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**Discovery of the heteromorph ammonoid *Amapondella amapondense* in the middle  
Campanian of Hokkaido, Japan**

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**Abstract.** The discovery of the heteromorph ammonoid *Amapondella amapondense* (van Hoepen) in the lower middle Campanian in the Urakawa, Biratori and Hidaka areas of Hokkaido, northern Japan, represents the first report of this taxon in the Northwest Pacific region. Because the species flourished in other regions during Santonian to early Campanian time, its final geographic occurrence in Hokkaido suggests that global environmental changes likely had a significant influence on ammonoid biogeography during early middle Campanian time.

**Keywords:** *Amapondella*, ammonoid, biogeography, Campanian, Cretaceous,

**Hokkaido**

**Introduction**

The shell of the monospecific Cretaceous heteromorph ammonoid genus *Amapondella* Klinger and Kennedy, 1997 (type species *Heteroceras amapondense* van Hoepen, 1921) is characterized by its tightly coiled helical phragmocone, which forms a low helix and a body chamber that curves upward until it reaches or slightly exceeds the height of the apex of the helical whorls (Klinger and Kennedy, 2003). The genus was first proposed as a subgenus of the genus *Eubostrychoceras* Matsumoto, 1967, but then was treated as an independent genus (e.g. Klinger *et al.*, 2007). Specimens assigned to the genus are known from the Santonian of Europe, the Middle East, southern Africa, Madagascar, southern USA, Pacific Coast of Canada and the lower Campanian offshore deposits of Madagascar and south of KwaZulu-Natal, southern Africa (Klinger and Kennedy, 2003; Haggart and Graham, 2018).

Coauthor Masataka Izukura recently discovered two specimens referable to *Amapondella amapondense* in the lower middle Campanian in the Biratori and Hidaka areas, south-central Hokkaido, northern Japan (Figure 1). The late Hide Kubota

collected two specimens referable to this species from the lower middle Campanian in the Urakawa area, southern central Hokkaido and the specimens were subsequently donated to the Hobetsu Museum (Mukawa, Hokkaido) by his wife Katsuko Kubota. We herein describe these four specimens and discuss their biogeographical significance.

### Notes on stratigraphy

The Upper Cretaceous Chinomigawa Formation of the Yezo Group, which is composed mainly of sandy mudstone and mudstone with sandstone, is widely distributed in the Urakawa area (Matsumoto, 1942; Kanie, 1966; Sakai and Kanie, 1986; Kanie and Sakai, 2002; Shigeta *et al.*, 2016), and sporadic outcrops occur in the Niikappu–Biratori–Hidaka areas of south-central Hokkaido (Shigeta *et al.*, 2019). These sporadic outcrops were originally described as the Hakobuchi Group in Yoshida *et al.* (1959) and Takahashi and Suzuki (1978, 1986).

The Chinomigawa Formation in the Urakawa area was divided into four members (U2–U5, Sakai and Kanie, 1986), and the lower two members (U2 and U3) are well exposed along the southern coast of Ikantai, 3 km west–northwest of Urakawa (Matsumoto and Kanie, 1982; Wada *et al.*, 1992). Member U2 contains *Sphenoceras*

*orientalis* (Sokolov, 1914) in the upper part and Member U3 includes *S. schmidtii* (Michael, 1899). Both fossils are index inoceramids of early middle Campanian time in the Northwest Pacific region, an age assignment confirmed by both magnetostratigraphy and zircon geochronology (e.g. Kodama, 1990; Shigeta and Tsutsumi, 2018). Outcrops of the portion of the formation yielding *S. orientalis* and *S. schmidtii* are exposed in a narrow area in the middle course of the Soushubetsu River in the Biratori area (Yoshida *et al.*, 1959) and are widely distributed in the upper course of the Pankeushappu River in the Hidaka area (Takahashi and Suzuki, 1986).

The four *Amapondella amapondense* specimens of the present study were collected from the Chinomigawa Formation in the following areas: two specimens from float calcareous concretions found along the southern coast of Ikantai in the Urakawa area together with *Sphenoceras orientalis*, one specimen from an exposure along the middle course of the Soushubetsu River in the Biratori area that also contained the early middle Campanian ammonoid *Urakawaites* sp. and one specimen from a float calcareous concretion found in the upper course of the Pankeushappu River in the Hidaka area together with *S. orientalis*.

**Paleontological description**

Systematic descriptions follow the classification established by Wright *et al.*

(1996). Morphological terms in the systematic description are those used in Arkell (1957).

*Institution abbreviations.*—HMG, Hobetsu Museum, Mukawa.

Suborder Ancyloceratina Wiedmann, 1966

Superfamily Turrilitoidea Gill, 1871

Family Nostoceratidae Hyatt, 1894

Genus *Amapondella* Klinger and Kennedy, 1997

*Type species.*—*Heteroceras amapondense* van Hoepen, 1921.

*Remarks.*—*Amapondella* was first proposed as a subgenus of *Eubostrychoceras* by Klinger and Kennedy (1997), but Klinger *et al.* (2007) later elevated the taxon to an independent genus. We herein follow the interpretation of Klinger *et al.* (2007).

*Amapondella amapondense* (van Hoepen, 1921)

Figures 2–4

*Heteroceras amapondense* van Hoepen, 1921, p. 17, pl. 4, figs. 1, 2.

*Eubostrychoceras (Amapondella) amapondense* (van Hoepen). Klinger and Kennedy, 2003, p. 235, figs. 5, 6, 7A, 8A–D, 9A–C (with synonymy).

*Amapondella amapondense* (van Hoepen). Klinger *et al.*, 2007, p. 101, figs. 5A–C, 10I–J, 11, 12B–I, 13A–E, M (with synonymy); Schaffert and Larson, 2021, p. 31, figs. 43–49.

*Amapondella cf. amapondense* (van Hoepen). Haggart and Graham, 2018, fig. 5.

*Type*.—The holotype, figured by van Hoepen (1921, p. 17, pl. 4, figs. 1, 2), from the upper Santonian or lower Campanian of the Mzamba Formation at the Mzamba River Estuary, Pondoland, Eastern Cape Province, South Africa, is curated in Ditsong Museum of Natural History, Pretoria.

*Material examined*.—HMG-2014 was extracted from a calcareous concretion found in the middle course of the Soushubetsu River (42°39'17.85"N, 142°25'12.44"E), in the Biratori area. HMG-2015 was extracted from a float calcareous concretion found 5.25 km upriver from the mouth of the Pankeushappu River (42°54'52.05"N, 142°25'15.17"E), a branch of the Saru River, in the Hidaka area. HMG-2016 and

HMG-2017 were extracted from float calcareous concretions found along the southern coast of Ikantai in the Urakawa area.

*Description.*—HMG-2014 (Figure 2A–F), consisting of almost half of 60 mm diameter helical phragmocone. Earliest whorls, less than about 5 mm in diameter, not preserved. Preserved initial three whorls (about 30 mm in diameter) helically and tightly coiled dextrally, forming apical angle of approximately  $95^{\circ}$ . As shell grows, apical angle becomes lower,  $112^{\circ}$  on the fourth whorl (about 60 mm in diameter). Whorl cross section nearly circular. Shell surface ornamented with dense, regularly spaced, normal ribs and strong, highly elevated, flared ribs occurring between every 2–3 normal ribs. Ribs slightly oblique, narrowly raised with slightly concave interspaces, and symmetrical in cross section with respect to adoral direction.

HMG-2016 (Figure 2G–I), consisting of a fragment of a phragmocone and a part of the body chamber. Coiling helical and dextral, forming low apical angle with whorls touching. Whorl cross section nearly circular. Shell surface ornamented with dense, regularly spaced, normal ribs and flared ribs occurring every 5–6 normal ribs. Ribs slightly oblique, narrowly raised with slightly concave interspaces, and symmetrical in cross section with respect to adoral direction.

HMG-2015 (Figure 3), consisting of a phragmocone with a diameter of about 60



mm and a fragment of body chamber with length of about 300°. Early whorls, less than about 15 mm in diameter, not preserved. Middle whorls (phragmocone), 15–60 mm in diameter, helically and tightly coiled dextrally, forming low apical angle of approximately 150°. Body chamber gradually grows downward and is located below in contact with the previous whorls. Whorl cross section nearly circular. Shell surface ornamented with dense, regularly spaced, normal ribs and flared ribs occurring between every 4–5 normal ribs. Ribs slightly oblique on phragmocone and early part of body chamber, but rursiradiate on lower whorl face on the remaining body chamber, narrowly raised with slightly concave interspaces, and symmetrical in cross section with respect to adoral direction.

HMG-2017 (Figure 4), consisting of a phragmocone with a diameter of 68 mm and a part of the body chamber with length of about 210°. Early whorls, less than about 15 mm in diameter, not preserved. Middle whorls (phragmocone), 15–68 mm in diameter, helically and tightly coiled dextrally, forming low apical angle of approximately 150°. Because the body chamber is broken at 90° from last septum, the ensuring part not in contact with the previous whorls. Whorl cross section nearly circular. Shell surface ornamented with dense, regularly spaced, normal ribs and flared ribs occurring every 3–7 ribs. Ribs slightly oblique, narrowly raised with slightly

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6 concave interspaces, and symmetrical in cross section with respect to adoral direction.  
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9 *Remarks.*—Klinger and Kennedy (2003, Figs. 6, 7A) illustrated a complete  
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11 specimen of *Amapondella amapondense* from the lower Campanian of South Africa.  
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14 The body chamber of their specimen, which begins at about 60 mm in diameter, is about  
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16 440° long and ends with the aperture facing upward. The body chambers of HMG-2015  
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18 and HMG-2017 begin at about 60 mm and 68 mm in diameter, but their lengths are  
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20 about 300° and 210° respectively, suggesting that the last third and half of their  
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22 respective body chambers are not preserved.  
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29 *Occurrence.*—Santonian of Europe (France, Austria), the Middle East (Israel),  
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31 southern Africa, Madagascar, southern USA (Mississippi) and Canadian Pacific Coast  
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33 (British Columbia), lower Campanian of Madagascar and South Africa, and lower  
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35 middle Campanian (*Sphenoceras orientalis* Zone) of Hokkaido.  
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## 45 Discussion

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51 It is plausibly assumed that *Amapondella amapondense* evolved from the early  
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53 Coniacian taxon *Eubostriochoceras auriculatum* (Collignon, 1965) of Madagascar  
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55 (Klinger and Kennedy, 1997), and then during Santonian time, extended its distribution  
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6 to the Canadian Pacific Coast (British Columbia), southern USA, Europe, the Middle  
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9 East, southern Africa and Madagascar (e.g. Klinger, 1976; Summesberger, 1979, 1980;  
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12 Lewy, 1983; Kennedy and Cobban, 1991; Kennedy *et al.*, 1995; Haggart and Graham,  
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15 2018; Figure 5). However, by early Campanian time, its distribution had decreased to  
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18 just southern Africa and Madagascar (Collignon, 1969; Klinger, 1976; Klinger *et al.*,  
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21 2007; Figure 5), and then by the early middle Campanian, it had completely disappeared  
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24 from the middle southern latitudes, leaving only the Hokkaido occurrence of the present  
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27 study (Figure 5).

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30 The Cretaceous Yezo Group in Hokkaido and Sakhalin, Far Eastern Russia yields  
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33 numerous well-preserved fossils from various horizons (e.g. Matsumoto, 1954;  
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36 Vereshchagin, 1977). Nevertheless, in spite of extensive search efforts, specimens  
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39 assignable to *Amapondella amapondense* have not yet been discovered in Santonian to  
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42 lower Campanian deposits (e.g. Tanabe *et al.*, 1977; Toshimitsu, 1988; Okamoto *et al.*,  
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45 2003; Aiba *et al.*, 2017), which strongly suggests that the species did not exist in the  
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48 Northwest Pacific during this time interval, and most likely extended its geographical  
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51 distribution from the middle southern latitudes into the Northwest Pacific region during  
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54 early middle Campanian time.

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57 It is well known that some ammonoid taxa, e.g. *Pseudophyllites* Kossmat, 1895,  
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6 *Desmophyllites* Spath, 1929, *Pachydiscus* Zittel, 1884, *Saghalinites* Wright and  
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9 Matsumoto, 1954, *Metaplacenticeras* Spath, 1926 and *Didymoceras* Hyatt, 1894  
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11 probably originated in other regions and extended their geographical distribution to the  
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13 Northwest Pacific region during late middle Campanian time (Shigeta, 1992; Shigeta *et*  
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15 *al.*, 2019). In contrast, some ammonoid species, e.g. *Tetragonites popetensis* Yabe,  
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17 1903 are widely distributed in the Upper Cretaceous successions in this particular  
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19 region (e.g. Shigeta, 1989; Maeda *et al.*, 2005). As Shigeta *et al.* (2016) earlier pointed  
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21 out, the resultant late middle Campanian ammonoid faunas of the Northwest Pacific  
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23 region may have been supplemented by the addition of “foreign taxa” that migrated  
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25 from other regions into the existing indigenous ammonoid population.  
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36 *Amapondella amapondense* was probably one of these “foreign taxa” in the  
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38 Northwest Pacific region during early middle Campanian time. Although the reason for  
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40 the extinction of *A. amapondense* in other regions and its subsequent migration to the  
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42 Northwest Pacific region are unknown, the final geographic occurrence of the species in  
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44 Hokkaido suggests that global environmental changes likely had a significant influence  
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46 on ammonoid biogeography during early middle Campanian time as well as late middle  
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48 Campanian time.  
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57 A similar fluctuating pattern of geographical distribution is also known for the  
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Albian–Cenomanian ammonoid *Tanabeceras* Shigeta *et al.*, 2012 of the family Gaudryceratidae Spath, 1927, which was widely distributed in California and the Mediterranean area during early to middle Albian time, but disappeared from both areas, and late Albian to Cenomanian members are known only from Hokkaido and Sakhalin (Shigeta *et al.*, 2012). Iba and Sano (2007, 2008) discussed the existence of a vicariance event which separated the North Pacific region from the Tethyan biotic realm during Albian time, and then Shigeta *et al.* (2012) stated that this Albian vicariance event and related chain episodes may have influenced the evolution of *Tanabeceras*.

It is unclear what type of global environmental changes affected ammonoid biogeography during middle Campanian time, but the changing pattern of geographical distribution for various ammonoid taxa may provide an important key for understanding the global environmental changes that occurred during middle Campanian time.

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Author contributions

M. I. collected fossils and contributed to the geological aspect of the study. Y. S.  
conducted taxonomic study. Both authors contributed to the writing of the paper.

Figure caption

Figure 1. Index map showing distribution of the Yezo Group (black area) in Hokkaido (A) and collection localities of *Amapondella amapondense* specimens in the Hidaka, Biratori and Urakawa areas (indicated by stars, B, C).

Figure 2. *Amapondella amapondense* (van Hoepen, 1921). A–F, HMG-2014, from outcrop of the Chinomigawa Formation exposed along the middle course of the Soushubetsu River in the Biratori area. A, B, apical views; C, D, lateral views; E, F, basal views; G–I, HMG-2016, from a float calcareous concretion found along the southern coast of Ikantai in the Urakawa area; G, apical view; H, basal view; I, lateral view. Arrowheads indicate position of last septum.

Figure 3. *Amapondella amapondense* (van Hoepen, 1921), HMG-2015, from a float calcareous concretion found in the upper course of Pankeushappu River in the Hidaka area. A, B, apical views; C, D, lateral views; E, F, basal views. Arrowheads indicate



position of last septum.

Figure 4. *Amapondella amapondense* (van Hoepen, 1921), HMG-2017, from a float calcareous concretion found along the southern coast of Ikantai in the Urakawa area. **A**, apical views; **B**, oblique apical view rotated 45° from A; **C**, lateral view rotated 90° from A; **D**, basal view; **E**, lateral view rotated 90° from D. Arrowheads indicate position of last septum.

Figure 5. Paleogeographical (**A**) and stratigraphical (**B**) distribution of *Amapondella amapondense* (van Hoepen, 1921) during Santonian to middle Campanian time. Paleomap from Smith *et al.* (1994). 1, British Columbia (Haggart and Graham, 2018); 2, Mississippi (Kennedy and Cobban, 1991); 3, France (Kennedy *et al.*, 1995); 4, Austria (e.g. Summesberger, 1979); 5, Israel (Lewy, 1983); 6, South Africa (e.g. Klinger and Kennedy, 2003); 7, Madagascar (e.g. Klinger *et al.*, 2007); 8, Hokkaido (this study).

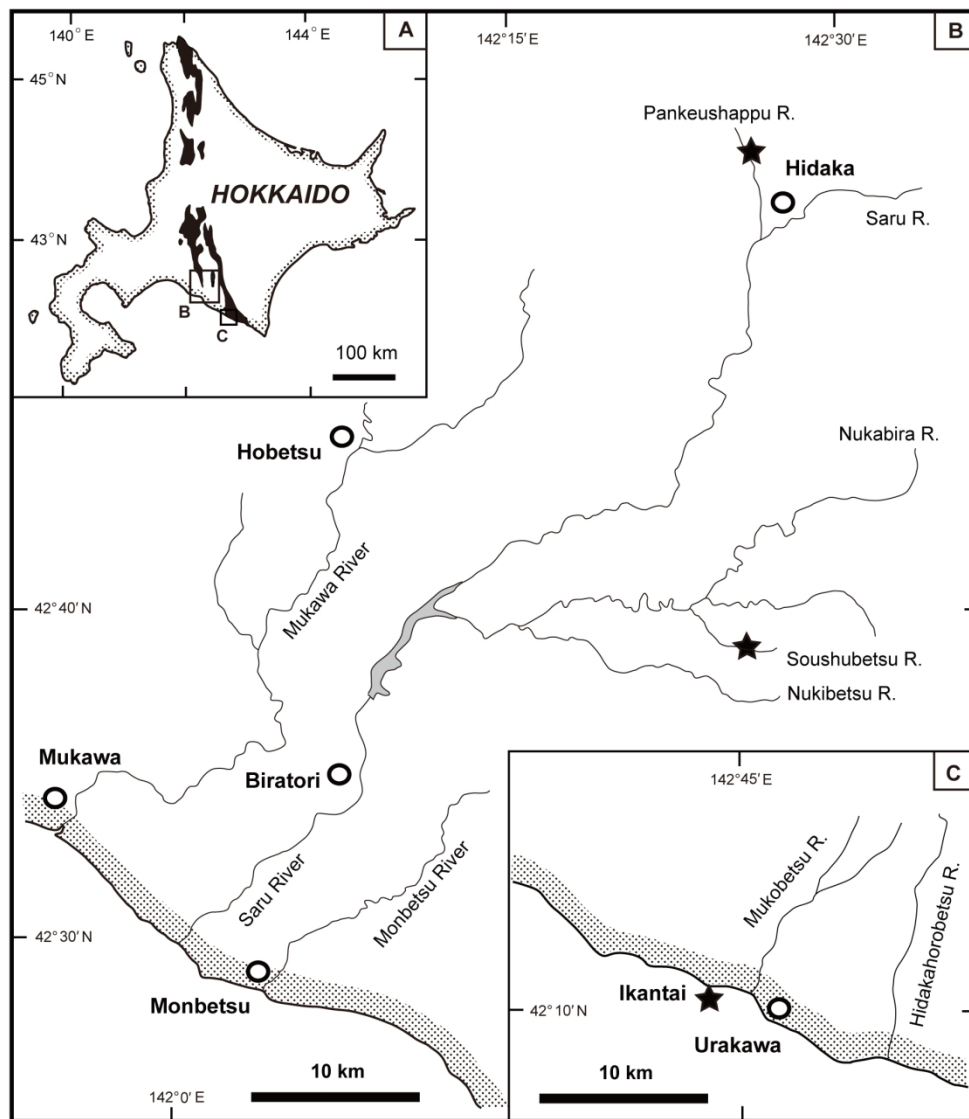


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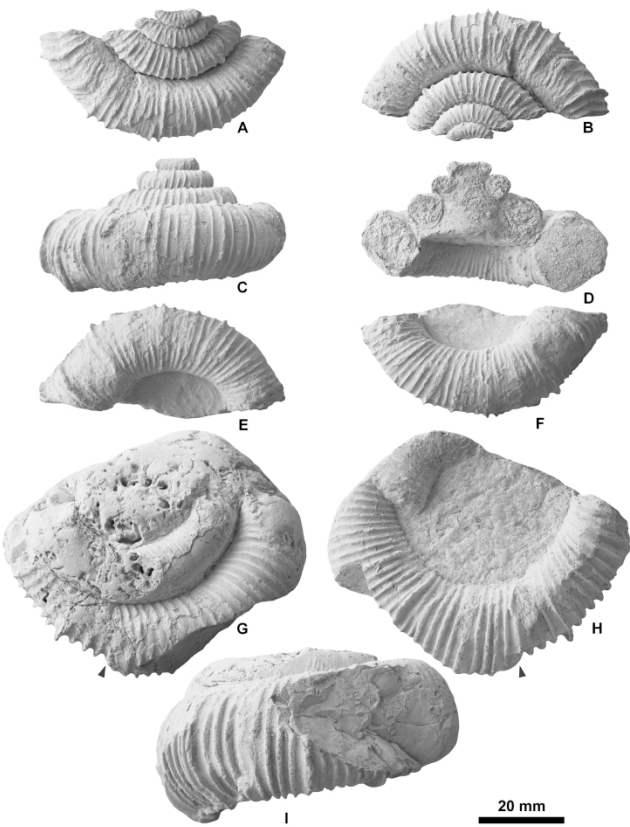


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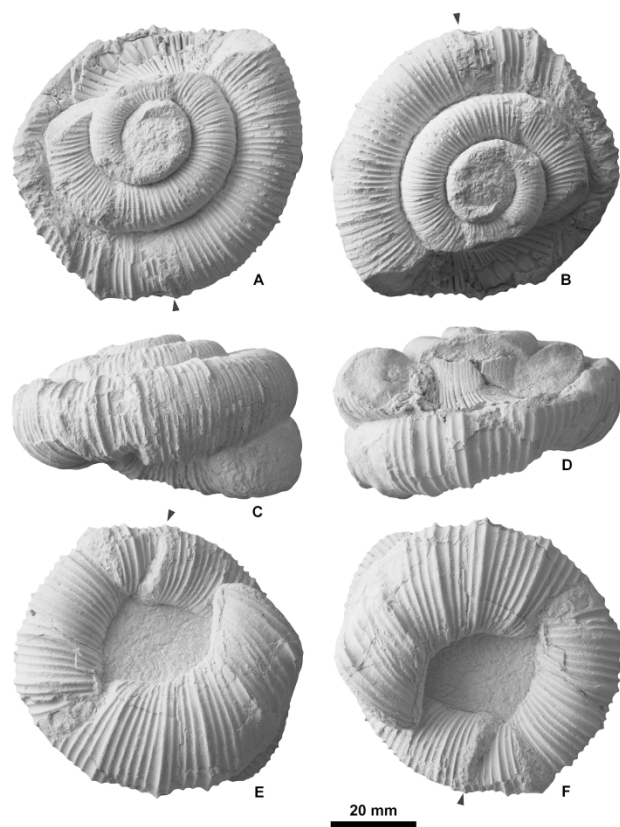


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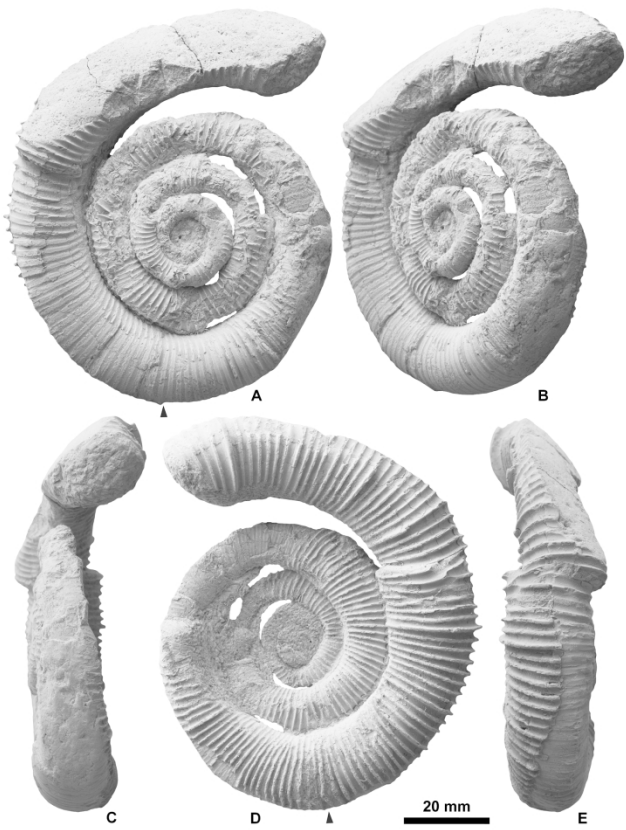


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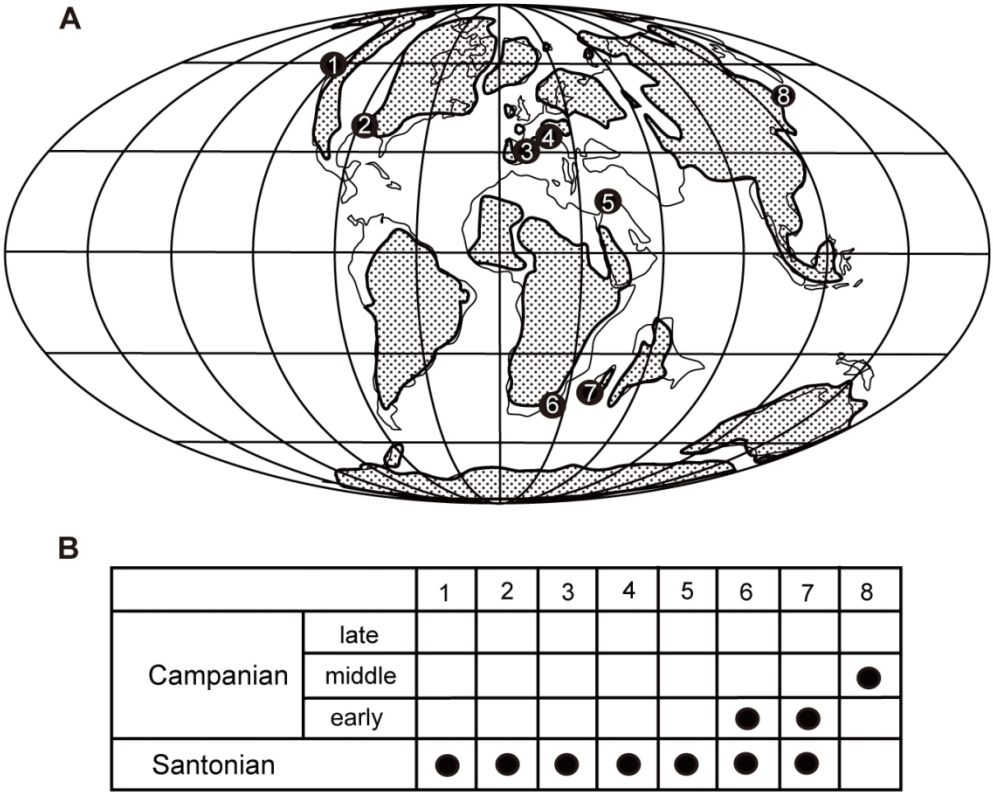


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115x94mm (300 x 300 DPI)