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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 newly found specimens with precise stratigraphic occurrences in the Kotanbetsu and Obira areas, northwestern Hokkaido. Two closely related species, *Hyphantoceras transitorium* and *H. orientale*, were recognized in the examined specimens from the Kotanbetsu and Obira areas. Specimens of *H. transitorium* show wide intraspecific variation in the whorl shape. The stratigraphic occurrences of the 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 *H. orientale* was derived from *H. transitorium*. The presumed lineage is likely indigenous to the northwestern Pacific realm in the Santonian–earliest Campanian. *Hyphantoceras venustum* and *H. heteromorphum* might stand outside a *H. transitorium–H. orientale* lineage, judging from differences of their shell surface ornamentation.

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 all species of *Hyphantoceras* were described from 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 the 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;

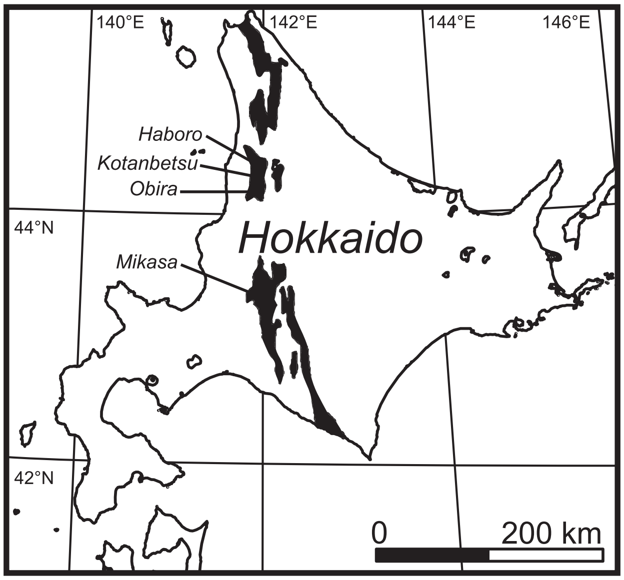

Figure 1. Index map of Hokkaido showing the distribution of the Yezo Group (black areas) and location of the Kotanbetsu and Obira areas. Modified from Takashima *et al*. (2004).

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 the latter two species to genus *Hyphantoceras*. Subsequently Wright and Matsumoto (1954) regarded "*Heteroceras*(?) *orientale*" as a species of *Hyphantoceras*. These identifications were accepted 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 the 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.

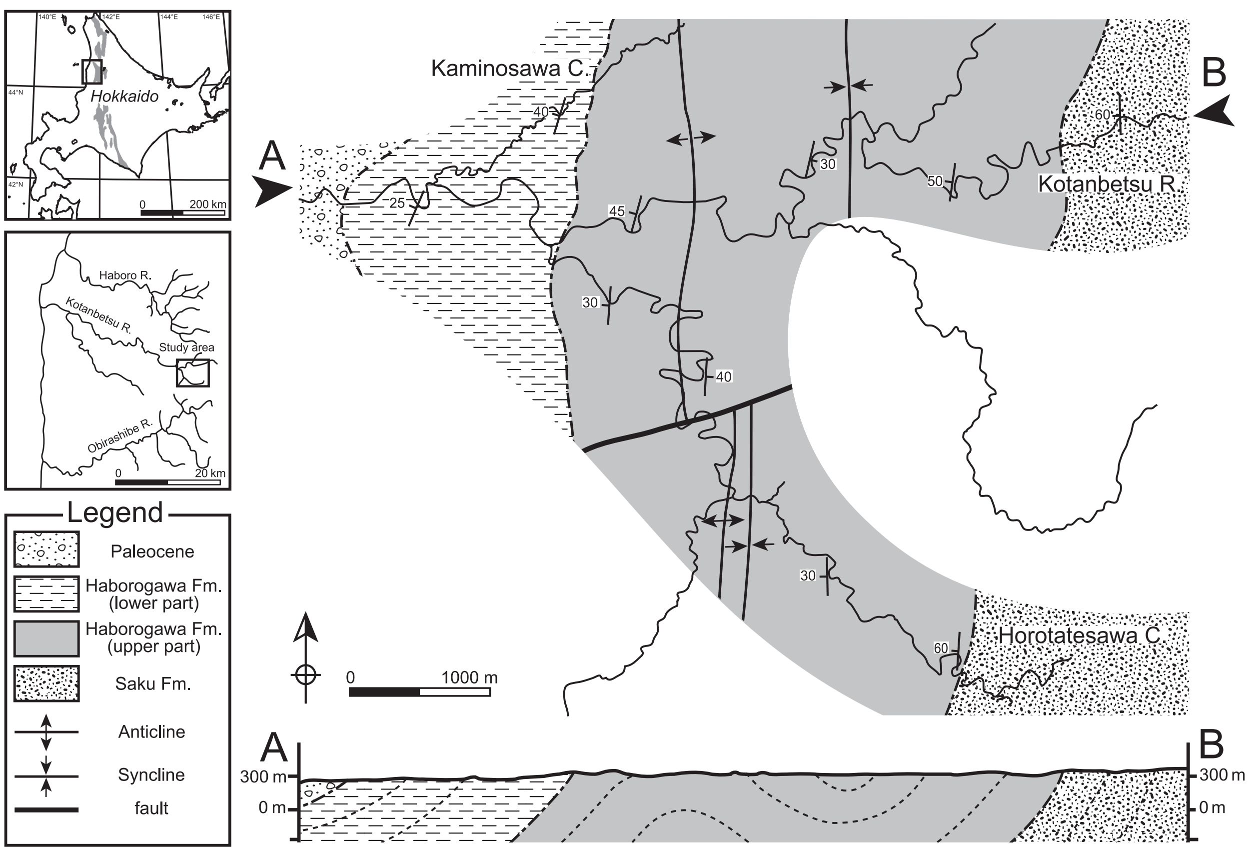

Figure 2. Geological map and cross section of the Kotanbetsu area, northwestern Hokkaido, northern Japan.

Table 1. The geographical and chronological distributions 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).

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

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, Russian Far East (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 the 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 the 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 into 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 sand-

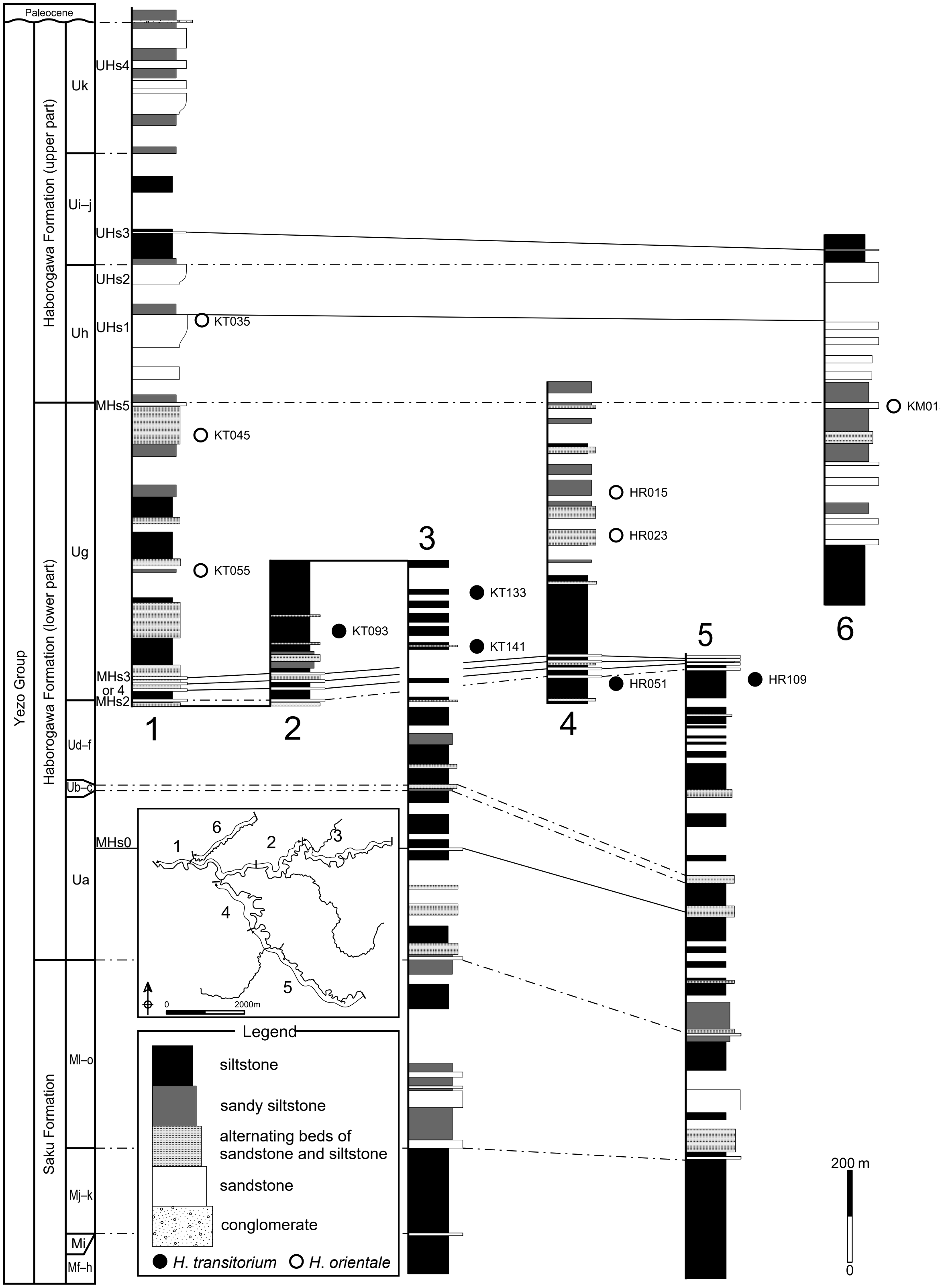

Figure 3. Columnar section of the Yezo Group in the Kotanbetsu area. 1–3, the Kotanbetsu River; 4, 5, the Horotate Creek; 6, the Kaminosawa Creek. The occurrences of *Hyphantoceras transitorium* (solid black circles) and *H. orientale* (white circles) are shown.

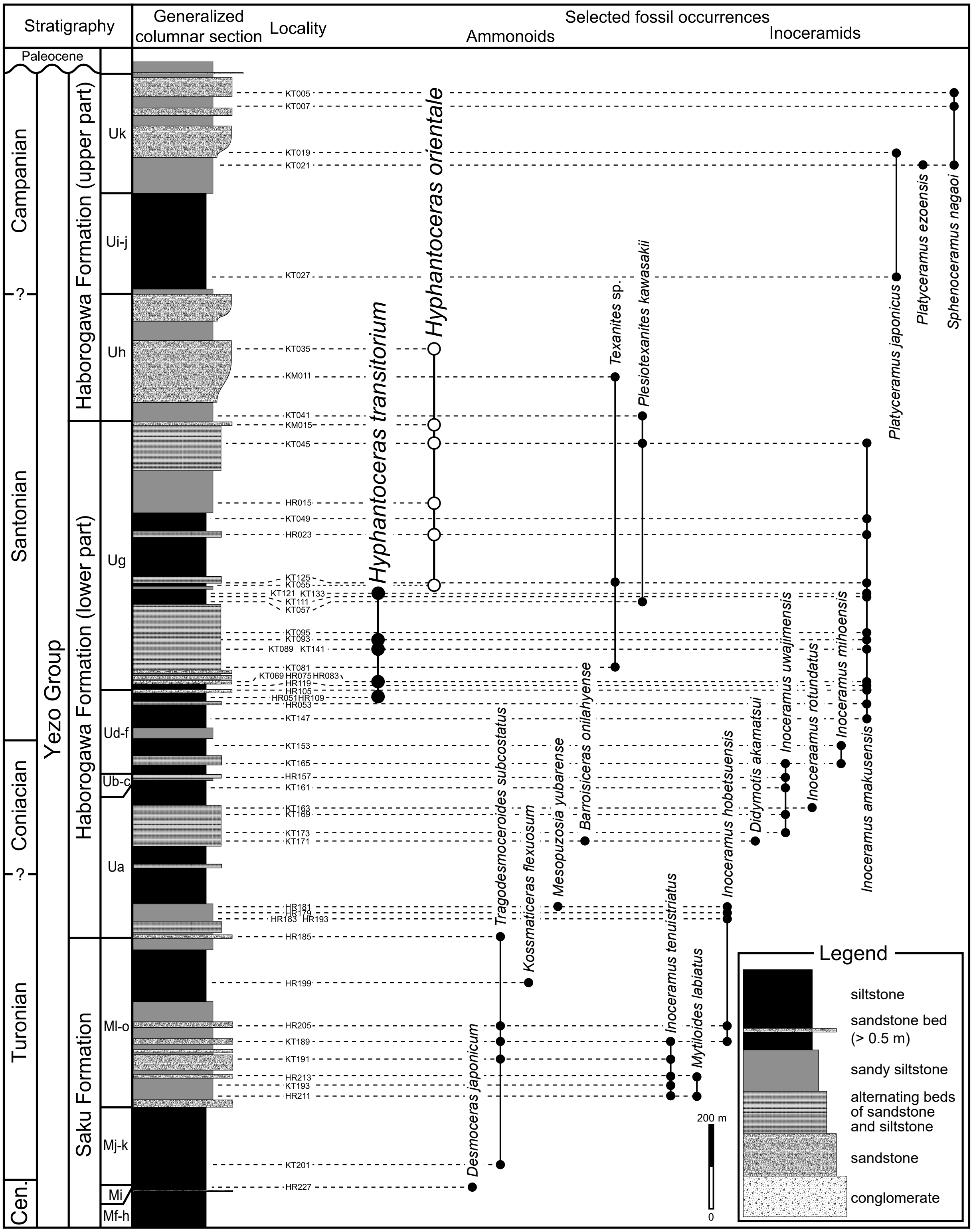

Figure 4. Generalized columnar section of the Yezo Group in the Kotanbetsu area, with the stratigraphic occurrences of *Hyphantoceras transitorium* and *H. orientale*, and the stage-diagnostic species of ammonoids and inoceramids. The numbers on the right side of the columnar section reflect the locality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

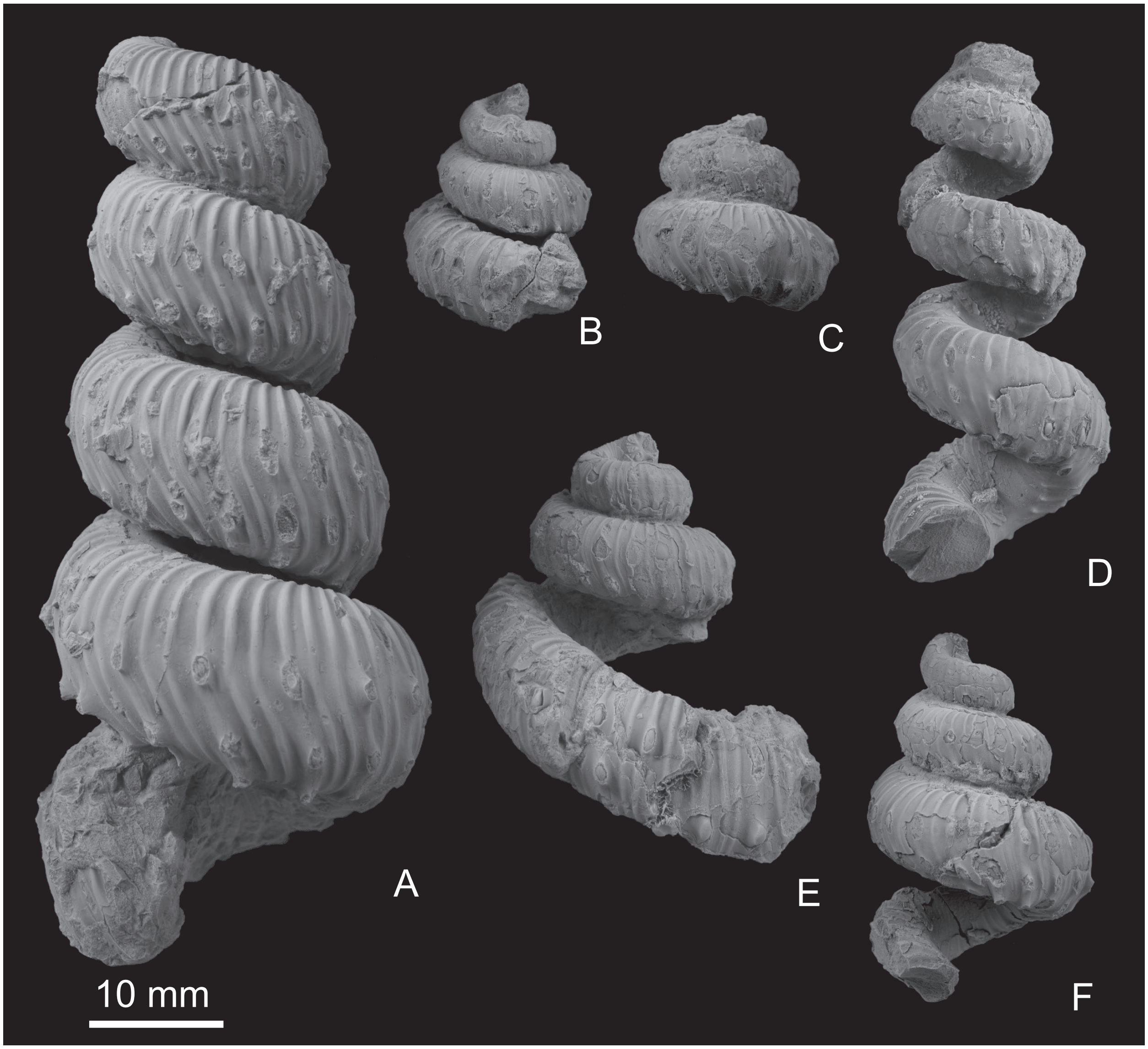

Figure 5. *Hyphantoceras transitorium* from the Kotanbetsu area. **A**, KYC86 from Kotanbetsu area; **B**, MCM-W1624 from locality HR109 of the Horotatesawa Creek; **C**, MCM-W1623 from locality HR051 of the Horotatesawa Creek; **D**, MCM-W1625 from locality KT133 of the Kotanbetsu River; **E**, MCM-W1622 from locality KT141 of the Kotanbetsu River; **F**, KYCH36 from the Kotanbetsu area.

stone layers 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 were 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, Tsukuba were also examined (Figure 7; Table 2).

Correspondence between abbreviations prefixed to registered number and institutions is as follows: MCM-W, Mikasa City Museum; KYC and KYCH, Nakagawa Museum of Natural History; UMUT MM, the University Museum, the University of Tokyo; NMNS PM, National Museum of Nature and Science, Tsukuba.

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.

Registered no.	Species	Type	Maximum height (mm)	Minimum major axis diameter in cross section (mm)	Maximum major axis diameter in cross section (mm)	Locality information		
						Locality no.	Area	Age
MCM-W1620	*Hyphantoceras transitorium*	–	15.8	4.8	7.3	KT093	Kotanbetsu	Santonian
MCM-W1621	*H. transitorium*	–	16.5	11.5	13.0	KT093	Kotanbetsu	Santonian
MCM-W1622	*H. transitorium*	–	28.1	2.9	8.8	KT141	Kotanbetsu	Santonian
MCM-W1623	*H. transitorium*	–	14.4	3.6	6.8	HR051	Kotanbetsu	Santonian
MCM-W1624	*H. transitorium*	–	16.0	2.4	6.2	HR109	Kotanbetsu	Santonian
MCM-W1625	*H. transitorium*	–	38.4	4.0	8.3	KT133	Kotanbetsu	Santonian
MCM-W1626	*H. transitorium*	–	7.0	4.9	5.8	KT133	Kotanbetsu	Santonian
MCM-W1627	*H. orientale*	–	50.8	4.5	5.1	KT035	Kotanbetsu	Santonian
MCM-W1628	*H. orientale*	–	13.3	3.4	4.2	KT035	Kotanbetsu	Santonian
MCM-W1629	*H. orientale*	–	11.3	3.0	3.4	KT035	Kotanbetsu	Santonian
MCM-W1630	*H. orientale*	–	28.4	6.5	7.0	KT035	Kotanbetsu	Santonian
MCM-W1631	*H. orientale*	–	16.8	4.0	4.7	KT035	Kotanbetsu	Santonian
MCM-W1632	*H. orientale*	–	12.3	3.5	4.0	KT035	Kotanbetsu	Santonian
MCM-W1633	*H. orientale*	–	15.9	4.4	4.9	KT035	Kotanbetsu	Santonian
MCM-W1634	*H. orientale*	–	28.3	4.6	5.4	KT035	Kotanbetsu	Santonian
MCM-W1635	*H. orientale*	–	54.6	4.8	6.8	KT035	Kotanbetsu	Santonian
MCM-W1636	*H. orientale*	–	70.0	5.2	7.1	KT035	Kotanbetsu	Santonian
MCM-W1637	*H. orientale*	–	40.3	3.3	4.4	KT045	Kotanbetsu	Santonian
MCM-W1638	*H. orientale*	–	35.1	3.6	5.7	KT045	Kotanbetsu	Santonian
MCM-W1639	*H. orientale*	–	14.6	4.0	4.9	KT045	Kotanbetsu	Santonian
MCM-W1640	*H. orientale*	–	31.6	5.7	6.2	KT045	Kotanbetsu	Santonian
MCM-W1641	*H. orientale*	–	35.3	3.3	4.7	KT055	Kotanbetsu	Santonian
MCM-W1642	*H. orientale*	–	17.1	5.7	6.4	KT055	Kotanbetsu	Santonian
MCM-W1643	*H. orientale*	–	63.2	6.9	8.5	HR015	Kotanbetsu	Santonian
MCM-W1644	*H. orientale*	–	41.8	7.7	10.1	HR023	Kotanbetsu	Santonian
MCM-W1645	*H. orientale*	–	29.9	11.1	11.8	HR023	Kotanbetsu	Santonian
MCM-W1646	*H. orientale*	–	26.6	9.3	9.5	HR023	Kotanbetsu	Santonian
MCM-W1647	*H. orientale*	–	64.7	8.5	11.6	KM015	Kotanbetsu	Santonian
MCM-W1648	*H. orientale*	–	59.3	5.7	7.6	KM015	Kotanbetsu	Santonian
MCM-W1649	*H. orientale*	–	37.0	8.2	9.2	KM015	Kotanbetsu	Santonian
MCM-W1650	*H. orientale*	–	20.4	3.3	4.1	KM015	Kotanbetsu	Santonian
KYC86	*H. transitorium*	–	58.4	7.2	13.9	unknown	Kotanbetsu	unknown
KYCH36	*H. transitorium*	–	24.1	2.9	8.4	unknown	Kotanbetsu	unknown
MCM-W0269-1	*H. transitorium*	–	11.4	3.0	5.9	OB35085	Obira	Santonian
MCM-W0335-1	*H. orientale*	–	36.7	5.1	6.7	OB36153	Obira	Santonian
UMUT MM7553	*H. oshimai*	holotype	99.9	26.6	38.2	"Ikushumbetsu River"	Mikasa	"*Scaphites*-beds"
UMUT MM7554	*H. oshimai*	paratype	23.5	–	–	"Shi-kuruki"	Yubari	"*Scaphites*-beds"
UMUT MM7572a	*H. orientale*	holotype	41.1	11.1	13.8	unknown	Urakawa	"the upper Ammonite-beds"
UMUT MM7572b	*H. orientale*	paratype	26.3	8.3	–	unknown	Mikasa	"*Pachydiscus*-beds"?
NMNS PM7261	*H. transitorium*	holotype	44.4	4.2	13.6	"Inarizawa"	Mikasa	Santonian?

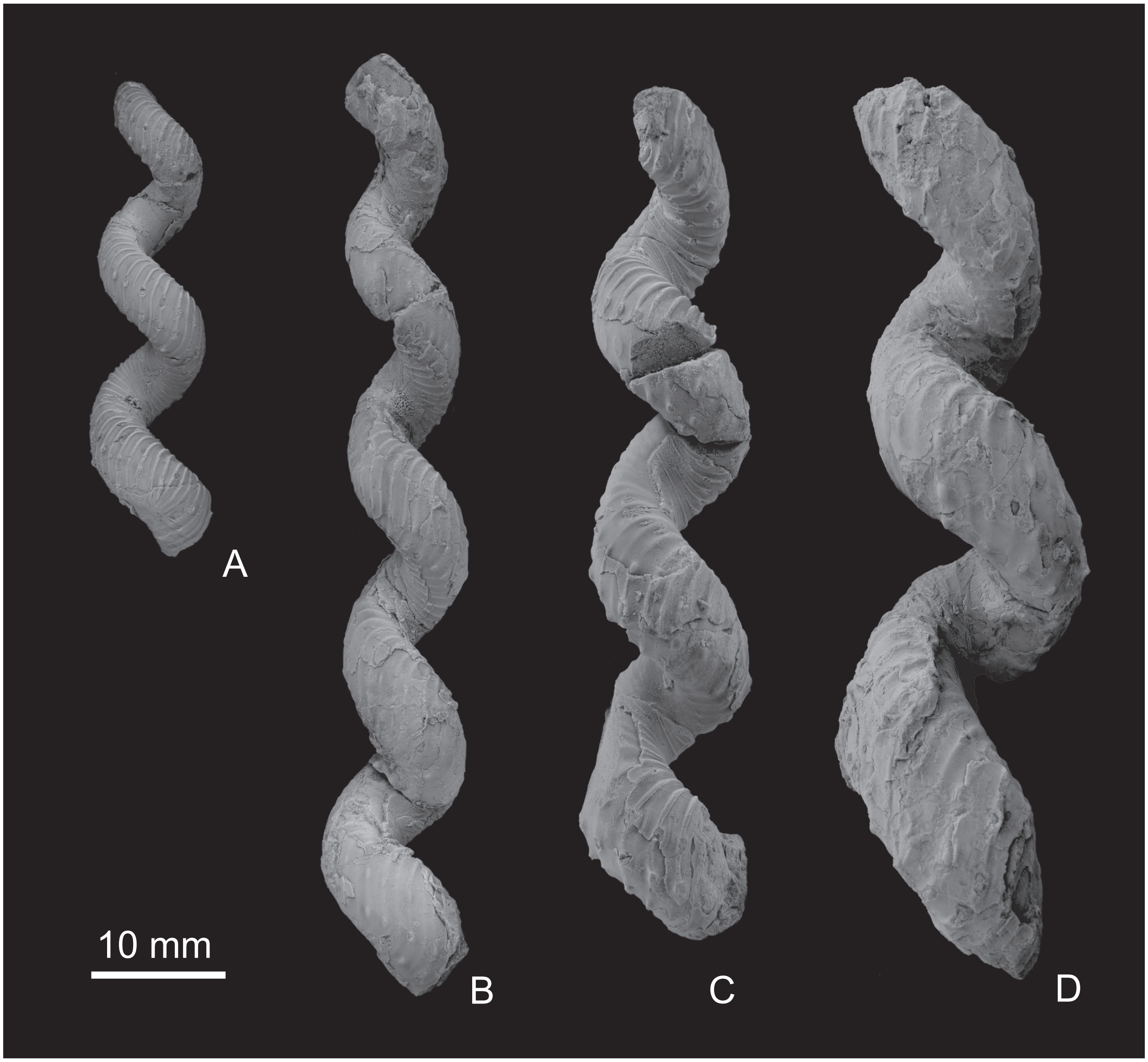

Figure 6. *Hyphantoceras orientale* from the Kotanbetsu area. **A**, MCM-W1638 from locality KT045 of the Kotanbetsu River; **B**, MCM-W1636 from locality KT035 of the Kotanbetsu River; **C**, MCM-W1643 from locality HR015 of the Kaminosawa Creek; **D**, MCM-W1647 from locality KM015 of the Kaminosawa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

Morphological characteristics of *Hyphantoceras transitorium*

Hyphantoceras transitorium Matsumoto, 1977b, described originally as a monotypic species, is characterized by a turreted shell with whorls slightly separated from each other (Matsumoto, 1977b; Figure 7E). Ten newly found 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 fall within the rangeof 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

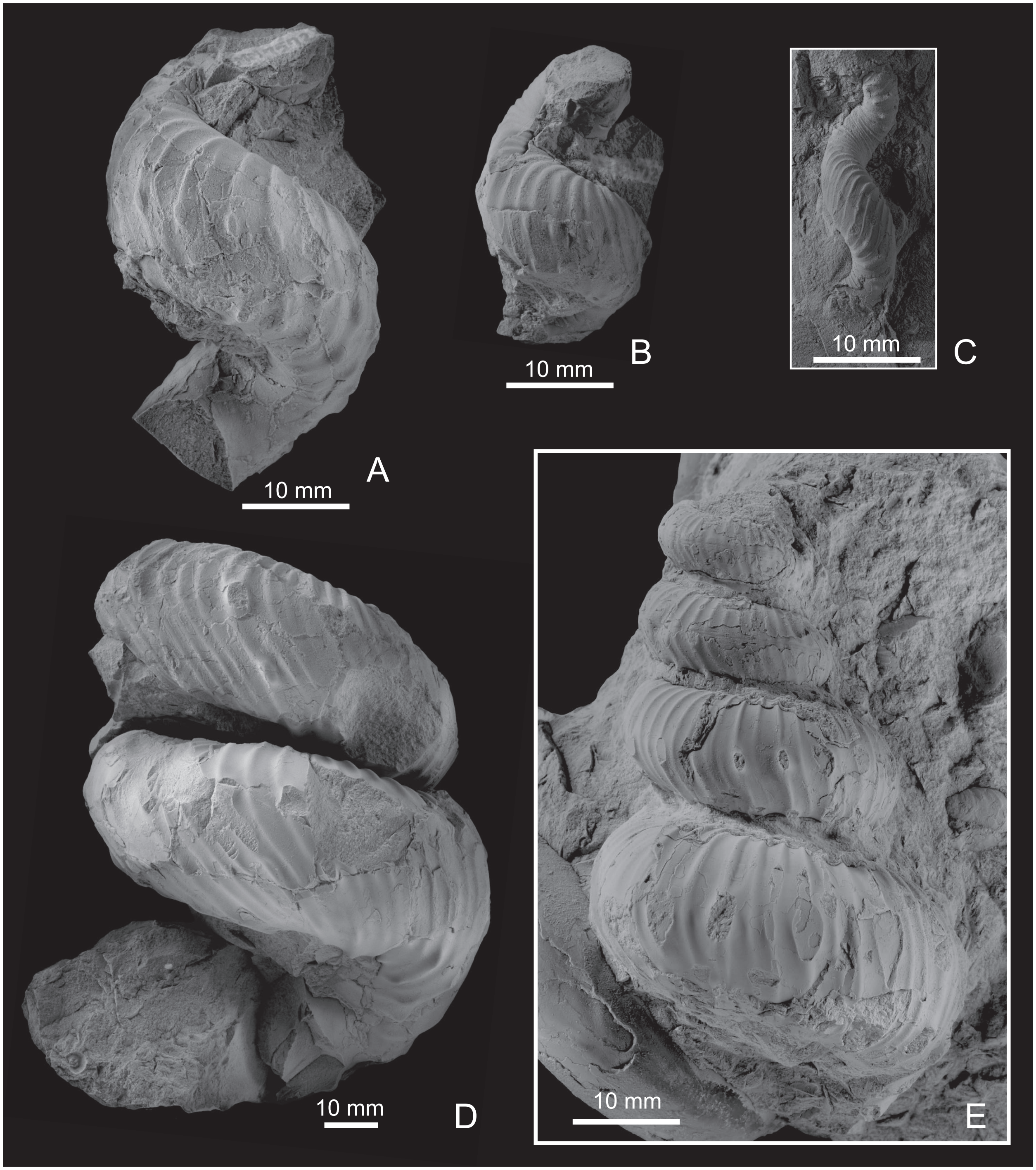

Figure 7. Type specimens of *Hyphantoceras orientale* (Yabe, 1904), *H. oshimai* (Yabe, 1904), and *H. transitorium* Matsumoto, 1977b. **A**, **B**, *H. orientale*; A, holotype (UMUT MM7572a); B, paratype (UMUT MM7572b); **C**, *H. orientale* (paratype of *H. oshimai* in the original description, UMUT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

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

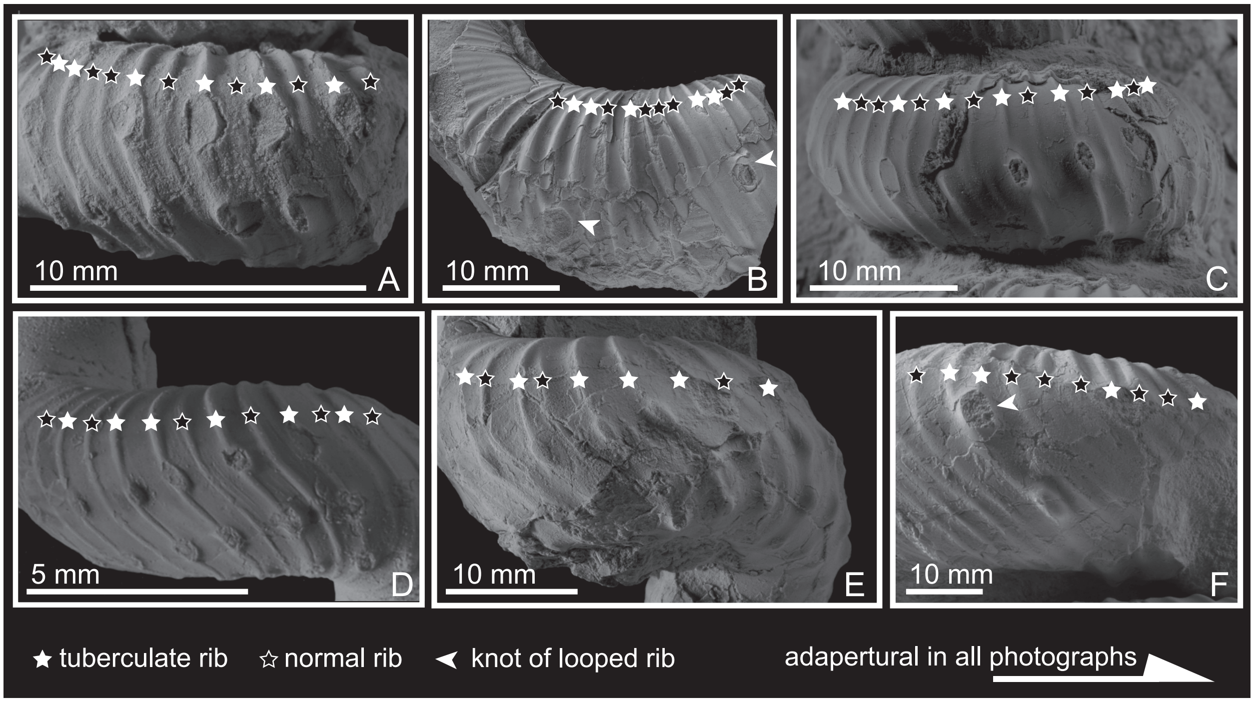

Figure 8. Photographs of shell surface ornamentation. **A**–**C**, *Hyphantoceras transitorium*; A, MCM-W1624; B, MCM-W1621; C, NMNS PM7261, holotype; **D**, **E**, *Hyphantoceras orientale*; D, MCM-W1638; E, UMUT MM7572a, holotype; **F**, *Hyphantoceras oshimai* (Yabe, 1904), UMUT MM7553, holotype.

5, 7E, 8A–C). Two ribs looped at a 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 the Kotanbetsu and Obira areas are assigned to this species (MCM-W0335-1, MCM-W1627–W1650; Figure 6). The shell sizes of the present specimens range within 3.0–11.8 mm in whorl tube diameter (Table 2). The whorl shapes do not change drastically in the range of the preserved part of the present specimens (Figure 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 coarser 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 *H. 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 upper part of units Ud-f and the lower part of Unit Ug of the Haborogawa Formation, which is in the *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 the *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 the Obira area.

Okamoto *et al*. (2003) listed *Hyphantoceras orientale* from the 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 the Haboro area.

Discussion

Variation of *Hyphantoceras transitorium*

Hyphantoceras transitorium was erected based on a single specimen from the Mikasa area, Hokkaido by monotypy (Matsumoto, 1977b; Figure 7E). However, ten newly found additional specimens of *H. transitorium* show that this species has wide intraspecific variation in the whorl shape and the timing of whorl shape change (Figure 5). 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 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 change in the mode of life (Okamoto, 1988a, b).

Matsumoto (1977b) pointed out that the deviated part of the 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 tightly coiled whorls are recognized in some of the present specimens (Figure 5A–C). Considering this, it is not certain that the deviation of the later whorl of the holotype is 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 ornamentation of the two species suggests that they are phylogenetically close. In addition, the 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 the 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 ribs looped at tubercles 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 the two species do not overlap (Figures 5, 7D; Table 2). *Hyphantoceras oshimai* is listed and reported from the same stratigraphic level (Unit Ug) in the Kotanbetsu area (Wani and Hirano, 2000) and the stratigraphic levels just below the occurrences of *H. transitorium* (Unit Uf) in the Haboro and Obira areas (Matsumoto, 1977b; Okamoto *et al*., 2003). Considering the similarities of the two species, there is a possibility that two species are closely related. However, the phylogenetic relationship between the two species cannot be concluded in this paper, because the whorl sizes of two species differ considerably and stratigraphic data is insufficient. Careful comparison throughout ontogeny and investigation of FAD of *H. transitorium* and LAD of *H. oshimai* are necessary for clarifying the relationship between them.

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* stand outside of the lineage of *H. transitorium–H. orientale*.

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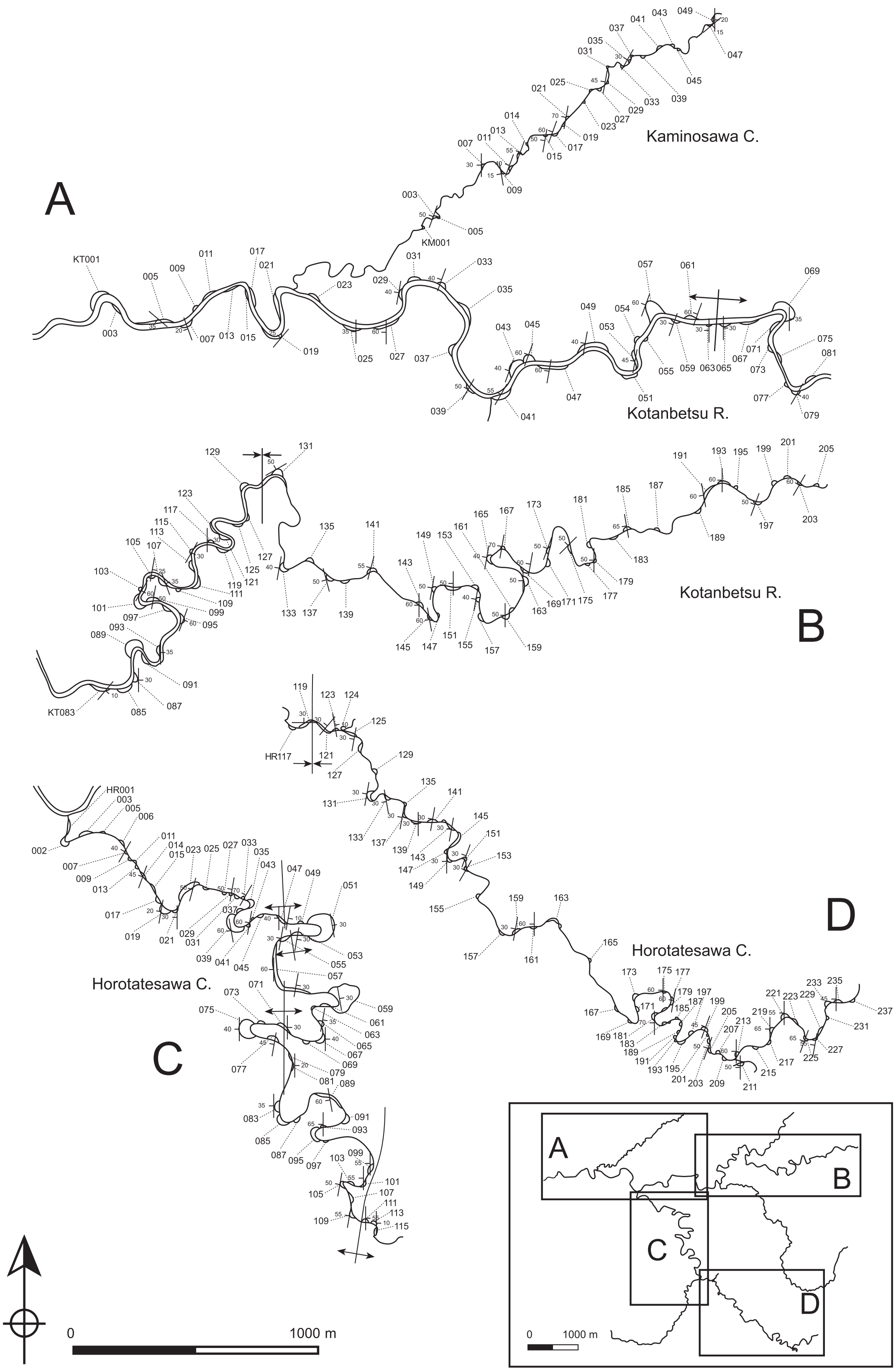

Appendix 1. Locality maps in the Kotanbetsu area.