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Living radiolarian feeding mechanisms: new light on past marine ecosystems

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ABSTRACT

Environmentally controlled studies on living radiolarians, especially on their feeding mechanisms are rare. In the same way, feeding behaviours of fossil radiolarians are poorly known. In this work, techniques for living radiolarian research, including plankton sampling at sea, observations using different types of microscopes, and laboratory culture, are introduced. Light microscope, epifluorescence microscope, and confocal laser scanning microscope images of selected radiolarian species are presented. Four types of feeding behaviour which correspond well to skeletal morphology are recognized and discussed. Multi-segmented nassellarians, represented by *Eucyrtidium, Pterocorys,* and *Spirocyrtis,* take relatively large prey, including ciliates and flagellates. Some other nassellarians, e.g. *Pseudocubus* and *Arachnocorallium,* are advantageous in collecting tiny prey including microflagellates and bacteria. Solitary spumellarians, represented by *Diplosphaera, Spongosphaera,* and *Spongaster,* also gather tiny prey. Colonial radiolarians such as *Collozoum* and *Buccinosphaera* seem to live exclusively on symbiotic algae. The wide variation in feeding behaviour means that radiolarians occupy several kinds of ecological niches in marine environments. Assuming that the radiolarian skeletal morphology indicates their feeding strategy, living forms can give some light on the feeding mechanisms of similar Mesozoic forms. By contrast, the unique curved conical skeleton of the Paleozoic Albaillellaria, unknown after the end-Permian mass extinction, suggests a different feeding behaviour.

Introduction

Radiolarians, marine protists, appeared during the Cambrian (de Wever et al. 2001) and are still spread worldwide in marine ecosystems. The study of the role of extant radiolarians is useful for a better understanding of the structure of past marine ecosystems. Radiolarians can be collected from the sea and cultured in laboratory under controlled environmental conditions.

In the 1980s, O.R. Anderson and his colleagues established an apparatus for radiolarian culture and presented a series of interesting results based on laboratory culture (Anderson et al. 1989a, b, c). I visited him in 1991 and stayed in the Carribean island Barbados to learn his culturing techniques. The results of this stay were published in Anderson & Matsuoka (1992), Matsuoka (1992a, b, 1993a), and Matsuoka & Anderson (1992). Upon return from the USA, I started to work on living radiolarians in Japan and established facilities for living radiolarian research. We are now successful in rearing radiolarians in environmentally controlled conditions and in making long term observations. This means that we can obtain direct evidence for ontogeny, skeletal morphogenesis, and physiological tolerance under various environmental conditions.

This paper introduces the techniques for research on living radiolarians (including plankton sampling at sea, observations using several kinds of microscopes, and laboratory cultures) and describes observations of a variety of feeding behaviours in the cultured radiolarian specimens; the relationship between skeletal morphology and feeding behaviour is discussed. An interesting application of studying living radiolarians is to try to make a link to the palaeoecology of Palaeozoic and Mesozoic forms, which is discussed herein.

Techniques to observe living radiolarians

Our research on living radiolarians has been performed at the Sesoko Marine Station of the University of Ryukyus since 1992, targeting subtropical radiolarians which dwell in the Kuroshio Warm Current in the East China Sea (Fig. 1).

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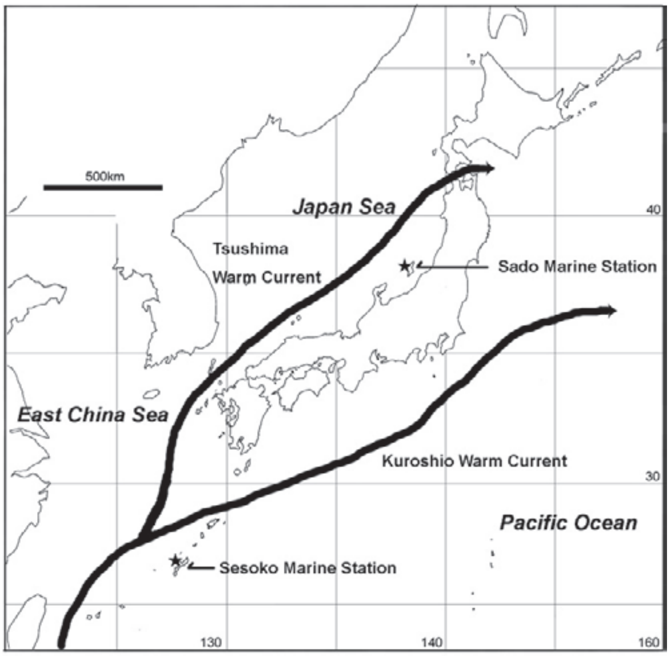

Fig. 1. Location of marine stations (Sesoko and Sado) where living radiolarian research is performed (East China Sea and Japan Sea). Sampling is conducted in the vicinity of these stations.

Fig. 2. Sampling technique of living radiolarians. a) Research vessel "IBIS 2000" and the Sado Marine Station (behind) of Niigata University. b) Sampling operation in the East China Sea using a plankton net.

The study started on temperate species at the Sado Marine Station of Niigata University (Fig. 1), upon the introduction of a small research vessel (Fig. 2a) in 2000. Radiolarians dwelling in the Tsushima Warm Current, a branch of the Kuroshio Warm Current, were collected in summer seasons, while those inhabiting in the cooler environments of the Japan Sea Proper Water were collected during the rest of the year. Detailed descriptions of the methods are given in Matsuoka et al. (2001, 2002).

Sampling

Living radiolarians are collected using plankton nets (mesh opening 44 or 100 μm) from a research vessel (Fig. 2b). In the East China Sea, plankton samples were collected by short duration (3-10 min) surface tows around Sesoko Island, Okinawa. In the Japan Sea, in addition to surface tows, subsurface tows up to 100 m in depth were performed. Plankton samples representative of different depth ranges were collected by closing the net at an intended depth by dropping a messenger. Sampling operations are usually carried out at a fixed site approximately 6 km west of Tassha in Sado Island, Niigata. At the sampling site we recorded the temperature profile with a digital thermometer.

Culture apparatus

The culture apparatus is composed of a water bath, temperature controller, and a light supply (Fig. 3a). The basic concept of this apparatus is the same as in Anderson et al. (1989c). Illumination is given from the top, instead of from the bottom as in Anderson's apparatus, to produce a more natural situation. Temperatures are controlled by a heater-chiller balance. Culture vials are placed in the temperature-controlled water bath with illumination from fluorescent fixtures. Two or three culture apparatus are simultaneously used to compare longevity and growth rate of reared specimens under various conditions.

Observation

Four kinds of microscopes are used for observations of living radiolarians: binocular stereomicroscope, inverted light microscope, epifluorescence microscope, and confocal laser scanning microscope.

The binocular stereomicroscope is used for separating radiolarian specimens from other organisms included in the plankton samples. Individual radiolarians are drawn using a Pasteur pipette and transferred to a multi well tissue culture plate filled

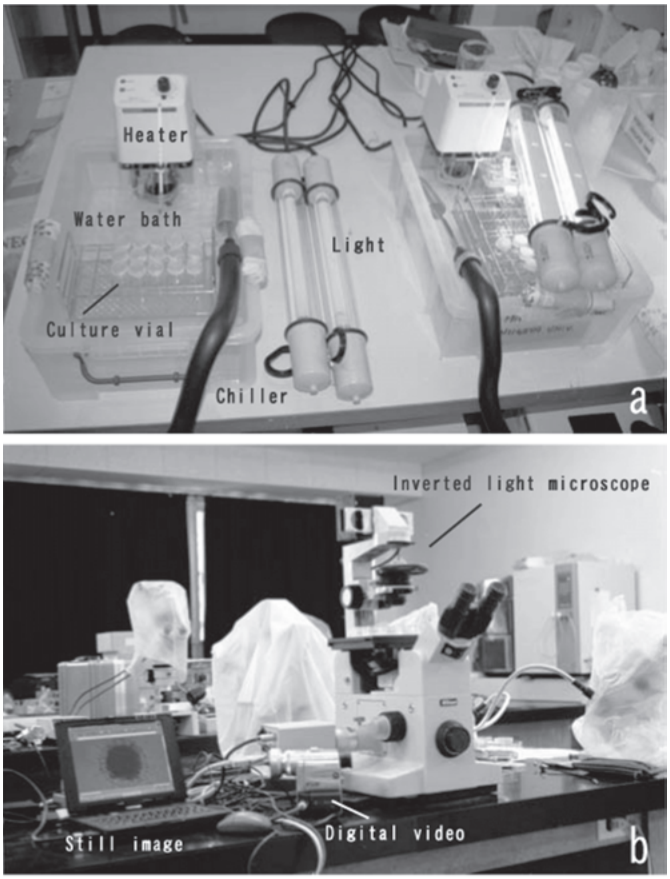

Fig. 3. Culture and observation materials for living radiolarian research. a) Culture apparatus composed of heater, chiller, water bath, and light supply. Two sets of culture apparatus are simultaneously used at different environmental conditions. b) Inverted light microscope connected to a digital video and a PC for image storage.

with ambient seawater from the sampling location. Low magnification does not allow us to observe detailed features of the living organisms. Separated specimens are further examined with the following microscopes.

Inverted light microscopy is the most common method for living radiolarian observations (Fig. 3b). Radiolarian specimens are observed from the bottom of a dish or culture vial. A normal camera or digital camera can be attached to the microscopes and gives still pictures of living organism. Vivid moving images are also recorded by connecting a video camera. Colour images of living radiolarians are presented in Matsuoka (1992b, 1993a, b) and Matsuoka et al. (2001). Some pictures of selected living radiolarian species are shown in Figures 4a–g and 5a1.

Epifluorescence microscopic observations give us useful information on symbiotic algae. The chloroplasts of algal symbionts emit autofluorescence under ultraviolet irradiation. We can easily detect the presence of symbiotic algae even if they are hidden within a silica skeleton or the host radiolarian cytoplasm. Some photomicrographs of living radiolarians from the East China Sea using an epifluorescence microscope are reported in Takahashi et al. (2003). A pair of light and epifluorescence microscopic images of the spumellarian species *Spongosphaera streptacantha* HAECKEL with symbiotic algae is shown in Figure 5 (a1 and a2, respectively).

Confocal laser microscope is another powerful tool to research living radiolarians. It shows the symbiotic algae but also a 3D image of the cytoplasm of living radiolarian specimens. Some confocal laser micrographic images are presented in Figure 5b–d. Symbiotic algae are clearly identified when the chloroplasts are highlighted (Figs. 5b2, d). Internal cell structures at any portion of the cytoplasm are also visible without any physical or chemical treatment.

Skeletal morphology and feeding behaviour

Detailed microscopic observations of living radiolarians reveal that skeletal morphology is deeply connected to their feeding behaviour. Four types of feeding strategies (Fig. 6) are recognized in subtropical radiolarians obtained from the East China Sea near Sesoko Island, Okinawa. Each strategy is described below together with the typical skeleton morphology of the different radiolarian species.

Multi-segmented nassellarians

This group of radiolarians has a conical multi-segmented skeleton. A circular large aperture is present at the distal end of the conical test. Representative genera include *Eucyrtidium* (Fig. 4a), *Pterocorys* (Fig. 4b) and *Spirocyrtis* (Fig. 4c). A typical feeding behaviour of multi-segmented nassellarians can be described as follows. The feeding apparatus is composed of an axial projection (XP) and terminal projections (TPs), and extends from the aperture (Fig. 4a). XP is one of the most prominent pseudopodia, in most cases thickest and longest, emerging outward from the center of the aperture. TPs are usually extending outward from the aperture and form a terminal cone (TC) surrounding XP (Fig. 4d). Feeding activity is divided into three phases: Phase 1, the extension phase, Phase 2, the capture phase and Phase 3, the retraction phase. The prey is captured by this cyclic movement of XP and TC, and is transferred into the radiolarian cell. The aperture acts as a mouth in the feeding mechanism. The prey is relatively large, but is smaller in diameter than the oral aperture. Prey includes ciliates and flagellates and can be engulfed by this feeding strategy. Sugiyama & Anderson (1997) described living features on three multi-segmented nassellarians together with their cytological fine structures.

Other nassellarians

Most of the other nassellarian species have a skeleton composed of spicular elements or a small number (one or two) of chambers. *Pseudocubus* (Fig. 4d) and *Arachnocorallium* are

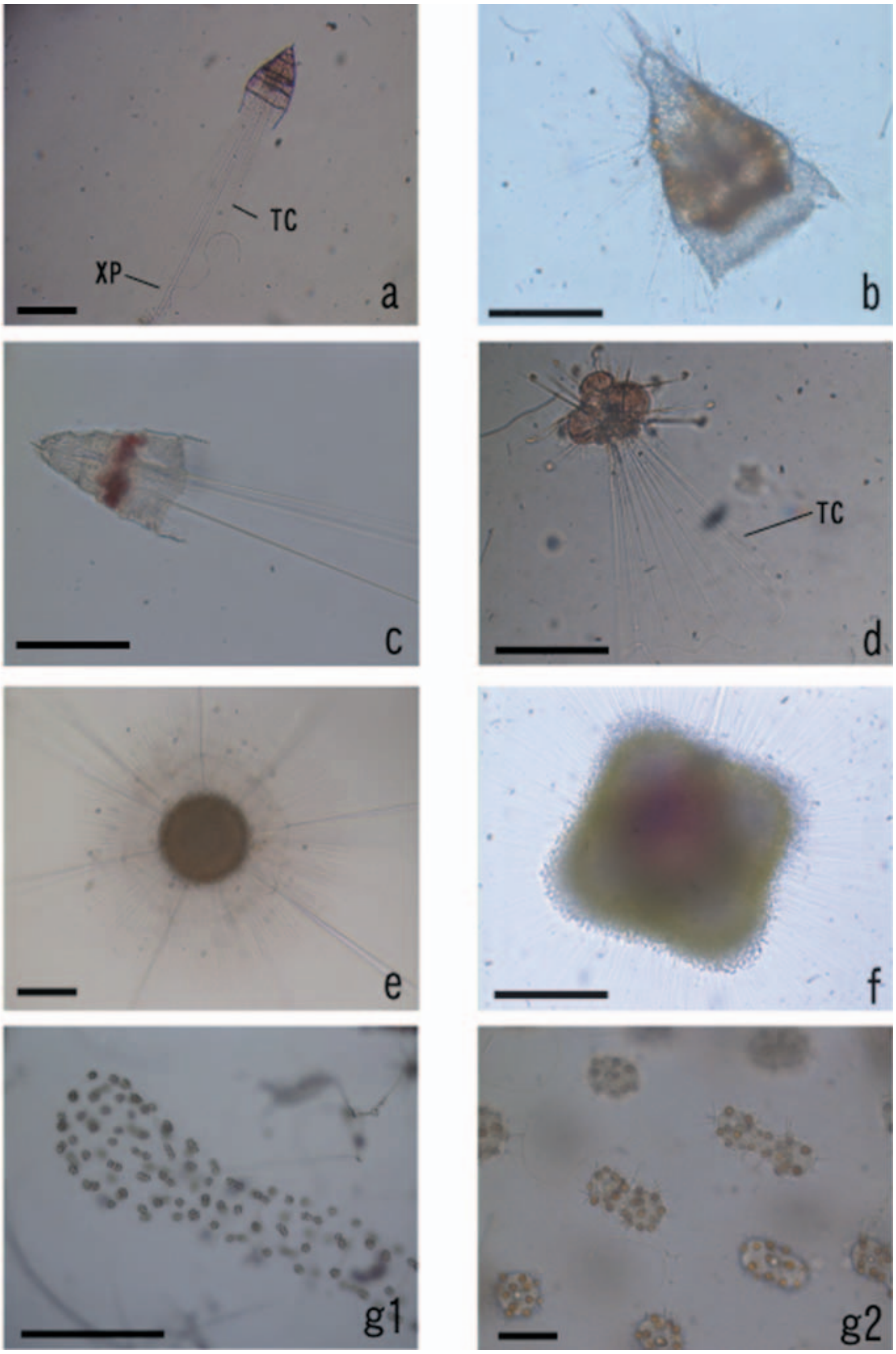

Fig. 4. Light microscopic images of living radiolarians from the East China Sea. a) *Eucyrtidium hexagonatum* HAECKEL. b) *Pteroeorys zancleus* (MÜLLER). c) *Spirocyrtis scalaris* HAECKEL. d) *Pseudocubus obeliscus* HAECKEL. e) *Diplosphaera hexagonalis* HAECKEL. f) *Spongaster tetras tetras* HAECKEL. g) *Collozoum* sp., g2 is an enlarged image of g1. Abbreviations: TC, terminal cone; XP, axial projection. Scale bars: 100 µm (a–f & g2); 500 µm (g1).

representative radiolarians which display another feeding behaviour. These radiolarians extend TC distally from the aperture or the base of the skeletal elements. TC consists of an axopodial strand and a membrane between the axopodia and resembles an umbrella. No XP is extended in this type of feeding behaviour. These radiolarians gather prey using TC as a fishing apparatus, like a casting net (Fig. 4d). Three phases in the feeding activity, similar to those in multi-segmented nassellarians, are distinguished. This strategy is advantageous in collecting tiny prey including microflagellates and bacteria. Sugiyama & Anderson (1998) examined cytological features of *Acanthodesmia vinculata* (MÜLLER) and *Lithocircus reticulatus* (EHRENBERG), both of which are categorized into the group "other nassellarians" as used herein, and showed light micrographs of living specimens of these species.

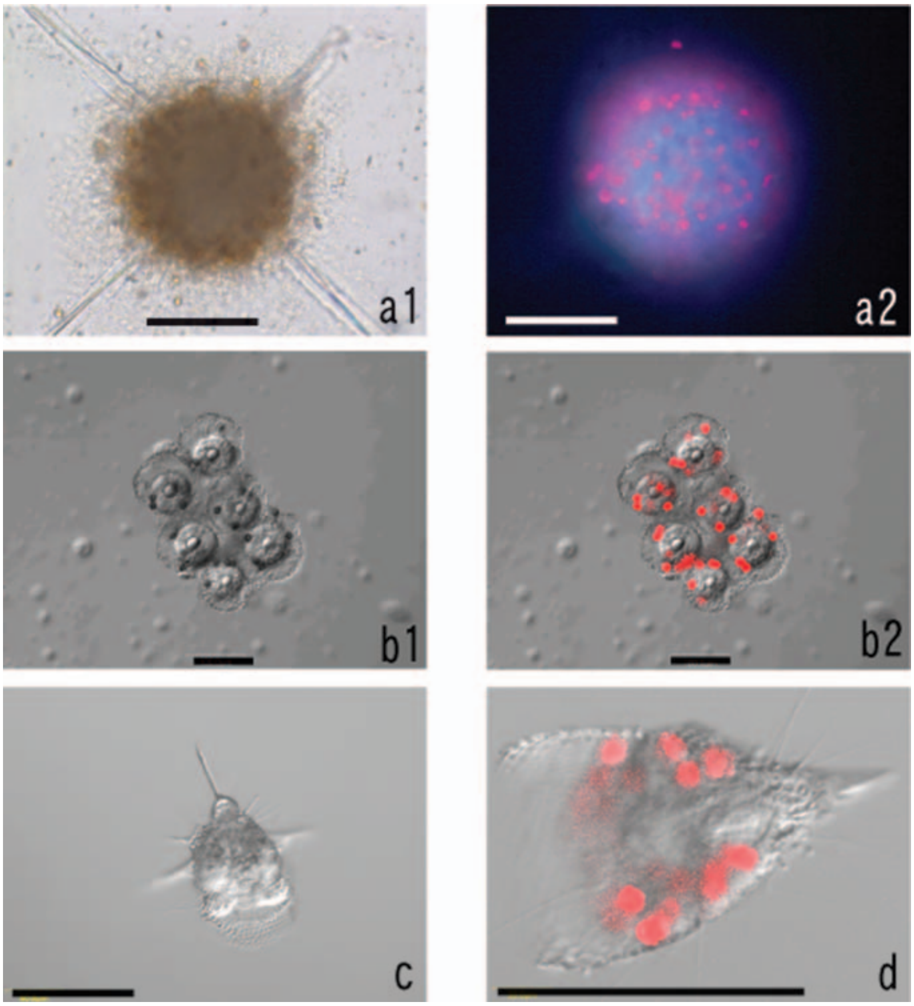

Fig. 5. Microscopic images of living radiolarians from the Japan Sea (a) and the East China Sea (b–d). a) *Spongosphaera streptacantha* HAECKEL (a1: light microscopic image, a2: epifluorescence microscopic image). b) *Buccinosphaera invaginata* HAECKEL (confocal laser microscopic images; b1: symbiotic algae not highlighted, b2: highlighted). c) *Lipmanella dictyoceras* (HAECKEL) (confocal laser microscopic image). d) *Pterocorys zancleus* (MÜLLER) (confocal laser microscopic image). Scale bars: 100 µm.

Solitary spumellarians

Solitary spumellarians display a great variety in their skeletal morphologies. One of the basic morphologies is spherical, represented by *Diplosphaera* (Fig. 4e) and *Spongosphaera* (Fig. 5a). Another typical form is discoidal such as *Spongaster* (Fig. 4f). Solitary spumellarians possess a large number of axopodia radiating in all directions. Tiny preys, including micro-algae and bacteria, are taken by contraction-extension movement of the axopodia. The movements vary among species. Symbiont-bearing species may live on the symbiotic algae as well. Feeding behaviours of *Diplosphaera hexagonalis* HAECKEL and *Rhizosphaera trigonacantha* HAECKEL are reported in Suzuki & Sugiyama (2001) and Suzuki (2005), respectively.

Colonial radiolarians

Colonial radiolarians are divided into two types: one has spicular skeletal elements such as *Collozoum* (Fig. 4g), and the other has spherical single-layered shells like *Buccinosphaera* (Fig. 5b). Radiolarian cells in both types of the colonial radiolarians are scattered in a gelatinous sheath with numerous symbiotic algae. No feeding behaviour has been observed and it is concluded that the colonial radiolarians seem to live exclusively on symbiotic algae.

Radiolarians in modern and past marine ecosystems

As stated in this paper, research on living radiolarians provides us with fundamental data for a better understanding of the past marine ecosystems. However, our knowledge on the role of radiolarians, even in modern marine environments, is still limited. There must be feeding strategies other than those presented herein. Extensive work on living radiolarians is required to better understand the changing marine environments from Cambrian to Present.

The four types of feeding strategy (Fig. 6) discussed herein correspond well to the skeletal morphology in extant radiolarian taxa. High diversity of radiolarian skeletal morphology is

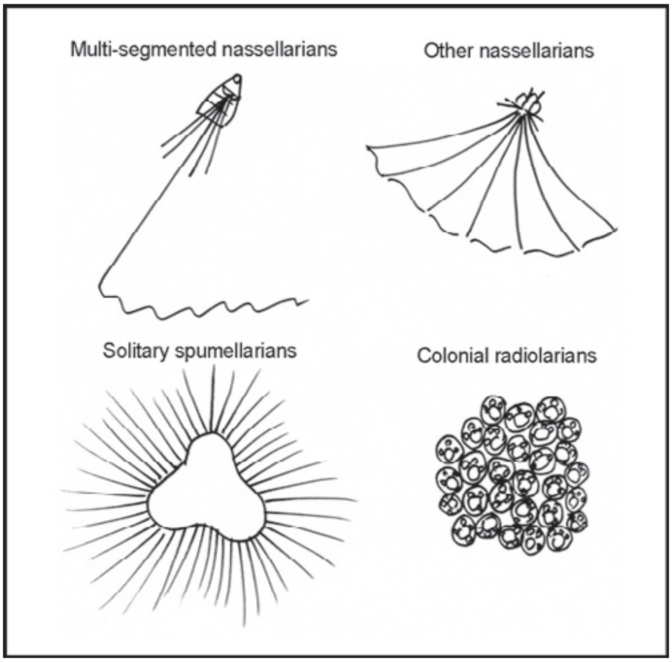

Fig. 6. Four types of feeding strategy found in living radiolarians. Multi-segmented nassellarians capture preys using both an axial projection and a terminal cone. Some other nassellarians gather prey using a terminal cone only. Solitary spumellarians collect prey by contraction-extension movement of numerous axopodia. Colonial radiolarians seem to live exclusively on symbiotic algae. See section "Skeletal morphology and feeding behaviour" for details.

partly related to a diversification in feeding strategies. The wide variation in feeding behaviour means that radiolarians occupy several kinds of ecological niches in the marine environments. We can infer the feeding behaviour of extinct radiolarian groups based on their skeletal morphology.

Once we recognize the role of radiolarians in the food web in modern marine environments, we can apply this knowledge to the reconstruction of past marine ecosystems. Fluctuation in the morphological diversity of radiolarian skeletons is well documented in the fossil record (de Wever et al. 2001). This fluctuation could be interpreted as a change in the number of ecological niches in the marine ecosystems through time.

Mesozoic radiolarians include most types of basic skeletal morphology of extant radiolarians except for colonial radiolaria. We can make assumptions that the skeletal morphology may be a reflection of a specific feeding behaviour, but it can also reflect the floating efficiency of the individual, or its capacity to stabilize/migrate at certain levels in the water column, or its efficiency at silica usage and the resulting optimization of cellular energetic balance, or it can change as a protection from predators. Anyway if we assume that the skeletal morphology indicates their feeding strategy, then at least three types of feeding behaviour (multi-segmented nassellarians, other nassellarians, and solitary spumellarians), as described in this paper were developed in the Mesozoic.

Paleozoic radiolarians are also characterized mostly by spherical, discoidal and cone-shaped shells (de Wever et al. 2001). One of the unique shell morphologies in Paleozoic radiolaria is the curved conical skeleton, typical in albaillellarians. It is noteworthy that after the end-Permian mass extinction, the curved conical skeletons have never been found in the fossil record, except for relict follicuculids in the lowermost Triassic (Sugiyama 1997, de Wever et al. 2006), and are unknown in living taxa. It could be assumed that the Albaillellaria might have adopted a different feeding strategy and that their ecological niche has never been occupied by any radiolarians after this major extinction event.

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