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Five species of *Microporina* (Bryozoa, Cheilostomata) from the Pleistocene Setana Formation at Kuromatsunai, Hokkaido, Japan

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Abstract. **Fossils of *Microporina* species were collected and examined from the Soebetsu Sandstone Member of the Pleistocene Setana Formation in southwestern Hokkaido. A description is provided for *M. japonica* Canu and Bassler, and four species (*M. sakakurai*, *M. minuta*, *M. quadristoma* and *M. soebetsuensis*) are newly described. Some of them were previously reported as *M. articulata* (Fabricius). Among the five species, three (*M. japonica*, *M. sakakurai*, *M. minuta*) have a semielliptical or elliptical orifice, relatively large and deep frontal pseudopores, opesiules occluded with a thin plate showing vein-like surface sculpturing, and avicularia that are longer than wide. The other two (*M. quadristoma*, *M. soebetsuensis*) have a rounded-quadrate orifice (sometimes with a convex proximal margin), smaller frontal pseudopores, opesiules occluded but lacking vein-like surface sculpturing, and avicularia that are circular or wider than long. Marked orificial dimorphism is observed in two species, *M. sakakurai* and *M. soebetsuensis*.**

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Keywords: Bryozoa, Hokkaido, *Microporina*, Pleistocene, Soebetsu Sandstone

Introduction

Species in the cheilostome bryozoan genus *Microporina* Levinsen, 1909 form flexible, erect colonies having cylindrical or club-shaped internodes, chitinous joints, and rootlet-like kenozooids for attachment. The type species, *Microporina articulata* (Fabricius, 1821), is a boreal species that has been reported from Japan and Korea (Silén, 1942; Mawatari, 1956; Rho and Seo, 1990), but some of the fossil and Recent records from Japan are incorrect (Arakawa, 2016).

Fossils of *Microporina* from the Pleistocene Setana Formation at Kuromatsunai, southwestern Hokkaido, Japan, were first studied by Sakakura (1936). The Setana Formation contains some of the most diverse, abundant, and well-preserved Pleistocene bryozoan deposits worldwide, particularly the bryozoan-rich outcrop at Utasai known as "Kokemushi (= bryozoan) Paradise" (Dick *et al.*, 2008a; Taylor *et al.*, 2012; see also Taylor, 2013). Internodes of *Microporina* are abundant in another locality of the Setana Formation along the Soebetsu River. Sakakura (1936) described the specimens from Kuromatsunai as *Microporina articulata* (Fabricius, 1821), but also recognized at least two types (one of which he termed the "thin type"); subsequent images of his material suggested the fauna might include several distinct species (Arakawa, 2016). In this study, I describe *Microporina* specimens newly collected from Kuromatsunai using scanning electron microscopy (SEM), recognizing five species and discussing the morphology of this genus in detail.

Geological setting

The Setana Formation comprises Pleistocene shallow marine deposits in Hokkaido, Japan. It is mainly distributed in the Imakane–Kamiyakumo area and the Kuromatsunai lowland, and uncomformably overlaps the Pliocene Kuromatsunai Formation. Nojo *et al.* (1999) redefined the Setana Formation in the Kuromatsunai lowland and divided it into the lower Nakasato Conglomerate Member and the upper Soebetsu Sandstone Member. The geological age of the Setana Formation has been studied biostratigraphically using diatoms (Tsuchi, 1979), planktonic foraminifera (e.g. Tsubakihara *et al.*, 1989; Nojo *et*

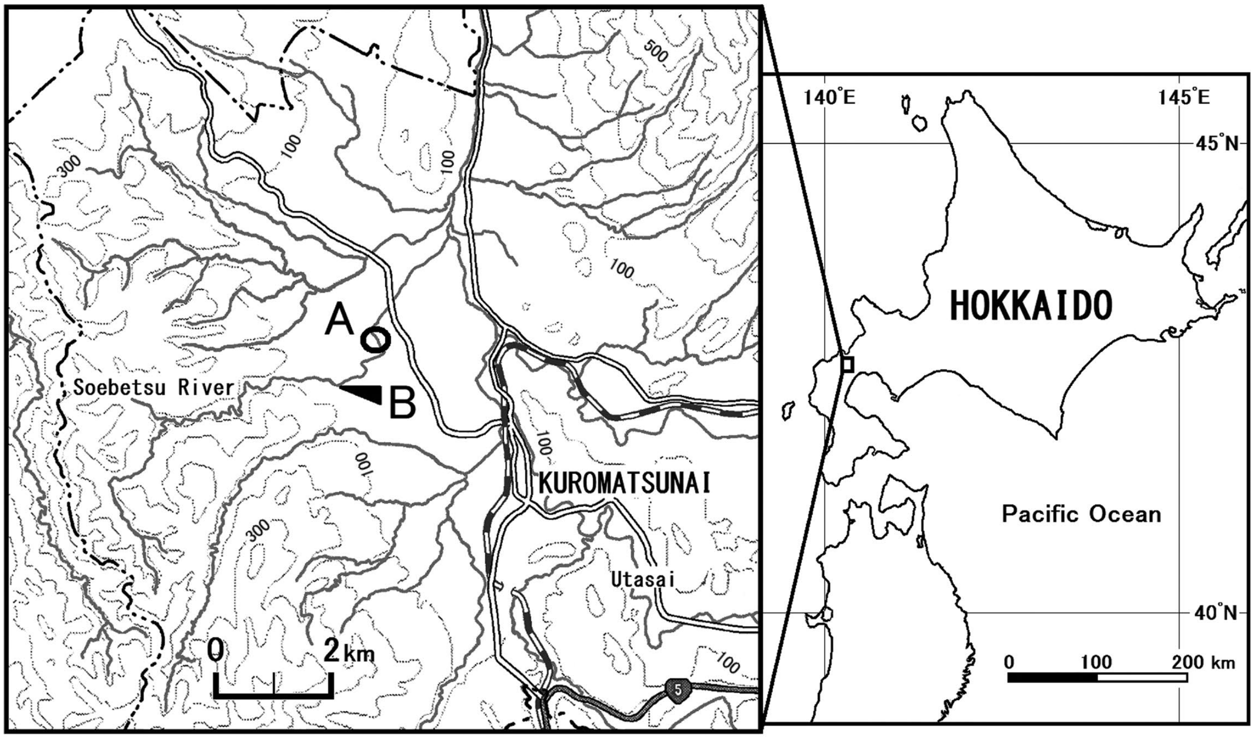

Figure 1. Map showing the location of the study area, based on a topographical map from the Geospatial Information Authority of Japan. **A,** sampling area of the material collected by Hokkaido University; **B,** locality of the samples taken by the author.

al., 1999) and calcareous nannofossils (Chitoku, 1983; Nojo *et al.*, 1999). Nojo *et al.* (1999) concluded that the Nakasato Member was deposited about 1.2 to 1.0 Ma, and the Soebetsu Member about 1.0 to 0.6 Ma, based on nannofossils (Zones CN13b and CN14a in Okada and Bukry, 1980).

The bryozoan fauna in the Nakasato Member is characterized by many colonies encrusting pebbles and cobbles, whereas that in the Soebetsu Member contains many erect colonies of *Microporina* and *Phidolopora* (Dick *et al.*, 2008a). The sedimentary environment of the Soebetsu Member has been interpreted as inner to outer shelf (Takashima *et al.*, 2008). Taylor *et al.* (2012) inferred that the depositional depth of the Soebetsu Member was shallower than the Nakasato Member due to the presence of stylasterid hydrocorals and absence of calcareous algae in the latter. The molluscan fauna of the Nakasato Member changed from subarctic to cool-temperate, and subtropical molluscs and warm-water planktonic foraminifers occur in the middle part of this member (Suzuki, 1989; Nojo *et al.*, 1999). Using the MART (mean annual range in temperature) technique, Dick *et al.* (2008b) estimated the average range in paleotemperature to be 8.6°C for eight bryozoan species in the Soebetsu Member, and 11.7°C for two species from the Nakasato Member. However, McClelland *et al.* (2014) showed the uncertainty (±4°C) for their revised MART equation.

Material and methods

Some of the study material was collected from the Soebetsu Sandstone Member of the Setana Formation along the Soebetsu River in Kuromatsunai ("A" in Figure 1), in stratigraphic samples taken in August, 2007 by Dr. Matthew Dick (Hokkaido University) and sorted in the laboratory of Dr. Reishi Takashima (Tohoku University). In 2018, I collected additional material from small riverside outcrops southward from the above sampling area ("B" in Figure 1, the lower part of the Soebetsu Member). Along the Soebetsu River, several coarse-grained layers show shell concentrations, and there is a concentration of calcareous algae in the middle of the member (Takashima *et al.*, 2008). The specimens of *Microporina* mainly came from a horizon about 2 m thick intercalated with a concentration of calcareous algae.

All fossils of *Microporina* occur as separated internodes. As illustrated in previous studies (Robertson, 1905; Kluge, 1962; Boardman *et al.*, 1983), the size of internodes varies even within the same colony. The Kuromatsunai material is well preserved and includes internodes from two to sixteen zooidal generations in length. For comparisons among species in this study, both small and large internodes were included as uniformly as possible.

Microporina internodes and fragments of internodes were picked from dried samples under a magnifying lens or a stereoscopic microscope, and were cleaned ultrasonically or in a hydrogen peroxide solution. After cleaning, specimens for SEM were mounted on aluminum stubs with adhesive tape, coated with Au in an ion sputter coater (model SC-701AT, Sanyu Denshi), and observed with a JEOL Model JSM-5310 microscope at the National Museum of Nature and Science, Tsukuba.

Zooidal characters were measured from SEM images taken at about 485× magnification. Measurements (in millimeters) are presented as the range, followed by the arithmetic mean and standard deviation. Sample sizes (n) are given as the number of zooids from which a character was measured, followed by the number of internodes or fragments of internodes from which measurements were taken. Abbreviations used for characters measured are as follows: ZL, autozooid length; ZW, autozooid width; OrL, orifice length; OrW, orifice width; AvL, avicularium length; AvW, avicularium width.

The type material and some of the other specimens examined in this study are deposited in the National Museum of Nature and Science, Tsukuba (catalog number prefix NMNS PA). Additional specimens are deposited in the collection of the science laboratory of Seishin-Gakuen, Kashima City, Ibaraki, Japan (SGBC).

Taxonomy

Order Cheilostomata Busk, 1852
Suborder Flustrina Smitt, 1868
Superfamily Microporoidea Gray, 1848
Family Microporidae Gray, 1848
Genus ***Microporina*** Levinsen, 1909

Type species.—*Salicornaria borealis* Busk, 1855 [now regarded as a synonym of *Cellularia articulata* Fabricius, 1821], Recent, from Greenland.

Occurrence.—Miocene to Recent.

Microporina japonica Canu and Bassler, 1929

Figures 2, 5A, 5D, 9A

Microporina japonica Canu and Bassler, 1929, p. 139, pl. 14, figs. 9–11; Arakawa, 2016, p. 18, figs. 6–8, 13B.

Microporina articulata (Fabricius, 1821): Sakakura, 1936, p. 259, pl. 15(5), figs. 1, 2; Arakawa, 1984, p. 74, pl. 8-1, fig. 2; Nishizawa, 1987, p. 182, pl. 1, fig. 3; Arakawa, 1995, p. 80; Arakawa, 1999, p. 57.

Material examined.—NMNS PA 18522, 18523, 18524, 18525 (two internodes, A, B), locality A in Figure 1; 18526 (two internodes, A, B), 18527 (two internodes, A, B), 18528, locality B in Figure 1; SGBC-0468 (two internodes, A, B), locality B in Figure 1. All from the Setana Formation, Soebetsu Sandstone Member, Pleistocene, Kuromatsunai, Hokkaido, Japan.

Measurements (in millimeters).—NMNS PA 18522–18528, and SGBC-0468. Autozooids (n = 288, 12): ZL, 0.49–1.09 (0.758 ± 0.099); ZW, 0.21–0.42 (0.295 ± 0.033); OrL, 0.06–0.15 (0.098 ± 0.010); OrW, 0.12–0.23 (0.177 ± 0.017). Avicularia (n = 113, 12): AvL, 0.14–0.26 (0.191 ± 0.022); AvW, 0.10–0.23 (0.160 ± 0.016).

Description.—Colony erect, consisting of pencil-shaped internodes (Figure 2). Minimum internode size 2.2 mm long (NMNS PA 18525A, Figure 2D) and 0.76 mm in diameter (SGBC-0468B); maximum size 11 mm long and 1.2 mm in diameter (NMNS PA 18528). Internodes generally circular in transverse section, composed of 8–13 columns of zooids; proximal end of internodes occupied by 4–7 kenozooids. Zooids elongate, rectangular or hexagonal, sometimes tapering proximally. Frontal wall cryptocystal, flat, granulated, covered with somewhat deep pseudopores occluded by reticulately fused elements (Figure 9A), and surrounded by salient mural rim. Mural rim finely granulated, and often thickened with secondary calcification. Opesiules (Figure 5D) large, elliptical or rounded triangular, completely occluded by smooth, calcification with vein-like surface sculpturing. Orifice (Figure 5A) not markedly dimorphic; semielliptical in most zooids, proximal border straight or concave, with rounded corners, sometimes nearly elliptical, especially when followed by avicularium. Oral spines and ovicells lacking. Avicularium distal to orifice of some zooids, longer than wide, directed proximally; mandibular portion of rostrum triangular; pivot bar complete, somewhat medially folded (Figure 5A).

Distribution.—Pleistocene to Recent, Japan. Known Recent localities are Tsugaru Strait (Canu and Bassler, 1929) and the continental shelf east of the Boso Peninsula (Arakawa, 2016). Pleistocene fossils have been collected from the Sawane Formation, Sado Island (Sakakura, 1936; Nishizawa, 1987); the Shimosa Group, Boso Peninsula (Arakawa, 1995); the Setana Formation, Hokkaido (Sakakura, 1936; this study).

Remarks.—As discussed by Arakawa (2016), this species shows large variations in the shape of the orifice, the proximal border of which can be nearly straight or broadly concave. The orifice with a straight proximal border is mainly observed in the autozooids not followed by an avicularium. In some internodes, most zooids have an orifice with a straight proximal border, as illustrated by Sakakura (1936, pl. 15(5), fig. 1).

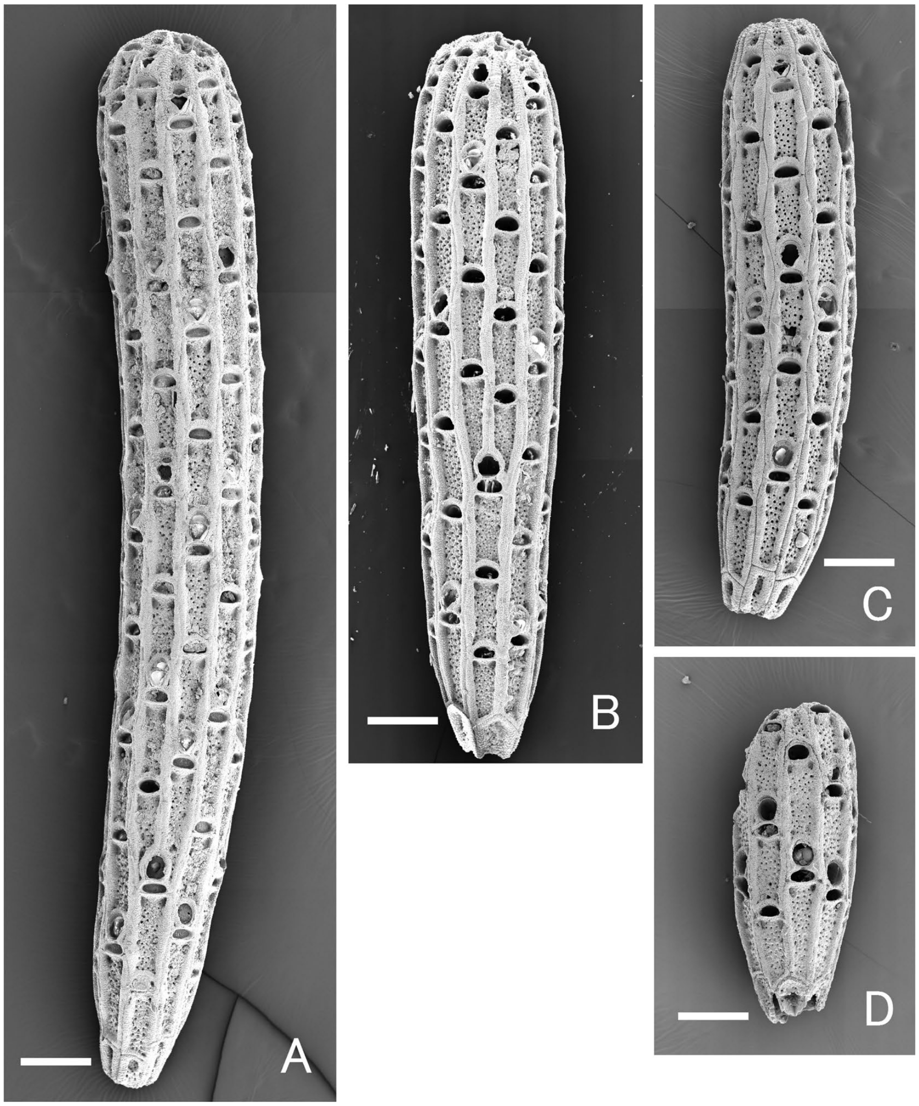

Figure 2. *Microporina japonica* Canu and Bassler, 1929. **A,** long internode (NMNS PA 18523); **B,** internode with zooids having somewhat larger orifices (NMNS PA 18524); **C,** typical internode (NMNS PA 18522); **D,** shortest internode (NMNS PA 18515A). Scale bars 500 µm.

Microporina sakakurai sp. nov.

Figures 3, 5B, 5E, 9B

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Microporina articulata (Fabricius, 1821): Sakakura, 1936, p. 260, pl. 15(5), figs. 3, 4.

Diagnosis.—Orifices dimorphic; mostly semielliptical, with sharp proximolateral corners in autozooids not followed by avicularium; smaller, longitudinally depressed, with rounded proximolateral corners, in autozooids followed by avicularium and in some proximal zooids in internode. Internodes with 13–20 columns of zooids, often markedly increasing in width distally.

Material examined.—Holotype, NMNS PA 18511, locality A in Figure 1. Paratypes, NMNS PA 18512 (two long internodes, A, B), and 18513 (an internode with small zooids), locality A in Figure 1. Other material examined, NMNS PA 18514, 18515, 18516, locality A in Figure 1, and 18517, locality B in Figure 1. All from the Setana Formation, Soebetsu Sandstone Member, Pleistocene, Kuromatsunai, Hokkaido, Japan.

Etymology.—Named for Japanese paleontologist Dr Katsuhiko Sakakura, who reported and illustrated this

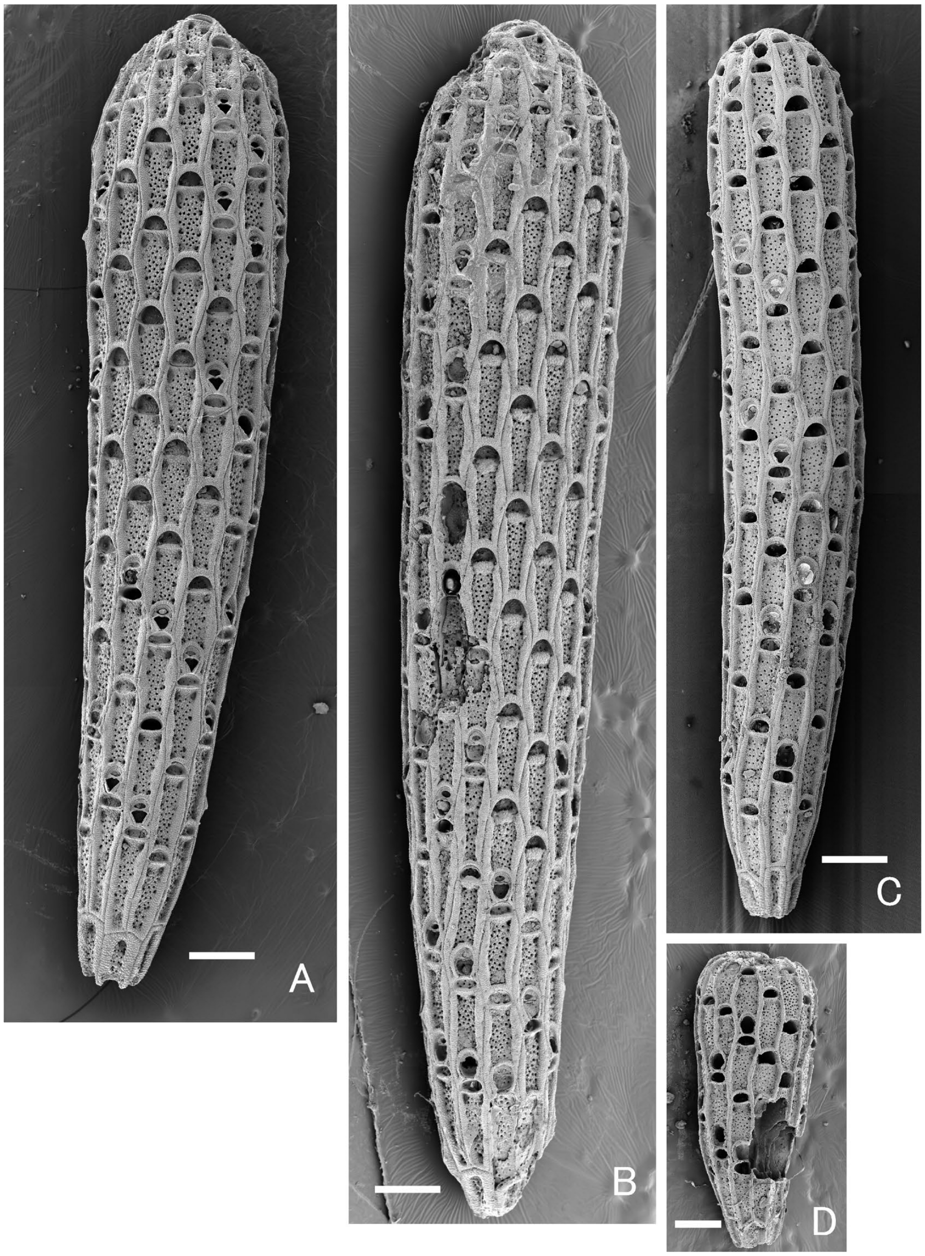

Figure 3. *Microporina sakakurai* sp. nov. **A,** holotype (NMNS PA 18511); **B,** paratype, long internode (NMNS PA 18512B); **C,** paratype, internode with small zooids (NMNS PA 18513); **D,** shortest internode (NMNS PA 18514). Scale bars 500 μm.

species (Sakakura, 1936).

Type locality.—Downstream part of the Soebetsu River (locality A in Figure 1), Kuromatsunai, Hokkaido, Japan, Pleistocene Setana Formation.

Measurements (in millimeters).—NMNS PA 18511 (holotype), 18512B (paratype), 18513 (paratype)–18517. Autozooids (n=298, 7): ZL, 0.58–1.06 (0.802±0.077); ZW, 0.21–0.38 (0.304±0.036); OrL, 0.09–0.16 (0.113±0.014); OrW, 0.14–0.24 (0.191±0.018). Avicularia (n=117, 7): AvL, 0.15–0.26 (0.215±0.019); AvW, 0.13–0.21 (0.166±0.013).

Description.—Colony erect, consisting of large internodes (Figure 3) often markedly increasing in width distally. Minimum internode size 3.2 mm long (NMNS PA 18514, Figure 3D) and 1.1 mm in diameter (NMNS PA 18513, Figure 3C); maximum size 10 mm long (NMNS PA 18516) and 2.0 mm in diameter (NMNS PA 18517). Internodes elliptical in transverse section, composed of

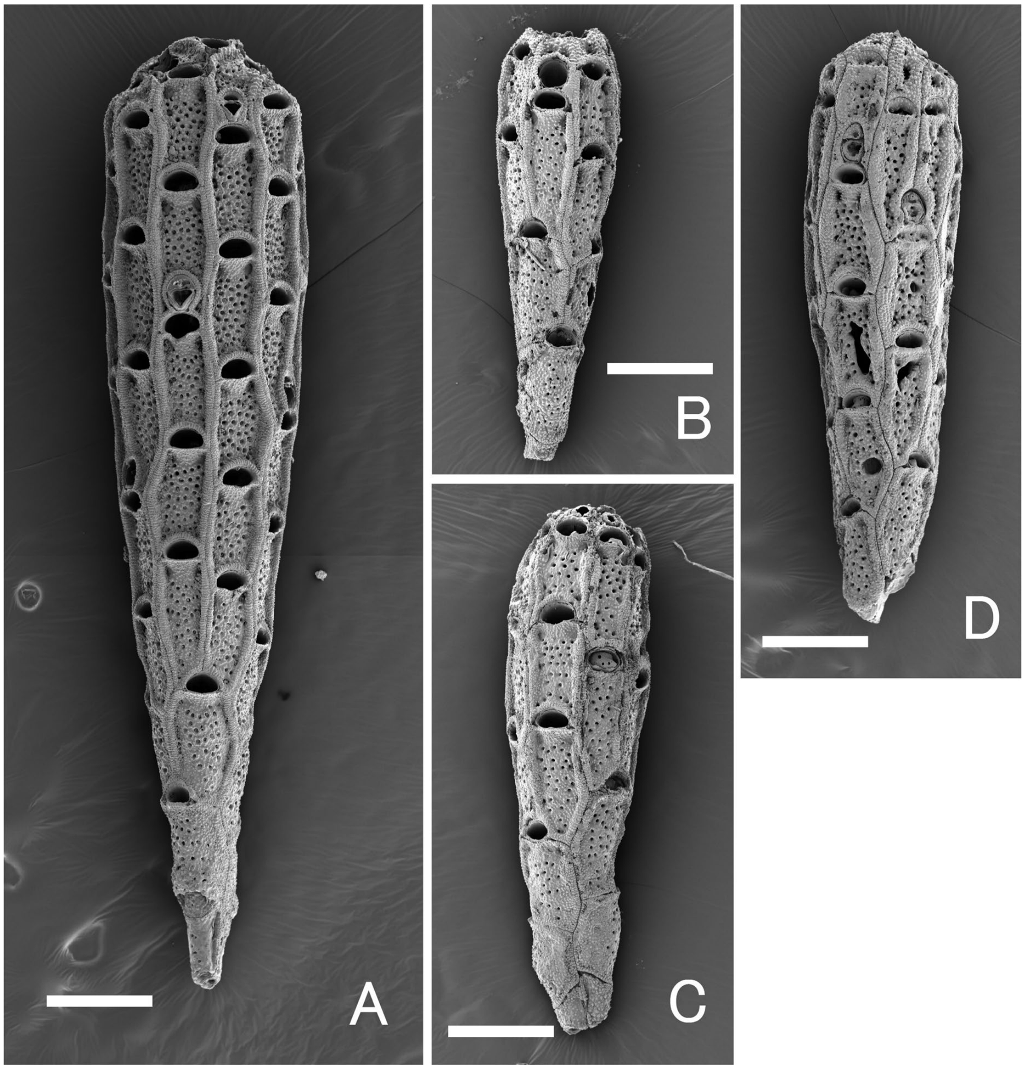

Figure 4. *Microporina minuta* sp. nov. **A,** holotype, longest internode (NMNS PA 18518); **B,** paratype, shortest internode (NMNS PA 18520A); **C,** paratype (NMNS PA 18520B); **D,** paratype, showing extensive secondary calcification (NMNS PA 18519). Scale bars 500 µm.

13–20 columns of zooids; proximal end of internodes occupied by 5–8 kenozooids. Zooids elongate; hexagonal in distal part of internodes, rectangular or proximally tapering in proximal part. Frontal wall cryptocystal, flat, finely granulated, uniformly covered with pseudopores, and surrounded by salient mural rim. Frontal pseudopores somewhat deep, occluded with reticulately fused elements (Figure 9B). Mural rim also finely granulated, and often thickened with secondary calcification. Opesiules (Figure 5E) large, circular or elliptical, completely occluded by smooth, calcified plate with vein-like surface sculpturing. In most autozooids, orifice D-shaped (Figure 5B), with sharp proximolateral corners and straight or concave proximal border; in zooids followed by avicularium and those in proximal part of internode, orifice smaller, longitudinally depressed, with rounded proximolateral corners. Rim of orifice also thickened with secondary calcification. Oral spines and ovicells lacking. Avicularium distal to orifice of some zooids; longer than wide, mandibular part of rostrum triangular, directed proximally; pivot bar complete, somewhat medially folded (Figure 5B).

Remarks.—Like *Microporina japonica* Canu and Bassler, 1929, *Microporina sakakurai* sp. nov. shows dimorphism in the autozooidal orifice, but the dimorphism is stronger in the latter. In *M. sakakurai*, orifices not preceding an avicularium tend to be longer and D-shaped with strongly arched distal border and acute proximal corners; those preceding an avicularium are longitudinally depressed with rounded corners. Some internodes of this species do not markedly increase in width distally,

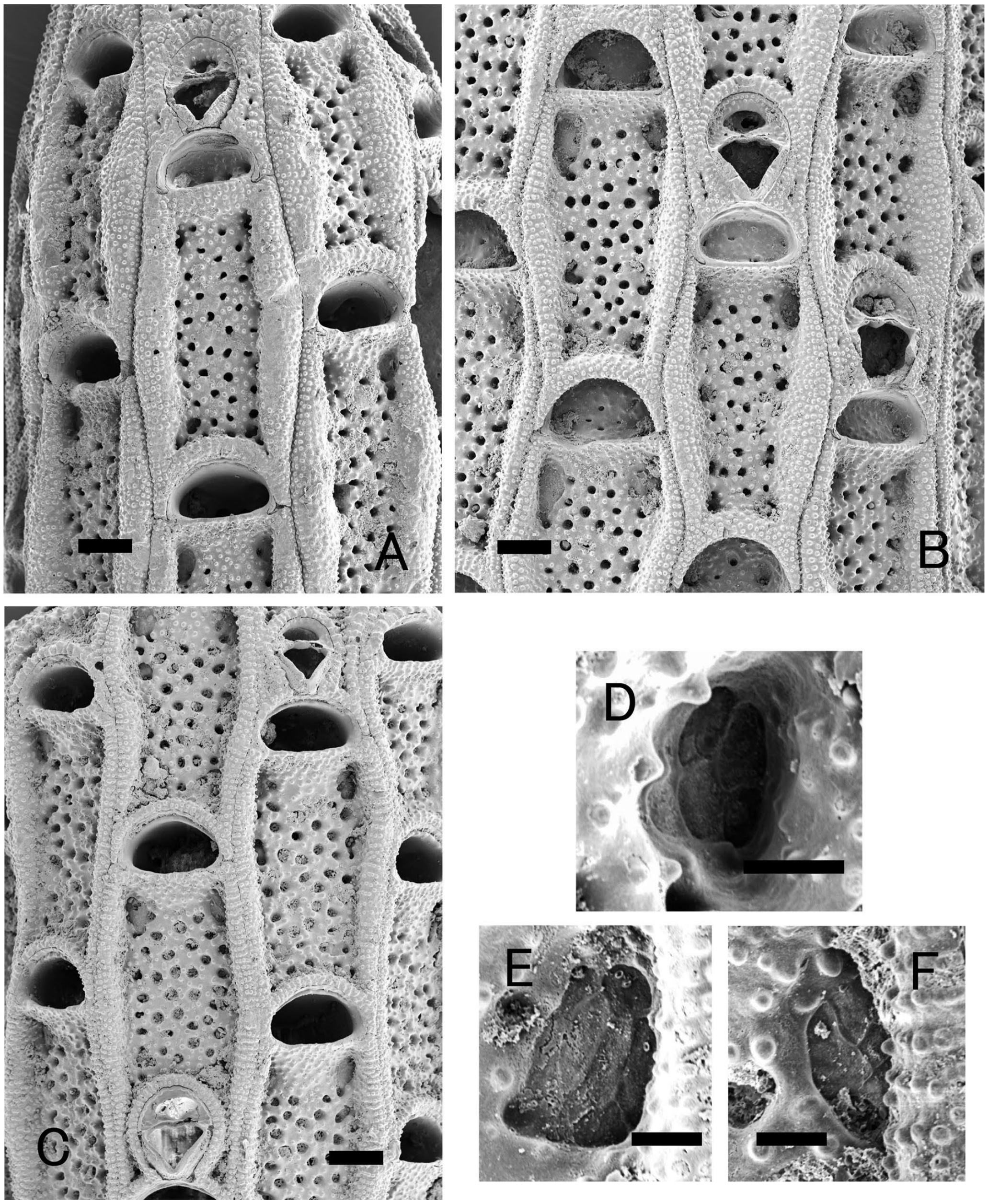

Figure 5. Comparison of zooids (A–C) and opesiules (D–F) in three species having semielliptical orifices. **A, D,** *Microporina japonica* Canu and Bassler, 1929, orifices not markedly dimorphic (NMNS PA 18522); **B, E,** *M. sakakurai* sp. nov., with dimorphic orifices (NMNS PA 18511); **C, F,** *M. minuta* sp. nov., orifices not markedly dimorphic (NMNS PA 18518, holotype). Scale bars 100 µm in A–C, 25 µm in D–F.

and they resemble *M. japonica* having semielliptical orifices with a straight proximal border. However, the orifice is not at all enlarged in *M. japonica*. Although Sakakura (1936) considered those two species to be conspecific (as *M. articulata*), the difference in the degree of orificial dimorphism is conspicuous even in his illustrations. And the two species also differ in the shape and width of internodes. The number of zooidal columns in this species (13–20) is larger than *M. japonica* (8–13). Most internodes of *M. sakakurai* are club-shaped (the width at the distal end up to three times that at the proximal end) and elliptical in transverse section.

Microporina minuta sp. nov.

Figures 4, 5C, 5F, 9C

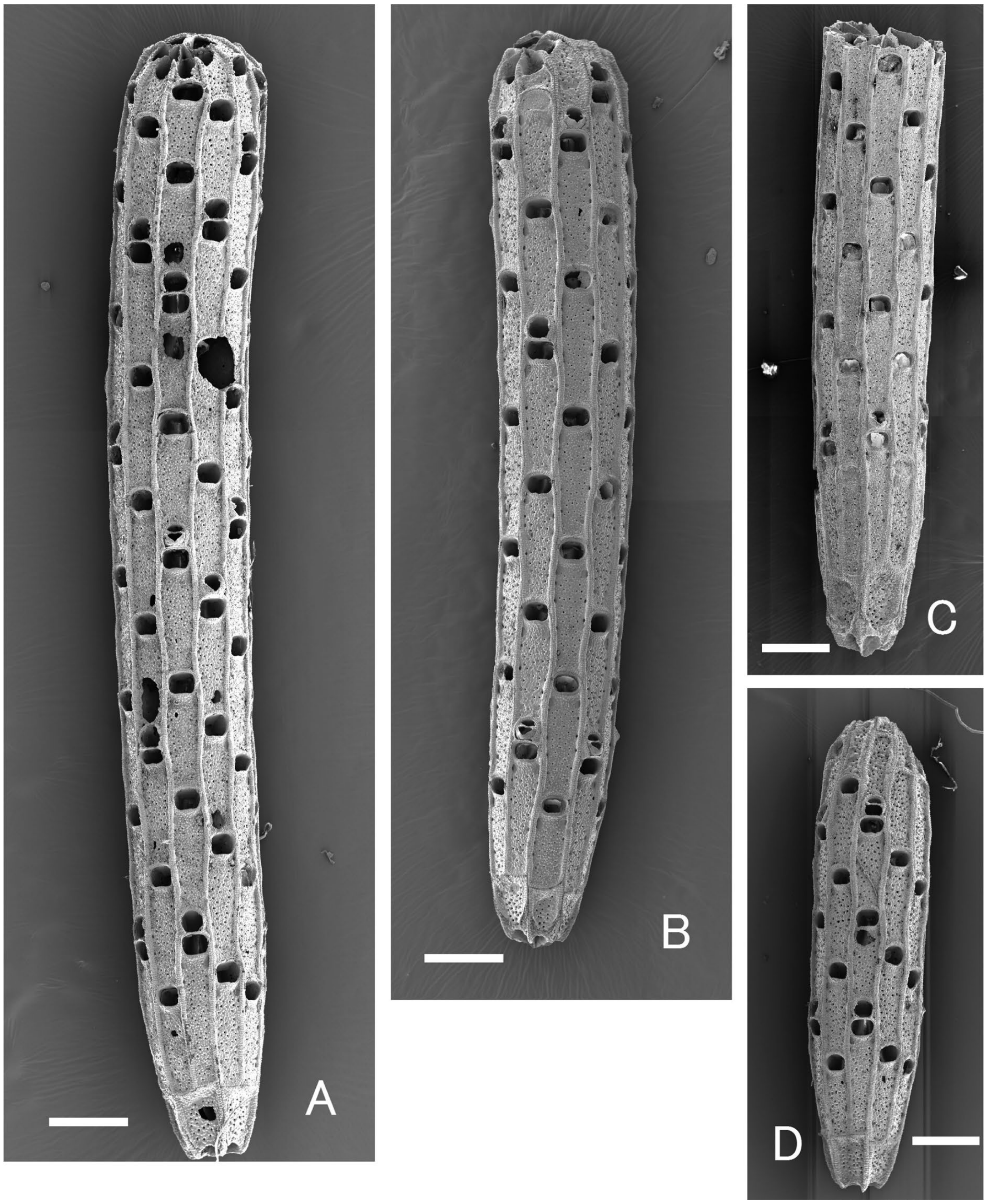

Figure 6. *Microporina quadristoma* sp. nov. **A,** holotype, longest internode (NMNS PA 18539); **B,** paratype, narrowest internode (NMNS PA 18541); **C,** paratype (NMNS PA 18540); **D,** shortest internode (NMNS PA 18542). Scale bars 500 μm.

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Diagnosis.—Internodes small, often markedly tapering proximally; zooids small, those at proximal end of internode with convex cryptocyst; orifice not noticeably dimorphic, semielliptical, proximal border straight or concave.

Material examined.—Holotype, NMNS PA 18518, locality A in Figure 1. Paratypes, NMNS PA 18519 (extensive secondary calcification), locality A in Figure 1, and 18520 (two short internodes, A, B), locality B in Figure 1. Other material examined, NMNS PA 18521, locality A in Figure 1, and SGBC-0458, locality B in Figure 1. All from the Setana Formation, Soebetsu Sandstone Member, Pleistocene, Kuromatsunai, Hokkaido, Japan.

Etymology.—The specific name comes from the Latin *minutus* (small), referring to the small-sized internodes.

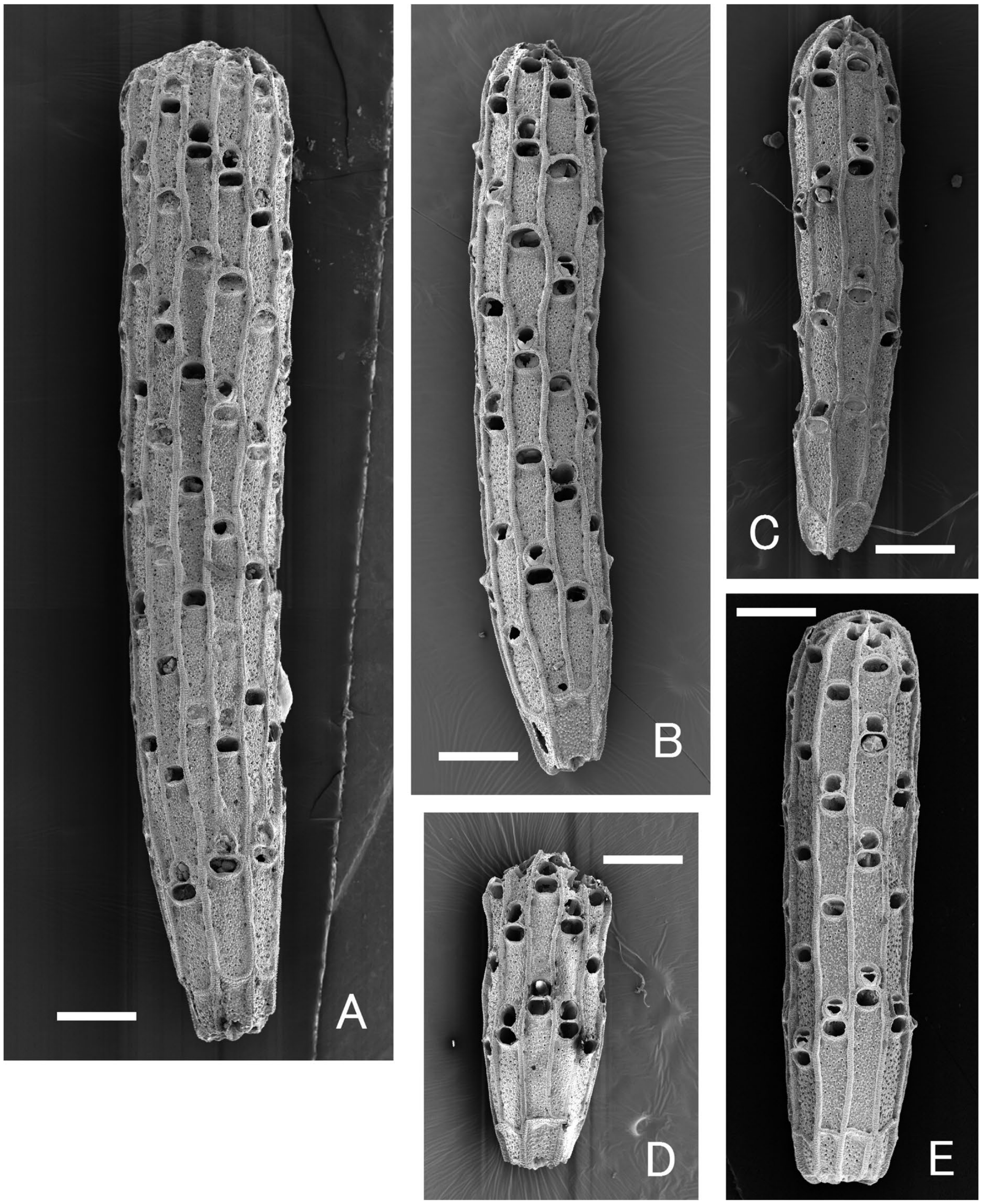

Figure 7. *Microporina soebetsuensis* sp. nov. **A,** paratype, long internode (NMNS PA 18530C); **B,** holotype (NMNS PA 18529); **C,** narrowest internode (NMNS PA 18533A); **D,** shortest internode (NMNS PA 18532A); **E,** paratype, internode with many proximal kenozooids (NMNS PA 18531). Scale bars 500 µm.

Type locality.—Downstream part of the Soebetsu River (locality A in Figure 1), Kuromatsunai, Hokkaido, Japan, Pleistocene Setana Formation.

Measurements (in millimeters).—NMNS PA 18518–18521 (includes all type series), and SGBC-0458. Autozooids (n = 57, 6): ZL, 0.47–0.86 (0.650 ± 0.081); ZW, 0.22–0.36 (0.296 ± 0.034); OrL, 0.08–0.11 (0.094 ± 0.008); OrW, 0.13–0.20 (0.165 ± 0.014). Avicularia (n = 10, 6): AvL, 0.13–0.20 (0.161 ± 0.023); AvW, 0.11–0.14 (0.130 ± 0.011).

Description.—Colony erect, consisting of small internodes (Figure 4) increasing in width distally. Minimum internode size 2.1 mm long and 0.63 mm in diameter (NMNS PA 18520A, Figure 4B); maximum size 4.6 mm long and 1.0 mm in diameter (NMNS PA 18518, holotype, Figure 4A). Internodes circular in transverse sec-

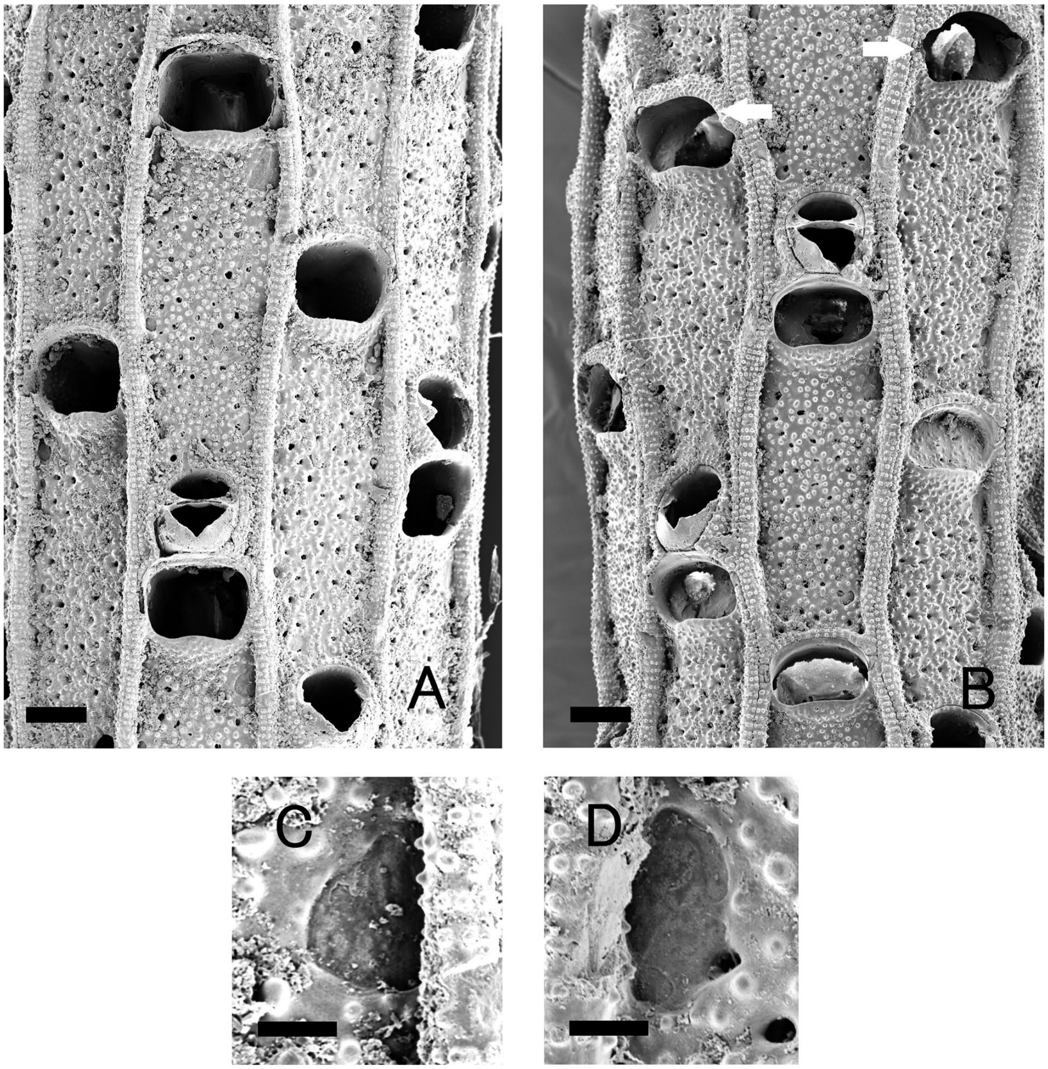

Figure 8. Comparison of zooids (A, B) and opesiules (C, D) in two species with rounded-quadrangular orifices. **A, C,** *Microporina quadristoma* sp. nov. (NMNS PA 18539, holotype); **B, D,** *M. soebetsuensis* sp. nov., with enlarged orifice (arrow) (NMNS PA 18529). Scale bars 100 µm in A, B, 25 µm in C, D.

tion, composed of 5–11 columns of zooids; proximal ends of internodes occupied by 2 or 4 kenozooids; kenozooids rarely formed two rows. Zooids elongate; pentagonal or hexagonal in outline. Frontal wall cryptocystal, flat in most zooids, convex in zooids at proximal end of internode, granulate, covered with somewhat deep pseudopores occluded by reticulately fused spicules (Figure 9C), and surrounded by salient, finely granulated mural rim. Mural rim thickening with secondary calcification. Opesiules (Figure 5F) elliptical, semielliptical, or triangular, usually longer than wide, occluded by smooth, calcified plate with vein-like surface sculpturing. Orifice (Figure 5C) semielliptical, proximal border straight or concave, with rounded corners, rarely elliptical. Oral spines and ovicells lacking. Avicularium distal to orifice of some zooids, longer than wide, directed proximally; mandibular portion of rostrum triangular; pivot bar complete, somewhat medially folded (Figure 5C).

Remarks.—*Microporina minuta* sp. nov. resembles *M. japonica* Canu and Bassler, 1929 in having semielliptical or elliptical orifices, with rounded corners, but differs from other *Microporina* species in the small size of internodes, and in the convex frontal wall of zooids at the extremely tapering proximal end of internodes.

Microporina quadristoma sp. nov.

Figures 6, 8A, 8C, 9D, 11C

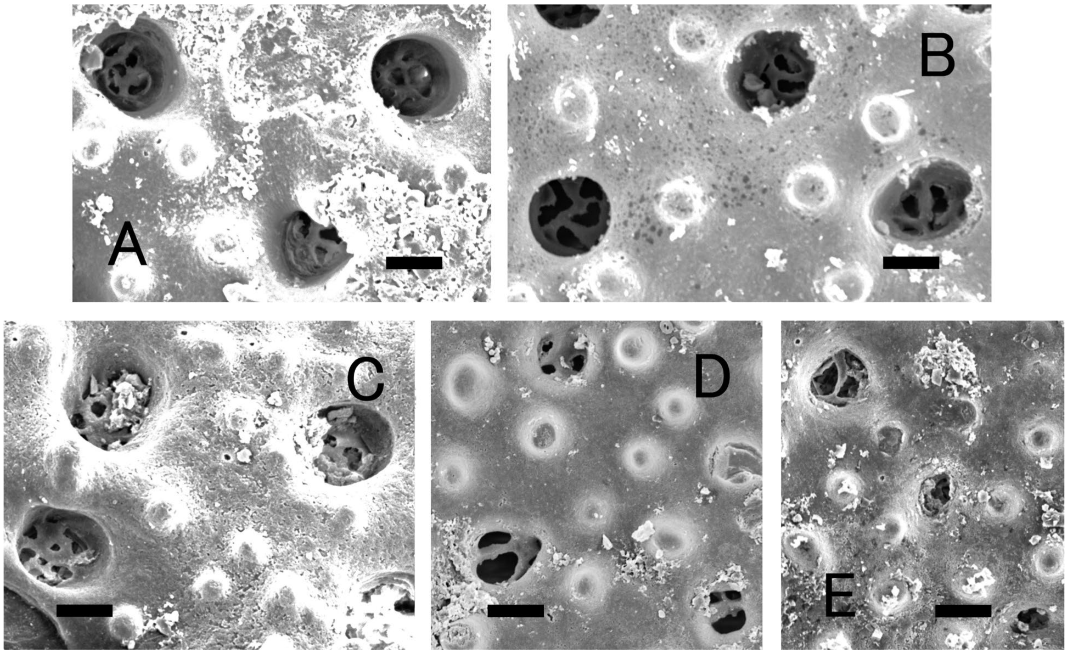

Figure 9. Pseudopores of *Microporina* species from Kuromatsunai. **A,** *Microporina japonica* Canu and Bassler, 1929 (NMNS PA 18522); **B,** *M. sakakurai* sp. nov. (NMNS PA 18511, holotype); **C,** *M. minuta* sp. nov. (NMNS PA 18518, holotype); **D,** *M. quadristoma* sp. nov. (NMNS PA 18539, holotype); **E,** *M. soebetsuensis* sp. nov. (NMNS PA 18530A, paratype). Scale bars 10 μm.

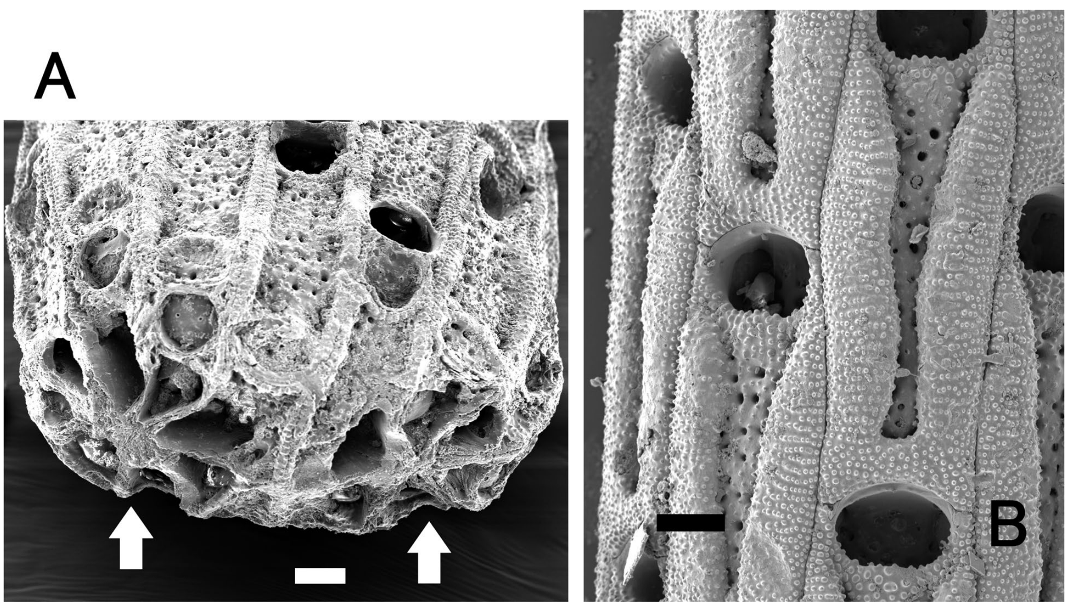

Figure 10. **A,** Position of the next internodes (arrows) at the distal end of an internode (*Microporina soebetsuensis* sp. nov., NMNS PA 18530C, paratype); **B,** Extremely thick secondary calcification of mural rim in *M. soebetsuensis* sp. nov. (NMNS PA 18538, paratype). Scale bars 100 μm.

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Microporina articulata (Fabricius, 1821): Sakakura, 1936, p. 260, pl. 15(5), fig. 5. (as "thin form")

Diagnosis.—Orifice large, rounded-quadrangular; no noticeable orificial dimorphism. Avicularium circular or elliptical, often wider than long, narrower than orifice.

Material examined.—Holotype, NMNS PA 18539,

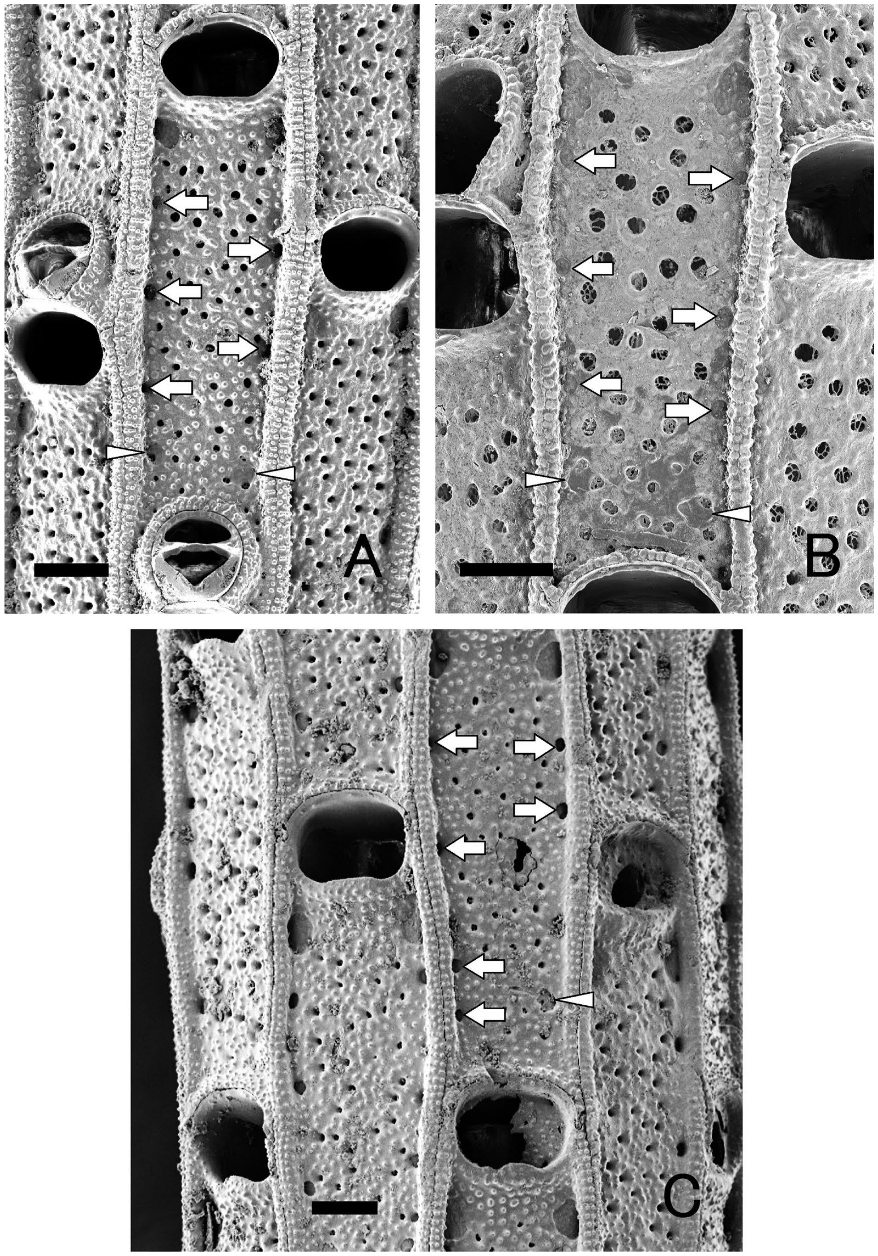

Figure 11. Small opesiule-like depressions (arrows) and large proximal depressions (arrowheads). **A,** *Microporina soebetsuensis* sp. nov., zooids showing relatively prominent opesiule-like depressions (NMNS PA 18453, paratype); **B,** *Microporina soebetsuensis* sp. nov., cryptocystal frontal wall after cessation of growth (NMNS PA 18537); **C,** *Microporina quadristoma* sp. nov. (NMNS PA 18541, paratype). Scale bars 100 µm.

locality B in Figure 1. Paratypes, NMNS PA 18540 (a narrowest internode), locality A in Figure 1, and 18541, locality B in Figure 1 (an internode with distinct opesiule-like depressions). Other material examined, NMNS PA 18542, 18543 (three internodes, A–C), 18544, locality A in Figure 1; 18545, locality B in Figure 1; SGBC-0472, locality B in Figure 1. All from the Setana Formation, Soebetsu Sandstone Member, Pleistocene, Kuromatsunai, Hokkaido, Japan.

Etymology.—The specific name comes from the Latin *quadri* (square) and *stoma* (opening), referring to the rounded quadrangular orifices.

Type locality.—Downstream part of the Soebetsu River (locality B in Figure 1), Kuromatsunai, Hokkaido, Japan, Pleistocene Setana Formation.

Measurements (in millimeters).—NMNS PA 18539 (holotype), 18540 (paratype), 18541 (paratype), 18542, 18543, 18544, 18545, and SGBC-0472. Autozooids (n = 177, 10): ZL, 0.60–1.08 (0.850 ± 0.086); ZW, 0.21–0.30 (0.265 ± 0.019); OrL, 0.11–0.16 (0.130 ± 0.012); OrW, 0.13–0.20 (0.175 ± 0.010). Avicularia (n = 47, 10): AvL, 0.12–0.16 (0.134 ± 0.009); AvW, 0.12–0.18 (0.144 ± 0.013).

Description.—Colony erect, consisting of long, cylindrical internodes (Figure 6). Minimum internode size 3.6 mm long (NMNS PA 18542, Figure 6D) and 0.88 mm in diameter (NMNS PA 18541, Figure 6B); maximum size 7.1 mm long (NMNS PA 18539, Figure 6A) and 1.2 mm in diameter (NMNS PA 18544). Internodes circular or elliptical in transverse section, composed of 10–12 columns of zooids; proximal ends of internodes occupied by 5 or 6 kenozooids. Zooids elongate; rectangular or hexagonal in outline, sides nearly parallel. Frontal wall cryptocystal, flat, finely granulated, covered with small pseudopores, surrounded by thin mural rim. Pseudopores relatively small, occluded by reticulately fused spicules (Figure 9D). Mural rim also finely granulated, rarely thickened with secondary calcification. Opesiules (Figure 8C) originally large, semielliptical or rounded-triangular, rarely elliptical; small opesiule-like depressions sometimes present along each side of cryptocyst (Figure 11C), not paired, covered with secondary calcification. Orifice wider than long; rounded-quadrangular, proximal margin straight, or slightly convex (Figure 8A). Oral spines and ovicells lacking. Avicularium distal to orifice of some zooids, circular or elliptical, generally wider than long directed proximally; mandibular portion of rostrum triangular; pivot bar complete, somewhat medially folded (Figure 8A).

Remarks.—Sakakura (1936: p. 260, text table; pl. 15(5), fig. 5) reported a "thin form" of what he considered to be *M. articulata* from the Setana Formation on Hokkaido. This form has slender internodes, rounded-quadrangular orifices (described as "elliptical" by Sakakura), and the avicularium is narrower than the orifice. The specimen he illustrated shows little variation in orifice shape; the orifice width, given as 0.17–0.18 mm, falls within the range of width in my material. Sakakura's "thin form" is unquestionably identified as this new species.

This species resembles Miocene fossils from Hokkaido assigned to *Microporina articulata* by Hayami (1970: p. 325, pl. 35, figs. 1, 2) in having rounded-quadrangular orifices that are not noticeably dimorphic. However, the sizes of the zooids (ZL, 0.88–1.32; ZW, 0.36) and orifices (OrL, 0.12; OrW, 0.22) in Hayami's specimens are larger than for all *Microporina* species from the Soebetsu Member.

Small opesiule-like depressions occur along the cryptocystal margins in both *Microporina quadristoma* and *M. soebetsuensis* (Figure 11) and these structures may be equivalent to the additional opesiules reported for *Microporina articulata notoensis* Sakakura, 1936 from the Miocene Nanao Calcareous Sandstone (see the Discussion).

Microporina soebetsuensis sp. nov.

Figures 7, 8B, 8D, 9E, 10, 11A, B

ZooBank lsid: urn:lsid:zoobank.org:act:91573D2F-8993-4945-8358-AD52BEC8B68E

Diagnosis.—Orifice typically rounded-quadrangular, proximal margin straight or convex; orifice markedly dimorphic in some internodes, being larger and less quadrate in some autozooids not followed by an avicularium. Avicularium circular, narrower than orifice.

Material examined.—Holotype, NMNS PA 18529, locality A in Figure 1. Paratypes, NMNS PA 18530 (long internodes, A, C and one of typical internodes B), and 18531 (an internode with many proximal kenozooids), locality A in Figure 1. Other material examined, NMNS PA 18453, 18532 (five internodes, A–E), 18533 (four internodes A–D), 18534, 18536, 18537, locality A in Figure 1; 18535, 18538, locality B in Figure 1; SGBC-0489 (six internodes, A–F), locality A in Figure 1. All from the Setana Formation, Soebetsu Sandstone Member, Pleistocene, Kuromatsunai, Hokkaido, Japan.

Etymology.—The specific name is derived from the Soebetsu River, the type locality.

Type locality.—Downstream part of the Soebetsu River (locality A in Figure 1), Kuromatsunai, Hokkaido, Japan, Pleistocene Setana Formation.

Measurements (in millimeters).—NMNS PA 18529 (holotype), 18530 (paratypes), 18531(A, C, E) (paratype), 18533(A, B, C), 18534–18536, and SGBC-0489(A, C, E). Autozooids (n = 280, 17): ZL, 0.51–1.08 (0.751 ± 0.098); ZW, 0.20–0.33 (0.258 ± 0.025); OrL, 0.08–0.15 (0.109 ± 0.011); OrW, 0.13–0.20 (0.162 ± 0.012). Avicularia (n = 98, 17): AvL, 0.10–0.17 (0.135 ± 0.011); AvW, 0.10–0.16 (0.132 ± 0.011).

Description.—Colony erect, consisting of internodes (Figure 7) increasing in width distally. Internodes often constricted in middle region or curved. Minimum internode size 2.0 mm long (NMNS PA 18532A, Figure 7D) and 0.72 mm in diameter (NMNS PA 18533A, Figure 7C); maximum size 8.9 mm long (NMNS PA 18535) and 1.1 mm in diameter (NMNS PA 18536). Internodes circular or elliptical in transverse section, composed of 8–15 columns of zooids; proximal ends of internodes occupied by 5–9 kenozooids. Zooids elongate; rectangular or hexagonal. Frontal wall cryptocystal, flat, finely granulated, covered with small pseudopores, and surrounded by thin mural rim. Pseudopores often occluded with reticulately fused spicules. Mural rim also finely granulated, and

Table 1. Comparison of five *Microporina* species from the Setana Formation. The numbers of the examined internodes or zooids are shown in parentheses.

	M. japonica	*M. sakakurai*	*M. minuta*	*M. quadristoma*	*M. soebetsuensis*
Shape of the internodes	mainly pencil-shaped	mainly club-shaped	club-shaped	pencil-shaped	mainly pencil-shaped
Length of the internode in mm	2.2–11 (12)	3.2–10 (10)	2.1–4.6 (3)	3.6–7.1 (6)	2.0–8.0 (18)
Width of the internode in mm	0.76–1.2 (12)	1.1–2.0 (10)	0.63–1.0 (6)	0.88–1.2 (11)	0.72–1.1 (18)
Number of zooidal columns	8–13 (12)	13–20 (10)	5–11 (6)	10–12 (11)	8–15 (18)
Number of proximal kenozooids	4–7 (12)	5–8 (10)	2 or 4 (3)	5–6 (6)	5–9 (18)
Average length of zooids in mm	0.76 (288)	0.80 (298)	0.65 (57)	0.85 (177)	0.75 (280)
Average width of zooids in mm	0.30 (288)	0.30 (298)	0.30 (57)	0.27 (177)	0.26 (280)
Frontal granulation	a little coarse	a little coarse	a little coarse	fine	fine
Frontal pseudopores	deep	deep	deep	small, shallow	small shallow
Secondary calcification	developed	developed	developed	not developed	developed
Vein-like surface sculpture of opesiules	developed	developed	developed	not developed	not developed
Small opesiule-like depressions	not developed	not developed	not developed	developed	developed
Shape of the orifice	semielliptical or elliptical	semielliptical or elliptical	semielliptical or elliptical	rounded-quadrate	rounded-quadrate
Dimorphism of the orifice	not developed	developed	not developed	developed	not developed
Average length of the orifice in mm	0.10 (288)	0.11 (298)	0.09 (57)	0.13 (177)	0.11 (280)
Average width of the orifice in mm	0.18 (288)	0.19 (298)	0.17 (57)	0.18 (177)	0.16 (280)
Average length of the avicularium in mm	0.19 (113)	0.22 (117)	0.16 (10)	0.13 (47)	0.14 (98)
Average width of the avicularium in mm	0.16 (113)	0.17 (117)	0.13 (10)	0.14 (47)	0.13 (98)

markedly thickened with secondary calcification (Figure 9D). Opesiules large, circular or semielliptical; two to five small, opesiule-like depressions along each side of cryptocyst (Figure 10A, B), not paired, covered with secondary calcification. Orifice rounded-quadrate, wider than long; proximal border straight or slightly convex; markedly enlarged and less quadrate in some autozooids not followed by avicularium (Figure 8B), with distal margin more curved. Proximal rim of orifice thickened with secondary calcification. Oral spines and ovicells lacking. Avicularium distal to orifice of some zooids, directed proximally; mandibular portion of rostrum triangular; pivot bar complete, somewhat medially folded (Figure 8B).

Remarks.—This species resembles *Microporina quadristoma* sp. nov. described above in the shape of orifice, but differs in the marked orificial dimorphism, which is similar to that in *M. sakakurai*. The zooidal length, orifice length and avicularium width are smaller than in *M. quadristoma*.

Discussion

This study indicates that characters diagnostic and perhaps synapomorphic for *Microporina* are frontal pseudopores occluded with reticulately fused elements, and the proximally directed avicularium with a medially folded pivot bar, in addition to the colony form and the cryptocystal frontal wall surrounded by a raised mural rim. On the other hand, the shape of the orifice and aspects of the opesiules may be important diagnostic characters among *Microporina* species, as noted by Arakawa (2016). The five *Microporina* species from Kuromatsunai, comprise two distinct groups based on alternative states of these two characters (Table 1). In one group (*M. japonica*, *M. sakakurai*, and *M. minuta*), the orifice is semielliptical or elliptical; the cryptocyst has relatively large and deep pseudopores; the opesiules are occluded with a thin plate showing vein-like surface sculpturing; and the avicularium is longer than wide. In the other group (*M. quadristoma* and *M. soebetsuensis*), the orifice is rounded-quadrangular, sometimes with a slightly convex proximal margin; the cryptocyst has smaller pseudopores; the occlusion of the opesiules lacks vein-like surface sculpturing; and the avicularium is circular or wider than long. Species with marked orificial dimorphism (*M. sakakurai* and *M. soebetsuensis*) occur in both groups.

Broad intraspecific variation in the following characters was observed in all of the *Microporina* species, with some noteworthy aspects as follows.

Shape of the internodes and number of zooidal columns.—The internodes in *Microporina sakakurai* increase conspicuously in width distally, but some internodes do not widen as much as in *M. japonica*, as remarked above. *Microporina minuta* also shows internodes increasing distally in width, but the number of zooidal columns does not increase in this species. *M. minuta* has the proximally tapering kenozooids and sometimes two rows of kenozooids (Figure 4C). If the number of new zooidal columns at the distal end of an internode (Figure 10A) indicate the number of the proximal kenozooids of the next internode, the number of the proximal kenozooids is roughly maintained among *Microporina* species from Soebetsu, except in the proximally tapering internodes in *M. minuta*.

Secondary calcification.—Except for *Microporina quadristoma*, all of the species from Kuromatsunai can show conspicuous thickening of the mural rim, the proximal part of the orificial rim, the frontal wall, and the rim of the avicularium. The orifice and the avicularium are also frequently occluded with a thin layer of calcification (e.g. Figures 5B, 8B). In particular, *M. soebetsuensis* sometimes shows extreme thickening of the mural rim (Figure 10B). Material identified as *M. articulata* from the Miocene Kaigarabashi Sandstone shows similarly heavy secondary calcification (Hayami, 1970: pl. 35, fig. 2).

Opesiule-like depression.—I observed small non-paired opesiule-like depressions along the cryptocystal margins in both *M. soebetsuensis* and *M. quadristoma* (Figure 11), with one or two larger, irregularly shaped depressions sometimes present near the proximal end. Zooids in which the cryptocyst has ceased growing show the original circular shape of these depressions (NMNS PA 18537, Figure 11B), as in *Metamicropora* (Arakawa, 2016), suggesting that these depressions are not simply due to unevenness in the frontal calcification. However, the irregularity of size and distribution of these depressions is different from *Metamicropora*, and these structures cannot be considered to be “additional opesiules”. They become more or less inconspicuous as the cryptocyst thickens and secondary calcification of the lateral mural rim eventually covers them.

Similar opesiule-like depressions are evident in two Miocene species, *Microporina articulata notoensis* Sakakura (1936: p. 261, pl. 15(5), figs. 6–9) and *M. articulata* sensu Hayami (1970: pl. 35, fig. 1). Sakakura concluded these depressions to be additional opesiules and stated that his Recent specimens of *M. articulata* from the Tsugaru Strait bore two or three small additional opesiules. I recently observed newly collected specimens of *M. articulata notoensis* Sakakura, in which the opesiule-like depressions have become more conspicuous due to secondary calcification (Arakawa, unpublished data). It is not clear whether Sakakura’s conclusion is correct, and further study of this character is needed.

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