleogene; **C**, local stratigraphy with a star indicating HMG-357 horizon. Geological map based on Tsushima *et al.*, 1958. Timescale follows Cohen *et al.* (2013).

Figure 2. Photograph (**A**) and interpretation (**B**) of the left lateral view of the five vertebrae of HMG-357 in articulation, and anterior (**C**), posterior (**D**) and ventral (**E**) views of the second vertebra. Hatching indicates damaged surface, and the open-circle-and-dot pattern marks matrix/adhesive in this and following figures. Abbreviations: rf, rib facet; tp, transverse process.

Figure 3. Photographs (**A to I**) and interpretation (**J to R**) of the ribs of HMG-357. **A and J**, dorsal (?) view of the 1st right rib (#11); **B and K**, dorso-posterior view of the 2nd right(?) rib (#10); **C and L**, posterior (?) view of the 3rd left

rib (#12); proximal (**D and M**), anterior (**E and N**), posterior (**F and O**) views of the 4th left rib (#7); posterodorsal (**G and P**) and anterior (**H and Q**) views of the 4th right rib (#15); **I and R**, posterior view of the 5th left rib (#13).

Figure 4. Photograph (**A to C**) and interpretation (**D to F**) of the clavicular arch of HMG-357 in anterior (**A, D**), ventral (**B, E**), and dorsal or visceral (**C, F**) views. Abbreviations: cl, clavicle; frag, fragmentary; icf, interclavicular foramen; icl, interclavicle; l, left; r, right.

Figure 5. Photograph (**A, B**) and interpretation (**C, D**) of the dorsal blade of the right (?) scapula of HMG-357 in lateral (**A, C**) and medial (**B, D**) views.

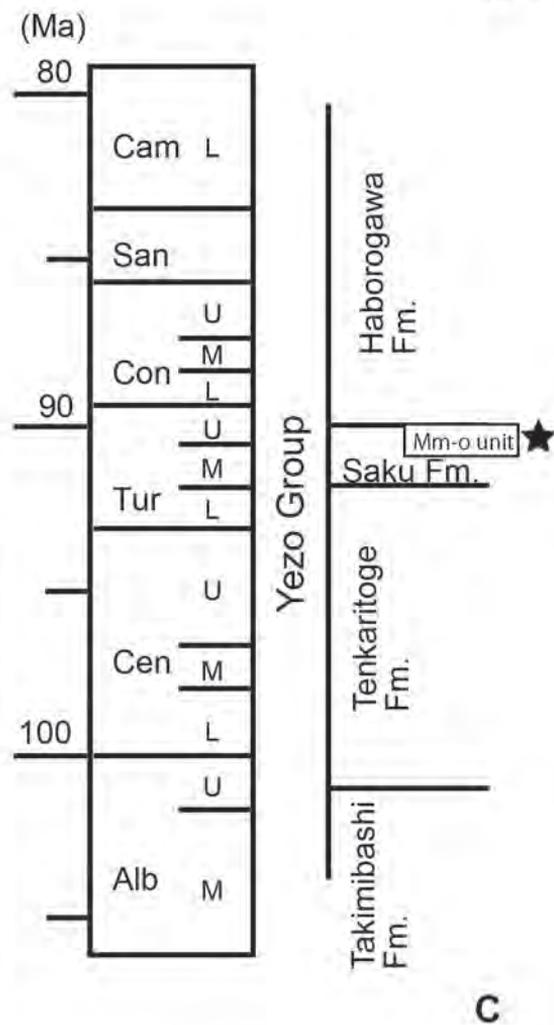
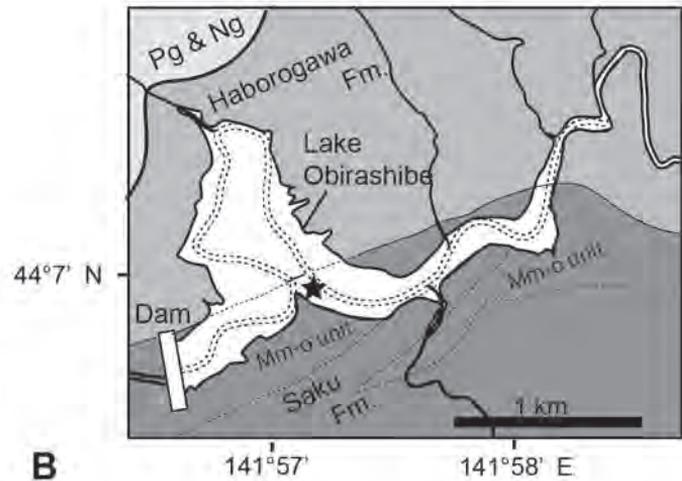
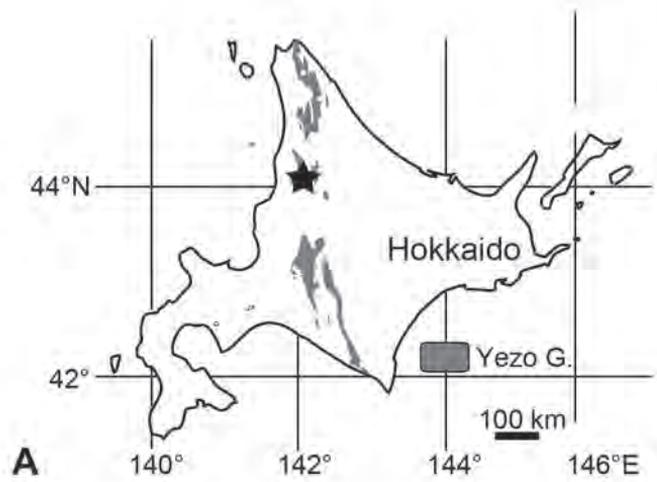
Figure 6. CT images of the proximal (**A**) and midshaft (**B**) portions of the left (?) antermost dorsal rib (#7) of HMG-357.

Figure 7. Histological thin sections of the right (?) antermost dorsal rib (#15) of HMG-357. **A**, longitudinal section of the proximal portion under natural transmitted light, with square D indicating the location of the close-up image in

D of this figure; **B and C**, transverse sections (B is a few millimeters more distal than C) under natural transmitted light, with squares E to I indicating locations of close-up images in E to I of this figure; **D to I**, close-ups under polarized microscope showing fiber bundles and the bands of alternating light and dark tissue (D), Haversian tissue (E), Howship's lacunae (arrow heads, F), primary parallel-fibered bone tissue (arrow head, G), secondary lamellar bone tissue (H), and avascular bone tissue with possible lines of arrested growth (arrow head, I).

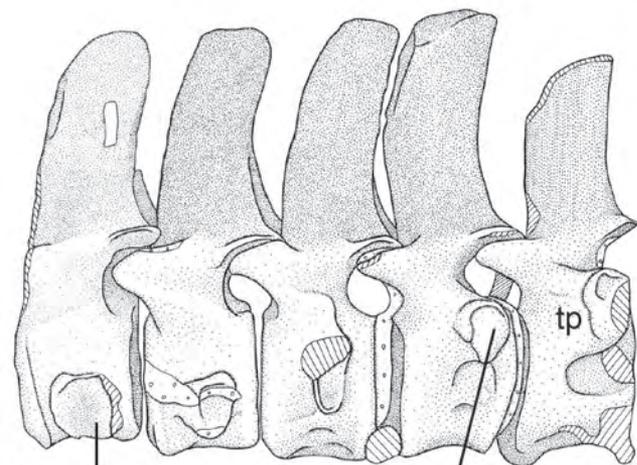
Table 1. Vertebral measurements of HMG-357. Length (L), height (H), and width (W) of the centrum in mm. Subscripts "d" and "e" refer to distorted centrum and estimated length, respectively.

Fig. 1.



**A**

100 mm

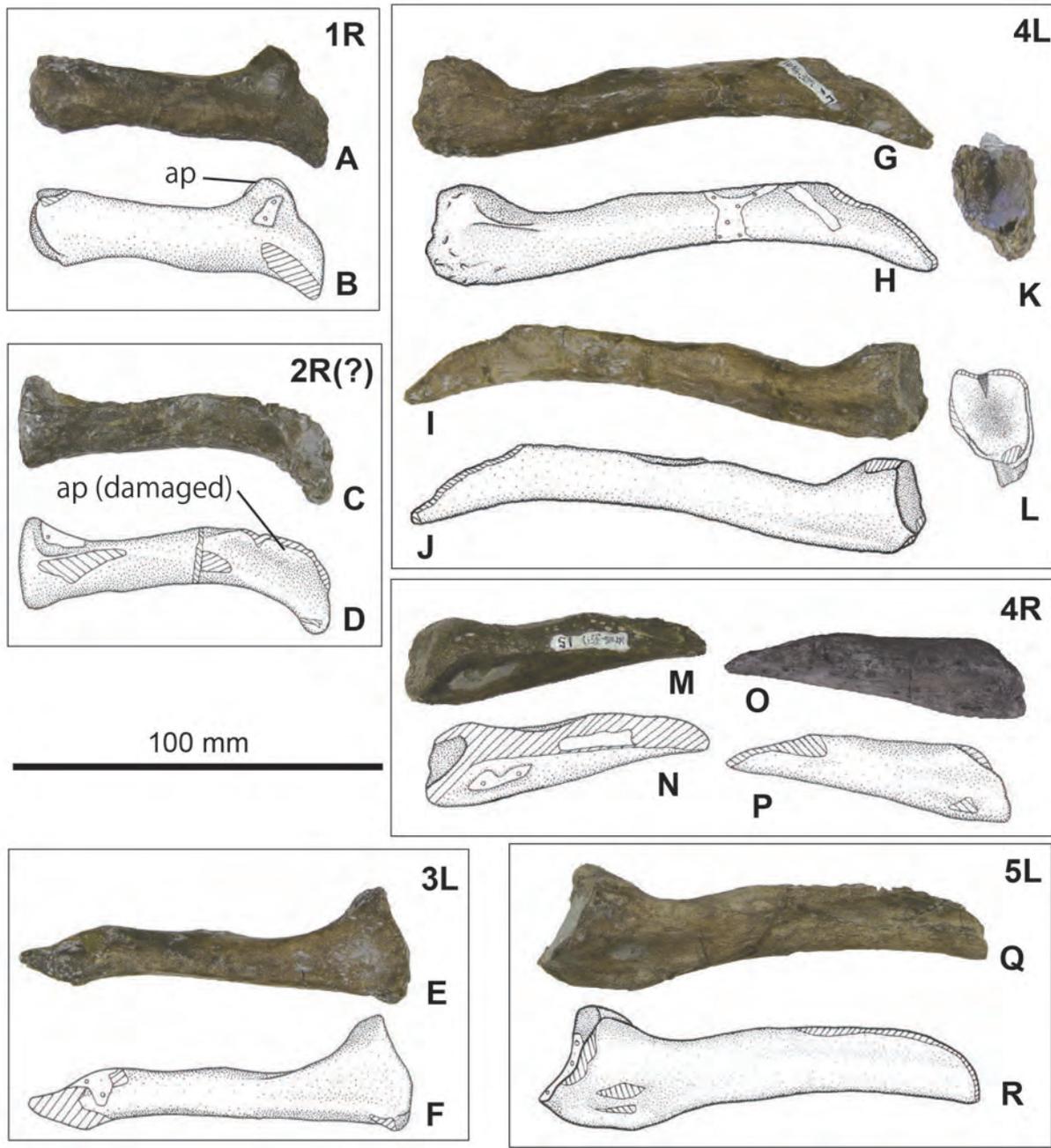
**B**

rf

rf

tp

**C****D****E**



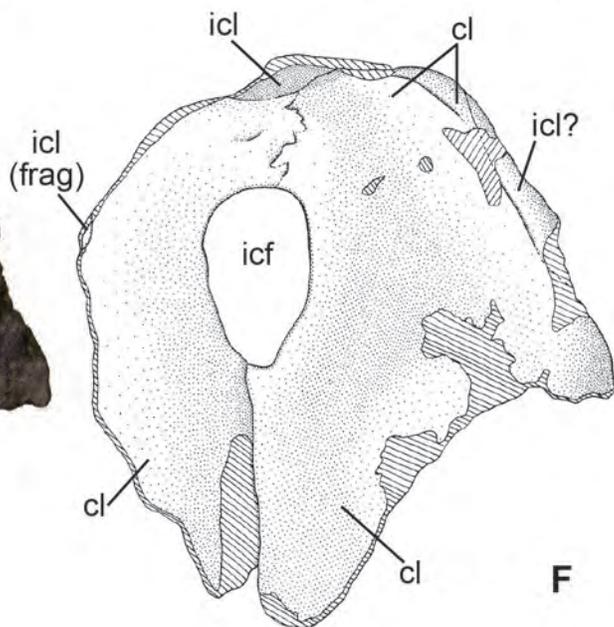
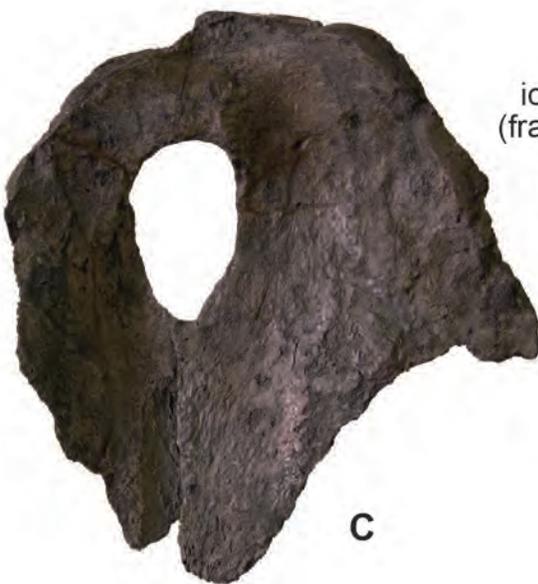
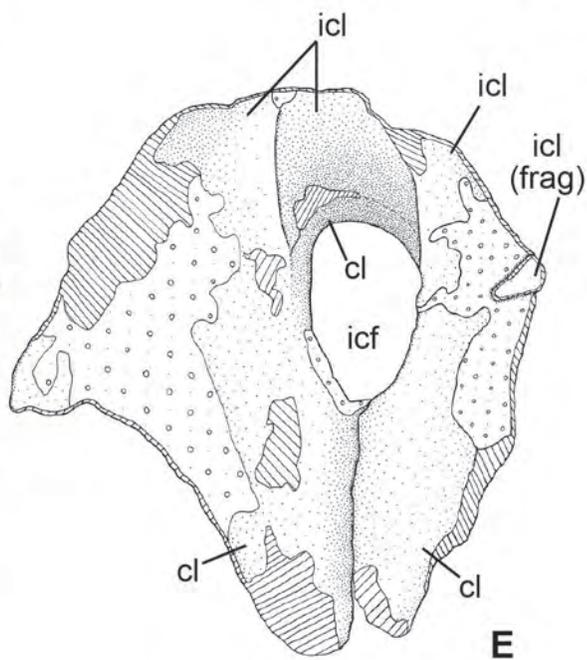
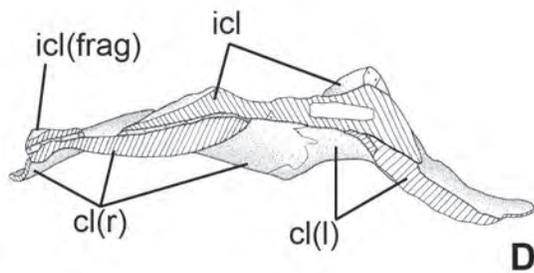


Fig. 5

half page width

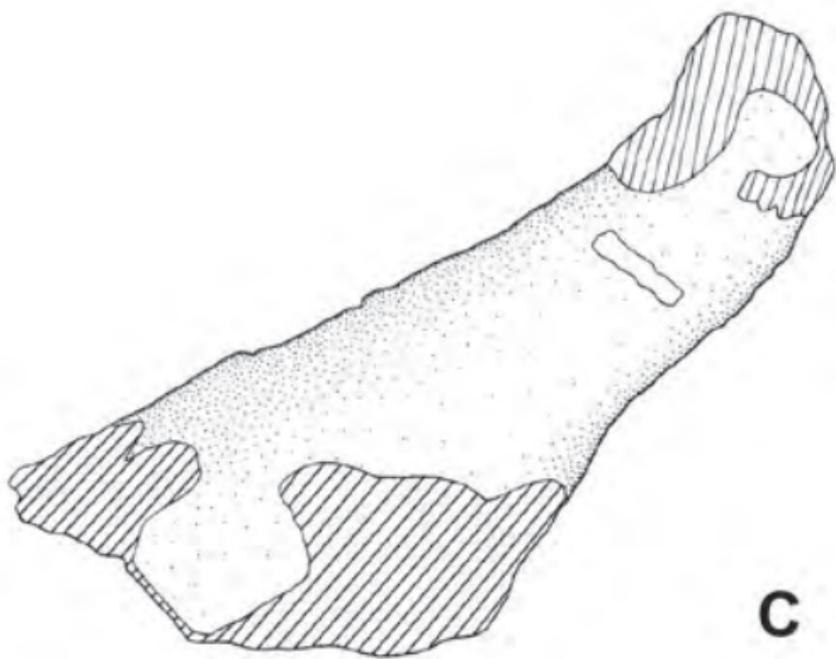


A

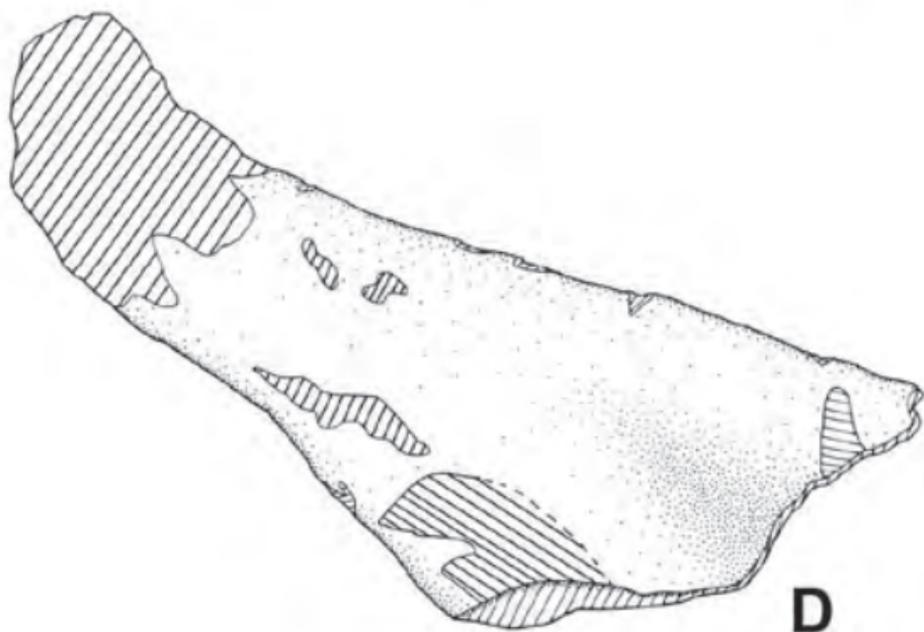
100 mm



B

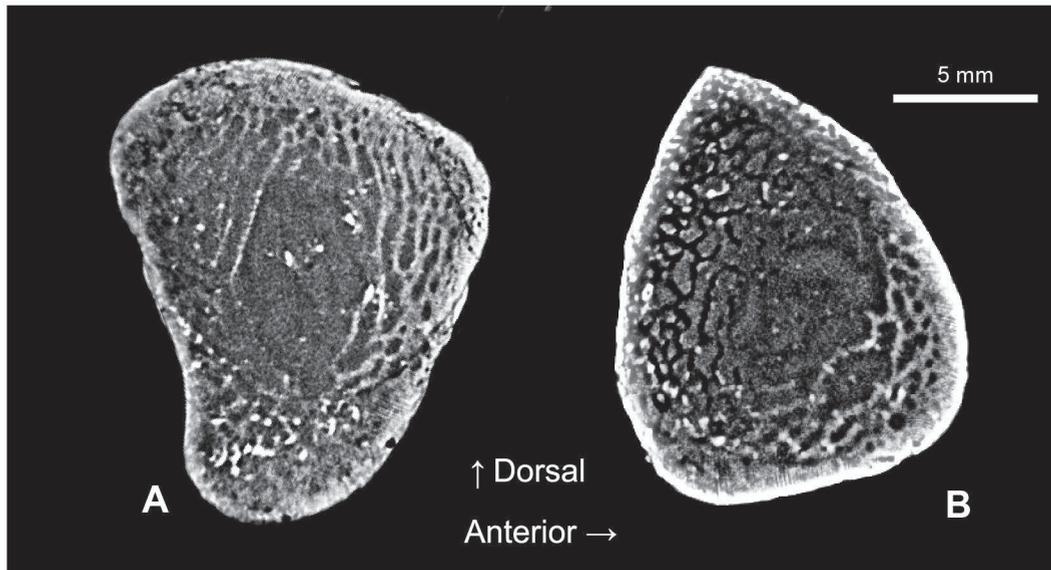


C



D

Fig 6



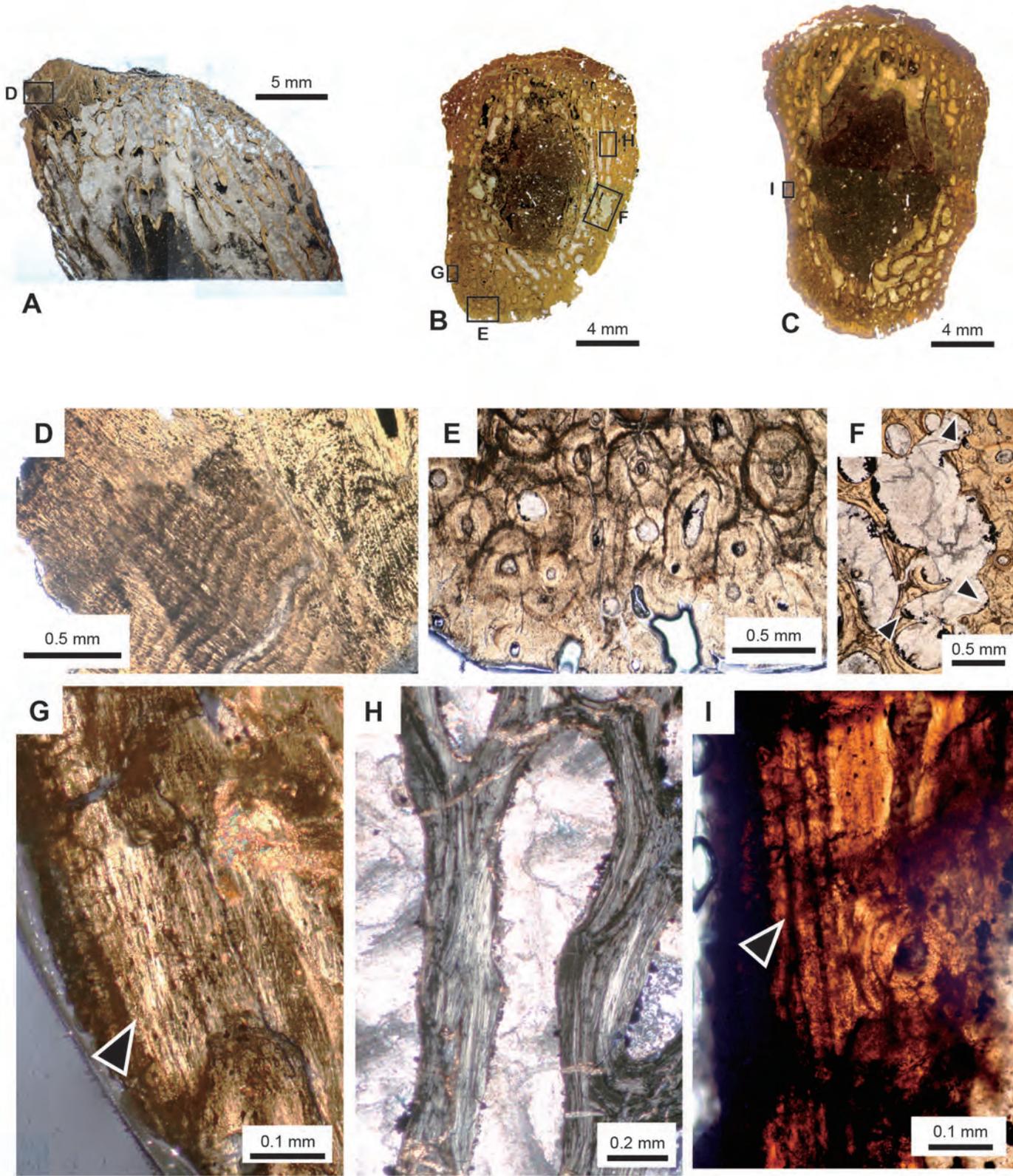


Table 1

	L	H	W
1 (anteromost)	42.9 _e	52.9	68.8
2	41.4	54.3	68.9
3	39.0	57.2	67.8
4	40.9	56.3	70.4
5	48.0 _d	61.8 _e	64.8

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