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Article

Ontogeny and variation of four species of Upper Cretaceous barroisiceratine ammonoids *Yabeiceras* and *Forresteria* by means of X-ray microcomputed tomography

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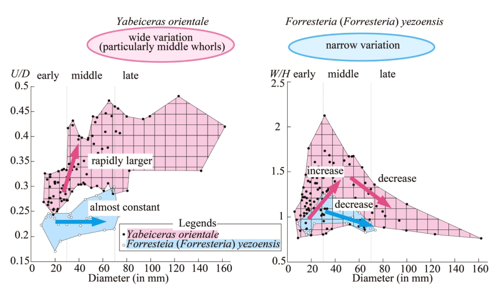
ABSTRACT

Ontogeny and variation of the three barroisiceratine ammonoids *Yabeiceras orientale* Tokunaga and Shimizu, *Yabeiceras* cf. *manasoaense* Collignon, and *Forresteria* (*F.*) *yezoensis* Matsumoto were studied by means of X-ray micro-computer tomography based on the well-preserved material from the probable upper Turonian Obisagawa Member of the Ashizawa Formation, Futaba Group in Fukushima Prefecture, northeast Japan. Specimens of *Y. orientale*, *F.* (*F.*) *yezoensis*, and *F.* (*F.*) *muramotoi* from the Coniacian of the Yezo Group in Mikasa City, central Hokkaido, northern Japan were also examined for comparison. As the shell of *Y. orientale* grows, the relative umbilical size (*U*/*D*) becomes rapidly larger at shell diameter (*D*) of 30–50 mm, and the relative whorl thickness (*W*/*H*) first increases to the stage of 30–50 mm in *D* and then decreases gradually. The growth rate of whorl width in costal section (*W*) is relatively constant up to a diameter of 30–50 mm and then decreases gradually, whereas that of whorl height (*H*) is relatively constant throughout ontogeny. The intraspecific variations in *U/D* and *W/H* in middle whorls are wider than those in early and late whorls, as evidenced by the data from the present and previous studies. As the shell of *F.* (*F.*) *yezoensis* grows, *U/D* is almost constant, and *W/H* decreases gradually after *D* exceeds 30–50 mm. *Forresteria* (*F.*) *yezoensis* shows relatively narrow intraspecific variations in relative umbilical size and whorl thickness, as evidenced by the measurement data from the present and previous studies.



Keywords: Ammonoida, Cretaceous, *Forresteria*, Futaba Group, intraspecific variation, *Yabeiceras*

Introduction

Ammonoids display profound intraspecific morphological variability in their shells (e.g. De Baets *et al.*, 2015). These intraspecific variations have been discussed in numerous studies on shell shape (e.g. Reeside and Cobban, 1960; Matsumoto, 1965; Korn and Klug, 2007; Wilmsen and Mosavinia, 2011), suture lines (e.g. Kraft *et al.*, 2008; Yacobucci and Manship, 2011; Aiba and Wani, 2016; Iwasaki *et al.*, 2020), color patterns (e.g. Mapes and Larson, 2015), and soft tissues (e.g. Klug *et al.*, 2012). These studies focusing on variations argued that wide intraspecific variabilities of shell and soft tissue morphologies are attributed to different regions (e.g. Dietl, 1978), paleoenvironments (e.g. Wilmsen and Mosavinia, 2011), hatchling size (Landman, 1987), septal spacing stress (e.g. Kraft *et al.*, 2008), and sexual dimorphism (Zatoń, 2008; Shigeta *et al.*, 2023). The mode and range of intraspecific variation might change during ontogeny, which may be particularly important for understanding the modes of growth, paleobiology, and paleoecology of ammonoids (De Baets *et al.*, 2015). However, studies on intraspecific variations during ontogeny have been limited due to the need for numerous well-preserved specimens.

Yabeiceras orientale, described by Tokunaga and

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Shimizu (1926) from the Upper Cretaceous Futaba Group in Sakurazawa Valley, Oriki, Hirono Town, Fukushima Prefecture, Northeast Japan, is an index fossil that exhibits its large intraspecific variation (Matsumoto *et al*., 1964; Matsumoto, 1969; Kennedy *et al*., 1983; Futakami *et al*., 2016; Futakami and Suzuki, 2018). However, ontogenetic shell development and intraspecific variation in shell morphology based on many specimens have not been studied. Kennedy *et al*. (1983) suggested that *Yabeiceras* evolved from *Forresteria*. However, comparisons of ontogenetic patterns and variation of shell form and ornament between species of the two genera have not yet been examined.

In this paper, we describe the ontogenetic shell development of *Yabeiceras orientale* based mainly on the specimens newly collected from the Sakurazawa Valley (type locality) by coauthor N. Watanabe. We also describe the ontogenetic shell development of *Y*. cf. *manasoaense* Collignon, 1965 and *Forresteria* (*Forresteria*) *yezoensis* Matsumoto, 1969 from the same locality as *Y. orientale* in the Sakurazawa Valley, and *Y. orientale*, *F*. (*F*.) *yezoensis*, and *F*. (*F*.) *muramotoi* Matsumoto, 1969 from the Yezo Group in Hokkaido, Northeast Japan for comparison with *Y. orientale* from the Sakurazawa Valley. In addition, we discuss intraspecific variation for the ontogenetic change of shell shape of *Y. orientale* and *F*. (*F*.) *yezoensis*.

Geological setting

The Futaba and Yezo groups in Japan are Cretaceous strata that include many ammonoids (e.g. Tokunaga and Shimizu, 1926; Saito, 1961, 1962; Shigeta, 2001). The specimens used in this study were from these groups.

The Upper Cretaceous Futaba Group comprises mainly fluvial to shallow marine deposits and is distributed in the Iwaki area of Fukushima Prefecture, northern Honshu, Japan (Figure 1). The group nonconformably overlies the Early Cretaceous intrusive granitic rocks (126–97.4 Ma: Kubo and Yamamoto, 1990) and is clino-unconformably overlain by the Paleogene Shiramizu Group (Otuka, 1939). The total thickness of this group is approximately 350 m (Ando *et al*., 1995). The lithofacies of this group are composed mainly of sandstone, siltstone, and conglomerates. The strata strike N5–25°E and dip 10–20°E.

In ascending order, the Futaba Group is divided into the Ashizawa, Kasamatsu, and Tamayama formations. The Ashizawa Formation is subdivided into the Asamigawa and Obisagawa members in ascending order (Kubo *et al*., 2002).

The Obisagawa Member is primarily composed of siltstone and fine sandstone that are frequently interbedded with thin calcareous conglomerate beds including fossils of vertebrates (Takakuwa *et al*., 2018), bivalves

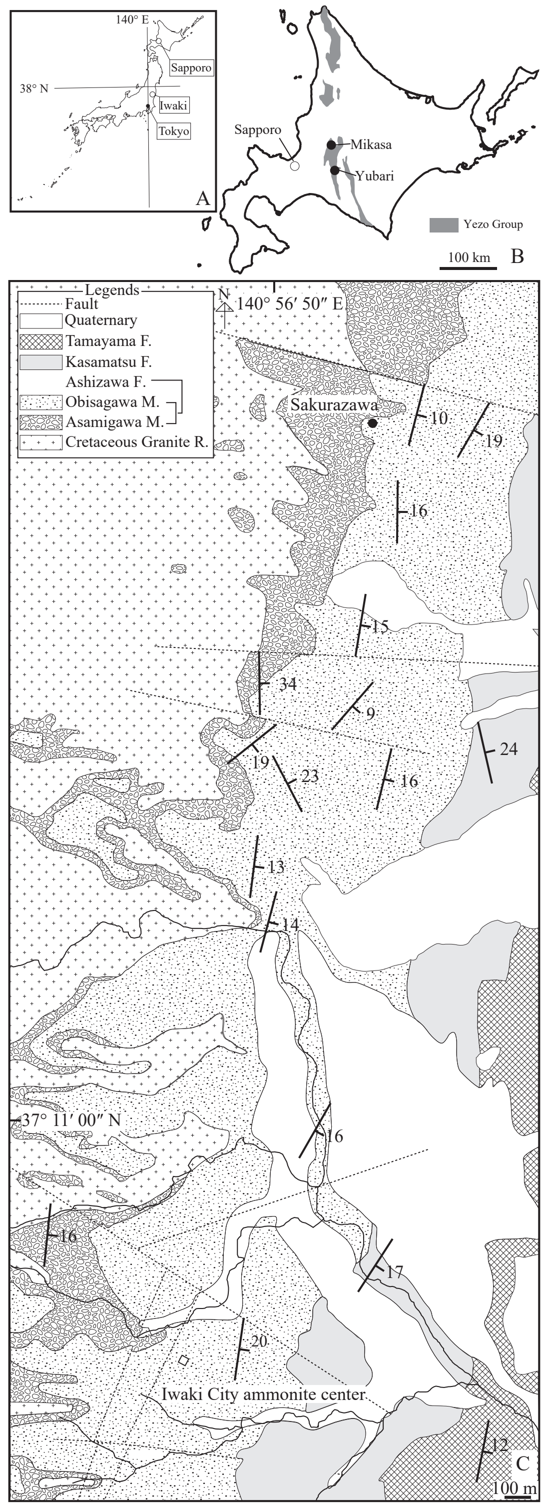

Figure 1. Index map of Japan (**A**) showing the location of Iwaki area, northeast Honshu. Map of Hokkaido (**B**) showing Miksa and Yubari areas from which the examined specimens were recovered (outcropping areas of the Yezo Group are shaded; modified from Takashima *et al*., 2004, fig. 1). Geological map of Iwaki area (**C**), showing the locality of the examined specimens in the Sakurazawa Valley (after Kubo *et al*., 2002).

(Inose and Watanabe, 2020), gastropods, and ammonoids (Tokunaga and Shimizu, 1926; Saito, 1962; Matsumoto *et al*., 1964; Futakami *et al*., 2016). *Yabeiceras orientale, Y*. cf. *manasoaense*, and *Forresteria* (*Forresteria*) *yezoensis* specimens used in the present study were obtained from calcareous conglomerates. Fine sandstone yields several types of fossils, such as vertebrates, bivalves, gastropods, and ammonoids, including *Y. orientale* (Futakami and Suzuki, 2018; Muramiya *et al*., 2022), and is used for digging at the Iwaki City Ammonite Center (e.g. Omori *et al.*, 2023). The thickness changes laterally by 60–170 m (Kubo *et al*., 2002), and the sedimentary environment ranges from the upper shoreface to the inner shelf (Ando *et al*., 1995). Kubo *et al*. (2002) correlated this member with the lower? to middle Coniacian. However, the lower part of the member, including the outcrop in the Sakurazawa Valley, that yielded the ammonoid specimens examined, was correlated with the upper Turonian based on the co-occurred inoceramids (Inose *et al*., 2024).

The Yezo Group is widely distributed in a 350 km long band running in a north-south direction in the central portion of Hokkaido and extends to the Sakhalin region, Russia (Figure 1; e.g. Takashima *et al*., 2004; Maeda and Shigeta, 2005). The group is correlated from the Aptian to the base of the Paleogene (e.g. Takashima *et al*., 2004). Numerous fossils, including ammonoids, have been reported by this group (e.g. Shigeta, 2001, 2021, 2024; Takashima *et al.*, 2004; Maeda and Shigeta, 2005; Shigeta and Maeda, 2023; Shigeta *et al*., 2023). One specimen of *Yabeiceras orientale* (NMNS PM17354) and one specimen of *Forresteria* (*Forresteria*) *yezoensis* (NMNS PM16870) were obtained from the group in Yubari City, Hokkaido. In addition, one specimen each of *F*. (*F*.) *muramotoi* (NMNS PM16869) and *F*. (*F*.) *yezoensis* (NMNS PM17044) was obtained from the group in Mikasa City, Hokkaido. These specimens were deposited in the Kawashita collection at the National Museum of Nature and Science, Tokyo (Shigeta, 2001). According to Matsumoto (1969), these ammonoids came from the Coniacian.

Material and methods

Six specimens of *Yabeiceras orientale* (HBE.P-103–105, 107–109) among the newly collected specimens, seven specimens of *Y. orientale* (HBE.P-101, NMNS PM 35062, 35064, 35065 described by Futakami *et al*., 2016), one specimen of *Y*. cf. *manasoaense* (HBE.P-106) and two specimens of *Forresteria* (*Forresteria*) *yezoensis* (HBE.P-112, 113) were subjected to a biometric analysis of the shell morphology (Figures 2–8). These specimens were recovered from a calcareous conglomerate bed in the lowermost part of the Obisagawa Member in the Sakurazawa Valley in Oriki, Hirono Town, Fukushima Prefecture, where the type locality of *Y*. *orientale* is located (Figure 1C). In addition, one specimen of *Y*. *orientale* (NMNS PM17354), one specimen of *F*. (*F*.) *muramotoi* (NMNS PM16869), and two specimens of *F*. (*F*.) *yezoensis* (NMNS PM16870, 17044) from the Yezo Group were also examined (Figures 5, 7–10).

We scanned 16 specimens using X-ray computed tomography (Tesco Corporation, TXS-CT300 model at the Fukushima Technology Centre; voxel size of 20–200 μm, 700–2000 slides, acceleration voltage of 100–300 kV, and current of 100–230 μA depending on the size of the specimens); six standard geometric parameters of the shell, namely, shell diameter (*D*), umbilical diameter (*U*), whorl height (*H*), aperture height (*h*), whorl width in costal section (*W*), and that in intercostal section (*w*), were measured every one-eighth whorl using an analysis software (TomoShop, Midorino Research Corporation; Figure 11). Subsequently, the five parameters (*U*/*D*, *W*/*H, w/H, whorl expansion rate (WER, (D/(D-h))^2), imprint zone rate (IZR, (H-h)/H)* were calculated. Six parameters (*D*, *U*, *H*, *h*, *W*, *w*) were also measured using vernier calipers for reducing errors. Unfortunately, only one specimen of *Forresteria* (*Forresteria*) *yezoensis* (NMNS PM16870) was measured using Vernier calipers because CT data were unavailable.

Institutional abbreviations.—**BMNH**, British Museum (Natural History), London, United Kingdom; **GK**, Kyushu University Museum, Fukuoka, Japan; **HBE**, Hirono Town Board of Education, Hirono, Fukushima, Japan; **I**, Iwaki City Board of Education, Iwaki, Fukushima, Japan; **IGPS**, Institute of Geology and Paleontology, Tohoku University, Sendai, Miyagi, Japan; **MB.C.**, Natural History Museum, Berlin, Germany; **NMNS**, National Museum of Nature and Science, Tsukuba, Ibaraki, Japan.

Paleontological description

A more detailed taxonomic nomenclature for ammonoids followed by Hoffmann *et al*. (2022). The systematic descriptions basically followed the classifications established by Klug *et al*. (2015a) except for the width of umbilicus. The description of width of umbilicus followed by Matsumoto (1954, p. 246) and Haggart (1989, table 8.1). Morphological terms are those used by Arkell (1957) for Mesozoic Ammonoida.

Family Collignoniceratidae Wright and Wright, 1951
Subfamily Barroisiceratinae Basse, 1947
Genus ***Yabeiceras*** Tokunaga and Shimizu, 1926

Type species.—Yabeiceras orientale Tokunaga and Shimizu, 1926.

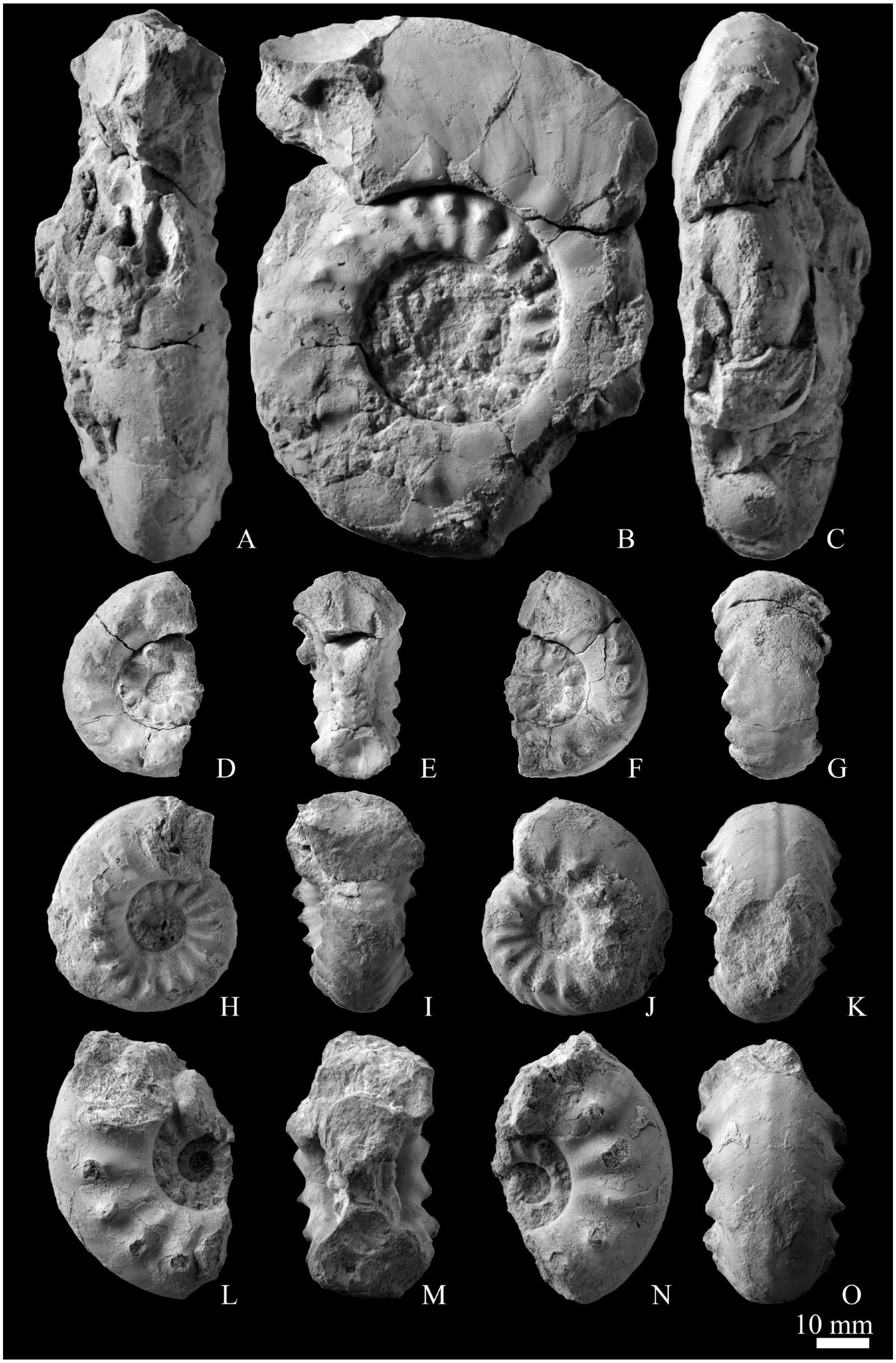

Figure 2. *Yabeiceras orientale* Tokunaga and Shimizu, 1926 from the Futaba Group. **A–C,** HBE.P-101; **D–G,** HBE.P-103; **H–K,** HBE.P-104; **L–O,** HBE.P-105. Left lateral (D, H, L), apertural (A, E, I, M), right lateral (B, F, J, N), and ventral (C, G, K, O) views. All photos were taken after whitening with ammonium chlorite.

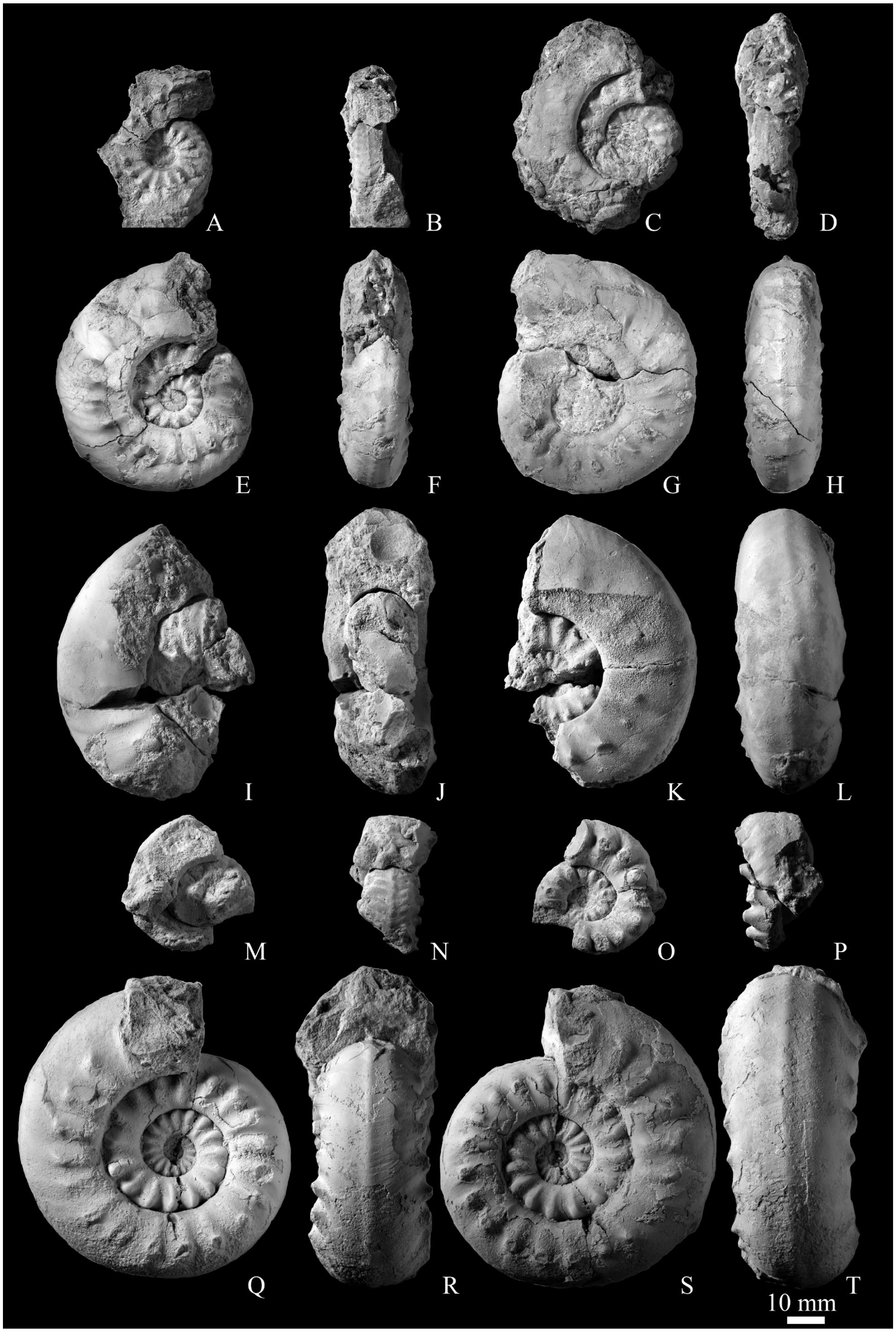

Figure 3. *Yabeiceras orientale* Tokunaga and Shimizu, 1926 from the Futaba Group. **A, B,** HBE.P-107; **C, D,** HBE.P-108; **E–H,** HBE.P-109; **I–L,** NMNS PM35062; **M–P,** NMNS PM35064; **Q–T,** NMNS PM35065. Left lateral (A, C, E, I, M, Q), apertural (B, D, F, J, N, R), right lateral (G, K, O, S), and ventral (H, L, P, T) views. All photos were taken after whitening with ammonium chlorite.

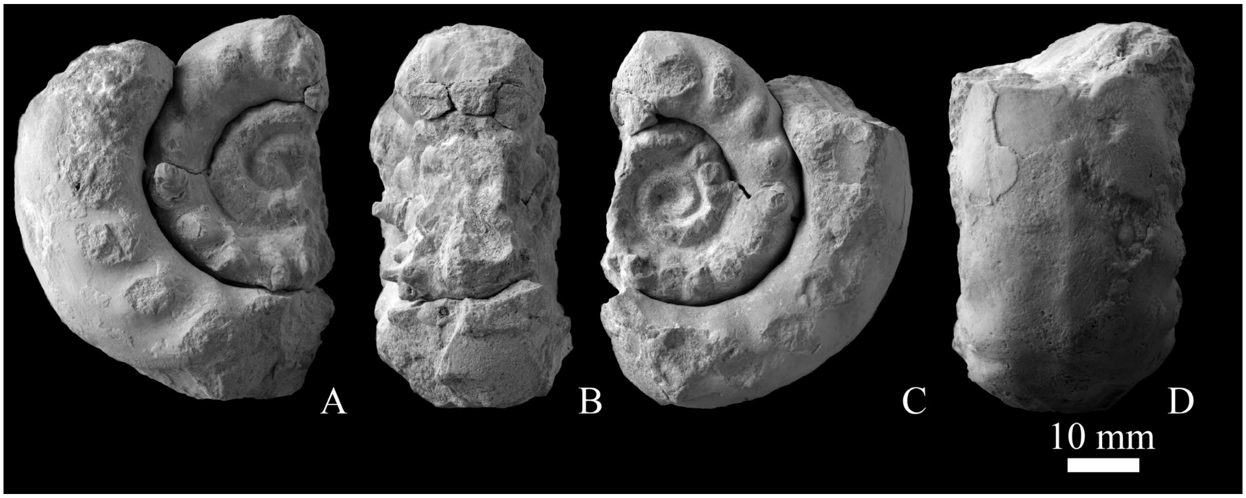

Figure 4. *Yabeiceras* cf. *manasoaense* Collignon, 1965 from the Futaba Group, HBE.P-106. **A,** left lateral view; **B,** Longitudinal view; **C,** right lateral view; **D,** ventral view. All photos were taken after whitening with ammonium chlorite.

Yabeiceras orientale Tokunaga and Shimizu, 1926

Figures 2, 3, 5A–K, 6A, 9

Yabeiceras orientale Tokunaga and Shimizu, 1926, p. 201, pl. 22, fig. 7, pl. 27, fig. 1a–c; Matsumoto *et al*., 1964, p. 323, pl. 48, figs. 1a–c, 2a–e, text-figs. 1a–d, 2a–e, 3; Matsumoto, 1969, p. 324, pl. 44, figs. 1, 2, pl. 45, fig. 1, text-figs. 12, 13; Kennedy *et al*., 1983, p. 295, figs. 41, 42G–I, 45; Futakami *et al*., 2016, p. 223, figs. 4–7, 8A–D; Futakami and Suzuki, 2018, p. 3, fig. 2.

Yabeiceras himuroi Tokunaga and Shimizu, 1926, p. 203, pl. 22, fig. 9, pl. 27, fig. 2a, b.

Yabeiceras cf. *orientale* Tokunaga and Shimizu, 1926, Kennedy *et al*., 1983, p. 302, fig. 42A–C.

Holotype.—Specimen described by Tokunaga and Shimizu (1926, pl. 27, fig. 1a–b). This specimen was destroyed by fire in 1944 (Matsumoto *et al*., 1964).

Neotype.—Specimen designated by Matsumoto *et al*. (1964, pl. 48, fig. 2a–e), is GK.H5556.

Material examined.—10 specimens (HBE.P-101, 103–105, 107–109, NMNS PM 35062, 35064, and 35065) from the Obisagawa Member of the Sakurazawa Valley in Oriki, Hirono Town, Fukushima Prefecture, and one specimen (NMNS PM17354) from the Yezo Group in Yubari City, Hokkaido, Japan (Figure 1). HBE.P-101, NMNS PM 35062, 35064, and 35065 were first described by Futakami *et al*. (2016).

Description.—Early whorls (up to approximately 30 mm in diameter): Evolute, weakly compressed to moderately depressed shell (*W*/*H* = 0.76–1.76) with arched venter, indistinct ventral shoulders, and slightly convex flanks at 10–20 mm in diameter. Umbilicus fairly narrow (*U*/*D* = 0.25–0.34) with a low, vertical wall. Whorl expansion rate is very low to extremely high (*WER* = 1.44–3.50) and the imprint zone rate is weakly embracing to very strongly embracing (*IZR* = 0.08–0.50). The ornamentation consists of prorsiradiate primary ribs and clavate tubercles at the mid-venter. As the shell grows, the relative umbilical size increases, and the whorl section becomes more depressed. The intraspecific variations of *U*/*D* and *W*/*H* at 30 mm diameter are approximately 0.28–0.34 and 1.03–1.76, respectively.

Middle whorls (approximately 30–70 mm in diameter): As the shell grows, the *U*/*D* becomes rapidly larger at a diameter of 30–50 mm. The whorl section becomes more depressed to 30–50 mm in diameter and subsequently becomes more compressed. The intraspecific variations of *U*/*D* and *W*/*H* at 40 mm and 60 mm diameter are approximately 0.30–0.39 and 0.89–1.47, and 0.29–0.45 and 0.90–1.55, respectively. Whorl expansion rate is moderate to extremely high (*WER* = 1.75–2.74) and imprint zone rate is weakly embracing to strongly embracing (*IZR* = 0.05–0.44). The ornamentation consists of strong conical mediolateral tubercles, prorsiradiate primary ribs, weak secondary ribs bifurcating from the mediolateral tubercles, and a weak mid-venter keel. The degree of ornamentation is the strongest at 40–50 mm diameters. The suture line is moderately incised using divided saddles (Figure 6A).

Late whorls (> approximately 70 mm in diameter): As the shell grows, *U*/*D* becomes even larger (*U*/*D* = 0.29–0.46), the whorl section becomes more compressed (*W*/*H* = 0.85–1.36), and the ornamentation becomes weakened except for growth lines. Whorl expansion rate is low to extremely high (*WER* = 1.74–2.61) and imprint zone rate is weakly embracing to moderately embracing (*IZR* = 0.14–0.29).

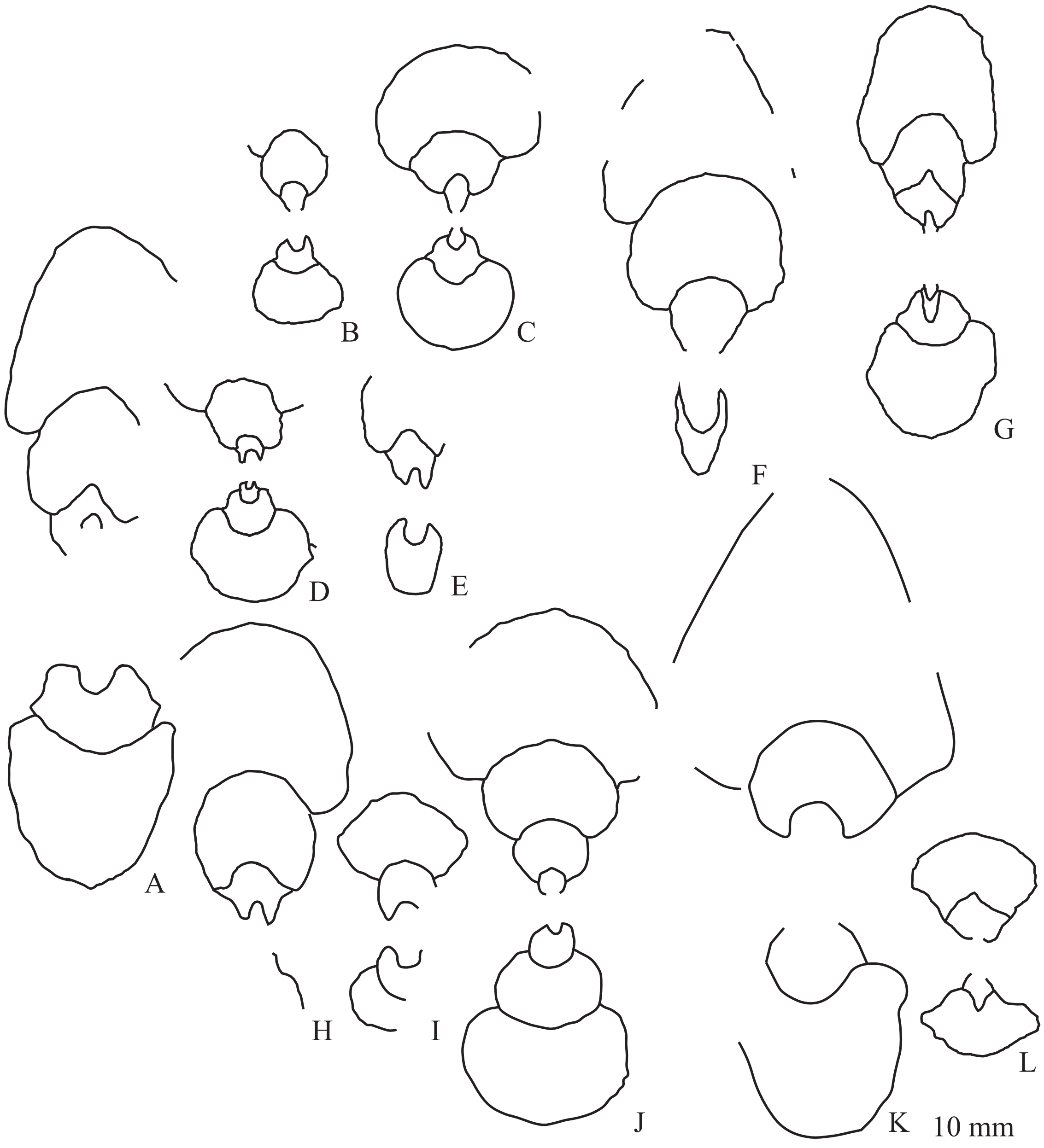

Figure 5. Whorl cross sections of *Yabeiceras orientale* Tokunaga and Shimizu, 1926 and *Y.* cf. *manasoaense* Collignon, 1965 based on CT data. **A**–**K,** *Y. orientale*; **L,** *Y.* cf. *manasoaense*. From the Futaba Group (A–J, L) and the Yezo Group (K). HBE.P-101 (A), HBE.P-103 (B), HBE.P-104 (C), HBE.P-105 (D), HBE.P-107(E), HBE.P-108 (F), HBE.P-109 (G), NMNS PM35062 (H), NMNS PM35064 (I), NMNS PM35065 (J), NMNS PM17354 (K), HBE.P-106 (L).

Remarks.—*Yabeiceras kotoi* Tokunaga and Shimizu, 1962 resembles *Y. orientale* in their ornamentation. Tokunaga and Shimizu (1926) distinguished *Y. kotoi* from *Y. orientale* based on the narrow umbilicus, compressed whorls, and different suture lines. The measurement data for *Y. kotoi* of *U/D* and *W/H* at a diameter of 80 mm were approximately 0.21 and 0.83, respectively (Tokunaga and Shimizu, 1926). Futakami *et al*. (2016) described one specimen from the same stratum, NMNS PM35066, as *Y. kotoi* based on its narrower umbilicus and compressed whorls. The measurement data for *Y. kotoi* with *U/D* at a diameter of 36.1 mm was approximately 0.20 (Futakami *et al*., 2016). Our *U/D* data for *Y. orientale* were limited to values > 0.25. These data suggest that this species can be distinguished from *Y. orientale* based on its narrow umbilicus.

Occurrence.—According to Futakami *et al*. (2016),

Figure 6. Suture lines of the specimens from the Futaba Group. **A,** *Yabeiceras orientale* Tokunaga and Shimizu, 1926, HBE.P-104, approximately 30 mm in diameter, approximately 14 mm in whorl height; **B,** *Forresteria* (*Forresteria*) *yezoensis* Matsumoto, 1969, HBE.P-113, approximately 50 mm in diameter, approximately 24 mm in whorl height. The arrow represents the siphuncle.

Yabeiceras orientale specimens were found in the Coniacian horizon of the Futaba Group. However, Inose *et al*. (2024) reported the co-occurrence of this species and the late Turonian inoceramids from the Obisagawa Member of the Ashizawa Formation in the Futaba Group. Therefore, this species appears to occur from the upper Turonian to the Coniacian in the Futaba Group. The present species has also been reported from the Coniacian of Hokkaido (Matsumoto, 1969) and South Africa (Kennedy *et al*., 1983).

Yabeiceras* cf. *manasoaense Collignon, 1965

Figures 4, 5L

Yabeiceras cf. *manasoaense* Collignon, 1965, Futakami *et al*., 2016, p. 230, figs. 6B, 7G.

Compare

Yabeiceras manasoaense Collignon, 1965, p. 84, pl. 452, fig. 1839; Matsumoto, 1971, p. 144, pl. 24, fig. 2; Klinger *et al*., 1976, p. 162, figs. 1–4; Kennedy *et al*., 1983, p. 311, figs. 47A, B, 51A–C; Wiese, 2000, p. 133, pl.2, fig. 5.

Material examined.—One specimen (HBE.P-106) from the Obisagawa Member of the Sakurazawa Valley in Oriki, Hirono Town, Fukushima Prefecture.

Description.—The specimen is moderate in size and comprises approximately half a whorl. Very evolute, moderately to strongly depressed shell (W/H = 1.67–2.51) with weakly arched venter and ventral shoulders. Umbilicus fairly wide (U/D = 0.46–0.49) with low, narrowly rounded wall. Whorl expansion rate is low to moderate (WER = 1.70–1.87) and imprint zone rate is weakly embracing to moderately embracing (IZR = 0.14–0.25). The ornamentation consists of strong conical mediolateral tubercles, prorsiradiate primary ribs, and a weak mid-venter keel. As the shell grows, the tubercles migrate from the mediolateral side toward the umbilical shoulders. The whorl section becomes more depressed to around 35 mm in diameter and subsequently becomes more compressed. The suture line is uncertain.

Remarks.—Futakami *et al*. (2016) described the specimen (I-424000) as *Yabeiceras* cf. *manasoaense* Collignon from the Futaba Group. Their specimen resembles HBE.P-106 concerning the position of the tubercles and umbilical size. HBE.P-106 has depressed whorl sections and a wide umbilicus, and is similar to the specimens of *Y. manasoaense* in the previous studies (Collignon, 1965; Matsumoto, 1971; Klinger *et al*., 1976; Kennedy *et al*., 1983; Wiese, 2000). However, we hesitated to classify it as this species because of the small specimen size.

Occurrence.—This species represented by a single specimen occurs in the upper Turonian to the Coniacian horizon of the Futaba Group.

Genus and Subgenus ***Forresteria*** Reeside, 1932

Type species.—*Barroisiceras* (*Forresteria*) *forresteri* Reeside (1932, p. 17; pl. 5, figs. 2–7), by the subsequent designation of Wright (1957, L432) = *Acanthoceras* (*Prionotropis*) *alluaudi* Boule *et al.* (1907, p. 32, pl. 8, figs. 6–7, text-fig. 17).

Forresteria* (*Forresteria*) *yezoensis Matsumoto, 1969

Figures 6B, 7, 8A–C

Forresteria (*Muramotoa*) *yezoensis* Matsumoto, 1969, p. 317, pl. 42, figs. 1, 2, text-figs. 9, 10.

Forresteria yezoensis Matsumoto, 1969, Shigeta, 2001, pl. 10, figs. 3, 4.

Holotype.—Specimen described by Matsumoto (1969), pl. 42, fig. 2 a–d, text-figs. 9, 10), is GK.H5462.

Material examined.—One specimen (NMNS PM16870) from the Yezo Group in Yubari City; one specimen (NMNS PM17044) from the Yezo Group in Mikasa City, Hokkaido; and two specimens (HBE.P-112, 113) from the Obisagawa Member, Ashizawa Formation, Futaba Group in the Sakurazawa Valley, Hirono Town, Fukushima Prefecture, Japan. NMNS PM16870 was first reported by Shigeta (2001).

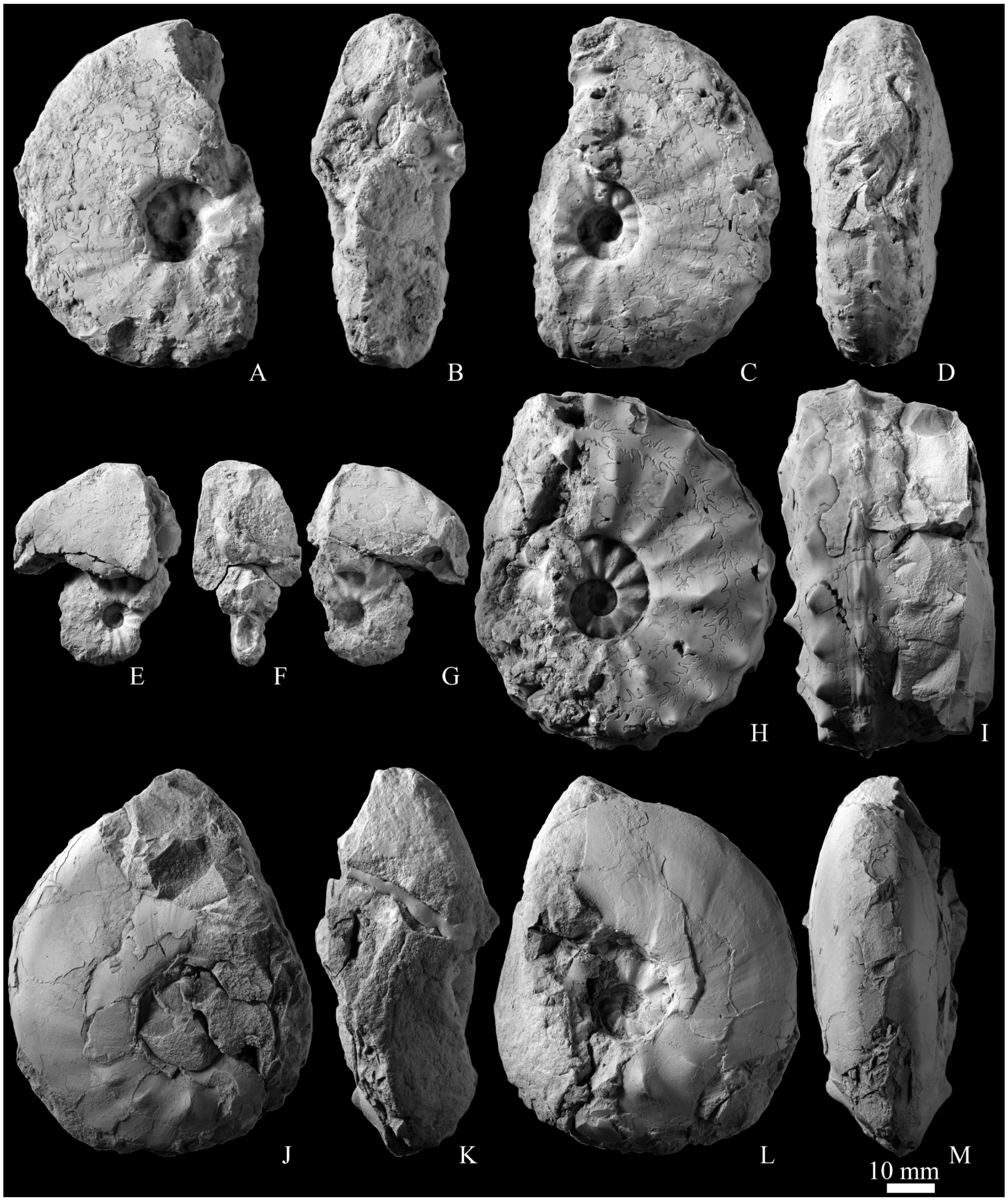

Figure 7. *Forresteria* (*Forresteria*) *yezoensis* Matsumoto, 1969. **A**–**D,** HBE.P-113 from the Futaba Group; **E**–**G,** HBE.P-112 from the Futaba Group; **H, I,** NMNS PM16870 from the Yezo Group; **J**–**M,** NMNS PM17044 from the Yezo Group. Left lateral (A, E, J), apertural (B, F, K), right lateral (C, G, H, L), ventral (D, I, M) views. All photos were taken after whitening with ammonium chlorite.

Description.—Early whorls (up to 30 mm in diameter): Evolute, weakly compressed to weakly depressed shell (W/H = 0.80–1.25) with arched venter and indistinct ventral shoulders. Umbilicus fairly narrow (U/D = 0.19–0.25) with a low, vertical wall. Whorl expansion rate is high to extremely high (WER = 2.09–2.67) and imprint zone rate is moderately embracing (IZR = 0.17–0.23). The ornamentation consists of prorsiradiate primary ribs, mediolateral and ventrolateral tubercles, and clavate tubercles at the mid-venter. As the shell grows, the whorl section becomes more depressed.

Late whorls (> 30 mm in diameter): As the shell grows, the whorl section becomes more compressed. The intraspecific variations of U/D and W/H around 60 mm diameter are approximately 0.21–0.30 and 0.88–0.94, respectively. Whorl expansion rate is moderate to

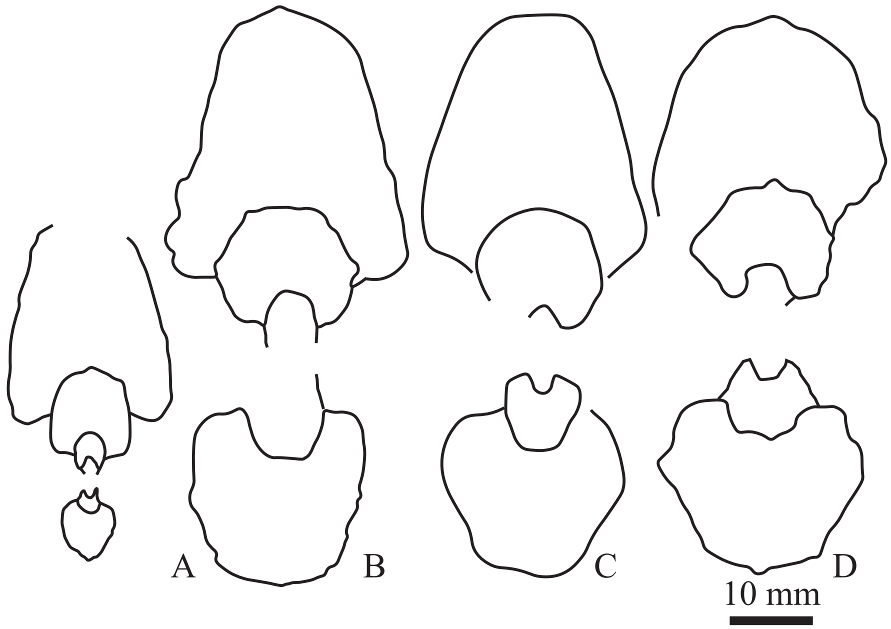

Figure 8. Whorl cross sections of *Forresteria* (*Forresteria*) *yezoensis* Matsumoto, 1969 and *F.* (*F.*) *muramotoi* Matsumoto, 1969 based on CT data. **A, B,** from the Futaba Group; **C, D,** from the Yezo Group. *F.* (*F.*) *yezoensis* Matsumoto, 1969 (A–C), *F.* (*F.*) *muramotoi* Matsumoto, 1969 (D). HBE.P-112 (A), HBE.P-113 (B), NMNS PM17044 (C), NMNS PM16869 (D).

extremely high (*WER* = 1.79–2.58) and the imprint zone rate is weakly to strongly embracing (*IZR* = 0.07–0.32). Ornamentation consists of umbilical, mediolateral, and ventrolateral tubercles; clavate tubercles on mid-venter; prorsiradiate primary ribs; and weak secondary ribs bifurcating from mediolateral tubercles. The ornamentation is weakened in the late whorls. The suture line is moderately incised using divided saddles (Figure 6B).

Remarks.—Matsumoto (1969) described the present species as the type species of the subgenus of *Muramotoa*. The subgenus was distinguished from the subgenus of *Forresteria* by Matsumoto (1969) based on the weakening and final disappearance of the ornaments in the adult whorl. However, Kennedy *et al*. (1983) and Kennedy (1984) suggested that *Muramotoa* is a specialized micromorph offshoot of *Forresteria* based on its restricted distribution and having the same immature whorls. According to these studies, species of the subgenus *Forresteria* have a wide intraspecific variation.

Occurrence.—Matsumoto (1969) reported this species from the Coniacian of the Yezo Group in Hokkaido. Specimens from the Futaba Group were obtained from the upper Turonian based on the co-occurred inoceramids (Inose *et al*., 2024).

Forresteria* (*Forresteria*) *muramotoi Matsumoto, 1969

Figures 8D, 10

Forresteria (*Muramotoa*) *Muramotoa* Matsumoto, 1969, p. 320, pl. 43, fig. 1a–d, text-fig. 11.

Forresteria muramotoi Matsumoto. Shigeta, 2001, pl. 10, figs. 1, 2.

Holotype.—Specimen described by Matsumoto (1969, pl. 43, fig. 1 a–d), is GK. H5620.

Material examined. One specimen (NMNS PM16869) from the Coniacian of the Yezo Group in the Pombetsu-gonosawa Creek, Mikasa City, Hokkaido, Japan. Same specimen as that figured by Shigeta (2001, pl. 10, figs. 1, 2).

Description.—The specimen is moderate in size and exhibits secondary deformation in the late whorls. Subevolute, weakly depressed shell (*W*/*H* = 1.08–1.46) with arched venter and ventral shoulders. Umbilicus fairly narrow (*U*/*D* = 0.22–0.27) with a low, vertical wall. Whorl expansion rate is moderate to very high (*WER* = 1.89–2.45) and imprint zone rate is moderately to strongly embracing (*IZR* = 0.16–0.38). The ornamentation consists of strong conical mediolateral tubercles, prorsiradiate primary ribs, and weak secondary ribs bifurcating from the mediolateral tubercles, ventrolateral tubercles, and ventral clavi. The degree of ornamentation is the strongest in the middle whorls. Ornamentation is weakened in the late whorls. As the shell grows, the whorl section becomes more depressed in early whorls. However, the whorl section becomes more compressed in the late whorls. The suture line is only partly exposed at the E/L.

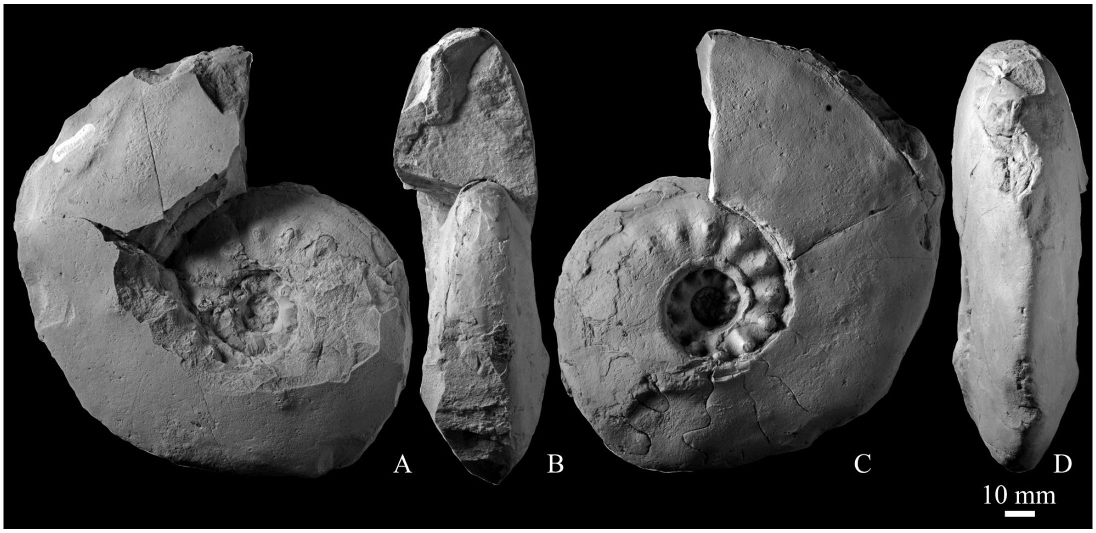

Figure 9. *Yabeiceras orientale* Tokunaga and Shimizu, 1926 from the Yezo Group, NMNS PM17354. **A,** left lateral view; **B,** apertural view; **C,** right lateral view; **D,** ventral view. All photos were taken after whitening with ammonium chlorite.

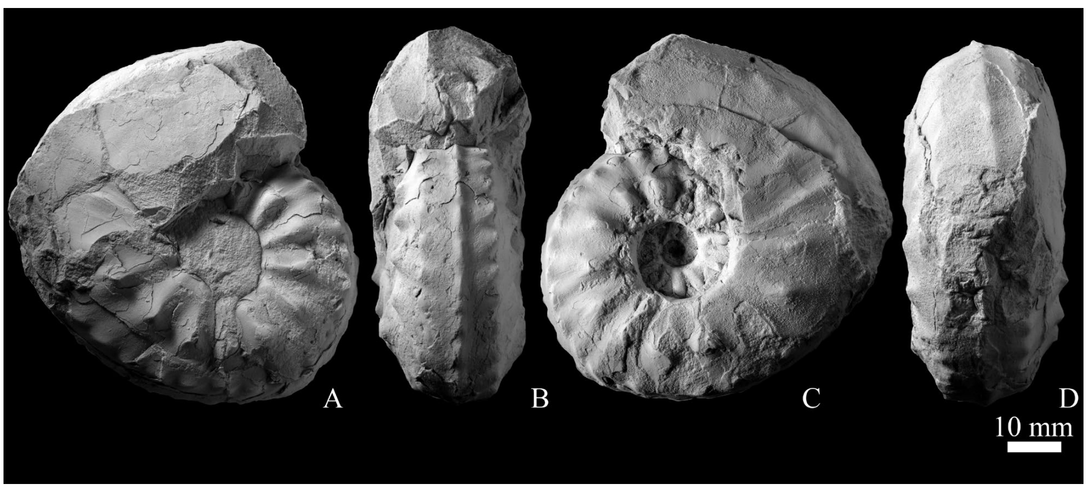

Figure 10. *Forresteria* (*Forresteria*) *muramotoi* Matsumoto, 1969 from the Yezo Group, NMNS PM16869. **A,** left lateral view; **B,** apertural view; **C,** right lateral view; **D,** ventral view. All photos were taken after whitening with ammonium chlorite.

Remarks.—This species is distinguished from *F*. (*F*.) *yezoensis* by having stronger mediolateral tubercles and numerous ventrolateral tubercles.

Occurrence.—This species is known from the Coniacian *Inoceramus uwajimensis* Zone in the Pombetsu-gonosawa Creek, Mikasa City, central Hokkaido (Matsumoto, 1969; Shigeta, 2001).

Results

The measurement data of the present study and previous studies of *Yabeiceras orientale* show wide intraspecific variation during ontogeny of the relative umbilical size (U/D = 0.25–0.48) and relative whorl thickness (W/H = 0.74–2.13, w/H = 0.58–1.58) (Figures 12–14). The measurement data for NMNS PM17354 from the Yezo Group falls in the range of intraspecific variation for specimens of *Y*. *orientale* from the Futaba Group (Figures 12 and 13). In addition, the range of the measurement data for *Y*. *orientale* were scarcely overlapped with those for *Y*. *kotoi*, *Y*. *manasoaense*, and *Y*. cf. *manasoaense* (Figures 12 and 13).

By studying the intraspecific shell variation during the ontogeny of *Yabeiceras orientale* using X-ray micro-

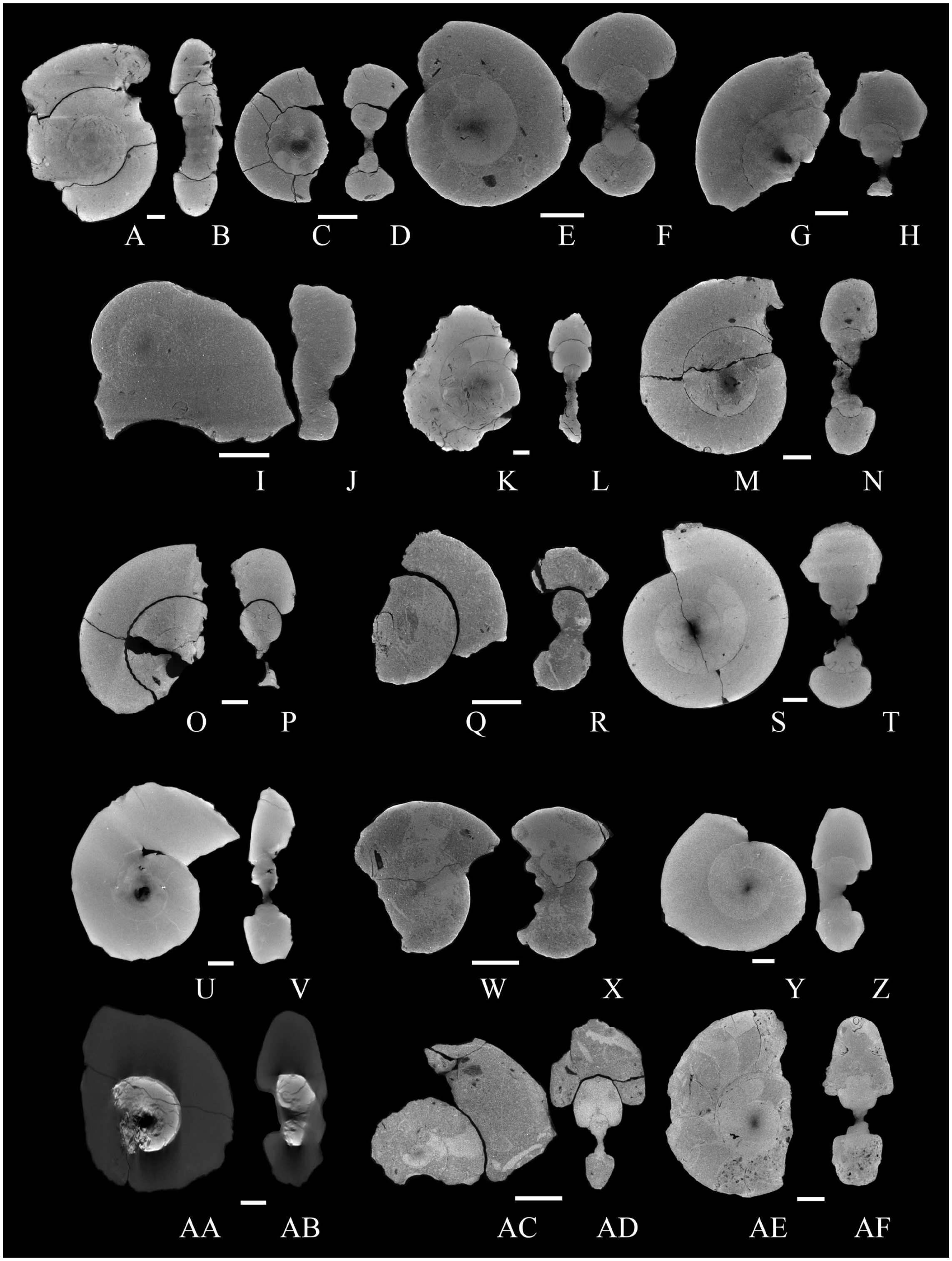

Figure 11. Cross-sectional images of *Yabeiceras* spp. and *Forresteria* spp. based on CT data. **A–V,** *Y. orientale* Tokunaga and Shimizu, 1926; **W, X,** *Y.* cf. *manasoaense* Collignon, 1965; **Y, Z,** *F.* (*F.*) *muramotoi* Matsumoto, 1969; **AA–AF,** *F.* (*F.*) *yezoensis* Matsumoto, 1969. From the Futaba Group (A–T, W, X, AC–AF) and the Yezo Group (U, V, Y–AB). HBE.P-101 (A, B), HBE.P-103 (C, D), HBE.P-104 (E, F), HBE.P-105 (G, H), HBE.P-107 (I, J), HBE.P-108 (K, L), HBE.P-109 (M, N), NMNS PM35062 (O, P), NMNS PM35064 (Q, R), NMNS PM35065 (S, T), NMNS PM17354 (U, V), HBE.P-106 (W, X), NMNS PM16869 (Y, Z), NMNS PM17044 (AA, AB), HBE.P-112 (AC, AD), HBE.P-113 (AE, AF). All scale bars are 10 mm.

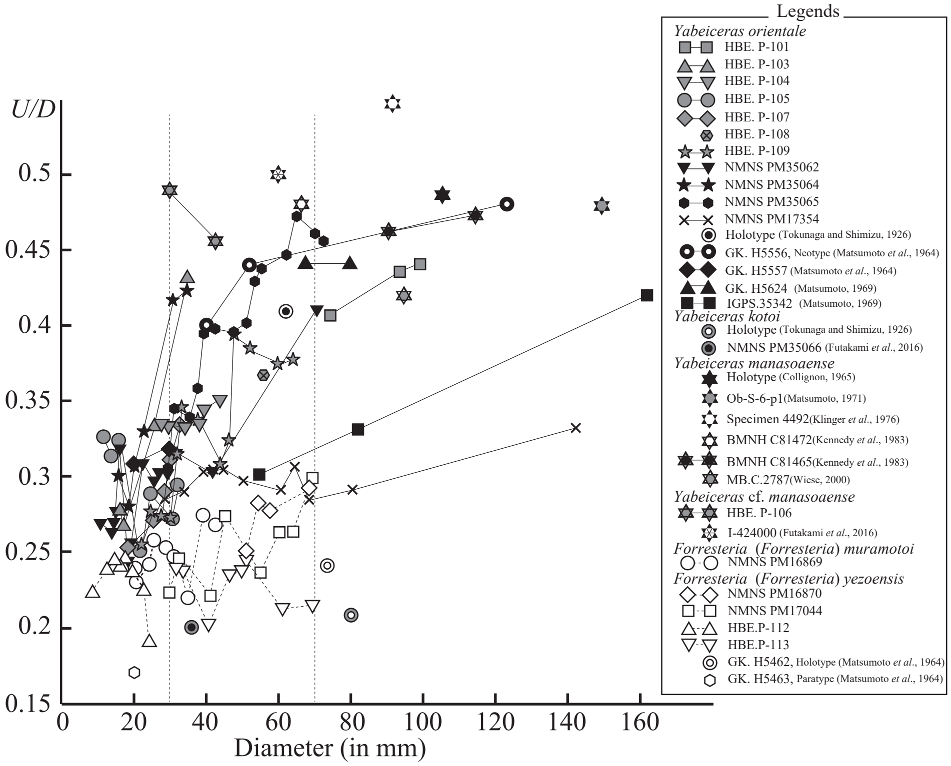

Figure 12. Scatter diagram showing ontogenetic variation in umbilical diameter/shell diameter (*U*/*D*) versus shell diameter (*D*) for specimens of *Yabeiceras* spp. and *Forresteria* spp. from the Futaba and Yezo groups used in this and previous studies. The measurement data of the specimens in previous studies were quoted from these studies. Vertical lines indicate the boundary of the growth stages (*D* = 30 and 70 mm).

computed tomography (CT) and the measurement data from previous studies, it was revealed that *U*/*D* becomes rapidly larger at a diameter of 30–50 mm and then increases gradually (Figure 12). The *W*/*H* first increases to a diameter of 30–50 mm and then decreases gradually (Figure 13). The intraspecific variations in *U*/*D*, *W*/*H* and *w*/*H* in the middle whorls (range of *U*/*D* = approximately 0.15; *W*/*H* = approximately 1.0; *w*/*H* = approximately 0.75) were wider than those in the early and late whorls (range of *U*/*D* = approximately 0.10; *W*/*H* = approximately 0.75; *w*/*H* = approximately 0.50; Figures 14 and 15). In addition, the growth rate of whorl width (*W*) versus shell diameter (*D*) is relatively constant up to a diameter of 30–50 mm and then decreases gradually, whereas that of whorl height (*H*) versus *D* is relatively constant through ontogeny (Figure 16). The intraspecific variations in the growth rates of *W* and *H* versus *D* in the early whorls are narrower than those in the middle and late whorls.

Our measurement data of the two specimens of *Forresteria* (*Forresteria*) *yezoensis* from the lowermost part of the Obisagawa Member in the Sakurazawa Valley show narrower intraspecific variations in the relative umbilical size (*U*/*D* = 0.19–0.30) and relative whorl thickness (*W*/*H* = 0.80–1.25, *w*/*H* = 0.73–1.24) than those of *Yabeiceras orientale* in the shells smaller than 80 mm in diameter (Figures 14 and 15). Furthermore, as the shell grew, *U*/*D* is almost constant, and *W*/*H* gradually decreases from a diameter of 30–50 mm (Figures 12 and 13). The holotype and paratype of *F*. (*F*.) *yezoensis* described by Matsumoto (1969) show similar measurement data to those of the examined specimens (Figures 12 and 13). The ontogenetic pattern of *F*. (*F*.) *yezoensis* in *U*/*D* is different from that of *Y*. *orientale* in *U*/*D*, whereas that of *F*. (*F*.) *yezoensis* in *W*/*H* resembles that of *Y*. *orientale* in *W*/*H*. In addition, the specimen of *F*. (*F*.) *muramotoi* from the Yezo Group (NMNS PM16869) exhibits a similar ontogenetic pattern of shell shape and ornament to the two specimens of *F*. (*F*.) *yezoensis* from the Obisagawa Member in Iwaki area (Figures 12 and 13). *Forresteria* (*F*.) *yezoensis* has narrower umbilicus than *Y*. *orientale*. Although *W*/*H* values of *F*. (*F*.) *yezoensis* and *Y*. *orientale* overlapped, *W*/*H* of the former has a tendency to be lower than that of the latter. The difference in our measurement data between specimens of *Forresteria* and *Yabeiceras* is consistent with those by Matsumoto (1969). Furthermore, intraspecific variation of whorl expansion rate (*WER* = 1.79–2.67) and imprint

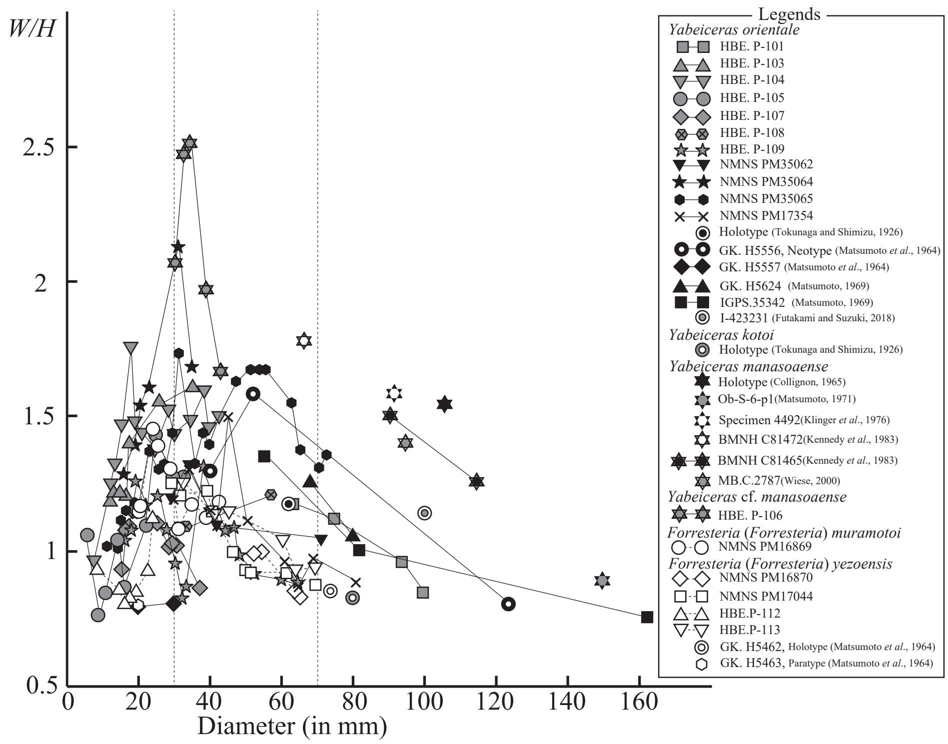

Figure 13. Scatter diagram showing ontogenetic variation in whorl width/whorl height in costal section (*W*/*H*) versus shell diameter (*D*) for specimens of *Yabeiceras* spp. and *Forresteria* spp. from the Futaba and Yezo groups used in this and previous studies. The measurement data of the specimens in previous studies were quoted from these studies. Vertical lines indicate the boundary of the growth stages (*D* = 30 and 70 mm).

zone rate (*IZR* = 0.07–0.32) of *F*. (*F*.) *yezoensis* is also narrower than that of *Y*. *orientale* (*WER* = 1.44–3.50, *IZR* = 0.05–0.50).

Discussion

Previous studies have noted intraspecific variation in *Yabeiceras orientale*. Matsumoto *et al*. (1964) reported intraspecific variations in the umbilical width, whorl width, ornamentation, and sutures of three specimens, including the neotype and holotype of *Y. orientale*. Matsumoto (1969) documented that one specimen from the Yezo Group in Hokkaido (IGPS.35342) and two specimens (GK.H5556 and GK.H5557) from the Futaba Group are all less widely umbilicate than the holotype from the Futaba Group, whereas the other specimen from the Yezo Group (GK.H5624) is very similar to the holotype. He attributed the difference among these specimens from the Yezo and Futaba groups as intraspecific variation in the present species. Kennedy *et al*. (1983) discussed intraspecific variations in the timing of changes in whorl width and ornamentation in one specimen from the St. Lucia Formation in South Africa and specimens described by Matsumoto *et al*. (1964). Futakami *et al*. (2016) reported intraspecific variations in the whorl section and ornamentation of nine specimens of *Y. orientale*, including the neotype. Recently, Futakami and Suzuki (2018) reported intraspecific variation in ornamentation among specimens (including the neotype and HBE.P-101) from the Futaba Group (Futakami *et al*., 2016). These previous studies showed characteristic ontogenetic changes in the shell shape and ornamentation in *Y. orientale*. Therefore, the present study investigated the ontogenetic change of the whorl shape in cross section for individual specimens and variation of the shell shape at a given shell size among specimens of *Y. orientale* from the Obisagawa Member of the Ashizawa Formation based on CT data. Based on the data in this study, the *U/D* becomes rapidly larger at a diameter of 30–50 mm and then increases gradually (Figure 12). In addition, the *W/H* first increases to a diameter of 30–50 mm and then decreases gradually (Figure 13). This ontogenetic tendency has been confirmed by previous studies (Tokunaga and Shimizu, 1926; Matsumoto *et al.*, 1964; Matsumoto, 1969; Kennedy *et al.*, 1983; Futakami *et al*., 2016). Futakami *et al*. (2016) suggested that variations in ornamentation and shell proportions in the early (up to 30–40 mm in diameter) to middle (30–80 mm in diameter) growth stages were greater than those

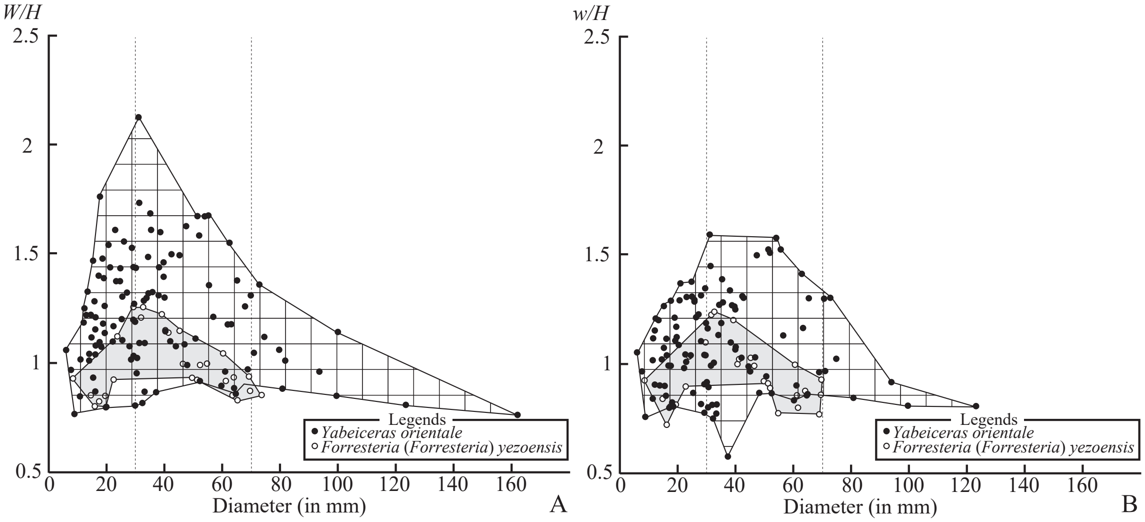

Figure 14. Scatter diagram showing the relationships between whorl width/whorl height in costal section (*W/H*) versus shell diameter (*D*) and whorl width/whorl height in intercostal section (*w/H*) versus shell diameter (*D*) for specimens of *Yabeiceras orientale* Tokunaga and Shimizu, 1926 and *Forresteria* (*Forresteria*) *yezoensis* Matsumoto, 1969 used in this and previous studies (Tokunaga and Shimizu, 1926; Matsumoto *et al*., 1964; Matsumoto, 1969; Futakami and Suzuki, 2018). The measurement data of the specimens in previous studies were quoted from these studies. **A,** relationships between *W/H* and *D*; **B,** relationships between *w/H* and *D*. Vertical lines indicate the boundary of the growth stages (*D* = 30 and 70 mm).

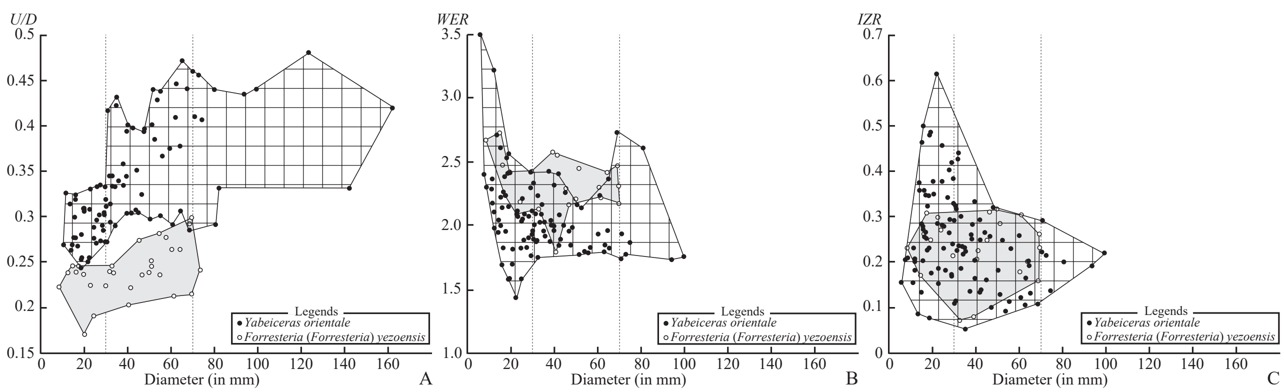

Figure 15. Scatter diagram showing the relationships between umbilical diameter/shell diameter (*U*/*D*) versus shell diameter (*D*), whorl expansion rate (*WER*, *(D/(D-h))^2*) versus shell diameter (*D*), and imprint zone rate (*IZR*, *(H-h)/H*) versus shell diameter (*D*) for specimens of *Yabeiceras orientale* Tokunaga and Shimizu, 1926 and *Forresteria* (*Forresteria*) *yezoensis* Matsumoto, 1969 used in this and previous studies (Tokunaga and Shimizu, 1926; Matsumoto *et al*., 1964; Matsumoto, 1969; Futakami and Suzuki, 2018). The measurement data of the specimens in previous studies were quoted from these studies. **A,** relationships between *U/D* and *D*; **B,** relationships between *WER* and *D*; **C,** relationships between *IZR* and *D*. Vertical lines indicate the boundary of the growth stages (*D* = 30 and 70 mm).

in the late growth stage (over 60–80 mm in diameter). This study confirmed that in *Y*. *orientale*, the intraspecific variations in *U/D*, *W/H*, and *w/H* in the middle whorls are wider than those in the early and late whorls (Figures 14 and 15). The data obtained in this study are consistent with the observations by Futakami *et al*. (2016).

Previous studies have shown that intraspecific variation in ammonoid shells is the largest during the early (Tanabe and Shigeta, 1987; Monnet *et al*., 2012; Klein and Landman, 2019) or middle growth stages (Dagys and Weitschat, 1993; Korn and Klug, 2007; De Baets *et al*., 2013), except for sexual dimorphism, which occurs in the late growth stage (Klug *et al*., 2015b). Tajika *et al*. (2020) reported that Cretaceous and living nautilids exhibited the largest intraspecific variation during the early growth stage. The results of our study on *Yabeiceras orientale* showed the largest intraspecific variation in the middle whorls. Let us consider the cause of intraspecific variation

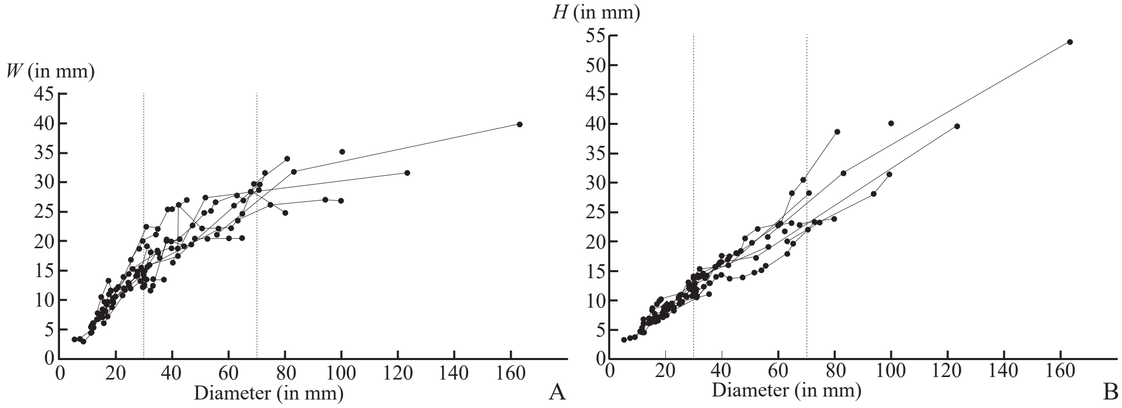

Figure 16. Scatter diagram showing the relationships between whorl width (*W*) versus shell diameter (*D*) and whorl height (*H*) versus shell diameter (*D*) for specimens of *Yabeiceras orientale* Tokunaga and Shimizu, 1926 used in this and previous studies (Tokunaga and Shimizu, 1926; Matsumoto *et al*., 1964; Matsumoto, 1969; Futakami and Suzuki, 2018). The measurement data of the specimens in previous studies were quoted from these studies. **A,** relationships between *W* and *D*; **B,** relationships between *H* and *D*. Vertical lines indicate the boundary of the growth stages (*D* = 30 and 70 mm).

in *Y. orientale* based on available data. First, explanations by different regions (e.g. Dietl, 1978) and paleoenvironments (e.g. Wilmsen and Mosavinia, 2011) were excluded because the examined specimens were mostly recovered from the same locality (type locality of *Y. orientale*) in the Sakurazawa Valley, Iwaki area (Fig. 1). In addition, sexual dimorphism might be excluded as the cause of the wide intraspecific variation in this species because the data of the specimens cannot be divided into two or more distinct groups. Intraspecific variation of shell growth patterns caused by septal spacing stress (e.g. Kraft *et al*., 2008) may be excluded because of successive changes throughout ontogeny and the same ontogenetic patterns among specimens. Finally, hatchling size (Landman, 1987) remains uncertain because of limited data on very early whorls in our material. However, as De Baets *et al*. (2015) suggested, the decrease in the intraspecific variation in the late growth stage may be biased by the usual higher abundance of intermediate-sized specimens within preserved "populations" of species. The observed intraspecific variations of shell form and ornament during ontogeny of *Y. orientale* might have been biased by insufficient number of large-sized specimens. Therefore, it is necessary to collect more large-sized specimens and conduct morphological analysis of a large number of specimens covering the whole ontogenetic stage for realization of the intraspecific variation of this species.

Kennedy *et al*. (1983) suggested that the Turonian to the Coniacian Barroisiceratine evolved from *Forresteria* (*Halreites*) through *Forresteria* (*Forresteria*) to *Yabeiceras*. Matsumoto (1969) allied *Yabeiceras* with *F.* (*F.*) *yezoensis* and *F.* (*F.*). *muramotoi* based on the weakened ornamentation in adult whorls.

A single specimen of *Forresteria* (*F.*) *alluaudi* (HBE-P1) was reported by Matsumoto *et al*., 1990, fig. 10) from the middle part of the Ashizawa Formation (= middle part of the Obisagawa Member) in Ashizawa, Iwaki City. Unfortunately, our CT observations show that the specimen, including the inner whorls, was secondarily deformed. In contrast, the lowermost part of the Obisagawa Member is exposed in the Sakurazawa Valley, from which examined specimens of *Yabeiceras orientale* were recovered. Therefore, we examined *F.* (*F.*) *yezoensis* from the Sakurazawa Valley, and *F.* (*F.*) *yezoensis* and *F.* (*F.*) *muramotoi* from the Yezo Group for comparison with *Y. orientale*.

Our measurement data of *Forresteria* (*Forresteria*) *yezoensis* show narrower intraspecific variations in the relative umbilical size (*U/D*), the relative whorl thickness (*W/H*), the whorl expansion rate (*WER*), and the imprint zone rate (*IZR*) than those of *Yabeiceras orientale* in the shells smaller than 80 mm in diameter (Figures 14 and 15). The range of the intraspecific variation of *w/H* of *Y. orientale* is wider than that of *w/H* of *F.* (*F.*) *yezoensis*. This study revealed that the examined specimens of *Y. orientale* and *F.* (*F.*) *yezoensis* can be distinguishable not only by the difference in surface ornamentations but also by the difference in *U/D*, although the range of intraspecific variations of other parameters versus shell diameter largely overlap between them.

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Author contributions

HI conducted the geological survey, analyzed the measurement data, and wrote the original draft. NW conducted the geological survey, collected the fossils, and contributed to the discussions. All authors contributed to the writing of the manuscript.

Appendix 1. Measurements (mm) of specimens of *Yabeiceras orientale* Tokunaga and Shimizu, 1926, from the Futaba Group used in the present study. *D*: shell diameter; *U*: umbilical diameter; *H*: whorl height; *h*: aperture height; *W*: whorl width in costal section; *w*: whorl width in intercostal section; *WER*: whorl expansion rate, (D/(D-h))^2, *IZR*: imprint zone rate, (H-h)/H.

species	register number	*D* (mm)	*U* (mm)	*H* (mm)	*h* (mm)	*W* (mm)	*w* (mm)	*U/D*	*W/H*	*w/H*	*WER*	*IZR*
Yabeiceras orientale	HBE.P-101	63.2	–	20.0	16.7	23.5	23.4	–	1.18	1.17	1.85	0.17
		74.7	30.4	23.3	20.1	26.1	24.0	0.41	1.12	1.03	1.87	0.14
		93.8	40.9	28.0	22.6	27.0	25.8	0.44	0.96	0.92	1.74	0.19
		99.5	43.9	31.4	24.5	26.8	25.6	0.44	0.85	0.82	1.76	0.22
Yabeiceras orientale	HBE.P-103	11.5	–	4.8	3.7	5.5	5.4	–	1.15	1.13	2.17	0.23
		12.2	–	4.8	3.8	6.0	5.8	–	1.25	1.21	2.11	0.21
		15.8	–	6.4	5.1	7.7	6.6	–	1.20	1.03	2.18	0.20
		16.5	4.6	6.7	4.3	8.1	6.7	0.28	1.21	1.00	1.83	0.36
		17.5	4.7	6.8	5.0	9.5	8.8	0.27	1.40	1.29	1.96	0.26
		26.2	8.8	9.9	8.1	15.4	12.1	0.34	1.56	1.22	2.10	0.18
		35.3	15.3	11.1	10.5	17.9	15.5	0.43	1.61	1.40	2.03	0.05
Yabeiceras orientale	HBE.P-104	7.6	–	3.4	2.7	3.3	3.3	–	0.97	0.97	2.41	0.21
		12.1	–	4.4	3.5	5.2	5.1	–	1.18	1.16	1.98	0.20
		13.5	–	5.8	5.3	7.7	7.0	–	1.33	1.21	2.71	0.09
		15.2	–	7.0	5.0	10.3	8.9	–	1.47	1.27	2.22	0.29
		17.6	–	7.5	5.8	13.2	9.7	–	1.76	1.29	2.22	0.23
		18.8	–	7.8	6.0	11.6	9.5	–	1.49	1.22	2.16	0.23
		20.9	–	8.3	5.4	12.0	11.4	–	1.45	1.37	1.82	0.35
		24.7	–	10.3	7.4	14.3	13.6	–	1.39	1.32	2.04	0.28
		25.7	–	10.8	7.8	16.7	14.1	–	1.55	1.31	2.06	0.28
		28.2	9.5	12.2	8.6	18.8	16.1	0.34	1.54	1.32	2.07	0.30
		29.8	10.0	13.9	9.3	20.0	16.6	0.34	1.44	1.19	2.11	0.33
		34.3	11.5	14.1	11.0	21.0	18.0	0.34	1.49	1.28	2.17	0.22
		38.6	13.0	15.9	11.4	25.4	20.3	0.34	1.60	1.28	2.01	0.28
		39.8	13.8	17.4	11.6	25.5	21.8	0.35	1.47	1.25	1.99	0.33
		42.3	15.1	17.3	13.0	26.1	22.8	0.36	1.51	1.32	2.08	0.25
Yabeiceras orientale	HBE.P-105	5.8	–	3.2	2.7	3.4	3.4	–	1.06	1.06	3.50	0.16
		8.8	–	3.8	3.0	2.9	2.9	–	0.76	0.76	2.30	0.21
		11.4	–	5.2	4.0	4.4	4.4	–	0.85	0.85	2.37	0.23
		12.2	4.0	6.6	5.4	6.1	6.0	0.33	0.91	0.91	3.22	0.18
		14.3	4.5	6.7	4.3	7.0	6.9	0.31	1.04	1.03	2.04	0.36
		16.0	5.2	7.1	5.1	6.2	6.1	0.33	0.87	0.86	2.15	0.28
		22.6	5.8	9.8	7.0	10.8	10.3	0.26	1.10	1.05	2.10	0.29
		24.8	7.2	9.4	5.1	13.4	13.0	0.29	1.43	1.38	1.58	0.46
		30.3	8.3	11.7	8.3	15.0	13.7	0.27	1.28	1.17	1.90	0.29
		32.4	9.6	14.1	7.9	18.1	14.3	0.30	1.28	1.01	1.75	0.44
Yabeiceras orientale	HBE.P-107	15.4	–	8.4	4.5	7.8	7.6	–	0.93	0.90	2.00	0.46
		17.0	–	9.2	6.0	9.8	7.4	–	1.07	0.80	2.39	0.35
		18.0	–	9.9	6.7	10.8	8.2	–	1.09	0.83	2.54	0.32
		18.5	4.7	10.1	6.6	11.6	8.2	0.25	1.15	0.81	2.42	0.35
		25.3	7.0	10.8	8.3	11.8	9.4	0.28	1.09	0.87	2.21	0.23
		29.1	8.5	12.5	10.4	13.2	9.8	0.29	1.06	0.78	2.42	0.17
		30.4	9.5	11.8	10.5	12.0	9.5	0.31	1.02	0.81	2.33	0.11
		33.3	11.2	12.3	10.0	13.4	9.6	0.34	1.09	0.78	2.04	0.19
		37.4	–	15.5	13.4	13.4	9.0	–	0.86	0.58	2.43	0.14
Yabeiceras orientale	HBE.P-108	29.1	–	12.0	9.9	12.3	11.0	–	1.03	0.92	2.30	0.18
		31.4	–	14.2	9.7	15.4	14.2	–	1.08	1.00	2.09	0.32
		56.4	20.8	19.1	14.7	22.1	21.7	0.37	1.16	1.14	1.83	0.23
Yabeiceras orientale	HBE.P-109	15.8	–	6.9	5.0	7.2	5.9	–	1.04	0.86	2.14	0.28
		17.6	–	6.7	5.0	7.3	6.7	–	1.09	1.00	1.95	0.25
		19.4	–	7.8	4.0	9.9	9.2	–	1.27	1.18	1.59	0.49
		22.2	5.6	9.6	3.7	11.3	9.5	0.25	1.18	0.99	1.44	0.61
		24.6	6.7	10.3	6.4	12.7	10.8	0.27	1.23	1.05	1.83	0.38
		28.0	7.7	12.9	7.7	14.0	10.6	0.28	1.09	0.82	1.90	0.40
		30.7	8.4	13.3	9.0	12.8	12.0	0.27	0.96	0.90	2.00	0.32
		32.3	10.2	14.0	10.7	11.7	10.6	0.32	0.84	0.76	2.24	0.24
		33.4	11.6	14.3	10.0	12.6	11.7	0.35	0.88	0.82	2.04	0.30
		38.3	13.0	15.4	11.5	20.3	17.0	0.34	1.32	1.10	2.04	0.25
		44.3	13.7	17.7	13.0	19.2	17.6	0.31	1.08	0.99	2.00	0.27
		46.7	15.2	17.9	13.3	19.6	18.5	0.33	1.09	1.03	1.95	0.26
		48.2	19.1	20.6	14.0	20.5	18.0	0.40	1.00	0.87	1.99	0.32
		52.5	20.3	22.1	16.6	20.5	19.2	0.39	0.93	0.87	2.13	0.25
		60.1	22.6	22.8	16.9	20.5	19.1	0.38	0.90	0.84	1.94	0.26
		64.5	24.5	23.2	18.5	20.5	20.0	0.38	0.88	0.86	1.97	0.20
Yabeiceras orientale	NMNS PM35062	28.0	7.6	11.7	8.6	14.6	13.0	0.27	1.25	1.11	2.08	0.26
		30.0	9.2	13.8	8.5	13.6	12.7	0.31	0.99	0.92	1.95	0.38
		32.0	10.1	15.2	8.7	15.9	12.4	0.32	1.05	0.82	1.89	0.43
		42.0	12.7	15.7	11.1	17.4	16.2	0.30	1.11	1.03	1.85	0.29
		71.0	29.2	28.2	20.0	29.6	27.5	0.41	1.05	0.98	1.94	0.29
Yabeiceras orientale	NMNS PM35064	16.0	4.8	7.4	3.7	9.6	8.3	0.30	1.30	1.12	1.69	0.50
		19.0	5.3	7.5	3.9	10.5	9.1	0.28	1.40	1.21	1.58	0.48
		20.6	6.3	7.7	4.8	11.9	10.0	0.31	1.55	1.30	1.70	0.38
		23.0	7.6	8.5	7.2	13.7	8.6	0.33	1.61	1.01	2.12	0.15
		31.0	12.9	10.5	9.3	22.4	16.8	0.42	2.13	1.60	2.04	0.11
		35.0	14.8	13.0	10.0	22.0	15.5	0.42	1.69	1.19	1.96	0.23

Appendix 2. Measurements (mm) of specimens of *Yabeiceras* spp. and *Forresteria* spp. from the Futaba and Yezo groups used in the present study. *D*: shell diameter; *U*: umbilical diameter; *H*: whorl height; *h*: aperture height; *W*: whorl width in costal section; *w*: whorl width in intercostal section; *WER*: whorl expansion rate, (D/(D-h))^2, *IZR*: imprint zone rate, (H-h)/H.

species	register number	*D* (mm)	*U* (mm)	*H* (mm)	*h* (mm)	*W* (mm)	*w* (mm)	*U/D*	*W/H*	*w/H*	*WER*	*IZR*
Yabeiceras orientale	NMNS PM35065	11.2	3.0	4.5	3.8	4.6	4.6	0.27	1.02	1.02	2.29	0.16
		14.1	3.7	6.4	4.0	6.5	5.8	0.26	1.02	0.91	1.95	0.38
		15.2	4.2	6.7	5.8	7.5	7.2	0.28	1.12	1.07	2.61	0.13
		16.4	5.2	7.4	5.5	8.5	7.7	0.32	1.15	1.04	2.26	0.26
		18.9	4.6	7.7	7.1	9.1	8.6	0.24	1.18	1.12	2.57	0.08
		19.6	5.0	8.5	7.0	9.7	9.6	0.26	1.14	1.13	2.42	0.18
		23.0	7.1	8.6	7.0	11.8	11.3	0.31	1.37	1.31	2.07	0.19
		25.7	7.6	9.7	7.0	12.7	12.5	0.30	1.31	1.29	1.89	0.28
		27.2	8.2	10.8	7.1	14.3	13.3	0.30	1.32	1.23	1.83	0.34
		29.4	8.9	10.8	8.2	15.5	14.6	0.30	1.44	1.35	1.92	0.24
		31.4	10.8	11.0	8.5	19.0	16.0	0.34	1.73	1.45	1.88	0.23
		35.7	12.1	12.9	10.0	17.1	16.6	0.34	1.33	1.29	1.93	0.22
		38.0	13.6	13.9	10.3	20.0	18.7	0.36	1.44	1.35	1.88	0.26
		39.7	15.6	14.3	11.4	20.0	18.1	0.39	1.40	1.27	1.97	0.20
		42.8	17.0	13.6	11.7	20.4	17.8	0.40	1.50	1.31	1.89	0.14
		47.4	18.7	13.9	12.5	22.6	20.9	0.39	1.63	1.50	1.84	0.10
		51.4	20.6	14.7	12.8	24.6	22.5	0.40	1.67	1.53	1.77	0.13
		53.9	23.1	15.1	13.7	25.2	23.9	0.43	1.67	1.58	1.80	0.09
		55.6	24.3	15.9	14.1	26.6	24.3	0.44	1.67	1.53	1.79	0.11
		62.9	28.1	17.9	16.0	27.7	25.4	0.45	1.55	1.42	1.80	0.11
		65.3	30.8	19.6	17.0	27.0	25.6	0.47	1.38	1.31	1.83	0.13
		70.6	32.5	22.0	17.1	28.8	28.7	0.46	1.31	1.30	1.74	0.22
		72.8	33.1	23.2	18.2	31.5	30.4	0.45	1.36	1.31	1.78	0.22
Yabeiceras orientale	NMNS PM17354	29.2	8.3	12.4	7.2	15.0	13.0	0.28	1.21	1.05	1.76	0.42
		34.1	9.9	13.7	10.5	18.1	15.6	0.29	1.32	1.14	2.09	0.23
		39.9	12.1	16.4	13.7	18.9	17.6	0.30	1.15	1.07	2.32	0.16
		41.9	12.8	17.2	14.9	18.8	17.8	0.31	1.09	1.03	2.41	0.13
		45.1	13.7	18.0	15.1	26.9	17.5	0.30	1.49	0.97	2.26	0.16
		50.5	15.0	19.8	16.2	22.1	18.8	0.30	1.12	0.95	2.17	0.18
		60.9	17.7	23.0	20.2	22.2	20.8	0.29	0.97	0.90	2.24	0.12
		64.8	19.8	28.1	22.7	24.6	24.4	0.31	0.88	0.87	2.37	0.19
		68.8	19.5	30.5	27.2	29.7	29.5	0.28	0.97	0.97	2.74	0.11
		80.8	23.5	38.5	–	34.0	32.7	0.29	0.88	0.85	2.61	0.20
		142.6	47.3	–	30.8	–	–	0.33	–	–	–	–
Yabeiceras cf. *manasoaense*	HBE.P-106	30.1	14.8	9.4	8.1	19.5	17.2	0.49	2.07	1.83	1.87	0.14
		32.7	–	9.5	7.8	23.5	17.9	–	2.47	1.88	1.72	0.18
		34.6	–	10.8	8.9	27.1	19.1	–	2.51	1.77	1.81	0.18
		39.0	–	12.1	10.1	23.9	20.7	0.46	1.98	1.46	1.82	0.17
		43.0	19.7	13.3	10.0	22.2	19.4	–	1.67	1.71	1.70	0.25
Forresteria (*Forresteria*) *yezoensis*	NMNS PM16870	51.9	13.0	23.0	–	23.2	20.6	0.25	1.01	0.90	–	–
		54.7	15.5	24.2	–	24.8	18.8	0.28	1.02	0.78	–	–
		61.6	17.0	27.0	–	23.4	21.7	0.28	0.87	0.80	–	–
		68.9	20.1	29.9	25.1	24.6	23.1	0.29	0.82	0.77	2.47	0.16
Forresteria (*Forresteria*) *yezoensis*	NMNS PM17044	29.6	6.6	13.5	10.6	16.9	14.9	0.22	1.25	1.10	2.43	0.21
		31.7	7.6	13.6	–	16.4	16.4	0.24	1.21	1.21	–	–
		39.2	–	16.1	14.8	19.6	19.4	–	1.22	1.20	2.58	0.08
		41.2	9.1	19.9	15.4	22.6	20.4	0.22	1.14	1.03	2.55	0.23
		45.3	12.4	20.5	15.4	23.5	21.1	0.27	1.15	1.03	2.30	0.25
		55.1	13.0	–	–	22.9	22.0	0.24	–	–	–	–
		60.5	15.9	25.1	20.6	26.2	25.1	0.26	1.04	1.00	2.30	0.18
		64.1	16.9	28.7	22.9	26.8	25.2	0.26	0.93	0.88	2.42	0.20
		69.6	20.8	29.2	22.4	27.5	27.2	0.30	0.94	0.93	2.17	0.23
Forresteria (*Forresteria*) *yezoensis*	HBE.P-112	8.5	1.9	4.3	3.3	4.0	4.0	0.22	0.93	0.93	2.67	0.23
		12.6	3.0	–	–	5.0	4.9	0.24	–	–	–	–
		14.7	3.6	7.0	5.8	6.0	5.9	0.24	0.86	0.84	2.73	0.17
		16.2	3.9	8.0	5.9	6.4	5.8	0.24	0.80	0.73	2.47	0.26
		17.5	4.3	8.4	5.8	6.9	6.8	0.25	0.82	0.81	2.24	0.31
		19.3	4.6	9.2	6.9	7.8	7.5	0.24	0.85	0.82	2.42	0.25
		22.7	5.1	10.0	7.0	9.3	9.0	0.22	0.93	0.90	2.09	0.30
		24.1	4.6	10.7	7.8	12.0	11.1	0.19	1.12	1.04	2.19	0.27
Forresteria (*Forresteria*) *yezoensis*	HBE.P-113	32.7	8.0	11.1	10.3	13.9	13.8	0.24	1.25	1.24	2.13	0.07
		33.7	8.0	–	–	–	–	0.24	–	–	–	–
		40.7	8.2	13.0	10.3	14.9	13.1	0.20	1.15	1.01	1.79	0.21
		46.5	10.9	21.6	14.9	21.6	21.5	0.23	1.00	1.00	2.17	0.31
		49.8	11.8	23.9	16.3	22.3	22.1	0.24	0.93	0.92	2.21	0.32
		51.2	12.5	25.9	18.5	23.8	23.7	0.24	0.92	0.92	2.45	0.29
		61.2	13.0	28.9	20.1	26.6	24.9	0.21	0.92	0.86	2.21	0.30
		69.5	14.9	32.3	23.8	28.4	27.9	0.21	0.88	0.86	2.31	0.26
Forresteria (*Forresteria*) *muramotoi*	NMNS PM16869	20.2	4.8	8.8	5.5	10.1	9.1	0.24	1.15	1.03	1.89	0.38
		20.5	4.7	9.8	6.5	11.4	11.3	0.23	1.16	1.15	2.14	0.34
		24.1	5.8	10.5	6.9	15.3	10.8	0.24	1.46	1.03	1.96	0.34
		25.6	6.6	11.4	7.1	15.9	13.3	0.26	1.39	1.17	1.91	0.38
		28.9	7.3	13.0	9.1	17.0	14.0	0.25	1.31	1.08	2.13	0.30
		31.4	7.7	14.5	10.6	15.7	14.8	0.25	1.08	1.02	2.28	0.27
		35.0	7.7	15.0	12.4	17.7	16.6	0.22	1.18	1.11	2.40	0.17
		39.0	10.7	16.8	14.1	18.9	18.8	0.27	1.13	1.12	2.45	0.16
		42.6	11.4	18.5	14.8	21.9	19.7	0.27	1.18	1.06	2.35	0.20