

Phylogenetic significance of a new cheilostome bryozoan species, *Dysnoetocella ? voighti* from the Upper Cretaceous Izumi Group in Shikoku, Japan

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Abstract. A new anascan cheilostome bryozoan species, *Dysnoetocella ? voighti*, is described from the Upper Cretaceous Izumi Group in the northwestern part of Shikoku Island, Japan. The zoarium is erect and unjointed, with subcylindrical multilamellar branches. Three types of fine structure are evident in the calcareous skeletal layers from well preserved specimens. The narrow frontal shields of the zooids show ontogenetic thickening, which suggests that the species is an anascan cryptocystidean. The zoarium, consisting of many zooid columns, is reminiscent of some Paleozoic trepostomes. Although the zooid column is sometimes found in the Ascophora, it also occurs rarely in the Anasca.

Key words : Bryozoans, Cheilostome, Izumi Group, Upper Cretaceous

Introduction

The Upper Cretaceous Izumi Group is distributed as a narrow belt about 300 km long stretching from the Izumi Mountains in the Kii Peninsula to Matsuyama City in the northwestern part of Shikoku Island (Matsumoto, 1954). In the Matsuyama area, some fossil localities of the Izumi Group yielding molluscan fossils such as *Inoceramus*, *Apiotrigonia*, *Steinmannella*, etc. are distributed. All of these fossils occur from the basal part of the group and indicate a Campanian age as defined by Tashiro *et al.* (1993).

The present bryozoan materials associated with many shell (bivalve) fragments were collected from an outcrop of the Yuyama basal conglomerate Member near Kuroya-ike (an artificial pond for agricultural use) located at Takanocho, eastern Matsuyama City (Figure 1). Some Upper Permian fusulines such as *Yabeina* and *Schwagerina* have been reported by Sada (1975) from the limestone pebbles of the conglomerate in the same locality, but we were unable to find any Paleozoic fossil remains.

The oldest calcified cheilostome reported from the Jurassic Period is morphologically simple and has an encrusting colony with uniserially budded autozooids. Rigidly erect colonies with higher states of integration are known from Late Cretaceous and Cenozoic deposits (Cheetham and Cook, 1983). Voigt (1964) established a genus *Dysnoetocella* based on the specimen from the Montian or Dano-Montian stage in Belgium and Poland. The type species, *D. aenigmatica*, has a rigidly erect, multilamellar growth habit. He

considered that this genus belongs to the Anasca, but further details of its systematic position are still obscure. He also compared the type species, *Dysnoetocella aenigmatica* Voigt, with an anascan *Conopeum ? damicornis* Canu and Bassler which has similar growth habit and zooid morphology.

In the present article, *Dysnoetocella ? voighti* sp. nov. is described, and its phylogenetic significance is discussed. This is the first descriptive report of Cretaceous bryozoan from Japan. Based on thin-section observations the fine skeletal structures are described in detail, although the original fine structures have been slightly damaged by diagenetic recrystallization and replacement (see Sandberg, 1975). The body cavities are completely filled with sparry calcite cement.

Systematic paleontology

Class Gymnolaemata Allman, 1856
Order Cheilostomata Busk, 1852
Suborder Anasca Levinsen, 1909
Genus *Dysnoetocella* Voigt, 1964

Type species.—*Dysnoetocella aenigmatica* Voigt, 1964

Generic diagnosis.—Zoarium dendroid, consisting of bilamellar axial zooecia and outer cumulating zooecia enveloping the axis. Axial zooecia large, slightly convex, with an oval aperture. Cumulating zooecia small, irregular and depressed. Ovicells and avicularia not observed.

Geological age.—Late Cretaceous (Campanian) ? to

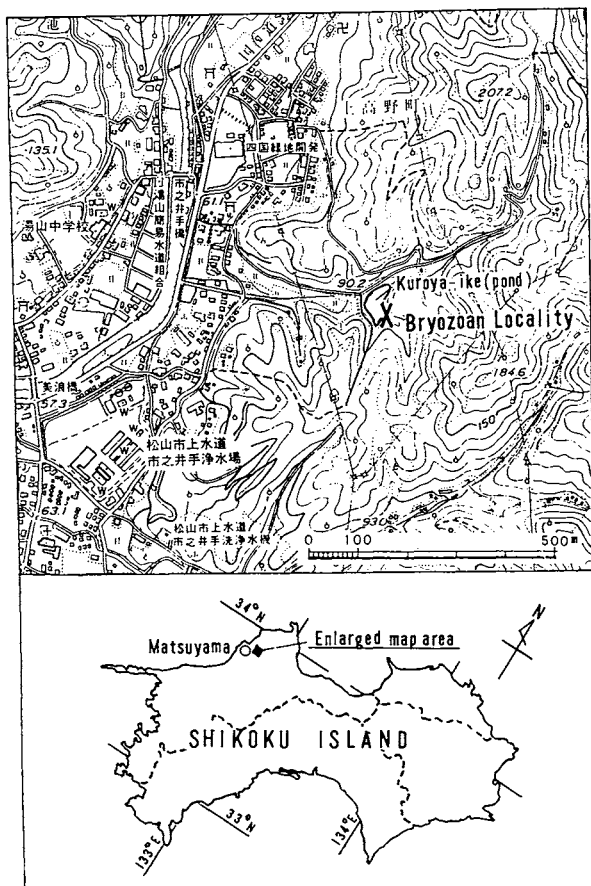


Figure 1. Localities map of bryozoan collections from the Izumi Group from "Matsuyama City" of the city planning map (scale: 1/10,000)

Early Tertiary (Montian or Dano-Montian).

Dysnoetocella? voighti sp. nov.

Figures 2-1—6, 3-1—10

Material.—Holotype: Reg. no. NSM-PA14018; Paratypes: Reg. nos. NSM-PA1401, NSM-PA14019, NSM-PA14020, NSM-PA14021, NSM-PA14022, NSM-PA14023, NSM-PA14024. All the specimens are stored in the Collections of National Science Museum (NSM) in Tokyo, Japan.

Description.—Zoarium erected without articulations, sub-cylindrical, branching dichotomously (Figures 2-1, 4), consisting of bilamellar zooecia which form a central axis and outer cumulating zooecia enveloping the axis. Each branch composed of two layers of back-to-back axial zooecia is initially flattened, and overgrown by approximately 20 zooid layers of cumulating zooecia at most, becoming subcylindrical and thick (Figures 2-2, 3). Bilamellar axial zooecia tubular, $0.34\text{--}0.49 \times 0.14\text{--}0.20$ mm in size; cryptocyst slightly convex, with a thickened superficial layer, extending one-quarter to one-third of the zooecial length from the proximal margin. Cumulating zooecia compressed, variable in size,

commonly $0.44\text{--}0.54 \times 0.26\text{--}0.32$ mm; cryptocyst narrow and flat, occupying about one-third of the front, with a thickened superficial layer. Ancestrula, ovicell and avicularia are absent.

Remarks.—The colony of *Dysnoetocella? voighti* is large. The branches measure about 50 mm in length and 6 mm in diameter. Thin sections show well preserved internal structures. Although colonies can not be observed from frontal view because of the consolidated conglomerate, the morphological features of the calcareous frontal shield are important in taxonomic studies of cheilostomes. The zooecia, which have interzoooidal communication organs in the lateral walls, demonstrate their cheilostomatous nature. Voigt (1964) considered that the genus *Dysnoetocella* belongs to the Anasca because of slight calcification of the frontal shield and the lack of an ascopore, and *Dysnoetocella? voighti* also lacks an ascopore. The encrusting base and ancestrula are not observed.

Occurrence and geological age.—The lowest horizon of the Yuyama conglomerate Member, which lies in the basal part of the Izumi Group. It is correlated to the Late Cretaceous Campanian age on the basis of the associated molluscan fossils (Tashiro *et al.*, 1993).

Fine structures of calcareous skeletal walls

The species produces two types of zooecia, namely, bilamellar axial and multilamellar outer zooecia. The branches are composed of 4 to 9 series of bilamellar axial zooecia initially (Figures 2-2, 3), and overgrown by multilamellar outer zooecia.

The axial zooecia, which are arranged in a brick-like pattern, are convex and slant distally upward (Figure 3-1). In longitudinal sections of the outer cumulating tissue (Figure 2-5), the multilamellar outer zooecia have a depressed box-shaped structure and differ in size. The total height of the zooecium is less than the axial one. The opecium is broad.

Dark-colored fibrous layer:—In transverse sections of the axial zooecia, dark-colored outermost skeletal layers of the basal and lateral walls are thin (about $20\text{ }\mu\text{m}$) and evenly distributed (Figure 3-5). The fine structure of the wall is fibrous, and resembles a planar spherulitic ultrastructure which lies against the cuticle and consists of acicular calcite needles (Sandberg, 1983). However, no arrangement of the calcite crystals in wedge- or fan-shaped arrays (Sandberg, 1983) is evident, because the exterior surface of the skeleton can not be observed in thin sections. There is a possibility of significant ultrastructural changes that are not visible by light microscopy (see Sandberg, 1975).

Wavy lamellar layer:—The dark-colored outermost skeletal layers of the basal and lateral walls are overlain by wavy lamellar layers composed of 4 to 9 lamellae (Figure 3-5). Lateral tracing of each lamella is difficult. The lamellar layers are generally thicker than the dark-colored outermost skeletal layers and continuous with the frontal and transverse walls. This fine structure is considered to be a lamellar ultrastructure (Cheetham *et al.*, 1969) composed of numerous, superimposed thin calcitic layers. As Sandberg (1971) pointed out, the lamination observed appears to be large-

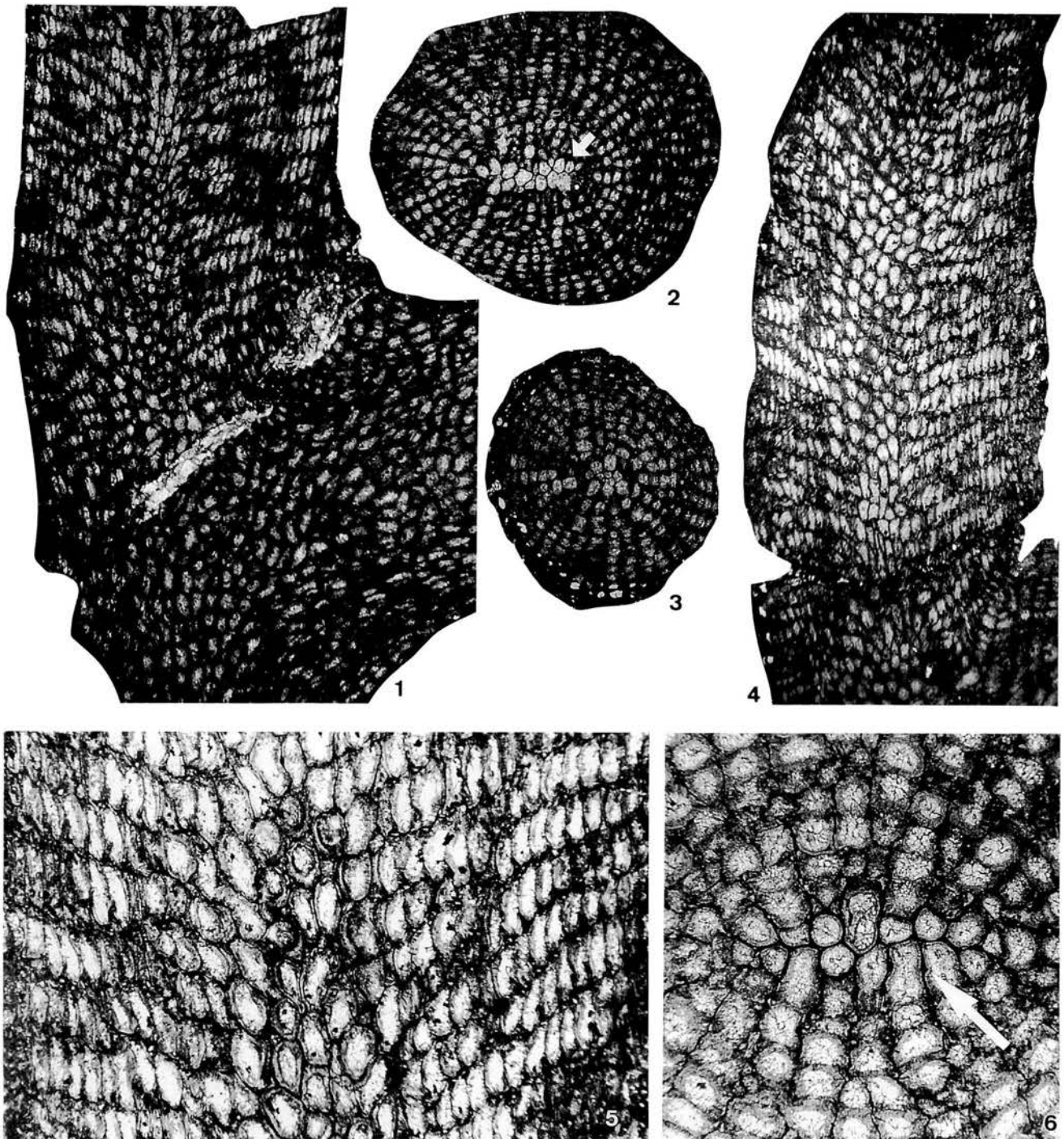
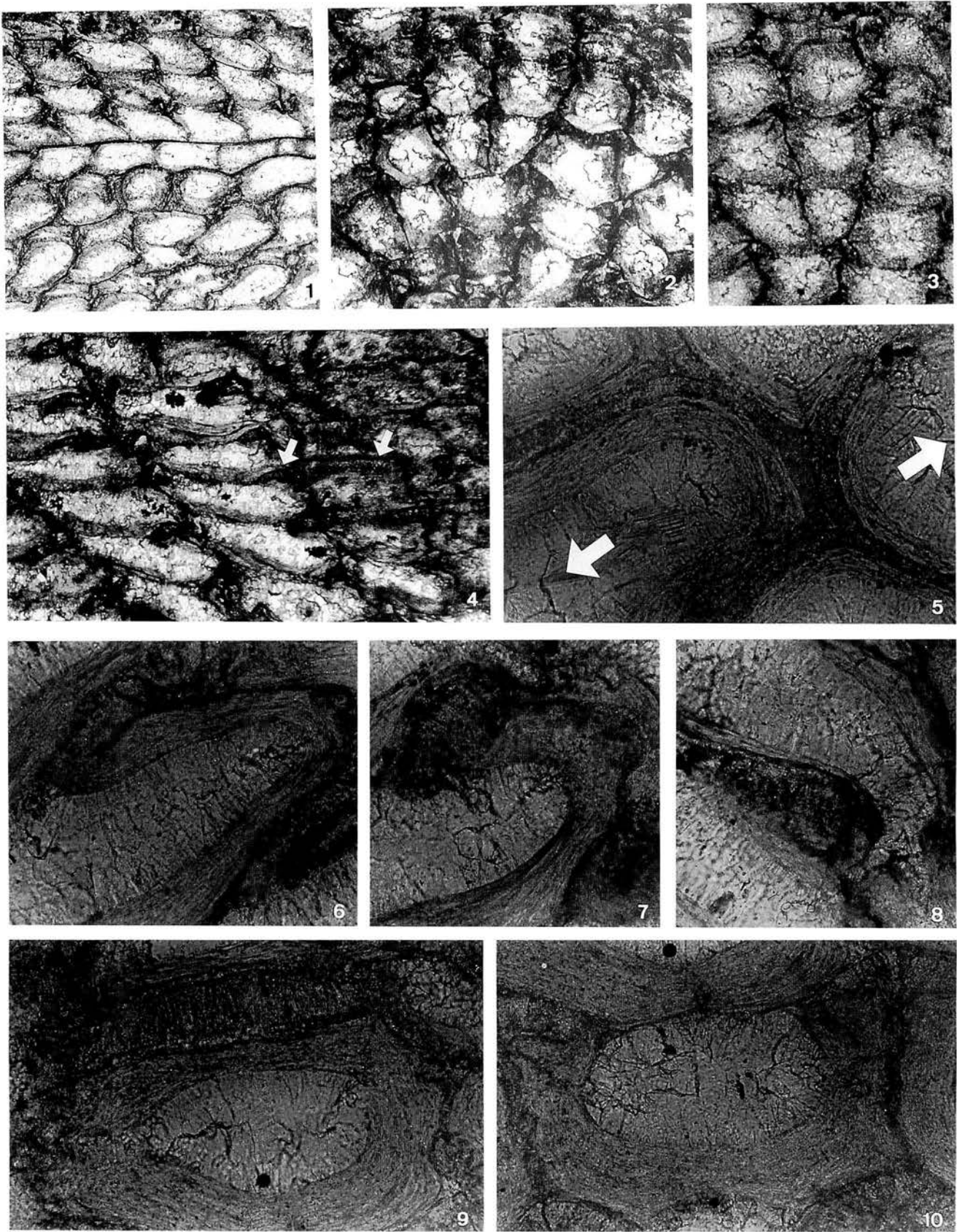


Figure 2. *Dysnoetocella? voighti* sp. nov. 1. Longitudinal section of branch, $\times 10$, NSM-PA14018. 2. Transverse section of branch, showing bilamellar axial zooecia (arrow), $\times 10$, NSM-PA14024. 3. Transverse section of branch, $\times 10$, NSM-PA14021. 4. Longitudinal section of branch, $\times 10$, NSM-PA14018. 5. Axial and cumulating zooecia, distal toward top, $\times 20$, NSM-PA14019. 6. Transverse section of branch, showing bilamellar axial zooecia and interzoooidal communication organs (arrow), $\times 30$, NSM-PA14022.

scale lamination, each composed of finer lamellae.

Fibrous superficial layer: —The frontal shield of the cumulating zoecium, which occupies one quarter to one

third of the total zooid length, is composed of two calcareous layers, the primary and superficial layers (Figure 3-4). The primary layer continuous with the lateral and transverse walls



is relatively thick, suggesting that calcareous deposition on the basal surface of the primary layer was not cut off by development of the ascus. The layer, which is smooth and laminated roughly parallel to the wall surface, has the same fine structure as the lamellar layers of the axial zooecia. There are also dark-colored thin skeletal layers between the lateral walls of adjacent zooecia (Figures 3-2, 3) like axial zooecia and between the transverse walls (Figure 3-4), but it appears that there are no dark-colored thin layers between the basal walls and the body cavities beneath, suggesting that the lateral and transverse walls are exterior and the basal walls interior.

The fibrous superficial layer that spreads over the primary layer and mural rim as a lamella, gradually thinning from the periphery to the center of the opesium, may begin exactly at the zooecial boundaries and spread distally (Figure 3-4). The fine structure of the fibrous superficial layer (Figures 3-7, 9) is somewhat similar to the conical bundles or clusters formed by acicular aragonitic crystals (see Sandberg, 1983). The calcification of the superficial layer is commonly heavy. This ontogenetic frontal thickening may occur after completion of the zooid. However, the time lag after which the superficial layer begins to develop on the upper surface of the primary layer is not known in *Dysnoetocella? voighti*, as Sandberg (1971) has pointed out that "the time lag between calcification of the primary calcitic frontal and the beginning of superficial aragonite formation is quite variable among species".

In some cases, pores piercing the two frontal calcareous layers are observed near the proximal margin (Figures 3-4, 8).

Phylogenetic consideration of *Dysnoetocella*

The multilamellar zooecia are commonly as large as the axial ones in *Dysnoetocella? voighti*, as in *Conopeum? damicornis* Canu and Bassler from the Paleocene Midway Group in North America, which has a similar growth habit. However, the multilamellar zooecia in *Dysnoetocella aenigmatica* and *D. foliacea* Voigt are much smaller than the axial ones (Voigt, 1964, 1967). The axial zooecia are taller than the cumulating zooecia in *Dysnoetocella? voighti*, as well as in *Dysnoetocella aenigmatica* and *D. foliacea*. In its growth form, *Dysnoetocella? voighti* resembles *Heteroconopeum janieresense* (Canu) from the Turonian age in France, but differs in its dimorphic zooecia like *D. aenigmatica* and has none of the small interopesia hollows that characterize the genera *Conopeum* and *Heteroconopeum* (Voigt, 1983).

In transverse section of axial zooecia, the lateral walls of the branch are breached to form interzooidal communication organs between adjacent axial zooecia (Figure 2-6). The

lineal series of subsequently budded axial zooecia is partitioned by small interior transverse walls. The outermost skeletal layers and bounding cuticles of the lateral and basal walls are presumably continuous from zooid to zooid within a lineal series (Figure 3-1).

There are three to five dark round spots in the lateral wall of a cumulating zooecium. They are calcareous protuberances and considered to be communication organs (Figure 3-4), through which the cumulating zooids communicate with zooids at the same depth in adjacent zooid columns. A longitudinal section of cumulating tissue shows that the transverse walls separated by the dark-colored thin layers (Figure 3-4) are double, and different from those of axial zooecia, suggesting that the transverse walls are formed in a different way from the latter. Unlike axial zooecia, the calcareous lateral and basal walls of the cumulating zooecia are not continuous with those of the distal and proximal zooecia at the same depth in the colony (Figure 3-1). Therefore, the transverse walls which form a double-walled structure with the intercalated cuticle layer like lateral walls are considered to be exterior. It is thus clear that the cumulating zooid does not bud from the proximal one at the same depth in the colony.

The basal wall of cumulating zooecia is commonly thick in the distal half, and becomes thinner proximally. Some longitudinal sections show that there is a pore at the proximal end of the wall, which sometimes connects with a corresponding pore in the frontal shield of the zooecium beneath it (Figure 3-8). The superficial layer wraps the pore, but does not extend down into it. Voigt (1964) stated that in *Dysnoetocella aenigmatica* "every zooecium contains a hole in the bottom, leading into the next lower zooecium". It is therefore reasonable to infer that the cumulating zooid erupts and buds through the pore frontally. Each new daughter zooid has the same polarity as its parent. On the other hand, Voigt (1964) mentioned that cumulating zooecia increase by "budding out from the apertures" in *Dysnoetocella aenigmatica*. The cuticle layer is considered to be continuous from the parent zooid to the frontally budded daughter, but the calcareous lateral and transverse walls are not continuous in *Dysnoetocella? voighti*. The daughter zooid does not use the frontal shield of the mother as a calcareous basal wall, but deposits the calcareous basal wall over the frontal shield. Although "distal" is "frontal" in frontally budded zooids, we will refer to directions in cumulating zooids as if they are axial zooids after the manner of Banta (1972).

Because thin sections show accretion of fibrous calcareous deposits on the frontal side of the frontal shield, and according to Cheetham and Cook (1983) "gymnocysts cease to be deposited relatively early in zooid life and characteristi-

Figure 3. *Dysnoetocella? voighti* sp. nov. 1. Longitudinal section, bilamellar axial zooecia, distal to left, $\times 30$, NSM-PA14020. 2. Transverse section, zooid column bifurcation and skeletal fine structures, $\times 60$, NSM-PA14024. 3. Transverse section, zooid column bifurcation and skeletal fine structures, $\times 60$, NSM-PA14022. 4. Longitudinal section, distal to left, showing fibrous superficial layers (arrows), $\times 60$, NSM-PA14019. 5. Transverse section of bilamellar axial zooecia, showing dark-colored outermost and wavy lamellar skeletal layers; arrows indicate frontal direction, $\times 250$, NSM-PA14022. 6. Longitudinal section, distal to left, cryptocyst, $\times 250$, NSM-PA14019. 7. Longitudinal section, distal to left, fibrous superficial layer, $\times 250$, NSM-PA14019. 8. Longitudinal section, distal to left, $\times 250$, NSM-PA14018. 9, 10. Transverse sections of cumulating zooecia, wavy lamellar and fibrous superficial layer, $\times 250$, NSM-PA14022.

cally remain relatively thin", the shield may not be a gymnocyst but a cryptocyst or an umbonuloid shield. Because the primary layer of the frontal shield has no dark-colored thin layer and resembles the cryptocysts of *Labioporella calypsonis* Cook and *Membranipora grandicella* (Canu and Bassler) (see Sandberg, 1983, Fig. 116; Sandberg, 1973, Fig. 13) in having lamellar layers around the distal end of the cryptocyst, the frontal shields are considered to be interior cryptocysts. Although thin sections demonstrate that the walls have neither condyles, characteristic of ascophoran cryptocystideans, nor opesiules through which the parietal muscles pass, characteristic of some anascan cryptocystideans, the species is considered to be an anascan cryptocystidean because of the narrow cryptocysts and development of the primary layers of the frontal shield.

The process of frontal budding of a cryptocystidean ascophoran species, *Schizoporella unicornis floridana* Osburn, was investigated in detail by Banta (1972). He observed that frontal budding is accomplished by swelling of the hyostegal coelom, and that the cryptocystal frontal wall of the mother zooid is the basal wall of the daughter. The cumulating zooids in *Dysnoetocella? voighti* are considered to have budded frontally through the uncalcified pores at the proximal end of the basal wall. In comparison with a cryptocystidean ascophoran *Schizoporella unicornis floridana* (Banta, 1972), the vertical walls of the daughter are not continuous with that of the parent, and the daughter deposits a new interior basal wall on the frontal shield of the mother.

As the frontal budding proceeds, radial zooid columns separated by an intercalated cuticle develop. Commonly in most anascan multilamellar colonies, the zooids are overgrown by subsequent zooid layers (Nishizawa, 1985) and do not produce zooid columns.

According to Cheetham and Cook (1983) and Gordon and Voigt (1996), some anascans and ascophorans known from Late Cretaceous and Cenozoic deposits exhibit a variety of growth habits, complex frontal structures and colonial integration. The cryptocystidean anascan *Dysnoetocella? voighti* is a complex anascan and similar to cryptocystidean ascophorans in frontal budding and ontogenetic thickening of the frontal shield.

What is the significance of frontal budding? As Banta (1972) has pointed out, it does not result in increasing the number of zooids, because a daughter zooid buds from the mother except for the bifurcation of the zooid column, and the mother is buried under the daughter. However, the frontal budding of erect rigid colonies of *Dysnoetocella? voighti* may increase the degree of structural support. The heavy ontogenetic thickening may indicate that frontal budding does not occur as soon as the cumulating daughter zooids are completed. Rigidly erect cheilostome colonies have a tendency to inhabit relatively deep sea areas with a low rate of sedimentation, little wave action and weak current, and the number of species decreases with increased depth (see Schopf, 1969). The Yuyama conglomerate Member contains only this species and no fragments of encrusting cheilostome colonies. Thus *Dysnoetocella? voighti* is considered to have lived on a calm ocean floor using gravel and shells as substrates. In *Dysnoetocella? voighti*

colonies, replacement of old zooids may have been preferable to rapidly increasing the number of zooids in such a stable environment after deposition of the basal conglomerate, because most of the colony fragments are thickly developed branches, and no early bilamellar branches are found.

As frontal budding proceeds, the colony forms zooid columns separated by cuticles. In the zooid column, each zooecium is broader than the one beneath it. If the width is excessive, the mother zooid gives rise to two daughters and the zooid column bifurcates.

Although the daughter zooids which bud from the axial zooid are as large as those which bud from the cumulating zooids in *Dysnoetocella? voighti*, the axial zooids produce many small cumulating zooids in *Dysnoetocella aenigmatica* and *D. foliacea*. The daughter zooecia at the point of bifurcation are narrow and distorted. There is an irregularly shaped dwarfed zooecium at the point of bifurcation in some cases. The zooecium is not considered to be an avicularium because of its inconsistent size and shape. Mostly one daughter is smaller than the other. The new column appears to arise by intercalation (Figures 3-2, 3) or bifurcation (Figure 3-2). In any event, the vertical walls between two daughters have a double-walled structure, and the mode of bifurcation is entirely different from that in *Schizoporella unicornis floridana*, separated by a single vertical wall (Banta, 1972).

Banta (1972) saw that "zooids overgrown by their own frontal buds soon undergo degeneration and brown body formation" in living specimens of *Schizoporella unicornis floridana*. The parent zooid of *Dysnoetocella? voighti* may have degenerated and formed brown bodies as well as *S. unicornis floridana*, though the parent zooid communicated with its daughter through the pores piercing the frontal shield. A dark and irregularly spherical spot is frequent in the zooecium. Perhaps these spots are altered brown bodies (Figure 2-5).

Summary

1. A new anascan cryptocystidean species, *Dysnoetocella? voighti*, is described from the Izumi Group in the northwestern part of Shikoku Island, Japan. This is the first Cretaceous bryozoan described from Japan. The rigidly erect colony shows high states of colonial integration.

2. The zooids communicate with lateral, distal and proximal zooids through interzooidal communication organs, demonstrating their cheilostomatous nature. Frontally budded daughter zooids also communicate with their mother through pores piercing the basal wall.

3. Although there is a possibility of diagenetic alteration, three types of fine structure of the calcareous skeletal layers are recognized in thin sections; a dark-colored fibrous structure in the outermost skeletal layers, a wavy lamellar structure in the lateral, basal and transverse walls and the primary layer of the cryptocyst, and a fibrous structure in the superficial layer of the cryptocyst. These structures are similar to some microstructures described in recent and fossil specimens.

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