Coral Reefs (2011) 30:925–933
DOI 10.1007/s00338-011-0765-z

REPORT

Sclerite calcification and reef-building in the fleshy octocoral genus *Sinularia* (Octocorallia: Alcyonacea)

M.-S. Jeng · H.-D. Huang · C.-F. Dai · Y.-C. Hsiao · Y. Benayahu

Received: 29 October 2010 / Accepted: 26 April 2011 / Published online: 15 May 2011

Abstract Alcyonacean octocorals in tropical reefs are usually not considered as reef builders. Some *Sinularia* species, however, are capable of consolidating sclerites at the colony base to form spiculite. Nanwan Bay, southern Taiwan, features both fossilized and recently formed boulders composed of spiculite, thus demonstrating the role of *Sinularia* in contributing to the reef structure. Section radiography of an 18.5 kg spiculite boulder demonstrated a regular density banding of 3–6-mm intervals. Core survey indicated spiculite coverage of 25–30% on the live reef and of 30–40% on the uplifted boulders. Cores taken from living *Sinularia* revealed a distinct transition from discrete sclerites to compact spiculite and amorphous calcium carbonate cementing the sclerites. In the widespread *S. gibberosa*, sclerite formation appeared to start intracellularly, followed by a prolonged extracellular calcification process. At the calcification site, multiple sclerocytes formed expanded pseudopod-like membranes that interconnected, forming multicellular vesicles (MCVs) around the sclerites. The MCVs and the pseudopods disappeared at sclerite maturation, followed by degradation of the sclerocytes around the mature sclerites. At the colony base, granular vesicles were distributed among the sclerites, indicating a cementing process in progress. These findings suggest that colonies of *Sinularia* are able to cement sclerites and consolidate them at their base into spiculite, thus making them reef builders.

Keywords Reef-building · Octocorals · Spiculite · *Sinularia* · Calcification · Sclerite cementation · Taiwan

Communicated by Geology Editor Prof. Bernhard Riegl

M.-S. Jeng (✉) · Y.-C. Hsiao
Biodiversity Research Center, Academia Sinica, Taipei 11529, Taiwan
e-mail: jengms@gate.sinica.edu.tw

H.-D. Huang
National Museum of Natural Science, Taichung 40453, Taiwan

C.-F. Dai
Institute of Oceanography, National Taiwan University, Taipei 10617, Taiwan

Y. Benayahu
Department of Zoology, Tel Aviv University, 69978 Ramat Aviv, Tel Aviv, Israel

Introduction

It is well accepted that the carbonate skeletons of stony corals form the foundations of coral reefs. New skeleton, in the form of aragonite crystals, is deposited externally by the calicoblastic epithelium of these corals onto previously formed ones (Le Tissier 1991; Muscatine et al. 1997). Octocorallia produce calcite sclerites within fleshy tissue as internal support (Fabricius and Alderslade 2001) and are generally not considered to contribute to the reef structure. The discovery of rocks composed of octocoral sclerites, termed spiculite (Konishi 1981; Accordi et al. 1989), led to the suggestion that fleshy octocorals may contribute to reef construction and growth (Schuhmacher 1997). Most spiculites are made of consolidated sclerites from octocorals of the family Alcyoniidae (order Alcyonacea). Cary (1931) first focused attention on sclerite masses left by colonies of *Alcyonium* (= *Sinularia*) *confertum* in American Samoa. Later, below flourishing living colonies of the fleshy octocoral, *Sinularia*, cemented layers of sclerites were found on modern coastal reefs in the Ryukyu Islands (southern Japan) and Australia that had been accreting for

thousands of years (Konishi 1981; Kleypas 1996). Fossil spiculites were found as distant as in Somalia (Accordi et al. 1989) and can be traced back to the Silurian period in fossils from the Island of Gotland in the Baltic Sea (Bengtson 1981). *Sinularia* spiculite has contributed to the basis of modern reefs in the central Great Barrier Reef since the end of the last Ice Age (Johnson and Risk 1987). Although spiculite rocks have been found in many regions, the mechanisms of sclerite cementation into solid calcareous rock layers are still not understood.

Among octocoral colonies, calcitic sclerites in the coenenchyme function as means of physical support and defense against predation (Alstyne et al. 1992) and may increase the ability of the organism to withstand shear forces caused by water flow (Grillo et al. 1993; Lin and Dai 1997). Sclerite formation could be initiated intracellularly in primary sclerocytes, followed by extracellular growth processes conducted by secondary sclerocytes (Goldberg and Benayahu 1987; Grillo et al. 1993). Another possible mechanism relates to the formation and growth within sclerocytes containing numerous sclerite-forming vacuoles (Kingsley and Watabe 1982; Kingsley and Dupree 1993). Konishi (1981) hypothesized that in *Sinularia* species, discrete sclerites may fuse and be incorporated into spiculite masses at the base of the colony. Thus, it was concluded that octocoral sclerites undergo cementation and fusion processes that imply persistent calcification, even after sclerite maturation.

In the present work, we studied spiculite of *Sinularia* spp. in southern Taiwan. Our findings demonstrate the extent of spiculite occurrence and, at the ultrastructural level, reveal the cellular activities that lead to sclerite cementation. We examined spiculite found in both living colonies and in uplifted (fossil) boulders and evaluate the roles and contribution of spiculite in building reef structures.

Materials and methods

Study site and sampling

Field surveys and collections of spiculite were conducted in Nanwan Bay, Kenting National Park, Hengchun Peninsula, southern Taiwan (Fig. 1), both along the shoreline and underwater by scuba diving (1997–2000). The seashore has a characteristic coastal Holocene coral reef dated to 2820 ± 40 years ago (Chen 1993). In addition to scleractinians, more than 50% of the subtidal reef surface there is covered by a high diversity of alcyonacean octocorals (Dai 1991a; Benayahu et al. 2004).

Surveys of spiculite boulders and rock formation were conducted in uplifted reefs of the upper intertidal zone of

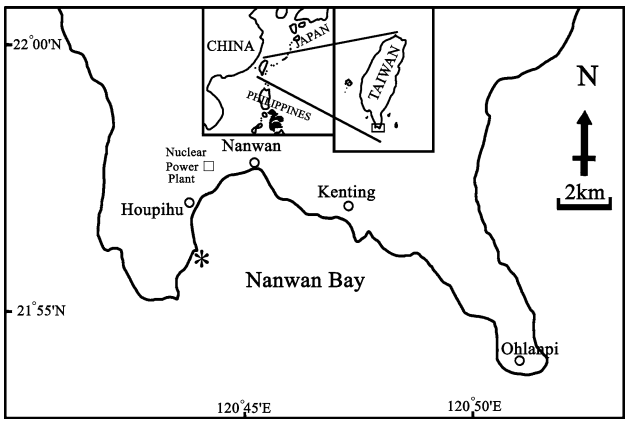

Fig. 1 Map of the study area, Nanwan Bay, southern Taiwan. Asterisk indicates the collection site near Houpihu

Houpihu, at approximately 10 m above sea level. Spiculite found embedded in the reef boulders was photographed and tape measured; the abundance of spiculite in the area was estimated according to size and occurrence. Thirty-five loose spiculite boulders were collected at random for microscopic examination. In the laboratory, thick sections (2.5–3.0 mm) were sampled from 10 boulders with a recognizable growth direction. Sections were cut parallel to the growth direction using a diamond saw and then examined with x-radiography (SOFTEX CMB-2). To determine the abundance of spiculite in the uplifted reefs, cores of spiculite masses from six exposed reef boulders (one for each) were taken, using a pump drill equipped with 50–cm-long steel tubes (70 mm inner and 80 mm outer diameter).

In order to examine the deposition of spiculite beneath living *Sinularia* colonies, core samples were obtained from the reef at 10–15 m deep. For this purpose, coverage of living *Sinularia* was determined by surveying two 50 m parallel transect lines, parallel to the shoreline and 10 m apart. For core sampling, colonies with a diameter of >1 m were selected, and a core was removed from each one by hammering a steel tube (1 m long, and 45 mm inner and 49 mm outer diameter) through the center of the upper surface down to the base (~20 cm deep). The morphological features of spiculite associated with the living colonies were recorded by underwater photography using a Nikon RS camera. The morphology of the sclerites found in the cores was examined under a compound microscope, and all of the sampled *Sinularia* colonies were identified to species level following Verseveldt (1980). Six samples from living colonies, which included the transition zone between discrete sclerites of the living parts and solid spiculite, were carefully excised from the cores using a knife and chisel. They were then subjected to critical-point drying, gold-coated, and examined with a scanning electron microscope (Hitachi S-2500).

Tissue preparation of *S. gibberosa* and electron microscopy

The process of sclerite consolidation, the function of the adjacent sclerocytes, and the features of spiculite were studied in *S. gibberosa* Tixier-Durivault, 1970. Six cuttings, 15 × 15 cm in size, with a spiculite layer were removed from the edge of six random colonies >1 m in diameter (November 2000). In order to obtain active sclerocytes, four cutting samples were transferred to the laboratory, kept for 5 days in aerated seawater tanks (90 × 30 × 30 cm) at 22°C with 12:12 h fluorescent illumination (Philips 36 W/865 tube light). The other two samples were transported on dry ice in a cooler to the laboratory and then stored in a freezer at −70°C for further examination (see below).

In order to study the process of sclerite cementation in the spiculite, we examined the structural features of individual and fused sclerites in *S. gibberosa*. Twenty-four tissue samples, 0.5 cm^3 in size, which included the surface layer and the interiors of the lobes and stalk, were removed from the six colony cuttings (four samples for each colony, see also Verseveldt 1980). They were individually placed in 5% sodium hypochloride for 24 h, and the remaining sclerites were repeatedly rinsed with distilled water and then air-dried. Six samples of fused sclerites, 0.25 cm^3 in size, one for each colony, were removed with a knife and chisel from the spiculite of the colonies. All preparations were mounted on stubs, gold-coated, and examined by scanning electron microscopy (SEM).

In order to examine sclerite deposition by sclerocytes, 35 tissue samples, each 1–2 mm^3 in size, were removed (8–9 samples per colony block) from the top and basal parts of the aforementioned four cuttings of *S. gibberosa* maintained in an aquarium. They were fixed for 1–2 h in a modified Karnovsky-type mixture containing 4% paraformaldehyde and 6.25% glutaraldehyde in 0.2 M phosphate buffer at pH 7.6–8.0. In order to improve fixation, 0.2% ruthenium red was added to the mixture (Goldberg and Benayahu 1987). Subsequent procedures included post-fixing samples in 1% OsO_4 in 0.2 M phosphate buffer with 0.1% ruthenium red for 1 h. After fixation, all samples were decalcified in 5% EDTA (buffered to pH 7.6 with 0.2 M phosphate) for 2–7 days, followed by dehydration in a graded series of ethanol and infiltration with Spurr resin. All steps were carried out at room temperature. Infiltration for final embedding was conducted in a 70°C vacuum oven for 18–24 h. Sections of the decalcified tissue samples were obtained using glass knives and stained with ethanol–uranyl acetate followed by lead citrate and then examined with a transmission electron microscope (TEM; Hitachi H-700).

Results

Distribution and morphology of spiculite

In Nanwan Bay, spiculites of *Sinularia* were found along the shoreline in different forms and sizes, ranging from pebbles weighing several grams to boulders of >100 kg (Fig. 2a), and on adjacent uplifted reefs (Fig. 2b). Figure 2c shows a dislodged, ~1.5 kg, dry octocoral mass that was deposited on the shore during a typhoon. The specimen included a rock of densely compacted sclerites cemented beneath its desiccated tissue. Examination of its sclerites indicated that it belonged to a colony of *S. nanolobata* Verseveldt, 1977. The exposed parts of the sampled reef boulders ranged from 60 to 110 cm in diameter. All core samples longer than 45 cm, from the six uplifted reef boulders, contained >90% continuous dense spiculite of fused sclerites (Fig. 2d). The estimated weight of the uplifted spiculite boulders exceeded 100 kg. Such spiculite boulders, according to the occurrence frequency and cored samples, covered approximately 30–40% of uplifted reefs in the study area. Radiographic images of sections from 10 spiculite boulders revealed delineated layers representing different densities of skeletal elements; a section from a spherical 18.5 kg boulder contained approximately 60 distinct density layers at 3–6 mm intervals (Fig. 2e).

The live coverage of *Sinularia* colonies on the reef at the time of this study was approximately 30%. From the 49 underwater cores obtained from live *Sinularia* colonies, five had no spiculite or fused sclerites, whereas the remaining 44, representing 22 species, contained spiculite ranging from 0.5 to 17 cm thick (Table 1). Of the 44 cores with spiculite, 17 samples representing 13 species contained spiculite masses of >5 cm thick (Fig. 3a). According to the abundance of the spiculite layer under living *Sinularia*, we estimate the spiculite coverage of a live reef as ranging from 25 to 30%. Cores of living *Sinularia* colonies contained a loosely consolidated sclerite layer in the tissue overlaying the spiculite. The spiculite mass beneath the base of the living colony had fused sclerites with no interstitial coenenchyme tissue. In most cases, there was a distinct boundary between the live tissue layer and the consolidated basal spiculite mass (Fig. 3b). SEM examination of sclerites of the newly deposited spiculite beneath the tissue layer revealed sclerites cemented by amorphous calcium carbonate, which also covered the surface of the spiculite (Fig. 3c).

Sclerocytes of *S. gibberosa*

Following examination of the morphology of the colonies and their sclerites, colonies employed for this part of the

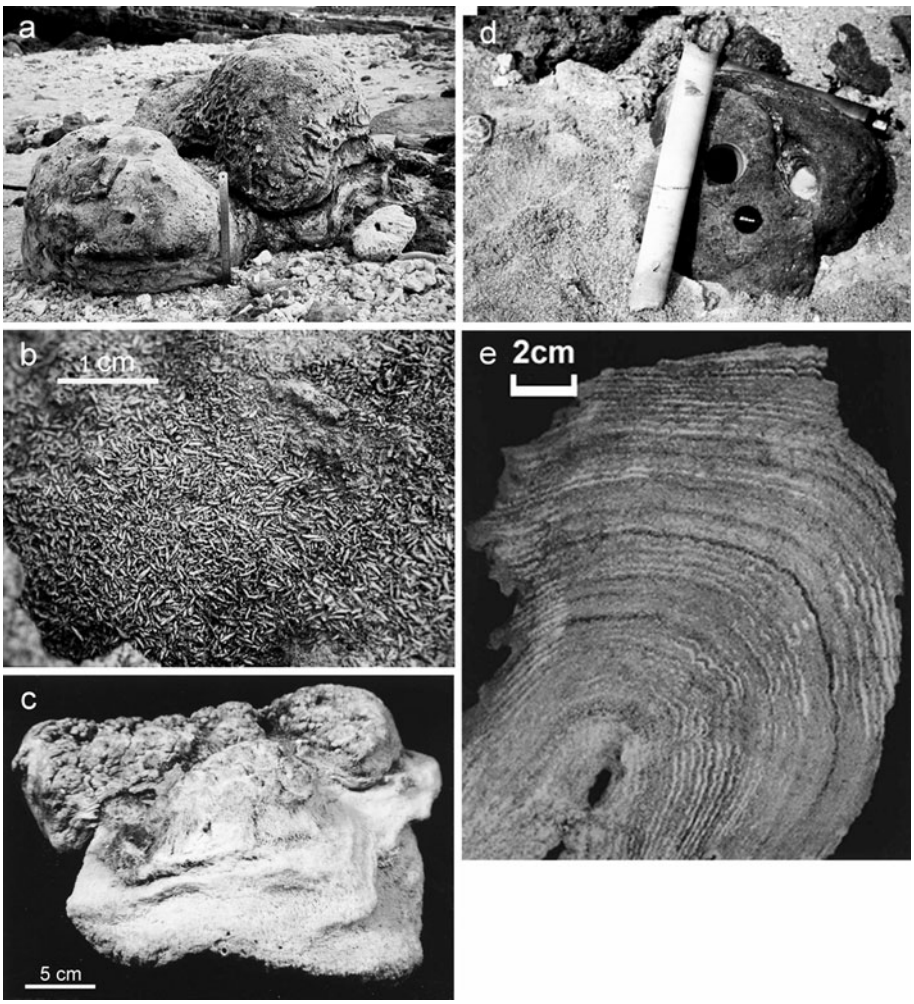

Fig. 2 Spiculite masses found on the shore of Nanwan Bay, southern Taiwan. **a** Fossil spiculite boulders approximately 50 and 70 cm high, half-embedded in coarse sand, ruler is 30 cm long. **b** Exposed on an uplifted beach, spiculite boulder illustrates surface texture of fused sclerites. **c** Desiccated soft coral colony (tissue) on top of its spiculite base (1.65 kg) of *Sinularia nanolobata*. This mass was deposited on the shore by a storm wave. **d** Land core sample of more than 50 cm in length through an uplifted, fossil spiculite mass. This boulder is composed solely of sclerites. Camera lens cap in the figure is 52 mm in diameter. **e** X-ray photograph of a section (2.5 mm thick) of 18.5-kg spiculite boulder showing periodic growth bands. Spiculite boulder growth direction is upward

study were assigned to *S. gibberosa.* In the interior of their bases, numerous sclerites were inter-cemented and their microstructure was still recognizable. At the location of cementation, there was amorphous calcium carbonate, which may function as an adhesive. Three crystal types of the adhesive were observed: blade like (Fig. 4a, b), botryoidal (Fig. 4c, d), and pillar shaped (Fig. 4e, f). Both primary and secondary sclerocytes were found scattered in the mesoglea. The primary sclerocytes were found exclusively, though in a relatively small amount, in the upper part of the colony and the cut wound, where new calcification had initiated. They were elliptic, mono-nucleated cells, approximately 4–7 μm in diameter, and contained vesicles surrounded by multiple electron-opaque vesicles (Fig. 5a). These vesicles, sometimes with a fibrous internal structure, may serve as the site of initial condensation of the sclerite microstructures. Numerous secondary sclerocytes were also observed (Fig. 5b). These relatively large cells, usually >8 μm in diameter, contained multiple free ribosomes and electron-opaque bodies. They possessed expanded pseudopod-like membranes that overlapped those of other cells, forming an extracellular structure in the shape of a multicellular vesicle (MCV). In decalcified tissues, MCVs appeared as electron-lucent structures that possessed an organic matrix. Several MCVs seemed to have further aggregated and connected among sclerocytes during the process of sclerite formation (Fig. 6a). Highly concentrated mesoglea fibers were observed adjacent to MCVs (Fig. 6b).

Sclerocytes, speculated to be inactive and degenerated, were found adjacent to mature sclerites within mesoglea fibers. They possessed a few calcitic vesicles but did not contain MCVs or signs of calcification (Fig. 7). In some cases, the sclerocytes were flattened and had engulfed the sclerites. Sclerocytes seldom appeared in the coenenchyme of the colony base. Instead, granular vesicles and organic matrix were distributed among the sclerites, which may indicate localized calcification/decalcification activity (Fig. 8).

Discussion

The findings of the field surveys revealed a continuous (for the last 2800 years) spiculite-forming zone of the *Sinularia*

Table 1 Shallow-water *Sinularia* species from Nanwan Bay cored for this study

Scientific name	No. cored	Spiculite base
Order ALCYONACEA Lamouroux, 1812		
Family ALCYONIIDAE Lamouroux, 1812		
Sinularia capillosa Tixier-Durivault, 1970	2	2*
Sinularia crassa Tixier-Durivault, 1945	1	1*
Sinularia cristata Tixier-Durivault, 1969	1	1*
Sinularia cruciata Tixier-Durivault, 1970	3	2*
Sinularia deformis Tixier-Durivault, 1969	1	1*
Sinularia dissecta Tixier-Durivault, 1945	1	1
Sinularia exilis Tixier-Durivault, 1970	3	3*
Sinularia fungoides Thomson & Henderson, 1906	1	1
Sinularia gibberosa Tixier-Durivault, 1970	5	5*
Sinularia inelegans Tixier-Durivault, 1970	6	5
Sinularia inexplicita Tixier-Durivault, 1970	2	2*
Sinularia leptoclados (Ehrenberg, 1834)	1	1
Sinularia lochmodes Kolonko, 1926	7	4*
Sinularia minima Verseveldt, 1971	2	2*
Sinularia muralis May, 1899	2	1
Sinularia nanolobata Verseveldt, 1977	2	2*
Sinularia notanda Tixier-Durivault, 1966	2	2
Sinularia numerosa Tixier-Durivault, 1970	1	1*
Sinularia parva Tixier-Durivault, 1970	1	1
Sinularia scabra Tixier-Durivault, 1970	3	3*
Sinularia sp. A	1	1
Sinularia sp. B	1	1

Of the 22 species of *Sinularia*, 49 cores were taken and 44 contained spiculite masses ranging from 0.5 to 17 cm thick. Asterisks indicate species with subjacent spiculite in excess of 5 cm thick

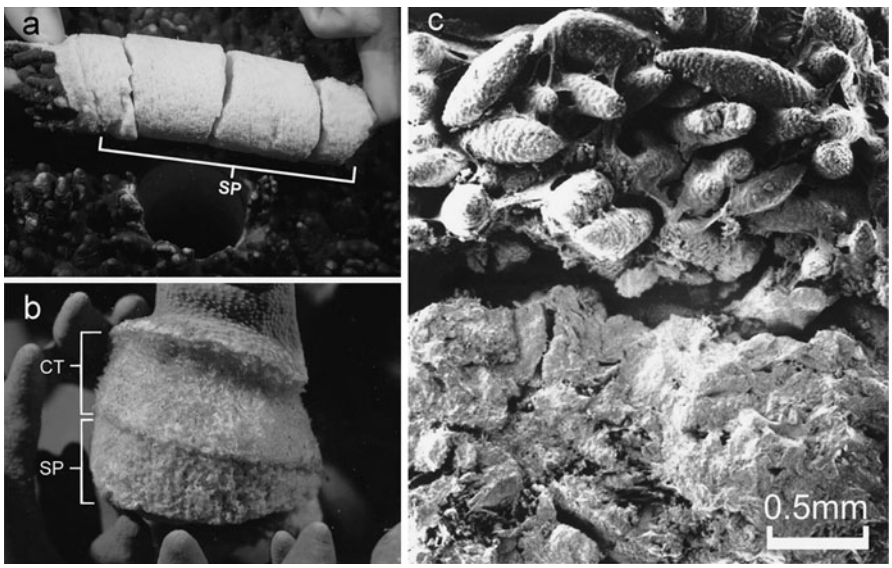

Fig. 3 Spiculites associated with living corals. **a** Core sample of *Sinularia nanolobata*, 17 cm long, which contains 5 cm of tissue with discrete sclerites and 12–cm-thick spiculite (SP) layer. **b** Close-up view of recently formed SP subjacent to colony, indicating coenenchyme tissue (CT) layer with discrete sclerites and solid SP. **c** SEM micrograph of boundary between soft tissue and SP layers. Upper part is composed of loosely cemented sclerites. Lower part is compact, tissue-free SP; surface structure of sclerites is obscured by amorphous $CaCO_3$

colonies from the subtidal zone to the uplifted reefs of Nanwan Bay, southern Taiwan (Chen 1993). In the lower part of living *Sinularia* colonies, discrete coenenchymal sclerites were cemented together by calcium carbonate adhesive. The fused sclerites formed solid spiculite beneath the colony. The size and thickness of the spiculite layer in the boulders suggested that, in addition to deposition of spiculite layers onto the existing reef platform, *Sinularia* colonies generate three-dimensional reef structures (Schuhmacher 1997).

The pattern of layered growth bands in the spiculite boulders (Fig. 2e) corresponded with the previous findings

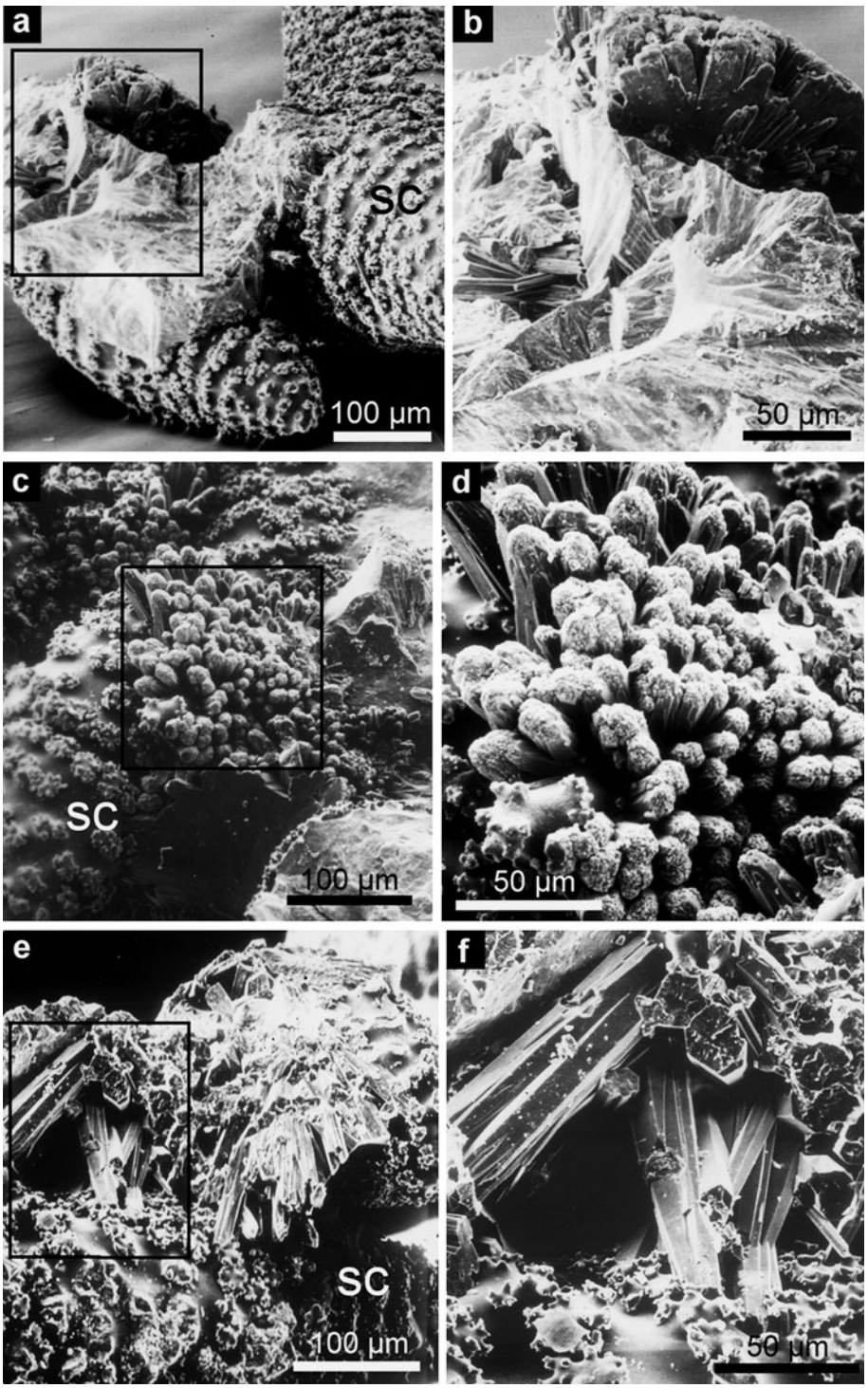

Fig. 4 SEM micrographs of three types of cementing crystals among sclerites at base of a colony. **b**, **d**, and **f** magnifications of *marked areas* in **a** **c** and **e**, respectively. **a** and **b** show bladed crystals; **c** and **d** botryoidal crystals; **e** and **f** pillar crystals. *sc* Cemented sclerites

of Schuhmacher (1997), indicating a distinct periodicity in spiculite deposition. Close ranges of band widths of the two study sites also indicated similar deposition rates between them. SEM showed that the surface of newly formed spiculite was covered with amorphous calcium carbonate, and thus, the microstructure of the sclerites could not be determined. This could have been caused by decalcification and re-deposition of calcium carbonate by octocoral colonies. Kingsley et al. (1996) reported seasonal changes in tissue characteristics of the gorgonian *Leptogorgia virgulata*. Its tissue becomes acidic in winter thus leading to sclerite decalcification; whereas in summer, sclerocytes redeposit calcium carbonate on the surface of the sclerites. Influenced by the warm Kuroshio current, the water

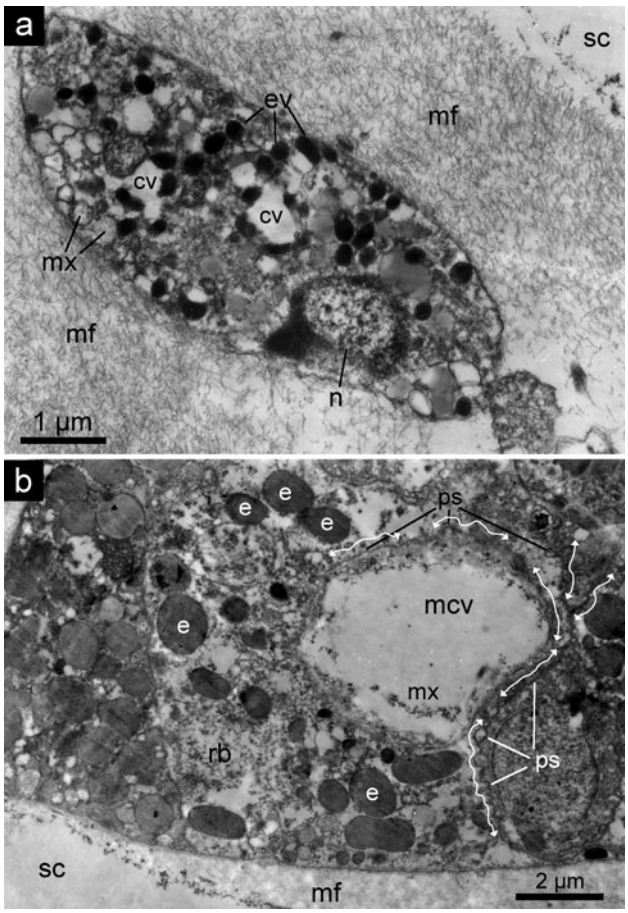

Fig. 5 Sclerocytes of *Sinularia gibberosa* under TEM. **a** Mononuclear, elliptic primary sclerocyte, usually found in upper stalk and sites where new calcification occurs. Primary sclerocytes contained calcitic vesicles (*cv*) accompanied by multiple electron-opaque vesicles (*ev*). Some vesicles contained insoluble organic matrix (*mx*). **b** Secondary sclerocytes expanded their pseudopod-like membranes (*ps*) and overlapped to form multicellular vesicle (*mcv*). *Arrowhead lines* around the multicellular vesicle indicate the overlapped membranes from multiple cells (e.g., the ones in *upper right corner*). Calcified structures in the MCV and sclerite were extracted after decalcification. *e* Electron-opaque body, *mf* mesoglea fibers, *n* nucleus, *r* free ribosome, *sc* sclerite

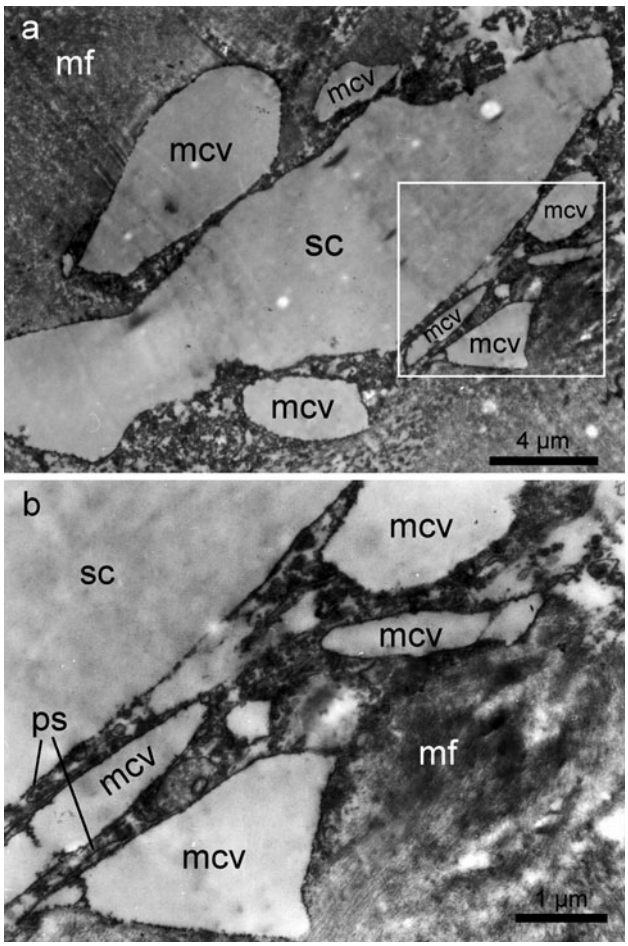

Fig. 6 Formation of large sclerite-structure formed by multicellular vesicles (MCVs). **b** Magnification of *marked area* in **a**. **a** Several MCVs connected among sclerocytes during sclerite formation. **b** MCVs surrounded by pseudopod-like membranes (*ps*) and numerous vesicles indicating calcification in process. *mcv* Multicellular vesicle, *mf* mesoglea fibers, *sc* sclerite

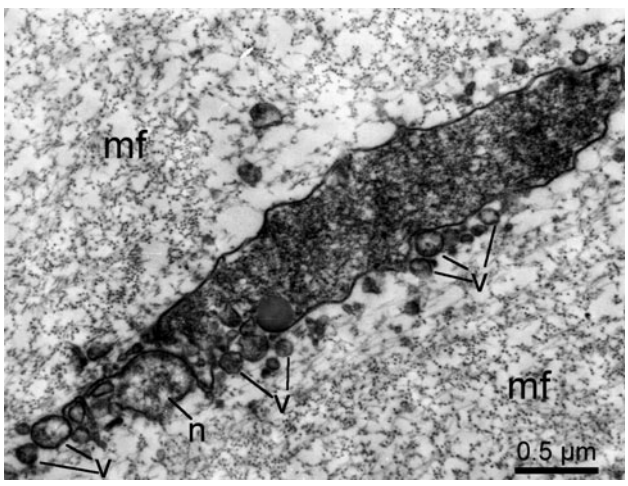

Fig. 7 Sclerocytes suspected as degenerated in the mesoglea; boundary of cell and degenerated nucleus are still visible. *mf* Mesoglea fibers, *n* degenerated nucleus, *v* vesicle

temperature in Nanwan Bay ranges between 22.5–29°C (Dai 1991b). It is possible that similar deposition and reabsorption cycles may also occur in *Sinularia* in Nanwan Bay, causing the formation and cementation of sclerites and seasonal changes in the spiculite density.

Inter-cemented coenenchyme sclerites in the basal part of *S. gibberosa* colonies revealed where sclerite consolidation into spiculite is initiated. Johnson and Risk (1987) noted that aragonite is the main component of the adhesive for cementing calcite sclerites of *Sinularia*. During sclerite calcification, calcium carbonate crystals are integrated by means of organic matrix (Rahman and Omura 2009). The chemical condition in deeper tissue of colonies is more acidic and may favor the production of amorphous calcium

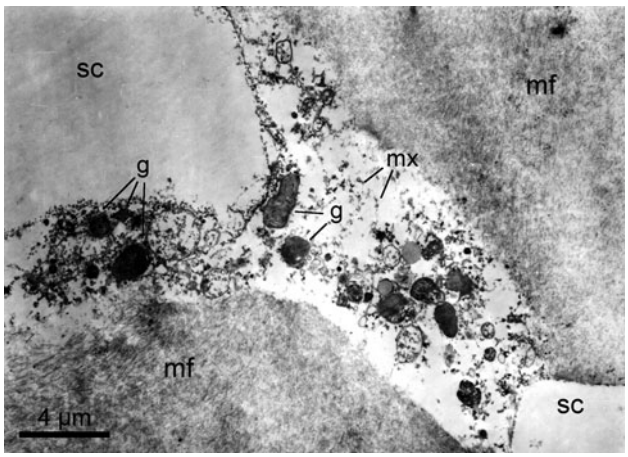

Fig. 8 Cellular activity between sclerites at colony base. Several granular structures (*g*) and organic matrix connected to two sclerites (*sc*). *mf* Mesoglea fibers. Calcified structures of sclerites were extracted

carbonate (Tentori and Van Ofwegen 2011); at the colony base, there were few sclerocytes containing multicellular vesicles, which leads to the amorphous calcification products that was noted as adhesives among sclerites. Therefore, the adhesive calcium carbonate is produced by a calcification mode which differs from that responsible for sclerite formation and growth.

The abundance and location of the sclerocytes suggested that *S. gibberosa* may synthesize sclerite primordia intracellularly and then extrude them for extracellular calcification. The intracellular stage occurs in primary sclerocytes (Fig. 5a). We suggest that in these primary sclerocytes, primordia of calcite crystals are secreted onto an organic matrix within the vesicles and then transported outside the cell for subsequent extracellular calcification similarly to sclerite formation in the gorgonian *Pseudoplexaura flagellosa* (Goldberg and Benayahu 1987). In the present study, although active primary sclerocytes were rarely observed after five days of tissue regeneration, there were no sign that primary sclerocytes had transformed into secondary ones. On the other hand, degenerated sclerocytes were found in most parts of the colonies. These findings led us to speculate that the sclerocytes are short-lived, may deposit sclerite primordia, and subsequently degenerate within a short period.

In the extracellular stage of sclerite growth of *S. gibberosa*, the sclerite primordia begin to grow inside the overlapping cell membrane extensions (MCVs) by means of multiple secondary sclerocytes (Figs. 5b, 6). Around MCVs, electron-opaque bodies in secondary sclerocytes may contain high concentrations of calcium (Kingsley 1990), which may be transported into the MCVs, and then deposited on the organic matrix for calcium carbonate crystal growth. In scleractinians, the organic matrix in the subepithelial space plays the role of a template determining the crystal morphology of the coral skeleton (Johnston 1980; Isa 1986; Le Tissier 1991). We assumed that the organic matrix in MCVs of *S. gibberosa* may have a similar function. Based upon the TEM findings (Fig. 6), MCVs serve as an isolated compartment in which sclerocytes deposit calcium carbonate. The locations and shapes of MCVs may determine the shape and size of the sclerites.

The mesoglea of *S. gibberosa* is the site where congregations of MCVs and sclerite formation occur. At that site, dense mesoglea fibers were observed (Fig. 6). Mesoglea fibers appeared to facilitate bonding between the MCVs and the developing sclerites. The distribution and array of mesoglea fibers may also determine the location where calcium carbonate is deposited, as well as sclerite morphology (see also Goldberg and Benayahu 1987).

The calcification process causes cementation of the sclerites, which takes place at the base of the colony, and differs from that leading to sclerite formation. At the colony base of *S. gibberosa*, active sclerocytes and MCVs, which are usually associated with developing sclerites in the mesoglea, were rarely observed. Rather, multiple free granular vesicles and the organic matrix occurring in the spaces among mature sclerites (Fig. 8) could be the source and template of the adhesive calcium carbonate. During the process of their degeneration, sclerocytes may release calcareous organelles or other materials outside the cell; these extruded organelles may retain the function of calcification. In the absence of facilitation of MCVs, calcium carbonate adhesives were deposited as amorphous aragonite in contrast to the calcite crystalline of the sclerites. This revealed that the sclerocytes and MCVs may also play roles in determining the calcite structure of the calcification products.

Fleshy octocorals are able to inhabit turbid environments that are less suitable for scleractinian corals, allowing them access to different ecological niches (Dai 1991a). The bias in common knowledge is toward viewing reefs as products of stony corals. We suggest that octocorals such as *Sinularia*, however, are also capable of accreting material into significant reef structures over geological time scales. This may allow the development of reef structures by spiculite-producing fleshy octocorals in areas where stony corals are unable to develop as a reef base.

Acknowledgments The authors thank Mr. T.-S. Chen and the Administration of Kenting National Park, Taiwan for assistance with the fieldwork. Y. Benayahu was partly supported by the Israel Cohen Chair in Environmental Zoology. We also acknowledge the funding and electron microscope support from the Research Center for Biodiversity, Academia Sinica, Taiwan.

References

Accordi G, Carbon F, Matteuci R (1989) 'Alcyonaria spiculite' nei calcari recifali quaternari della costa Somala. Rend Soc Geol Italia 12:17–20

Alstyne LLV, Waylie CR, Paul VJ, Meyer K (1992) Antipredator defenses in tropical Pacific soft corals (Coelenterata: Alcyonacea). I. Sclerites as defenses against generalist carnivorous fishes. Biol Bull 182:231–240

Benayahu Y, Jeng M-S, Perkol-Finkel S, Dai C-F (2004) Soft corals (Octocorallia: Alcyonacea) from southern Taiwan. II. Species diversity and distributional patterns. Zool Stud 43:548–560

Bengtson S (1981) *Atractosella*, a Silurian alcyonacean octocoral. J Paleontol 55:281–294

Cary LR (1931) Studies on the coral reefs of Tutuila, American Samoa, with special reference to the *Alcyonaria*. Carnegie Inst Wash Publ 27:53–98

Chen Y-G (1993) Sea-level change and neotectonics in southern part of Taiwan region since Late Pleistocene. Ph.D. dissertation, National Taiwan University, p 158

Dai C-F (1991a) Distribution and adaptive strategies of alcyonacean corals in Nanwan Bay, Taiwan. Hydrobiologia 216(217):241–246

Dai C-F (1991b) Reef environment and coral fauna of southern Taiwan. Atoll Res Bull 354:1–24

Fabricius K, Alderslade P (2001) Soft corals and sea fans: a comprehensive guide to the tropical shallow water genera of the central-west Pacific, the Indian Ocean and the Red Sea. Australia Institute of Marine Science, Townsville, p 264

Goldberg WM, Benayahu Y (1987) Spicule formation in the gorgonian coral *Pseudoplexaura flagellosa*. 1. Demonstration of intracellular and extracellular growth and the effect of ruthenium red during decalcification. Bull Mar Sci 40:287–303

Grillo MC, Goldberg WM, Allemand D (1993) Skeleton and sclerite formation in the precious red coral *Corallium rubrum*. Mar Biol 117:119–128

Isa Y (1986) An electron microscope study on the mineralization of the skeleton of the staghorn coral *Acropora hebes*. Mar Biol 93:91–101

Johnson DP, Risk MJ (1987) Fringing reef growth on a terrigenous mud foundation, Fantome Island, central Great Barrier Reef, Australia. Sedimentology 34:275–287

Johnston IS (1980) The ultrastructure of skeletogenesis in hermatypic corals. Int Rev Cytol 67:171–214

Kingsley RJ (1990) Calcium carbonate spicules in the invertebrates. In: Joseph GC (ed) Skeletal biomineralization: patterns, processes and evolutionary trends, vol I. Van Nostrand Reinhold, New York, pp 27–34

Kingsley RJ, Dupree JL (1993) Seasonal localization of a collagenous protein in the organic matrix of sclerites from the gorgonian *Leptogorgia virgulata* (Cnudarua: Gorgonacea). Cell Tiss Res 273:309–316

Kingsley RJ, Watabe N (1982) Ultrastructure of the axial region in *Leptogorgia virgulata* (Cnidria: Gorgonacea). Cell Tiss Res 233:325–334

Kingsley RJ, Melaro EW, Flory KE, Skorupa AM, Harclerode KA (1996) Mechanisms of the annual cycling of organic-matrix collagen from spicules of the gorgonian *Leptogorgia virgulata*. Invert Biol 115:89–98

Kleypas JA (1996) Coral reef development under naturally turbid conditions: fringing reefs near Broad Sound, Australia. Coral Reefs 15:153–167

Konishi K (1981) Alcyonarian spiculite: Limestone of soft corals. Proc 4th Int Coral Reef Symp 1:643–649

Le Tissier MD (1991) The nature of the skeleton and skeletogenic tissues in the Cnidaria. Hydrobiologia 216(217):397–402

Lin M-C, Dai C-F (1997) Morphological and mechanical properties of two Alcyonaceans, *Sinularia flexibilis* and *S. capillosa*. Zool Stud 36:58–63

Muscatine L, Tambutte E, Allemand D (1997) Morphology of coral desmocytes, cells that anchor the calicoblastic epithelium to the skeleton. Coral Reefs 16:205–213

Rahman MA, Omura T (2009) In vitro regulation of $CaCO_3$ crystal growth by the highly acidic proteins of calcitic sclerites in soft coral, *Sinularia polydactyla*. Connect Tissue Res 50:285–293

Schuhmacher H (1997) Soft corals as reef builders. Proc 8th Int Coral Reef Symp 1:499–502

Tentori E, Van Ofwegen LP (2011) Patterns of distribution of calcite crystals in soft corals sclerites. J Morph. doi:10.1002/jmor.10942

Verseveldt J (1980) A revision of the genus *Sinularia* May (Octocorallia, Alcyonacea). Zool Verh Leiden 179:166