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Taphonomy of large *Canadoceras* (ammonoid) shells in the Upper Cretaceous Series in South Sakhalin, Russia

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Abstract. Based on materials from the Krasnoyarka Formation in the Naiba area in south Sakhalin, Russia, taphonomic histories of a large Campanian ammonoid, *Canadoceras kossmati* Matsumoto, 1954, were closely investigated. Large *Canadoceras* shells exceeding 30 cm in diameter are usually embedded horizontally and solitarily in muddy sandstone. A thin, lenticular calcareous concretion envelopes the shell (= envelope concretion). Their body chambers are mostly lost. The inner whorls comprising the center of the umbilicus completely disappear without exception, and only two or three outer whorls are preserved. The body and air chambers are somewhat compressed by compaction and are filled with sediments. *Phycosiphon* burrows are common not only in open body chambers but also in inner air chambers, which were originally closed. These observations suggest that the thin-shelled inner whorls and organic-rich siphuncular tubes degraded before final burial of the shell, and sediment infilling to the inside of the chambers followed. The early loss of inner whorls and siphuncular tubes gave rise to "draft-through currents." The continuous supply of oxygen and nutrients by the draft-through currents supported the *Phycosiphon* producers in the inner air chambers. Compared with other calcareous concretions containing intact fossils, values of minus-cement porosity (MCP) remain relatively low (63–74%) and vary by areas even in the same envelope concretion. This indicates that the envelope concretions were cemented under a progressive increase of compaction during the later diagenetic stage. The formation of the envelope concretion appears to be a long-term phenomenon. Various events at different stages have been overprinted in a single large ammonoid fossil.

Key words: *Canadoceras kossmati*, Cretaceous ammonoid, diagenesis, envelope concretion, minus-cement porosity, taphonomy

Introduction

A full understanding of the taphonomy of any preserved fauna is essential to ensure that the evidence it provides is correctly interpreted (Orr *et al.*, 2000). It is particularly essential in extinct fossil animals without any allied recent groups such as ammonoids. Increasing numbers of taphonomic studies on ammonoid fossils since the 1970's may underlie this trend (e.g., Kennedy and Cobban, 1976; Fernández-López, 1984, 1991; Maeda, 1991; Fernández-López and Meléndez, 1994, 2004; Gómez and Fernández-López, 1994; Oloriz *et al.*, 2004; Zaton and Marynowski, 2006; Olivero, 2007). Their scope and interest have been mainly focused on the biostratinomical (= sedimentological) aspects of empty ammonoid shells.

In contrast, the diagenetic processes undergone by ammonoid shells are less well studied and have been investigated by a few works (Minato, 1953; Seilacher, 1971; Seilacher *et al.*, 1976; Hagdorn and Mundlos, 1983; Maeda, 1987; Fernández-López, 2007, 2008; etc.). Except for rare cases of snapshots or "taphonomic windows" in Konservat Lagerstätten (Seilacher, 1970; Seilacher *et al.*, 1985), post-burial taphonomic processes involved in the preservation of fossils are usually very complicated. However, they can play a decisive role in their final preservations. Investigation of diagenetic processes is therefore a key to unravelling whole overprint histories in most fossils.

A Late Cretaceous pachydiscid ammonite species, *Canadoceras kossmati* Matsumoto, 1954, is widely distributed in the circum-North Pacific region (Matsumoto, 1954; Wright *et al.*, 1996). Adult shells of this species exceeding 30 cm in diameter are found abundantly in the Campanian deposits in the Krasnoyarka Formation in the Naiba area, south Sakhalin, Russia (Figures 1–4). They are never

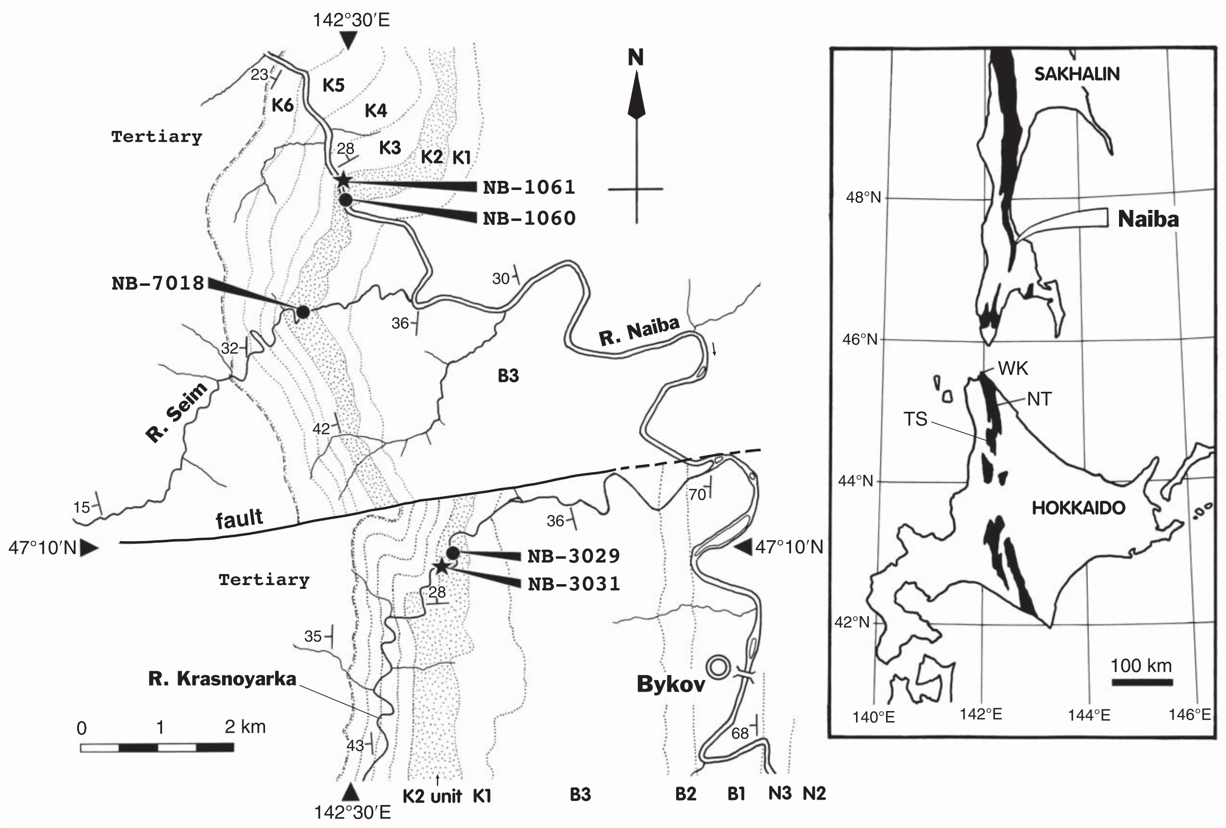


Figure 1. Maps showing distribution of the Cretaceous Yezo Group (right) and localities of *Canadoceras kossmati* Matsumoto in the Naiba area, south Sakhalin (left). In the right figure, WK: Wakkanai area; NT: Nakatombetsu area (the type locality of *C. kossmati*); TS: Teshio area; dark area: distribution of the Yezo Group. In the left figure, N2 and N3: the Naiba Formation; B1-B3: the Bykov Formation; K1-K6: the Krasnoyarka Formation (see Kodama *et al.*, 2002 for detailed stratigraphy and localities); dotted area on the left: distribution of the K2 unit, Krasnoyarka Formation; solid circles: occurrences of *C. kossmati*; stars: occurrences of *C. multicostatum* (a descendant species of *C. kossmati*).

perfectly preserved because of various kinds of taphonomic damage, such as compaction and dissolution, that have been overprinted on their shells. They are, however, useful for taphonomic investigation from the above-stated point of view (Figures 5–8).

Kase *et al.* (1994) reported limpet home-depressions on large *C. kossmati* shells, and discussed the bathymetry of the ammonoid animal. In contrast, this study focuses on synsedimentary and post-burial processes of the same material, and attempts to unravel the taphonomic histories of large *Canadoceras* fossils.

Outline of stratigraphy

The Naiba area near Bykov represents one of the best Cretaceous sections in the Far East region (Figure 1; Matsumoto, 1942; Vereshchagin and Salikov, 1968; Pergament, 1974; Zhakarov *et al.*, 1984; Poyarkova, 1987; Zonova *et al.*, 1993; Kodama *et al.*, 2000, 2002; Shigeta and Maeda, 2005; Shigeta *et al.*, 1999). The Cretaceous Yezo Group extending from Hokkaido to Sakhalin attains a thickness of 5,000 m there. The Ai (Albian; not illustrated here), Naiba (Cenomanian), Bykov (Upper Cenomanian-lower Campanian), and Krasnoyarka (Campanian-Maastrichtian) formations are successively exposed in upward sequence (Figures 1, 2). The lower three formations dominated by fine-grained deposits represent an offshore mudstone facies in a slope-basin environment (Okada, 1979, 1983). These are equivalent to the Middle and Upper Yezo groups in Hokkaido (Matsumoto, 1942, 1954). The overlying Krasnoyarka Formation is equivalent to the Hakobuchi Formation in Hokkaido (Kodama *et al.*, 2002). It frequently intercalates sandstone and conglomerate, and exhibits a shallowing-upward succession suggesting a prodelta-delta facies (Figure 2; Bhattacharya and Walker, 1992).

Materials and methods

Four biostratigraphic zones are discriminated in the Krasnoyarka Formation, namely, the *Sphenoceramus schmidti*,

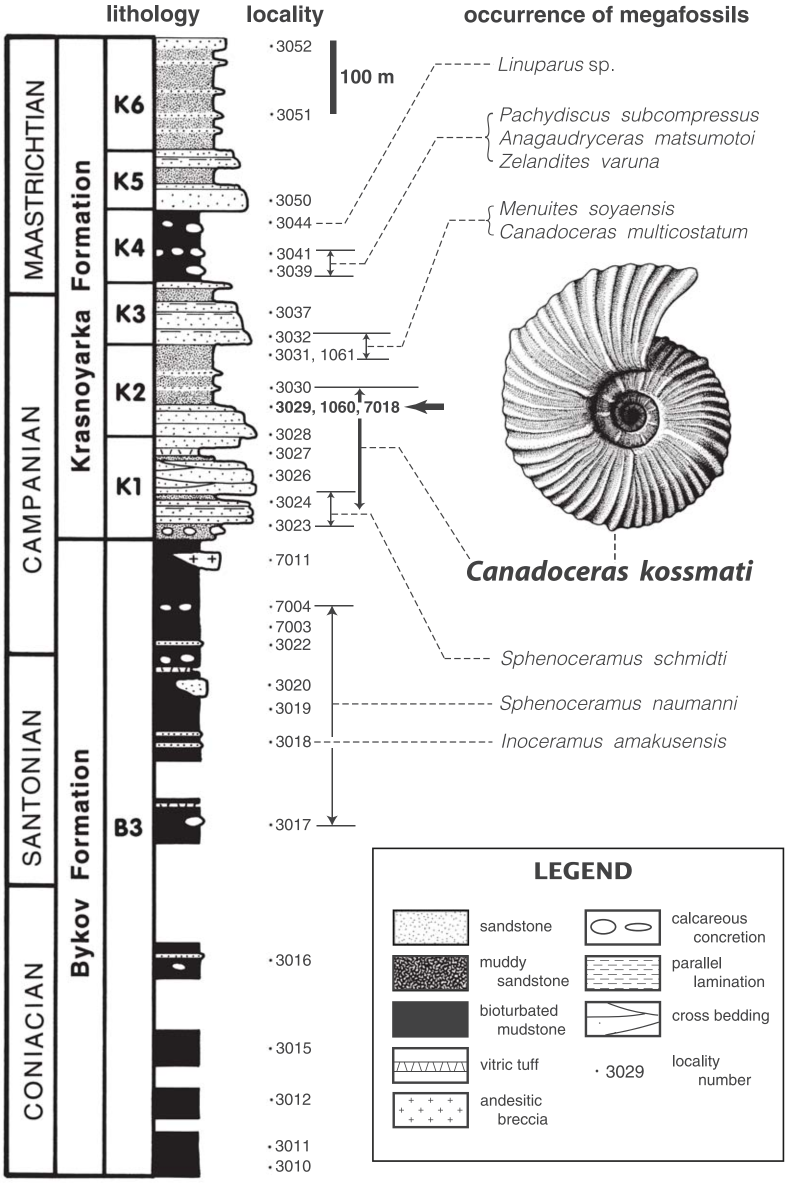
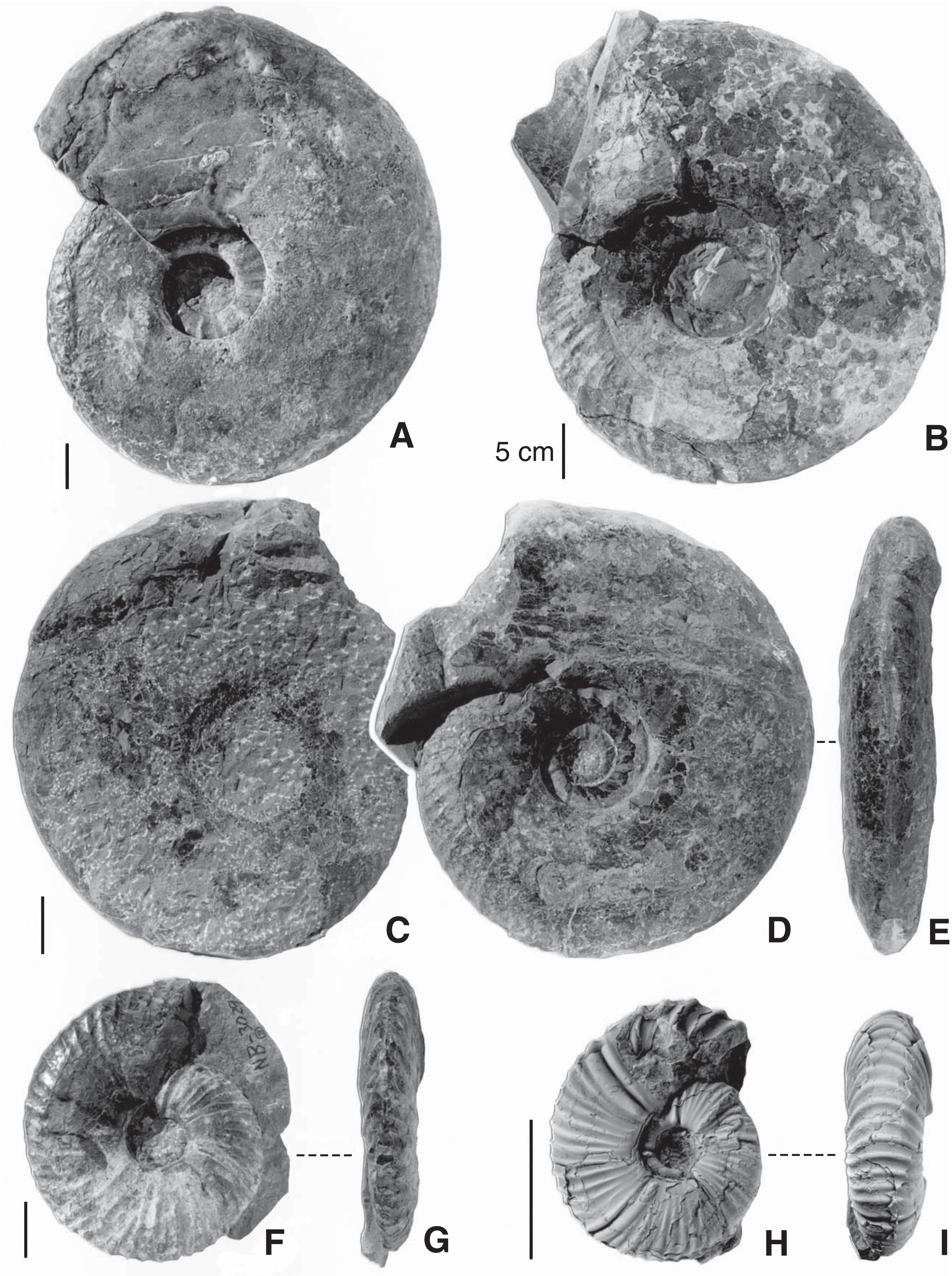


Figure 2. Columnar section of the Upper Cretaceous Series along the River Krasnoyarka in the Naiba area. The upper part of the Bykov Formation and the Krasnoyarka Formation (Coniacian to Maastrichtian), attaining a thickness of 1,500 m thick, are successively exposed. *Canadoceras kossmati* Matsumoto occurs from the lower part of the Krasnoyarka Formation (lower to middle Campanian), particularly from the middle part of the K2 unit. *C. kossmati* Matsumoto is replaced stratigraphically by a descendant species, *C. multicostatum* Matsumoto in the uppermost part of the K2 unit. *Pachydiscus* (*Pachydiscus*) *subcompressus* Matsumoto occurs abundantly from the overlying muddy K4 unit. Stratigraphic division is based on Matsumoto (1942), Poyarkova (1987), Kodama *et al.* (2002), and Hasegawa *et al.* (2003).

➡ **Figure 3.** *Canadoceras kossmati* Matsumoto of various shell sizes. Scale bars are 5 cm long. Photographs connected with dashed lines indicate different views of the same specimen. **A**. Lower side of a large phragmocone from the River Seim (locality NB-7018). The shell surface is slightly worn by weathering. **B**. Lower side of another adult shell (phragmocone) from the River Krasnoyarka (locality NB-3029). Many limpet boreholes discussed by Kase *et al.* (1994) are visible on the shell surface. **C**. Upper side of a nearly adult shell from the River Krasnoyarka (locality NB-3029). Shell test (in dark color) is preserved only in part. White scratch marks are due to trimming by chisel. **D**. Lower side of the same specimen as in Figure 3C. Compared to the upper side, much more of the shell test remains. However, the inner whorls are not preserved. **E**. Ventral view of the same specimen as in Figures 3C, D. The upper side (right) is remarkably flattened. Note that the venter partly shows the original curvature of the shell (uppermost part in the figure). **F**. Upper side of a middle-grown stage shell from the River Krasnoyarka (locality NB-3029). **G**. Ventral view of the same specimen as in Figure 3F. The shell is flattened, and fracture patterns run longitudinally. **H**. Immature shell housed in a mushroom-shaped calcareous concretion from the River Krasnoyarka (locality NB-3029). **I**, Ventral view of the same specimen as in Figure H. In contrast to large specimens, small shells in spherical concretions are less flattened, and inner whorls are preserved.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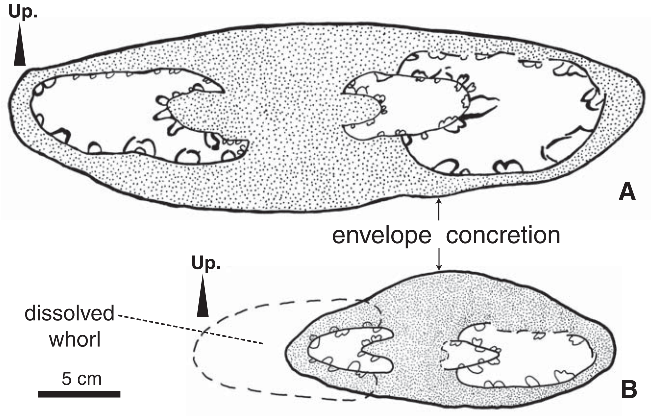

Figure 3. Mode of occurrence of large *Canadoceras kossmati* shells. **A**, **B**. Vertical profiles of the shells from the River Naiba (locality NB-1060). The shells are horizontally embedded in ill-sorted sandy mudstone. In most cases, a lenticular calcareous concretion envelopes the shell (= envelope concretion). Body chamber is lost in most cases. Even in concretions, the inner whorls are not preserved. The whorls were asymmetrically compressed and flattened by compaction particularly on the upper side. The siphuncular tube is not preserved, and the air chambers are filled with sediments.

Canadoceras kossmati, C. multicostatum, and *Pachydiscus subcompressus* zones in upward sequence (Kodama *et al.*, 2002; Maeda *et al.*, 2005). *C. kossmati* Matsumoto occurs from the lower part of the Krasnoyarka Formation (lower to middle Campanian), particularly from the middle part of the K2 unit, e.g., at localities NB-3029, -7018, and -1060 (Figure 1). *C. kossmati* is succeeded stratigraphically by the descendant species: *C. multicostatum* Matsumoto in the uppermost part of the K2 unit (Figure 2). We follow the stratigraphic divisions of Kodama *et al.* (2002). See Poyarkova (1987) and Kodama *et al.* (2002) for detailed stratigraphy and localities.

Taxonomic assignment

All individuals used in this study are assignable to the single species *Canadoceras kossmati* Matsumoto, 1954. The present species was first named as *Pachydiscus denisonianus* by Jimbo (1894) based on an immature specimen from Nakatombetsu in Hokkaido (NT in Figure 1, right), and was redescribed as *Canadoceras kossmati* sp. nov. by Matsumoto (1954). Since then, the allied species "*C. mysticum* Matsumoto, 1954" and "*C. minimum* Matsumoto, 1986" have been proposed from the Campanian in Teshio (TS) and Wakkanai (WK) in Hokkaido, respectively (Figure 1, right; Matsumoto, 1954; Matsumoto and Miyauchi, 1986).

Specimens from the Naiba area typologically resemble "*C. mysticum*" in having relatively compressed whorls. However, the splitting of "*C. mysticum*" and "*C. minimum*" from *C. kossmati* seems insignificant because these "species" share almost the same biostratigraphic ranges, and many individuals show intermediate features even in their diagnostic characters. Therefore, we assign all the specimens utilized in this study to *Canadoceras kossmati* Matsumoto, 1954, following the rule of priority in taxonomic nomenclature.

Materials

More than 25 specimens of *Canadoceras kossmati* ranging 5–80 cm in diameter were utilized here. They were collected from sandy mudstone of the K2 unit (middle Campanian) at localities NB-3029, -1060, and -7018 during an expedition of the Japan-Russia (USSR) joint research program directed by K. Kodama (Kochi University) in 1990. All the specimens occur in the upper part of the taxon range zone of this species (Figure 2).

Specimens utilized here are housed in Kyoto University, Kochi University, and the National Museum of Nature and Science, Tokyo.

Methods

Recovered specimens were carefully prepared for various observation purposes. Several specimens were excavated from matrices to describe whole-shell morphology (Figure 3). Some concretions were vertically cut in whole specimens to see their internal structures (Figure 4). To observe internal shell destruction, modes of sediment infill, and burrowing in detail, several specimens were longitudinally cut, polished, and thin-sectioned (Figures 5–8). Various parts were thin-sectioned, e.g., deposits outside of ammonoid shells and sediment infill of body and air chambers, and were photographed (Figure 7).

The original pores of the sediment infills are now cemented by microcrystalline calcite. The porosity that a sedimentary deposit would have if it contained no chemical cement can be measured (= minus-cement porosity, MCP; Huggett, 1994; Jackson, 1997; Raiswell and Fischer, 2000). To determine MCP, the volume of calcite cement in thin sections was measured by the point-counting method, in which 1,000 counts were repeated 3 times for every thin section. The measured values were averaged (Figure 8).

Modes of occurrence and preservation

Macroscopic observation

Preservational features of *Canadoceras kossmati* shells are typically observable at riverbeds and riverbank cliffs at locality NB-3029 along the River Krasnoyarka (Figure 1; Kodama *et al.*, 2002, fig. 4; Shigeta and Maeda, 2005, p. 7, fig. 4, upper left). The large adult shells attaining 30–80 cm diameter are horizontally embedded in dark greenish gray sandy mudstone containing abundant pumiceous volcanic-glass fragments (Figures 2, 7).

The large *Canadoceras* shells are mostly enveloped by thin lenticular calcareous concretions that just fit the shell size (= envelope concretion; Figure 4). Their body chambers are lost

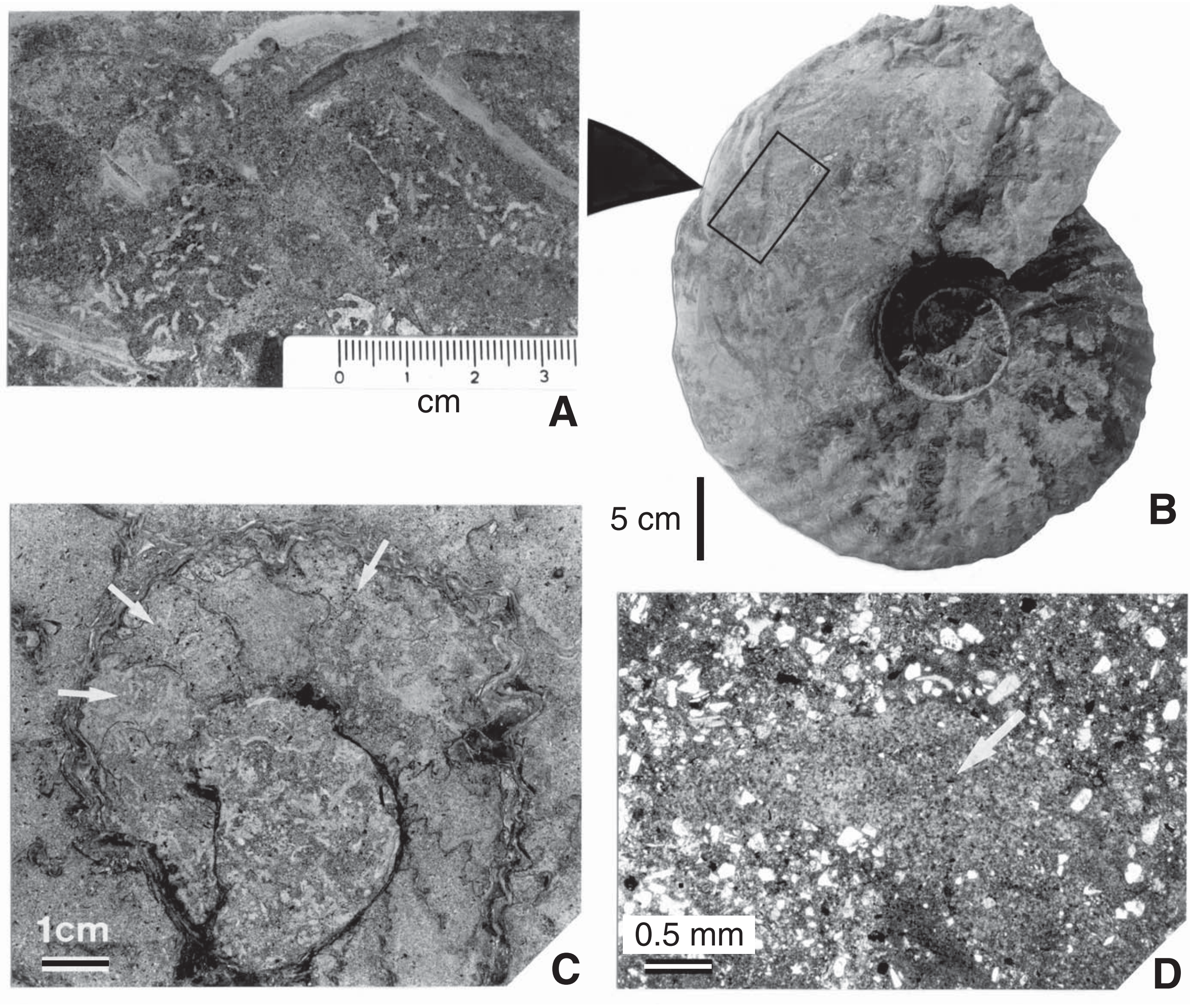

Figure 5. Trace fossils in sediment infills of *Canadoceras kossmati* shells. **A**. Worn surface of body chamber; close-up of the rectangle in Figure 5B. Small *Phycosiphon* burrows are aggregated patchily in sediment infill of the body chamber. **B**. Lateral view of a naturally worn specimen of middle growth stage from the River Krasnoyarka (locality NB-3029). **C**. Close-up of inner whorls of another worn specimen from the River Krasnoyarka (locality NB-3029). *Phycosiphon* burrows are aggregated in the sediment infills of a few air chambers (white arrows). **D**. Photomicrograph of a *Phycosiphon* burrow in an air chamber of a specimen from the River Krasnoyarka (locality NB-3029). Note that the tube burrow (indicated by a white arrow) is filled with finer-grained sediments than the surrounding rocks.

or partly preserved (Figures 3A, B, 5B). Besides the body chamber loss, the large shells have suffered other damage even with preservation in calcareous concretions. The inner whorls comprising the center of the umbilicus have completely disappeared without exception, and only two or three outer whorls are preserved (Figures 3A–G, 4, 5C, 6).

Like the body chamber, the air chambers have also collapsed due to compaction, so that the breadth-height ratio of the whorl (B/H) has apparently decreased 5–20% from the original shell morphology. Such compression rates are almost uniform both in the body chamber and the phragmocone. The major fracture lines usually run longitudinally along the ventrolateral periphery (Figure 3A). In addition, many minor fracture lines are visible on the flanks and umbilical periphery. Attachment lines of the umbilical wall of the outer whorl, which is now lost, are occasionally imprinted on the inner whorl surfaces (Figure 3B).

The lower burial side of the whorls is relatively well preserved and somewhat retains the original shell test. Therefore, the original shell surface ornaments, such as radial

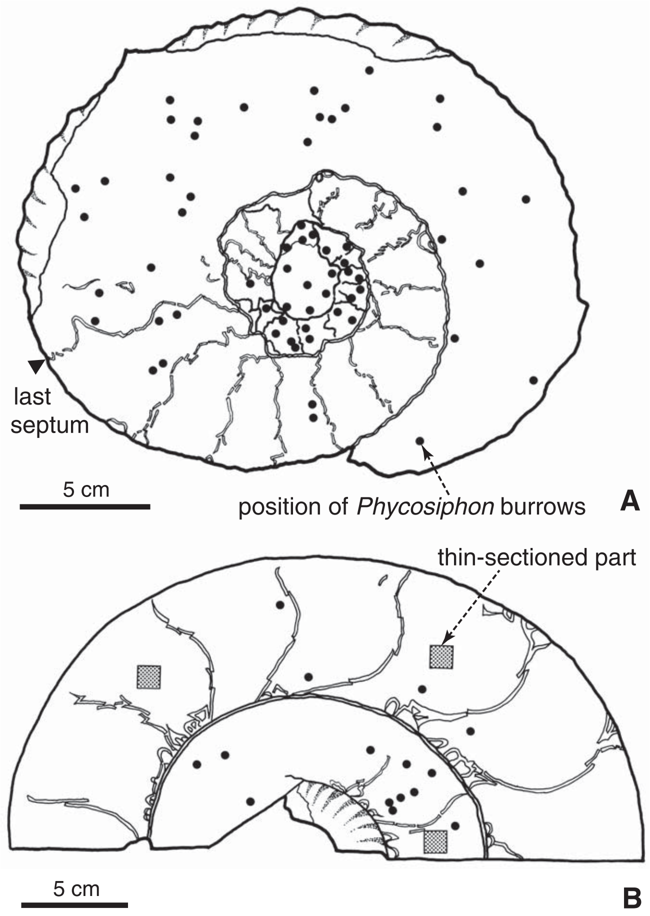

Figure 6. Median longitudinal sections of large *Canadoceras kossmati* shells. Solid circle: positional plot of aggregation of *Phycosiphon* burrows (more than 3 burrows); square: thin-sectioned part. **A**. Naturally worn specimen from the River Krasnoyarka (locality NB-3029). **B**. Polished section of another specimen from the River Krasnoyarka (locality NB-3029). The septal walls are fractured, and all air chambers are filled with sediments. The *Phycosiphon* burrows are preserved not only in the body chamber but also in several air chambers that were originally closed. They are particularly abundant in the both terminals of the preserved phragmocone whorls, namely outermost and innermost chambers.

costae and umbilical bullae, are well-distinguished (Figure 3A, 3B, 3D). In contrast, the upper burial side of the whorls is more crushed and somewhat flattened (Figure 3C, 3E). The original shell test is partly preserved as crushed patches in the upper flank so that the original shell sculptures, such as costae and umbilical bullae, are indiscernible (Figure 3C). However, the specimens did not exhibit typical "half-ammonoid" preservation (Figure 3E; Seilacher *et al.*, 1976; Maeda, 1987, 2001; Maeda and Seilacher, 1996; Kondo and Maeda, 2004). They are asymmetrically compressed (Fernández-López, 2007).

Septal walls are more or less compressed (Figures 4, 6, 8). The broken septal walls are easily observed in longitudinal sections of the phragmocones (Figures 5C, 6, 8). The septal fragments overlap each other due to compressional force (Figure 7A).

The body and air chambers are filled with sandy mudstone, which is essentially similar to the host sediment outside the shell (Figures 5, 7). No intact air chambers are filled with drusy calcite in large *C. kossmati* shells exceeding 30 cm diameter. Siphuncular tubes are lost in most cases.

Besides large shells, a few immature shells of *C. kossmati* up to several centimeters in diameter are preserved in mushroom-shaped calcareous concretions together with other small ammonoids, plant remains, and pumice grains (Maeda, 1987; Maeda and Seilacher, 1996; Kondo and Maeda, 2004). Except for slight compactional crush, they retain the original shell morphology and show better preservational states than the larger shells (Figure 3H, I).

Phycosiphon burrows in air chambers

Phycosiphon tube burrows are commonly found in matrices of the envelope concretions and the surrounding sandy mudstone. It is noteworthy that *Phycosiphon* tube burrows are common not only in the sediment infills of the body chamber but also in air chambers that were originally closed (Figure 5). The burrows are straight or curved, about 2–4 mm long, and 1 mm in diameter (Figure 5A–C). They are filled with much finer-grained muddy particles than the surrounding deposits (Figure 5D). The *Phycosiphon* producers are considered to be deposit feeders (Wetzel and Uchman, 2001; Naruse and Nifuku, 2008). In phragmocones, *Phycosiphon* burrows are most common in a few innermost air chambers that are adjacent to the lost inner whorls and/or in the last air chambers (Figures 6, 8). The burrows are rare in the intermediate chambers (Figure 6A).

Signs of bioturbation by larger animals are present in the body chambers (Figure 5A) but are absent from air chambers.

Microscopic observation

Sedimentary features, i.e., size, shape, and composition of grains, textures in host sediment and sediment infills in *Canadoceras* shells were observed. Detailed destruction patterns of septal walls were also investigated. MCP was also measured.

Surrounding sediment.—The host sediment consists of dark greenish gray, ill-sorted lithic fine sandy mudstone. Figure 7C shows a photomicrograph of the deposits outside of a *Canadoceras* shell in an envelope concretion. Grains are angular to subangular, fine-sand size. Among the grains, andesitic volcanic fragments showing a light-green color are abundant. Light yellowish-green pumiceous volcanic glass fragments showing a typical bubble-wall texture are also very common (see also Figure 7D, 7E). In addition, quartz, feldspar, plant remains, and foraminifer tests are common.

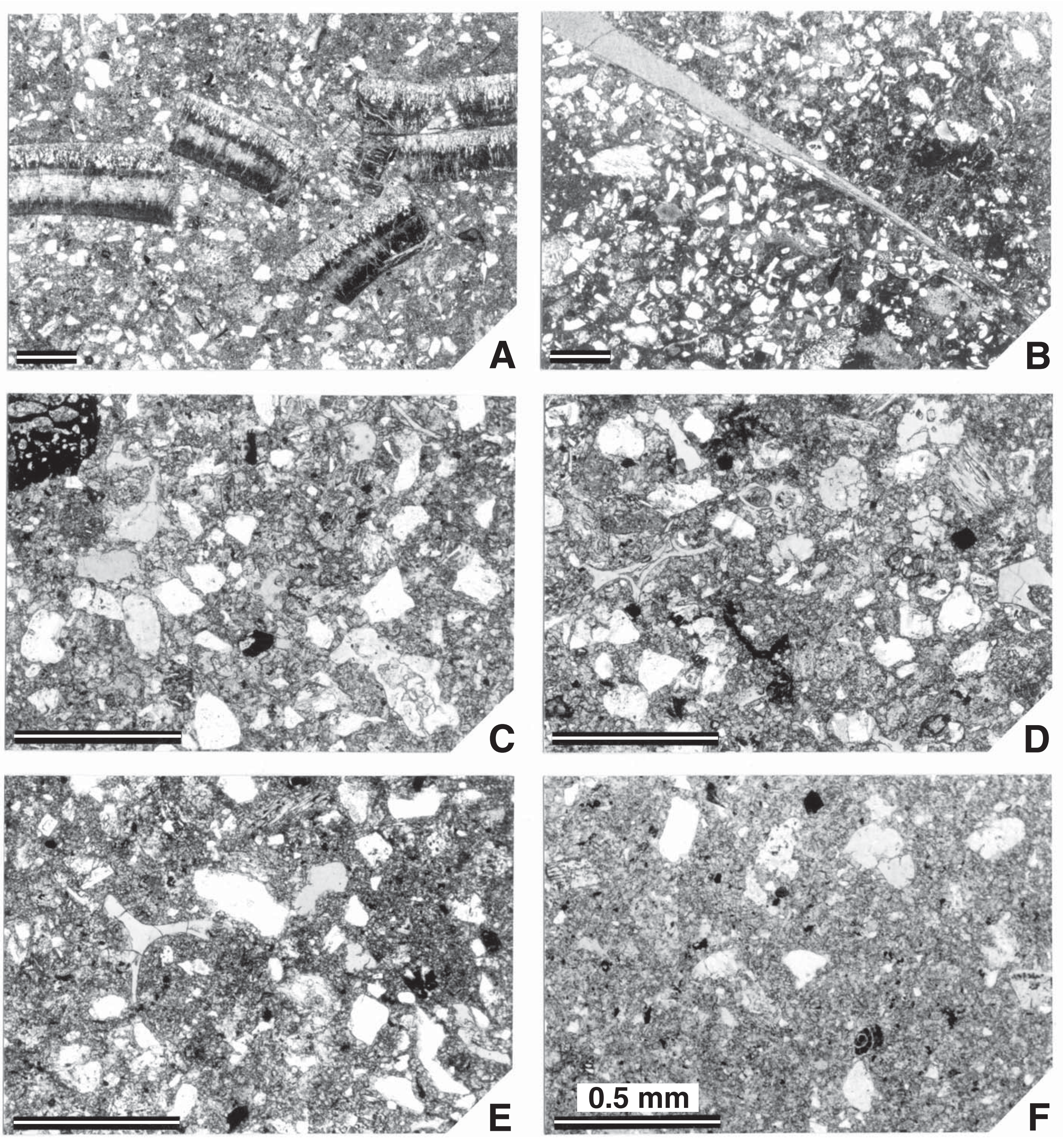

Figure 7. Photomicrographs of sediment infill of *Canadoceras kossmati* shells and surrounding deposits. Open nicols; scale bars are 0.5 mm long. **A**, **B**. Different patterns of diagenetic destruction of septal walls. A: rigid fracturing caused probably by mechanical stress during compaction, in an outermost air chamber of a specimen from the River Krasnoyarka (locality NB-3029); B: gradual thinning of a septal wall originated by chemical dissolution, in an innermost air chamber of another specimen from the River Naiba (locality NB-1056). **C–F**. Variation of concretionary microsparite volumes by places in a single envelope concretion (see Figure 8), from the River Krasnoyarka (locality NB-3029). C: matrix of an envelope concretion (outside of the *Canadoceras kossmati* shell) showing relatively low minus-cement porosity (MCP; 63.4%). D: sediment infill in body chamber with moderate minus-cement porosity (66.4%; see Figure 8). E: sediment infill in air chamber 1 in Figure 8A. The minus-cement porosity (MCP) is 68.9%. F: sediment infill in air chamber 2 in Figure 8A. Relatively high minus-cement porosity (73.9%) is measured here.

The sand grains touch each other or somewhat float in a matrix consisting mainly of clay minerals and in calcite cements.

The original pore spaces are cemented by secondary microcrystalline calcite (Figure 7C). MCP measured by volume is approximately 63.4% (average of 1,000 point-counts × 3 times). This is lower than that of sediment infills of *Canadoceras* shells.

Body chamber infill.—The size, shape, and composition of grains are essentially similar to the host sediment (Figure 7D). MCP is 66.4%, which is slightly larger than that of the host sediment.

Air chamber infill.—In most air chambers, size, shape, and composition of grains are essentially similar to the host sediment (Figure 7E). Pumiceous volcanic glass fragments show a typical bubble-wall texture (Figure 7E). However, the sand grains are more dispersed (Figure 7E). In a few air chambers, opaque grains mainly represented by pyrite are common, and the microcrystalline calcite cement covers a very wide area (Figure 7F). MCP is higher than in the other areas and reaches 68.9–73.9%.

Modification patterns of septa.—Two different modification patterns of septal walls are distinguished. In the first type, the septal wall is broken into rectangular to trapezoidal fragments that overlap each other (Figure 7A). The wall still retains a layered shell structure, and the fractured edges are still sharp and are not corroded.

In the second type, the septal wall thins gradually and finally disappears (Figure 7B). The layered shell structure is obscure. The former can be attributed to compression by gravitational compaction and is widespread in the septa of whole air chambers. The latter may suggest chemical dissolution of the septal wall and is particularly common in the thinner septal walls of inner air chambers.

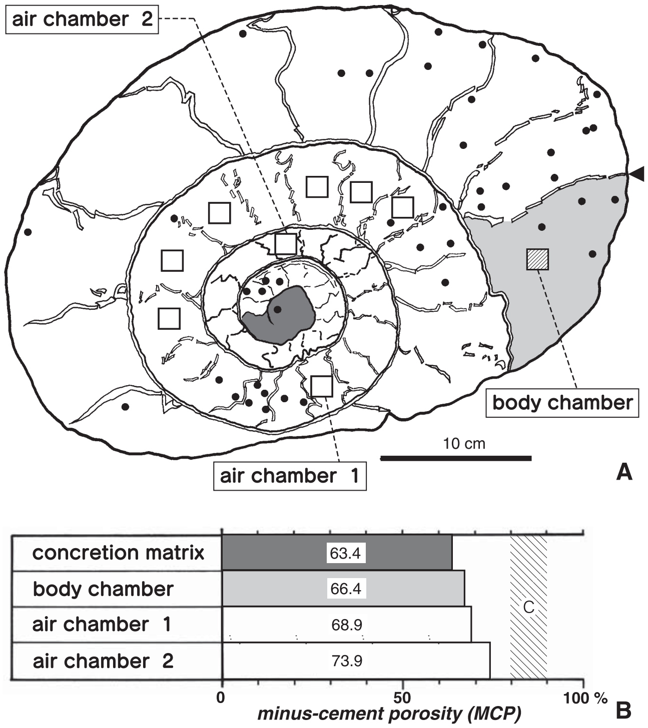

Figure 8. Variation of minus-cement porosity values at places in a single envelope concretion from the River Krasnoyarka (locality NB-3029). **A**. Median longitudinal section of a large *Canadoceras kossmati* shell enveloped in the concretion. Outside of the shell is not illustrated here. Solid triangle: position of the last septum; solid circles: positional plot of aggregation of *Phycosiphon* burrows; squares: thin-sectioned parts (see Figure 7C–F). **B**. Diagram showing selected minus-cement porosity values in a single envelope concretion. Position of measured parts is shown in Figure 8A except for concretion matrix. Note that the minus-cement porosity (MCP) values decrease from the inside of the phragmocone to the outside of the shell via the body chamber in a single envelope concretion. Concretions housing intact fossils usually show much higher minus-cement porosity values (80–90%) that are usually plotted in the shadowed area (C) (Raiswell, 1976).

Discussion

Early loss of inner whorls

It seems natural that an open body chamber of the empty *Canadoceras kossmati* shell was filled with sediments and colonized by benthic animals on the seafloor (Figure 5A, B). The *Phycosiphon* burrows are also abundant in the sediment infills of certain air chambers that were originally closed (Figure 6). However, large *C. kossmati* shells usually lack inner whorls comprising the center of the umbilicus like other large coiled ammonoid fossils (Maeda, 1987). It is noteworthy that such *Phycosiphon* burrows are particularly concentrated in a few innermost air chambers that are adjacent to the lost inner whorls (Figures 5A, 5B, 8A). There is no notable difference between the sediment infills of the chambers and surrounding deposits, particularly in terms of grain size and composition (Figure 7C–F). These observations suggest the following:

1) Degradation of the shell wall first occurred in the thin-shelled inner whorls before final burial of the shell (= early loss of inner whorls).

2) Sediments intruded into the air chambers via openings on the whorls after the shell was damaged.

3) *Phycosiphon* producers particularly colonized the innermost air chambers that were close to such openings.

In addition, organic-rich siphuncular tubes are not preserved (Figures 4, 6, 8). They would have also decomposed before burial in aerobic conditions on the seafloor (Maeda and Seilacher, 1996). The early loss of inner whorls and the siphuncular tube may also give rise to a “draft-through current” (Seilacher, 1968). Early decay of the siphuncular tube and septal necks, and the loss of the innermost whorls created terminal openings allowing a unidirectional water current to penetrate the nearly closed phragmocone (Seilacher, 1968). The draft-through current carries a large amount of sediments

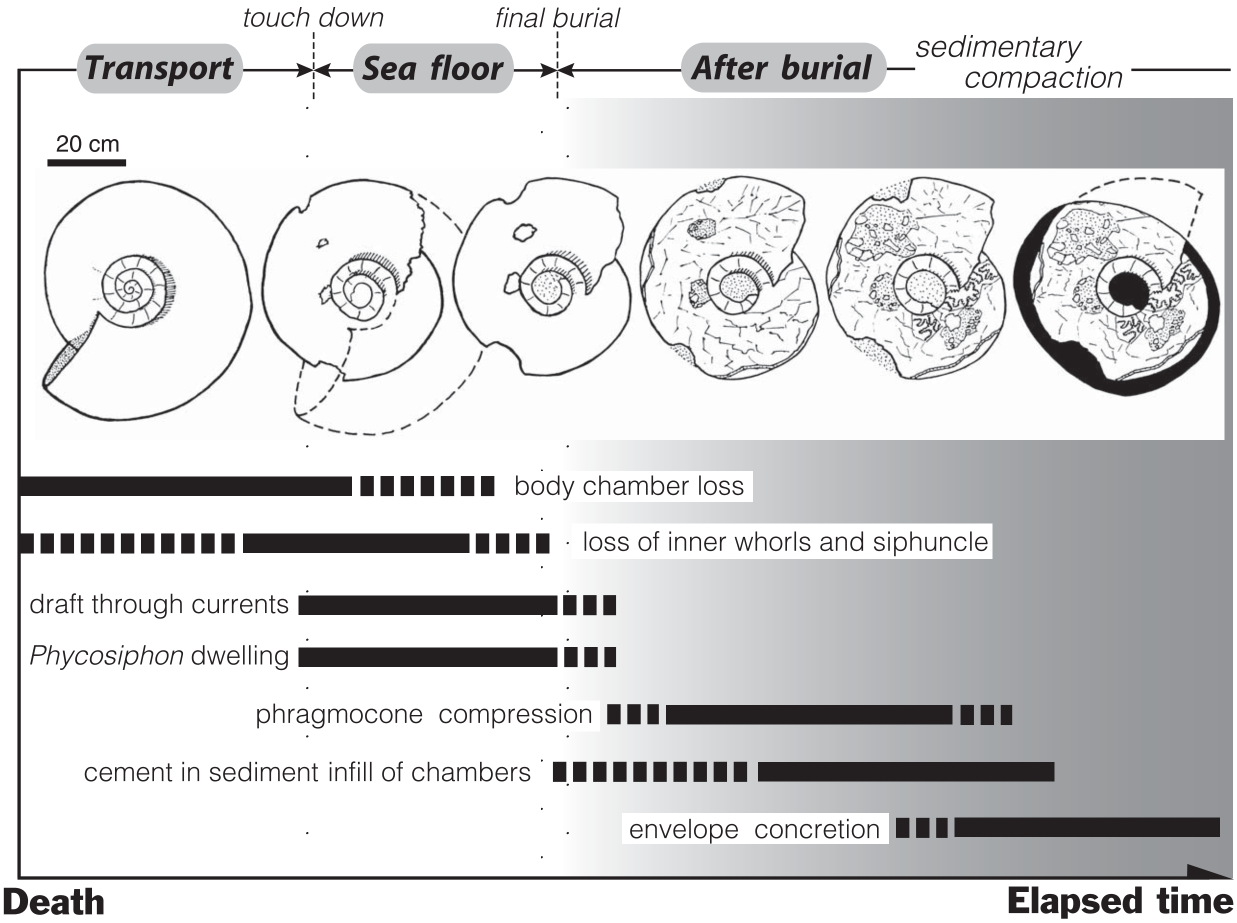

Figure 9. Taphonomic history of a large empty shell of *Canadoceras kossmati* Matsumoto in the Cretaceous Yezo Group deposited in a slope basin on an active margin. The extremely high sedimentation rate (0.3–1.0 mm/y) prevented ammonoid remains from repeated reworking. Formation of envelope concretion is a longtime phenomenon, and various events at different stages have been overprinted in a large ammonoid fossil.

into the air chambers and forms heavy sediment infills until the openings are closed (Seilacher, 1968, 1971; Hagdorn and Mundlos, 1983; Maeda, 1987; Fernández-López, 2008). This also provided continuous "ventilation" to the inside chambers, and ensured the maintenance of "lifelines," e.g., oxygen and nutrients, for the *Phycosiphon* producers over a considerable period. This is suggested by the concentration of *Phycosiphon* burrows in areas close to the entrance or exit of the draft-through current (Figures 6A, 8B).

Empty ammonoid shells were reused in various ways by other organisms. The most outstanding examples are the inhabitation of empty shells by hermit crabs (Fraaije, 2003) and their use as scaffoldings for cirripedes (Witter, 1996; Ifrim and Stinnesbeck, 2007). In addition, shells lying on the seafloor often trapped lightweight materials, such as smaller ammonoid shells, plant remains, and pumice grains, that were swept by weak bottom currents (= sheltered preservation; Maeda, 1987, 1991; Zaton and Marynowski, 2006; Olivero, 2007). Such trapping spots created by large ammonoid shells would be useful for benthic dwellers not only as a residence but also as a nutrient-rich food source (Maeda, 1987; Maeda and Seilacher, 1996).

Slowly formed envelope concretion

Many intact ammonoid shells occur in carbonate concretions in mudrocks from different ages and areas (Lehmann, 1976; Landman and Waage, 1993; Maeda, 1993; Maeda and Shigeta, 2005; Zaton and Marynowski, 2006). These concretions (= "snapshot concretions") are almost compaction-free and are thought to have been quickly consolidated in very early diagenetic stages in which bacterial sulfate reduction was active (Raiswell, 1976; Allison, 1990). Reflecting the high original porosity of muddy deposits, MCP values of these snapshot concretions are usually high, around 80–90% (area C in Figure 8B; Raiswell, 1976; Huggett, 1994; Raiswell and Fischer, 2000).

In contrast, envelope concretions of large *Canadoceras* shells show different preservational features. Even though they were contained in calcareous concretions, the ammonoid shells suffered severe diagenetic damage, such as compactional compression by overburden of sediments and dissolution of shell walls (Figures 3, 4, 7A, 7B). Compared with snapshot concretions, MCP values in envelope concretions usually remain low, i.e., around 63–74% (Figures 7C–F, 8). This clearly suggests that the cementation of the envelope concretion occurred in the later stages of diagenesis, after the compactional process had already started (Figure 9).

It is noteworthy that MCP values vary by areas even in the same envelope concretion (Figure 8). For example, MCP values decrease from 73.9% (air chamber 2; Figures 7F, 8), 68.9% (air chamber 1; Figures 7E, 8), or 66.4% (body chamber; Figures 7D, 8) to 63.4% (outside the shell; Figures 7C, 8) in descending order. This indicates that consolidation of microcrystalline calcite occurred in different compactional stages and places in the envelope concretion. Cementation first occurred in sediment infills in air chambers, then in body chambers, and finally in sediments outside of the shell under progressively increasing compaction in later diagenetic stages.

On the other hand, an alternative interpretation that the inner chamber may be protected from intensive compaction compared with the outer whorl and outside matrix even during the same cementation process should be tested. This situation actually occurs in ammonoid preservation within fossiliferous calcareous concretions, in which phragmocones are almost intact while brittle body chambers are compressed (Maeda, 1987). However, both body chambers and phragmocones are similarly compressed in large *Canadoceras* shells in envelope concretions (Figure 3). This suggests that structural reinforcement by septal walls was not advantageous in preventing sediment infill of the inner whorls from compression by compaction in large *Canadoceras* shells.

The evidence suggests the following taphonomic scenario (Figure 9). First, the empty *Canadoceras* shells were waterlogged and sank to the bottom after death (Kennedy and Cobban, 1976; Maeda, 1987; Maeda and Seilacher, 1996). Loss of the body chamber might occur during transport or by resedimentation on the seafloor. Subsequently, the thin-shelled inner whorls and the organic-rich siphuncular tube were quickly lost, and sediments intruded into the air chambers via openings on the shell walls. *Phycosiphon* producers particularly concentrated in the innermost air chambers that were close to such openings. Their requirements, such as oxygen and nutrients, were continuously supplied by the draft-through current until the openings were closed by complete burial (Seilacher, 1968, Maeda, 1987). After complete burial, the envelope concretion was gradually formed under the progressive increase of compaction during later diagenetic stages (Figure 9).

Conclusions

The formation of an envelope concretion of a large *Canadoceras* shell is a long-term phenomenon in which many taphonomic processes in various stages are overprinted. First, degradation of the shell wall occurred in the relatively thin-shelled inner whorls before final burial of the shell (= early loss of inner whorls). Second, sediment infilling to the inside chambers occurred. Maintenance of lifelines by the draft-through current supported colonization by *Phycosiphon* producers in the almost closed inner air chambers.

Even after complete burial, cementation in the envelope concretion did not occur quickly. The envelope concretions were cemented under the progressive increase of compaction during later diagenetic stages. Detailed observations of the envelope concretions of large *Canadoceras* shells allow assessment of the various fossilization processes particularly during the post-burial stages.

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