Regular axopodial activity of *Diplosphaera hexagonalis* Haeckel (spheroidal spumellarian, Radiolaria)

NORITOSHI SUZUKI[1] and KAZUHIRO SUGIYAMA[2]

[1]*Institute of Geology and Paleontology, Graduate School of Science, Tohoku University,
Aramaki, Aoba, Aoba-ku, Sendai, 980–8587, Japan*
[2]*Marine Geology Department, Geological Survey of Japan, Tsukuba, 305–8567, Japan.*

Abstract. The physiological ecology of a spherical polycystine species, *Diplosphaera hexagonalis* collected from the surface water of the Kuroshio Current in the East China Sea off Sesoko Island, Okinawa, was observed in a culture dish for three days. The observed specimen demonstrated cyclic extension and contraction of axopodia by a regular interval of ca. 630 seconds. Each cycle was divided intro four phases based on the state of the axopodia and movement of axopodial vacuoles. Vertical migration in response to axopodial motility was also observed. The specimen began to rise accompanied with the axopodial extension, floated in the seawater and often moved horizontally when its axopodia were radiated symmetrically, and began to sink in correspondence with the axopodial contraction. The effect of thermal currents on this behavior is easily neglected on the ground of the definite coincidence with the rhythmic extension and contraction of axopodia. The rhythm appears to play important roles in the physiological ecology of this species, including food capture and possibly buoyancy. The taxonomic section presents a nearly complete synonym list of *D. hexagonalis* and summarizes that the genus *Diplosphaera* is a senior synonym of *Astrosphaera*, *Drymosphaera* and *Leptosphaera*. Thus, *Diplosphaera hexagonalis* is the only valid name for this species, according to ICZN Article 55.3. *Diplosphaera* is considered herein to belong not to the family Actinommidae but to the Astrosphaeridae, unlike in most previous paleontological and biological studies. The family Macrosphaeridae Hollande and Enjumet, 1960, to which the genus *Diplosphaera* was assigned, is treated as an invalid name because the type genus *Macrosphaera* has not been established yet.

Key words: axopodia, *Diplosphaera hexagonalis*, East China Sea, living radiolaria, Okinawa, physiological ecology

Introduction

Radiolaria is an informal taxonomic group of planktonic unicellular Protoctista generally possessing a plane, line or point skeletal symmetry of the test. This group includes the classes Polycystina possessing a siliceous test, Acantharia with a strontium sulfate test, and Phaeodaria having a siliceous test with incorporated organic substances (Margulis and Schwartz, 1988; The Committee on Systematics and Evolution of the Society of Protozoologists, 1980). Of these radiolarians, solitary spheroidal Polycystina ranges in age from the middle Cambrian to the present (Nazarov, 1988). Since the polycystine group is widely distributed in the open oceans, information on its physiological ecology will provide new insights both in analysis of paleoceanographic analyses and the establishment of a natural classification.

Although previous studies have revealed detailed information on physiological and ecological information (living features, longevity, prey, and skeletal growth under culture conditions and some fine structures) of some discoidal spumellarians such as *Dictyocoryne truncatum* (Ehrenberg) and *Spongaster tetras* (Haeckel) (e.g. Anderson *et al.*, 1989a, 1989b; Anderson and Matsuoka, 1992; Matsuoka, 1992; Matsuoka and Anderson, 1992; Sugiyama and Anderson, 1997), we know little about the physiological ecology of spheroidal spumellarians. Examination of the cytological structures of solitary spherical polycystines has provided some groundwork for these analyses (Anderson, 1976, 1981, 1983; Anderson *et al.*, 1998; Cachon and Cachon, 1972a, 1972b, 1976, 1985; Haeckel, 1862; Haecker, 1907; Hertwig, 1879, 1932; Hollande and Enjumet, 1954, 1960; Hollande *et al.*, 1965; Swanberg *et al.*, 1990),
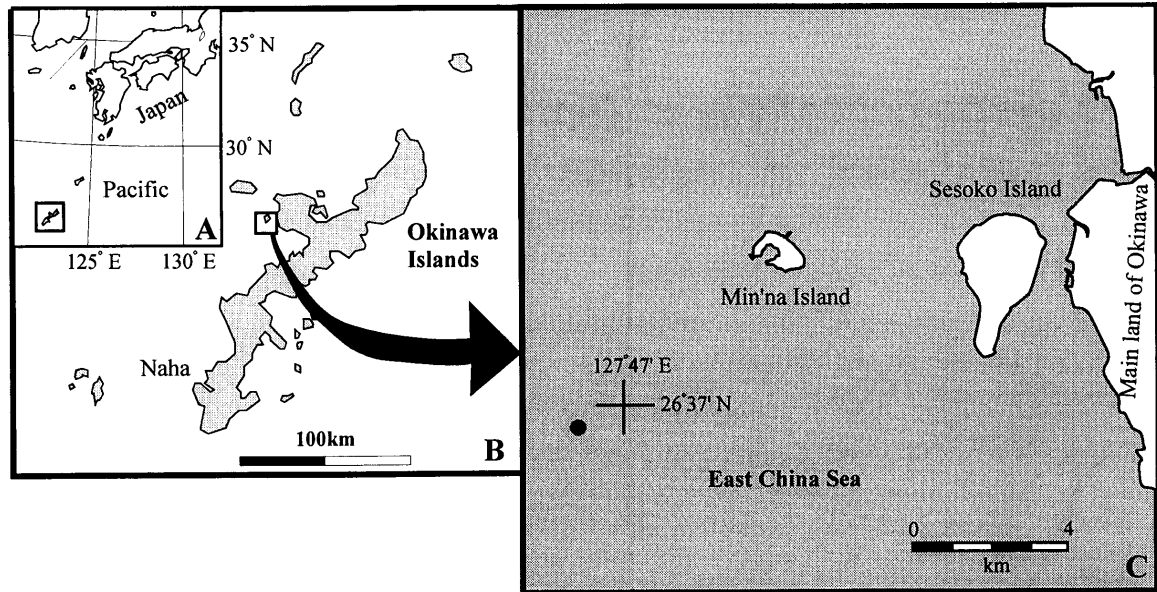
Figure 1. Sampling location. **A.** A map showing the position of Okinawa Islands (open square). **B.** The Okinawa Islands and its adjacent islands. **C.** The sampling location (solid circle).

but there have been only limited investigations of the nutritional role of symbionts (Anderson et al., 1983, 1985) and the possible reproductive role of swarm cells released by mature specimens during laboratory culture (Anderson, 1978, 1984 and others).

In order to observe living features of radiolarians in the surface seawater of the Kuroshio Current, some Japanese radiolarian paleontologists have collaborated on observation tours of living organisms at the Sesoko Tropical Biosphere Research Center (STBRC), University of the Ryukyus, Sesoko Island, Okinawa Prefecture, Southwest Japan, since 1997 (Figure 1). During the 2nd tour held on October 5th to 14th, 1998, we made three samplings on October 7th, 8th and 12th, 1998, and encountered approximately 40 species in laboratory examinations. As a result, we obtained extensive information about their pseudopodial behavior using normal still and video photography.

Among the observed radiolarians, we particularly traced continuous axopodial activity of one specimen of *Diplosphaera hexagonalis* Haeckel, a solitary spheroidal spumellarian representative of the observed radiolarian fauna, during four days from October 7th to 10th, 1998. Our interest was especially aroused since it systematically repeated axopodial extension and contraction cycles at regular intervals. In this report, we present a detailed description of the features of the extension and contraction cycles and possible implication for the physiological ecology of *D. hexagonalis* in relation to this cyclical axopodial activity. A probable physiological function and an explanation of a mechanism of the cycles are also discussed. This paper also describes the taxonomic classification of *D. hexagonalis* in order to resolve the confusion surrounding its generic and family positions.

Materials and methods

Plankton samples containing the observed *Diplosphaera hexagonalis* were collected on October 7th, 1998, at a locality (Station 1; Figure 1) approximately 12 km west of Sesoko Island and more or less affected by the warm-water Kuroshio Current. Ambient seawater temperature and salinity at the sampling location were 28.5 °C and 34.0 ‰, respectively. The sample was collected by 3 min. tow using a 36 μm mesh net. On return to the laboratory at STBRC, small portions of the sample were placed into sorting dishes, examined with binocular microscopes, and each individual radiolarian was separated from other matter using a Pasteur pipette into a glass vial (ca. 25 mm diam. ×50 mm tall), a glass culture dish (50 mm or 90 mm diam.) or a single well of a multiwell tissue culture plate (23 mm diam. ×20 mm tall) (FALCON® 3043, Becton Dickinson Labware, Lincoln Park, N. J.) previously filled with ambient seawater from the sampling location. These culture containers with radiolarians were placed either in a temperature-controlled bath with fluorescent light units or in temperature-uncontrolled baths without fluorescent light units. The temperature of the former bath was kept at 28 °C by a heater-chiller balance, whereas that of the latter was about 27 °C, the room temperature of the laboratory, throughout the culture work. Both types of baths were covered by metal foil during the night to produce a day/night cycle. The radiolarians were cultured without exchange of the seawater, no supply of food, nor removal of any filth.

Continuous axopodial activity of one *D. hexagonalis* individual was observed from October 7th to 10th October, 1998, using Nikon Diaphot and Olympus CK2 inverted microscopes, mainly following previously established protocols

(Anderson et al., 1989a). We used a video camera (SONY HANDYCAM DCR-TRV9), with a resolution of 0.76 million pixels, attached to the Nikon Diaphot microscope through a TV adapter and digital camera (FUJIFIX HC-300) in order to record vivid images of radiolarian activity. The observations were recorded on five 60-minute videotapes and more than 10 pictures. Only for one individual was the continuous axopodial activity described in this paper ascertained. Although six to ten other individuals were observed with two inverted microscopes for snapshots using normal cameras as well, we did not confirm whether other specimens show continuous axopodial behavior or not.

Observational results of living *Diplosphaera hexagonalis*

The skeleton of *Diplosphaera hexagonalis* (Figure 2.1) consists of one spherical primus exosphere, one polyhedral secondus exosphere with triangular frameworks, and a dozen triradiate auxiliary spines radiating from the primus exosphere (for skeletal terms see Suzuki, 1998). This species was assigned to the family Astrosphaeridae based on criteria published by Hollande and Enjumet (1960).

Living *D. hexagonalis* possesses a dark, grayish red, spherical cell body within the secondus exosphere, and fine, transparent axopodia radiating from the surface of the cell body (Figure 2.2, 2.3). The spherical cell is composed of
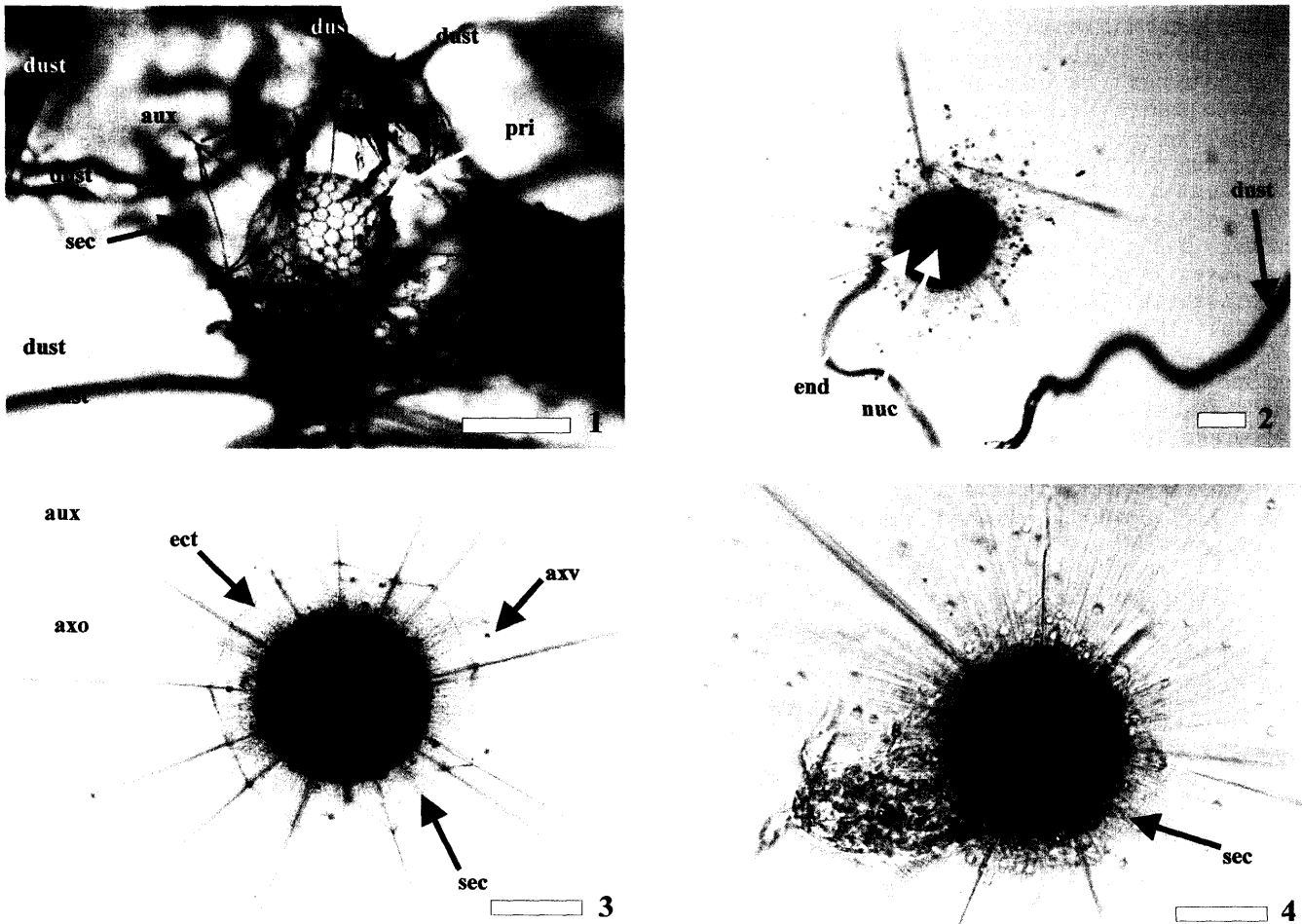

Figure 2. General view of *Diplosphaera hexagonalis* Haeckel. 1. Light transmitted microscopic photograph. 2–4. Inverted microscopic photographs, showing a bottom view. Scale bars are equal to 100 μm. 1. Skeleton structure of *D. hexagonalis* possessing a spherical primus exosphere (pri) and a polygonal frame of the secondus exosphere (sec). These two shells are connected with numerous auxiliary spines (aux). 2. Numerous yellow–brown axopodial vacuoles surround the endoplasm. Axopodia may begin to extend (EII-subphase). 3. This specimen has a small amount of axopodial vacuoles. Both the fine axopodia and axopodial vacuoles near the endoplasm indicate that this specimen is in the EI-subphase. 4. A copepod attached to *D. hexagonalis* is partially digested by the specimen. Abbreviations: nuc, nucleus; end, endoplasm; cop, copepod; ect, ectoplasm; axo, axopodia; aux, auxiliary spine; axv, axopodium vacuole; pri, primus exosphere.

two parts: (1) a more transparent light-colored, bubble-like outer part between the primus and secondus exospheres, corresponding to ectoplasm, and (2) a more opaque, spherical inner part within the primus exosphere. The latter is further subdivided into a deeper-colored central part, and the surrounding endoplasm which is slightly lighter-colored. The inner part is referred to as a nucleus according to Hollande and Enjumet (1960).

The length of the axopodia changes periodically from a minimum of 0.12 – 0.13 mm to longer than 2.0 mm. Vacuoles, dark amber or reddish gray in color, globular in shape and of a few to ten μm in diameter are displayed on each axopodium. The total number of vacuoles varies among specimens but it typically is about 200. The distribution of the vacuoles on the axopodia changes with the length of the axopodia. The biological function and physical composition remains unknown.

We observed the specimen with a copepod (ca. 400 μm in length) attached to its axopodia outside the secondus exosphere at noon on the 7th (Figure 2.4). On the next day, the entrails of the copepod began to dissolve, and the entire copepod body completely disappeared on October 9th. After the digestion of the copepod, the ectoplasm of *D. hexagonalis* increased in volume to fill the secondus exosphere. During the observations, other organisms, probably ciliates, moved around the halo of axopodia of *D. hexagonalis*, and became momentarily immobilized on the axopodia. However, all of these microorganisms were soon released by the shortening of the axopodia. This seems to indicate that these microorganisms were not captured but only snared accidentally. Some of the microorganisms escaped from *D. hexagonalis*, but those which failed to escape from the specimen were again snared by the axopodia.

Systematic repetition pattern of axopodial extension and contraction

On October 9th, a series of 17 extension and contraction cycles of the axopodia was observed over a duration of 2 hrs. 44 min. 21 sec. (Figure 4). The cycles described herein have a reasonably regular interval; the longest interval was 677 sec, the shortest 550 sec and the mean 633 sec. Each cycle is divisible into four phases based on the state of the axopodia and movement of axopodial vacuoles. These phases are as follows: S-phase (short phase, Figures 3.1, 5), E-phase (extension phase, Figures 3.2–3.5, 5), L-phase (long phase, Figures 3.6–3.7, 5) and C-phase (contraction phase, Figres 3.8–3.12, 5). Among them, the E-phase is further subdivided into three subphases (EI-subphase, EII-subphase and EIII-subphase), and the C-phase into two subphases (CI-subphase and CII-subphase). Although each cycle has almost the same interval, as mentioned above, phase and subphase intervals in each cycle differ considerably as shown in Figure 4. We tried to interrupt the axopodial movement by vibrations produced by tapping the dish with sticks but the cyclicity was uninterrupted, and what is more, the regularity was maintained in spite of contact by ciliates and other small organisms.

S-phase (Figure 3.1).—This phase is defined as an interval after C-phase, during which axopodial length is at a minimum. Axopodia in this phase are composed of two kinds; one is named H-index type and the other is L-index type. The former type of axopodia has relatively high refractive index against seawater under the microscope, whereas the refractive index of the latter type is lower. Usually, H-index type axopodia are shorter than the L-index type in this phase. The length of the H-index type axopodia is about half of the primus exosphere diameter, while that of the L-index type axopodia is approximately double that of the H-index type. In this phase, most vacuoles on both types of axopodia are rarely moved outside the ectoplasm. The shortest interval of this phase is 4 sec, the longest 18 sec and the mean 12 sec.

E-phase.— This phase is defined as an interval after S-phase, during which most axopodia are extending. The shortest interval of this phase is 160 sec, the longest 474 sec and the mean 302 sec. The E-phase is subdivided into the following EI-, EII- and EIII-subphases.

During the EI-subphase, we still cannot see the outward movement of the axopodial vacuoles situated in the secondus exosphere (Figure 3.2). In contrast, vacuoles on the L-index type axopodia begin to move slowly inwards. H-index type axopodia begin to extend slowly and become more slender. The refractive index of both types of axopodia decreases with their extension. During this subphase, the difference between the L- and H- type axopodia becomes indistinct. The shortest interval of this subphase is 14 sec, the longest 86 sec and the mean 31 sec.

The EII-subphase starts by the outward movement of axopodial vacuoles, and ends by the event that the distal parts of axopodia become invisible (Figure 3.3). Within this subphase the axopodia maintain a continuous and slow extension. Most axopodial vacuoles continue to move outward, but a few return to the inside of the secondus exosphere. The shortest interval of this subphase is 2 sec, the longest 140 sec and the mean 85 sec.

The end of the subsequent EIII-subphase is defined by unrecognizableness of the outward extension of axopodia (Figure 3.4, 3.5). During this subphase, the distal parts of axopodia are invisible but the outward extension can be discerned by the movement of axopodial vacuoles. The shortest interval of this subphase is 46 sec, the longest 433 sec and the mean 217 sec.

L-phase (Figure 3.6, 3.7).—This phase is defined as an interval during which the specimen keeps radiate, long axopodia with immobile vacuoles. Axopodia in this phase are finer than those in the S-phase, and the refractive difference between the axopodia and seawater is negligible. Axopodial vacuoles are heterogeneously distributed around the halo of axopodia. The shortest interval of this phase is 29 sec, the longest 205 sec and the mean 100 sec.

C-phase. —This phase subsequent to the L-phase is marked by an abrupt contraction of axopodia towards the endoplasm, and ends when most axopodia finish shrinking. The shortest interval of this phase is 59 sec, the longest 282 sec and the mean 168 sec. This phase is subdivided into CI- and CII-subphases as follows.

In the CI-subphase, axopodial vacuoles begin to be moved back to the ectoplasm although the axopodia are not
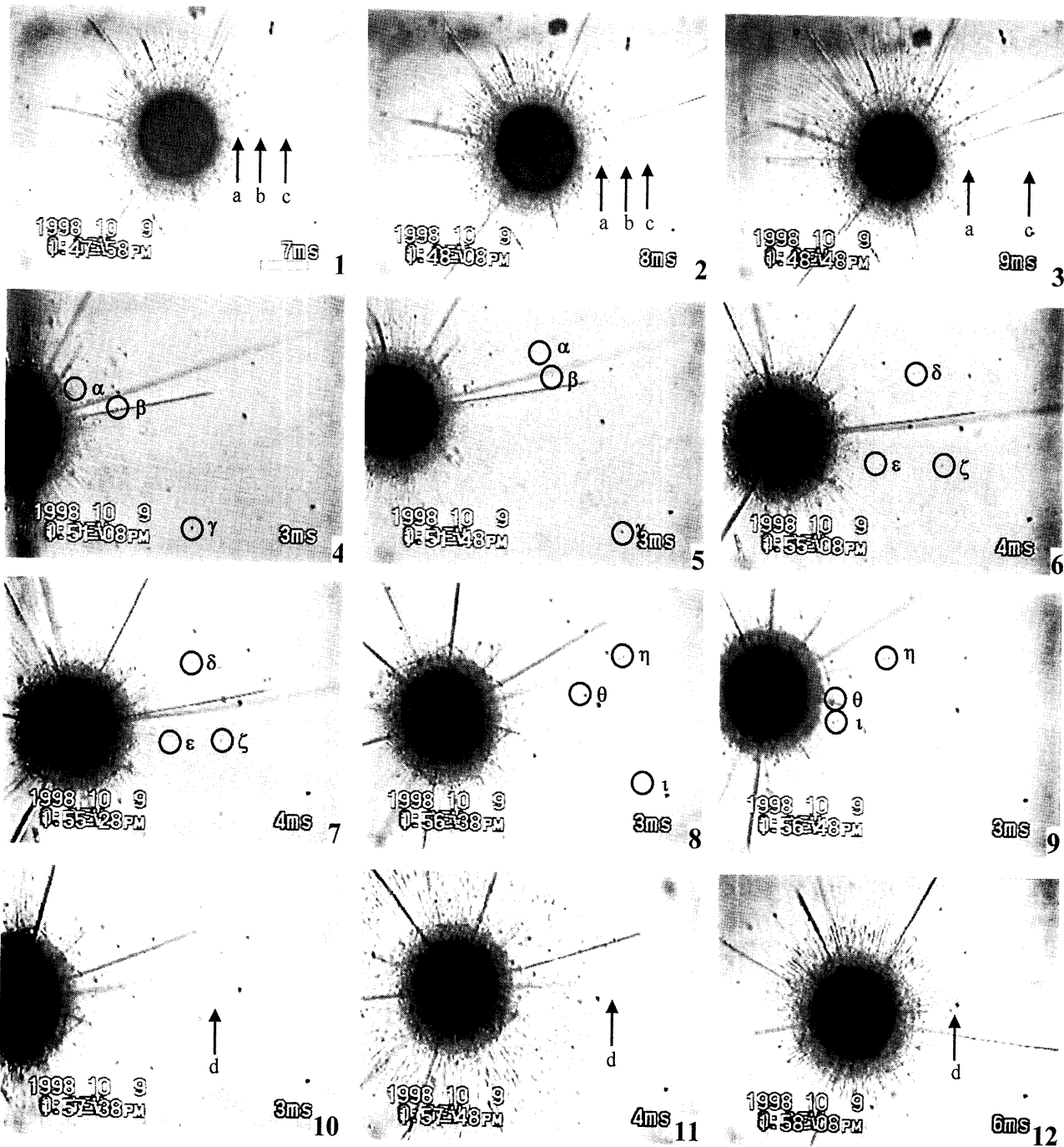
Figure 3. Four phases of extension and contraction of the axopodia. Scale bar is equal to 100 μm. **1**. S-phase. **2**. EI-subphase. **3**. EII-subphase. **4, 5**. EIII-subphase. **6, 7**. L-phase. **8, 9**. CI-subphase. **10-12**. CII-subphase. Arrows: a, the periphery of the dominant axopodial vacuoles; b, the distal part of H-index type axopodia; c, the distal part of L-index type axopodia; and d, the distal part of the contractile axopodia. Open circles with Greek symbols in Figure 3.4-3.9 represent axopodial vacuoles. The same Greek symbols in different figures imply the same axopodial vacuole.

yet contracted (Figure 3.8, 3.9). During this subphase the refractive index of the axopodia increases gradually accompanied by thickening of the axopodial diameter at the proximal point where it attaches to the cell body. A few axopodial vacuoles are moved inward relatively quickly. These vacuoles pass the secondus exosphere and reach near the surface of endoplasm. The shortest interval of this subphase is 34 sec, the longest 227 sec and the mean 133 sec.

The CII-subphase is characterized by an abrupt contraction of axopodia and followed by the S-phase after complete cessation of axopodial shrinking. At the beginning of this
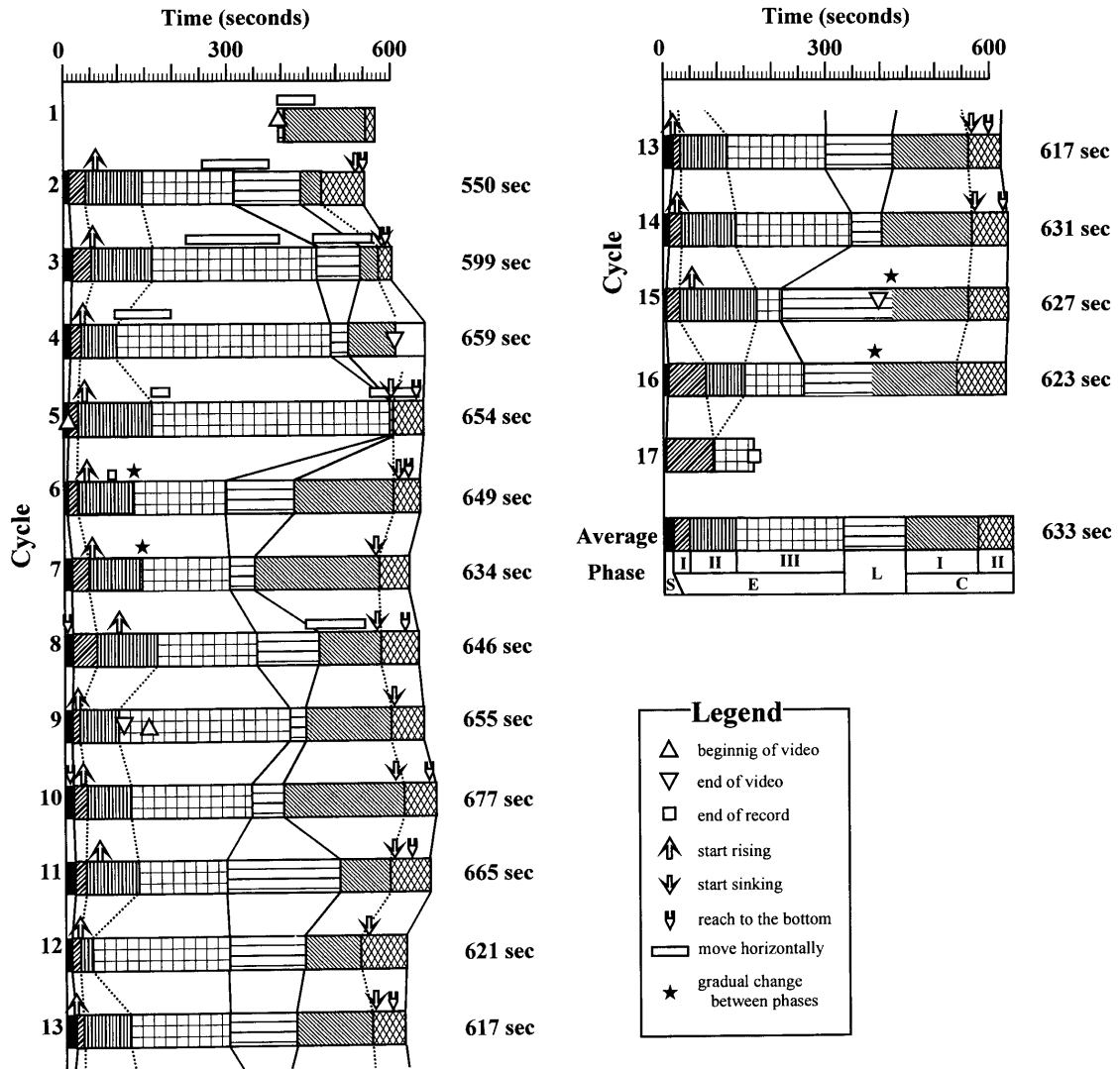
Figure 4. Diagram illustrating the four phases of the axopodia on 9th, Oct, 1998.

subphase, the periphery of the axopodia shrinks suddenly (arrow d in the Figure 3.10–3.12). The vacuoles on the distal part of the axopodia are moved inwards by this action, and the refractive index of the axopodia increases immediately (Figure 3.10). Subsequently, the axopodia shorten in a stepwise fashion with a concomitant increase of the refractive index at each step. The axopodial vacuoles are also moved inwards in the same stepwise fashion. The halo of axopodia in this subphase has a gelatinous spherical envelope with numerous pigmented dots (Figure 3.11). The shortest portion of this subphase is 25 sec, the longest 90 sec and the mean 64 sec.

Vertical migration in connection to axopodial motility

During the observation of *Diplosphaera hexagonalis*, we found that rising, floating and sinking motions in the culture vessel are always related to axopodial extension and contraction. Vertical migration was confirmed with video re-

cords and was counted 14 times at each expansion and contraction rhythm of the axopodia except for the last two rhythmic cycles which were not recorded on the video tape (Figure 4). It would be doubtful if this behavior depended on the effect of thermal currents in the observed dish, but the possibility of this effect is easily discarded: the relation of floating and sinking correlated with the changes in axopodial rhythm is so strict, and the radiolarian specimen did not show any other irregular rising and sinking movement in spite of particular careful observation as shown in Figure 4.

The specimen begins to rise from the bottom of the vessel during the interval from the middle EI-subphase to early EII-subphase accompanied with the axopodial extension (the up-arrows in Figure 4). Cessation of this movement is quite gradual. The specimen floats in the seawater and often moves horizontally during the EII-subphase through the middle CII subphase (the open rectangles in Figure 4). When the specimen is floating, its axopodia are radiated symmetri-
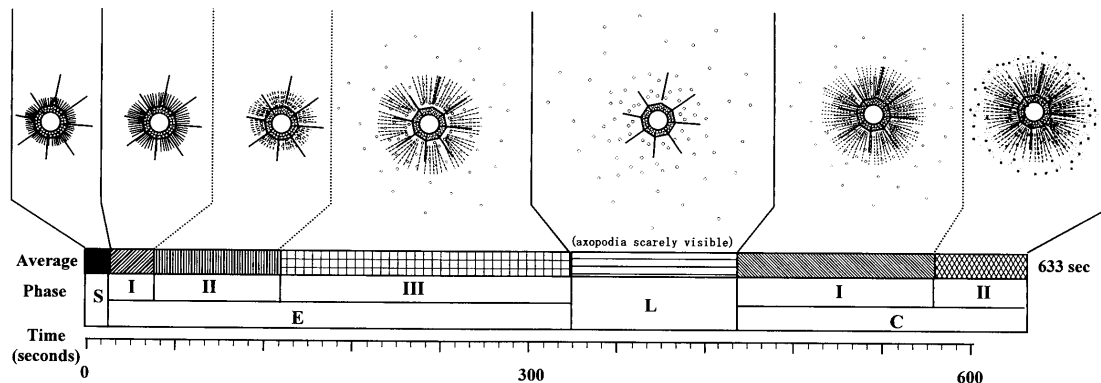
Figure 5. Schematic illustration of the cycle of extension and contraction of the axopodia. Solid thick line: siliceous skeleton. Solid fine line: H–index type axopodia. Dark gray small dot: axopodium vacuole. Dark to light gray fine lines: L–index type axopodia. The darkness of lines indicates a refractive index between the axopodia and the seawater.

cally from the cell body, which drifts in all directions very slowly. Around the late CI-subphase to the early CII-subphase, the specimen begins to sink in correspondence with the axopodial contraction (the down-arrows in Figure 4). After a few to 60 seconds, the body of the specimen reaches the bottom of the culture vessel.

Discussion

Although a rhythmic extension and contraction of radiolarian axopodia has been reported by Anderson (1983), the observation herein is the first evidence showing a regular rhythm of axopodial movement at approximately ten and a half-minute intervals. Our observation demonstrated that videotape recording is a fairly useful and advanced method by which to document the continuous activities of radiolarian axopodia. We accumulated a continuous record of *D. hexagonalis* with cyclic axopodial motions only from one specimen using videotapes, but other collected specimens (more than ten specimens) also appeared to have the same kind of rhythmical activity, judging from a series of still photograph images. Consequently, we can conclude that the above described cyclical motions are a common physical behavior of *D. hexagonalis*.

Spherical symmetry is probably not a major predictive factor in the occurrence of the regular, cyclical axopodial contractions observed in *D. hexagonalis*. Several spherical spumellarian species of genera with a double shell (e.g. *Hexacontium* spp. and *Spongodrymus* sp. indet.) also were observed during this experiment, but they never exhibited a similar rhythmic motion of the axopodial array. Likewise, other protista, including Acantharia and Heliozoa, have a symmetric distribution of axopodia around the cell body, but we have no information if they possess possible cyclical patterns as observed in *D. hexagonalis*. Currently, therefore, we can infer that the observed regular rhythm is peculiar to *D. hexagonalis* and its related taxa, and that a particular cytological apparatus of *D. hexagonalis* likely produces this rhythm.

The cytology of *D. hexagonalis* is unusual. There is no axoplast and the nucleus is surrounded by large vacuoles

(Hollande and Enjumet, 1960). However, as with other axopodial-bearing species, the axopodium contains an array of axially oriented internal microtubules (axoneme). An axoplast is absent also in other spherical polycystine genera including *Rhizoplegma, Centrocubus, Octodendron* and *Haplosphaera* (Cachon and Cachon, 1985). It is not known presently whether the absence of an axoplast is related to the regular rhythmic cycles of extension and contraction of the axopodia in *D. hexagonalis*. When the axoplast is present in other species, it is rich in tubulin monomers that polymerize to form microtubules and is usually located centrally where the microtubules of the axonemes converge. Hence, the axoplast may provide an organizing center for the axonemes. In the absence of an axoplast, the regular array of large vacuoles in *D. hexagonalis* could serve to support the axonemes and in addition may contribute to the cytoplasmic volume as the periphery array of axopodia expands. If the expansion of the axopodial array indeed contributes to enhanced buoyancy, then there must be a source of additional cytoplasmic volume to supply the added low-density mass produced by the expansion of the peripheral corona of axopodia. If the expanding axopodia were simply constructed at the expanse of existing cytoplasmic mass in the main cell body, without further expansion of internal volume, there would be no net gain in buoyancy. If, however, the vacuoles increase in size as the axopodia expand, this could result in less mass per unit volume, and produce an increased buoyancy. Likewise, according to this model, as the axopodia contract, the vacuoles may decrease in volume, thus accommodating the inward flow of cytoplasm toward the central body and producing a concomitant decrease in buoyancy. A dynamic adjustment in volume by the central vacuoles may provide a necessary mechanism for maintaining appropriate mass balance required to control buoyancy as the peripheral axopodial array expands and contracts. The rhythmic extension and contraction of the axopodia appear to play important roles in the physiological ecology and physical functioning of *D. hexagonalis*, including food capture and possibly the regulation of buoyancy as reported here.

The extension of protozoan axopodia usually occurs by

elongation of the microtubules when additional tubulin is polymerized at one end and they are shortened by disassembly of the tubulin, all in response to biochemically regulated cycles (e.g., Tilney and Byers, 1969). To understand the mechanism of the observed rhythmic extension and contraction of axopodia, it is essential to investigate more thoroughly changes in cytological structures and correlated biochemical processes with the aim of creating a more complete model of the rhythmic activity of axopodia in *D. hexagonalis*.

Systematic description

Family Astrosphaeridae Haeckel 1882,
sensu Hollande and Enjumet 1960
Genus *Diplosphaera* Haeckel 1860, emend.
Hollande and Enjumet, 1960

Type species.—*Astrosphaera gracilis* Haeckel 1862, designated by Campbell (1954).

Diplosphaera Haeckel, 1860, p. 804; Haeckel 1887, p. 246; Campbell, 1954, D.62; Hollande and Enjumet, 1960, p. 116; Kozur and Mostler, 1979, p. 12.
Astrosphaera Haeckel 1887, p. 250; Campbell, 1954, D61.
Drymosphaera Haeckel 1882, p. 452; Haeckel 1887, p. 248; Campbell, 1954, D.62.
Leptosphaera Haeckel, 1887, p. 243-244; Campbell, 1954, D.62.

Remarks.—*Diplosphaera* is regarded as the senior synonym of three other genera, *Astrosphaera*, *Drymosphaera* and *Leptosphaera*, based on the ontogenetic growth change of their skeletal structures and similarity of their cytological structures (Hollande and Enjumet, 1960). According to them, the *Leptosphaera*-form, the youngest, possesses two exospheres without by-spines. *Diplosphaera*- and *Drymosphaera*- forms appear in the next ontogenetic growth stage through the development of by-spines on one of these. When both exospheres have by-spines, this form is referred as an *Astrosphaera*-form.

Diplosphaera has been assigned to three different families: classical studies described it as a member of the Astrosphaeridae Haeckel 1882 (e.g. Haeckel, 1882, 1887; Campbell, 1954; Mast, 1910). Recent paleontologists and paleoceanographers prefer to assign it to the Actinommidae Haeckel 1862 (e.g. Kozur and Mostler, 1979; Takahashi, 1991). Finally, cytological researchers have regarded it as a member of "Macrosphaeridae" Hollande and Enjumet 1960 (e.g. Anderson, 1983; Cachon and Cachon, 1985; Hollande and Enjumet, 1960). However, since *Macrosphaera* had not been proposed as a genus name, the family name "Macrosphaeridae" violates Art 29.1 of ICZN (1999), which states that a family-group name is formed by adding the termination -idae to the stem of the name of the type genus, or to the entire name of the type genus. *Diplosphaera* is cytologically closely similar to the genus *Haplosphaera* Hollande and Enjumet 1960, the type genus of the "Macrosphaeridae" (Hollande and Enjumet, 1960). The phylogenetically close relationship between *Diplosphaera* and *Haplosphaera* suggests that the family

"Macrosphaeridae" is included in the Astrosphaeridae.

Hollande and Enjumet (1960) revealed that the genus *Actinomma* Haeckel 1862, the type genus of the Actinommidae, is one of the centroaxoplastid spumellarians with the axoplast enclosed by the nuclear membranous envelope, whereas the genus *Diplosphaera* of the Astrosphaeridae belongs to the anaxoplastid spumellarians without axoplast. This cytological difference between the Actinommidae and Astrosphaeridae suggests that *Diplosphaera* does not belong to the Actinommidae.

Almost all species assigned to *Diplosphaera* have been recovered from surface sediment or plankton samples due to their fragile skeletons. Only one species, *Drymosphaera ? pseudosagenoscena* Sugiyama 1992, is known from the lower Miocene (Sugiyama, 1992). All assigned species other than *D.? pseudosagenoscena* lack a microsphere, so that the lower Miocene species appears to belong to another genus.

Range.—Recent as far as known.
Known occurrence.—Equatorial and North Pacific, equatorial Atlantic and Mediterranean.

Diplosphaera hexagonalis Haeckel, 1887

Diplosphaera hexagonalis Haeckel 1887, p. 246, pl. 19, fig. 3; Hollande and Enjumet, 1960, p. 116, pl. 12, fig. 6, pl. 15, fig. 11, pl. 23, fig. 2, pl. 26, fig. 2: Cachon and Cachon, 1972a, pl. 35, figs. b, c; Anderson, 1983, p. 66-67; Fujioka, 1990, p. 136, pl. 39, fig. 7.
Astrosphaera hexagonalis Haeckel 1887, p. 250, pl. 19, fig. 4; Mast, 1910, p. 52; Popofsky, 1912, p. 105-106, text-fig. 16, pl. 8, fig. 2; Sugano, 1937, p. 64, figs. 21; Renz, 1976, p. 100-101, pl. 2, fig. 12; Tan and Tchang, 1976, p. 229, figs. 4a, b; Takahashi and Honjo, 1981, p. 147, pl. 2, fig. 12; Nishimura and Yamauchi, 1984, p. 24, pl. 14, figs. 1, 2; Boltovskoy and Jankilevich, 1985, pl. 1, fig. 17; Yamauchi, 1986, pl. 2, fig. 3; Fujioka, 1990, p. 136, pl. 38, fig. 7; Yeh and Cheng, 1990, pl. 3, fig. 2; Takahashi, 1991, p. 69, pl. 11, figs. 1-3; Boltovskoy, Alder and Abelmann, 1993, p. 1891; Tan, 1998, p. 164, figs. 152a, b (= the same figures of Tan and Tchang, 1976); Boltovskoy, 1998, p. 41, figs. 15-40.
Leptosphaera hexagonalis Haeckel 1887, p. 244, pl. 19, fig. 2. [nomen oblitum]

Remarks. — Most previous authors have identified *D. hexagonalis* as a species of *Astrosphaera*. As mentioned in the generic remarks, *Astrosphaera* is a junior synonym of the genus *Diplosphaera* (Hollande and Enjumet, 1960; Kozur and Mostler, 1979), which means that *Astrosphaera hexagonalis* is an unavailable name (Article 53.3 of ICZN, 1999). Thus, *Diplosphaera hexagonalis* is the valid name of this species.

Skeletal residues are obtained from surface sediment in the eastern Pacific Ocean, China Sea, and the Mediterranean (Tan and Tchang, 1976; Nishimura and Yamauchi, 1984), whereas they are not found in the sediment from the center of the equatorial Pacific (Renz, 1976; Takahashi, 1991). The skeleton of this species appears to dissolve easily at greater water depth as discussed by Takahashi (1991).

Known Range.—Recent.

Occurrences.—Equatorial Pacific, equatorial Atlantic, East China Sea, South China Sea, east off Okinawa, Shikoku and Taiwan, Mediterranean and west Patagonia.

Habitat.—Warm seawater. Surface to 300 m depth (Hollande and Enjumet, 1960; Renz, 1976).

Acknowledgements

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