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Late Maastrichtian (latest Cretaceous) ammonoids from the Naiba area, southern Sakhalin, Russian Far East

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Abstract. Six early late Maastrichtian (Late Cretaceous) ammonoid taxa are reported from the Krasnoyarka Formation of the Yezo Group in the Naiba area, southern Sakhalin, Russian Far East. These taxa are grouped into "immigrant species", i.e., those that migrated from other regions (*Pachydiscus subcompressus*, *Anagaudryceras mikobokense*, *Gaudryceras seymouriense* and *Zelandites varuna*) and "indigenous species" with a North Pacific distribution (*Anagaudryceras matsumotoi*). It is unclear to which group *Tetragonites* sp. belongs. *Zelandites varuna* and *G. seymouriense* occur in both the lower upper Maastrichtian as well as the upper lower Maastrichtian in southern Sakhalin, but they have never been found in the middle Maastrichtian. The appearance of these two species in the cold-water regions, i.e., North Pacific and Antarctic, as well as intermediate southern mid-latitudes regions suggests that cooling events occurred during the late early and early late Maastrichtian in the Northwest Pacific region. Their disappearance during the middle Maastrichtian may indicate that the Northwest Pacific region was affected by the greenhouse Middle Maastrichtian Event (MME). This hypothesis suggests that the influx (e.g. *P. subcompressus* and *A. mikobokense*) and reappearance (e.g. *Z. varuna* and *G. seymouriense*) of many immigrant species into the Northwest Pacific region during late Maastrichtian time may have been associated with the post-MME cooling.

Keywords: ammonoid, Cretaceous, Krasnoyarka Formation, Middle Maastrichtian Event, Naiba, Sakhalin

Introduction

Late Maastrichtian (latest Cretaceous) ammonoids were poorly known in the Northwest Pacific region in the 1990's (Toshimitsu *et al*., 1995), but more recent integration of bio- and magnetostratigraphic studies of the Maastrichtian Senpohshi Formation of the Nemuro Group exposed along the western coast of Akkeshi Bay, eastern Hokkaido, revealed that the early late Maastrichtian ammonoid assemblage includes the following seven ammonoid taxa: *Zelandites varuna* (Forbes, 1846), *Anagaudryceras matsumotoi* Morozumi, 1985, *Gaudryceras* cf. *seymouriense* (Macellari, 1986), *Diplomoceras* cf. *notabile* Whiteaves, 1903, *Gaudryceras* sp., *Pseudophyllites* sp., and *Neophylloceras* sp. (Nifuku *et al*., 2009; Shigeta *et al*., 2015). However, the presence of juvenile shells only, combined with the fragmental nature of many specimens precluded definitive species assignments for the latter five taxa. In addition, their faunal properties as well as species composition and intraspecific variation were not fully understood.

Similar ammonoid assemblages are known from the Shimonada Formation of the Izumi Group on Awaji Island, Southwest Japan (Morozumi, 1985), the Heitaro-zawa Formation of the Yezo Group in the Nakatonbetsu area, northern Hokkaido (Ando *et al*., 2001), and the Krasnoyarka Formation of the Yezo Group in the Naiba area (Yazykova, 1994; Kodama *et al*., 2002), southern Sakhalin, Russian Far East (Figure 1). Although these formations yield many well preserved ammonoids, their taxonomy has not yet been thoroughly investigated.

In the 1990s, Japanese and Russian workers organized a joint working group and various members conducted several scientific expeditions to Sakhalin where they studied lithostratigraphy, biostratigraphy, magnetostratigraphy, isotope stratigraphy, paleobiology, and taphonomy (Shigeta, 1993; Kase *et al*., 1994; Kase and Shigeta, 1996; Maeda and Seilacher, 1996; Shigeta *et al*., 1999; Kodama *et al*., 2000, 2002; Hasegawa *et al*., 2003; Shigeta and Maeda, 2005; Maeda *et al*., 2005; Maeda and Shigeta, 2005; Maeda *et al*., 2010). The group collected many well-preserved Maastrichtian ammonoids from the

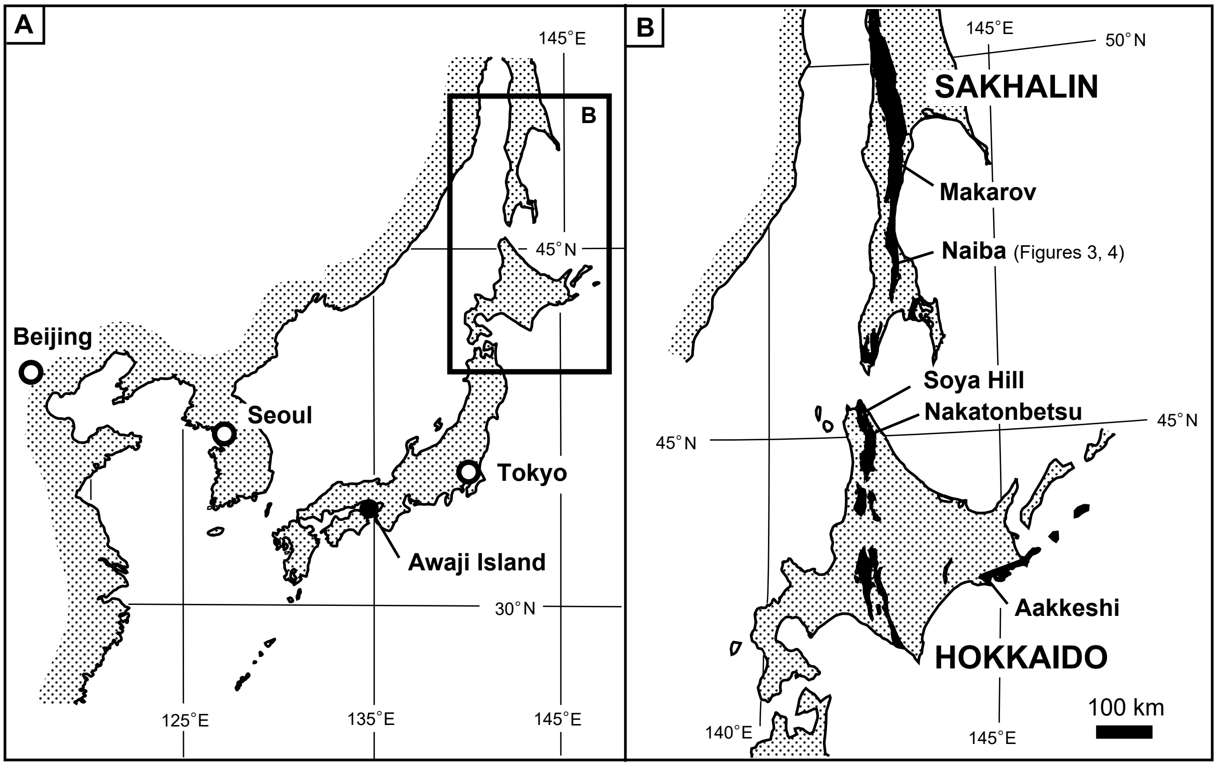

Figure 1. Generalized map (**A**) showing relative locations of Hokkaido, Japan and Sakhalin, Russia (B) and Awaji Island, Southwest Japan. Index map (**B**) showing distribution of Cretaceous Yezo Group (central Hokkaido and Sakhalin) and Nemuro Group (eastern Hokkaido) exposures (black areas), as well as the Maastrichtian fossil localities mentioned in the text.

Naiba area, but their taxonomy and biostratigraphy have not been fully investigated until now. In this paper, we document these late Maastrichtian ammonoids from the Naiba area and discuss their faunal properties.

All specimens studied herein were collected during the field expeditions of the Japan-Russia joint research program in the 1990's and were transported from Russia to Japan with permission from the Russian Government, the State Government of Sakhalin, and other concerned authorities.

Biostratigraphic scheme of the Maastrichtian in the Northwest Pacific region

Toshimitsu *et al*. (1995) and Zonova *et al.* (1993) established biostratigraphic zonation schemes based mainly on ammonoids and inoceramid bivalves for the Maastrichtian in Japan and Russian Far East, respectively. Shigeta and Tsutsumi (2019) recently revised these schemes and correlated the ammonoid zones with the geomagnetic polarity time scale (GPTS) based on recent works of biostratigraphy, magnetostratigraphy and zircon-based geochronology in the Northwest Pacific region. In this paper, we provisionally subdivide the Maastrichtian into three substages of approximately equal duration, but there are as yet no formal recommendations for primary markers or boundary stratotypes for substages (Gradstein *et al*., 2020).

According to Shigeta and Tsutsumi (2019), four Maastrichtian ammonoid zones (taxon-range zones) in the Northwest Pacific region are recognized as follows, in ascending order: *Nostoceras hetonaiense*, *Gaudryceras izumiense*, *Pachydiscus flexuosus* and *P. subcompressus* (Figure 2). The *N. hetonaiense* Zone on Awaji Island, Southwest Japan was correlated with polarity chron C32.2n to C32.1n (= early Maastrichtian) by Kodama (1990). Although the magnetostratigraphic correlation for the *G. izumiense* Zone and the lower to middle parts of the *P. flexuosus* Zone has not yet been completed, the U–Pb age of a tuff bed overlying the *G. izumiense*-bearing beds in the Soya Hill area, northern Hokkaido was determined to be 70.5 ± 1.1 Ma (95% conf.) (= late early Maastrichtian) by Shigeta *et al*. (2017). Shigeta and Tsutsumi (2019) also determined the U–Pb age of a tuff bed in the middle part of the *P. flexuosus* Zone in the Nakatonbetsu area, northern Hokkaido to be 69.8 ± 0.8 Ma (95% conf.) (= late early to early middle Maastrichtian). The upper part of the *P. flexuosus* Zone and the *Zelandites*

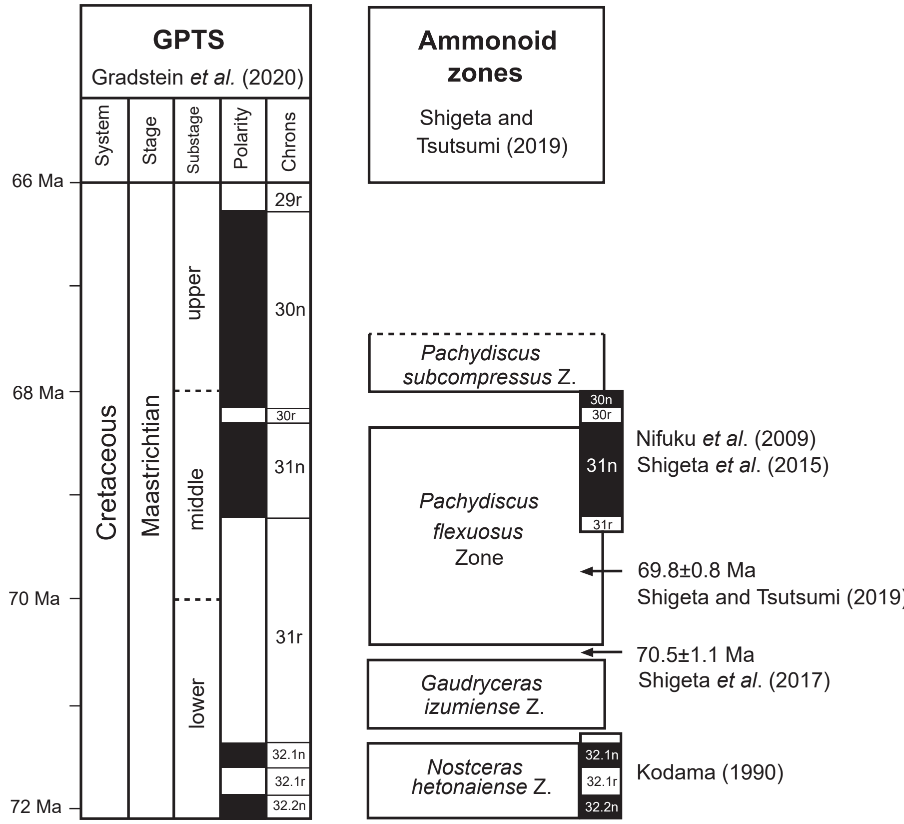

Figure 2. Diagram showing Maastrichtian ammonoid zones (taxon-range zones) in the Northwest Pacific region (Shigeta and Tsutsumi, 2019) and their correlation with the geomagnetic polarity time scale (GPTS) based on recent works of magnetostratigraphy (Kodama, 1990; Nifuku *et al*., 2009; Shigeta *et al*., 2015) and zircon-based geochronology (Shigeta *et al*., 2017; Shigeta and Tsutsumi, 2019). The three-subdivision scheme for the Maastrichtian is provisional, and there are as yet no formal recommendations for primary markers or boundary stratotypes for substages.

varuna-bearing beds in the Akkeshi area, eastern Hokkaido area were correlated with polarity chron C31n (= middle to late middle Maastrichtian) and most likely the lower part of polarity chron C30n (= early late Maastrichtian) respectively by Shigeta *et al*. (2015). *Zelandites varuna* and *P*. *subcompressus* Matsumoto, 1954 co-occur on Awaji Island (Morozumi, 1985) and in southern Sakhalin (e.g. Matsumoto, 1988).

The Maastrichtian ammonoid zones in the Northwest Pacific region therefore correlate as follows based on the three-subdivision scheme for the Maastrichtian: *Nostoceras hetonaiense* Zone with the lower lower Maastrichtian, *Gaudryceras izumiense* Zone with the middle lower Maastrichtian, *Pachydiscus flexuosus* Zone with the upper lower to upper middle Maastrichtian, and *P*. *subcompressus* Zone with the lower upper Maastrichtian (Figure 2). As indicated earlier by Shigeta *et al*. (2010, 2012), Shigeta and Nishimura (2013) and Shigeta and Tsutsumi (2019), *Gaudryceras* is an ideal ammonoid genus for precise biostratigraphic correlation of the Maastrichtian in the Northwest Pacific region, e.g. *G*. *hobetsense* Shigeta and Nishimura, 2013, *G*. *izumiense* Matsumoto and Morozumi, 1980, *G*. *tombetsense* Matsumoto, 1984, *G*. *hamanakense* Matsumoto and Yoshida, 1979, *Gaudryceras* sp. and *G*. *makarovense* Shigeta and Maeda in Maeda *et al*., 2005 all occur in ascending stratigraphic order. Future taxonomic and biostratigraphic studies of these *Gaudryceras* taxa will more accurately define the subdivisions of the Maastrichtian in the Northwest Pacific region.

Notes on stratigraphy

In the Naiba area near Bykov, deposits of the Yezo Group, which are widely distributed in a north-south direction in central Hokkaido and the West Sakhalin Mountains, crop out continuously. Unlike carbonate platforms, the group represents a thick clastic sequence deposited in a forearc basin along the eastern margin of the paleo-Asian continent (Okada, 1983; Kodama *et al*., 2002; Takashima *et al*., 2004). It attains a thickness of over 5,000 m and ranges in age from Albian to Maastrichtian (Figures 1, 3). This area represents one of the best known Cretaceous reference sections in the Northwest Pacific region (Matsumoto, 1942b, 1954; Vereshchagin and Salnikov, 1968; Pergament, 1974; Vereshchagin, 1977; Zakharov *et al*., 1984; Poyarkova, 1987; Zonova *et al*., 1993; Kodama *et al*., 2000, 2002; Shigeta and Maeda, 2005).

The Ai (Albian, not studied here), Naiba (upper Albian–Cenomanian), Bykov (upper Cenomanian–lower Campanian), and Krasnoyarka (Campanian–Maastrichtian, Paleocene?) formations are successively exposed along the middle course of the Naiba River and its tributaries, i.e., the Krasnoyarka, Nagornaya, and Seim rivers (Figures 3, 4). The lower three formations are dominated by fine-grained deposits and turbiditic sandstones that represent an offshore facies in a slope–basin environment (Okada, 1979, 1983), while the Krasnoyarka Formation, which is intercalated by sandstone and conglomerate, exhibits a shallowing-upward succession that suggests a prodelta–delta facies (Kodama *et al*., 2002; Maeda *et al*., 2010).

Kodama *et al*. (2002) divided the Krasnoyarka Formation into six lithostratigraphic units, i.e., K1–K6. The 170 m thick K1 Unit, is composed of greenish grey, poorly sorted, muddy sandstone in the lowest part, light greenish grey, cross-stratified, coarse to medium grained sandstone in the main part, and dark grey, intensely bioturbated sandy mudstone in the uppermost part. Fossils in the K1 Unit include the inoceramid bivalve *Sphenoceramus schmidti* (Michael, 1899) in the lower part and the ammonoid *Canadoceras kossmati* Matsumoto, 1954 in the lower and middle parts. The *S. schmidti* Zone in the Northwest Pacific region has been correlated with the lower middle Campanian under the three-subdivision scheme for the Campanian by magnetostratigraphic correlation (Kodama, 1990; Tamaki *et al*., 2008) and zircon-based geochronology (Shigeta and Tsutsumi, 2018).

The 150 m thick K2 Unit, consisting of light greenish grey, coarse grained sandstone in association with conglomerate in the lower part and intensely bioturbated, muddy sandstone in the middle and upper parts, includes *Canadoceras kossmati* (Kodama *et al*., 2002, fig. 8A, B) in the middle part and the late middle Campanian ammonoid *C. multicostatum* Matsumoto, 1954 (Kodama *et al*., 2002, fig. 8E, F) in the upper part.

The 170 m thick K3 Unit, composed mainly of greenish grey, bedded, medium to fine grained sandstone in the lower to middle parts and poorly sorted, muddy sandstone in the upper part, contains *Canadoceras multicostatum* and *Menuites soyaensis* (Matsumoto and Miyauchi, 1984) (Kodama *et al*., 2002, fig. 8C, D) in the lower part and the upper lower and middle Maastrichtian index ammonoid *Pachydiscus flexuosus* Matsumoto, 1979 in the uppermost part (Figure 5).

The 140 m thick K4 Unit, consisting mainly of dark grey, intensely bioturbated massive mudstone, includes the early late Maastrichtian ammonoid *Pachydiscus subcompressus*. Assuming that the high sedimentation rate of the K4 Unit is similar to the 200 m/Myr of the 1,290 m thick B3 Unit (upper Turonian to lower Campanian) of the Bykov Formation with similar lithology (Kodama *et al*., 2002), it follows that the duration of the K4 Unit is estimated to be about 0.7 Myr, which means that the entirety of this unit is included in the lower upper Maastrichtian.

The 140 m thick K5 Unit, composed mainly of grey, intensely bioturbated, sandy mudstone in association with greenish grey, coarse grained sandstone, contains the lobster *Linuparus* sp. and the bivalve *Goniomya* sp. in the lowest part. And finally, the 120–180 m thick K6 Unit, consisting mainly of unfossiliferous, intensely bioturbated, sandy mudstone and mudstone, is unconformably overlain by the Eocene Lower Duye Formation. The fauna in Unit K5 and K6 is termed the "Sinegorsk Fauna", and its makeup suggests a possible Paleocene age (Kalishevitch and Posylny, 1958; Kalishevitch *et al*., 1981). The stratigraphic relationship between the K4 and K5 units is similar to that in the Nakatombetsu area of northern Hokkaido, where the uppermost part of the Heitaro-zawa Formation, which yields *Pachydiscus subcompressus* is unconformably overlain by the upper Paleogene Oku-utsunai Formation. Strata from the uppermost Maastrichtian to middle Paleocene, including the Cretaceous/Paleogene boundary, have presumably been eroded away (Ando *et al*., 2001). This evidence suggests that the uppermost Maastrichtian to middle Paleocene strata in the Naiba area have also been eroded away.

Material and methods

Material

Figures 3 and 4 show the localities and horizons from which the upper Maastrichtian ammonoids were collected in the K4 Unit of the Krasnoyarka Formation along the Naiba and Krasnoyarka rivers in the Naiba area. A total of 34 specimens were utilized for the following paleontological description.

Methods

Nearly all specimens were utilized for biometric analysis of the shell form. The four classic geometric parameters of the shell, i.e., diameter (*D*), umbilical diameter

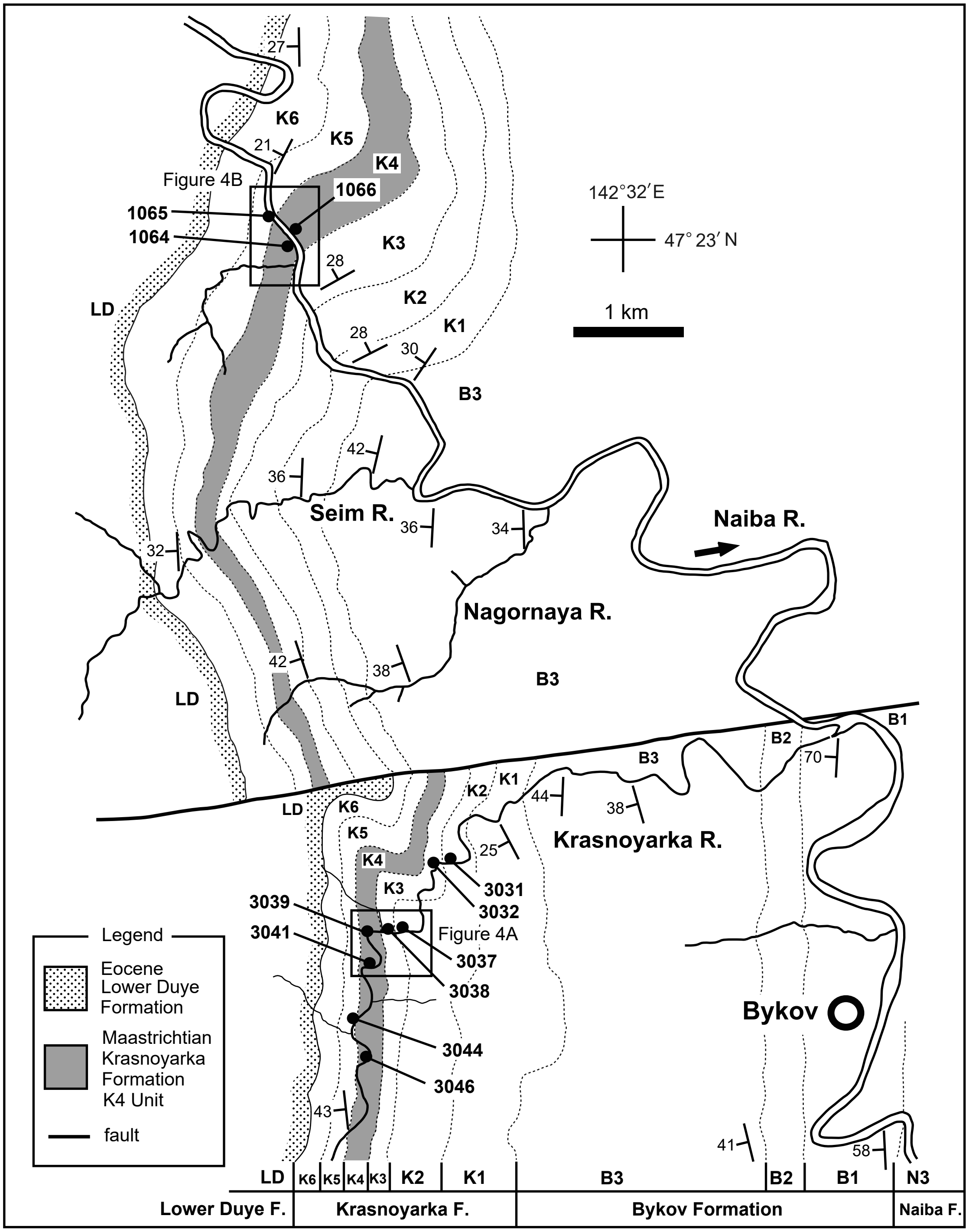

Figure 3. Geological map showing fossil localities mentioned in the text in the Naiba area, southern Sakhalin. N3, Naiba Formation; B1–B3, Bykov Formation; K1–K6, Krasnoyarka Formation; LD, Lower Duye Formation. See Kodama *et al*. (2002) for detailed stratigraphy. Locality numbers in the text are preceded by prefix "NB". The areas enclosed by the rectangles in this figure are enlarged and shown in Figure 4.

(U), whorl height (H) and whorl width (W) were measured with the aid of a slide caliper (accuracy, ± 0.05 mm) and two ratios, relative umbilical size (U/D) and relative whorl thickness (W/H), were calculated for each specimen (Figure 6).

Seven specimens (NSM PM35926–35930, *Zelandites*

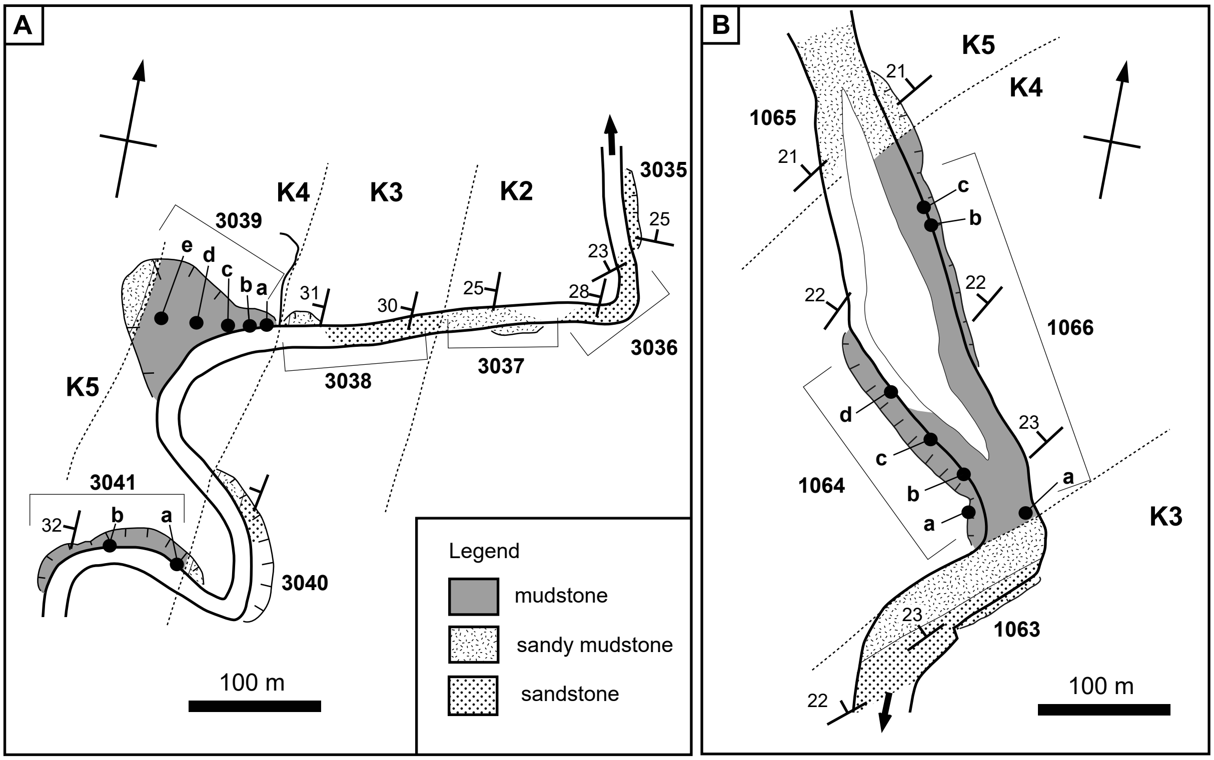

Figure 4. Maps of the areas along the Krasnoyarka River (**A**) and the upper course of the Naiba River (**B**) showing rock types as well as locality numbers, which are preceded by prefix "NB" in the text.

varuna, and PM35931–35932, *Anagaudryceras matsumotoi*) were cut into cross sections that passed through the center of the initial chamber, and each cross-sectioned surface was etched with 5% acetic acid for three minutes. Then an acetate peel was prepared by pressing a sheet of triacetylcellulose film (0.025 mm in thickness) onto the etched surface while flooded with acetone. The four parameters (*D*, *U*, *H*, *W*) were measured every half whorl using a digital micrometer (accuracy, ± 0.001 mm) attached to a profile projector (Nikon Model V-20B) on the peeled cross section.

The inner whorl of specimen NMNS PM35918, *Anagaudryceras mikobokense* Collignon, 1956, with a diameter of 35 mm was scanned utilizing X-ray computed tomography (inspeXio SMX-225CT FPD HR, Shimadzu). The four parameters (*D*, *U*, *H*, *W*) were measured every half whorl using X-ray CT image of the cross section.

Specimen NMNS PM35919, *Gaudryceras seymouriense* (Macellari, 1986), was prepared in the following manner for ontogenetic study of the shell form. Its outer whorl was removed in two segments of about half whorl each, and then *D*, *U*, *H* and *W* were measured for each remaining shell with the aid of a slide caliper. Its inner whorl with a diameter of 30 mm was scanned utilizing X-ray computed tomography, and the four parameters (*D*, *U*, *H*, *W*) were measured every half whorl using X-ray CT image of the cross section.

Paleontological description

Morphological terms are those used in Arkell (1957). Quantifiers used to describe the shape of ammonoid shell replicate those proposed by Matsumoto (1954, p. 246) and modified by Haggart (1989, table 8.1).

Abbreviations for shell dimensions.—*D*, shell diameter; *U*, umbilical diameter; *H*, whorl height; *W*, whorl width.

Institution abbreviations.—BMNH, Natural History Museum, London; KYUM, the Kyushu University Museum, Fukuoka; MNHN, National Muséum of Natural History, Paris; NMNS, National Museum of Nature and Science, Tsukuba; OSU, Orton Geological Museum, the Ohio State University, Columbus; UMUT, the University Museum, the University of Tokyo, Tokyo.

Suborder Lytoceratina Hyatt, 1889
Superfamily Tetragonitoidea Hyatt, 1900

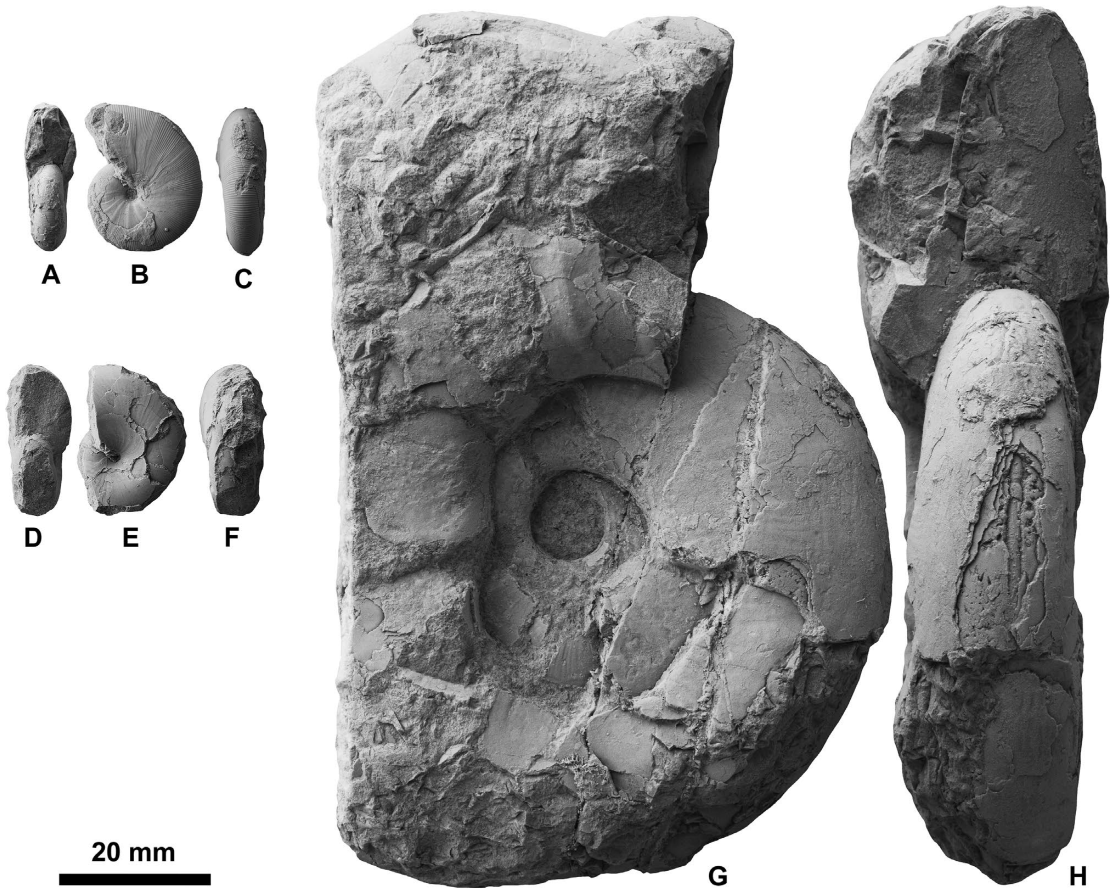

Figure 5. Middle Maastrichtian ammonoids from the uppermost part of the K3 Unit of the Krasnoyarka Formation at NB3038. **A–C,** *Neophylloceras* sp., NMNS PM35933; **D–F,** *Phyllopachyceras* sp., NMNS PM35934; **G, H,** *Pachydiscus flexuosus* Matsumoto, 1979, NMNS PM35935. A, D, H, apertural views; B, E, right lateral views; C, F, ventral views; G, left lateral view.

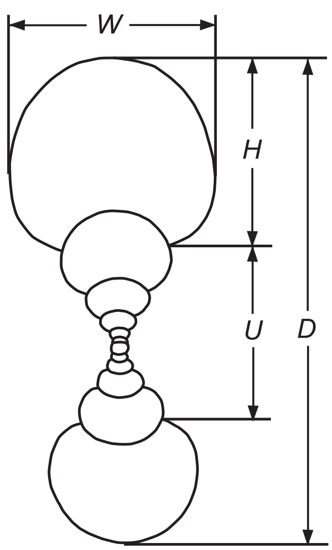

Figure 6. Classic measurements of ammonoid whorl cross section. *D*, shell diameter; *U*, umbilical diameter; *H*, whorl height; *W*, whorl width.

Family Tetragonitidae Hyatt, 1900
Genus ***Tetragonites*** Kossmat, 1895

Type species.—*Ammonites timotheanus* Pictet, 1847.

Tetragonites sp.

Figures 7, 8A

Material examined.—Two specimens: NMNS PM35900 from NB1066a; NMNS PM35901 from NB3046.

Description.—Very involute, fairly depressed shell with sub-rounded to sub-quadrate whorl-section, low arched venter, rounded ventral shoulders and slightly convex flanks with maximum whorl width at mid-flank. Umbilicus fairly narrow and deep with high, vertical wall and rounded shoulders. Ornamentation consists of very fine growth lines, which are prorsiradiate on flanks but become slightly sinuous at ventral shoulders before crossing over venter with very shallow concave arch. Suture

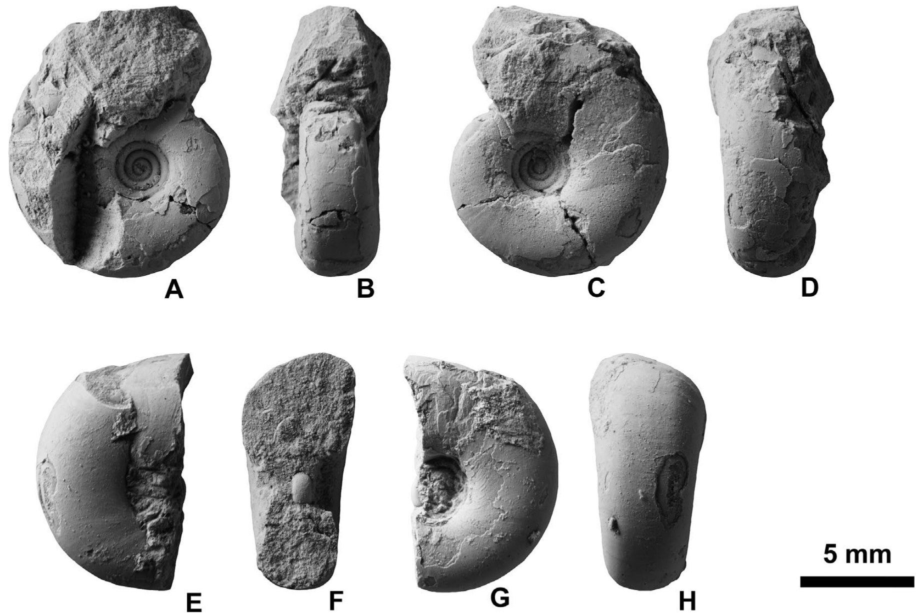

Figure 7. *Tetragonites* sp. from the K4 Unit of the Krasnoyarka Formation. **A–D,** NMNS PM35901 from NB3046; **E–H,** NMNS PM35900 from NB1066a. A, E, left lateral views; B, F, apertural views; C, G, right lateral views; D, H, ventral views.

line with large asymmetric trified first lateral saddle, smaller trified lateral saddle, and suspensive lobe with large trified first auxiliary saddle (Figure 8A). First lateral lobe large and irregularly subdivided.

Measurements.—See Appendix.

Remarks.—The present species is distinguished from *Tetragonites popetensis* Yabe, 1903 by having a narrower umbilicus. The specimens of the present species are somewhat similar to those described as *T. terminus* Shigeta, 1989 from the lower Maastrichtian in Hokkaido by Shigeta (1989, figs. 13.8–13.10) and Shigeta *et al*. (2017, fig. 17), *T. superstes* van Hoepen, 1921 from the lower Maastrichtian in north-eastern Mexico by Ifrim *et al*. (2004, pl. 1, figs. 5–8), *Pseudophyllites indra* (Forbes, 1846) from the Maastrichtian in southern Sakhalin by Maeda *et al.* (2005, figs. 38.12, 38.13, 38.16, 38.17) and specimens described as *Pseudophyllites* sp. from the upper Maastrichtian in eastern Hokkaido by Shigeta *et al*. (2015, fig. 4). The absence of adult features precludes a definitive species assignment, but their sub-rounded to sub-quadrate whorl-section and trifid major saddles enable us to assign them with reasonable confidence to the genus *Tetragonites*. *Tetragonites* is a long ranging genus known from the upper Aptian to the Maastrichtian (Wright *et al*., 1996).

Genus ***Zelandites*** Marshall, 1926

Type species.—*Zelandites kaiparaensis* Marshall, 1926.

Zelandites varuna (Forbes, 1846)

Figures 8B, 9, 10A–E, 11

Ammonites varuna Forbes, 1846, p. 107, pl. 8, fig. 5.
Lytoceras (*Gaudryceras*) *varuna* (Forbes). Kossmat, 1895, p. 161, pl. 16, fig. 4, pl. 17, fig. 8.
Lytoceras varuna (Forbes). Steinmann, 1895, p. 84, pl. 5, fig. 2, text-fig. 7.
Zelandites varuna var. *japonica* Matsumoto, 1938, p. 140, pl. 14, figs. 5–7, text-fig. 1.
Zelandites varuna (Forbes). Stinnesbeck, 1986, pl. 195, pl. 8, figs. 5, 6, text-fig. 20; Macellari, 1986, p. 14, figs. 11.11, 11.12, 12; Matsumoto, 1988, p. 184, pl. 51, fig. 4; Kennedy and Henderson, 1992, p. 404, pl. 5, figs. 13–15, pl. 17, figs. 2, 3; Ando *et al*., 2001, pl. 1, figs. 19–21; Kodama *et al*., 2002, fig. 8I, J; Maeda *et al*., 2005, p. 84, fig. 38.1–38.4; Salazar *et al*., 2010, p. 196, fig. 6b, c, e, f, I; Shigeta *et al*., 2015, p. 112, fig. 3M–U.
Zelandites cf. *varuna* (Forbes). Morozumi, 1985, p. 32, pl. 9, fig. 2, text-fig. 8.
Zelandites aff. *varuna* (Forbes). Yazykova, 1991, pl. 2, fig. 2.
non *Zelandites varuna* (Forbes). Zonova *et al*., 1993, p. 148, pl. 98, fig. 4; Yazykova, 1994, p. 289, pl. 1, fig. 8 (= *Anagaudryceras matsumotoi*); Ifrim *et al*., 2004, p. 1592, text-figs. 3O–P, 6F, G, J.
Zelandites japonicus Matsumoto. Zonova *et al*., 1993, p. 149, pl. 90, figs. 2, 3, pl. 98, fig. 3, pl. 99, figs. 3–13, pl. 101, figs. 4–7, pl. 102, figs. 3–10; Yazykova, 1994, p. 290, pl. 1, figs. 1–4, pl. 2, figs. 1–18; Matsumoto, 1995, p. 133; Alabushev and Wiedmann, 1997, p. 11, pl. 2, fig. 6, text-fig. 2.

Lectotype.—Specimen designated by Matsumoto (1988, p. 184), BMNH C51059, is the original of Forbes

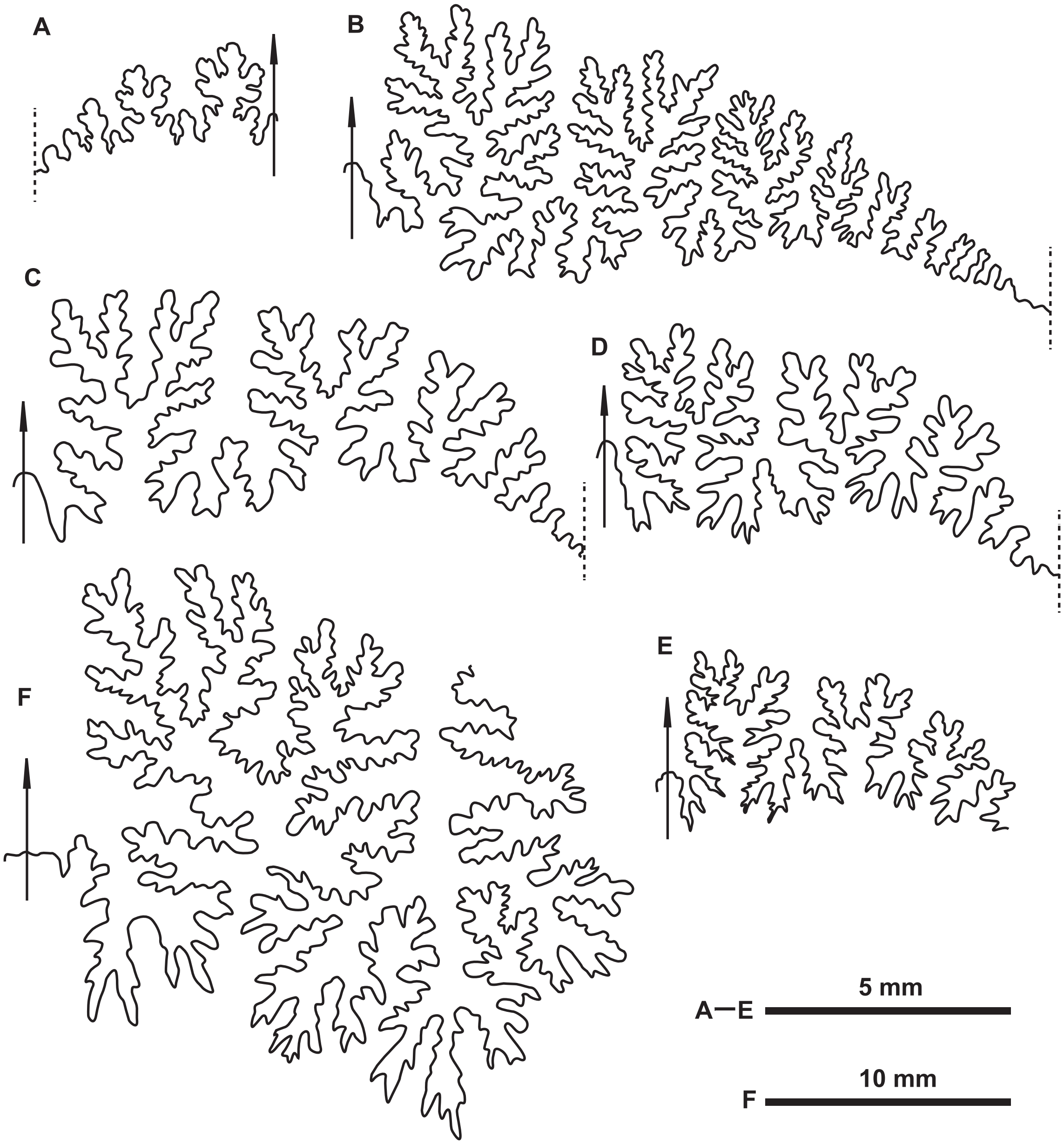

Figure 8. Suture lines of ammonoids from the K4 Unit of the Krasnoyarka Formation. **A,** *Tetragonites* sp., NMNS PM35901 from NB3046; **B,** *Zelandites varuna* (Forbes, 1846), NMNS PM35909 from NB3039c; **C,** *Anagaudryceras matsumotoi* Morozumi, 1985, NMNS PM35917 from NB3041a; **D,** *A. mikobokense* Collignon, 1956, NMNS PM35918 from NB1066b; **E,** *Gaudryceras seymouriense* (Macellari, 1986), NMNS PM35919 from NB1066b; **F,** *Pachydiscus subcompressus* Matsumoto, 1954, KYUM GKP00016 from a float concretion found at NB3035. Solid line represents the siphuncle, and broken line indicates the position of the umbilical seam.

(1846, p. 107, pl. 8, fig. 5) from the Maastrichtian of Pondicherry, southern India.

Material examined.—Thirteen specimens: NMNS PM35902 from NB1064c; NMNS PM35903–35909, 35926–35930 from NB3039c.

Description.—Early whorls (up to 4 mm in diameter): Very evolute, very depressed shell with rounded whorl section, arched venter, indistinct ventral shoulders, and slightly convex flanks with maximum whorl width at mid-flank. Umbilicus fairly wide with low, rounded wall.

Middle to late whorls (over 4 mm in diameter): As shell grows, whorl section becomes more compressed, while relative umbilical size (*U*/*D*) becomes progressively smaller (Figure 11). Shell with a diameter of 20 to 40 mm is very involute, fairly compressed and exhibits elliptical whorl-section with narrowly rounded venter,

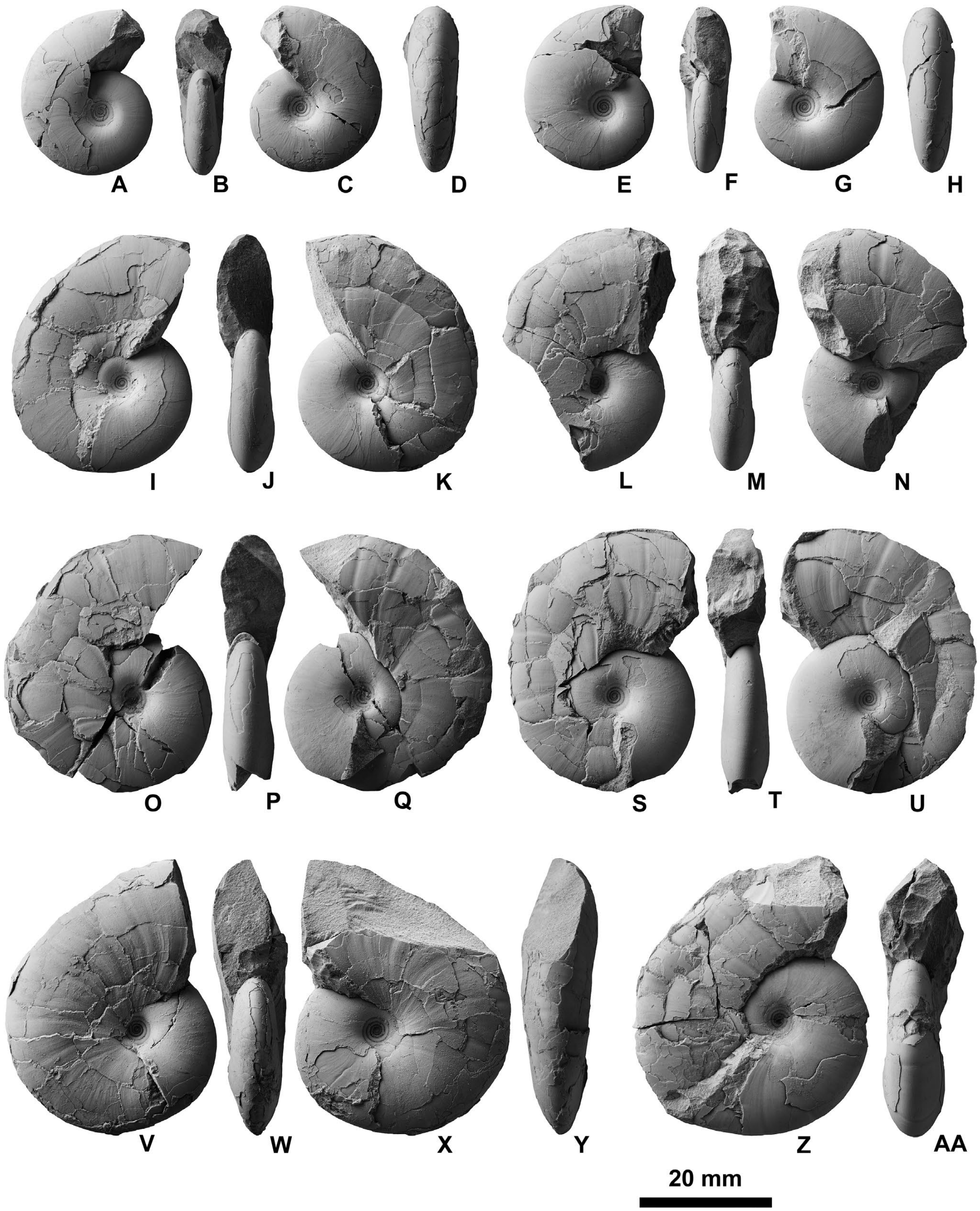

Figure 9. *Zelandites varuna* (Forbes, 1846) from the K4 Unit of the Krasnoyarka Formation. **A–D,** NMNS PM35902 from NB1064c; **E–H,** NMNS PM35904 from 3039c; **I–K,** NMNS PM35907 from NB3039c; **L–N,** NMNS PM35903 from NB3039c; **O–Q,** NMNS PM35905 from NB3039c; **S–U,** NMNS PM35906 from NB3039c; **V–Y,** NMNS PM35908 from NB3039c; **Z, AA,** NMNS PM35909 from NB3039c. A, E, I, L, O, S, V, Z, left lateral views; B, F, J, M, P, T, W, AA, apertural views; C, G, K, N, Q, U, X, right lateral views; D, H, Y, ventral views.

indistinct ventral shoulders and slightly convex flanks with maximum whorl width on inner flank at one third of whorl height. Umbilicus fairly narrow and shallow with low, rounded wall. Ornamentation consists of very weak constrictions and fine growth lines, which are prorsiradiate on inner flank, convex at mid-flank and rectiradiate

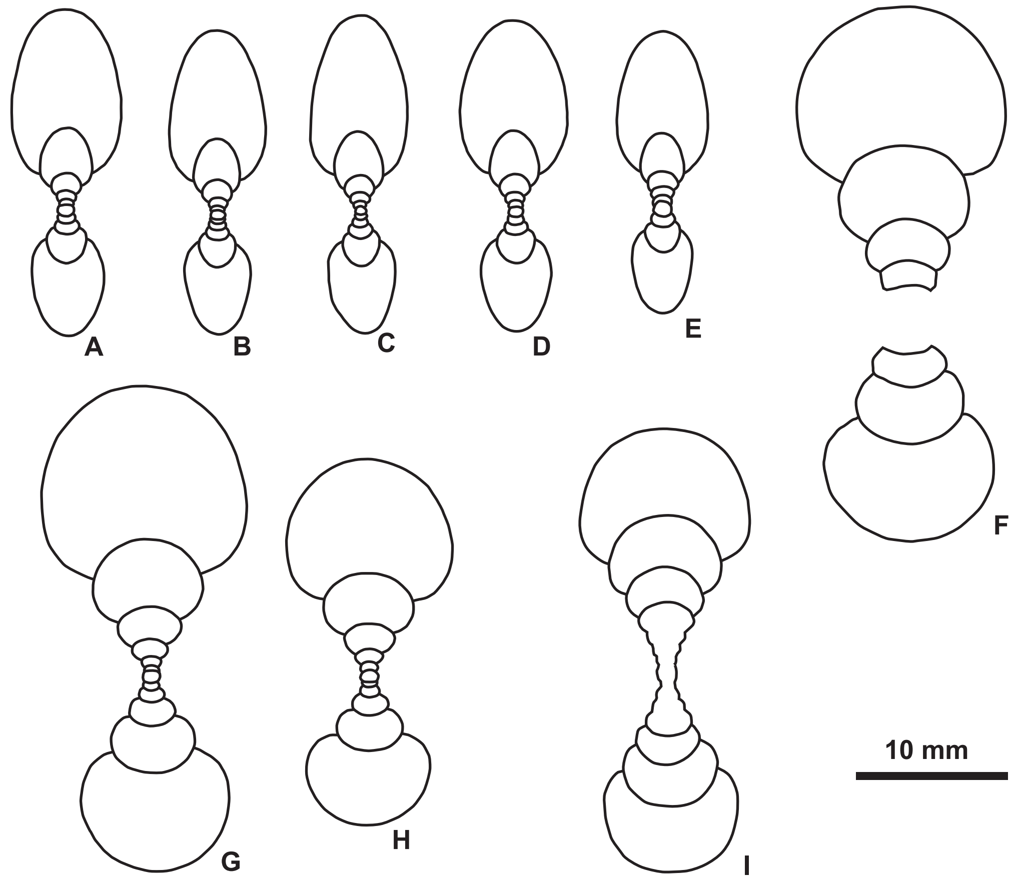

Figure 10. Whorl cross sections of ammonoids from the K4 Unit of the Krasnoyarka Formation. **A–E,** *Zelandites varuna* (Forbes, 1846) from NB3039c; A, NMNS PM35926; B, NMNS PM35927; C, NMNS PM35928; D, NMNS PM35929; E, NMNS PM35930; **F,** *Anagaudryceras mikobokense* Collignon, 1956, NMNS PM35918 from NB1066b; **G, H,** *A. matsumotoi* Morozumi, 1985 from NB3039c; G, NMNS PM35931; H, NMNS PM35932; **I,** *Gaudryceras seymouriense* (Macellari, 1986), NMNS PM35919 from NB1066b.

on outer flank. Body chamber adorned with low, broad, gently flexed band-like ribs, that are separated by constrictions of various width. Suture line with large, deeply incised, asymmetric bifid first lateral saddle, smaller bifid lateral saddle, and suspensive lobe with large bifid first auxiliary saddle (Figure 8B). First lateral lobe large and irregularly subdivided.

Measurements.—See Appendix.

Remarks.—Matsumoto (1938, p. 140) proposed *Zelandites varuna* var. *japonica* based on specimens collected from the Naiba area, which supposedly exhibit a more involute coiling, narrower umbilicus, and more compressed whorl section than typical specimens of *Z. varuna*. However, Macellari (1986, p. 14) pointed out that these differences are not evident when observing the figured syntype and regarded it as a synonym of *Z. varuna*. Matsumoto (1988) subsequently agreed with Macellari's interpretation and we also concur.

Salazar *et al*. (2010, p. 197) stated that the specimens identified as *Zelandites varuna* by Macellari (1986, p. 14, fig. 11.11, 11.12) from Seymour Island in Antarctica should be referred to another taxon because they have much smaller *W*/*H* and *U*/*D* ratios. However, the diameters of Macellari's (1986, table 2) specimens shown in Salazar *et al*. (2010, fig. 12) are 1/10 of the original values; this discrepancy is apparently caused by failure to recognize that the values were expressed in cm and not mm. The *W*/*H* and *U*/*D* of the Macellari's specimens fall within the variation of the type and other specimens of *Z. varuna* at the same diameter.

Zonova *et al*. (1993, pl. 98, fig. 4) and Yazykova (1994, pl. 1, fig. 8) assigned a specimen from the Maastrichtian in the Pugachevo area, southern Sakhalin to *Zelandites varuna*, but as Maeda *et al*. (2005) and Shigeta *et al*. (2015) pointed out, the specimen is identical to *Anagaudryceras matsumotoi* with respect to its whorl section, mode of coiling, and ornamentation. One of the four specimens described as *Z. varuna* by Ifrim *et al*. (2004, text-fig. 6G)

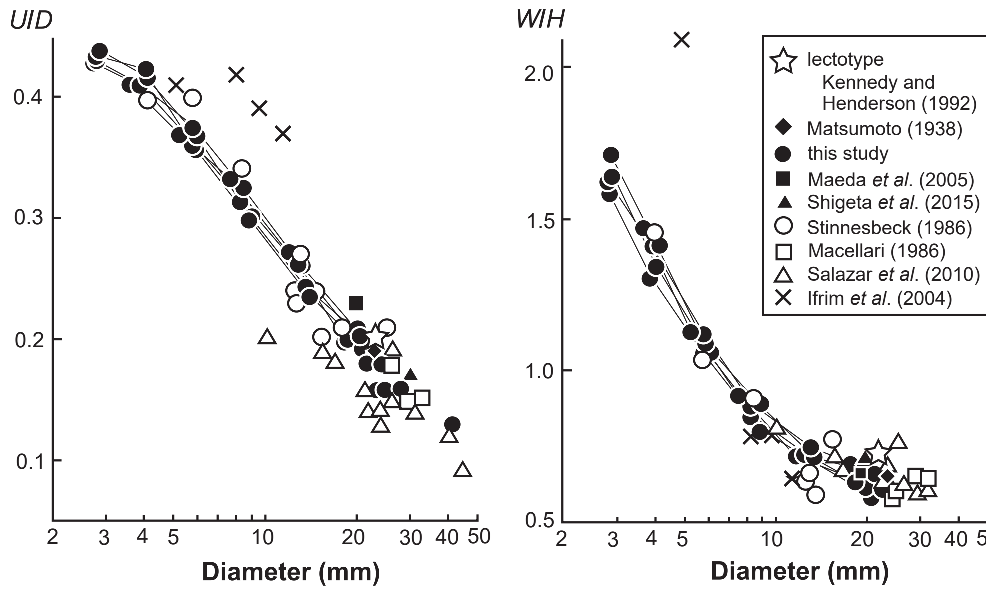

Figure 11. Scatter diagrams of umbilical diameter/shell diameter (*U*/*D*) versus shell diameter (*D*) and whorl width/whorl height (*W*/*H*) versus shell diameter for thirteen specimens of *Zelandites varuna* (Forbes, 1846) from the K4 Unit of the Krasnoyarka Formation, the lectotype from southern India and specimens assigned to this taxon by Matsumoto (1938) and Maeda *et al*. (2005) from southern Sakhalin, Shigeta *et al*. (2015) from eastern Hokkaido, Stinnesbeck (1986) and Salazar *et al*. (2010) from central Chile, Macellari (1986) from Seymour Island in Antarctica and Ifrim *et al*. (2004) from northeastern Mexico (see Material and methods section).

has a trapezoidal whorl section with a broad, flat venter, and exhibits a much larger *W*/*H* value than the typical specimens of *Z. varuna* (Figure 11); this specimen should be considered to be a juvenile shell of *Anagaudryceras* or *Gaudryceras*. The other three specimens (Ifrim *et al*., 2004, text-fig. 6F, J) exhibit a much wider umbilicus than the typical *Z. varuna* (Figure 11), and should be assigned to a different species of *Zelandites.*

Occurrence.—Middle Maastrichtian in southern India, upper Maastrichtian in Chile, Seymour Island in Antarctica, and Hokkaido and Awaji Island (Japan). Upper lower Maastrichtian and lower upper Maastrichtian in southern Sakhalin.

Genus ***Anagaudryceras*** Shimizu, 1934

Type species.—*Ammonites sacya* Forbes, 1846.

Anagaudryceras matsumotoi Morozumi, 1985

Figures 8C, 10G, H, 12, 13

Anagaudryceras matsumotoi Morozumi, 1985, p. 29, pl. 9, fig. 1, text-fig. 7; Matsumoto, 1985, p. 27, pl. 4, figs. 1–10; Matsumoto, 1988, p. 183, pl. 51, fig. 3; Ando *et al*., 2001, pl. 1, figs. 12–14; Maeda *et al*., 2005, p. 81, fig. 39.1–39.15; Shigeta *et al*., 2015, p. 112, fig. 5A–P; Shigeta *et al*., 2017, p. 21, fig. 13D–G.

Zelandites varuna (Forbes). Zonova *et al*., 1993, p. 148, pl. 98, fig. 4; Yazykova, 1994, p. 289, pl. 1, fig. 8.

Holotype.—KYUM GKH6882, figured by Morozumi (1985, p. 29, pl. 9, fig. 1, text-fig. 7), from the Maastrichtian *Pachydiscus* aff. *subcompressus* Zone in the Shimonada Formation of the Izumi Group on Awaji Island, Southwest Japan.

Material examined.—Ten specimens: NMNS PM35910 from NB1064b; NMNS PM35911 from NB1066a; NMNS PM35912–35916, 35931, 35932 from NB3039c; NMNS PM35917 from NB3041a.

Description.—Early whorls (up to 5 mm in diameter): Very evolute, very depressed shell with rounded whorl section, arched venter, indistinct ventral shoulders, and slightly convex flanks with maximum whorl width at mid-flank. Umbilicus fairly wide with moderately high, rounded wall and rounded shoulder.

Middle to late whorls (over 5 mm in diameter): As shell grows, whorl section becomes more compressed, while relative umbilical size (*U*/*D*) becomes progressively smaller (Figure 13). Shell with a diameter of 20 to 40 mm moderately involute and has whorl nearly as high as broad. Whorl cross-section circular with arched venter, indistinct ventral shoulders and gently convex flanks with maximum whorl width slightly below mid-flank. Umbilicus moderately wide with moderately high, rounded umbilical wall. Ornamentation consists of very fine, slightly sinuous growth lines, which pass over the venter in a broad convex arch. Suture line with large, deeply

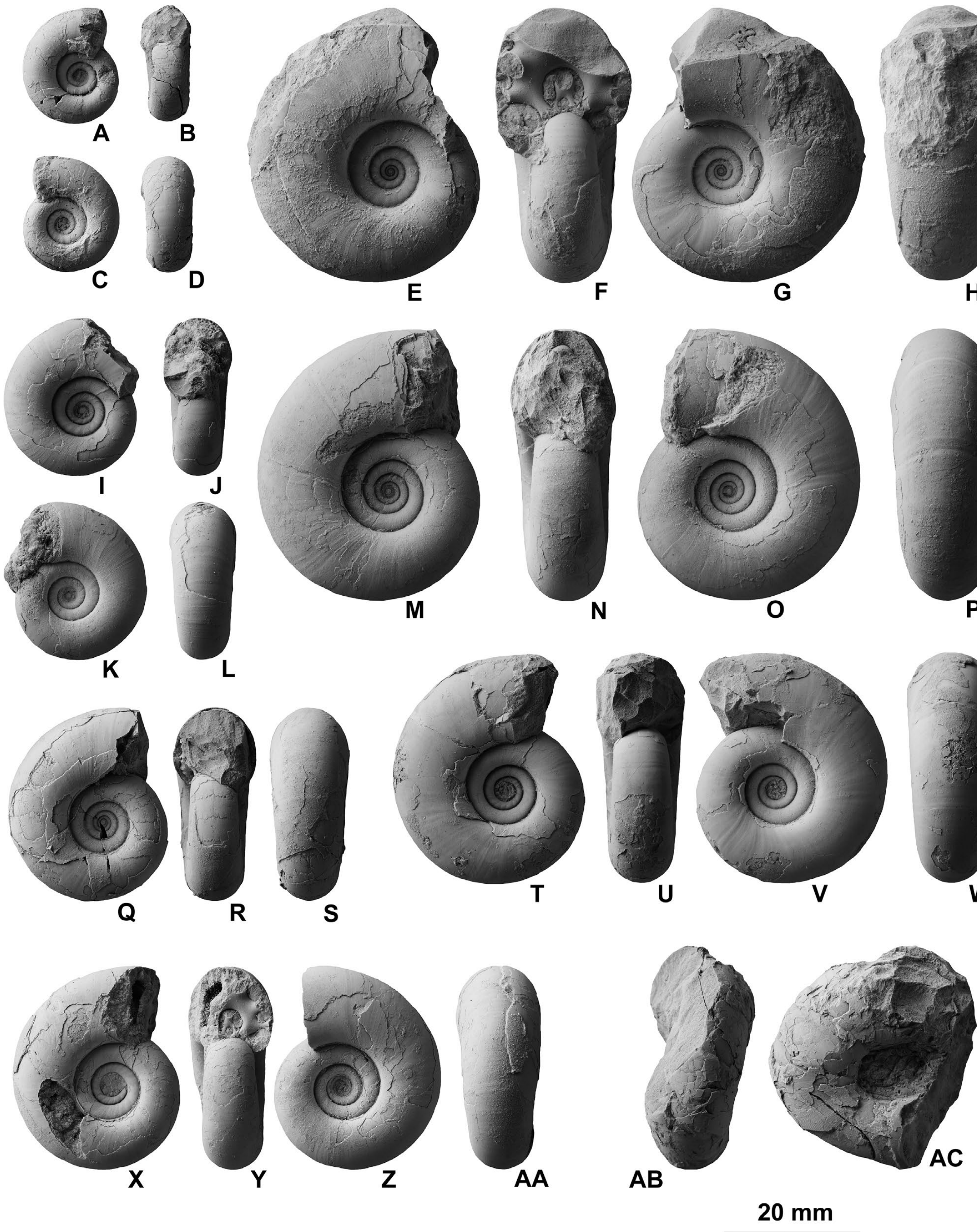

Figure 12. *Anagaudryceras matsumotoi* Morozumi, 1985, from the K4 Unit of the Krasnoyarka Formation. **A–D,** NMNS PM35916 from NB3039c; **E–H,** NMNS PM35912 from NB3039c; **I–L,** NMNS PM35914 from NB3039c; **M–P,** NMNS PM35913 from NB3039c; **Q–S,** NMNS PM35917 from NB3041a; **T–W,** NMNS PM35915 from NB3039c; **X–AA,** NMNS PM35910 from NB1064b; **AB, AC,** NMNS PM35911 from NB1066a. A, E, I, M, Q, T, X, AC, left lateral views; B, F, J, N, R, U, Y, apertural views; C, G, K, O, V, Z, right lateral views; D, H, L, P, S, W, AA, AB, ventral views.

incised, asymmetric bifid first lateral saddle, slightly smaller bifid lateral saddle, and strongly retraced suspensive lobe with large bifid first auxiliary saddle (Figure 8C). First lateral lobe large and irregularly subdivided.

Measurements.—See Appendix.

Remarks.—Ornamentation on the adult body chamber

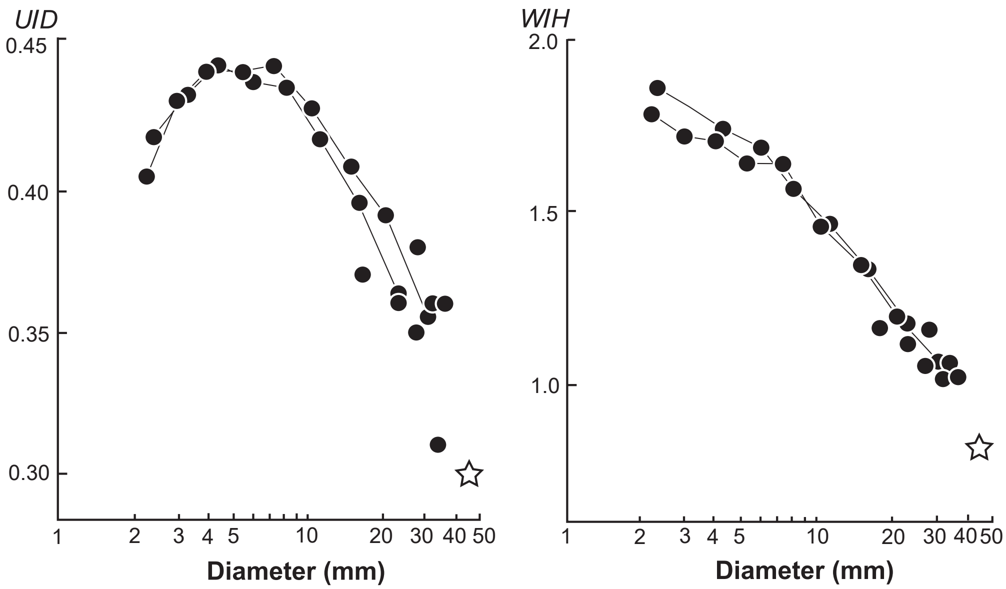

Figure 13. Scatter diagrams of umbilical diameter/shell diameter (*U*/*D*) versus shell diameter (*D*) and whorl width/whorl height (*W*/*H*) versus shell diameter for nine specimens of *Anagaudryceras matsumotoi* Morozumi, 1985 from the K4 Unit of the Krasnoyarka Formation (black circles) and the holotype (open star) from Awaji Island, Southwest Japan (see Material and methods section).

of *Anagaudryceras matsumotoi* consists of low, broad, gently flexed band-like ribs that are separated by constrictions of various width (Maeda *et al*., 2005). Because these ribs are not observed on the studied specimens, they are considered to be juvenile shells.

Occurrence.—Maastrichtian of southern Sakhalin, Hokkaido and Awaji Island.

Anagaudryceras mikobokense Collignon, 1956

Figures 8D, 10F, 14–16

Gaudryceras politissimum (Kossmat). Collignon, 1938, p. 92, pl. 7, fig. 2.

Anagaudryceras mikobokense Collignon, 1956, p. 59, pl. 8, fig. 1; Matsumoto, 1959, p. 139, pl. 38, fig. 1, text-fig. 70; Howarth, 1965, p. 358, pl. 4, figs. 1–3, text-figs. 1.

?*Lytoceras* (*Gaudryceras*) *aureum* Anderson, 1958, p. 184, pl. 71, fig. 1.

Anagaudryceras politissimum (Kossmat). Salazar *et al*., 2010, p. 193, figs. 5i, j, 6d, g, h, 7b, 8b, 9.

Holotype.—MNHN.F.R00657, figured by Collignon (1956, p. 59, pl. 8, fig. 1), from the Maastrichtian of Ianjona, Madagascar.

Material examined.—One specimen: NMNS PM35918 from NB1066b.

Description.—Fairly evolute shell with fairly depressed, rounded whorl section, arched venter, indistinct ventral shoulders, and slightly convex flanks with maximum whorl width at mid-flank in early growth stage. Umbilicus fairly wide with rounded umbilical wall. As shell grows, whorl section becomes more compressed, while relative umbilical size (*U*/*D*) decreases (Figure 16), becoming only moderately wide. Ornamentation consists of very fine, slightly sinuous, markedly prorsiradiate growth lines and five rounded, collar-like ribs per whorl, which bend gently forward on outer flank before crossing venter in a convex arch. Suture line with large, deeply incised, asymmetric bifid first lateral saddle, slightly smaller bifid lateral saddle, and strongly retraced suspensive lobe with large bifid first auxiliary saddle (Figure 8D). First lateral lobe large and irregularly subdivided.

Measurements.—See Appendix.

Remarks.—As Matsumoto (1959) earlier pointed out, the holotype of *Lytoceras* (*Gaudryceras*) *aureum* Anderson, 1958 is probably referable to *Anagaudryceras mikobokense*. Specimens assigned to *A*. *politissimum* (Kossmat, 1895) by Salazar *et al*. (2010) with their markedly prorsiradiate growth lines and rounded, collar-like ribs, and slightly convex flanks with maximum whorl width at mid-flank, are identical to the present species. *Anagaudryceras politissimum* has more compressed whorls than *A*. *mikobokense* and the maximum whorl width is situated below mid-flank (Kennedy and Klinger, 1979; Matsumoto, 1985).

Occurrence.—Upper Campanian of Angola and Maastrichtian of Madagascar, southern Sakhalin, Chile and California.

Figure 14. *Anagaudryceras mikobokense* Collignon, 1956, NMNS PM35918, from NB1066b in the K4 Unit of the Krasnoyarka Formation. **A,** ventral view; **B,** left lateral view.

Genus *Gaudryceras* de Grossouvre, 1894

Type species.—*Ammonites mitis* Hauer, 1866.

Gaudryceras seymouriense (Macellari, 1986)

Figures 8E, 10I, 17–20

Anagaudryceras seymouriense Macellari, 1986, p. 10, figs. 9.1–9.6, 10.1–10.4; Maeda *et al*., 2005, p. 82, figs. 40.4–40.6, 41.

Anagaudryceras cf. *seymouriense* Macellari. Matsumoto, 1988, p. 183, pl. 51, fig. 2, pl. 53, fig. 1; Shigeta *et al*., 2015, p. 115, fig. 8.

Vertebrites? cf. *kayei* (Forbes). Morozumi, 1985, p. 26, pl. 9, fig. 3, text-fig. 6.

Gaudryceras (*Vertebrites*) *kayei* (Forbes). Stinnesbeck, 1986, p. 198, pl. 8, figs. 2, 3, text-fig. 21.

Gaudryceras kayei (Forbes). Salazar *et al*., 2010, p. 195, figs. 5a–f, 7c–f, 10, 11a, b, 13d, e.

Gaudryceras hamanakense Matsumoto and Yoshida. Zonova *et al*., 1993, p. 154, pl. 103, fig. 2; Yazykova, 1994, p. 292, pl. 6, fig. 2.

Holotype.—OSU38333, figured by Macellari (1986, p. 10, fig. 9.1, 9.2), from the upper Maastrichtian of Seymour Island in the Antarctic Peninsula.

Material examined.—Three specimens: NMNS PM35919 from NB1066b; NMNS PM35920 from NB3039c; NMNS PM35921 from NB3041a.

Description.—Very evolute, slightly depressed shell with rounded whorl section, arched venter, indistinct ventral shoulders, and slightly convex flanks with maximum whorl width below mid-flank on early to middle whorls (up to 50 mm in diameter). Umbilicus wide with moderately high, vertical wall and moderately rounded shoulders. As shell grows, whorl expansion rate increases, and whorl section becomes more compressed, while relative

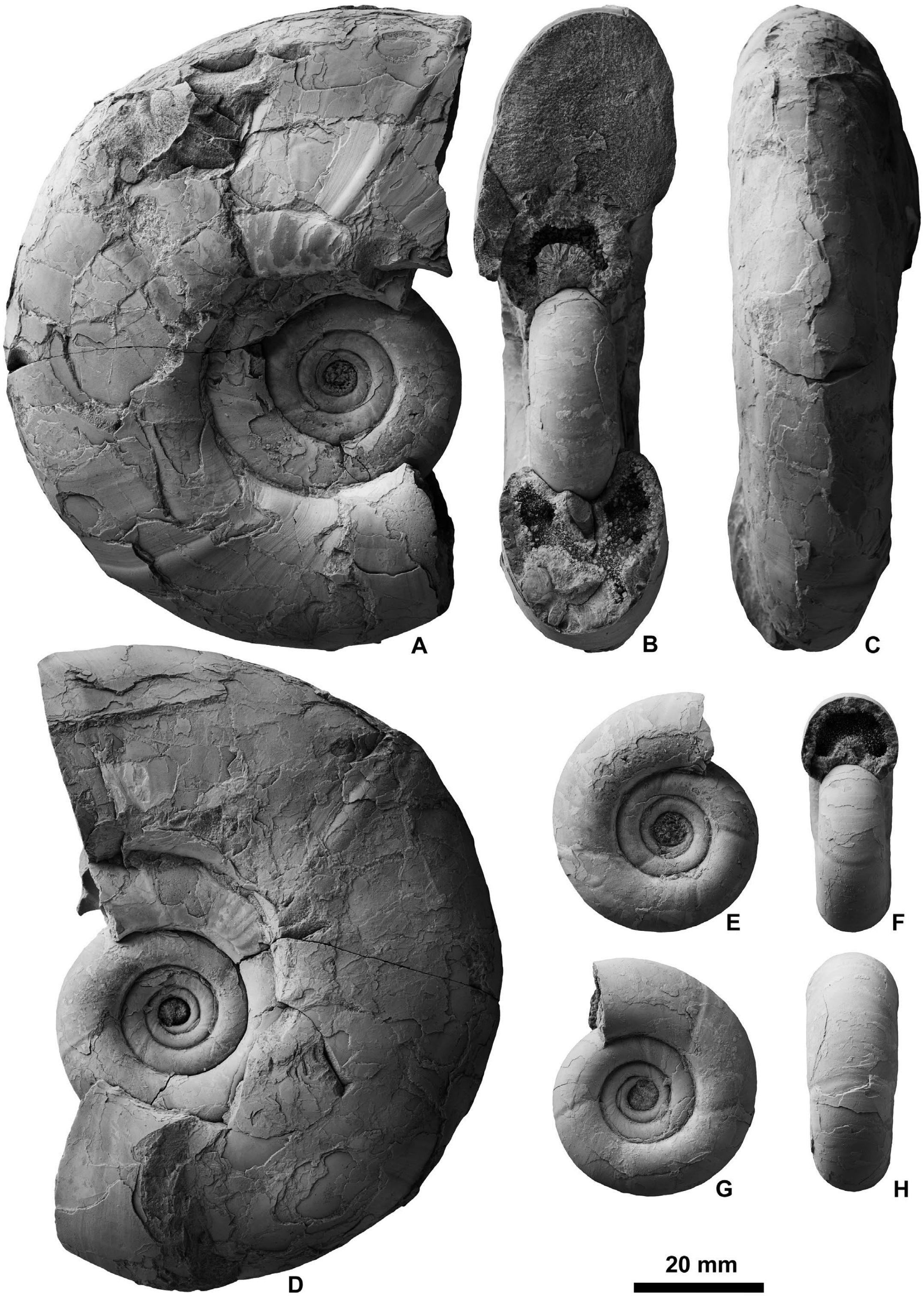

Figure 15. *Anagaudryceras mikobokense* Collignon, 1956, NMNS PM35918, from NB1066b in the K4 Unit of the Krasnoyarka Formation. **A,** left lateral view; **B,** apertural view; **C,** ventral view; **D,** right lateral view; **E–H,** inner whorls after removal of parts of phragmocone and body chamber; E, left lateral view; F, apertural view; G, right lateral view; H, ventral view.

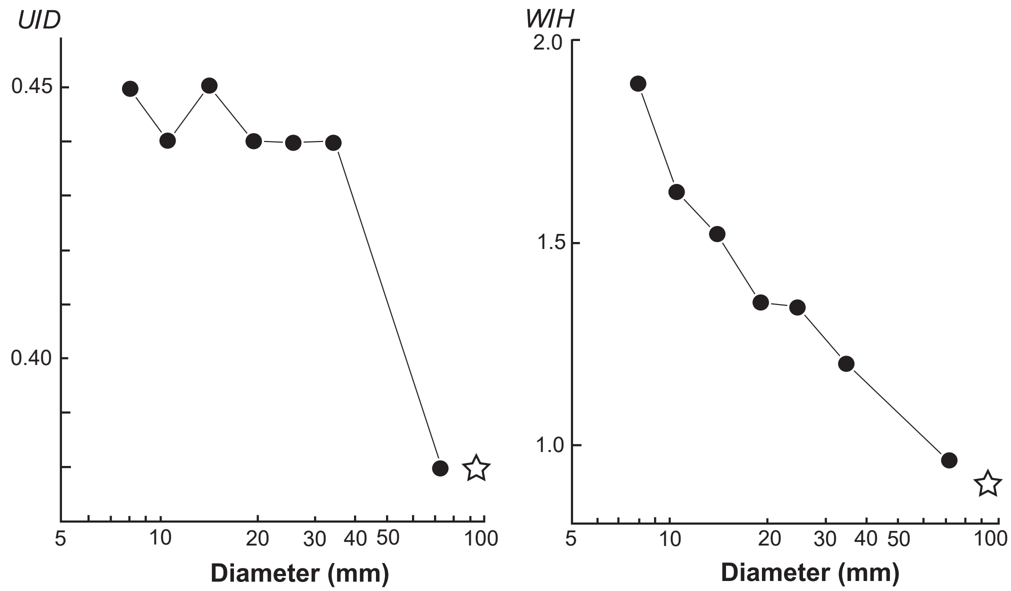

Figure 16. Scatter diagrams of umbilical diameter/shell diameter (*U*/*D*) versus shell diameter (*D*) and whorl width/whorl height (*W*/*H*) versus shell diameter for inner whorls of specimen (NMNS PM35918) of *Anagaudryceras mikobokense* Collignon, 1956, from the K4 Unit of the Krasnoyarka Formation (black circles) and the holotype (open star) from Madagascar (see Material and methods section).

umbilical size (*U*/*D*) becomes smaller (Figure 20). Ornamentation consists of very fine lirae and rounded, collar-like ribs, which arise at umbilical seam and approach a sigmoidal pattern before passing over the venter in a broad convex arch. Lirae gradually develop into slightly more distant, narrowly raised ribs, and collar-like ribs become more frequent on later whorls. Very weak spiral lirae visible on outer flank and venter. Suture line with large, deeply incised, asymmetric bifid first lateral saddle, slightly smaller bifid lateral saddle, and suspensive lobe with large bifid first auxiliary saddle (Figure 8E). First lateral lobe large and irregularly subdivided.

Measurements.—See Appendix.

Remarks.—This species was described as *Anagaudryceras* by Macellari (1986), but Shigeta *et al*. (2015) assigned it to *Gaudryceras*, because its evolute shell and wide umbilicus during its early to middle growth stages, and slightly sigmoidal lirae and ribs are all characteristic features of *Gaudryceras*. Specimens assigned to *G. kayei* by Stinnesbeck (1986) and Salazar *et al*. (2010), *Vertebrites*? cf. *kayei* by Morozumi (1985), and *G. hamanakense* by Zonova *et al*. (1993, pl. 103, fig. 2) and Yazykova (1994, pl. 6, fig. 2) are identical to *G. seymouriense* with respect to whorl section, mode of coiling and ornamentation.

Occurrence.—Upper lower Maastrichtian of southern Sakhalin and upper Maastrichtian of Hokkaido and Awaji Island (Japan), southern Sakhalin, Chile and Seymour Island in Antarctica.

Suborder Ammonitina Hyatt, 1889
Superfamily Desmoceratoidea Zittel, 1895
Family Pachydiscidae Spath, 1922
Genus ***Pachydiscus*** Zittel, 1884

Type species.—*Ammonites neubergicus* Hauer, 1858.

Pachydiscus subcompressus Matsumoto, 1954

Figures 8F, 21–23

Pachydiscus subcompressus Matsumoto, 1954, p. 287, pl. 10, fig. 4; Vereshchagin *et al*., 1965, p. 56, pl. 70, fig. 1; Matsumoto, 1979, fig. 5; Poyarkova, 1987, p. 143, pl. 28, fig. 4; Matsumoto, 1988, p. 186, pl. 53, fig. 2; Zonova *et al*., 1993, p. 167, pl. 89, fig. 1, pl. 97, fig. 2; Yazykova, 1994, p. 298, pl. 10, fig. 2; Kodama *et al*., 2002, fig. 8G, H; Maeda *et al*., 2005, fig. 14.3, 14.6.

Pachydiscus aff. *subcompressus* Matsumoto. Morozumi, 1985, p. 21, pl. 5, fig. 1, pl. 7, fig. 1, text-fig. 5.

Pachydiscus gollevillensis Orbigny. Yazykova, 1994, p. 297, pl. 11, fig. 2; Zonova *et al*., 1993, p. 166, pl. 89, fig. 2.

non *Pachydiscus subcompressus* Matsumoto. Matsumoto, 1954, p. 287, pl. 12, fig. 1 (= *Pachydiscus flexuosus*, after Matsumoto, 1979, p. 53); Yazykova, 1992, p. 198, pl. 111, fig. 4 (= *P. flexuosus*); Zonova *et al*., 1993, p. 167, pl. 93, fig. 1, pl. 95, fig. 1, pl. 96, fig. 1 (= *Canadoceras*), pl. 94, fig. 1, pl. 96, fig. 2 (= *P. excelsus*); Yazykova, 1994, p. 298, pl. 8, fig. 3 (= *Canadoceras*?), pl. 10, fig. 3 (= *P. flexuosus*), pl. 13, fig. 2 (= *P. excelsus*), pl. 15, fig. 1, pls. 16, 17, pl. 18, fig. 1 (= *Canadoceras*).

Holotype.—UMUT MM.6821, figured by Matsumoto (1954, p. 287, pl. 10, fig. 4), from Rdy1 Unit at Loc. 105 along the Miho (= Krasnoyarka River) in the Naibuchi

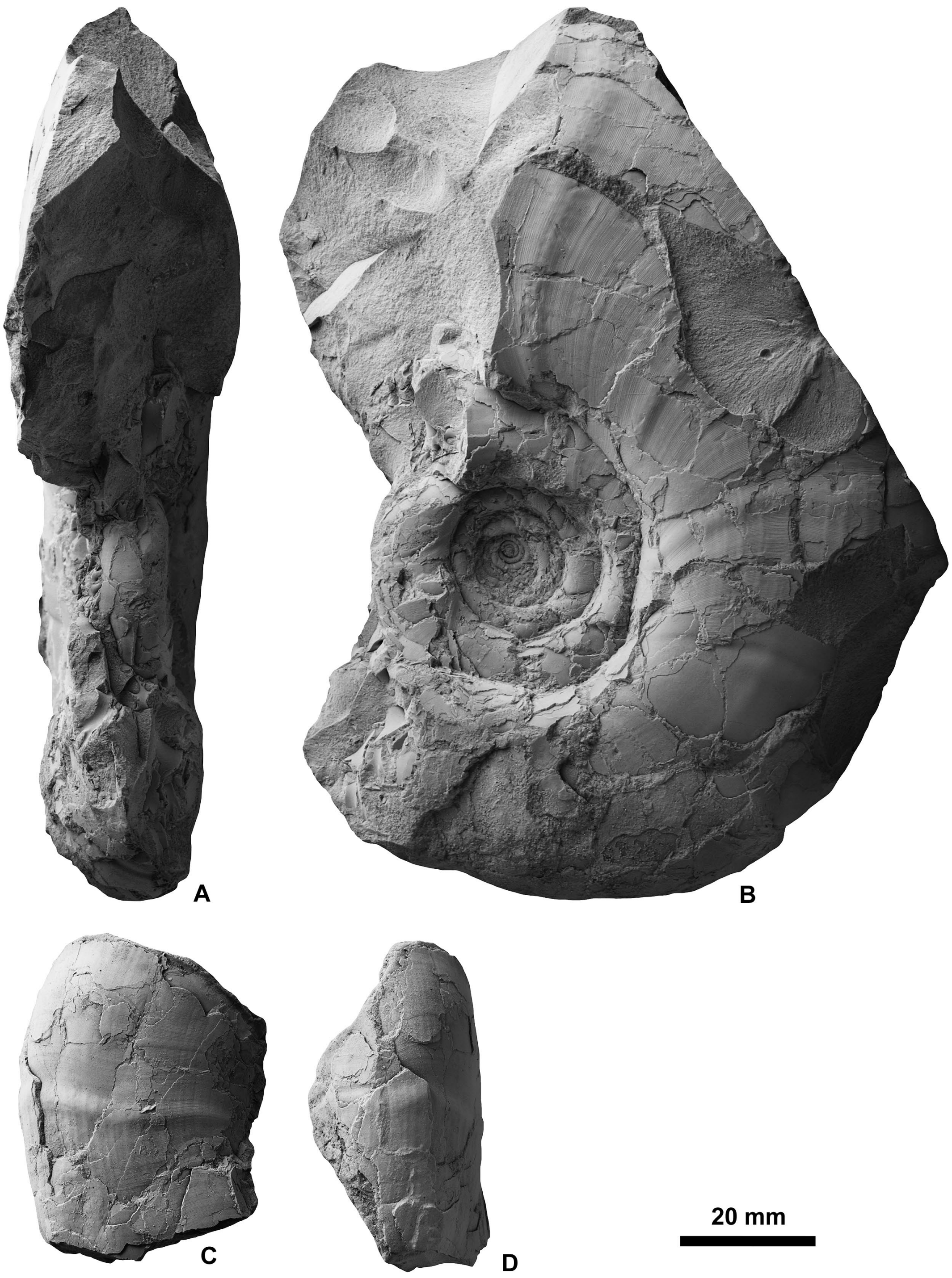

Figure 17. *Gaudryceras seymouriense* (Macellari, 1986) from the K4 Unit of the Krasnoyarka Formation. **A, B,** NMNS PM35921 from NB3041a; A, apertural view; B, right lateral view; **C, D,** NMNS PM35920 from NB3039c; C, left lateral view; D, ventral view.

(= Naiba) area, southern Sakhalin. Because the only exposure at Loc. 105 (= NB3035 in Figure 4) consists of sandy mudstone of the K2 Unit, it is reasonable to assume that the holotype was extracted from a float concretion derived from the K4 Unit.

Material examined.—Five specimens: NMNS PM35922 from NB3039a; NMNS PM35923 from NB3039b; NMNS PM35924 from NB3039d; NMNS

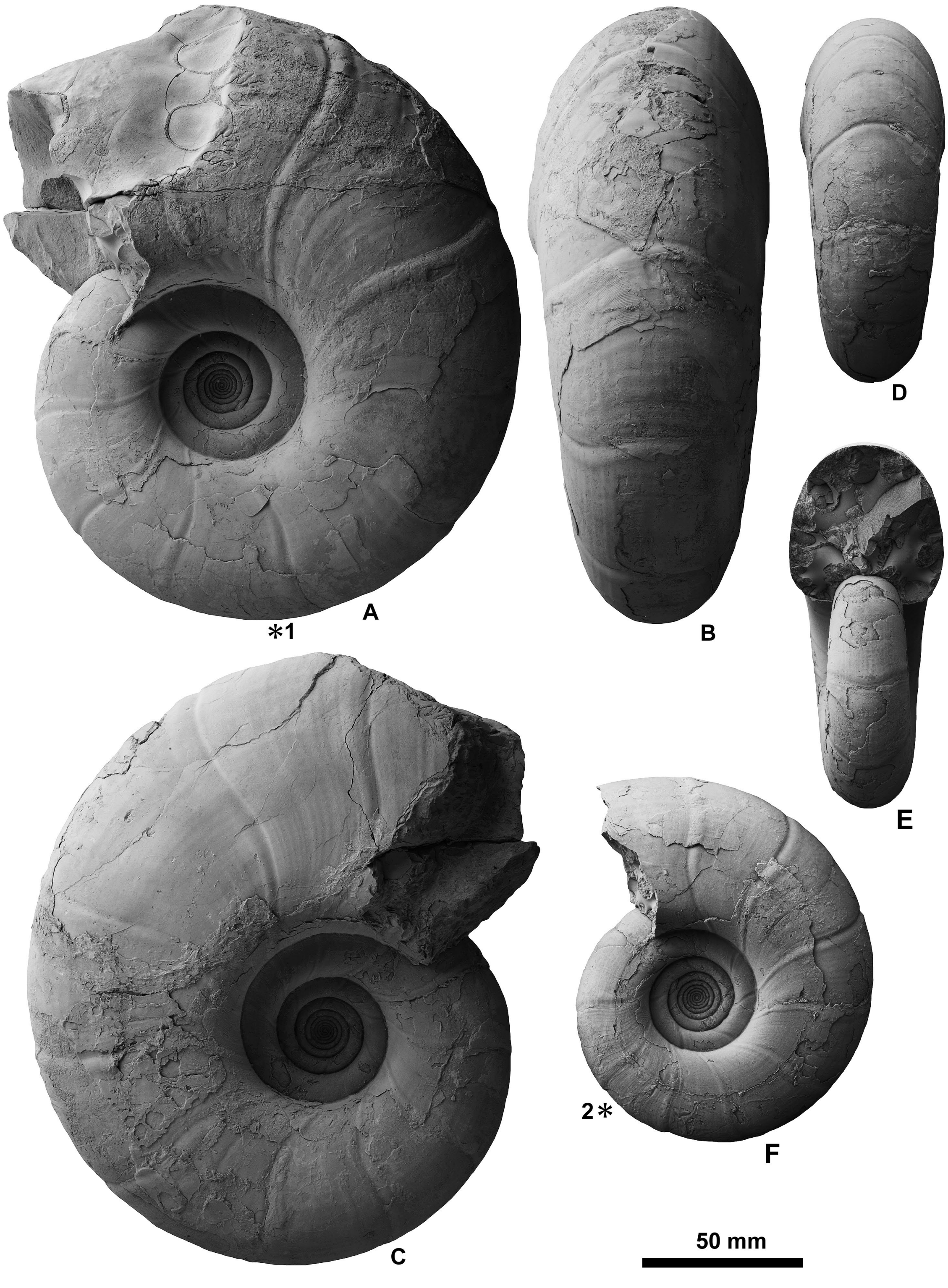

Figure 18. *Gaudryceras seymouriense* (Macellari, 1986), NMNS PM35919, from NB1066b in the K4 Unit of the Krasnoyarka Formation. **A–C,** original specimen; **D–F,** the same specimen following the removal of successive ~1/2 whorl segments. Numbered asterisks 1 and 2 indicate positions where whorl segments were removed, resulting in D–F and Figure 19A–C, respectively (see Material and methods section). A, F, right lateral views; B, D, ventral views; C, left lateral view; E, apertural view.

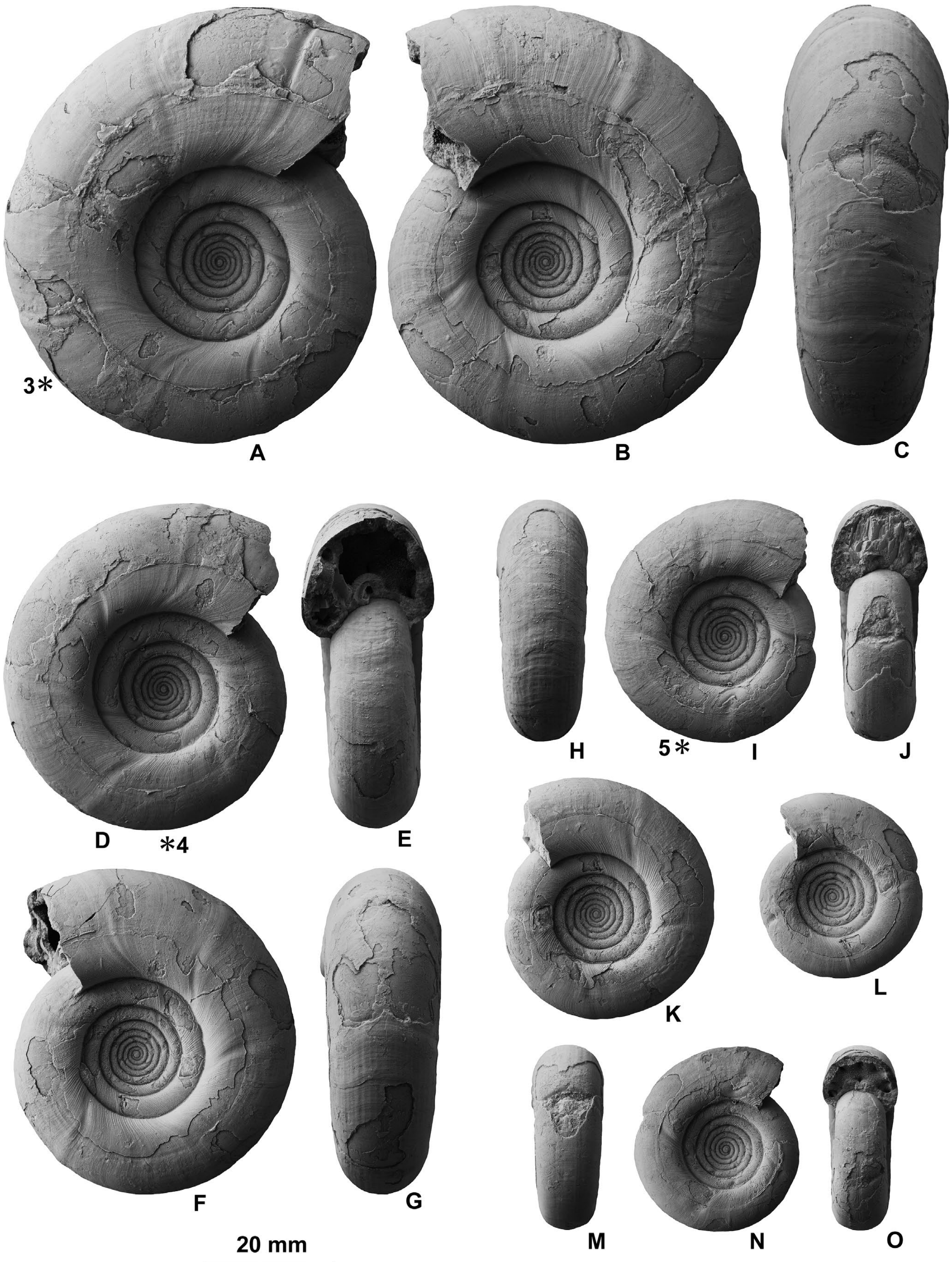

Figure 19. *Gaudryceras seymouriense* (Macellari, 1986), NMNS PM35919, from NB1066b in the K4 Unit of the Krasnoyarka Formation. **A, D, I, N,** left lateral views; **B, F, K, L,** right lateral views; **C, G, H, M,** ventral views; **E, J, O,** apertural views. Numbered asterisks 3–5 indicate positions where whorl segments were removed, resulting in D–G, H–K and L–O, respectively (see Material and methods section).

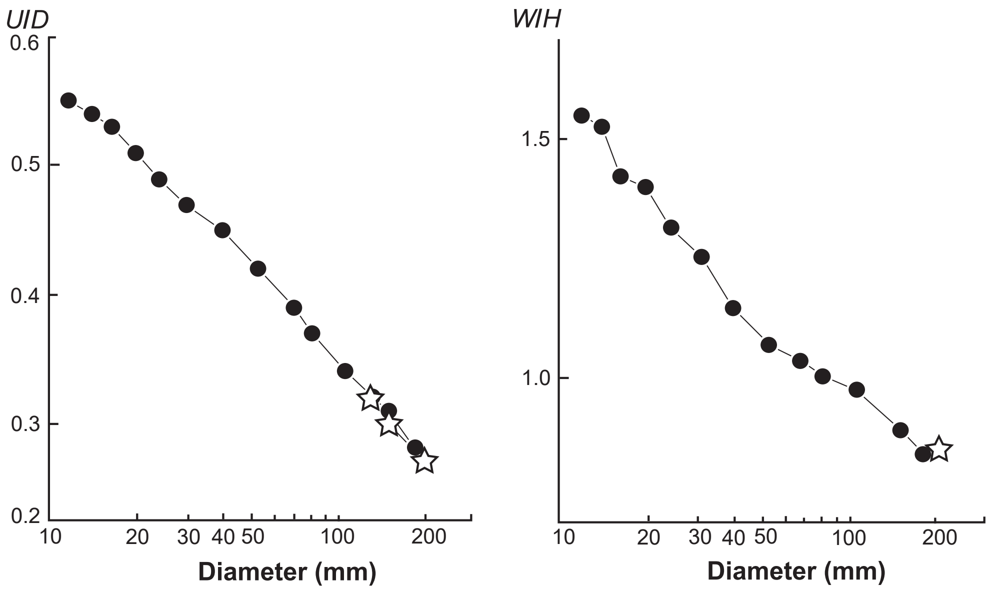

Figure 20. Scatter diagrams of umbilical diameter/shell diameter (*U*/*D*) versus shell diameter (*D*) and whorl width/whorl height (*W*/*H*) versus shell diameter for specimen (NMNS PM35919) of *Gaudryceras seymouriense* (Macellari, 1986), from the K4 Unit of the Krasnoyarka Formation (black circles) and the holotype (open stars) from Seymour Island in Antarctica (see Material and methods section).

PM35925 from NB3039e; KYUM GKP00016 from a float concretion found near NB3035.

Description.—Moderately involute, very compressed shell with oval whorl section, rounded venter, rounded ventral shoulders, and subparallel flanks. Umbilicus fairly narrow with moderately high, vertical wall and rounded shoulders. Ornamentation tends to be restricted to just the umbilical- and ventral areas. Ribs arise on umbilical wall, strengthen markedly on umbilical shoulder, becoming concave and forming umbilical bullae, and then become prorsiradiate on inner flank, before fading in strength at about mid-flank. Strong ribs reappear on outer flank and cross venter in a broad convex arch. At diameter of 100–170 mm, umbilical ribs number 18 and ventral ribs 70–80 per whorl. Ribs on flanks almost disappear at middle and later growth stages (Figures 22, 23). Suture line with deeply incised, asymmetric trifid lateral saddle and trifed first lateral lobe (Figure 8F).

Measurements.—See Appendix.

Remarks.—Specimens attributed to *Pachydiscus subcompressus* from southern Sakhalin by Matsumoto (1954), Zonova *et al*. (1993) and Yazykova (1992, 1994) actually include different species of *Pachydiscus* as well as *Canadoceras*. One of these specimens (Matsumoto, 1954, pl. 12, fig. 1) is identical to *P. flexuosus* Matsumoto, 1979, as Matsumoto (1979, p. 53) later pointed out. Specimen no. 89/12769 (Zonova *et al*., 1993, pl. 94, fig. 1, pl. 96, fig. 2; Yazykova, 1994, pl. 13, fig. 2), with its fairly compressed shell with numerous, weakly prorsiradiate ribs and intercalated ribs, which strengthen on the outer flank and venter, is assignable to *P. excelsus* Matsumoto, 1979. Specimen no. 28/12632 (Yazykova, 1992, pl. 111, fig. 4) and no. 93/12769 (Yazykova, 1994, pl. 10, fig. 3), both of which are characterized by weak, flexuous ribs, are clearly identifiable as *P. flexuosus*. Specimens numbered no. 88/12769 (Zonova *et al*., 1993, pl. 93, fig. 1; Yazykova, 1994, pl. 17, pl. 18, fig. 1), no. 92/12769 (Zonova *et al*., 1993, pl. 95, fig. 1; Yazykova, 1994, pl. 15, fig. 1, pl. 16) and no. 245/12769 (Yazykova, 1994, p. 298, pl. 8, fig. 3), all of which exhibit numerous, prorsiradiate ribs as well as constrictions followed immediately by major ribs, and intercalated ribs occurring between the inner and mid-flank, probably belong to *Canadoceras*.

Matsumoto (1954, p. 289) proposed *Pachydiscus subcompressus obsoletus*, but the paratypes are identical to *P. flexuosus* with respect to whorl section, mode of coiling and ornamentation (Matsumoto, 1979, p. 56). *Pachydiscus subcompressus* is similar to *P. compressus* (Spath, 1922) from the Maastrichtian of southern India with its very compressed shell and fairly narrow umbilicus, but differs by having much denser umbilical and ventral ribbing. This species also resembles *P. gollevilensis* (Orbigny, 1850) from the Maastrichtian of Europe and other areas, but differs by its much more compressed shell with a narrower umbilicus and much denser ribbing.

Occurrence.—Lower upper Maastrichtian of southern Sakhalin, Hokkaido and Awaji Island.

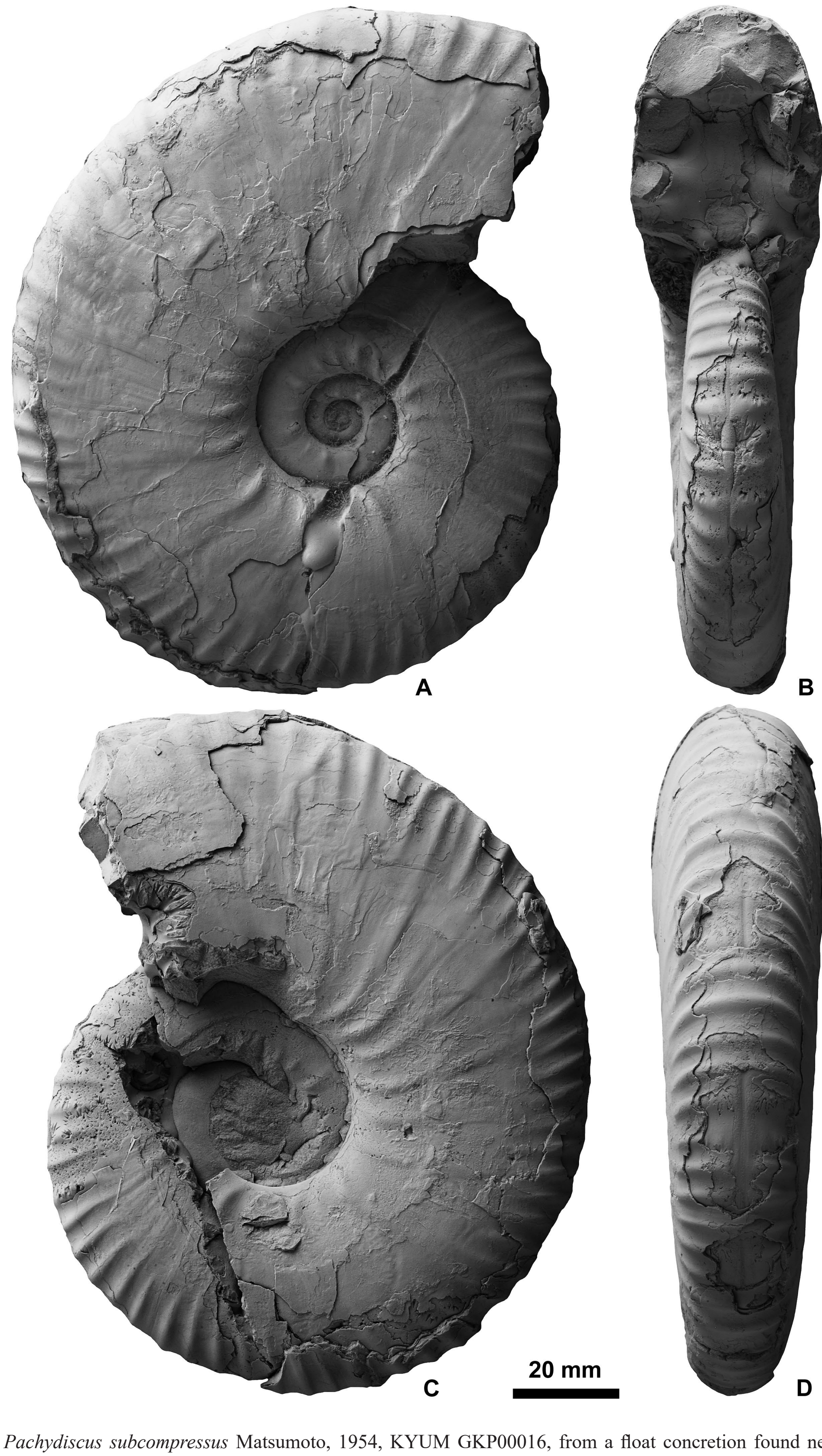

Figure 21. *Pachydiscus subcompressus* Matsumoto, 1954, KYUM GKP00016, from a float concretion found near NB3035. **A,** left lateral view; **B,** apertural view; **C,** right lateral view; **D,** ventral view.

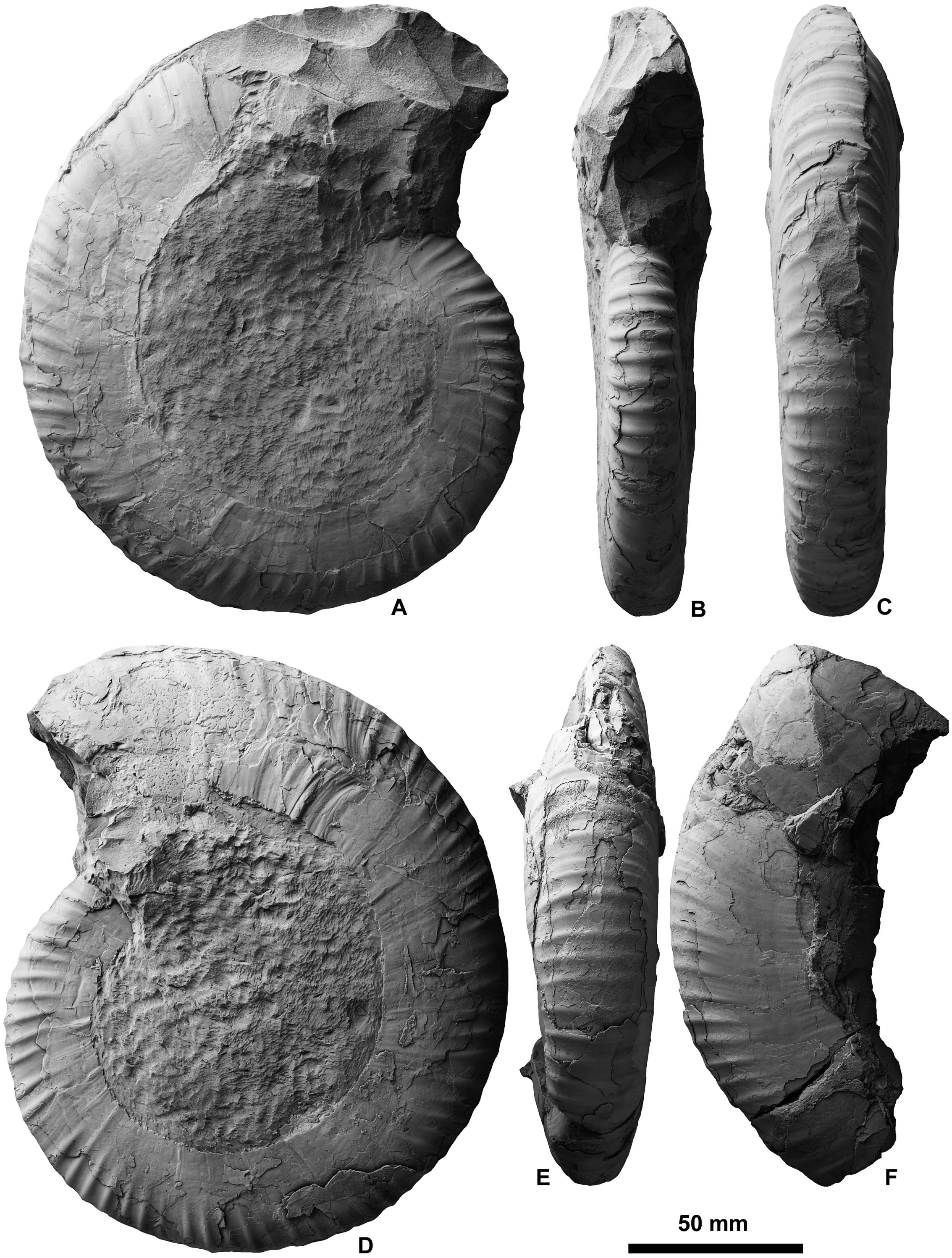

Figure 22. *Pachydiscus subcompressus* Matsumoto, 1954 from the K4 Unit of the Krasnoyarka Formation. **A–D,** NMNS PM35924 from NB3039d; **E, F,** NMNS PM35925 from NB3039e. A, F, left lateral views; B, apertural view; C, E, ventral views; D, right lateral view.

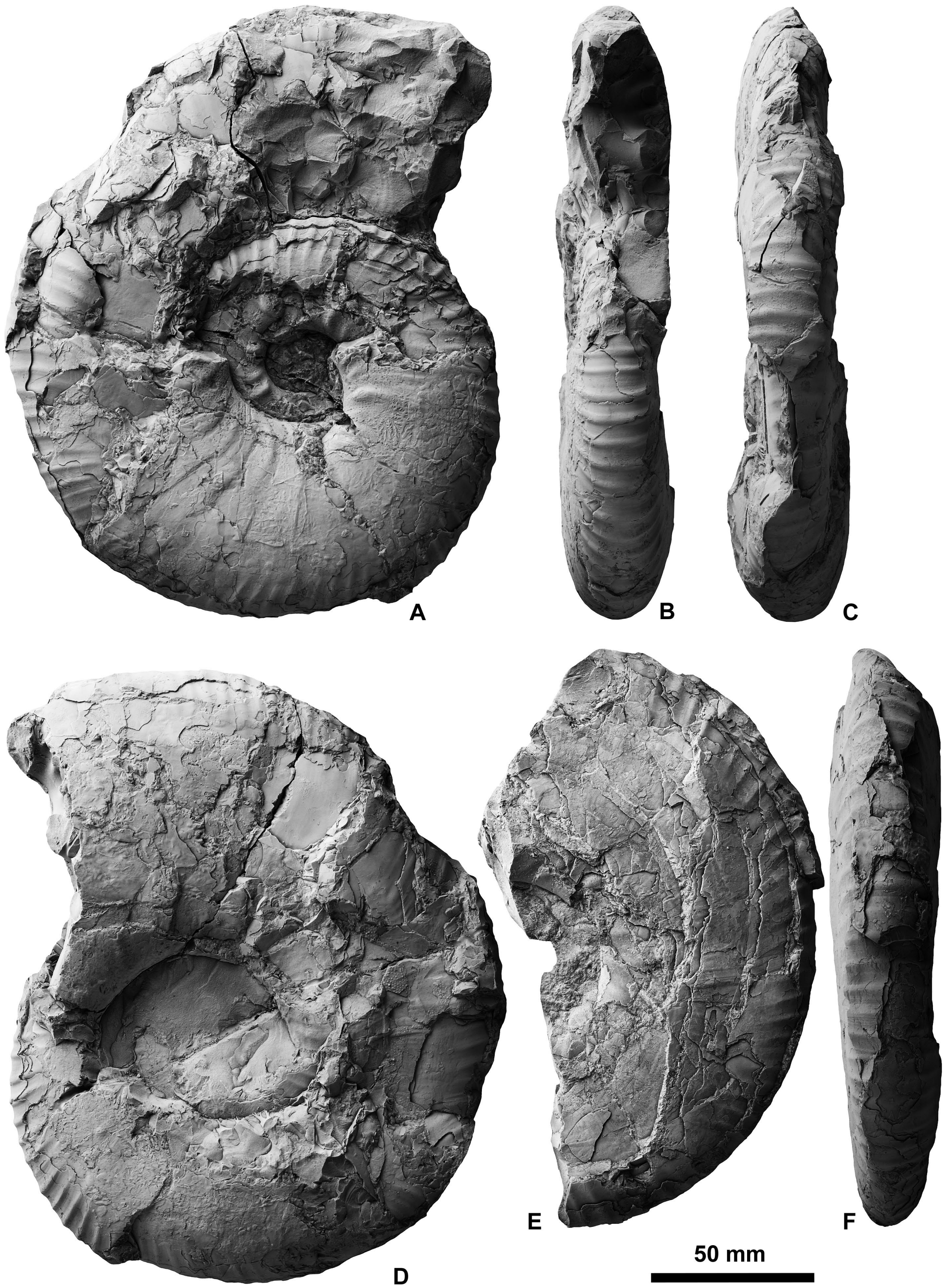

Figure 23. *Pachydiscus subcompressus* Matsumoto, 1954 from the K4 Unit of the Krasnoyarka Formation. **A–D,** NMNS PM35923 from NB3039b; **E, F,** NMNS PM35922 from NB3039a. A, left lateral view; B, apertural view; C, F, ventral views; D, E, right lateral views.

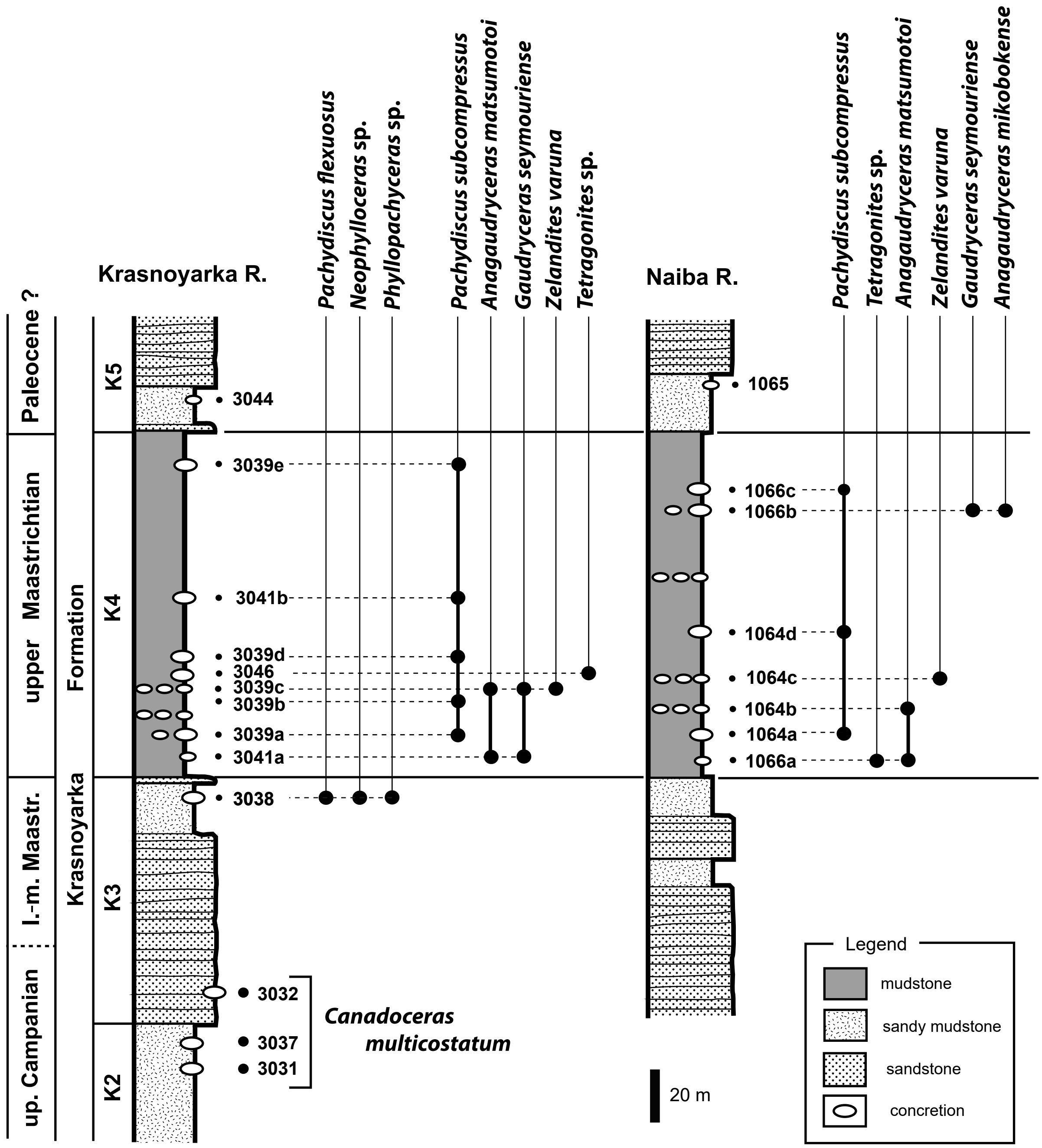

Figure 24. Lithology and stratigraphic occurrence of ammonoids in the Krasnoyarka Formation. Specimens of *Pachydiscus subcompressus* at NB1064a, 1064d, 1066c and 3041b were not collected, but their occurrences in the outcrops were confirmed (see Kodama *et al*., 2002). Additional collected fossils are stored at National Museum of Nature and Science, Tsukuba and Kyushu University Museum, Fukuoka.

Discussion

The following six ammonoid species have been recognized in the K4 Unit of the Krasnoyarka Formation in the Naiba area (Figure 24): *Pachydiscus subcompressus*, *Gaudryceras seymouriense*, *Anagaudryceras mikobokense*, *A. matsumotoi*, *Zelandites varuna* and *Tetragonites* sp.

Of these species, *Anagaudryceras matsumotoi* exhibits an endemic distribution restricted to the Northwest Pacific region and a relatively wide stratigraphic range throughout the Maastrichtian. It probably evolved from

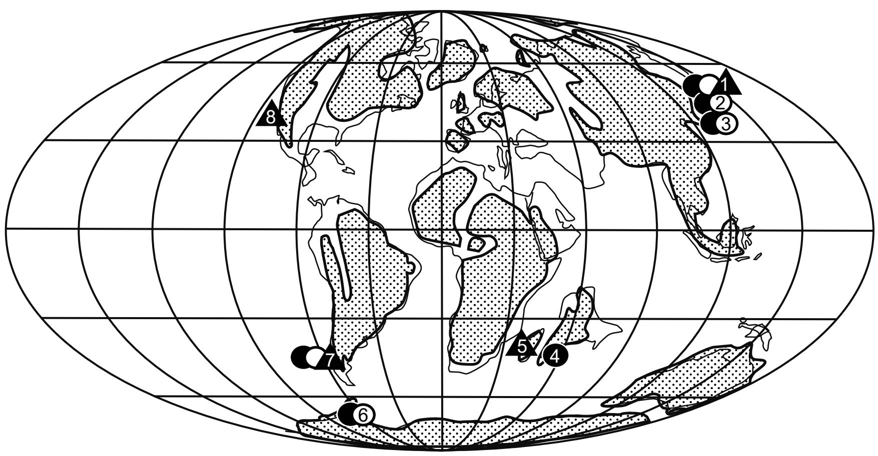

Figure 25. Paleogeographical distribution of *Zelandites varuna* (black circles), *Gaudryceras seymouriense* (open circles) and *Anagaudryceras mikobokense* (black triangles) during Maastrichtian time. Paleomap modified after Smith *et al*. (1994) and Ifrim *et al*. (2004). 1, southern Sakhalin (e.g. Matsumoto, 1938, 1988); 2, Hokkaido (e.g. Shigeta *et al*., 2015); 3, Awaji Island in Southwest Japan (Morozumi, 1985); 4, southern India (e.g. Forbes, 1846); 5, Madagascar (Collignon, 1956); 6, Seymour Island in Antarctica (Macellari, 1986); 7, Chile (Stinnesbeck, 1986; Salazar *et al*., 2010); 8, California (Matsumoto, 1959).

A. *compressum* Shigeta and Nishimura, 2014 during the early Maastrichtian and then flourished in the Northwest Pacific region during Maastrichtian time (Shigeta and Nishimura, 2014; Shigeta *et al*., 2017).

Pachydiscus subcompressus is known only from the upper Maastrichtian in the Northwest Pacific region. However, the studied specimens exhibit features that closely resemble *P*. *compressus* (Spath, 1922) from the Maastrichtian of southern India and *P. gollevilensis* (Orbigny, 1850) from the Maastrichtian of Europe and other areas, namely 1) the very compressed whorl with subparallel flanks, 2) rounded venter, and 3) ornamentation characterized by distinctly differentiated umbilical and ventral ribs. These features suggest close phylogenetic relationships. These species are clearly distinguishable morphologically from *P. flexuosus*, which occurs in the middle Maastrichtian of Hokkaido and Sakhalin, by its slightly rounded converging flanks and continuous flexuous ribs (Maeda *et al.*, 2005, p. 46–47, figs. 14, 15; Maeda and Shigeta, 2005, p. 130, fig. 8). This evidence suggests that the *P*. *compressus*- *P. gollevilensis* group extended its geographical distribution from other areas to the Northwest Pacific region at the beginning of late Maastrichtian time and gave rise to *P. subcompressus* (Maeda *et al*., 2005, p. 54).

Zelandites varuna is known from the Maastrichtian in the Indo-Pacific region (southern mid-latitudes, North Pacific and Antarctic; Ifrim *et al*., 2004; Figure 25). Although five species of *Zelandites* are known from the upper Albian to middle Campanian, the genus has not been found in the upper Campanian to middle lower Maastrichtian in the Northwest Pacific region (Matsumoto, 1938, 1995; Matsumoto and Miyauchi, 1984). Very involute and fairly compressed specimens of *Zelandites*, similar to *Z. varuna*, were described as *Zelandites* sp. 2 from the upper Santonian to early Campanian in Natal, South Africa (Kennedy and Klinger, 1979), *Z. pujatoi* Raffi *et al*., 2019 from the lower Campanian in the James Basin, Antarctica (Raffi *et al*., 2019) and *Z. kaiparaensis* Marshall, 1926 from the Campanian–Maastrichtian in New Zealand (Henderson, 1970). This evidence suggests that *Z. varuna* probably originated in other areas and then extended its geographical distribution to the Northwest Pacific region.

Gaudryceras seymouriense is also known from the Maastrichtian in the Indo-Pacific region (southern mid-latitudes, North Pacific and Antarctic; Figure 25). Several successive species of *Gaudryceras*, which have more or less stronger ribs, occur in the lower to middle Maastrichtian in Hokkaido and Sakhalin (Maeda *et al*., 2005; Shigeta *et al*., 2010; Shigeta and Nishimura, 2013; Shigeta and Tsutsumi, 2019), but the ancestor of *G. seymouriense* has not been found in the Northwest Pacific (Matsumoto, 1995). Specimens of *Gaudryceras*, with very fine lirae and rounded, collar-like ribs, similar to *G. seymouriense*, are known as *G. luenesburgense* (Schlüter,

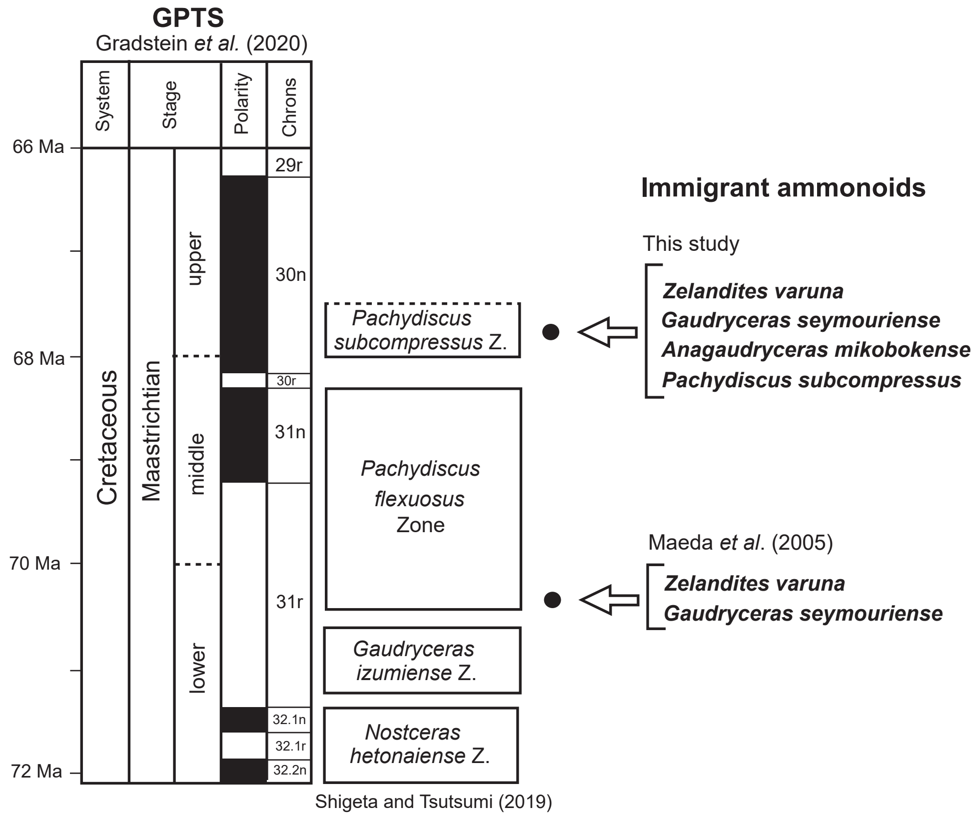

Figure 26. Diagram showing Maastrichtian ammonoid zones (taxon-range zones) by Shigeta and Tsutsumi (2019) and stratigraphic occurrences of immigrant ammonoid species in the Yezo Group in southern Sakhalin based on data from the present paper and Maeda *et al*. (2005).

1872) from the upper Campanian to upper Maastrichtian in central Europe (Birkelund, 1982, 1993; Kennedy and Summesberger, 1986). This evidence suggests that *G. seymouriense* probably originated in other areas and then extended its geographical distribution to the Northwest Pacific region.

Anagaudryceras mikobokense is known from the Maastrichtian in the Indo-Pacific region (southern mid-latitudes, North Pacific; Figure 25), but the oldest record is from the upper Campanian of Angola. Because its ancestor has not been found in the Northwest Pacific (Matsumoto, 1995), the taxon also probably originated in other areas and then extended its geographical distribution to the Northwest Pacific region.

Tetragonites sp. from the K4 Unit is somewhat similar to *T. terminus* from the lower Maastrichtian in Hokkaido (Shigeta, 1989; Shigeta *et al*., 2017) and *T. superstes* from the lower Maastrichtian in northeastern Mexico (Ifrim *et al*., 2004), but the absence of adult features precludes a definitive species assignment.

In addition to the above-mentioned six species, *Neophylloceras* sp. and *Diplomoceras* cf. *notabile* have also been found in the *Zelandites varuna*-bearing beds of the Senpohshi Formation in eastern Hokkaido (Shigeta *et al*., 2015). The specimens of *Neophylloceras* sp. were later assigned to *N. hetonaiense* Matsumoto, 1942a, which occurs abundantly in the lower and middle Maastrichtian in Hokkaido and southern Sakhalin (Maeda *et al*., 2005; Shigeta *et al*., 2017). *Diplomoceras notabile*, a long-ranging species known from the Campanian and Maastrichtian in the North Pacific region, occurs in the upper middle Campanian to upper Maastrichtian in Japan and southern Sakhalin (e.g. Matsumoto and Miyauchi, 1984; Maeda *et al*., 2005).

In the western North Pacific region, Maastrichtian ammonoid assemblages consist of mixtures of "immigrant species" and "indigenous species". Immigrant species, which migrated from the other regions (Ifrim *et al*., 2015), include *Pachydiscus subcompressus*, *Anagaudryceras mikobokense*, *Gaudryceras seymouriense* and *Zelandites varuna*. Species indigenous to the North Pacific region include *Anagaudryceras matsumotoi*, *Neo-*

phylloceras hetonaiense and *Diplomoceras notabile*.

Zelandites varuna and *Gaudryceras seymouriense* occur not only in the lower upper Maastrichtian but also in the upper lower Maastrichtian (lowest part of the *Pachydiscus flexuosus* Zone; Shigeta and Tsutsumi, 2019) in southern Sakhalin (Maeda *et al*., 2005; Figure 26). In spite of carefully controlled bed-by-bed sampling, neither taxon has been found in the middle Maastrichtian in southern Sakhalin and Hokkaido (Ando *et al*., 2001; Maeda *et al*., 2005; Shigeta *et al*., 2015). Because both species appear in the North Pacific and Antarctic cold-water regions as well as the intermediate southern mid-latitudes regions (Ifrim *et al*., 2004; Figure 25), their appearance may suggest that cooling events occurred during the late early and early late Maastrichtian in the Northwest Pacific region.

It is well known that a long-term global cooling trend during the Late Cretaceous was interrupted by an intense greenhouse episode known as the Middle Maastrichtian Event (MME) at approximately 69 Ma, based on isotopic data from paleosol carbonate in west Texas and Alaska (Nordt *et al*., 2003; Dworkin *et al*., 2005; Salazar-Jaramillo *et al*., 2016) and marine cores in the northwestern Pacific (Bralower *et al*., 2002; Frank *et al*., 2005). Although detailed studies of paleoclimate during the Maastrichtian have not been conducted, the disappearance of *Zelandites varuna* and *Gaudryceras seymouriense* in the middle Maastrichtian may suggest that the Northwest Pacific region was also affected by the MME. This hypothesis suggests that the influx (e.g. *Pachydiscus subcompressus* and *Anagaudryceras mikobokense*) of and reappearance (e.g. *Z. varuna* and *G. seymouriense*) of many immigrant species into the Northwest Pacific region during late Maastrichtian time may have been associated with the post-MME cooling.

Concluding remarks

The Late Cretaceous ammonoid assemblages of the Northwest Pacific region resulted from the inclusion of immigrant species to the existing indigenous fauna, many of which may have also included descendants of earlier immigrant taxa. The ability to distinguish these immigrant species from indigenous ones will eventually provide an important key for a detailed understanding of this faunal turnover. It is still unclear as to how this significant change in faunal makeup during the late Maastrichtian may have been affected by concurrent global environmental changes, but a better understanding of this relationship will provide contextual information for the K/Pg mass extinction event.

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References

Alabushev, A. and Wiedmann, J., 1997: Upper Cretaceous ammonites from southern Sakhalin and northwestern Kamchatka (North-East Russia). *Palaeontographica Abteilung A*, Band 244, p. 1–36.

Anderson, F. M., 1958: Upper Cretaceous of the Pacific Coast. *Geological Society of America Memoir*, vol. 71, p. 1–378.

Ando, H., Tomosugi, T. and Kanakubo, T., 2001: Upper Cretaceous to Paleocene Hakobuchi Group, Nakatonbetsu area, northern Hokkaido—lithostratigraphy and megafossil biostratigraphy. *Journal of the Geological Society of Japan*, vol. 107, p. 142–162. (*in Japanese with English abstract*)

Arkell, W. J., 1957: Introduction to Mesozoic Ammonoidea. *In*, Arkell, W. J., Furnish, W. M., Kummel, B., Miller, A. K., Moore, R. C., Schindewolf, O. H., Sylvester-Bradley, P. C. and Wright, C. W. *eds*., *Treatise on Invertebrate Paleontology*, *Part L*, *Mollusca 4*, *Cephalopoda*, *Ammonoidea*, p. L81–129. Geological Society of America, New York and University of Kansas Press, Lawrence.

Birkelund, T., 1982: Maastrichtian ammonites from Hemmoor, Niederelbe (NW Germany). *Geologisches Jahrbuch*, Band A61, p. 13–33.

Birkelund, T., 1993: Ammonites from the Maastrichtian White Chalk of Denmark. *Bulletin of the Geological Society of Denmark*, vol. 40, p. 33–81.

Bralower, T. J., Silva, I. P., Malone, M. J., Scientific participants of Leg 198, 2002: New evidence for abrupt climate change in the Cretaceous and Paleogene: an ocean drilling program expedition to Shatsky Rise, northwest Pacific. *GSA Today*, vol. 12, p. 4–10.

Collignon, M., 1938: Ammonites Campaniennes et Maestrichtiennes de l'ouest et du sud de Madagascar. *Annales géologiques du Service des Mines*, *Madagascar*, vol. 9, p. 53–118.

Collignon, M., 1956: Ammonites néocrétacées du Menabe (Madagascar). IV. Les Phylloceratidae. V. Les Gaudryceratidae, VI. Les Tetragonitidae. *Annales géologiques du Service des Mines*, *Madagascar*, vol. 23, p. 1–106.

Dworkin, S. I., Nordt, L. and Atchley, S., 2005: Determining terrestrial paleotemperatures using the oxygen isotopic composition of

pedogenic carbonate. *Earth and Planetary Science Letters*, vol. 237, p. 56–68.
Forbes, E., 1846: Report on the fossil Invertebrata from southern India, collected by Mr. Kaye and Mr. Cunliffe. *Transactions of the Geological Society of London*, *Series 2*, vol. 7, p. 97–174.
Frank, T. D., Thomas, D. J., Leckie, R. M., Arthur, M. A., Bown, P. R., Jones, K. *et al*., 2005: The Maastrichtian record from Shatsky Rise (northwest Pacific): a tropical perspective on global ecological and oceanographic changes. *Paleoceanography*, vol. 20, doi:10.1029/2004PA001052.
Gradstein, F. M., Ogg, J. G., Schmitz, M. D. and Ogg, G. M., 2020: *Geologic Time Scale 2020, volume 2*, 1357 p. Elsevier, Amsterdam.
Grossouvre, A. de., 1894: Recherches sur la Craie supérieure. Deuxième partie: paléontologie. Les ammonites de la Craie supérieure. *Mémoires du Service de la Carte Géologique Detaillée de la France*, p. 1–264.
Haggart, J. W., 1989: New and revised ammonites from the Upper Cretaceous Nanaimo Group of British Columbia and Washington State. *Geological Survey of Canada Bulletin 396*, p. 181–221.
Hasegawa, T., Pratt, L. M., Maeda, H., Shigeta, Y., Okamoto, T., Kase, T. *et al*., 2003: Upper Cretaceous stable carbon isotope stratigraphy of terrestrial organic matter from Sakhalin, Russian Far East: a proxy for the isotopic composition of paleoatmospheric CO_2. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, vol. 189, p. 97–115.
Hauer, F. R. von, 1858: Über die Cephalopoden der Gosauschichten. *Beiträge zur Paläontographie von Österreich*, Band 1, p. 7–14.
Hauer, F. R. von, 1866: Neue Cephalopoden aus den Gosaugebilden der Alpen. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien*, *Mathematisch-Naturwissenschafliche Klasse*, Band 53, p. 300–308.
Henderson, R., 1970: Ammonoidea from the Mata Series (Santonian–Maastrichtian) of New Zealand. *Special Papers in Palaeontology*, no. 6, p. 1–82.
Hoepen, E. C. N. van, 1921: Cretaceous Cephalopoda from Pondoland. *Annals of the Transvaal Museum*, vol. 8, p. 1–48.
Howarth, M. K., 1965: Cretaceous ammonites and nautiloides from Angola. *Bulletin of the British Museum (Natural History)*, *Geology*, vol. 10, p. 335–412.
Hyatt, A., 1889: Genesis of the Arietidae. *Smithsonian Contributions to Knowledge*, no. 673, p. 1–238.
Hyatt, A., 1900: Cephalopoda. *In*, Zittel, K. A. *ed*., *Textbook of Palaeontology*, *English ed.*, *Translated by C. R. Eastman*, p. 502–592. Macmillan, London and New York.
Ifrim, C., Lehman, J. and Ward, P., 2015: Paleobiogeography of Late Cretaceous ammonoids. *In*, Klug, C., Korn, D., De Baets, K., Kruta, I. and Mapes, R. H. *eds*., *Ammonoid Paleobiology: From macroevolution to paleogeography*, p. 259–274. Topics in Geobiology, vol. 44, Springer, Dordrecht.
Ifrim, C., Stinnesbeck, W. and López-Oliva, J. G., 2004: Maastrichtian cephalopods from Cerralvo, north-eastern Mexico. *Palaeontology*, vol. 47, p. 1575–1627.
Kalishevitch, T. G. and Posylny, V. Y., 1958: About absence of break of sedimentation between Cenozoic and Mesozoic in the Sinegorsk-Zagorsk region on Sakhalin. *Doklady Akademii Nauk SSSR*, *Series Geology*, vol. 119, p. 766–768.
Kalishevitch, T. G., Zaklinskaya, E. D. and Serova, M. Y., 1981: *Organic Evolution of the Circum-Pacific during the Mesozoic-Cenozoic Transition*, 164 p. Nauk, Moscow. (*in Russian; original title translated*)
Kase, T. and Shigeta, Y., 1996: New species of Patellogastropoda (Mollusca) from the Cretaceous of Hokkaido, Japan and Sakhalin, Russia. *Journal of Paleontology*, vol. 70, p. 762–771.
Kase, T., Shigeta, Y. and Futakami, M., 1994: Limpet home depressions in Cretaceous ammonites. *Lethaia*, vol. 27, p. 49–58.
Kennedy, W. J. and Henderson, R. A., 1992: Non-heteromorph ammonites from the upper Maastrichtian of Pondicherry, South India. *Palaeontology*, vol. 35, p. 381–442.
Kennedy, W. J. and Klinger, H. C., 1979: Cretaceous faunas from Zululand and Natal, South Africa. The ammonite family Gaudryceratidae. *Bulletin of the British Museum (Natural History)*, *Geology Series*, vol. 31, p. 121–174.
Kennedy, W. J. and Summesberger, H., 1986: Lower Maastrichtian ammonites from Neuberg, Steiermark, Austria. *Beiträge zur Paläontologie von Österreich*, Nummer 12, p. 181–242.
Kodama, K., 1990: Magnetostratigraphy of the Izumi Group along the Median Tectonic Line in Shikoku and Awaji Islands, Southwest Japan. *Journal of the Geological Society of Japan*, vol. 96, p. 265–278. (*in Japanese with English abstract*)
Kodama, K., Maeda, H., Shigeta, Y., Kase, T. and Takeuchi, T., 2000: Magnetostratigraphy of Upper Cretaceous strata in South Sakhalin, Russian Far East. *Cretaceous Research*, vol. 21, p. 469–478.
Kodama, K., Maeda, H., Shigeta, Y., Kase, T. and Takeuchi, T., 2002: Integrated biostratigraphy and magnetostratigraphy of the upper Cretaceous System along the River Naiba in southern Sakhalin, Russia. *Journal of the Geological Society of Japan*, vol. 108, p. 366–384. (*in Japanese with English abstract*)
Kossmat, F., 1895: Untersuchungen über die Südindische Kreideformation. Teil 1. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients*, Band 9, p. 97–203.
Macellari, C. E., 1986: *Late Campanian–Maastrichtian Ammonites Fauna from Seymour Island (Antarctic Peninsula)*, 55 p. *Paleontological Society Memoir*, vol. 18, Paleontological Society, Ithaca.
Maeda, H., Kumagae, T., Matsuoka, H. and Yamazaki, Y., 2010: Taphonomy of large *Canadoceras* (ammonoid) shells in the Upper Cretaceous Series in South Sakhalin, Russia. *Paleontological Research*, vol. 14, p. 56–68.
Maeda, H. and Seilacher, A., 1996: Ammonoid taphonomy. *In*, Landman, N. H., Tanabe, K. and Davis, R. *eds*., *Ammonoid Paleobiology*, p. 543–578. Plenum Press, New York.
Maeda, H. and Shigeta, Y., 2005: Maastrichtian ammonoid fauna from the Pugachevo area, southern Sakhalin, Russian Far East. *National Science Museum Monographs*, vol. 31, p. 121–136.
Maeda, H., Shigeta, Y., Fernando, A. G. S. and Okada, H., 2005: Stratigraphy and fossil assemblages of the Upper Cretaceous System in the Makarov area, southern Sakhalin, Russian Far East. *National Science Museum Monographs*, vol. 31, p. 25–120.
Marshall, P., 1926: The Upper Cretaceous ammonites of New Zealand. *Transactions of the New Zealand Institute*, vol. 56, p. 129–210.
Matsumoto [= Matumoto], T., 1938: *Zelandites*, a genus of Cretaceous ammonite. *Japanese Journal of Geology and Geography*, vol. 15, p. 137–148.
Matsumoto [= Matumoto], T., 1942a: A short note on the Japanese Cretaceous Phylloceratidae. *Proceedings of the Imperial Academy*, *Tokyo*, vol. 18, p. 674–676.
Matsumoto [= Matumoto], T., 1942b: Fundamentals in the Cretaceous stratigraphy of Japan, Part 1. *Memoirs of the Faculty of Science*, *Kyushu Imperial University*, *Series D*, *Geology*, vol. 1, p. 129–280.
Matsumoto, T., 1954: *The Cretaceous System in the Japanese Islands*, 324 p. Japan Society for the Promotion of Science, Tokyo.
Matsumoto, T., 1959: Upper Cretaceous ammonites of California. Part 2. *Memoirs of the Faculty of Science*, *Kyushu University*, *Series D*, *Geology*, special vol. 1, p. 1–172.
Matsumoto, T., 1979: Palaeontological descriptions Part 1. Some new species of *Pachydiscus* from the Tombetsu and the Hobetsu val-

leys. *Memoirs of the Faculty of Science*, *Kyushu University*, *Series D*, *Geology*, vol. 24, p. 50–64.

Matsumoto, T., 1984: Some gaudryceratid ammonites from the Campanian and Maastrichtian of Hokkaido. Part 1. *Science Report of the Yokosuka City Museum*, no. 32, p. 1–10.

Matsumoto, T., 1985: Three species of *Anagaudryceras* from the Campanian and Maastrichtian of Hokkaido. *Science Report of the Yokosuka City Museum*, no. 33, p. 22–29.

Matsumoto, T., 1988: Notes on some Cretaceous ammonites from South Sakhalin held at Tohoku University, Sendai. *Science Report of the Tohoku University*, *2nd Series (Geology)*, vol. 59, p. 177–190.

Matsumoto, T., 1995: Notes on gaudryceratid ammonites from Hokkaido and Sakhalin. *Palaeontological Society of Japan*, *Special Paper*, no. 35, p. 1–152.

Matsumoto, T. and Miyauchi, T., 1984: Some Campanian ammonites from the Soya area. *Palaeontological Society of Japan*, *Special Paper*, no. 27, p. 33–76.

Matsumoto, T. and Morozumi, Y., 1980: Late Cretaceous ammonites from the Izumi Mountains, Southwest Japan. *Bulletin of the Osaka Museum of Natural History*, no. 33, p. 1–31.

Matsumoto, T. and Yoshida, S., 1979: A new gaudryceratid ammonite from eastern Hokkaido. *Transactions and Proceedings of the Palaeontological Society of Japan*, n. ser., no. 114, p. 65–76.

Michael, R., 1899: Über Kreidefossilien von der Insel Sachalin. *Jahrbuch der Königlichen Preussischen Geologischen Landsanstalt und Bergakademie zu Berlin*, Band 18, p. 153–164.

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

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

Nordt, L., Atchley, S. and Dworkin, S., 2003: Terrestrial evidence for two greenhouse events in the latest Cretaceous. *GSA Today*, vol. 13, p. 4–9.

Okada, H., 1979: The geology of Hokkaido and its plate tectonics. *Earth Monthly*, vol. 1, p. 869–877. (*in Japanese*)

Okada, H., 1983: Collision orogenesis and sedimentation in Hokkaido, Japan. *In*, Hashimoto, M. and Ueda, S. *eds*., *Accretion Tectonics in the Circum-Pacific Regions*, p. 91–105. Terra Scientific Publishing Co., Tokyo.

Orbigny, A. d'., 1850: *Prodrome de Paléontologie stratigraphique universelle des animaux mollusques et rayonnés*, 428 p. Masson, Paris.

Pergament, M. A., 1974: Biostratigraphy and *Inoceramus* of Senonian (Santonian–Maastrichtian) of the USSR Pacific region. *Trudy Geologicheskogo Instituta Akademii Nauk SSSR*, vol. 260, p. 1–267. (*in Russian; original title translated*)

Pictet, F. J., 1847: Description des mollusques fossils qui se trouvent dans le Grès Vers des environs de Genève. *Mémoires de la Société de Physique et d'Histoire Naturelle de Genève*, vol. 11, p. 257–412.

Poyarkova, Z. N., 1987: *Reference Section of Cretaceous Deposits in Sakhalin (Naiba Section)*, 197 p. Nauka, Leningrad. (*in Russian*)

Raffi, M. E., Olivero, E. B. and Milanese, F. N., 2019: The gaudryceratid ammonoids from the Upper Cretaceous of the James Ross Basin, Antarctica. *Acta Palaeontologica Polonica*, vol. 64, p. 523–542.

Salazar, C., Stinnesbeck, W. and Quinzio-Sinn, L. A., 2010: Ammonites from the Maastrichtian (Upper Cretaceous) Quiriquina Formation in central Chile. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, Band 257, p. 181–236.

Salazar-Jaramillo, S., Fowell, S. J., McCarthy, P. J., Benowitz, J. A., Śliwiński, M. G. and Tomsich, C. S., 2016: Terrestrial isotopic evidence for a Middle-Maatrichtian warming event from the lower Cantwell Formation, Alaska. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, vol. 441, p. 360–376.

Schlüter, C. A., 1872: Cephalopoden der oberen deutschen Kreide. *Palaeontographica*, Band 22, p. 25–120.

Shigeta, Y., 1989: Systematics of the ammonite genus *Tetragonites* from the Upper Cretaceous of Hokkaido. *Transactions and Proceedings of the Palaeontological Society of Japan*, n. ser., no. 156, p. 319–342.

Shigeta, Y., 1993: A record of *Pseudophyllites indra* (Lytoceratina, Tetragonitidae) from the Upper Cretaceous of Hokkaido and Sakhalin. *Transactions and Proceedings of the Palaeontological Society of Japan*, n. ser., no. 166, p. 1157–1163.

Shigeta, Y., Izukura, M. and Tsutsumi, Y., 2017: An early Maastrichtian (latest Cretaceous) ammonoid fauna from the Soya Hill area, Hokkaido, northern Japan. *Bulletin of the Hobetsu Museum*, no. 32, p. 7–41.

Shigeta, Y. and Maeda, H., 2005: Yezo Group research in Sakhalin—a historical review. *National Science Museum Monographs*, vol. 31, p. 1–24.

Shigeta, Y., Maeda, H., Uemura, K. and Solov'yov, A. V., 1999: Stratigraphy of the Upper Cretaceous System in the Kurl'on Peninsula, South Sakhalin, Russia. *Bulletin of the National Science Museum*, *Series C*, vol. 25, p. 1–27.

Shigeta, Y., Misaki, A. and Ohara, M., 2012: *Gaudryceras tombetsense* Matsumoto, a Maastrichtian ammonoid from the Aridagawa area, Wakayama, southwestern Japan. *Paleontological Research*, vol. 16, p. 244–251.

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

Shigeta, Y. and Nishimura, T., 2014: A new species of *Anagaudryceras* (Ammonoidea, Gaudryceratidae) from the lowest Maastrichtian of Hokkaido, Japan. *Paleontological Research*, vol. 18, p. 176–185.

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

Shigeta, Y, Tanabe, K. and Izukura, M., 2010: *Gaudryceras izumiense* Matsumoto and Morozumi, a Maastrichtian ammonoid from Hokkaido and Alaska and its biostratigraphic implications. *Paleontological Research*, vol. 14, p. 202–211.

Shigeta, Y. and Tsutsumi, Y., 2018: U–Pb age of the *Sphenoceramus schmidti* Zone (middle Campanian, Cretaceous) in Hokkaido, northern Japan. *Bulletin of the National Museum of Nature and Science*, *Series C*, vol. 44, p. 13–18.

Shigeta, Y. and Tsutsumi, Y., 2019: U–Pb age of the *Pachydiscus flexuosus* Zone (Maastrichtian, Cretaceous) in the Nakatonbetsu area, Hokkaido, northern Japan. *Bulletin of the National Museum of Nature and Science*, *Series C*, vol. 45, p. 29–36.

Shimizu, S., 1934: Ammonites. *In*, Shimizu, S. and Obata, T. *eds*., *Cephalopoda*, 137 p. Iwanami's Lecture Series of Geology and Palaeontology, Iwanami Shoten, Tokyo. (*in Japanese; original title translated*)

Smith, A. G., Smith, D. G. and Funnel, B. M., 1994: *Atlas of Mesozoic and Cenozoic Coastlines*, 99 p. Cambridge University Press, Cambridge.

Spath, L. F., 1922: On the Senonian ammonite fauna of Pondoland. *Transactions of the Royal Society of South Africa*, vol. 10, p. 113–148.

Spath, L. F., 1927: Revision of the Jurassic cephalopod fauna of Kachh (Cutch), part 1. *Memoirs of the Geological Survey of India*, *Palaeontologia Indica*, *New Series*, vol. 9, memoir 2, p. 1–71.

Steinmann, G., 1895: Die Cephalopoden der Quiriquina-Schichten. *Neues Jahrbuch für Mineralogie Geologie und Paläontologie*, Band 10, p. 64–94.

Stinnesbeck, W., 1986: Zu den faunistischen und paläökologischen Verhältnissen in der Quiriquina Formation (Maastrichtian) Zentrales-Chiles. *Palaeontographica*, *Abteilung A*, Band 194, p. 99–237.

Takashima, R., Kawabe, F., Nishi, H., Moriya, K., Wani, R. and Ando, H., 2004: Geology and stratigraphy of forearc basin sediments in Hokkaido, Japan: Cretaceous environmental events on the north-west Pacific margin. *Cretaceous Research*, vol. 25, p. 365–390.

Tamaki, M., Oshimbe, S. and Itoh, Y., 2008: A large latitudinal displacement of a part of Cretaceous forearc basin in Hokkaido, Japan: paleomagnetism of the Yezo Supergroup in the Urakawa area. *Journal of the Geological Society of Japan*, vol. 114, p. 207–217. (*in Japanese with English abstract*)

Toshimitsu, S., Matsumoto, T., Noda, M., Nishida, T. and Maiya, S., 1995: Towards an integrated mega-, micro- and magneto-stratigraphy of the Upper Cretaceous in Japan. *Journal of the Geological Society of Japan*, vol. 101, p. 19–29. (*in Japanese with English abstract*)

Vereshchagin, V. N., 1977: The Cretaceous System of Far East. *Trudy Vsesoyunogo Nauchno-Issledovatel'skogo Geologicheskogo Instituta (VSEGEI)*, *New Series*, vol. 245, p. 1–207. (*in Russian; original title translated*)

Vereshchagin, V. N., Kinasov, V. P., Paraketsov, K. V. and Terekhova, G. P., 1965: *Field Atlas of the Cretaceous Fauna from Northeast USSR*, 216 p. Magadanskoye Knizhnoye Izdatyelstovo, Magadan. (*in Russian; original title translated*)

Vereshchagin, V. N. and Salnikov, B. A., 1968: On principles and methods of studying of reference stratigraphical sections on the example of the stratotypical sections of the Upper Cretaceous of the Pacific biogeographical area (Sakhalin Island). *Trudy Vsesoyunogo Nauchno-Issledovatel'skogo Geologicheskogo Instituta (VSEGEI*), *Novaya Seriya*, vol. 143, p. 45–58. (*in Russian; original title translated*)

Whiteaves, J., 1903: On some additional fossils from the Vancouver Cretaceous, with a revised list of the species therefrom. *Geological Survey of Canada*, *Mesozoic Fossils*, vol. 1, part V, p. 309–415.

Wright, C. W., Calloman, J. H. and Howarth, M. K., 1996: *Treatise on Invertebrate Paleontology*, *Part L*, *Mollusca 4*, *Revised*, *vol. 4*, *Cretaceous Ammonoidea*, 362 p. Geological Society of America, Boulder and University of Kansas Press, Lawrence.

Yabe, H., 1903: Cretaceous Cephalopoda from the Hokkaido. Part 1: *Lytoceras*, *Gaudryceras*, and *Tetragonites*. *Journal of the College of Science*, *Imperial University of Tokyo*, vol. 18, p. 1–55.

Yazykova, E. A., 1991: Maastrichtian ammonites of eastern USSR and their stratigraphical significance. *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody*, *Otdel Geologicheskii*, vol. 66, p. 68–73. (*in Russian with English summary*)

Yazykova, E. A., 1992: Upper Cretaceous ammonites from East USSR. *Trudy Vssoyungo Nauchno-Issledovatel'skogo Geologicheskogo Instituta (VSEGEI)*, *Novaya Seriya*, vol. 350, p. 192–200. (*in Russian; original title translated*)

Yazykova [= Yazikova], E. A., 1994: Maastrichtian ammonites and biostratigraphy of the Sakhalin and the Shikotan Islands, Far East Russia. *Acta Geologica Polonica*, vol. 44, p. 277–303.

Zakharov, Y. D., Grabovskaya, V. S. and Kalishevich, T. G., 1984: Late Cretaceous successions of the marine communities in South Sakhalin and climatic conditions of the North-West Pacific. *In*, Gramm, M. N. and Zakharov, Y. D. *eds*., *Systematics and Evolution of Far Eastern Invertebrates*, p. 41–90. Akademiya Nauk SSSR, Dal'nevostochnyi Nauchnyi Tsentr, Biologo-Pochvennyi Institut, Vladivostok. (*in Russian; original title translated*)

Zittel, K. A., 1884: Cephalopoda. *In*, Zittel, K. A. *ed*., *Handbuch der Paläontologie, Band 1, Abt. 2, Lief 3*, p. 329–522. Oldenbourg, Munich and Leipzig.

Zittel, K. A., 1895: *Grundzüge der Paläontologie*, 971 p. Oldenbourg, Munich and Leipzig.

Zonova, T. D., Kazintsova, L. I. and Yazykova, E. A., 1993: *Atlas of Index Fossils in the Cretaceous Fauna of Sakhalin*, 327 p. Nedra, St. Petersburg. (*in Russian; original title translated*)

Author contributions

Both authors conducted the geological survey, collected fossils and contributed to the writing of the paper. The taxonomic study was conducted by Y. S. for Lytoceratina and H. M. for Ammonitina.

Appendix. Measurements (in mm) of ammonoid specimens studied herein from the K4 Unit of the Krasnoyarka Formation. *D*, shell diameter; *U*, umbilical diameter; *H*, whorl height; *W*, whorl width.

taxon	register number	*D* (mm)	*U* (mm)	*H* (mm)	*W* (mm)	*U*/*D*	*W*/*H*
Tetragonites sp.	NMNS PM35900	10.10	2.40	4.60	5.00	0.23	1.08
	NMNS PM35901	10.20	2.50	4.50	—	0.24	—
Zelandites varuna	NMNS PM35902	22.40	4.00	11.10	7.20	0.17	0.64
	NMNS PM35903	18.00	3.60	9.10	6.20	0.20	0.68
	NMNS PM35904	24.80	4.50	12.60	8.10	0.18	0.64
	NMNS PM35905	22.00	4.00	11.10	7.40	0.18	0.66
	NMNS PM35906	23.20	3.90	12.10	7.50	0.16	0.61
	NMNS PM35907	23.30	3.80	12.20	7.90	0.16	0.64
	NMNS PM35908	43.60	5.90	—	—	0.13	—
	NMNS PM35909	28.00	4.60	14.40	9.40	0.16	0.65
	NMNS PM35926	2.925	1.266	1.613	0.942	0.432	1.712
		4.052	1.708	2.015	1.421	0.422	1.418
		5.958	2.129	2.587	2.370	0.357	1.091
		8.970	2.690	3.476	3.924	0.300	0.886
		13.792	3.315	4.696	6.578	0.240	0.710
		21.516	4.121	7.151	10.865	0.192	0.658
	NMNS PM35927	2.844	1.222	1.445	0.910	0.430	1.588
		3.978	1.631	1.902	1.452	0.410	1.310
		5.801	2.088	2.367	2.244	0.360	1.055
		8.474	2.668	2.994	3.537	0.315	0.846
		12.891	3.367	4.310	6.002	0.261	0.718
		20.006	3.983	6.086	9.995	0.199	0.609
	NMNS PM35928	3.004	1.306	1.589	0.966	0.435	1.645
		4.154	1.746	1.942	1.444	0.420	1.345
		6.038	2.234	2.478	2.350	0.370	1.054
		8.969	2.697	3.141	3.911	0.301	0.803
		13.454	3.272	4.321	6.241	0.243	0.692
		21.009	4.245	6.119	10.520	0.202	0.582
	NMNS PM35929	2.827	1.215	1.508	0.925	0.430	1.630
		4.026	1.651	2.080	1.465	0.410	1.420
		5.850	2.197	2.495	2.211	0.376	1.128
		8.677	2.823	3.247	3.658	0.325	0.888
		13.106	3.400	4.475	6.058	0.259	0.739
		20.299	4.136	6.786	10.142	0.204	0.669
	NMNS PM35930	3.703	1.519	1.914	1.309	0.410	1.462
		5.372	1.991	2.324	2.062	0.371	1.127
		7.874	2.619	2.941	3.209	0.333	0.916
		11.901	3.226	3.881	5.455	0.270	0.711
		18.523	3.670	5.847	9.309	0.198	0.628
Anagaudryceras matsumotoi	NMNS PM35910	28.30	11.00	10.50	12.20	0.38	1.16
	NMNS PM35912	34.20	10.90	15.00	16.00	0.31	1.06
	NMNS PM35913	37.80	13.80	14.70	15.10	0.36	1.02
	NMNS PM35914	23.40	8.60	9.00	10.00	0.36	1.11

	NMNS PM35915	32.10	11.60	12.50	12.70	0.36	1.01
	NMNS PM35916	17.20	6.40	6.50	7.60	0.37	1.16
	NMNS PM35917	28.30	10.10	11.00	11.60	0.35	1.05
	NMNS PM35931	2.274	0.921	1.366	0.766	0.405	1.783
		3.031	1.310	1.661	0.970	0.432	1.712
		4.142	1.832	2.279	1.340	0.442	1.701
		5.647	2.497	2.967	1.813	0.442	1.637
		7.708	3.422	4.058	2.472	0.444	1.642
		10.671	4.573	5.381	3.631	0.429	1.454
		15.019	6.148	7.032	5.221	0.409	1.347
		21.497	8.397	9.389	7.877	0.391	1.192
		31.316	11.130	13.019	12.251	0.355	1.063
	NMNS PM35932	2.407	1.008	1.305	0.780	0.419	1861.000
		3.229	1.402	1.760	0.976	0.434	1.803
		4.409	1.962	2.462	1.415	0.445	1.740
		6.037	2.646	3.266	1.938	0.438	1.685
		8.328	3.632	4.270	2.729	0.436	1.565
		11.571	4.834	5.835	3.995	0.418	1.461
		16.407	6.503	7.873	5.942	0.396	1.325
		23.704	8.614	10.522	9.075	0.363	1.159
Anagaudryceras mikobokense	NMNS PM35918	8.20	3.70	3.40	1.80	0.45	1.89
		10.80	4.80	5.50	3.40	0.44	1.62
		14.40	6.50	7.00	4.60	0.45	1.52
		19.60	8.60	8.40	6.20	0.44	1.35
		25.80	11.30	11.00	8.20	0.44	1.34
		35.00	15.50	13.40	11.20	0.44	1.20
		71.00	27.60	25.40	26.20	0.38	0.96
Gaudryceras seymouriense	NMNS PM35919	11.70	6.40	4.50	3.00	0.55	1.50
		13.90	7.50	5.00	3.30	0.54	1.52
		16.70	8.80	6.40	4.50	0.53	1.42
		20.00	10.20	7.70	5.50	0.51	1.40
		24.50	11.90	9.20	7.00	0.49	1.31
		30.30	13.60	11.50	9.20	0.45	1.25
		39.40	18.20	15.00	13.10	0.46	1.15
		53.00	22.40	19.80	18.50	0.42	1.07
		70.60	27.50	26.50	25.60	0.39	1.04
		81.40	30.40	32.00	31.70	0.37	1.01
		107.60	36.80	43.30	44.00	0.34	0.98
		151.00	46.20	59.70	66.80	0.31	0.89
		187.10	53.50	86.00	73.00	0.28	0.84
	NMNS PM35921	55.00	28.00	—	—	0.51	—
Pachydiscus subcompressus	NMNS PM35922	—	—	82.50	—	—	—
	NMNS PM35923	200.00	—	—	—	—	—
	NMNS PM35924	175.00	—	—	—	—	—
	KYUM GKP00016	125.40	30.50	57.40	33.10	0.24	0.57