Shell structure and morphologic variation in *Spongosphaera streptacantha* Haeckel (Spumellaria, Radiolaria)

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Abstract

The detailed shell structures of *Spongosphaera streptacantha* Haeckel collected from the Sea of Japan, off Tassha, Aikawa Town, Sado Island, Niigata Prefecture, central Japan, are described based on high magnification SEM and transmitted light microscopic observations. The shell of *S. streptacantha* consists of a dodecahedral inner microsphere, spherical latticed outer microsphere, long three-bladed main spines arising from the surface of the outer microsphere, and a surrounding three-dimensional spongiose network. Main spines commonly number six or seven, rarely eight or nine, and the number shows no correlation with the size of the spongiose shell. Results of observations on 19 individuals reveal that the differences between the number and arrangement of the main spines and size, shape, and density of a spongiose shell produce morphologic variations in *S. streptacantha*. Since variability of the spongiose shell depends largely on the number of the main spines and the crude density of sponge-forming apophyses, morphologic variation of *S. streptacantha* has much to do with how many main spines arise from the outer microsphere during the early ontogenic process.

key words: morphologic variation, Radiolaria, Sado Island, Sea of Japan, shell structure, skeletal growth, *Spongosphaera streptacantha*.

Introduction

Recent advancements in living radiolarian studies show that the skeletal growth processes of several species can be useful for understanding the morphogenesis of Radiolaria (e.g., Anderson and Bennett, 1985; Anderson et al., 1986; Swanberg and Bjørklund, 1987). Skeletal growth of *Dictyocoryne truncatum* (Ehrenberg) which is a discoidal spumellarian species possessing a spongiose shell has been demonstrated by Matsuoka (1992) using laboratory

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(Manuscript received 6 February, 2004; accepted 12 March, 2004)

culture experiments and observations of various sized specimens collected from plankton tow samples near Barbados.

Spongiose taxa like *Dictyocoryne truncatum* grow basically by supplementation of the spongiose meshwork during late juvenile to mature stages and befit morphogenetic study due to their simple shell development. However, most thick mature shells of spongiose taxa prevent us from analyzing fine shell structures, especially the internal structure. *Spongosphaera streptacantha* Haeckel, which is characterized by having two small internal shells, long three-bladed spines, and a thick surrounding spongiose layer, is one of the most common constituents of the middle to late summer radiolarian fauna of the Sea of Japan (Matsuoka et al., 2001). Work on radiolarians of the Sea of Japan is progressing off Tassha, Sado Island favorably by the second author (A.M.) and his collaborators (Matsuoka et al., 2002; Itaki et al., 2003; research in progress by S. Machidori, Niigata University) and we can collect living radiolarian specimens in various growth stages. In the foreseeable future, attention will be focused on the ecology and morphometry of *S. streptacantha*, as this is an easily-accessible example of spheroidal Radiolaria. However, little is known about the fine shell structure of *S. streptacantha*, except for the pioneering work by Haeckel (1862), Popofsky (1912), and Hollande and Enjumet (1960). It is clearly shown in these works that a comparative study of scanning electron microscopic morphometry of various sized specimens and tracing the growth process of living specimens only provides fundamental information on skeletal development. We add to the cumulative knowledge of radiolarian skeletal growth processes by describing here whole skeletal features and fine structures of the skeletal elements of *S. streptacantha* based on SEM and transmitted light microscopic observations. The variability of *S. streptacantha* is also discussed.

Materials and methods

Plankton samples were collected from sea water of 100-0 m depth at a location approximately 6 km west of Tassha, Aikawa Town, Sado Island, Niigata Prefecture, central Japan (Fig. 1). Sampling was carried out on the mornings of July 22 and August 18, 2003 and eight samples were obtained each day, using a 100 μm opening net of the Marukawa type with a 0.3 m diameter mouth.

Each individual specimen of *Spongosphaera streptacantha* was transferred to a vial (9 ml) and preserved in ethanol, and was then picked and dried on a glass slide. Organic matter of specimens in the sample collected on July 22 was incinerated with an electric furnace. Specimens obtained from the August 18 sample were placed in ca. 50% sulfuric acid for a day to free the organic matter; 37 cleaned specimens of *S. streptacantha* were obtained. Nineteen specimens (ID number s-01 to s-19) were mounted in Canada balsam and observed by a digital transmitted light microscope (Keyence VH-7000). The specimens were then picked by rinsing with solvent (xylene) and mounted on a stub for observation by scanning electron microscope (SEM, JEOL

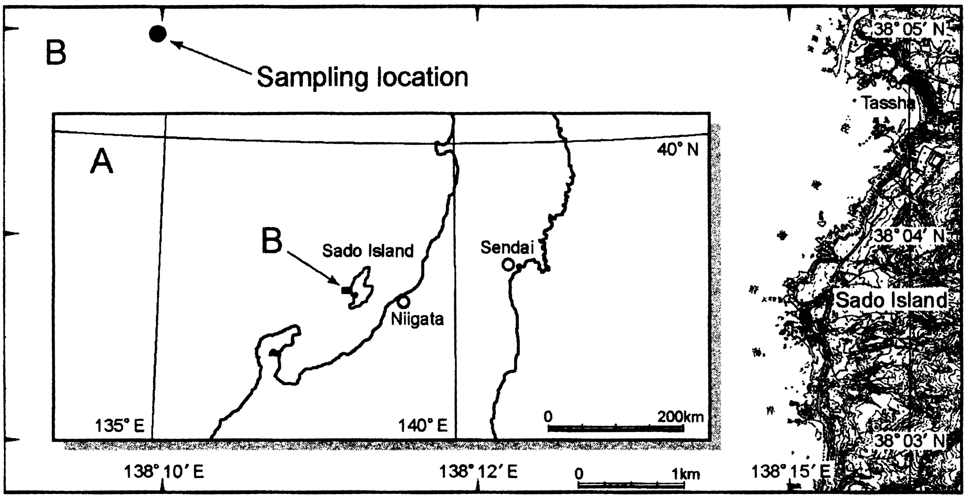

Fig. 1. Index map showing the sampling location (solid circle). The topography is from the 1:25,000 scale "Aikawa" map sheet published by the Geographical Survey Institute of Japan.

JSM-5600). In order to observe the internal shell structure by SEM, four specimens (s-22 to s-25) were mounted on a SEM stub and their spongiose layers were directly scraped off under a stereoscopic microscope by a micromanipulator (Eppendorf MicroDissector 5190). Two specimens (s-20 and s-21) were fixed within Canada balsam on a glass slide. When the Canada balsam hardened completely, the spongiose layer was scraped off using the same equipment. Following this process, specimens were picked from the Canada balsam using xylene and mounted on a SEM stub. Other specimens (s-26 to s-37) were prepared for SEM observations of their external shell structure.

Description of shell structure

The nomenclature for skeletal elements of spheroidal polycystines is still confusing and needs revision (Paverd, 1995; Suzuki, 1998). Terms for major skeletal elements mentioned in this paper are used in accordance with the following definition and as shown in Figs. 2, 3, 5, and 7. (1) *microsphere*, proposed by Hollande and Enjumet (1960) with extended use by Dumitrica (1982, 1985, 1988, 1991) and Paverd (1995), is less than 50μm in diameter (Hollande and Enjumet, 1960). This is almost synonymous with the "medullary shell (formed intracapsularly)" of Haeckel (1887), but the former is a purely descriptive term (Paverd, 1995). (2) *bar*, a part of the "pore-frame" of Campbell (1954), which is synonymous with "gephura" of Suzuki (1998); the connection and enclosure of several bars make *pore*. (3) *radial beam* (Campbell, 1954) connects the individual shells and sometimes penetrates a shell.

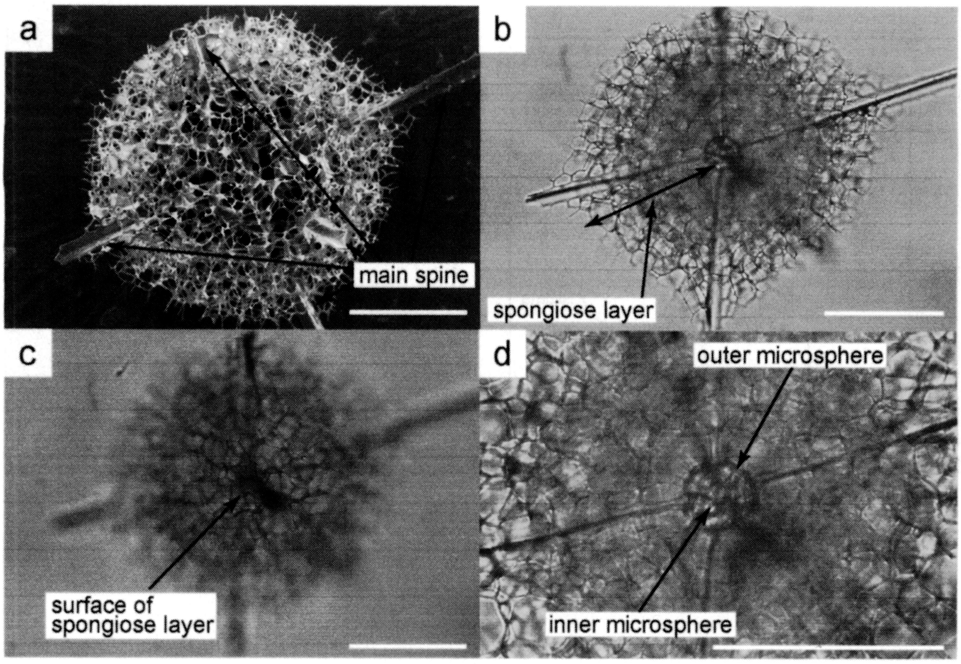

Fig. 2. SEM and transmitted light microscopic images showing the overview of skeletal features of *Spongosphaera streptacantha* Haeckel and nomenclature for skeletal elements. ID number of this specimen is s-14. a: SEM image of the external appearance. Six main spines (One is invisible) arise from the inner microsphere. b and c: Transmitted light microscopic images of the spongiose layer. d: Transmitted light microscopic image showing the inner and outer microspheres. All scale bars equal to 100 μm.

(4) *main spine* and *accessory spine* (Haeckel, 1887), kinds of "radial spine" (Haeckel, 1860), are synonymous with "principal spine" and "by-spine" of Campbell (1954), respectively. (5) *apophysis* is the lateral transverse process of a radial spine (Campbell, 1954). Subdivision of the radial beam (3) and the main spine (4) has been proposed by Suzuki (1998, figs. 3 and 16).

SEM and transmitted light microscopic images of *Spongosphaera streptacantha* give an overview of the skeletal features. The shell of *S. streptacantha* is composed of the following three skeletal elements; two microspheres (Fig. 2d), main spines (Fig. 2a), and a spongiose layer (Fig. 2b, c). The external appearance formed by the outline of the dense spongiose layer is spherical, irregularly spherical, irregularly polyhedral, or slightly elliptical. More than five long, three-bladed main spines whose length is three to four times the diameter of the spherical shell are present. In the following section, we describe the above-mentioned skeletal elements.

The two microspheres are located centrally (Fig. 3). Based on observations of 19 specimens with a transmitted light microscope, the diameter of the inner and outer microspheres varies from 11.2 to 18.2 μm (average 15.2 μm) and from 31.6 to 39.4 μm (average 35.5 μm), respectively (Fig. 4). The inner microsphere, consisting of a three-dimensional connection of bars, is

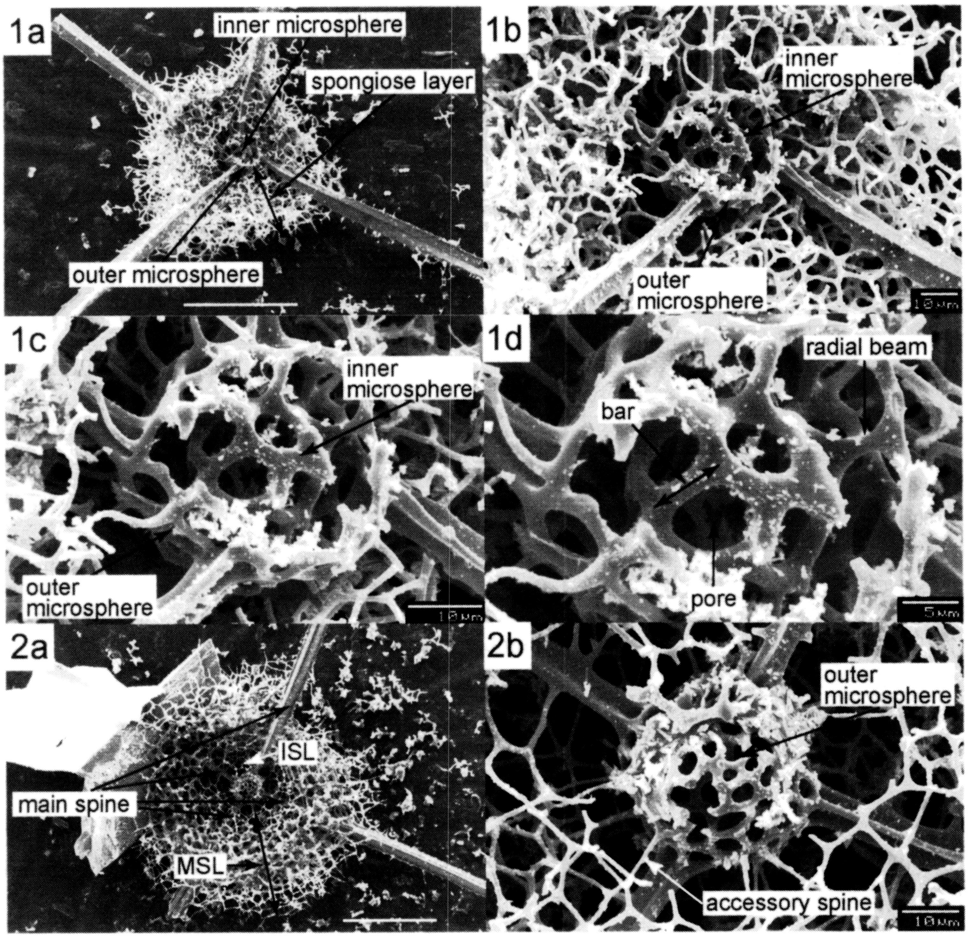

Fig. 3. SEM images showing detail structures of the microspheres and nomenclature for skeletal elements. ID numbers of specimens figured in 1 and 2 are s-23 and s-22, respectively. 1a and 2a: SEM images showing the observed specimens, of which spongiose layers were scraped by a micromanipulator (Eppendorf MicroDissector 5190). 1b, 1c, 1d, and 2b: SEM images of high magnification view of the microspheres. Scale bars of 1a and 2a equal to 100 μm.

irregularly spherical to polyhedral in shape. Based on high magnification SEM observation, five bars usually frame each pore, and an assemblage of nearly pentagonal-shaped planes partitioned by these bars makes a closed space with a shape similar to a regular dodecahedron (Fig. 3-1a-d). There are thus usually 12 pores on the inner microsphere. The outer microsphere is latticed, spherical, irregularly spherical, and slightly elliptical in shape (Fig. 3-2a, b); pores are irregular in shape and size, subrounded or ovate in shape. Radial beams arise from bars of the inner microsphere and connect the inner and outer microspheres (Fig. 3-1d). These radial

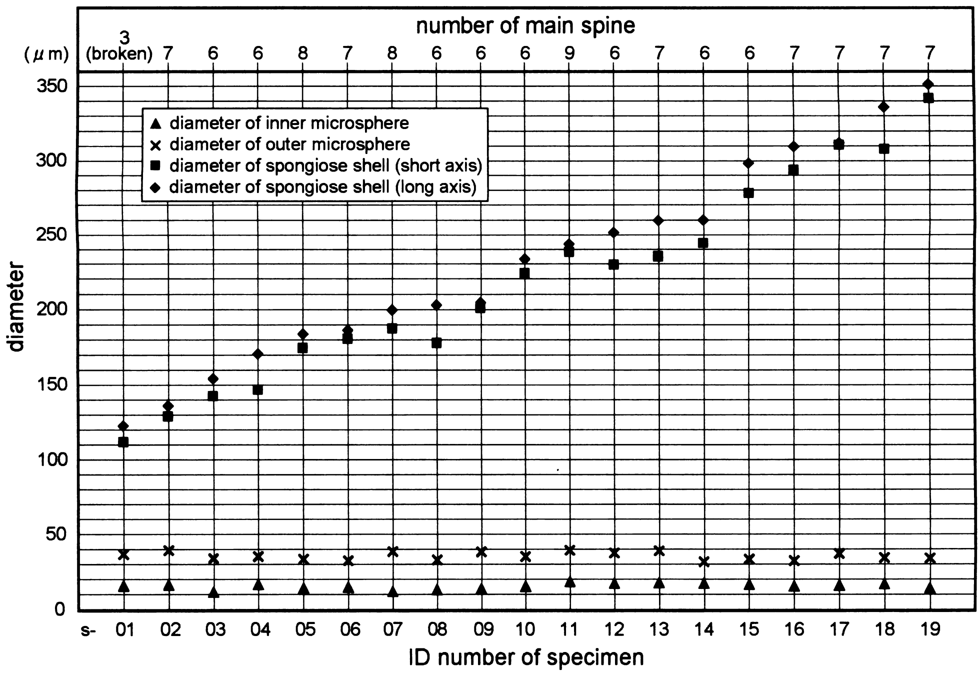

Fig. 4. Diameters of the inner and outer microspheres and spongiose shell (apparent short and long axes) and number of the main spine on nineteen individuals.

beams correspond to the "microsphere beam" of Suzuki (1998, fig. 16). They are irregularly arranged.

The main spines have distinct thin ridges and deeply developed grooves and exhibit a Y-shape in cross section (Fig. 5-1). The main spines arise only from the surface of the outer microsphere (Fig. 5-6) and do not connect to the inner microsphere by radial beams (Fig. 3-1b). The proximal part of the main spine is thinner than the middle part of it, but it also has distinct ridges and grooves (Fig. 3-2a, b). The proximal parts of these main spines are slightly thickened toward the middle. From the middle part of the main spine, thin apophyses arise at almost even intervals and extend inwardly (Fig. 5-2). In the individual shown in Fig. 5-2, the intervals between apophyses range from 7.3 to 14.4 μm. The apophyses divide repeatedly into a spongiose meshwork. The main spine tapers distally and has many teeth-like apophyses on the distal part (Fig. 5-3). Some of the main spines are slightly twisted (Fig. 5-1). The number and arrangement of the main spines can be divided broadly into two types. One type is characterized by having six main spines. Main spines of this type are symmetrically arranged and radiate at right angles to each of the adjacent spines (Fig. 5-4). The other type has more than six main spines. These main spines are arranged irregularly (Fig. 5-5), and are commonly seven in number; individuals having eight or nine main spines are rare (Fig. 6).

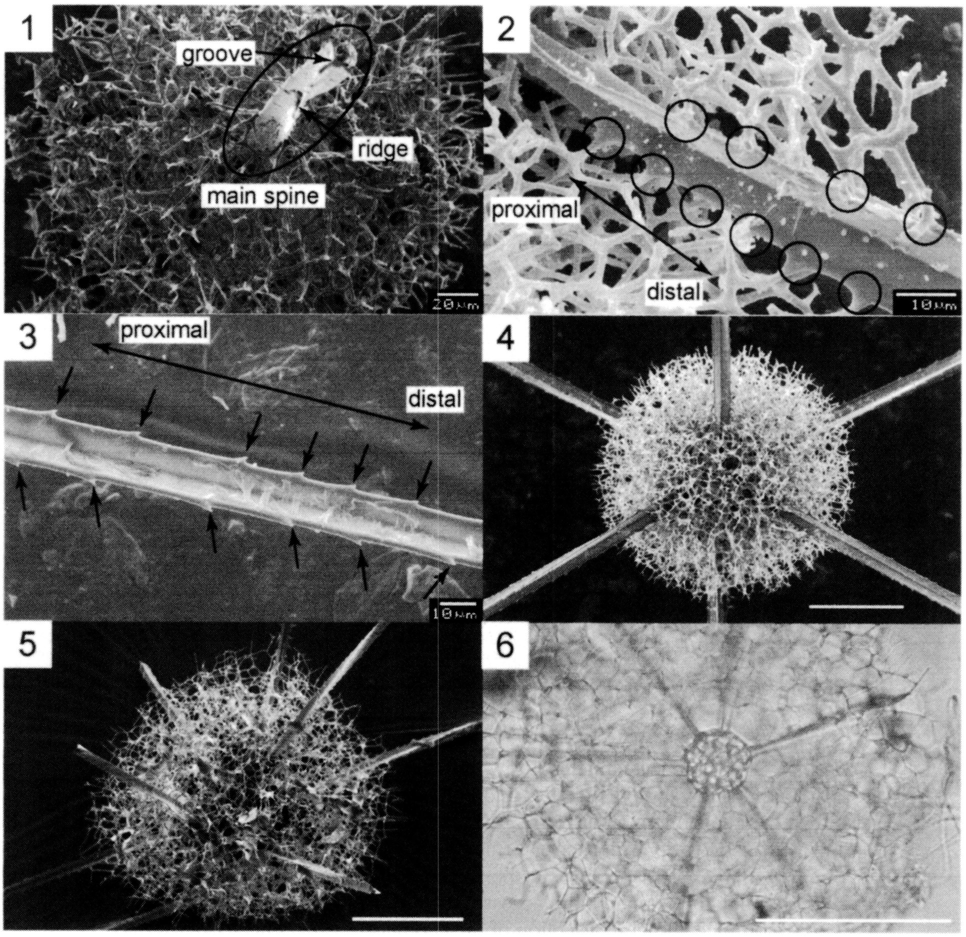

Fig. 5. SEM and transmitted light microscopic images showing detailed structures and arrangement patterns of the main spine and nomenclature for skeletal elements. ID numbers of specimens figured in 1 to 6 are s-35, s-23, s-24, s-26, s-13, and s-10, respectively. 1: SEM image showing the shape and structures of the main spine (circled area). 2: SEM image of apophyses arising from a main spine (circled areas). 3: SEM image showing teeth-like apophyses in the distal part of the main spine. 4: SEM image showing a symmetric arrangement of six main spines. 5: SEM image showing a irregular arrangement of main spines. 6: Transmitted light microscopic image showing the proximal ends of the main spines. All main spines arise from the outer surface of the outer microsphere. Scale bars of 4 to 6 equal to 100 μm.

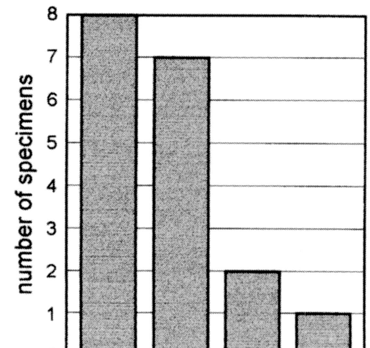

Fig. 6. Bar chart showing a variation in main spine numbers for 18 specimens (s-02 to s-19).

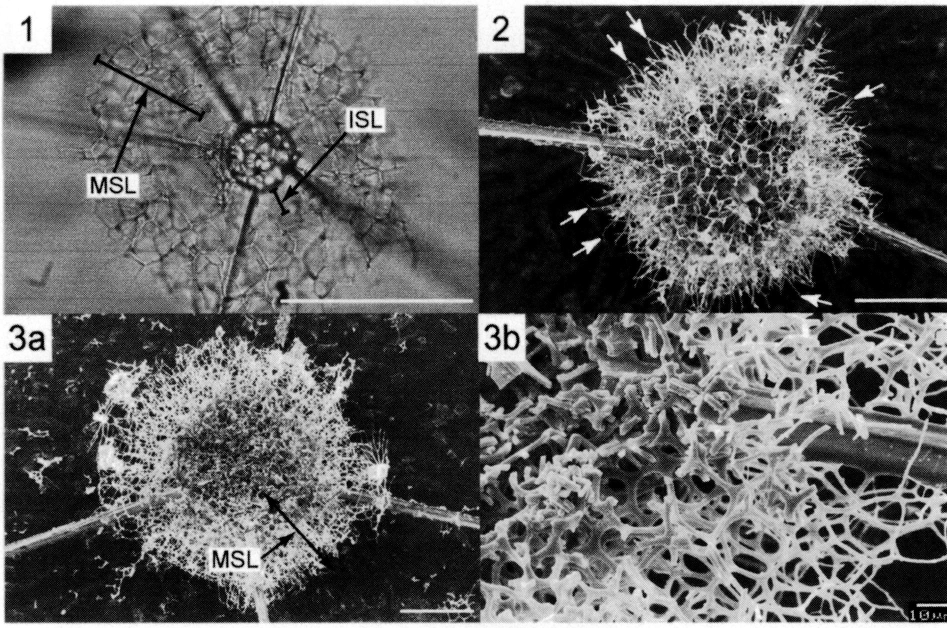

Fig. 7. SEM and transmitted light microscopic images showing detailed structures of the spongiose layer and nomenclature for skeletal elements. ID numbers of specimens figured in 1 to 3 are s-04, s-36, and s-24, respectively. 1: Transmitted light microscopic image showing a very loose spongiose innermost layer (ISL) and a fine spongiose main layer (MSL). 2: SEM image showing radially extended thin accessory spines from the MSL (white arrows). 3a: SEM image showing a section of the spongiose layer. The spongiose layer of this specimen was scraped by a micromanipulator (Eppendorf MicroDissector 5190). 3b: SEM image of high magnification view of a delicate layer. Scale bars of 1 to 3 equal to 100 μm.

The spongiose layer, which is composed of a three-dimensional network of accessory spines and apophyses, is divided into two parts: (1) a very loose spongiose innermost layer (ISL) formed by accessory spines arising directly from the surface of the outer microsphere (Fig. 3-2a, b), and (2) a fine spongiose main layer (MSL) consisting of the extension of apophyses to form a three-dimensional network (Fig. 3-2a, Fig. 7-1, 3a). The outermost part of the MSL forms a rather delicate layer which consists of a combination of both extended thin accessory spines from the MSL (Fig. 7-2) and thin apophyses (Fig. 7-3b). This layer frequently thickens in the vicinity of the main spines and is especially prominent in specimens having a large diameter (Fig. 7-3a). The mean thickness of the ISL, MSL, the delicate layer of the MSL, and the diameter of apparent long and short axes of spongiose shells, measured by

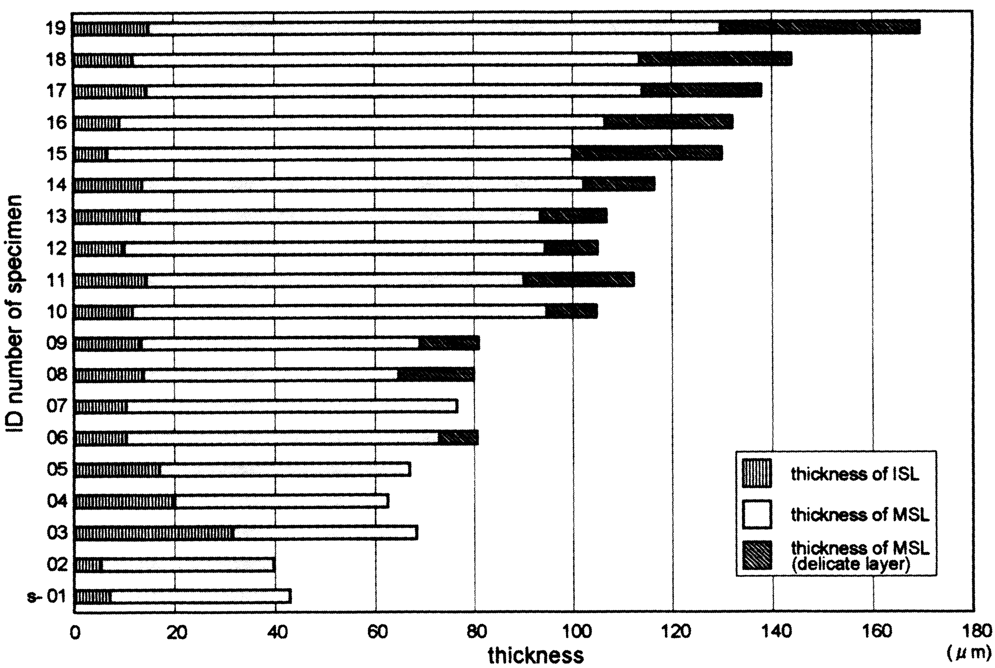

Fig. 8. Bar chart showing mean thicknesses of the ISL, MSL, and delicate layer of the MSL (nineteen individuals). The mean thickness of each layer for a individual was calculated by the average of any four measured values.

transmitted light microscope, are shown in Figs. 8 and 4, respectively. SEM and transmitted light microscope images of various sized specimens are figured in Fig. 9.

Morphologic variation of *Spongosphaera streptacantha*

It is essential to know which skeletal elements have major variability. Based on our SEM and transmitted light microscopic observations, the microspheres of *Spongosphaera streptacantha* have almost the same structure. Furthermore, as shown in Fig. 4, it is clear that the diameters of both the inner and outer microspheres are virtually constant, regardless of the thickness of their spongiose layers. Morphology of the main spines has little variation as far as we observed. According to the systematic descriptions of Haeckel (1862, 1887), *S. streptacantha* is characterized by an irregular outlined, polyhedral spongiose shell and six to twelve (Haeckel, 1862) or eight to twelve (Haeckel, 1887) irregularly arranged spines. Results of the present study, combined with Haeckel's (1862, 1887) description, suggest that the shell morphology of *S. streptacantha* varies in the number and arrangement of the main spines and the size, shape, and density of the spongiose shell.

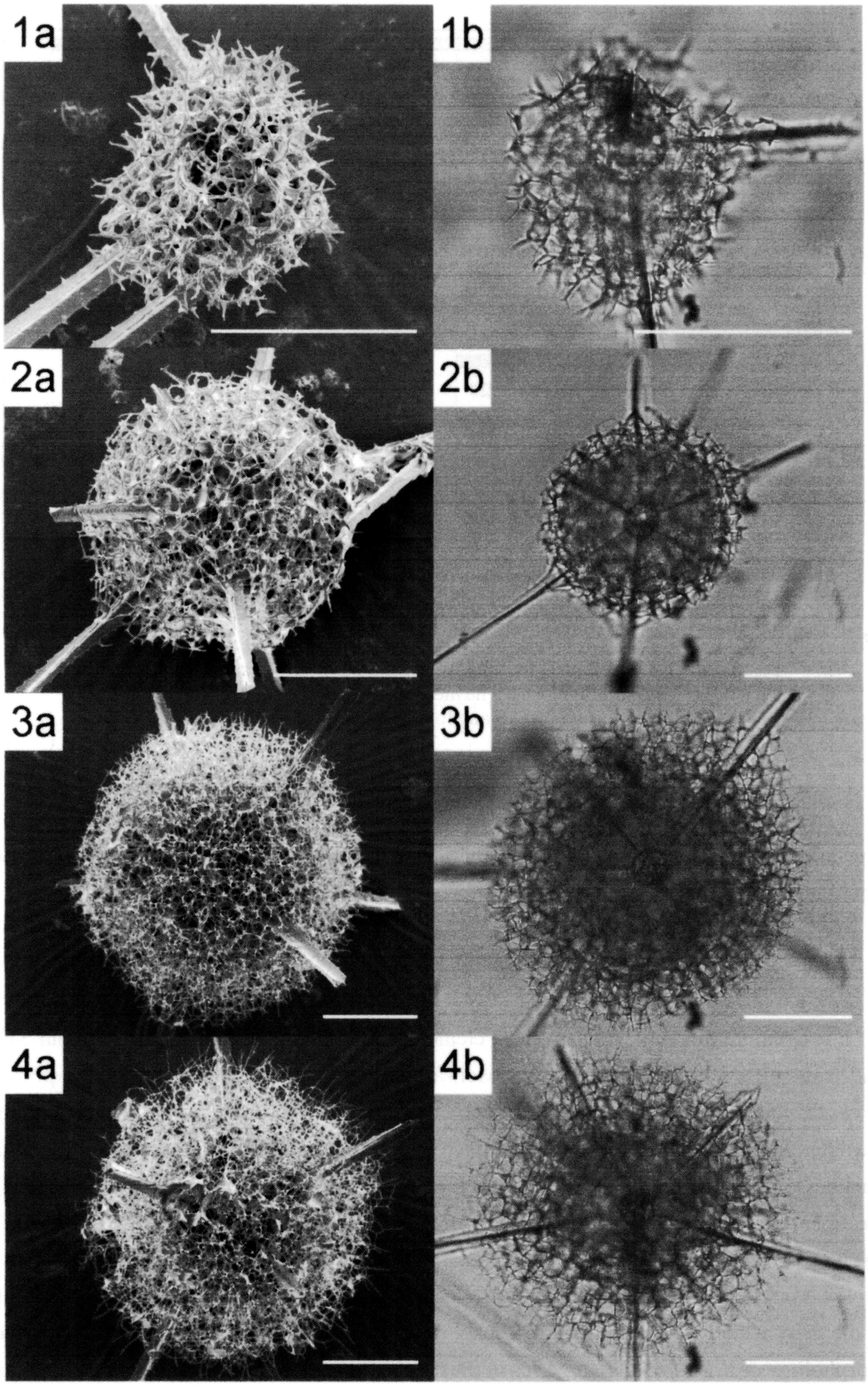

Fig. 9. SEM and transmitted light microscopic images of various sized individuals. ID numbers of specimens figured in 1 to 4 are s-01, s-06, s-16, and s-18, respectively. All scale bars equal to 100 μm.

As mentioned above, two different types about the number and arrangement pattern of main spines (six, symmetrically arranged-spine type and more than six, irregularly arranged-spine type) are recognized. Concerning the classification of the main spines, Suzuki (1998) has proposed the following four types of main spines; "primary spine" that arises from the "microsphere" (= inner microsphere of this study), "subordinate spine" that arises from the "macrosphere" (= outer microsphere of this study), "auxiliary spine" that arises from the "exosphere" (defined as outer shells having more than 80 μm in diameter), and "outer spine" that arises from the outermost "exosphere" (Suzuki, 1998, Fig. 3). In the case of *Spongosphaera streptacantha*, the main spines of both the types arise from the outer surface of the outer microsphere and are classified as the "subordinate spines". Therefore, there is a possibility that the differing number and arrangement of the main spines between these two types is not caused by the difference of these kinds of main spines. However, this presumption is based solely on high magnification observations of two specimens. Further investigation is needed to recognize the presence or absence of other types of main spines. Definite correlation between the number of spines and shell size can not be recognized at this time (see Fig. 4).

The size of the spongiose shell varies greatly; minimum and maximum diameters of observed specimens are 122.8 μm and 351.4 μm, respectively (Fig. 4). The spongiose layer of *Spongosphaera streptacantha* has skeletal features similar to those of the patagial spongiose layer of *Euchitonia elegance* (Ehrenberg) (Anderson and Bennett, 1985, pl. II, fig. 3). For example, radial extension of fragile accessory spines and an arching connection made by very thin beams are present in both species as sponge-forming structures. The structures of *E. elegance* are interpreted to be formed by additional skeletal deposition on the basic skeleton. Therefore, the spongiose layer of *Spongosphaera streptacantha* is most likely to be made by skeletal supplementation, and it is reasonable to think that the size difference between these specimens is not critical and can be approximated by the growth process of an individual. The shape of the spongiose shell of the individual varies widely. In many cases, the spherical spongiose shell takes on a polyhedral appearance due to the heterogeneous development of the MSL, especially in the outermost part, which is thicker near the main spine. The density of the spongiose shell is also variable and does not seem to depend on the differing size and shape of the spongiose shell. It is noteworthy that some individuals with more than six spines exhibit a rather loose spongiose shell. To summarize, it is likely that the shape and density of the spongy shell of *S. streptacantha* have some relationship to the number of spines that arise from the outer microsphere in the early ontogenic stage.

In this paper, we have focused on the shell structure and variation of *Spongosphaera streptacantha*. Recent improvements in the cultured study of living radiolarians facilitate the observation of their ecology (prey capture, symbionts, etc.) and for tracing of skeletal growth. Comparison of the present results together with future studies for tracing growth process will provide essential information on skeletogenesis. We will also be concerned with the correspondence of morphologic variation to ecological features.

Systematic description

Family Actinommidae Haeckel, 1862, emend. Sanfilippo and Riedel, 1980
Subfamily Actinomminae Haeckel, 1862
Genus *Spongosphaera* Ehrenberg, 1847

Spongosphaera streptacantha Haeckel, 1862
Figs. 2, 3, 5, 7, 9

Spongosphaera streptacantha Haeckel, 1962, p. 455, pl. 26, figs. 1-3; 1887, p. 282; Mast, 1910, p. 187; Popofsky, 1912, p. 109, text-fig. 22; Hollande and Enjumet, 1960, pl. 20, figs. 5-7, pl. 45, fig. 5; Tan and Tchang, 1976, p. 234, text-fig. 11; Nishimura and Yamauchi, 1984, p. 33, pl. 15, figs. 4a, b, pl. 52, fig. 2; Yamauchi, 1986, pl. 2,fig. 3; Takahashi, 1991, p. 64, pl. 7, fig. 6; Paverd, 1995, p. 114, pl. 28, figs. 2, 5, 7; Chen and Tan, 1996, p. 176, pl. 10, figs. 5-7; Tan, 1998, p. 185, fig. 176; Matsuoka et al., 2001, pl. 2, fig. 6.

Remarks.—Haeckel (1862, 1887) mentioned that the present species has six to twelve or eight to twelve main spines. Anderson (1983) suggested that the number of main spines is six or generally eight. Based on our observation, individuals having six or seven main spines are the most common (Figs. 4 and 6). Some of our specimens possessing more than six, irregularly arranged spines are somewhat similar to *Spongosphaera polycantha* Müller in external appearance. *Spongosphaera streptacantha*, however, differs from *S. polycantha* in having a more dense spongy layer. Furthermore, according to Haeckel (1887), *S. polycantha* has a large number of spines (10 to 12) which makes *S. polycantha* easily distinguished from *S. streptacantha*. *Spongosphaera helioides* Haeckel is very different from the present species in having numerous, long radial accessory spines arising from the spongiose layer.

Habitat.—Cosmopolitan, common in warm seawater (Haeckel, 1887; Yamauchi, 1986).

Acknowledgments

Prof. M. Nozaki at the Sado Marine Biological Station, Niigata University, allowed us use of facilities in the station. We would like to thank Mr. T. Shimotani, captain of the vessel "IBIS 2000", and Mr. S. Machidori of Niigata University for their assistance in plankton sampling. Mr. T. Aoki of Niigata University assisted with sample preparations using an electric furnace. We gratefully acknowledge Dr. E.S. Carter for reviewing the manuscript and valuable comments. We also thank Dr. H. Kurita of Niigata University for his review.

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