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Iodictyum akaishiensis sp. nov.: a new Miocene phidoloporid (Bryozoa, Cheilostomata) from the Moniwa Formation, Sendai, Japan

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Abstract. **A new Miocene phidoloporid, *Iodictyum akaishiensis* sp. nov., was collected from the Moniwa Formation (Langhian) near the Akaishi Bridge, Sendai City, Japan. It is the first fossil record of *Iodictyum* in Japan, and the fifth discovery of Miocene fossils of the genus from the Indo-Pacific area. The species resembles some Recent species from the western Pacific, especially in the large marginal pores, an open peristomial sinus and shaft, and subtriangular ooecial labellum. The characteristics of *Iodictyum* from Eocene to Recent are compared, and the trend of evolution in the genus is inferred.**

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Keywords: Bryozoa, *Iodictyum*, Langhian, northern Japan, Sendai

Introduction

Iodictyum Harmer, 1933 is one of 26 genera in the cheilostomatous bryozoan family Phidoloporidae Gabb and Horn, 1862 (Bock, 2017). This family had been historically mainly treated under the invalid name Reteporidae Smitt, 1868 (see discussion in Gordon, 1989), and is well known for including many species of fenestrate erect colonies. In Japanese, it has been called the "*Amikokemushi*" group (Mawatari, 1965), meaning the reticular bryozoans.

Although some of the Recent species, such as *Iodictyum axillare* (Ortmann, 1890) and *I. sanguineum* (Ortmann, 1890), are well known in Japan, no fossil of *Iodictyum* has been described from there. Among the previous studies in Japan, only *Schizoretepora tumescens* (Ortmann, 1890) and *S. tamagawensis* Zágoršek, Takashima and Hirose, 2015 have been described from Japan (Hayami, 1971, 1975; Nishizawa and Sakagami, 1986; Nishizawa, 1987; Zágoršek *et al.*, 2015), and other phidoloporids have been only listed as indeterminable species (Hayami, 1980, 1981; Arakawa, 1995). One of the reasons for the rarity of fossil records is their generally poor preservation, resulting from post-mortem transportation in most phidoloporid fossils. Especially, the frontal wall of the ovicell, a key character in the identification of phidoloporid genera, is easily broken.

In 2017, I visited a riverside outcrop of the Moniwa Formation near the Akaishi Bridge (known as "Kita-Akaishi"), Sendai City, Miyagi Prefecture, a famous locality for Miocene fossils, and found only one well-preserved fossil of *Iodictyum*. After comparison with fossil and Recent species of the genus, I concluded that this is a new bryozoan species.

This is only the fifth record of Miocene *Iodictyum* from the Indo–Pacific area. The first study was made by Brown (1952) who proposed two species, *I. acanthoides* Brown, 1952 (Serravallian) and *I. ligarense* Brown, 1952 (Burdigalian) from New Zealand. The third species is *I. megapora* Guha and Gopikrishna, 2007, from the Aquitanian of India (Guha and Gopikrishna, 2007). *Filiflustrella pacifica* Stoliczka, 1865, from the Burdigalian of New Zealand was placed in *Iodictyum* by Gordon *et al.* (2009), representing the fourth species. Brown (1958) reported one more species, *Iodictyum* sp., but its ovicell was not found. This species is not counted here.

Thus, I here provide a description of this new *Iodictyum* species, which may contribute to the study of the evolution and radiation in the genus.

Geological setting and bryozoan fauna

The Moniwa Formation comprises the lower part of the Natori Group distributed in the southwestern part of the Sendai Plain. The Natori Group consists of the Tsukinoki, Takadate, Moniwa, Hatatate and Tsunaki formations in ascending order (Kitamura *et al.*, 1986). Volcanic rocks (mainly andesite and andesitic breccia) of the Takadate Formation are unconformably overlain by the basal conglomerate of the Moniwa Formation around the locality of this study. Nomura and Maeda (2008), who studied the taphonomy of fossil barnacles in these two formations, interpreted their boundary as a ravinement surface, based on autochthonous barnacles and abundant perforation by stone borers on the boulder surface. The Moniwa Formation is composed mainly of coarse-grained sandstone and conglomerate, and conformably overlain by fine-grained sandstone of the Hatatate Formation. The K–Ar age of the Takadate Formation was dated about 22 Ma for andesite lava, and about 15 to 13 Ma for basalt and dacite (Konda and Ueda, 1980; Uto *et al.*, 1989). On the other hand, the biostratigraphy of the Moniwa and Hatatate formations have been studied using planktonic foraminifers (Saito, 1963; Oda and Sakai, 1977; Ibaraki, 1981; Kitamura *et al.*, 1986; Shimamoto *et al.*, 2001; Fujiwara *et al.*, 2008; Idehara *et al.*, 2013), diatom (Maruyama, 1984; Yanagisawa, 1999), calcareous nannofossils (Honda, 1982; Yanagisawa, 1999) and radiolarians (Oda and Sakai, 1977). The Moniwa Formation is interpreted as the N8 to N9 planktonic foraminiferal zone of Blow (1969), and the CN3 to 4 calcareous nannofossil zone of Okada and Bukry (1980). Therefore, the age of the Moniwa Formation is assigned to the Langhian (see Suzuki *et al.*, 2019).

The Moniwa Formation yields abundant fossils, such as foraminifers, sponges, corals, bryozoans, brachiopods, molluscs, ostracods, barnacles, crabs, echinoids, etc. According to Kitamura *et al.* (1986), the benthic foraminifers mainly indicate deposition in the lower sublittoral zone. Masuda (1969) and Sato (1991) compared molluscan assemblages of the fossil localities, and concluded that the Moniwa Formation at "Kita-Akaishi" was deposited in a rocky or gravelly tidal to shallow marine zone. Saijo (2010) listed the fauna at the sampling locality of this study.

The presence of bryozoan fossils in the Moniwa Formation was referred to in early studies (e.g. Nomura, 1940). Only Hayami (1976) has described the bryozoans, listing 27 species of cheilostomes from the vicinity of the type locality, eight of which were illustrated. Unfortunately, however, the whereabouts of Hayami's bryozoans are unknown. Most of the 27 cheilostomes are encrusting species, but *Caberea hataii* Okada, 1929, *Micropora articulata* (Fabricius, 1821) and *Cellaria nanaoensis* Hayami, 1973 form rooted erect colonies, and *Membranipora arborescens* (Canu and Bassler, 1928) (now in *Biflustra* or *Acanthodesia*) and *Myriapora subgracilis* (d'Orbigny, 1852) (as *M. subgracila*) are erect rigid species. These erect bryozoans may need to be taxonomically restudied.

Material and method

The study material is a colony of a fenestrated phidoloporid collected from an outcrop by the Natorigawa River immediately downstream from the Akaishi Bridge (Figure 1). It was broken into four parts during extraction. These were cleaned ultrasonically and in a hydrogen peroxide solution. After the cleaning, specimens were mounted on aluminum stubs with adhesive tape, for scanning electron microscopy (SEM) observation. They were Au-coated in an ion coater (model SC-701, Sanyu Denshi) and observed with a JSM-5310 microscope (JEOL) at the Department of Geology and Paleontology, National Museum of Nature and Science, Tsukuba. Type material is deposited in the Paleontological Collection of the Department of Geology and Paleontology, National Museum of Nature and Science, Tsukuba (collection code NMNS PA).

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. Abbreviations used for characters measured are as follows: ZL, autozooid length; ZW, autozooid width; OrL, orifice length; OrW, orifice width; OvL, ovicell length; OvW, ovicell width; AvL, avicularium length; AvW, avicularium width.

Systematic description

Order Cheilostomatida Busk, 1852
Suborder Flustrina Smitt, 1868
Superfamily Celleporoidea Johnston, 1838
Family Phidoloporidae Gabb and Horn, 1862
Genus ***Iodictyum*** Harmer, 1933

Type species.—*Retepora phoenicea* Busk, 1854.

Diagnosis.—Colony usually fenestrate. Frontal wall without pseudopores, with or without marginal pores. Primary orifice generally sinuate with condyles, immersed within a peristome. Peristome at first projecting; secondary orifice sinuate or bearing a pseudospiramen, sometimes marginally denticulate. Oral spines absent. Avicularia present or absent, frontal or fenestral, rarely

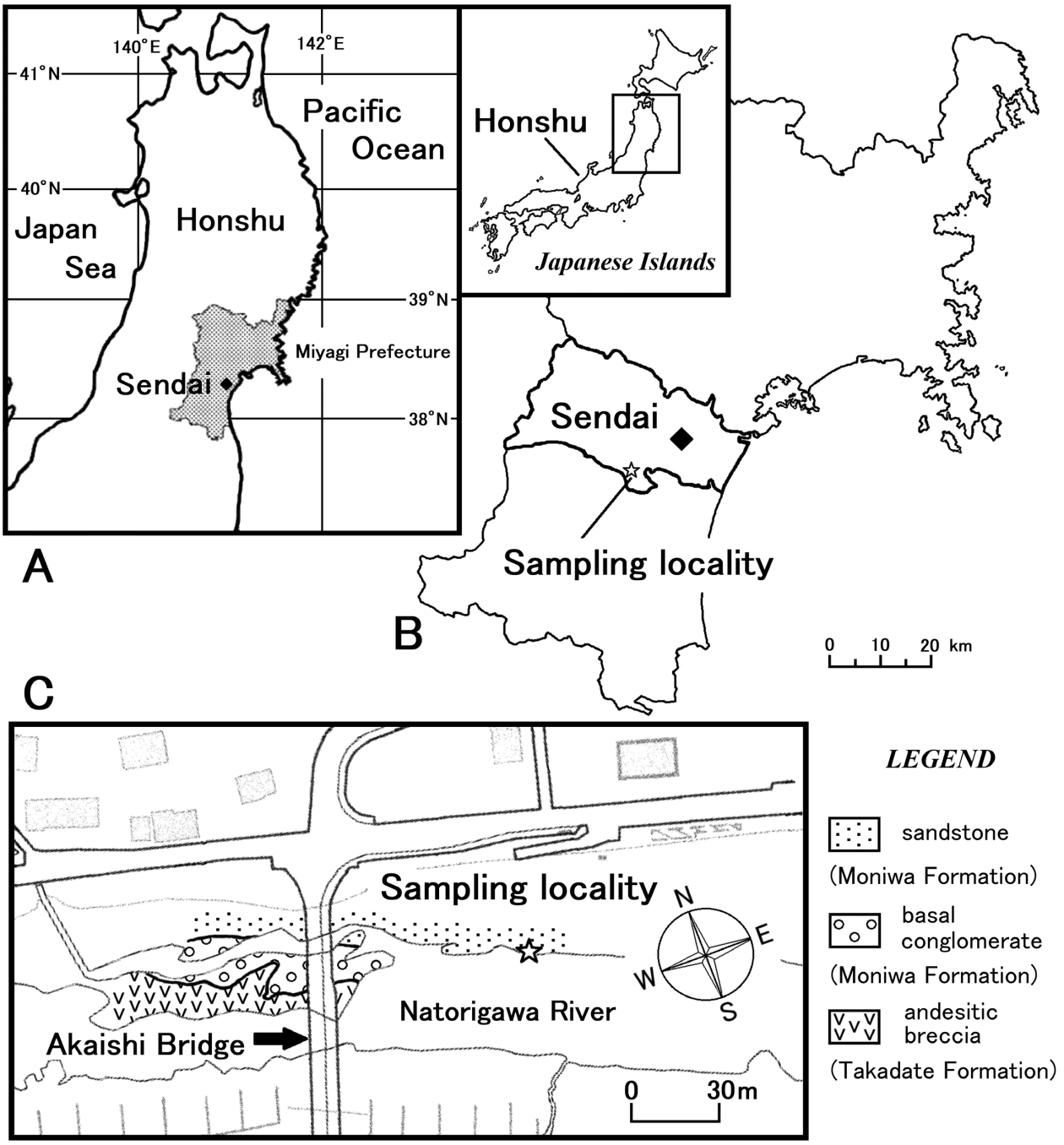

Figure 1. The sampling locality of the holotype material of *Iodictyum akaishiensis* sp. nov. **A**, northern Honshu and Miyagi Prefecture; **B**, Sendai City and the sampling locality; **C**, detail of the sampling locality and geology around the Akaishi Bridge based on Saijo (2010).

peristomial. Ovicell usually having a proximal labellum flanked by lateral sinus. (see Discussion)

Iodictyum akaishiensis sp. nov.

Figures 2–4

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Diagnosis.—*Iodictyum* bearing large marginal pores, open peristomial sinus, massive orificial condyles, triangular frontal avicularia near the median line of zooid,

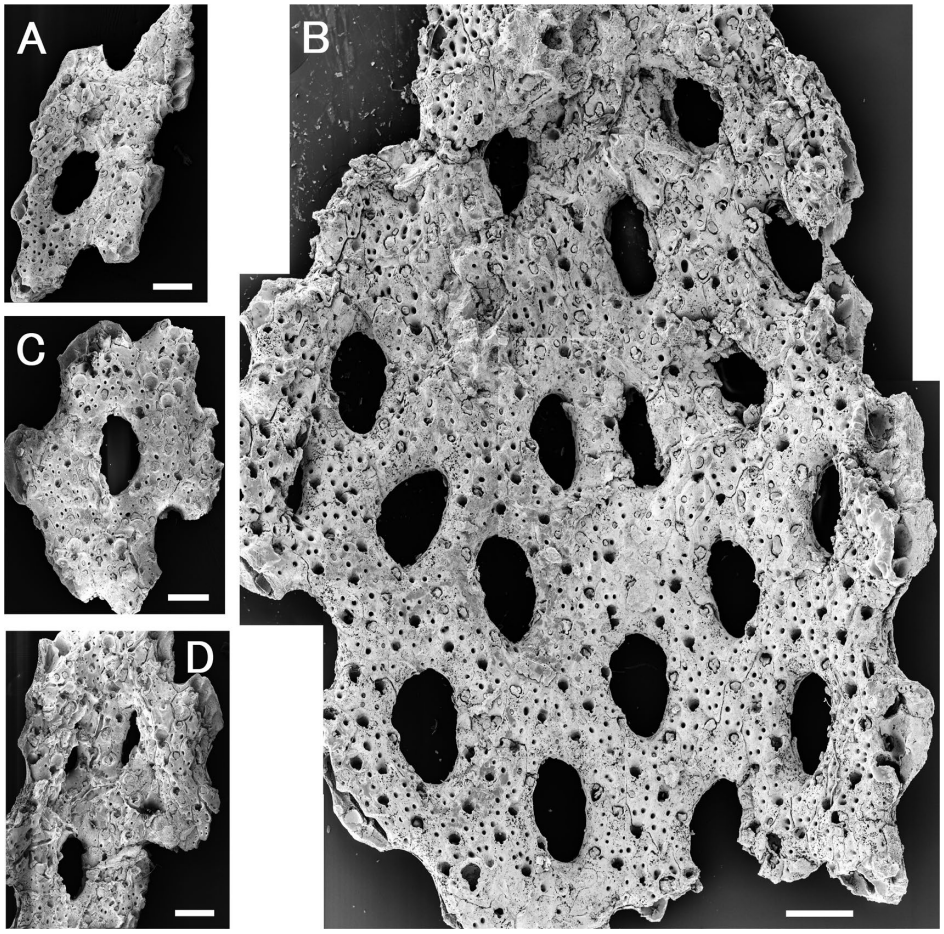

Figure 2. Holotype of *Iodictyum akaishiensis* sp. nov. **A**, NMNS PA 18692A; **B**, NMNS PA 18692B; **C**, NMNS PA 18692C; **D**, NMNS PA 18692D. Scale bars: 500 μm.

directed proximolaterally, and ovicell with tapering median labellum that creates an M-shaped proximal margin.

Etymology.—Species name alludes to the name of the type locality, the *Akaishi Bridge*.

Type material.—Holotype, NMNS PA 18692, Moniwa Formation, near Akaishi Bridge, Sendai City, Miyagi Prefecture, Japan, consisting of four fragments A to D originated from a single colony.

Type locality.—About 70 m east of the Akaishi Bridge (38°12′54.7″N, 140°45′21.5″E), the left side of the Natorigawa River, Moniwa, Taihaku Ward, Sendai City, Miyagi Prefecture, Japan, middle Miocene Moniwa Formation (Langhian).

Measurements (in millimeters).—NMNS PA 18692. Autozooids (n = 81, 1): ZL, 0.37–0.57 (0.461 ± 0.040); ZW, 0.18–0.36 (0.246 ± 0.029); OrL, 0.08–0.13 (0.108 ± 0.012); OrW, 0.08–0.12 (0.103 ± 0.009). Avicularia (n = 13, 1): AvL, 0.10–0.17 (0.140 ± 0.019); AvW, 0.06–0.11 (0.087 ± 0.010). Ovicell (n = 18, 1): OvL, 0.15–0.26 (0.205 ± 0.030); OvW, 0.16–0.22 (0.194 ± 0.016).

Description.—Colony erect, reticulate; trabeculae consisting of 3 to 7 autozooidal series (Figure 2). Fenestrae generally oval, 0.85 mm long and 0.41 mm wide on average. Zooids hexagonal. Frontal a little convex, almost smooth, with 4 to 6 large marginal pores (Figure 3A, B). Primary orifice keyhole-shaped, longer than wide, immersed in the peristome and thick frontal wall; rarely a pair of very large condyles preserved (Figure 3D); peristome not especially projecting, with a U-shaped sinus. Oral spines absent. Frontal avicularia occasionally present near the median line of zooid, directed proximolaterally; mandibular portion of rostrum triangular; pivot bar narrow, complete (Figure 3A, C). Intrafenestral avicularium rarely present, situated at the proximal end of the fenestrae, about 0.15 mm long, directed laterally; mandibular portion of rostrum triangular, some rostral tip curved upward along the wall of fenestra, pivot bar lack-

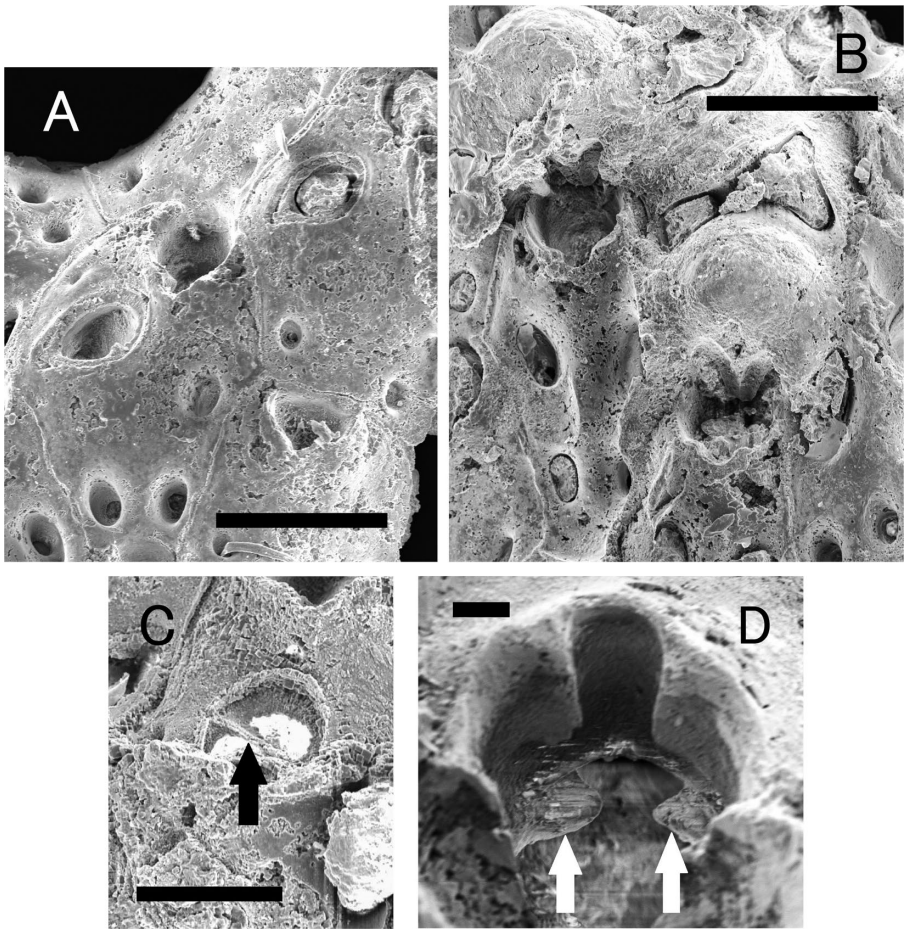

Figure 3. Close up of zooids, orifices, avicularia and ovicells of *Iodictyum akaishiensis* sp. nov., holotype. **A**, autozooids with frontal avicularia (NMNS PA 18692A); **B**, ovicellate zooids (NMNS PA 18692A); **C**, pivot bar of frontal avicularium (arrow) (NMNS PA 18692B); **D**, primary orifice with a pair of very large condyles (arrows) and U-shaped peristomial sinus with sinus shaft (NMNS PA 18692C). Scale bars: 200 μm in A, B, 100 μm in C, 20 μm in D.

ing (Figure 4B, C). Ovicell globular, almost smooth, with a subtriangular tapering median labellum and indentations either side that create an M-shaped proximal margin to the ovicell; a tiny median pore also present in the distal part of the labellum (Figure 3B).

Remarks.—This species resembles three Recent species of the genus in Japan, *Iodictyum axillare* (Ortmann, 1890), *I. sanguineum* (Ortmann, 1890) and *I. deliciosum* (Buchner, 1924), and is also similar to *I. willeyi* Harmer, 1934, ranging from Indonesia to Australia, and *I. spicatum* Harmer, 1934, from the Torres Strait. All of these species and *I. akaishiensis* sp. nov. have salient marginal pores and frontal avicularia directed proximally to proximolaterally, and a pseudospiramen is not formed. Especially, *I. sanguineum* and *I. willeyi* also have an ovicell with a proximally tapering subtriangular ooecial labellum and a median pore, as in the new species (Harmer, 1934; Hayward, 2004). However, *I. akaishiensis* sp. nov. is distinguished from the other species by the shape of avicularia. The mandibular portion of rostrum is short in the frontal avicularia of *I. sanguineum*, and the large fenestral avicularium is spatulate in both *I. sanguineum* and *I. willeyi*.

Among six fossil species of *Iodictyum* (see Bock, 2016), *I. acanthoides* Brown, 1952, from the Miocene of New Zealand resembles *I. akaishiensis* sp. nov. in the subtriangular labellum and the M-shaped proximal margin of the ovicell, but differs in the smaller marginal pores and small rounded avicularia. *Iodictyum megapora* Guha and Gopikrishna, 2007, from the Miocene of India is somewhat similar to *I. akaishiensis* sp. nov. in having large marginal pores and a subtriangular labellum, but has a pseudospiraminal pore and no avicularia.

Occurrence.—Known only from the type locality, middle Miocene (Langhian).

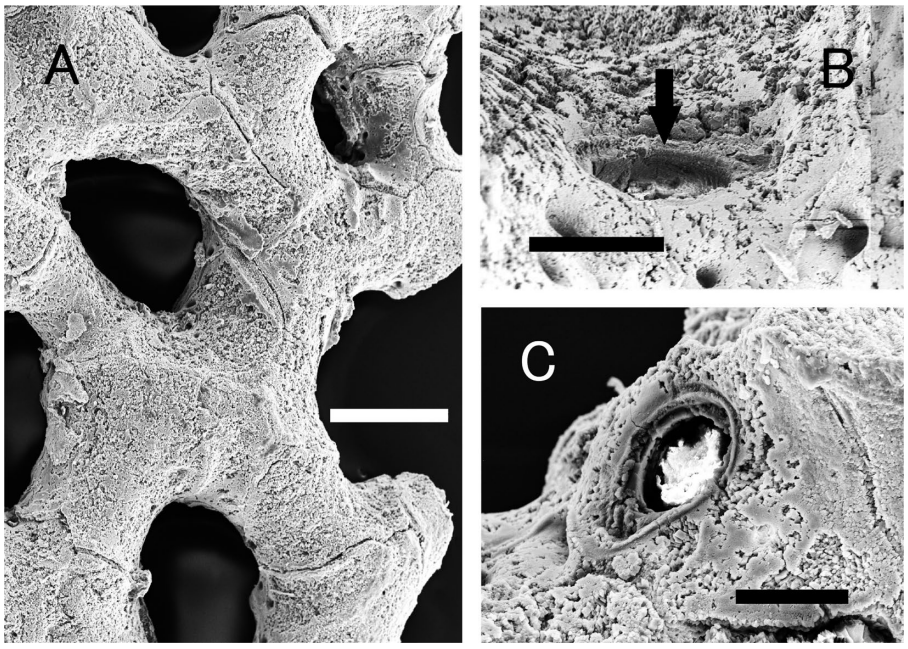

Figure 4. Dorsal surface of colony and fenestral avicularium of *Iodictyum akaishiensis* sp. nov. (NMNS PA 18692B), holotype. **A**, dorsal surface of colony; **B**, fenestral avicularium (arrow) with upward curving tip; **C**, fenestral avicularium showing distinct outline. Scale bars: 500 μm in A, 100 μm in B and C.

Discussion

The present new species is assigned to the genus *Iodictyum*, although the marginal denticulation of peristome was not observed. It is the first fossil record of *Iodictyum* in Japan.

According to Harmer's (1933) original concept of the genus, *Iodictyum* has: (1) fenestrate colonies with rare exceptions, (2) a peristome at first projecting (less so with the secondary calcification), with marginal teeth or internal denticles, (3) no oral spines, and (4) an ovicell with a free tongue or labellum, a median carina (= longitudinal ridge) and usually a minute pore. In the report of the Siboga Expedition, he stated that the genera in Reteporidae (= Phidoloporidae) are distinguished mainly by the characters of the ovicells (Harmer, 1934). However, both the shape and the development of the ooecial labellum are diverse. Species may lack a labellum, e.g. *Iodictyum bicuspidatum* Gordon and d'Hondt, 1997. On the other hand, it is known that other genera in Phidoloporidae also have ovicells with a subtriangular labellum. For example, *Reteporellina babelensis* (Chapman, 1941) bears not only a longitudinal fissure but also a minute pore distal to the labellum (Hayward, 2004). To my best knowledge, the mode of ovicell formation in *Iodictyum* shown by Harmer (1934), which starts with a longitudinal median sinus as in *Schizoretepora*, can be reasonably applied to other genera.

Although Harmer (1933, 1934) did not emphasize the absence of suboral or peristomial avicularia, his "labial avicularia" constitute one of the distinct characters in *Iodictyum*. Genera such as *Reteporella* and *Reteporellina* include many species with "labial avicularia". In contrast, such avicularia are absent in most species in *Iodictyum*, although *I. trochus* Gordon and d'Hondt, 1997 has peristomial avicularia.

Therefore, the diagnosis of *Iodictyum* may be said to include the absence of oral spines and rarity of suboral or peristomial avicularia, as well as having a well-developed ooecial labellum flanked by lateral sinus. However, there is ambiguity in the difference among three genera, *Iodictyum*, *Reteporella*, and *Reteporellina* (Table 1). Zágoršek (2010) suggested in his generic diagnosis that *Iodictyum* may have no labial avicularia. In this study, I avoid making any conclusions on this problem, because no definite evidence was supplied.

On the other hand, Harmer (1933, 1934) divided *Iodictyum* into "Section A" with brilliantly coloured colonies and "Section B" with white colonies. The former has large marginal pores, a thickly chitinized operculum and symmetrical ovicellular sinus. Although the colour of *I. akaishiensis* sp. nov. in life is not known, all the above five similar Recent species are included in Harmer's "Section A". The discovery of *I. akaishiensis* sp. nov.

Table 1. Comparison between *Iodictyum*, *Reteporella* and *Reteporellina*. (* *Reteporellina projecta* Gordon and d'Hondt, 1997, with oral spines)

	Iodictyum	*Reteporella*	*Reteporellina*
Colony form	fenestrate with rare exception	fenestrate or open branching	sometimes anastomosing
Peristome	not so projecting marginal teeth present or absent	generaly not projecting	generally projecting with distinct marginal teeth
Oral spines	absent	present or absent	very rare *
Lavial avicularium	very rare	generally present	present or absent
Ovicell	labellum distinct median fissure rare	labellum rare median fissure distinct	labellum distinct median fissure generally present

demonstrates that this species group had already radiated in the Indo–Pacific region by the middle Miocene.

However, the oldest species of the genus *Iodictyum*, *I. rubeschi* (Reuss, 1848) and *I. labellatum* Zágoršek, 2001, from the latest Eocene (Priabonian) of Hungary do not have salient marginal pores (Zágoršek, 2001). The long median suture lines of their ovicells rather resemble those of *Reteporella* and *Reteporellina*. A similar structure is restricted to the proximal part of the ovicell in most Recent species of *Iodictyum*. An exception is *I. illinguum* Gordon and d'Hondt, 1997, from New Caledonia. Thus, I infer that the diminution of the occluded median sinus of the ovicell had occurred in *Iodictyum* during the radiation from Europe to the Indo-Pacific area. Further discovery of well-preserved fossils of this genus is still required.

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