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A possible phylogenetic relationship of two species of *Hyphantoceras* (Ammonoidea: Nostoceratidae) in the Cretaceous Yezo Group, northern Japan

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Abstract. A possible phylogenetic relationship of two species of *Hyphantoceras* (Ammonoidea: Nostoceratidae) was proposed, based on the newly found specimens with precise stratigraphic occurrences in the Kotanbetsu and Obira areas, northwestern Hokkaido. Two closely related species, *Hyphantoceras transitorium* and *Hyphantoceras orientale*, were recognized in the examined specimens from the Kotanbetsu and Obira areas. Specimens of *H. transitorium* show the wide intraspecific variation in the whorl shape. The stratigraphic occurrences of two species indicate that they occur successively in the Santonian–lowermost Campanian, without stratigraphic overlapping. The similarity of their shell surface ornamentations and the stratigraphic relationships possibly suggest that *Hyphantoceras orientale* was derived from *Hyphantoceras transitorium*. The presumed lineage is likely indigenous to the northwestern Pacific realm in Santonian–earliest Campanian. *Hyphantoceras venustum* and *H. heteromorphum* might be out of a lineage of *Hyphantoceras transitorium*–*Hyphantoceras orientale*, judging from differences of their shell surface ornamentations.

Key words: Cretaceous, heteromorph ammonoid, *Hyphantoceras*, intraspecific

variation, lineage

Introduction

The genus *Hyphantoceras* Hyatt, 1900, belonging to the family Nostoceratidae Hyatt, 1894, has helically coiled (or sometimes irregularly coiled) whorls with slightly oblique, dense ribs and 2–4 tubercle rows (Wright *et al*., 1996). More than 10 species assigned to this genus have been reported from the Turonian–Campanian in various regions of the world (Europe: d'Orbigny, 1850; Schlüter, 1876; Kaplan and Schmidt, 1988; Santamaría-Zabala, 1992; Tarkowski, 1996; Wiese, 2000; Metzdorf and Sowiak, 2003; Wiese *et al*., 2004; Wilmsen and Wiese, 2004; Kennedy and Gale, 2015, New Zealand: Wright, 1957, Japan and Russian Far East: Yabe, 1904; Shimizu, 1935; Matsumoto, 1942, 1943, 1959, 1977b; Zonova and Yazykova, 1998, Madagascar: Collignon, 1966; Walaszczyk *et al*., 2004, 2014, USA: Anderson, 1902, 1958). Five species assigned to *Hyphantoceras* have been described from Hokkaido, northern Japan and Sakhalin, Russian Far East (e.g. Yabe, 1904; Shimizu, 1935; Matsumoto, 1942, 1943, 1959, 1977b; Wright and Matsumoto, 1954; Kodama et al., 2002; Yazykova, 2004; Jagt-Yazykova, 2011). However, the phylogenetic relationships among these

species remained obscure. The main reason is the uncertainty of the stratigraphic horizons of the type specimens of each species, because most of them were collected from river floats in various areas. Additionally, almost species of *Hyphantoceras* were described by small numbers of fragmentary specimens. Therefore, the intraspecific variation of each species is not understood adequately.

During the field survey, more than 30 specimens of *Hyphantoceras orientale* and *H. transitorium* were collected from the Santonian–lowermost Campanian outcrops in the Kotanbetsu area, northwestern Hokkaido (Figures 1, 2). Based on these specimens with the exact stratigraphic horizon from the Kotanbetsu area and some specimens collected in the Obira area by Oizumi *et al*. (2005), the intraspecific variation and the phylogeny of two species were discussed.

Note on *Hyphantoceras* in the Yezo Group

Five species of *Hyphantoceras* have been described and/or reported from the Yezo Group (Yabe, 1904; Shimizu, 1935; Matsumoto, 1942, 1943, 1959, 1977b; Wright and Matsumoto, 1954; Ohya *et al*., 2012). *Hyphantoceras orientale*, *H. oshimai*, and *H.*

venustum were originally described by Yabe (1904) as "*Heteroceras*(?) *orientale*", "*Heteroceras*(?) *oshimai*", and "*Helicoceras*(?) *venustum*" respectively. Shimizu (1935) assigned later two species to genus *Hyphantoceras*. Wright and Matsumoto (1954) regarded "*Heteroceras*(?) *orientale*" as a species of *Hyphantoceras*. These identifications are acceptable in later studies (e.g. Matsumoto, 1977b; Okamoto, 1988a; Okamoto *et al*., 2003). *Hyphantoceras transitorium* and "*H*.(?) *heteromorphum*" were described by Matsumoto (1977b). Ohya *et al*. (2012) regarded "*H*.(?) *heteromorphum*" as a species of genus *Hyphantoceras*. Following above previous studies, *H. orientale*, *H. oshimai*, *H. venustum*, *H. transitorium* and *H. heteromorphum* are available as species of *Hyphantoceras* in this study. Geographical and chronological distributions of these species are compiled in Table 1.

Geological setting and material

The marine deposits of the Yezo Group are distributed over 1000 km in a north to south direction, from Hokkaido, northern Japan, to Sakhalin, Far East of Russia (Figure 1; Takashima *et al*., 2004; Maeda *et al*., 2005). The sediments were deposited in the

Yezo forearc basin during the Aptian–Maastrichtian of the Cretaceous (Takashima *et al*., 2004).

The Yezo Group is widely distributed in the Kotanbetsu area, northwestern Hokkaido (Figures 1, 2; Igi *et al*., 1958; Tsushima *et al*., 1958; Okada and Matsumoto, 1969; Toshimitsu, 1988; Nishida *et al*., 1992, 1993, 1996, 1997; Wani and Hirano, 1999, 2000; Wani, 2003; Takashima *et al.*, 2004; Tsujino, 2009), and subdivided into the Maruyama, Hikagenosawa, Saku, Haborogawa and Hakobuchi formations, in ascending order (Takashima *et al.*, 2004; Tsujino, 2009). The Hakobuchi Formation is exposed only around the Nakanosawa River (Tsujino, 2009), but this area was not investigated in this study (Figure 2).

The Haborogawa Formation in the Kotanbetsu area is subdivided into two parts (Figures 2–4; Takashima *et al*., 2010; Ikeda and Wani, 2012). The lower part of the Haborogawa Formation in the Kotanbetsu area is composed of siltstone, siltstone with interbedded sandstone, sandy siltstone, and sandstone (Figures 3, 4; Toshimitsu, 1988; Wani and Hirano, 2000; Wani, 2003). The upper part of the Haborogawa Formation in the Kotanbetsu area consists of three sequences that coarsen upwards from sandy siltstone to sandstone (Figures 3, 4; Toshimitsu, 1988; Wani and Hirano, 1999, 2000; Wani, 2003). The thickness of the Haborogawa Formation in Kotanbetsu area is

approximately 2100 m (Figure 4). Based on age index ammonoids and inoceramids, the geological age of the Haborogawa Formation in the Kotanbetsu area is estimated to be Turonian–early Campanian (Figure 4; Wani and Hirano, 1999, 2000; Wani, 2003; Ikeda and Wani, 2012).

The stratigraphy of the Yezo Group in the Obira area has been studied in detail (Igi *et al*., 1958; Tsushima *et al*., 1958; Takayanagi, 1960; Tanaka, 1963; Tanabe *et al*., 1977; Taketani, 1982; Sekine *et al*., 1985; Toshimitsu, 1988; Asai and Hirano, 1990; Hasegawa and Saito, 1993; Nishi *et al*., 2003; Funaki and Hirano, 2004; Oizumi *et al*., 2005; Hayakawa and Hirano, 2013; Honda and Hirano, 2014). The Yezo Group is subdivided into the Takimibashi, Tenkaritoge, Saku, and Haborogawa formations in the Obira area, in ascending order (Funaki and Hirano, 2004). The Haborogawa Formation in the Obira area consists of siltstone with interbedded sandstone, alternating beds of sandstone and siltstone, and sandstone (Funaki and Hirano, 2004; Oizumi *et al*., 2005). The thickness of the Haborogawa Formation in Obira area is approximately 2200 m (Funaki and Hirano, 2004; Oizumi *et al*., 2005). The geological age of the Haborogawa Formation in the Obira area is estimated to be Turonian–early Campanian based on age index ammonoids and inoceramids (Funaki and Hirano, 2004; Oizumi *et al*., 2005; Hayakawa and Hirano, 2013).

The Haborogawa Formation in these areas is subdivided to twelve units (Ua–Ul) by Tsushima *et al*. (1958) and Tanaka (1963). After that, the uppermost Unit Ul is identified as the Hakobuchi Formation in the Kotanbetsu area by Tsujino (2009). In the northwestern area including, the Kotanbetsu and Obira areas, several thick sandstones can be traced as key beds of the Haborogawa Formation (e.g. MHs0, MHs2–MHs5, UHs1–UHs4, named by Toshimitsu, 1985, 1988).

Thirty-three specimens assigned to *Hyphantoceras orientale* and *H. transitorium* obtained from the units Ud–f, Ug and Uh in the Kotanbetsu and Obira areas were examined in this study (Figures 5B–E, 6; Table 2). These specimens are housed in the Mikasa City Museum. In addition to these specimens, two specimens assigned to *H. transitorium* obtained from the Kotanbetsu area without precise locality records, housed in the Nakagawa Museum of Natural History are also examined (Figure 5A, F; Table 2). All specimens have been recovered from spherical or mushroom-shaped calcareous concretions. The type specimens of *H. orientale*, *H. transitorium*, and *H. oshimai*, housed in the University Museum, the University of Tokyo and the National Museum of Nature and Science were also examined (Figure 7; Table 2).

Correspondence between abbreviations prefixed to registered number and institutions is as follows: MCM-W = Mikasa City Museum; NYC and NYCH =

Nakagawa Museum of Natural History; UMUT MM = the University Museum, the University of Tokyo; NMNS PM= National Museum of Nature and Science, Tsukuba.

Morphological characteristics of *Hyphantoceras transitorium*

Hyphantoceras transitorium Matsumoto, 1977, described originally as a monotypic species, is characterized by turreted shell with whorls slightly separated from each other (Matsumoto, 1977b; Figure 7E). Newly found ten additional specimens examined in the present study are regarded to this species (MCM-W0269-1, MCM-W1620–W1626, KYC86, KYCH36; Figure 5; Table 2). The shell sizes of the present specimens are ranged within 2.4–13.9 mm in whorl tube diameter (Table 2). The present specimens show a wide range of variation for the degree of separation of each whorl. Specifically, some have simple tightly-coiled whorls (Figure 5A–C), while others have tightly coiled whorls followed by loosely coiled whorls (Figure 5D–F). Furthermore, there is intraspecific variation on timing of the change of whorl shapes among the specimens (Figure 5D–F). For instance, the whorl shape transition occurs on 5.0 mm in whorl tube diameter in MCM-W1625 (Figure 5D), and on 8.0 mm in whorl tube diameter in MCM-W1622 (Figure 5E) and KYCH36 (Figure 5F), respectively. A

retroversally hooked body chamber is not observed in the present specimens. The ribs are coarse (19–24 ribs per half whorl), and slightly prorsiradiate (Matsumoto, 1977b; Figures 5, 7E, 8A–C). Ribs with three or four tubercles occur on every other or every third rib (Matsumoto, 1977b; Figures 5, 7E, 8A–C). Two ribs looped at tubercle are observed in some ribs of some specimens (Matsumoto, 1977b; Figure 8B). The siphuncle is positioned at the middle of the external side (Matsumoto, 1977b). The coiling is sinistral in all examined specimens (Figures 5, 7E; Table 2).

Morphological characteristics of *Hyphantoceras orientale*

Hyphantoceras orientale (Yabe, 1904) is characterized by extremely elongated and slowly enlarging whorls (Yabe, 1904; Matsumoto, 1977b; Figure 7A, B). Twenty-five specimens from Kotanbetsu and Obira areas are assigned to this species (MCM-W0335-1, MCM-W1627–W1650; Figure 6). The shell sizes of present specimens are ranged within 3.0–11.8 mm in whorl tube diameter (Table 2). The whorl shapes do not change drastically in the range of preserved part of the present specimens (Figures 6). Okamoto (1988a) described the initial straight whorl of *H. orientale*, but that part is not preserved in the present specimens. The ribs are not dense (11–20 ribs

per half whorl; Figures 6, 7A, B, 8D, E), much coarse in some specimens (Figures 6D, 7A, 8E), and rather prorsiradiate (Matsumoto, 1977b; Figures 6, 7A, B, 8 D, E). Ribs with three or four tubercles occur on every other rib or in higher frequency (Figures 6, 7A, B, 8D, E). The coiling is mostly sinistral (Matsumoto, 1977b). The paratype of *Hyphantoceras oshimai* (Yabe, 1904) can be assigned to this species (Shimizu, 1935; Wright and Matsumoto, 1954; Matsumoto, 1977b; Figure 7C).

Stratigraphic occurrences of *Hyphantoceras transitorium* and *H. orientale*

The stratigraphic occurrences of *Hyphantoceras transitorium* and *H. orientale* in the Kotanbetsu area are shown in Figures 3 and 4. The stratigraphic ranges of two species do not overlap. *Hyphantoceras transitorium* occurs in the lower part of Unit Ug and the upper part of units Ud–f of the Haborogawa Formation, which is in *Inoceramus amakusensis* Zone (= Santonian; Toshimitsu *et al*., 1995; 2007), and *H. orientale* appears in the upper part of Unit Ug and Unit Uh of the Haborogawa Formation, which is in *Inoceramus amakusensis* Zone (= Santonian; Toshimitsu *et al*., 1995; 2007).

In the Obira area, one specimen (MCM-W0269-1) assigned to *Hyphantoceras transitorium* occurs in the horizon between MHs 3 or MHs 4 and MHs 2, and the other

specimen (MCM-W0335-1) assigned to *H. orientale* occurs in the horizon a few meters below UHs1 (Oizumi *et al*., 2005). The horizons of two species in the Obira area are concordant with those in the Kotanbetsu area. Matsumoto (1977b) reported the specimens assigned to *H. orientale* probably derived from units Ui–j (*Platyceramus japonicus* Zone; = lowermost Campanian; Toshimitsu *et al*., 1995; 2007) in Obira area.

Okamoto *et al*. (2003) listed *Hyphantoceras orientale* from upper part of Unit Ug and Unit Uh in Haboro area. The results of this study in Kotanbetsu and Obira areas are concordant with the stratigraphic occurrence of *H. orientale* in Haboro area.

Discussion

Variation of *Hyphantoceras transitorium*

Hyphantoceras transitorium was elected by single specimen from Mikasa area, Hokkaido as a monotypy (Matsumoto, 1977b; Figure 7E). However, newly found additional ten specimens of *H. transitorium* show that this species is not monotypy, but has the wide intraspecific variation for the whorl shape and the timing of whorl shape change (Figure 5). The wide intraspecific variations for whorl shape are observed in other nostoceratid ammonoids (e.g. *Ainoceras*: Matsumoto and Kanie, 1967; *Yezoceras*:

Matsumoto, 1977b; *Eubostrychoceras*: Matsumoto, 1977b; Okamoto, 1989; Misaki and Maeda, 2010). Switching timing of the shell ornament phase is also variable even in the single species of some heteromorph ammonoids (*Polyptychoceras*: Okamoto and Shibata, 1997; *Baculites*: Tsujino *et al*., 2003). Several previous studies presume that the ontogenetic change of whorl shape is related to the change of the mode of life (Okamoto, 1988a, b).

Matsumoto (1977b) pointed out that the deviated part of later whorl in the holotype of *Hyphantoceras transitorium* could be a partially preserved retroversally hooked body chamber. On the other hand, more loosely coiled parts following to the tightly coiled whorls are recognized in some present specimens (Figure 5A–C). Considering this, it is not certain to regard the deviation of whorl of holotype as an indication of the end of growth.

Phylogenetic lineage of two *Hyphantoceras* species

Two species, *Hyphantoceras transitorium*, and *H. orientale* share many characters of shell ornamentation characteristics, such as prorsiradiate and relatively frequent tuberculate ribs, no flared ribs, and three or four tubercles on each tuberculate rib (Figures 5, 6, 7A–C, E, 8A–E; Table 2). The similarity of the shell surface

ornamentations of the two species suggests that they are close in the phylogeny. In addition, two species occur successively (Figures 3, 4), and the specimen (MCM-W1625) of *H. transitorium* with the loosely coiled whorl for the most part occurs in the topmost horizon of the stratigraphic range (Figure 5D). The specimen might be the intermediate form between *H. transitorium* (e.g. holotype; Figure 7E) and *H. orientale*. Several lines of evidence indicate a high possibility that *H. orientale* was derived from *H. transitorium* during Santonian. This lineage was probably indigenous to the northwestern Pacific realm.

Relationships with the other species of *Hyphantoceras* in the Yezo Group

Hyphantoceras oshimai (Yabe, 1904, p. 12, pl. 3, fig. 5; Figure 7D) shares the loosely coiled whorls and many features of shell surface ornamentation such as coarse, slightly prorsiradiate, and sometimes looped at tubercles ribs with some specimens of *H. transitorium* (Figures 5D–F, 8A–C, F). However, *H. oshimai* is much larger than *H. transitorium*, and the whorl sizes of two species are not overlapped (Figures 5, 7D; Table 2). *Hyphantoceras oshimai* is listed and reported from the same stratigraphic level (Unit Ug) in Kotanbetsu area (Wani and Hirano, 2000) and the stratigraphic levels just below the occurrences of *H. transitorium* (Unit Uf) in Haboro and Obira areas

(Matsumoto, 1977b; Okamoto *et al*., 2003). Considering similarities of two species, there is a possibility that two species are closely related. However, the phylogenetic relationship between two species cannot be concluded in this paper, because the whorl sizes of two species differ considerably and stratigraphic data is insufficient. The careful comparison through the ontogeny, and investigation of FAD of *H. transitorium* and LAD of *H. oshimai* are necessary for clarifying the relationship between two species.

Hyphantoceras venustum (Yabe, 1904, p. 11, pl. 3, fig. 4, pl. 5, figs. 1 and 2) differs from *H. transitorium*, *H. orientale*, and *H. oshimai* by its periodic tuberculate flared ribs, numerous intervening fine ribs, and the wide umbilicus. *Hyphantoceras heteromorphum* (Matsumoto, 1977b, p. 314, pl. 47, fig. 2) also differs from *H. transitorium*, *H. orientale*, and *H. oshimai*, by its periodic tuberculate flared ribs, numerous intervening fine ribs, and irregularly coiled whorls. These comparisons suggest that *H. venustum* and *H. heteromorphum* are out of the lineage of *H. transitorium–H. orientale*.

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Figure and Table captions

Figure 1. Index map of Hokkaido showing the distribution of the Yezo Group (black areas) and location of the Kotanbetsu and Obira areas. Modified from Takashima *et al*. (2004).

Figure 2. Geological map and cross section of the Kotanbetsu, northwestern Hokkaido, northern Japan.

Figure 3. Columnar section of the Yezo Group in the Kotanbetsu area. 1–3, the Kotanbetsu River; 4–5, the Horotate Creek; 6, the Kaminosawa Creek. The occurrences of *Hyphantoceras transitorium* and *H. orientale* are shown.

Figure 4. Generalized columnar section of the Yezo Group in the Kotanbetsu area, with the stratigraphic occurrences of *Hyphantoceras transitorium* and *H. orientale*, and the stage diagnostic species of ammonoids and inoceramids. The numbers on the right side of the columnar section reflect the locality numbers in Appendix 1.

Figure 5. *Hyphantoceras transitorium* from the Kotanbetsu area. **A**, KYC86 from Kotanbetsu area; **B**, MCM-W1624 from locality HR109 of the Horotatesawa Creek; **C**, MCM-W1623 from locality HR051 of the Horotatesawa Creek; **D**, MCM-W1625 from locality KT133 of the Kotanbetsu River; **E**, MCM-W1622

from locality KT141 of the Kotanbetsu River; **F**, KYCH36 from Kotanbetsu area.

Figure 6. *Hyphantoceras orientale* from the Kotanbetsu area. **A**, MCM-W1638 from locality KT045 of the Kotanbetsu River; **B**, MCM-W1636 from locality KT035 of the Kotanbetsu River; **C**, MCM-W1643 from locality HR015 of the Kaminosawa; **D**, MCM-W1647 from locality KM015 of the Kaminosawa Creek.

Figure 7. Type specimens of *Hyphantoceras orientale* (Yabe, 1904), *H. oshimai* (Yabe, 1904), and *H. transitorium* Matsumoto, 1977. **A**, **B**, *H. orientale*; A, holotype (UMUT MM7572a); B, paratype (UMUT MM7572b); **C**, *H. orientale* (*H. oshimai*, paratype in the original description; UMUT MM7554); **D**, *H. oshimai*, holotype (UMUT MM7553); **E**, *H. transitorium*, holotype (NMNS PM7261).

Figure 8. Photographs of shell surface ornamentations. **A**–**C**, *Hyphantoceras transitorium*; A, MCM-W1624; B, MCM-W1621; C, NMNS PM7261, holotype; **D**, **E**, *Hyphantoceras orientale*; D, MCM-W1638; E, UMUT MM7572a, holotype; **F**, *Hyphantoceras oshimai* (Yabe, 1904), UMUT MM7553, holotype.

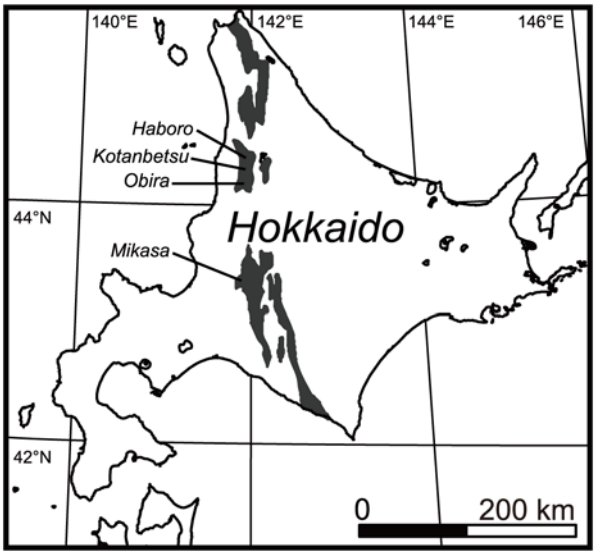
Table 1. The geographical and chronological distribution of five *Hyphantoceras* species. These data are compiled from previous studies (Yabe, 1904; Shimizu, 1935; Matsumoto, 1942, 1943, 1959, 1977a, b; Igi *et al*., 1958; Tsushima *et al*., 1958; Haggart, 1984; Toshimitsu, 1988; Zonova and Yazykova, 1998; Wani and Hirano,

2000; Moriya and Hirano, 2001; Kodama *et al*., 2002; Okamoto *et al*., 2003; Yazykova, 2004; Oizumi *et al*., 2005; Jagt-Yazykova, 2011).

Table 2. List and measurements of specimens. The locality numbers of the specimens from the Kotanbetsu area correspond to these in Appendix 1. MCM-W0269-1 and MCM-W0335-1 are specimens listed in Oizumi *et al*. (2005). The localities of the specimens are cited in Oizumi *et al*. (2005). See Aiba *et al*. (2017, fig. 7) for the measuring method.

Appendix

Appendix 1. Route maps in the Kotanbetsu area.



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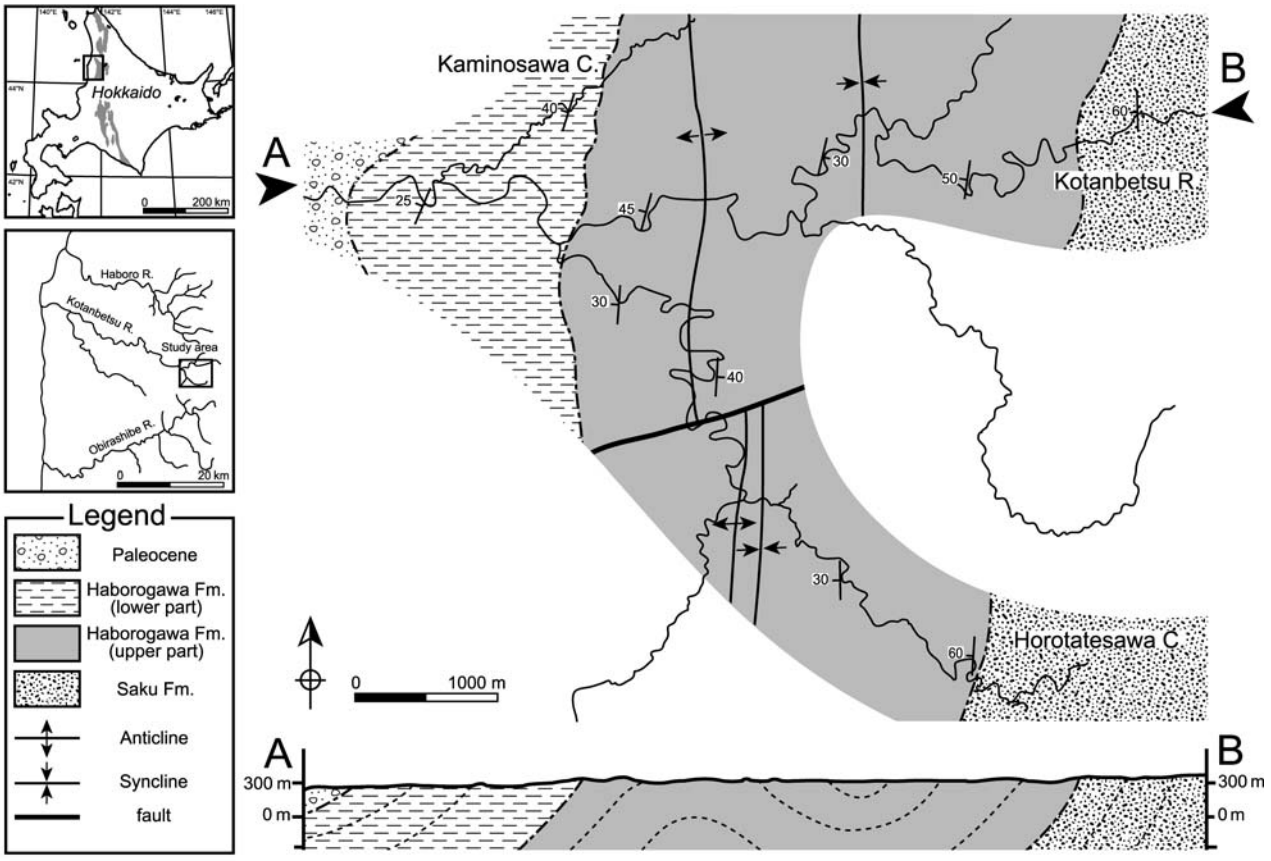

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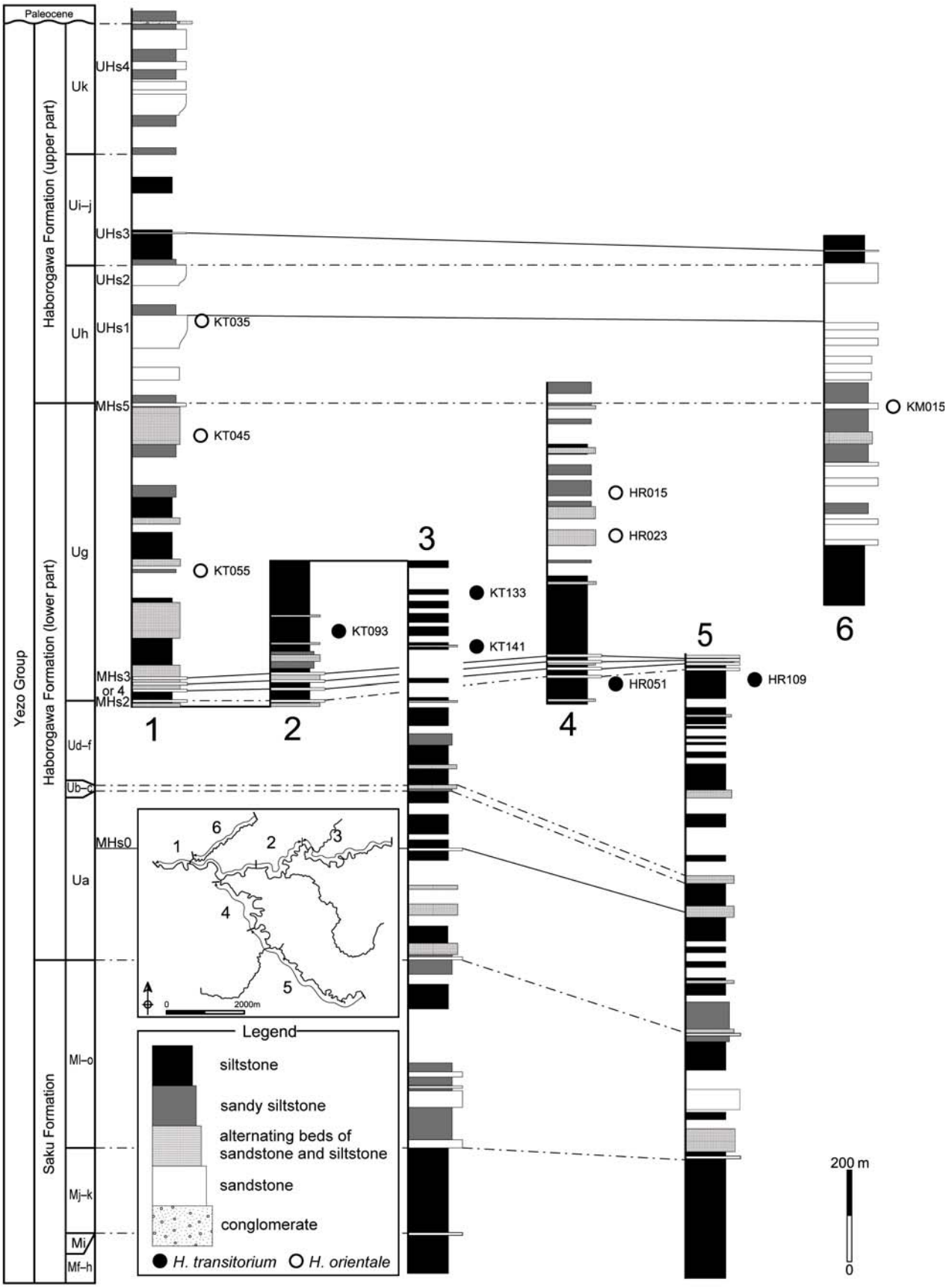

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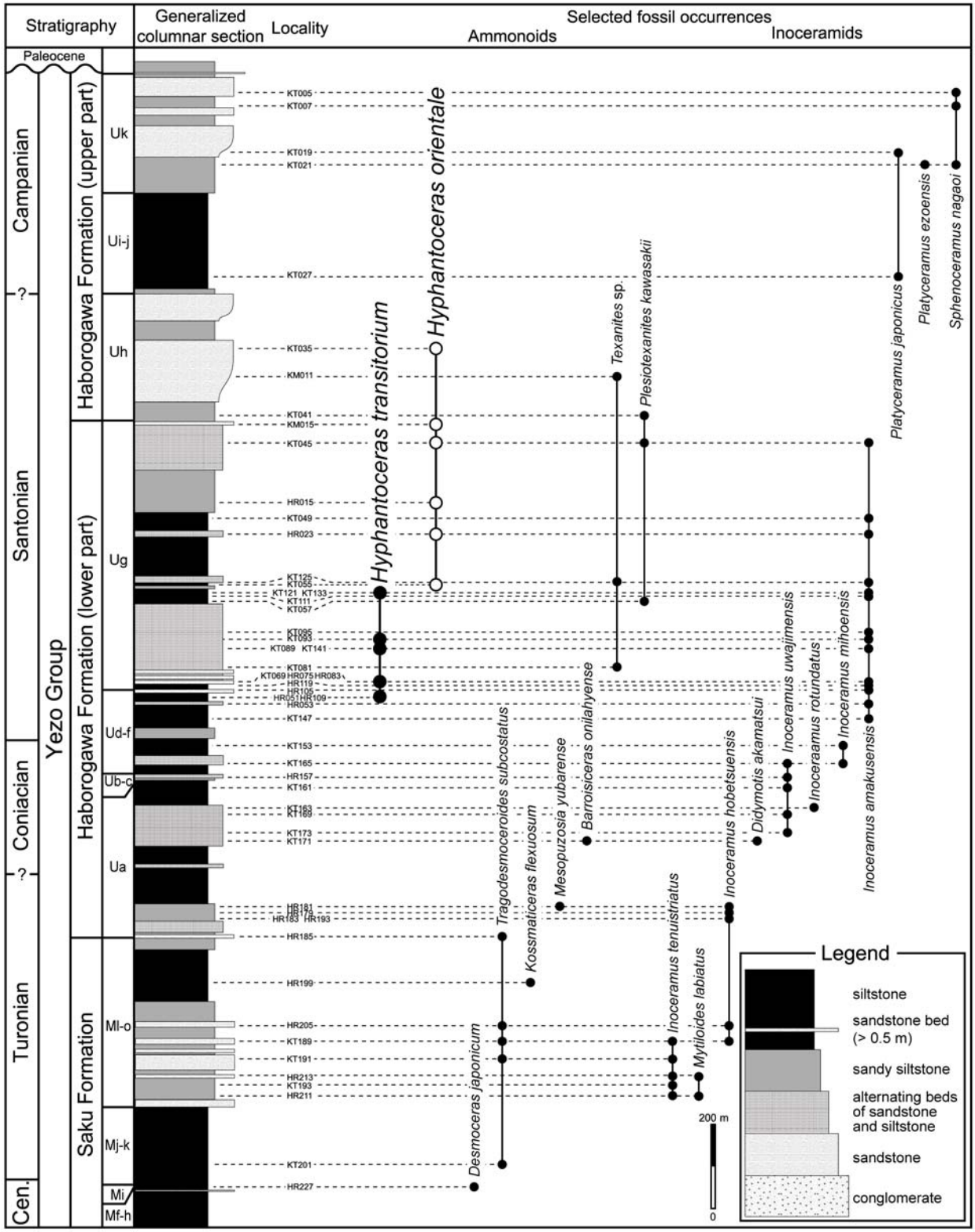

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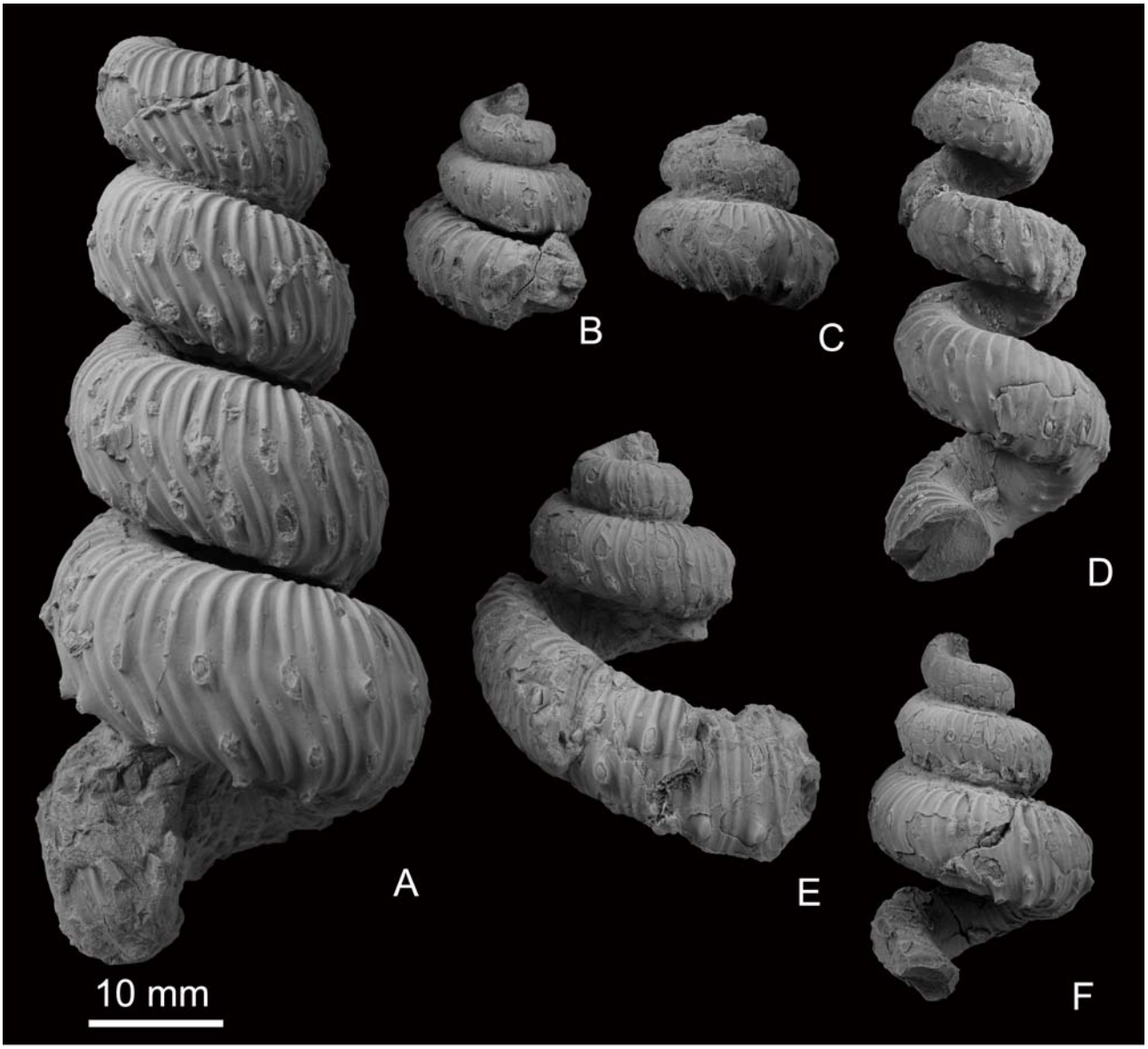

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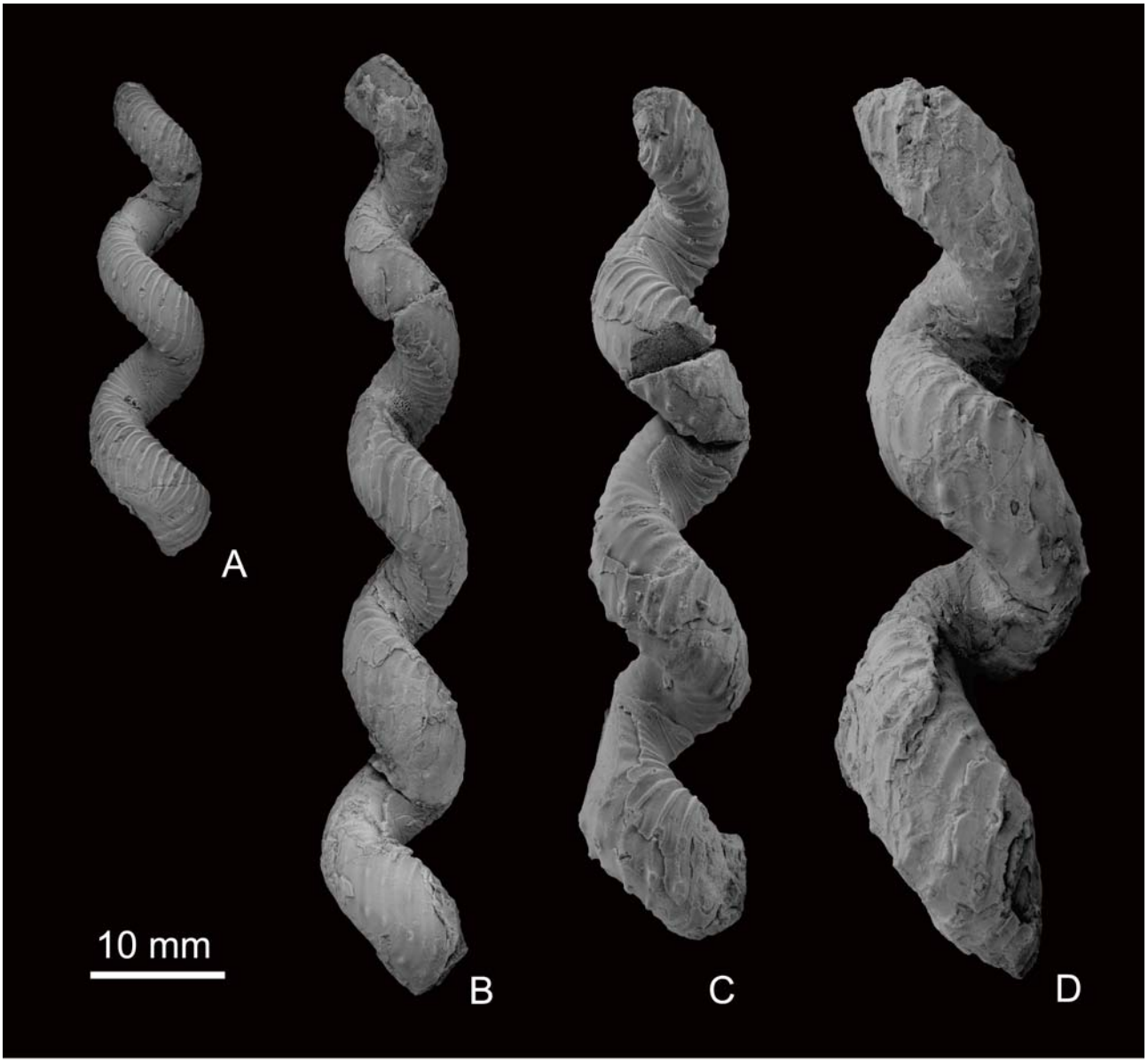

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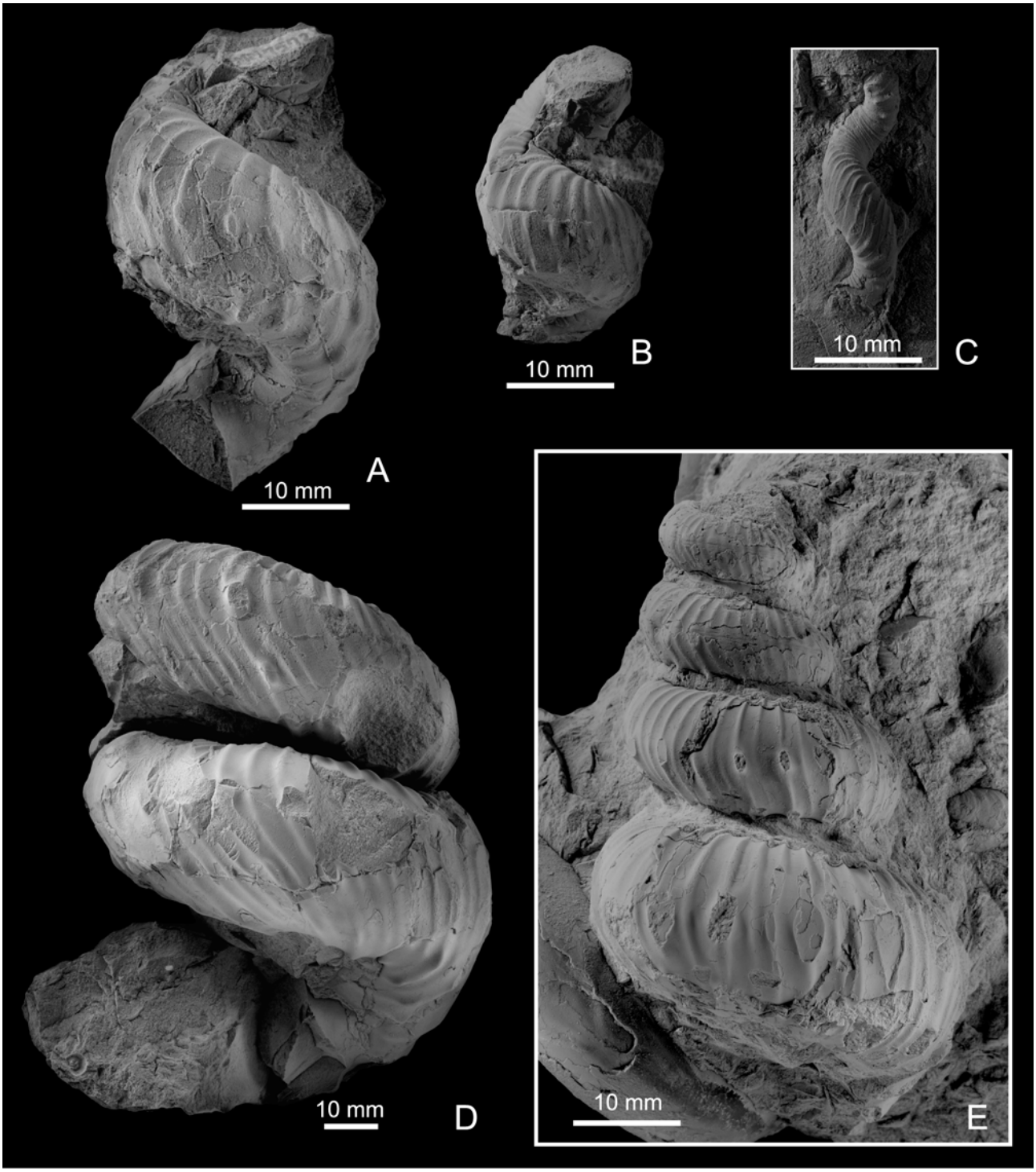

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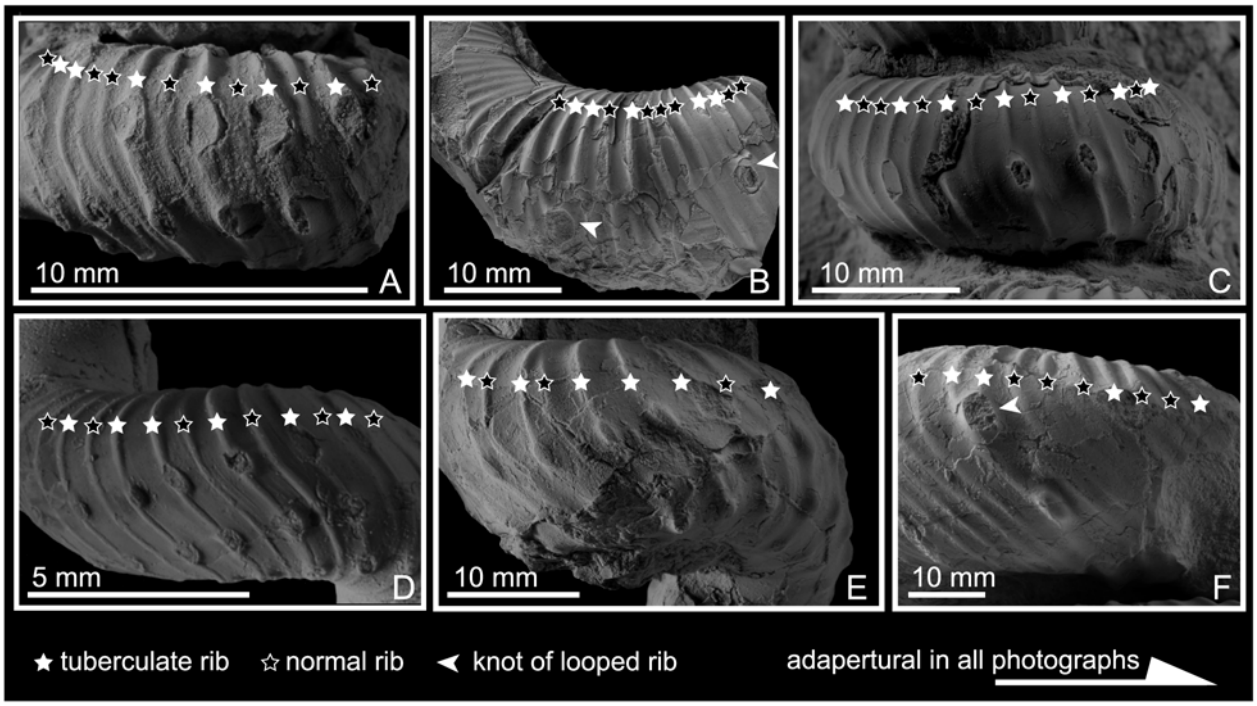

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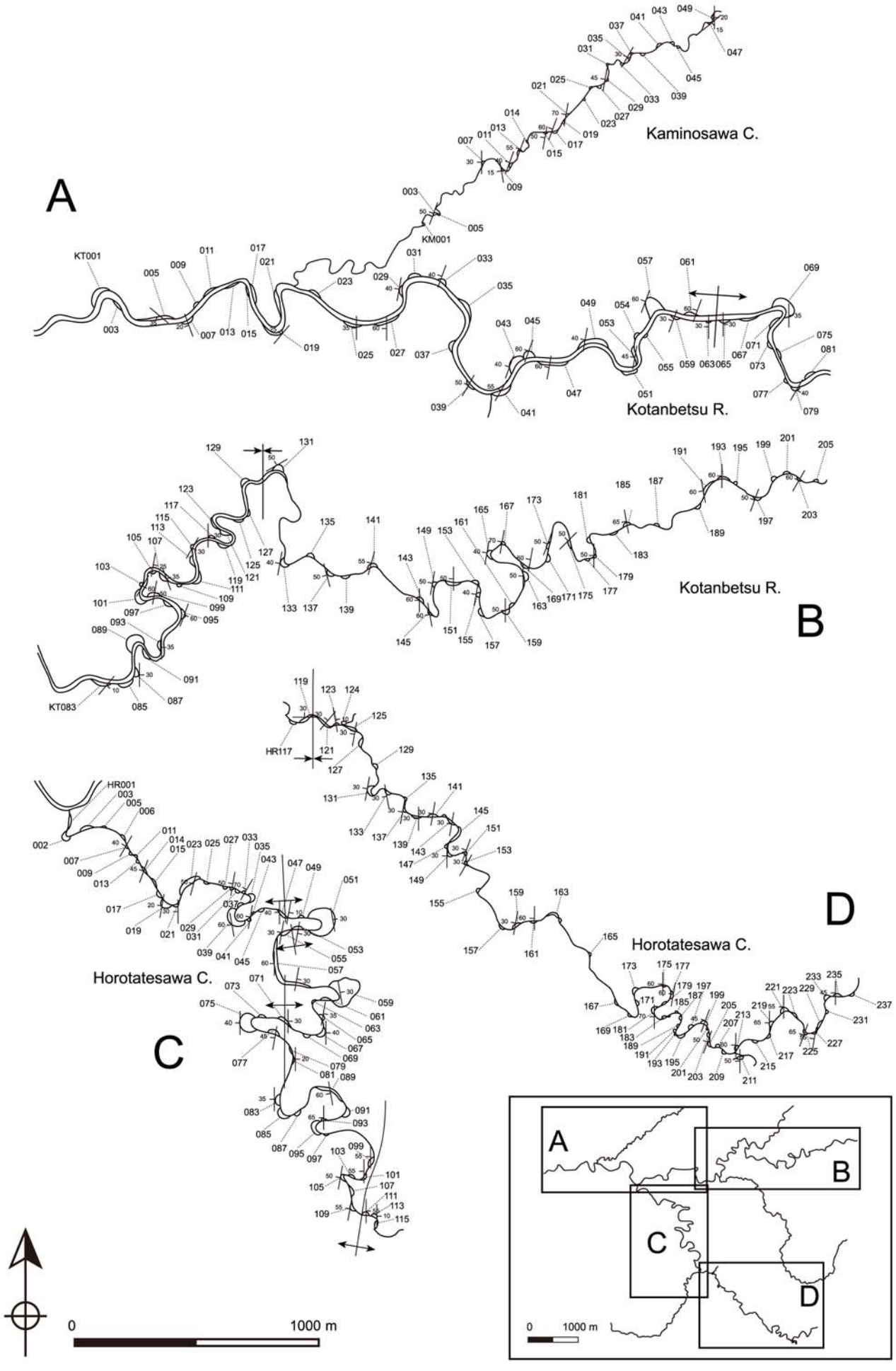
Species	Geographical distribution	Chronological distribution
H. venustum (Yabe, 1904)	Hokkaido, northern Japan; southern Sakhalin, Russian Far East; California, USA	Turonian–Campanian
H. oshimai (Yabe, 1904)	Hokkaido, northern Japan; southern Sakhalin, Russian Far East	Santonian
H. orientale (Yabe, 1904)	Hokkaido, northern Japan; southern Sakhalin, Russian Far East	Santonian–Campanian
H. transitorium Matsumoto, 1977	Hokkaido, northern Japan	Santonian
H. heteromorphum Matsumoto, 1977	Hokkaido, northern Japan; southern Sakhalin, Russian Far East	Coniacian–Santonian

Registered no.	Species	Type	Maximum height (mm)	Minimum major axis diameter in cross section (mm)
MCM-W1620	*H . transitorium*	-	15.8	4.8
MCM-W1621	*H . transitorium*	-	16.5	11.5
MCM-W1622	*H . transitorium*	-	28.1	2.9
MCM-W1623	*H . transitorium*	-	14.4	3.6
MCM-W1624	*H . transitorium*	-	16.0	2.4
MCM-W1625	*H . transitorium*	-	38.4	4.0
MCM-W1626	*H . transitorium*	-	7.0	4.9
MCM-W1627	*H . orientale*	-	50.8	4.5
MCM-W1628	*H . orientale*	-	13.3	3.4
MCM-W1629	*H . orientale*	-	11.3	3.0
MCM-W1630	*H . orientale*	-	28.4	6.5
MCM-W1631	*H . orientale*	-	16.8	4.0
MCM-W1632	*H . orientale*	-	12.3	3.5
MCM-W1633	*H . orientale*	-	15.9	4.4
MCM-W1634	*H . orientale*	-	28.3	4.6
MCM-W1635	*H . orientale*	-	54.6	4.8
MCM-W1636	*H . orientale*	-	70.0	5.2
MCM-W1637	*H . orientale*	-	40.3	3.3
MCM-W1638	*H . orientale*	-	35.1	3.6
MCM-W1639	*H . orientale*	-	14.6	4.0
MCM-W1640	*H . orientale*	-	31.6	5.7
MCM-W1641	*H . orientale*	-	35.3	3.3
MCM-W1642	*H . orientale*	-	17.1	5.7
MCM-W1643	*H . orientale*	-	63.2	6.9
MCM-W1644	*H . orientale*	-	41.8	7.7
MCM-W1645	*H . orientale*	-	29.9	11.1
MCM-W1646	*H . orientale*	-	26.6	9.3
MCM-W1647	*H . orientale*	-	64.7	8.5
MCM-W1648	*H . orientale*	-	59.3	5.7
MCM-W1649	*H . orientale*	-	37.0	8.2
MCM-W1650	*H . orientale*	-	20.4	3.3
KYC86	*H . transitorium*	-	58.4	7.2
KYCH36	*H . transitorium*	-	24.1	2.9
MCM-W0269-1	*H . transitorium*	-	11.4	3.0
MCM-W0335-1	*H . orientale*	-	36.7	5.1
UMUT MM7553	*H . oshimai* (Yabe, 1904)	holotype	99.9	26.6
UMUT MM7554	*H . oshimai* (Yabe, 1904)	paratype	23.5	-
UMUT MM7572a	*H . orientale* (Yabe, 1904)	holotype	41.1	11.1
UMUT MM7572b	*H . orientale* (Yabe, 1904)	paratype	26.3	8.3
NMNS PM7261	*H . transitorium* Matsumoto, 1977	holotype	44.4	4.2

Maximum major axis diameter in cross section (mm)	Locality information		
	Locality no.	Area	Age
7.3	KT093	Kotanbetsu	Santonian
13.0	KT093	Kotanbetsu	Santonian
8.8	KT141	Kotanbetsu	Santonian
6.8	HR051	Kotanbetsu	Santonian
6.2	HR109	Kotanbetsu	Santonian
8.3	KT133	Kotanbetsu	Santonian
5.8	KT133	Kotanbetsu	Santonian
5.1	KT035	Kotanbetsu	Santonian
4.2	KT035	Kotanbetsu	Santonian
3.4	KT035	Kotanbetsu	Santonian
7.0	KT035	Kotanbetsu	Santonian
4.7	KT035	Kotanbetsu	Santonian
4.0	KT035	Kotanbetsu	Santonian
4.9	KT035	Kotanbetsu	Santonian
5.4	KT035	Kotanbetsu	Santonian
6.8	KT035	Kotanbetsu	Santonian
7.1	KT035	Kotanbetsu	Santonian
4.4	KT045	Kotanbetsu	Santonian
5.7	KT045	Kotanbetsu	Santonian
4.9	KT045	Kotanbetsu	Santonian
6.2	KT045	Kotanbetsu	Santonian
4.7	KT055	Kotanbetsu	Santonian
6.4	KT055	Kotanbetsu	Santonian
8.5	HR015	Kotanbetsu	Santonian
10.1	HR023	Kotanbetsu	Santonian
11.8	HR023	Kotanbetsu	Santonian
9.5	HR023	Kotanbetsu	Santonian
11.6	KM015	Kotanbetsu	Santonian
7.6	KM015	Kotanbetsu	Santonian
9.2	KM015	Kotanbetsu	Santonian
4.1	KM015	Kotanbetsu	Santonian
13.9	unknown	Kotanbetsu	unknown
8.4	unknown	Kotanbetsu	unknown
5.9	OB35085	Obira	Santonian
6.7	OB36153	Obira	Santonian
38.2	"Ikushumbetsu River"	Mikasa	"*Scaphites* -beds"
-	"Shi-kuruki"	Yubari	"*Scaphites* -beds"
13.8	unknown	Urakawa	"the upper Ammonite-beds"
-	unknown	Mikasa	"*Pachydiscus* -beds"?
13.6	"Inarizawa"	Mikasa	Santonian?



Aiba, Appendix 1, 100%