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SPATIAL COMPETITION BETWEEN ORGANISMS OF DIFFERENT GROWTH FORMS

Sung-Wook Kwon[1,*], Suk-Joo Choh[1], and Dong-Jin Lee[2] (cotigoksw@korea.ac.kr)

[1]Department of Earth and Environmental Sciences, Korea University, Seoul, Korea

[2]Department of Earth and Environmental Sciences, Andong National University, Andong, Korea

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ABSTRACT

Spatial competition between dendritic tetradiid (*Rhabdotetradium jiangshanense* Lin and Zou, 1980) and massive encrusting siliceous sponge were analyzed in order to understand life-history strategy of branching form organism in competition with that of massive encrusting type. Tetradiid is a problematic Ordovician fossil characterized by mm-sized tubes. *Rhabdotetradium* is composed of slender single tube dividing into four tubes at long interval. *R. jiangshanense* analyzed in this study is composed of poorly preserved tube with average diameter of 1.6 mm. Tetradiid-sponge and tetradiid-dominated boundstones from the Upper Ordovician (late Katian) Xiazhen Formation of south China were compared based on transverse serial thin sections. Both boundstones are from the same horizon with close proximity and considered to be formed under comparable environmental conditions. Tetradiid tubes from tetradiid-dominated boundstone show predominance of typical quadripartite fission (69% of axial increase; n=11) with vertical distance between 3 to 7 mm. On the other hand, in tetradiid-sponge boundstone, 56 % of tetradiid tubes occur at the outer margin of sponge showing predominance of atypical bipartite division (66% of axial increase; n=4) with 2 to 4.5 mm of vertical distance. Other 31% of tetradiids are completely enveloped by sponge and dominantly display bipartite fission (63% of axial increase; n=5) with 1 to 2.5 mm vertical distance. There are predominance of bipartite fission and strikingly shorter vertical distance in those from tetradiid-sponge boundstone compared to dominant quadripartite fission with longer vertical distance in tetradiid-dominated boundstone without sponge. These contradistinctive growth patterns of tetradiid appear to be an adaptive survival strategy by ecologic stress derived from competing siliceous sponges. This result provides a new insight for understanding competition between organisms of different growth forms in ancient reefs, and reaffirms the potential of serial thin sections for study of biologic interactions in fossil benthic communities.

1. PURPOSE

A. Assess spatial competition between non-compatible organisms of branching and dendritic tetradiids and massive siliceous sponges

B. Describe and interpret the life-history strategies of a dendritic type tetradiid in response to ecologic stress by competitive organism

2. COMPETITIVE ORGANISMS

A. *Rhabdotetradium jiangshanense* Lin and Zou, 1980
- Erect branching growth form of tetradiid composed of slender, sinuous, and millimeter size calcareous tubes
- Growth characteristics: four-fold axial division of tubes (i.e., quadripartite)
- Range: Middle to Upper Ordovician
- Affinity: uncertain (Tabulate coral? Chaetitid? Red alga?)

B. Siliceous sponge
- No regular external morphology
- Recognized by well to poorly preserved spicule networks (Warnke, 1995; Kwon et al., 2012)

3. METHODS

A. Serial thin sections
- Transverse serial thin sections cut perpendicular to dominant growth axis of tetradiids
- **6 sets** of serial thin sections of **tetradiid-sponge boundstone** at each 0.5 mm interval, a total of **over 130** thin sections
- **5 sets** of serial thin sectionis of t**etradiid-dominated boundstone**, at same interval, a total of **over 100** thin sections

B. Thin section mapping
- Using **one set** of serial thin sections of **tetradiid-sponge boundstone (n=20)**
- Mapping of area occupied by **6 constituents of tetradiid-sponge boundstone (Fig. 1B)**
- Designation of **3 different classes** of tetradiid tubes
- Measurement of **cross-sectional tube area**

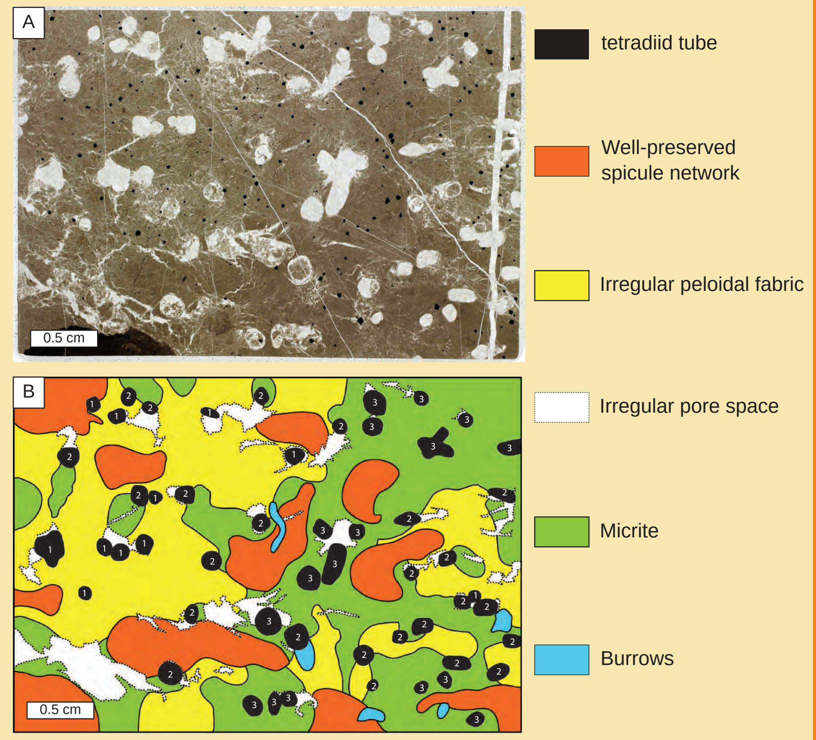


Fig. 1. (B) Map of the boundstone (A) shows tetradiid tubes in different fabrics (each class of tubes are marked by 1 to 3). The irregular peloidal fabrics containing spicules are considered as the product of degraded and incomplete calcification of sponge soft tissue (Warnke, 1995).

Classification	Criteria and distribution within boundstone
Class 1	Tetradiid tubes completely surrounded by sponge
Class 2	Tetradiid tubes at the outer margin of sponge
Class 3	Tetradiid tubes occurring outside of sponge

C. Types of tube division
- Using all serial thin sections (11 sets, over 230 serial thin sections)
- Normal quadripartite division vs. atypical bipartite and tripartite
- Measurement of vertical distance of tube divisions

4. SPATIAL COMPETITION?

Initiation of tetradiid tube on sponge

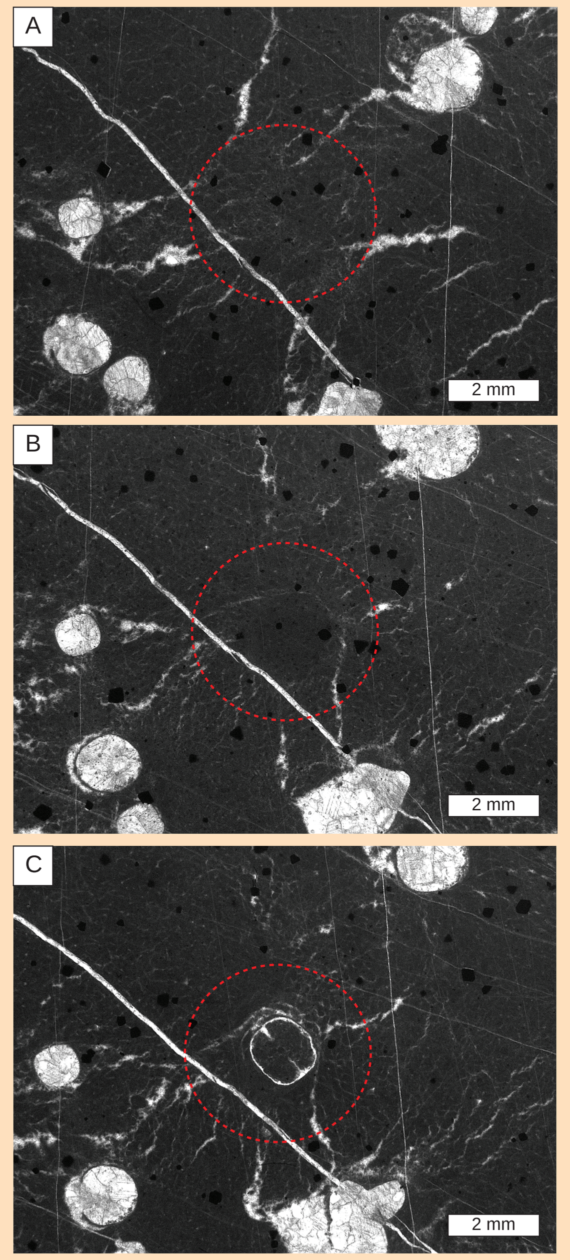


Fig. 2. Transverse serial thin sections showing the initiation of a tetradiid tube (class 1) on top of sponge. (A) Well-preserved spicule networks occupy the space between the tubes of tetradiid. (B) A circular patch (1.3 mm in diameter) of micrite without spicules appears in the center of the spicule networks. (C) A new tube of tetradiid first appears at the location of the circular micritic patch. Figured sections spaced 1.5, 0.5 mm apart, respectively.

Encroachment of sponge between dividing tetradiid

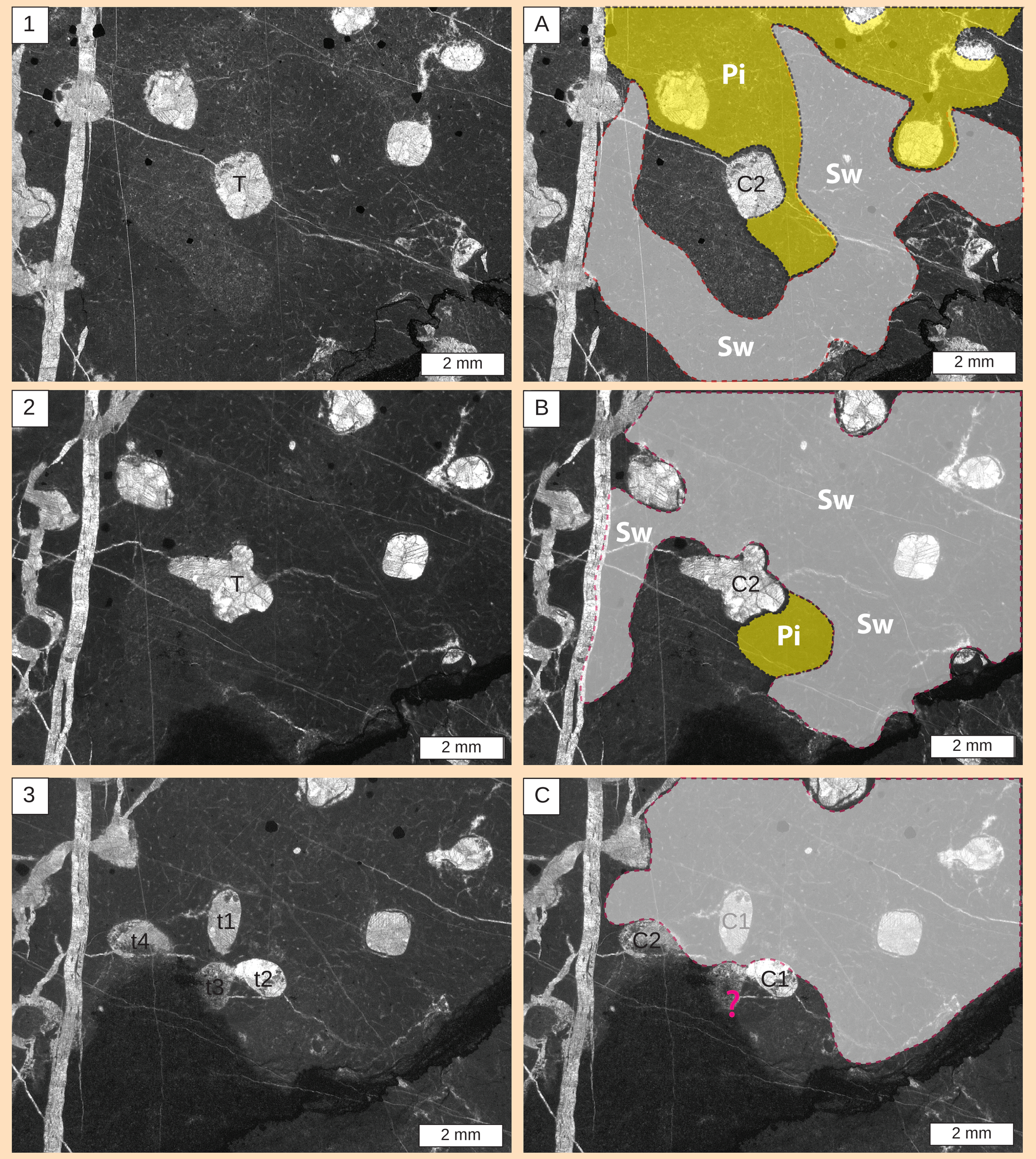


Fig. 3. Transverse serial thin section photomicrographs showing the encroachment of siliceous sponge between the dividing tetradiid tubes. (1, A) The tetradiid tube in the center of the photomicrograph occurs at the outer margin of siliceous sponge (i.e., class 2). (2, B) The tube (class 2) is dividing into four tubes. (3, C) Once the newly divided tubes are separated from each other, siliceous sponge invades the space between the tubes and completely surrounds two of the newly formed tubes (t1, t2; class 1). Figured sections spaced 1.5, 1.0 mm apart, respectively.

Termination of tetradiid tube

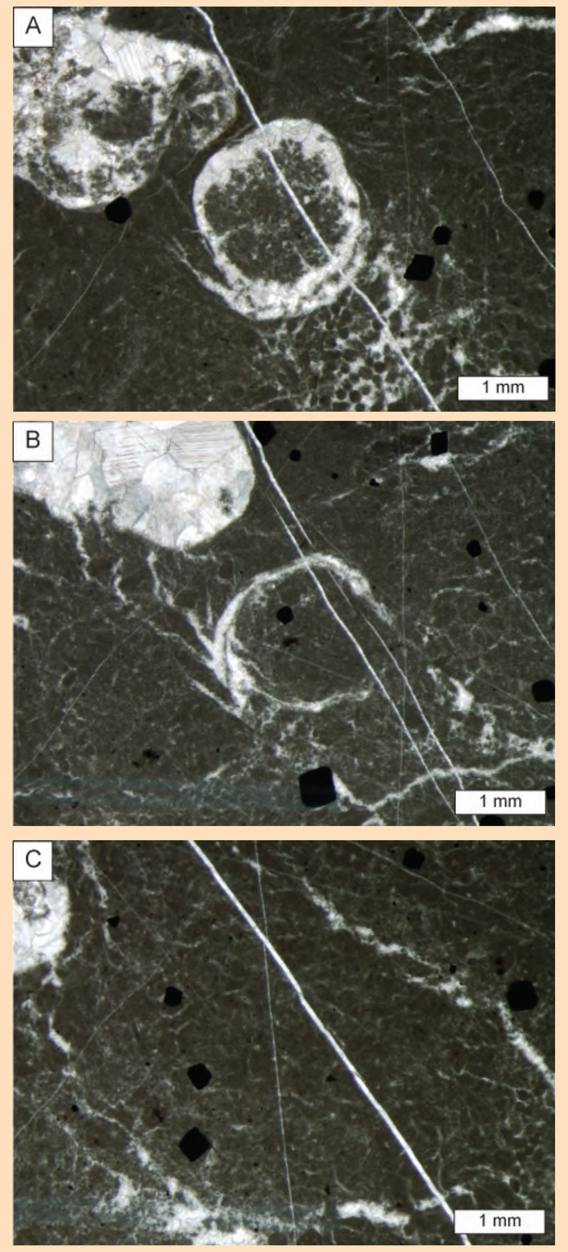
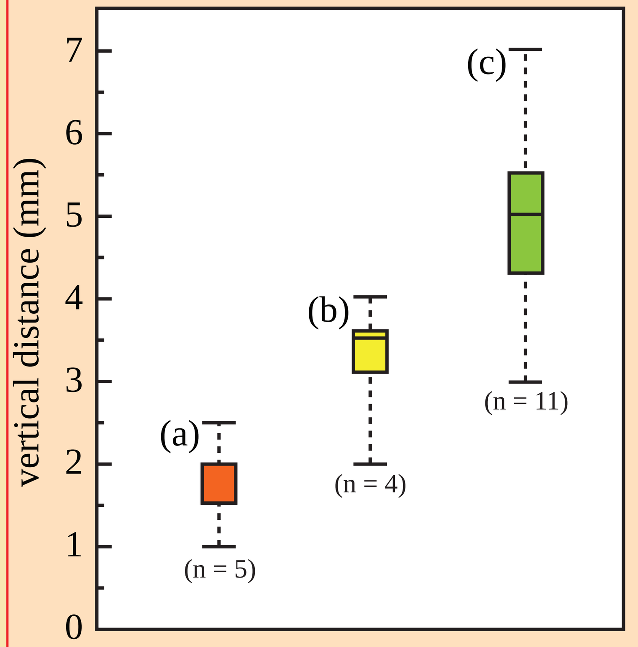


Fig. 4. Transverse serial thin section photomicrographs showing the termination of a tetradiid tube (class 1). (A) A single tube of a tetradiid with partially preserved septa filled with peloidal micrite with spicules. (B) and (C) show that sponge subsequently reclaim the former space occupied by the terminated tetradiid tube. Figured sections spaced 1.0, 0.5 mm apart, respectively.

5. EFFECTS OF COMPETITION TO DENDRITIC TETRADIID



- Predominance of non-quadripartite division of tetradiid from tetradiid-sponge boundstone (Kwon et al., 2012)

Fig. 5. Vertical axial division distance of tetradiid tubes by class and division types of tetradiid tubes: (a) class 1 and (b) class 2 tube dividing into two (i.e., bipartite division); (c) class 3 tube dividing into four tubes (i.e., typical quadripartite division)

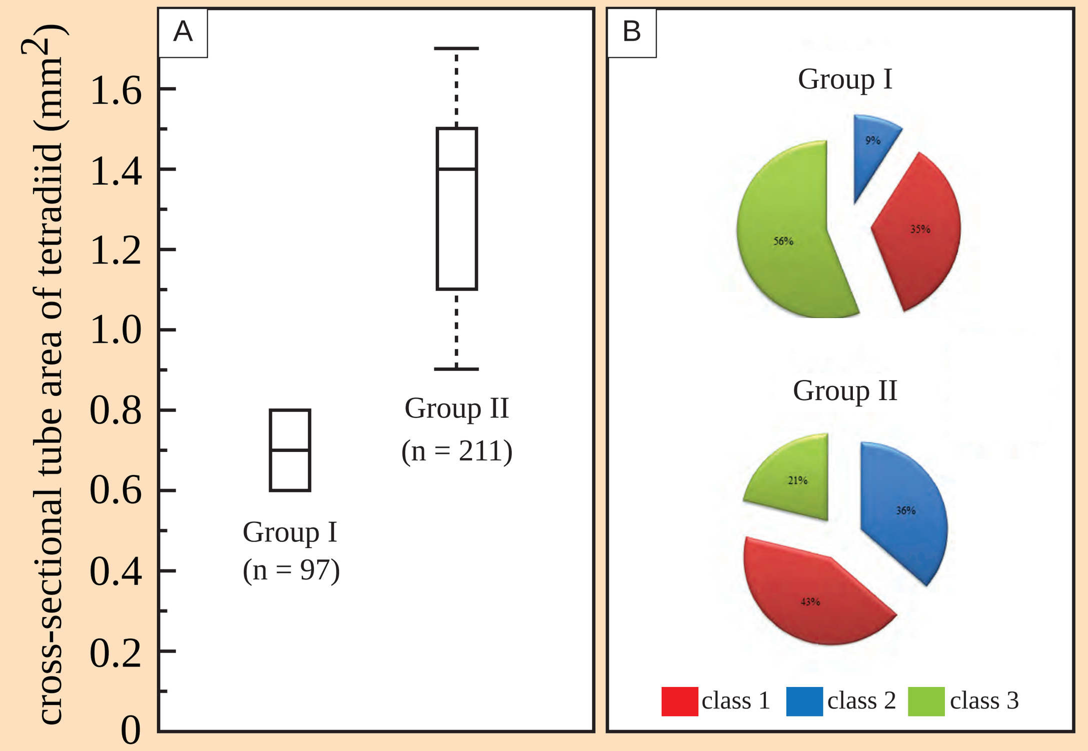


Fig. 6. Cross-sectional area range of tetradiid tubes by class and division types of tetradiid tubes. (A) Two groups of tetradiid differentiated by bimodal cross-sectional tube area. (B) The group I tetradiid tubes are dominantly composed of class 1 and 2 types, which indicates that the growth of tetradiid tubes was heavily influenced by sponge. In group II, on the other hand, 56% of tetradiid tubes belong to class 3, which indicates that the growth of the tubes was less affected by sponge than that of the group I.

Yes!! Direct spatial competition!

A. Skeletal distortion at contact
- Distortion of spicule networks at contact to initiating sponge

B. Overgrowth reversals or repeated overgrowth between competing organisms
- Overtoping of tetradiid on top of sponge
- Reoccupation of sponge atop of terminated tetradiid tube
- Encroachment of sponge between dividing tetradiid tubes
- "Cul-de-Sac" pattern possibly due to partial mortality of sponge at contact to tetradiid (cf., Fagerstrom and West, 2011)

6. DISCUSSION AND SUMMARY

A. During initiation, growth, and termination of tetradiid tubes, skeletal distortion of spicule networks at contact with initiating tetradiid and overgrowth reversal as overrunning by sponge of the tubes are indicative of direct spatial competition (Liddell and Brett, 1982; Jackson, 1983; Fagerstrom et al., 2000; McCook et al., 2001; West et al., 2011).

B. Based on sequence of encroachment pattern of sponges characterized by "Cul-de-Sac" pattern as well as overgrowth reversal and predominant overtopping of tetradiid tubes, it is unlikely that the competition between the massive sponge and the dendritic form tetradiid correspond to hierarchy of competition (e.g., Jackson, 1983; West et al., 2011) stating that encrusting colonial organism can easily overwhelm an organism with erect growth form.

C. It has been proposed that faster upward growth of erect branching form organisms is considered as a survival strategy in response to ecologic stress caused by massive encrusting organisms as competitor (Fagerstrom et al., 2000; West et al., 2011). In addition, the change of growth or reproduction strategy has been considered as adaption of cateniform coral and stromatoporoid in response to external physical factors such as sedimentation rate or current energy (e.g., Lee and Elias, 1991; Young and Kershaw, 2005; Bae et al., 2006).

D. Contradistinctive growth patterns (i.e., predominant non-quadripartite division and shorter vertical distance of tube divisions, Fig. 5; Kwon et al., 2012) and dimensions (i.e., cross-sectional area of tubes, Fig. 6) of tetradiid tubes documented in this study record previously unknown life-history strategy of dendritic organism in direct ecologic stress by competitive encrusting massive organisms.

E. This composite life-history strategy of dendritic tetradiids of the Late Ordovician tetradiid-sponge boundstone could provide crucial insight from fossil record deciphering the main causes of life-history strategy change.

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