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Article

Azooxanthellate colonial corals from the Miocene Omori Formation, Shimane, Japan

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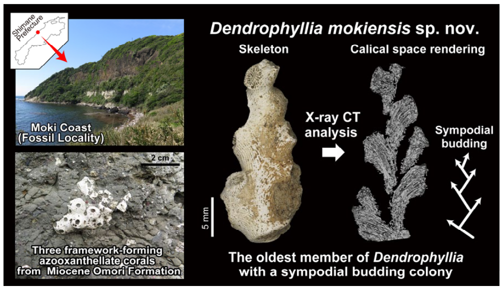
ABSTRACT

Azooxanthellate colonial corals are important habitat-formers in deep-water ecosystems. Here, we provide detailed descriptions of three framework-forming azooxanthellate corals (*Petrophyllia niimiensis*, *Dendrophyllia okamotoi* and *Dendrophyllia mokiensis* sp. nov.) from the Miocene Omori Formation on the Moki coast in Oda, Shimane, Japan using microfocus X-ray computed tomography. With an estimated age of 17.65–13.60 Ma based on nannofossils, *Dendrophyllia mokiensis* sp. nov. represents the oldest member of *Dendrophyllia* with a sympodial budding colony. Moreover, this is the first report of the co-occurrence of *Petrophyllia* and *Dendrophyllia* in a high density fossil assemblage. *Petrophyllia* has been reported as a framework builder in cold-water coral reefs or a member of dense accumulations of azooxanthellate corals during the Turonian (Late Cretaceous), thereby raising the possibility that an azooxanthellate coral community dominated by *Petrophyllia* also existed in the Miocene. This discovery sheds light on changes in azooxanthellate coral communities in deep-water coral habitats during the Cenozoic.



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Keywords: *Dendrophyllia*, Microfocus X-ray CT, *Petrophyllia*, Scleractinia, Taxonomy

Introduction

Approximately 50% of the 1698 known extant scleractinian species are azooxanthellates, most of which are regarded as deep-water taxa (Cairns, 2007; Hoeksema and Cairns, 2024). Although fossil azooxanthellate scleractinian corals have been reported from Japan (e.g. Makiyama, 1926; Yabe and Eguchi, 1932, 1942a, 1942b, 1944; Eguchi, 1944; Niko *et al.*, 2015, 2016, 2017), only six species have been described from Miocene strata (Eguchi, 1944; Yabe and Eguchi, 1944; Niko *et al.*, 2015, 2016, 2017). Hayashi *et al.* (2015) reported the occurrence of scleractinian corals from the Miocene Omori Formation on the Moki coast in Oda, Shimane, Japan. A detailed description of the coral assemblage of the Omori Formation has potential to provide valuable insights into the poorly studied Miocene scleractinian corals of the Northwest Pacific region. However, the taxonomic details, diversity, and distribution of these corals have remained undescribed.

The calical parts of corals, including the inter-septal and columellate spaces, possess characteristics that are

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useful for taxonomic study, but these are typically filled with sediment in fossil specimens. In addition, fossil corals are easily damaged and fragmented during preparation for analysis; therefore, morphological analyses are generally performed by means of serial thin sections (e.g. Stolarski, 1996). However, this method tends to lose three-dimensional information of the skeletal morphology. Recently, fossil and extant corals have been analyzed using computed tomography to understand both the inner and outer structures (e.g. Zapalski and Dohnalik, 2013; Sentoku *et al*., 2015a, 2015b). Here, we utilize microfocus X-ray computed tomography to describe three colonial scleractinian coral species from the Miocene Omori Formation on the Moki coast, one of which is a new species. We also elucidate the paleoenvironmental setting in which these Miocene azooxanthellate corals thrived. The study of these fossils provides an opportunity to clarify the evolution of colonial azooxanthellate corals and the transition of azooxanthellate coral communities in deep-water coral habitats during the Cenozoic.

Geologic setting

The specimens described here were collected from the Miocene Omori Formation on the Moki coast in Isotake, Oda, Shimane, Japan (Figure 1). The Omori Formation unconformably overlies the Kuri Formation and in the Oda area is composed mainly of conglomerates and pyroclastic rocks (Sawada and Yamauchi, 2009). On the Moki coast, andesitic volcanic breccia, chaotic rocks with andesite and mudstone blocks (~12 m thick), grayish-white tuffaceous sandstone (~16 m thick), and andesite lava (>15 m thick) are exposed. The chaotic rock unit is characterized by non-layered bodies consisting of siltstone boulders (maximum 4 m diameter) within a poorly sorted silty to pebbly matrix that contains andesite and pumice cobbles (maximum clast diameter 20 cm), coral fragments (maximum 15 cm wide), and mollusks (Hayashi *et al*., 2023). There is a sharp boundary between the lower andesitic volcanic breccia and the chaotic rock unit. Hayashi *et al*. (2015) inferred that the chaotic rock unit was formed by a submarine landslide triggered by a volcanic eruption, which led to the deposition of the lower andesitic volcanic breccia. The age of the chaotic rock unit was estimated to be *ca.* 11–12 Ma based on the co-occurrence of the foraminifera *Globorotalia quinifaicata*, *G. rikuchuensis*, and *Neogloboquadrina pseudopachyderma* in siltstone blocks within the chaotic rock unit (Hayashi *et al*., 2015). However, Hayashi *et al*. (2023) concluded that the Omori Formation was deposited at 17.65–13.60 Ma based on nannofossils (Zone CN3 to CN4 in Okada and Bukry, 1980), indicating the possibility of diachroneity of foraminiferal faunal events between lower and higher latitudes in Japan.

Material and methods

Coral fragments and fractured cobbles (up to 20 cm long) are scattered throughout the chaotic rock unit. The exposure consists of a continuous outcrop that is ~15 m long, 6 m high, and oriented NW-SE (Figure 1C–E). More than 200 colonial coral specimens were randomly collected from the outcrop. Almost all coralla show no conspicuous bioerosion. We estimated the density of coralla by counting the number of coralla in randomly selected 30 cm × 30 cm quadrats. The mean density of corals within the matrix was 0.35 coralla/cm^2 (n = 5). Macroskeletal features were observed using a stereomicroscope (Leica M165FC, Germany) and a digital microscope (Keyence VHX-7000, Japan). Thirty well-preserved coralla were photographed at various angles and magnifications for documentation. Measurements were performed using Adobe Photoshop CC (Adobe Inc., USA), ImageJ Fiji (NIH, USA; Schindelin *et al*., 2012), and electronic calipers. We scanned of 21 well-preserved fossil coralla selected from the photographed specimens using a microfocus X-ray computed tomography (CT) system (inspeXio SMX-225CT, SHIMADZU, Japan) at the Tottori Institute of Industrial Technology in Tottori, Japan for structural analysis. The spatial resolution of CT images is determined principally by the size and number of detector elements, the size of the X-ray focal spot, and the source object–detector distance. We achieved an isotropic voxel resolution of 6 µm with a focal spot size of 4 µm and a source-to-detector distance of 800 mm. Each specimen was placed in a 25- or 50-mL polypropylene centrifuge microtube (VIO-25B, VIO-50BN, VIOLAMO, Japan) and secured in the middle using melamine foam (Gekiochikun: LEC, Inc., Japan). The capped tube was then fixed on the stage using curing tape. The specimens were scanned using the microfocal subsystem with X-ray settings of 80–100 kV and 40 µA. The major axes of the specimens were carefully aligned with the rotational axis of the sample stage. During each scan, a series of 1024 × 1024 or 2048 × 2048 pixel grayscale images were captured, representing cross-sectional views of the specimen perpendicular to the rotational axis.

CT image data were processed and analyzed using Slice software (Nakano *et al*., 2006) via Cygwin software on Windows 10 OS, ImageJ Fiji, Adobe Photoshop CC, and 3D Slicer (Fedorov *et al*., 2012). Discrimination between sediment filling the calice and the skeleton was not accurately achieved, so we extracted the skeletal structure by manually selecting and removing sediments within the CT images using the Polygonal Lasso tool in Photoshop CC. Because of the difficulty in distinguish-

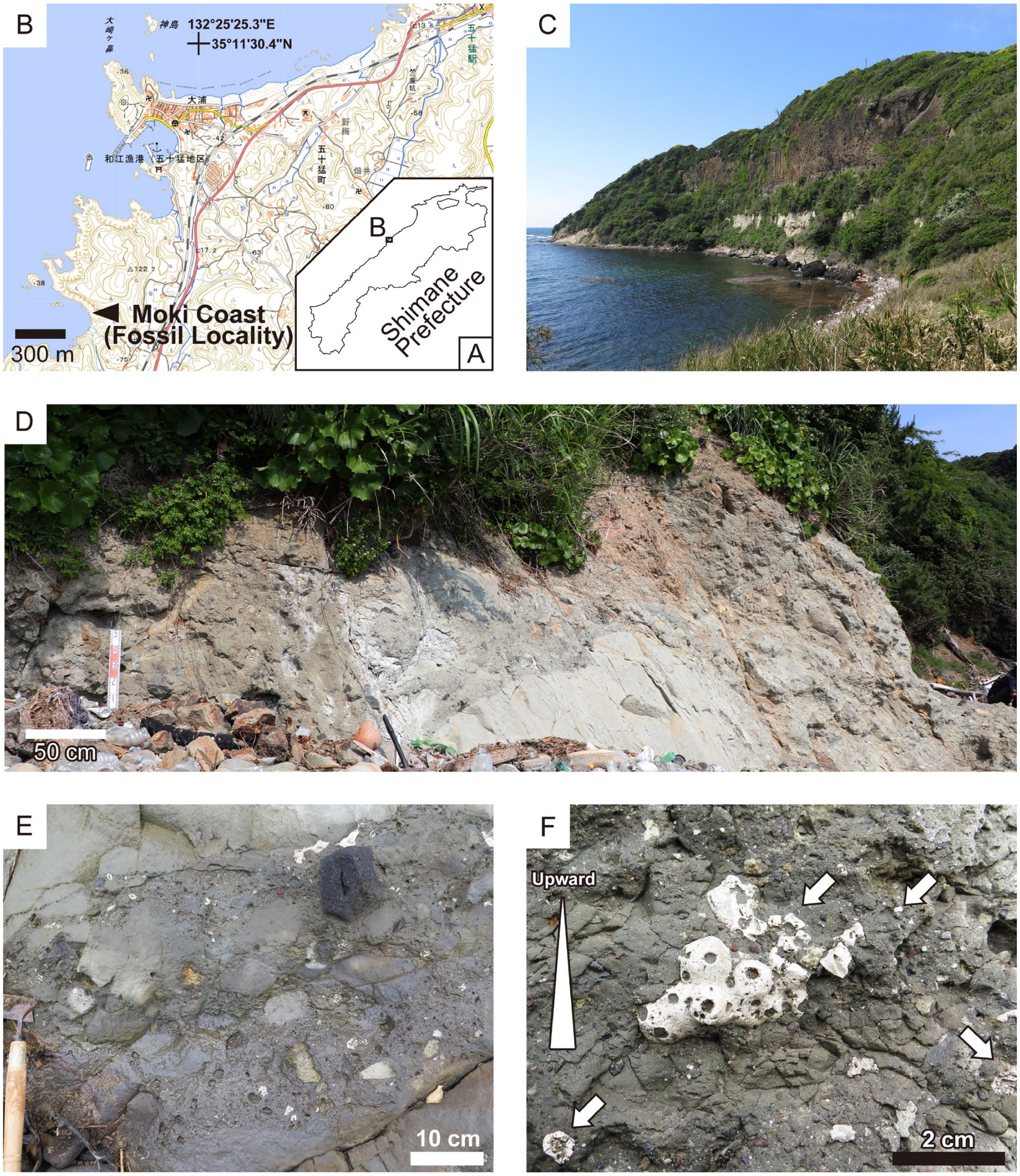

Figure 1. Map and field photographs of the study area. **A**, **B**, location of the fossil locality on the Moki coast in Shimane, Japan. The base map is from the "Oura" 1:25,000 topographic map published by the Geospatial Information Authority of Japan. **C**, panoramic view of the outcrop on the Moki coast. **D**, part of the outcrop of the chaotic rock unit that contains colonial corals. **E**, close-up view of the chaotic rock unit. A siltstone block (upper part of the photo) is visible within a poorly sorted silty to pebbly matrix containing andesite and pumice breccia, and corals. **F**, vertical section of the matrix containing corals (white arrows).

ing the budding patterns of the colony from consecutive cross-sectional images, we used Adobe Photoshop CC to selectively retain only the voids within the calice (calical cavity), removing both the coenosteum and skeletal elements. In the consecutive cross-sectional images of the sample where skeletal parts needed to be removed, we opened a cross-sectional image of the middle part of the specimen in Adobe Photoshop CC and used the Magic Wand tool to select the background. If the selection was incomplete, the tolerance of the magic wand tool was adjusted until the appropriate range was selected. Once the selection was satisfactory, the background part was removed by using the Cut command. Then, binary conversion was applied to the image via the Threshold command, producing an image with the background and coenosteum in white and the calical cavity in black. Subsequently, the image was inverted so that the background and coenosteum were shown in black and the calical cavity in white. This series of steps was saved as a new action within Adobe Photoshop CC and applied to all the other consecutive cross-sectional images. When using automated selection, outline areas located at the boundary between the coenosteum and the background were occasionally not selected, resulting in them remaining as white residues resembling outlines during binarization. In such cases, we initially performed binarization to eliminate the ambiguous areas between the coenosteum and the background and then conducted automatic selection to extract the calical cavity. In images where the calical cavity was completely surrounded by the coenosteum, this process resulted in the retention of only the calical cavity and minimal noise. However, when the calical cavity was contiguous with the background, binarization led to assimilation between the spaces and the background, preventing the extraction of only the calical cavity. In such cases, we first filled the background with white and then performed binarization.

The holotype and paratypes of *Dendrophyllia mokiensis* sp. nov. were numbered with the prefix SNMS-F and stored at the Shimane Nature Museum of Mt. Sanbe in Oda, Shimane, Japan.

Systematic paleontology

by Y. Tokuda, N. Yamada, H. Endo, A. Sentoku and Y. Ezaki

Order Scleractinia Bourne, 1900
Family Oculinidae Gray, 1847
Genus *Petrophyllia* Conrad, 1855
Petrophyllia niimiensis Niko, Suzuki and Taguchi, 2017

Figures 2 and 3

Petrophyllia niimiensis Niko, Suzuki and Taguchi, 2017, pl. 3, figs. 1–9.

Description.—Coralla are arborescent with robust branches, often forming subflabellate colonies (Figure 2A). Basal stems of coralla are a maximum of 2.5 cm in diameter. Coenosteum on branches is dense, almost smooth, with a porcelaneous surface and faintly developed costae. In transverse section of the proximal branch, the coenosteum is up to 4 mm thick around the axial corallite. The branches are fused with each other, especially in the proximal part of the corallum (Figure 2A). Some specimens have galleries of approximately 0.4 mm diameter in the coenosteum. Bryozoans are rarely encrusted on the surface of coenosteum. Individual corallites are widely spaced on the surface of branches (Figure 2A–C). The calical rims of each corallite are typically ridged in the distal parts of branches but not in the proximal parts (Figure 2C).

The CT image of the longitudinal section of one branch shows an axial corallite through the center of the branch (Figure 2C). The greater calicular diameter (GCD *sensu* Cairns, 1989, 1994) of axial corallites is 3.8–5.6 mm (mean ± SE = 4.63 ± 0.3 mm, n = 5). A new branch is formed by monopodial lateral budding of a daughter axial corallite from the parent axial corallite (Figure 2A, B). All lateral corallites arise from the axial corallite by lateral extra-tentacular budding (Figure 2B, D). The inclination of 21 lateral corallites from the four colonies (i.e., the smaller angle between the growth direction of the lateral corallites and a horizontal line oriented perpendicular to the maximum growth direction of the axial corallite) is 68.3° ± 1.5° (mean ± SE). The budding of lateral corallites periodically occurs on a specific horizontal plane of the axial corallite. Three lateral corallites simultaneously originate from the axial corallite on a horizontal plane at regular intervals of approximately 120° (Figure 2E, F). The budding sites are each rotated by approximately 60° on the axial corallite relative to the previous budding sites on the lower budding plane (Figure 2D–F). The greater calicular diameter of lateral corallites is 2.9–3.4 mm (mean ± SE = 3.12 ± 0.5 mm, n = 11).

The septa of the axial corallites are hexamerally arranged in four cycles, but the last is incomplete (up to 31 total septa; Figure 3A). The septa are not vertically exerted from the calical rim. Almost all the septa of the axial corallites are short (maximum 0.4 mm) in transverse section (Figures 2E, 3A), but its first- and second-order septa (S1 and S2, respectively) extend to the center of the calice only on tabular endothecal dissepiment parts (Figures 2F, 3F, G). Septal edges are smoothly curved toward the dissepiments (Figure 3F, G). The longer septa are weakly fused with each other in the center of the calice without forming a columella (Figures 2F, 3F). The third-order septa (S3) are very short (maximum 0.12 mm) in transverse section. The fossa is deep and vacuous (Figure 2C, E). Pali and paliform lobes are absent.

The septa of the lateral corallites show a hexameral arrangement in two complete cycles (12 total septa; Figure 3B). S1 and S2 are elongated to the center of the calice and are fused with a rudimentary columella. Pali are absent (Figure 3B, C). The third-order septa are very short and rudimentary. Thin, tabular endothecal dissepi-

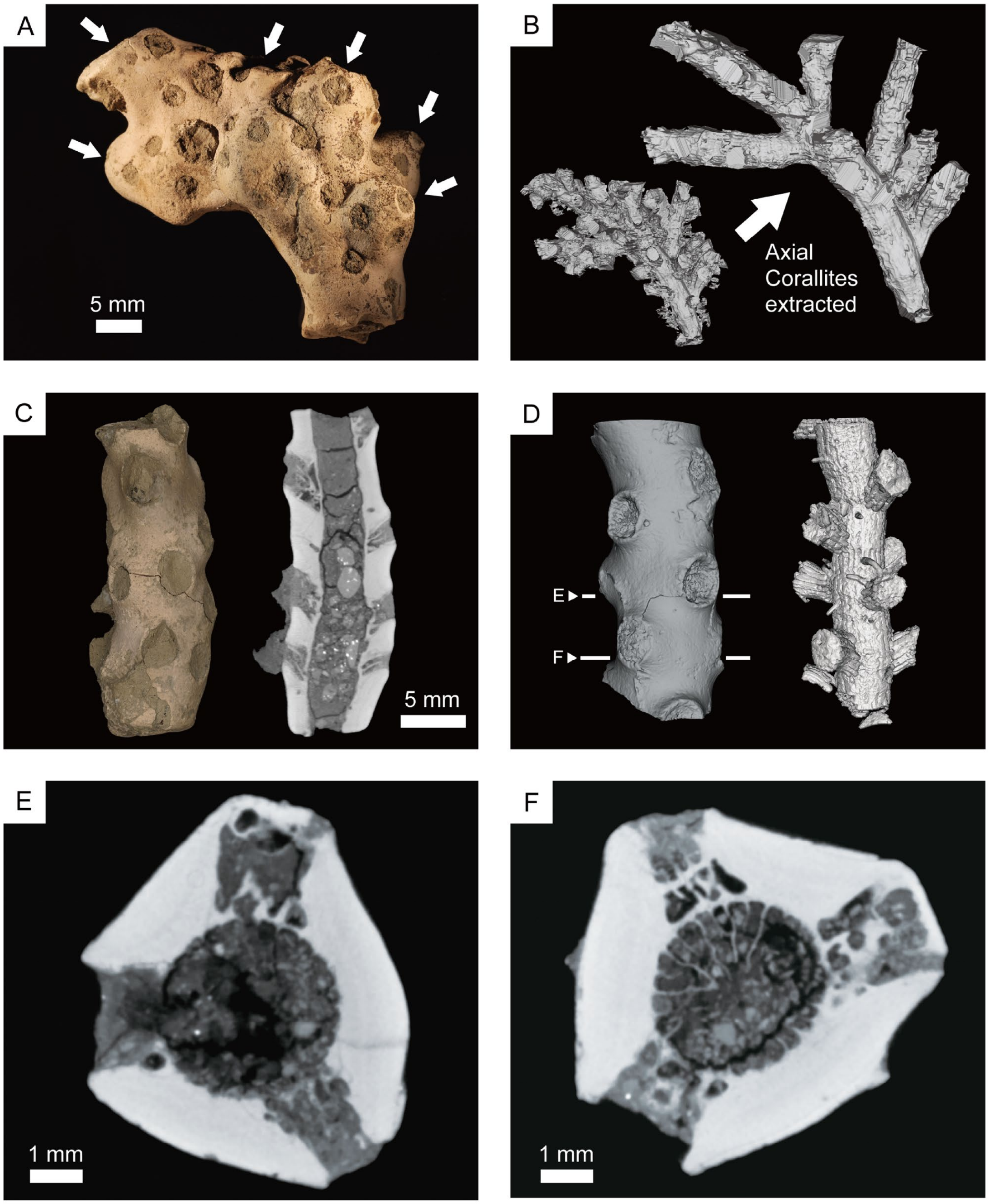

Figure 2. Morphology of *Petrophyllia niimiensis*. **A**, side view of a proximal part of corallum. White arrows indicate axial corallites. **B**, side views of the 3D reconstruction of the corallum without the coenosteum skeletons of A, showing all corallites (lower left) and only axial corallites (upper right). Axial corallites arise from previous generations of axial corallites. **C**, side view of a branch and a longitudinal section of the branch. **D**, side views of the branch of the 3D reconstruction of X-ray CT images. Surface rendering image of the corallum (left) and the corallum without the coenosteum skeletons (right). **E**, **F**, transverse sections of the corallum corresponding to the positions marked in D.

ments, which are perpendicular to the maximum growth direction of the corallite, are occasionally formed in both axial and lateral corallites (Figure 3D–F).

Discussion.—In the specimens described here, three lateral corallites simultaneously bud from an axial corallite on a horizontal plane at regular intervals of approximately 120°. Similar budding is also recognized in the extant *P. rediviva* (Wells and Alderslade, 1979, fig. 2d).

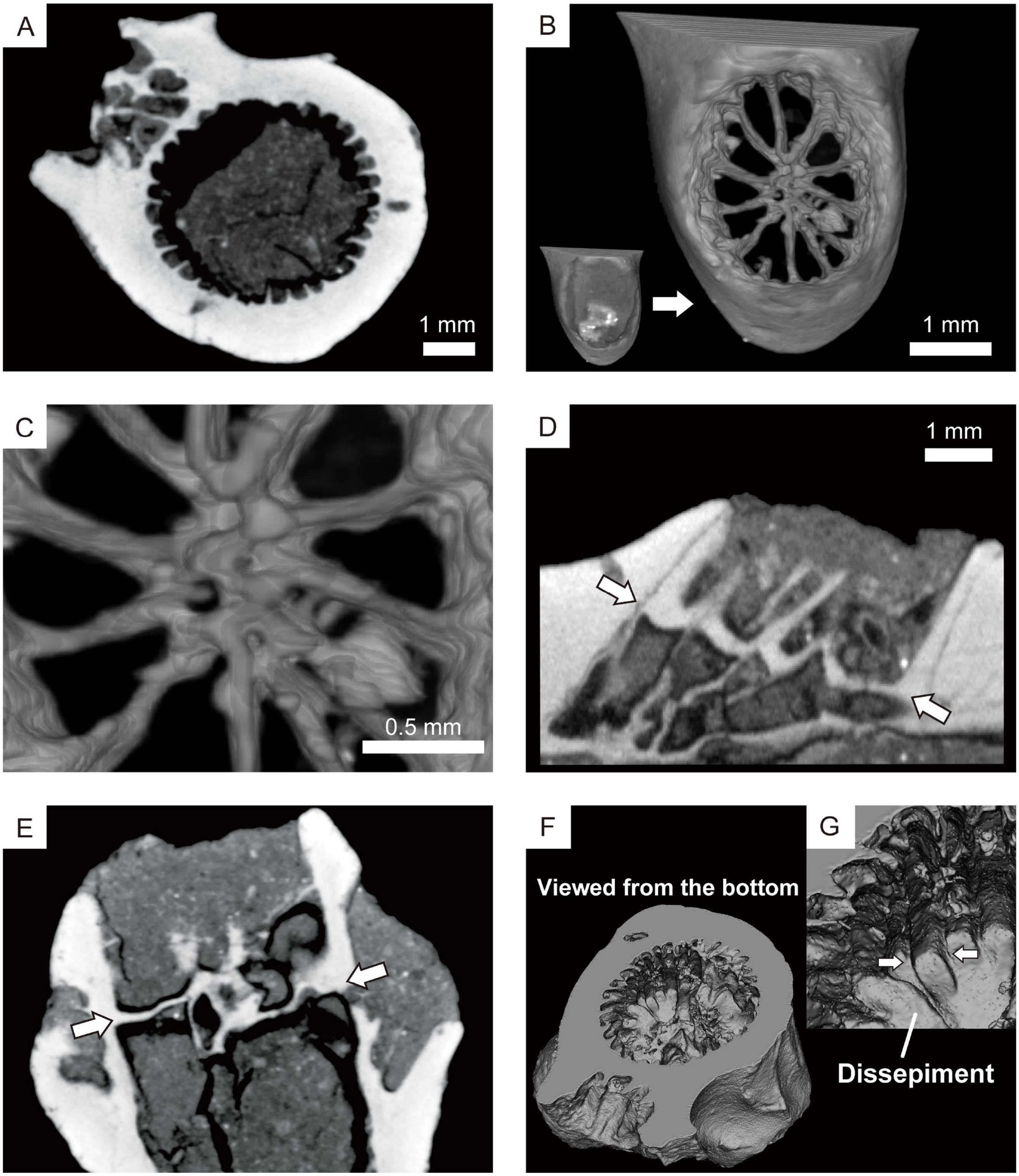

Figure 3. Morphology of corallites of *Petrophyllia niimiensis*. **A**, transverse section of an axial corallite. **B**, calical view of a lateral corallite. The skeletal structures were extracted from the sediment-filled calice (lower left) by using X-ray computed tomography. **C**, enlarged view of the center of the calice in B. **D**, dissepiments (white arrows) of a lateral corallite. **E**, dissepiments (white arrows) of an axial corallite. **F**, 3D reconstruction of the dissepiments in E viewed from the bottom. **G**, enlarged septa and dissepiments in F. Septal edges are smoothly curved toward the dissepiments (white arrows).

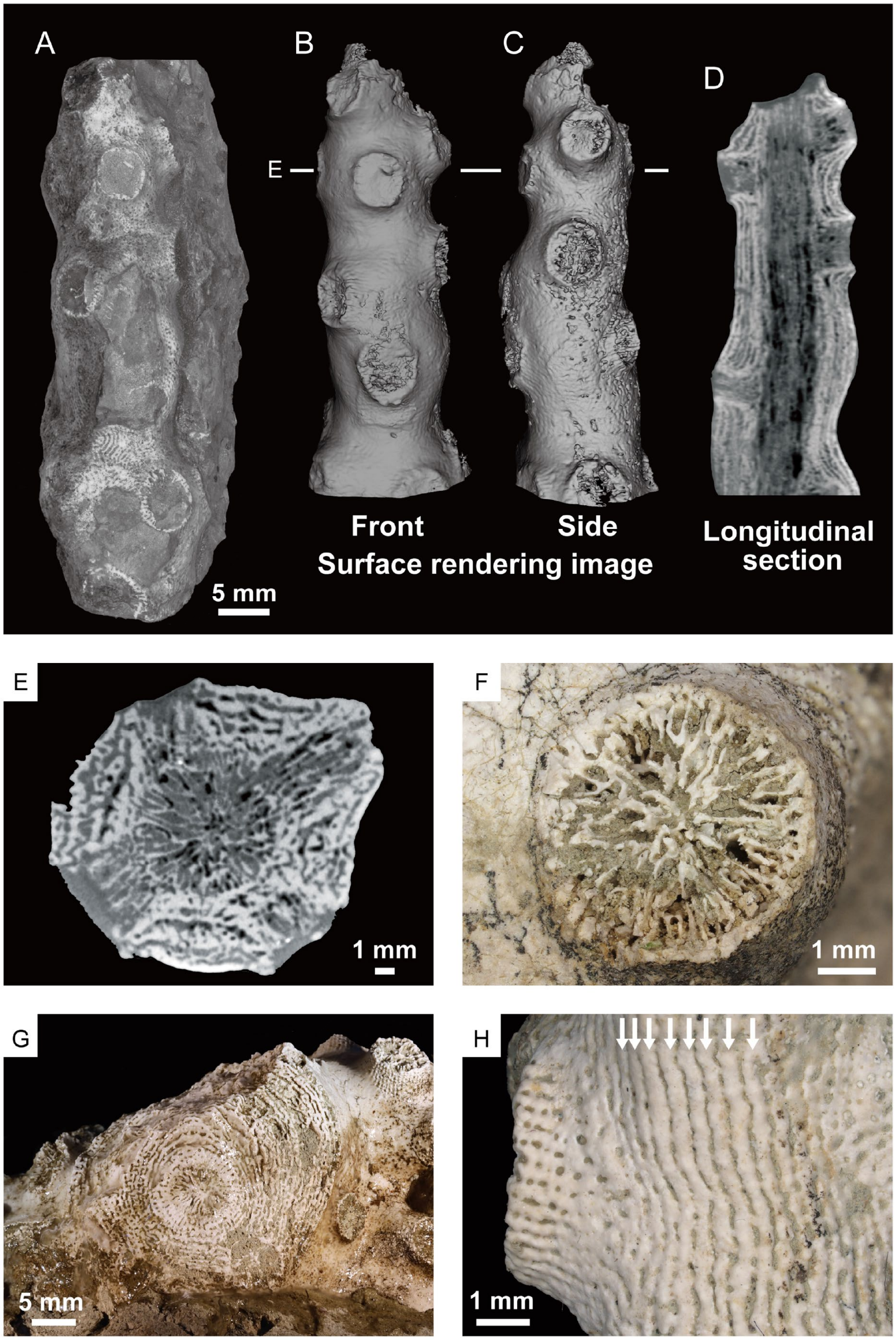

Figure 4. Morphology of *Dendrophyllia okamotoi*. **A**, side view of a branch; **B**, **C**, surface rendering images of the 3D reconstruction of the branches; **D**, longitudinal section of the branch; **E**, transverse sections of the corallum corresponding to the positions marked in B and C; **F**, calice of a lateral corallite; **G**, thick coenosteum and an axial corallite of the proximal part of the corallum; **H**, costae (white arrows) on the corallum surface of the distal part of a branch with a lateral corallite.

The mode of budding could be an important taxonomic characteristic of the genus *Petrophyllia*.

Petrophyllia arkansensis, the type species of this genus, shows pali before the S1 and S2 septa (Cairns, 2001). The extant species *P. rediviva* shows paliform lobes before the S1 septa (Wells and Alderslade, 1979); however, *P. niimiensis* does not possess pali or paliform lobes. As the holotype of *Petrophyllia arkansensis* shows distinct pali before S1 and S2, the taxonomic position of *P. niimiensis* should be reexamined, at least at the genus level.

The holotype of *P. niimiensis* was collected from the Bihoku Group (Middle Miocene: Langhian) of Niimi, Okayama, Japan (Niko *et al*., 2017). The age of that site is almost identical to that of the fossil locality of this study (17.65–13.60 Ma based on nannofossils: Hayashi *et al*., 2023).

Family Dendrophylliidae Gray, 1847

Dendrophyllia okamotoi Niko, Suzuki and Taguchi, 2015

Figure 4

Dendrophyllia okamotoi Niko, Suzuki and Taguchi, 2015, pl. 2, figs. 1–7, pl. 3, figs. 1–7.

Description.—Large colonies are arborescent with stout, basal stems (maximum 35 mm diameter) with robust branches (Figure 4A–C). Axial corallites are relatively straight (Figure 4D). Short lateral corallites (3.2–6.1 mm high) bud extratentacularly at the growth tip of the axial corallite (Figure 4A–D). The mean inclination of the lateral corallites, defined as the angle between the growth direction of the lateral corallites and a horizontal line oriented perpendicular to the growth direction of the axial corallite, is 10.3° ± 8.6° (n = 7). The GCD of the axial and lateral corallites is 7.7–8.4 and 6.2–6.9 mm, respectively (Figure 4E, F). Thick coenosteum is developed between individual corallites. In transverse section, the coenosteum shows nearly concentric growth lines with pores derived from synapticulotheca (Figure 4G). The lateral corallites simultaneously bud around the axial corallite (Figure 4D, E). Costae of axial corallites are well developed, especially in growth tips of coralla (Figure 4H). The costae are 0.39–0.46 mm wide, separated by narrow intercostal striae (0.07–0.15 mm). Costae on lateral corallites (0.20–0.27 mm wide) are connected by horizontal bars, leading to highly porous inner spaces (Figure 4H). The pores are 0.12–0.21 mm in diameter. The outer wall surfaces are not covered with epitheca, but the lower part of the coralla has smoother surfaces of the coenosteum. Septa are hexamerally arranged in four cycles (48 septa) in a Pourtalès Plan. Each pair of S4 fuses before their adjacent S3. Fossae of lateral corallites show moderate depth and contain small, spongy columellae.

Discussion.—*Dendrophyllia okamotoi* belongs to Group 1 *sensu* Cairns (1994, 2001): tall arborescent colonies, often flabellate, with several larger axial corallites. Two species of *Dendrophyllia*, *Dendrophyllia koiwaii* Yabe and Eguchi, 1944 and *D. okamotoi* Niko *et al*., 2015, have been described from Miocene strata in Japan. *Dendrophyllia okamotoi* is distinguished from *D. koiwaii* by its larger GCD (6.2–8.4 mm vs. 3–4 mm) and larger number of septa (48 vs. 32).

Dendrophyllia mokiensis Tokuda, Yamada, Endo, Sentoku and Ezaki, sp. nov.

[New Japanese name: Mōki-Kisango]

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Figures 5 and 6

Etymology.—The new species name *mokiensis* is derived from the Moki coast, the type locality.

Type specimens.—Holotype, SNMS-F-1553; Paratypes, SNMS-F-1554, SNMS-F-1555.

Type locality.—The holotype was collected from a poorly sorted silty to pebbly matrix of the chaotic rock unit of the Miocene Omori Formation on the Moki coast in Oda, Shimane, Japan (35°10′40.0″N, 132°25′0.3″E).

Diagnosis.—Small uniplanar or arborescent colonies formed by extratentacular sympodial branching. Corallites slightly elliptical with a GCD of 4.6–6.7 mm and a lesser calicular diameter (LCD) of 3.5–5.5 mm. Calicular edges of corallites moderately lanceted. Septa hexamerally arranged in four cycles (6, 6, 12, 24) in a Pourtalès Plan. Two directive septa of corallites oriented subparallel to the maximum growth direction of a branch. Columella elongate and spongy.

Description.—Small uniplanar or arborescent colonies are formed by extratentacular sympodial branching (Figures 5 and 6). The mean angle between the maximum growth direction of the daughter corallites and that of the parent corallite is 33.6° ± 0.9° (n = 5). The orientation of the two directive septa of the corallites tends to be subparallel to the maximum growth direction of the branch (Figure 5A, B, D). Occasionally, lateral corallites secondarily bud from the axillary part of the sympodial branches (Figure 6D–F). Theca are synapticulothecal costate without epitheca (Figure 5C). The coenosteum is thicker in the lower part of the corallum. The maximum branch diameter is 8.5 mm. Corallites are slightly elliptical, with a GCD of 4.6–6.7 mm (mean ± SE = 5.55 ± 0.21 mm, n = 11) and LCD of 3.5–5.5 mm (mean ± SE = 4.71 ± 0.23 mm, n = 11) (Figure 5B). The calicular margins of the corallites are slightly projecting (mean ± SE = 1.21 ±

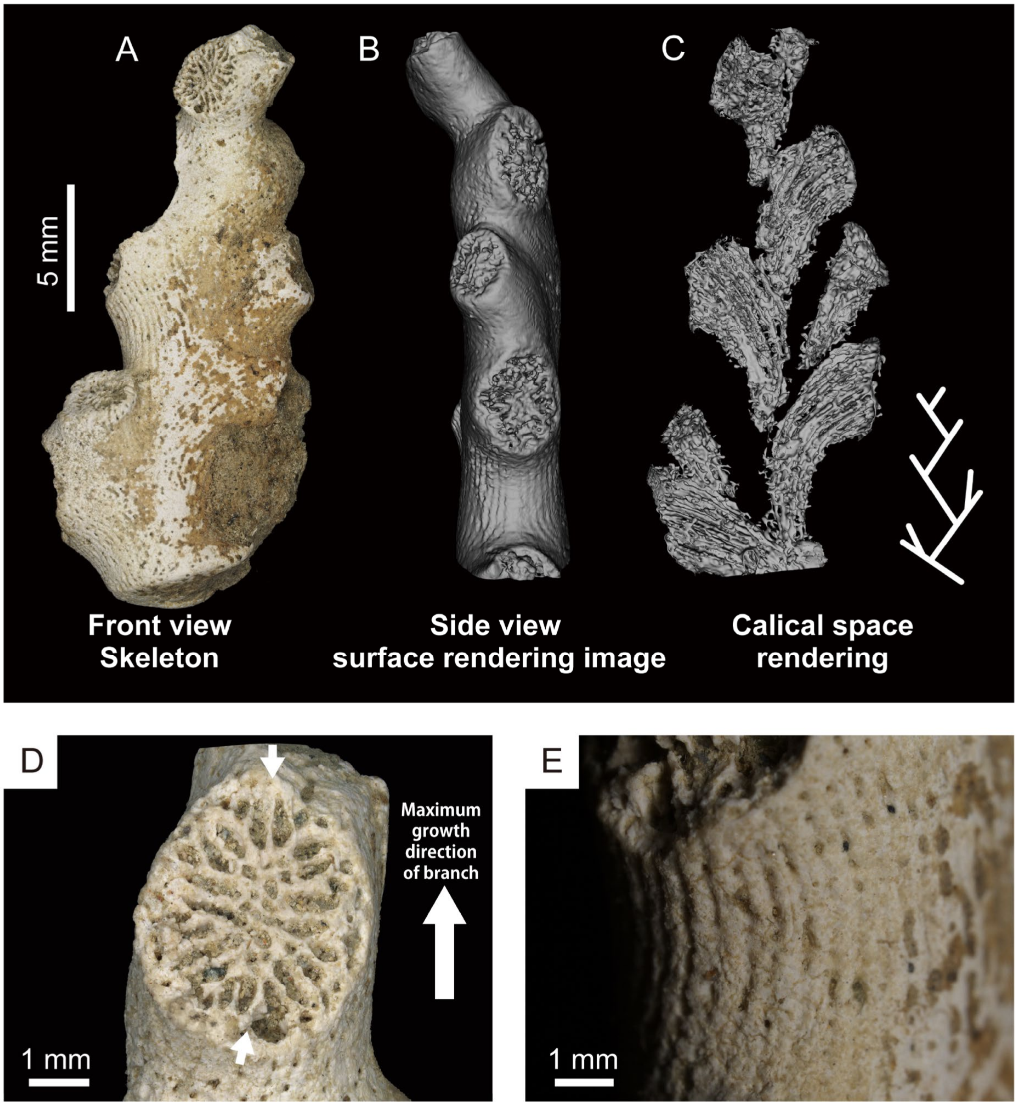

Figure 5. Morphology of *Dendrophyllia mokiensis* sp. nov. (SNMS-F-1553, holotype). **A**, front view of the distal part of a branch. **B**, surface rendering image of A, showing the side view of the corallum. **C**, side view of the 3D reconstruction of X-ray CT images of the branch without the coenosteum skeletons of A, showing sympodial budding. A diagram of the budding pattern is provided at lower right. **D**, close-up view of a corallite. The orientation of the two directive septa (short white arrows) of the corallites tends to be sub-parallel to the maximum growth direction of the branch. **E**, costae on the corallum surface.

0.13 mm, *n* = 5). The calicular edges of corallites are moderately lanceted. The costae of the corallites are well developed, 0.32–0.51 mm wide, and separated by narrow intercostal striae (0.12–0.16 mm), especially at the growth tips of coralla (Figure 5A, E). Septa are hexamerally arranged in four cycles (6, 6, 12, 24) in a Pourtalès Plan (Figure 5B). S1 and S2 are equal in size. S3 are short; pairs of S4 are fused before their adjacent S3 and extend to the columella. An elongate spongy columella is slightly developed.

Discussion.—*Dendrophyllia mokiensis* can be distinguished from *D. koiwaii* by its larger GCD (4.6–6.7 mm vs. 3–4 mm) and greater number of septa (48 vs. 32). *Dendrophyllia mokiensis* shows extratentacular sympodial branching with no main axis. Although details of the budding patterns of *D. koiwaii* were not described by Yabe and Eguchi (1944), *D. koiwaii* does not show any sympodial branching (pl. 7(4), figure 1 in Yabe and Eguchi, 1944); therefore, the two species have different budding patterns. *Dendrophyllia mokiensis* is distinguished from *D. okamotoi* by the mode of budding (i.e., sympodial vs. monopodial budding).

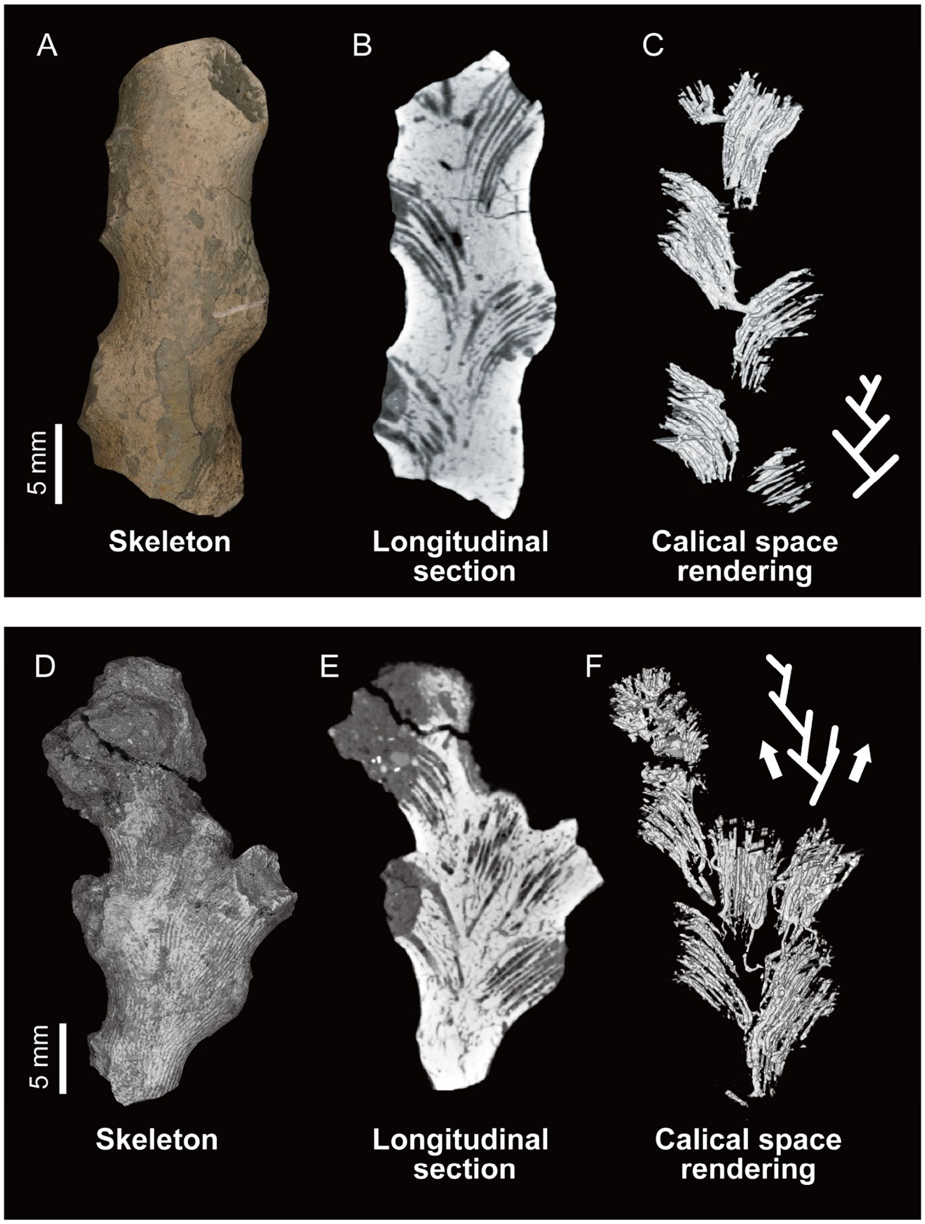

Figure 6. Mode of budding in *Dendrophyllia mokiensis* sp. nov. **A**, paratype (SNMS-F-1554), side view of a branch. **B**, longitudinal section of the branch shown in A. **C**, side view of the 3D reconstruction of X-ray CT images of the branch without the coenosteum skeletons of A, showing sympodial budding. A diagram of the budding pattern is provided at lower right. **D**, paratype (SNMS-F-1555), side view of a branch. **E**, longitudinal section of the branch shown in D. **F**, side view of the 3D reconstruction of the corallum without the coenosteum skeletons of D, showing sympodial budding and branching. A diagram of the budding and branching patterns is provided at upper right.

Eight valid extant species of *Dendrophyllia* showing sympodial budding are known (Cairns, 1979, 1991, 1994, 2001; Kitahara and Cairns, 2021): *D. alcocki* (Wells, 1954); *D. alternata* Pourtales, 1880; *D. boschmai* van der Horst, 1926; *D. dilatata* van der Horst, 1927; *D. johnsoni* Cairns, 1991; *D. oldroydae* Oldroyd, 1924; *D. florulenta* Alcock, 1902; and *D. romanoae* Kitahara and Cairns, 2021. *Dendrophyllia mokiensis* is distinguished from *D. alcocki* by a greater number of septa and a spongy columella (48 vs. 32; elongate spongy vs. papillose); from *D. alternata* by a greater number of septa (48 vs 39–45); from *D. boschmai* by a smaller calical diameter (maximum 6.7 mm vs. maximum 11 mm); from *D. romanoae* by its uniplanar branching colony, smaller calice (mean

Table 1. Fossil and Recent azooxanthellate coral framework composed of *Dendrophyllia* and/or *Petrophyllia* after Coates and Kauffman (1973), Stanley and Cairns (1988).

Location	Framework builder	Age	Structure	Depth	Reference
Ireland to Northeast Africa	*Dendrophyllia cornigera*	Recent	Thicket	200–450 m	Le Danois (1948)
off Casablanca, Morroco	*Dendrophyllia ramea*	Recent	Thicket	80–110 m	Gruvel (1923)
Niger Delta	*Madracis asperula* *Dendrophyllia* cf. *ramea*	Recent	Thicket Coppice	50–120 m	Allen and Wells (1962)
Gulf of Aqaba, Red Sea	*Madracis interjecta* *Dendrophyllia minuscula*	Recent	Bioherm	120–200 m	Fricke and Hottinger (1983)
Shimane, Japan	***Petrophyllia niimiensis*** ***Dendrophyllia okamotoi*** ***Dendrophyllia mokiensis* sp. nov.**	**Middle Miocene Langhian (17.65–13.60 Ma)**	**Unknown**	**100–200 m (interpreted)**	**This study**
Fakse, Denmark	*Dendrophyllia candelabrum* *Faksephyllia faxoensis* *Oculina becki*	Paleocene Danian	Banks	50 m	Fløris (1979, 1980)
Fakse, Denmark	*Dendrophyllia candelabrum* *Faksephyllia faxoensis* *Oculina becki* Stylasterid corals Bryozoa	Paleocene Danian	Mounds	100–300 m (interpreted)	Bernecker and Weidlich (1990)
Nuussuaq, Greenland	*Dendrophyllia candelabrum* *Faksephyllia faxoensis* *Oculina becki* *Lophelia*? sp.	Paleocene Danian	Thicket Coppice	?50–80 m	Fløris (1972)
Limhamn, Sweden	*Dendrophyllia candelabrum* *Faksephyllia faxoensis* *Oculina becki*	Paleocene Danian	Unknown	Photic zone	Holland and Gabrielson (1979)
Western Interior, USA	*Petrophyllia dartoni*	Late Cretaceous Turonian	Thicket	200–500 feet = 61–152.5 m (interpreted)	Coates and Kauffman (1973)

5.6 × 4.7 mm vs. 8.7 × 6.9 mm) and the calicular edge morphology (moderately lanceted vs. highly lanceted); from *D. dilatata* by the orientation of the two directive septa of the corallites (sub-parallel vs. sub-perpendicular to the maximum growth direction); from *D. johnsoni* by its hexamerally arranged septal insertion and greater number of septa (octamerally arranged, 32 septa in *D. johnsoni*); from *D. oldroydae* by a smaller number of septa (48 vs 72 septa) and smaller corallites (maximum 6.7 mm vs. maximum 15 mm); and from *D. florulenta* by its smaller corallites (maximum 6.7 mm vs. maximum 9 mm).

Dendrophyllia oldroydae, the only previous example of fossil *Dendrophyllia* with sympodial budding, has been reported only from middle Pliocene strata of the San Diego Formation in California, USA (Hertlein and Grant, 1960). Therefore, *Dendrophyllia mokiensis* is the oldest species of Group 3 of the genus *Dendrophyllia sensu* Cairns (1994, 2001).

Discussion

The large, exposed surface (15 m long and 6 m high) of the chaotic rock unit contains a high concentration of coral remains (0.35 coralla/cm^2). Almost all coralla are fragmented, but the absence of conspicuous bioerosion patterns within the skeletons indicates rapid burial (e.g. Freiwald and Wilson, 1998). The existence of coral thickets consisting of live corals on steeply inclined hard substrates and submarine cliffs can be inferred from redeposited coral-rich sediment showing a similar coral concentration to that in the chaotic rock unit of this study (Titschack and Freiwald, 2005; Aguirre *et al.*, 2020). Therefore, we conclude that a community with abundant azooxanthellate corals lived near the source area of the chaotic rock.

Freiwald *et al.* (2004) indicated that the preferred locations or environments of cold-water coral habitats are characterized by (1) being below the seasonal storm wave base; (2) strong topographically guided bottom currents that prevent the deposition of sediments, thereby creating current-swept conditions; (3) hard substrates that facilitate colonization by habitat-forming corals; (4) a flow of water that is funneled through narrow passages such as straits or channels, fjord troughs, and submerged canyons and gullies; and (5) nutrient-rich waters that stimulate the development of high phyto- and zooplankton levels, providing a major food source for the coral communities. Hayashi *et al*. (2015) reconstructed the sedimentary environments and the source of the chaotic rocks. They concluded that the original sedimentary depth of the siltstone blocks in the chaotic rock was deeper than 100–200 m from the high planktonic/total foraminiferal ratio (77.6%; following Gibson, 1989) and the occurrence of *Fissidentalium yokoyamai* (Makiyama, 1931) in the matrix of the chaotic rock unit, as reported by Ogasawara and Masuda (1989). Moreover, they showed that one-third of the total foraminifera from the siltstone blocks were *Globigerina praebulloides* Blow, 1959, indicating an environment with strong upwelling (Hayashi *et al*., 2015). Therefore, the environment of the source area has been interpreted as an offshore setting (below the storm wave base) with a strong upwelling current, which may have prevented sediment deposition and supplied nutrient-rich waters from depth, leading to the blooming of phyto- and zooplankton and eventually forming a suitable habitat for azooxanthellate corals.

Petrophyllia and *Dendrophyllia* are known to be framework builders of coral thickets and reefs (Table 1). Fossil *Petrophyllia* coral thickets, indicating a paleodepth of 60–150 m, have been reported only from the Cretaceous strata of the Western Interior, USA (Coates and Kauffman, 1973). Reefs, banks, and thickets formed by *Dendrophyllia* frameworks are known from the Paleocene to Recent from inferred paleodepths of 100–300 m (Paleocene, Fakse, Denmark: Bernecker and Weidlich, 1990), 50–120 m (Recent, Niger Delta: Allen and Wells, 1962), 80–110 m (Recent, Morocco: Gruvel, 1923), and 120–200 m (Recent, Gulf of Aqaba, Red Sea: Fricke and Hottinger, 1983). The inferred paleodepths of these *Petrophyllia* and *Dendrophyllia* frameworks are generally consistent with the paleobathymetry of the original sedimentary depth of silt in the chaotic rocks containing the fossil corals of this study. To date, there have been no reports of coral reefs or thickets formed by a combination of *Petrophyllia* and *Dendrophyllia* as major framework builders. In addition, *Petrophyllia* has been reported as a framework builder in cold-water coral reefs or high-density azooxanthellate coral assemblages only during the Turonian (Late Cretaceous: Coates and Kauffman, 1973). Therefore, this study is the first report of an azooxanthellate coral community dominated by *Petrophyllia* from the Cenozoic. Nevertheless, further research is needed to elucidate the details of Miocene azooxanthellate coral habitats, community structures, and geomorphology through the finding of an autochthonous fossil coral assemblage in the Shimane area.

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Author contribution

Y. T., N. Y., and H. E. designed and performed all the experiments. Y. T., N. Y., H. E., A. S., and Y. E. analysed the results and wrote the manuscript. Y. T., N. Y., A. S., H. H., Y. M., and S. K. collected fossils and contributed to the geological aspects of the study. All authors gave final approval for publication.