An Exceptionally Well Preserved Middle Pleistocene Epiphytic Diatom, *Arachnoidiscus ornatus*, from Japan: A Possible Taphonomic Process

Yoshihiro Tanimura¹, Megumi Kato², Tamotu Nagumo³, Atsushi Kobayashi⁴ and Kazumi Yokoyama¹

¹Department of Geology and Paleontology, National Science Museum, 3–23–1 Hyakunin-cho, Shinjuku-ku, Tokyo 169–0073, Japan
²Department of Geology and Paleontology, National Science Museum, 3–23–1 Hyakunin-cho, Shinjuku-ku, Tokyo 169–0073, Japan
(Research fellow of the Japan Society for the Promotion of Science) ³Department of Biology, Nihon Dental University, 1–9–20 Fujimi, Chiyoda-ku, Tokyo 102–8159, Japan ⁴Department of Education, Bunkyo University, 3337 Minami-Ogishima, Koshigaya, Saitama 343–8511, Japan ⁵Department of Geology and Paleontology, National Science Museum, 3–23–1 Hyakunin-cho, Shinjuku-ku, Tokyo 169–0073, Japan

Abstract Exceptionally well preserved frustules of a single diatom species, Arachnoidiscus ornatus Ehrenberg, were found on mid-Pleistocene seaweed-like remains. The distribution of frustules on the remains were compared with the distribution of A. ornatus cells on modern seaweeds. This comparison indicated that the fossil frustules were likely preserved epiphytic assemblages that occurred on seaweeds. Almost all modern A. ornatus cells are attached to seaweeds with epivalves, and 97% of the fossil A. ornatus frustules had epivalves on the exposed upper face. This finding and the occurrence of flattened thin frustules of a single naviculoid diatom speices on the fossil epivalve surfaces suggested a possible taphonomic process for the exceptional state of preservation. Seaweeds, which acted as impermeable films within sediments during the taphonomic process, probably prevented interstitial waters from permeating the tiny pores of the frustules. These films were peeled off when the fossils were excavated. To infer the possible physicochemical conditions of preservation, the framboidal pyrite (FeS₂) preserved in the fossil A. ornatus valves was compared with cytoplasmic masses in living A. ornatus cells collected from modern coastal waters off Japan. The following two scenarios were inferred: the cytoplasmic masses in Arachnoidiscus cells may be the source of the framboids, and the rapid burial of cells in mud under saline conditions probably led to the superior preservation.

Key words: Arachnoidiscus ornatus, diatom, Japan, middle Pleistocene, taphonomic process.

Introduction

Arachnoidiscus ornatus is an epiphytic diatom occurring mainly on seaweeds (Round et al., 1990). It attaches on surfaces of seaweed species such as Dilophus okamurae, Gelidiopsis hachijoensis, Gelidium elegans, Grateloupia livida, Lomentaria catenata, Odonthalia annae, Plocamium recurvatum, P. relfairiae, Postieria hornemannii, and Psilothallia dentata (Kobayashi et al., 1998). Despite its common occurrence in modern coastal waters of the circum-Pacific, fossil epiphyton on seaweeds have rarely been found along the Pacific coast.

In a field excursion hosted by the National Science Museum, many frustules of a single *Arachnoidiscus* species, *A. ornatus*, were found on the remains of seaweed-like flats within the Renkoji Formation. This formation is part of the Kazusa Group that outcrops in the Tama River in Tokyo. The Kazusa Group is divided into seven formations in the Tama district: the Terada, Oyabe, Hirayama, Oyamada, Renkoji, Inagi, and



Figs. 1, 2. Light and scanning electron micrographs of *Arachnoidiscus ornatus* frustules from the middle Pleistocene Renkoji Formation, and a distribution map of *A. ornatus* frustules on a seaweed-like remain. (1) a seaweed-like remain with *A. ornatus* frustules. (2) *Arachnoidiscus ornatus* frustules on the seaweed-like remain (a), and the distribution map of *A. ornatus* frustules on the remain (b).

Dedana formations in ascending order (Takano, 1994). The group is composed mainly of fluvial conglomerates in the lower portion, tidal-flat and inner-bay mudstone in the middle, and littoral-to-upper neritic sandstone in the upper part. At the Tama River outcrops, the Renkoji Formation is approximately 10-m thick and composed mainly of pale-blue mudstone with a 1-m-thick basal conglomerate layer (Baba *et al.*, 1986). Tephra chronology has dated the formation to be middle Pleistocene in age (Takano, 1994).

This report describes the exceptionally well preserved fossil *A. ornatus* found on middle Pleistocene seaweed-like remains within the formation and discusses a possible taphonomy for the preservation process. The ecology of *Arachnoidiscus* species is poorly understood. The well preserved fossils and taphonomic evidence presented here will elucidate *Arachnoidiscus* ecology and facilitate future research.

Materials and Methods

Three fossil remains were recovered from mudstone excavated from the Renkoji Formation in the Tama River (35°40′50″N, 139°24′23″E). Figure 1 shows one of the fossils. Another fossil was prepared for scanning electron microscopy (SEM) analysis. Carbon paste was used to attach the fossil to a brass stub, and gold was used for coating. Based on the SEM observations, we created a distribution map of the frustules on the fossil remain, also indicating whether the epivalve or the hypovalve was on the upper face of each fossil frustule and whether each upper valve had raphe-like slits.

Further observations and analyses examined opaque granules preserved in some valves. The number of granules per valve and the granule sizes, chemical compositions, and distributions within the valves were determined. Energy-dispersive spectrometry (EDS; Link QX2000, JEOL 5400; JEOL, Tokyo, Japan) was used to determine the chemical composition. The granules found in the fossil valves were then compared with cytoplasmic masses from living *A. ornatus*



Fig. 3. An energy-dispersive spectrometry spectrum of framboidal pyrite preserved in an *Arachnoidiscus ornatus* valve.

cells collected from the Banda area of Tateyama, Chiba Prefecture, Japan (date of collection, 23 July 1996).

Results

The SEM observations revealed 23 valves and 137 frustules of *A. ornatus* in the fossil remain (Fig. 2a). Of the frustules, 97% had epivalves on the exposed upper face, and 25.5% of the upper valves were slit-bearing (Fig. 2b). Many rounded granules were distributed rather peripherally in the valves. An EDS analysis revealed these granules to be framboidal pyrite (FeS₂; Fig. 3). In living *Arachnoidiscus* species collected from modern coastal waters, cells contained many cytoplasmic masses that were rounded in shape and distributed densely in the cell periphery (Fig. 4).

Discussion

Almost all cells of modern *A. ornatus* are found attached via epivalves to seaweeds (Kobayashi *et al.*, 1998; Kobayashi *et al.*, 2001). For example, on the surface of the *Laurencia* sp. shown in Fig. 5, all *A. ornatus* frustules are attached by epivalves. In the fossil *A. ornatus*, 97% of the frustules had epivalves on the upper side (Fig. 2b). Fine volate occlusions in the areolae, which are characteristic of this species, were also well preserved in several valve surfaces of the



Figs. 4–7. Light and scanning electron micrographs of *Arachnoidiscus ornatus* cells, frustules, and valves. (4) *Arachnoidiscus ornatus* cells on *Gelidium elegans* (Banda, Tateyama, Chiba Pref., Japan). (5) *Arachnoidiscus ornatus* cells on *Laurencia* sp. (Fukui Pref., Japan). (6) Framboidal pyrite in an *A. ornatus* valve (a), and details showing its entire shape (b) and crystals (c). (7) Flattened frustules of a single naviculoid diatom species on an *A. ornatus* frustule (a), and details of this species (b).

fossil frustules (Fig. 7b). The flattened frustules of a single naviculoid diatom species were additionally found on the epivalve surfaces, with fine structures such as the cingula well preserved (Fig. 7). These features and the close similarity in frustule distributions between the fossil remains and modern specimens found on seaweeds suggest the following taphonomic process for this thanatocoenosis.

A broken piece of seaweed with epiphytic A. ornatus cells was buried in mud beneath the sediment-water interface, and spaces on and around the cells filled with mud. The A. ornatus frustules and the flattened frustules of epiphytic naviculoid diatom species were corrosion-resistant due to mucilage contact with the seaweed surfaces. The seaweed probably acted as impermeable films during the taphonomic process and thus prevented interstitial waters in the sediments from permeating through tiny pores such as the volate occlusions in the areolae of the A. ornatus frustules and the cingula in the naviculoid-diatom frustules. These films were peeled off when the fossils were excavated in the outcrop. Frustules of the naviculoid diatom species, which are epiphytic on A. ornatus epivalves, were flattened by A. ornatus cells either during their lifetimes or after their deaths.

Comparison of framboidal pyrite in fossil *A.* ornatus frustules from the Renkoji Formation with the cytoplasmic masses of modern *A. orna*tus cells from coastal waters off Japan suggests that the cytoplasmic masses were the source of the framboids. The shape (rounded), number (many), size (generally ca. $3-5 \mu$ m in diameter), and distribution (densely in the cell periphery) of cytoplasmic masses in the modern *Arachnoidis*cus cells are similar to the framboids seen in the diatom frustules from the Renkoji Formation (Figs. 4, 5a-c). The framboids may be a kind of sedimentary pyrite formed by microbial preservation, as reported in Schieber (2002).

If this inference is correct, this excellent preservation required rapid burial under a saline condition. Allison (1988) studied the depositional conditions required to preserve soft parts of organisms such as the pyrite, phosphate, and carbonate, and concluded that pyrite preservation requires saline conditions and rapid (catastrophic) burial. Rapid burial probably prevented decomposition of the silica frustules by aerobic bacteria (Bidle and Azam, 1999). Water movement in the coastal waters probably detached the seaweed; currents may then have rapidly buried the seaweed deep beneath a "taphonomic active zone" (Martin, 1999) in the muddy bottom layer. Common occurrences of shell aggregations, composed mainly of shell fragments with intact shells, foraminifers, and ostracodes, in the mudstone within this formation suggest rather strong water movements at the bottom.

Taxonomic Notes

Arachnoidiscus ornatus Ehrenberg, 1849, Ber. Bekanntm. Ver. K. Preuf. Akad. Wiss. Berlin, p. 64.

Based on comparisons of valve morphology between *Arachnoidiscus ornatus* and *A. ehrenbergii* frustules from ten coastal localities off Japan, Kobayashi *et al.* (1998) determined that these two species have no difference in morphology except for a larger average valve diameter in the latter; their research concluded that the recent *Arachnoidiscus* entity from Japan can be classified under *A. ornatus*, as synonymous with *A. ehrenbergii*. The present report follows Kobayashi *et al.* (1998) and assigns the specimens found in the formation to *A. ornatus*.

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