

Diverse Interactions between Corals and the Coral-Killing Sponge, *Terpios hoshinota* (Suberitidae: Hadromerida)

Jih-Terng Wang^{1,*}, Yi-Yun Chen¹, Pei-Jie Meng^{2,3}, Yu-Hsuan Sune³, Chia-Min Hsu⁴, Kuo-Yen Wei¹, and Chaolun Allen Chen^{4,5,6}

¹Graduate Institute of Biotechnology, Tajen Univ., Pingtung 907, Taiwan

²National Museum of Marine Biology and Aquarium, Pingtung 944, Taiwan

³Institute of Marine Biodiversity and Evolution, National Dong Hwa Univ., Checheng, Pingtung 944, Taiwan

⁴Institute of Oceanography, National Taiwan Univ., Taipei 108, Taiwan

⁵Biodiversity Research Center, Academia Sinica, Nangang, Taipei 115, Taiwan

⁶Taiwan International Graduate Program (TIGP)- Biodiversity, Academia Sinica, Nangang, Taipei 115, Taiwan

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Jih-Terng Wang, Yi-Yun Chen, Pei-Jie Meng, Yu-Hsuan Sune, Chia-Min Hsu, Kuo-Yen Wei, and Chaolun Allen Chen (2012) Diverse interactions between corals and the coral-killing sponge, *Terpios hoshinota* (Suberitidae: Hadromerida). *Zoological Studies* 51(2): 150-159. *Terpios hoshinota* is an encrusting sponge which can kill corals by overgrowing them. However, little is known about interactions between sponges and corals. Using visual observations and scanning electron microscopy (SEM), 4 features, including hairy tips, thick tissue threads, compact edges, and disintegrated tissues, displayed at the coral-facing front of *Terpios* were summarized from examining 20 species of corals. Hairy tips, found on 13 species of coral victims, were occupied by cyanobacteria, sponge tissues, and spicules. Thick tissue threads, found on only 7 coral species, were obviously an extension of *Terpios* tissues. Twelve coral species displayed a compact edge at the *Terpios*-coral border, in which some *Terpios* fronts had extruding spicules. Disintegrated tissue was only found on the coral side in 5 species of coral, but that on the sponge side was only found on 1 coral species. Only a few disintegrated tissues being found at the *Terpios*-coral border suggests that allelochemicals are not the major player in *Terpios*-coral interactions. The interactions also did not display species specificity, except in the case of *Terpios* having been retrogressively grown over by a coral, which was only found in *Millepora exaesa*. Under SEM examination, coral nematocysts were usually found on the surface of the invading *Terpios*, but they did not seem to retard the growth of the sponge. In summary, exploitation of the substratum by *T. hoshinota* on coral does not move forward in a consistent manner. The performance of *Terpios*, such as when overgrowing a coral, building a clear border, or being retrogressively overgrown by a coral, may rely on the viability status of both organisms. <http://zoolstud.sinica.edu.tw/Journals/51.2/150.pdf>

Key words: *Terpios*, Cyanobacteria, Coral-killing sponge, Substrata competition.

In coral reefs, sponges are a well-known space competitor (Suchanek et al. 1983, Rützler 2002), but few are recognized as real threats to the survival of corals. *Terpios hoshinota* Rützler and Muzik, 1993, a cyanobacteriosponge, is an exception, as its high growth rate can encrust almost every type of hermatypic coral encountered.

Its widespread infection was first reported in Guam (Bryan 1973), and subsequently in the Ryukyus, Japan (Rützler and Muzik 1993, Reimer et al. 2011) and Green I. (*Lyudao*), Taiwan (Liao et al. 2007). *Terpios hoshinota* was also found in Truk Lagoon in American Samoa, Cebu I. in the Philippines, Thailand (Plucer-Rosario 1987), and even on the

*To whom correspondence and reprint requests should be addressed. Tel: 886-8-7624002. Fax: 886-8-7621645. E-mail: jtw@mail.tajen.edu.tw

Great Barrier Reef (Fujii et al. 2011). Damage caused by an invasion of *Terpios* caused nearly 30% loss of coral coverage on some reefs in Guam (Plucer-Rosario 1987). At Green I., Taiwan, an unprecedented overgrowth by *Terpios* on corals was found in 2006, which also caused almost 30% coral coverage loss along a 100-m transect belt (Liao et al. 2007). The complete recovery from a *Terpios* encrustation, e.g., at Anae I. in Guam, took more than 10 yr, when the disturbance level decreased (Plucer-Rosario 1987). Therefore, once a *Terpios* outbreak occurs, there will be long-term impacts on a coral reef ecosystem and on activities that rely on a healthy condition of the reefs.

Ecologically, *T. hoshinota* is distributed above the limit of the euphotic zone, probably due to the presence of endosymbiotic photosynthetic cyanobacteria (Bryan 1973, Plucer-Rosario 1987, Rützler and Muzik 1993). A histological examination of *T. hoshinota* indicated that the sponge contained a high percentage (> 50%) of intercellular cyanobacteria and 5%-18% of cells were in the dividing stage (Rützler and Muzik 1993, Hirose and Murakami 2011). High abundances and activities of cyanobacteria contained in *T. hoshinota* suggest that a potential source of the sponge's nutrients is derived from photosynthetic bacteria (Rützler and Muzik 1993). It was hypothesized by Bryan (1973) that *Terpios* probably kills coral for nutrients with toxic chemicals, but comparisons between tissue-depleted and healthy coral suggested that the sponge might just overgrow the coral surface to occupy more space (Plucer-Rosario 1987). During growth, *Terpios* moves forward by lateral propagation, extending short, fine tendrils across crevices to new substrate (Rützler and Muzik 1993). *Terpios hoshinota* can also develop tissue threads, instead of whole sheets of tissue, to move over a shaded area and establish new territory (Soong et al. 2009). However, *Terpios* occasionally exhibits retrogression (i.e., negative growth) and can even be overgrown by some corals (e.g., *Montipora* and *Porites*) or red calcareous algae (Plucer-Rosario 1987). Thus, *Terpios* does not always win during its advance. Interactions between *Terpios* and corals were examined from the viewpoint of changes in the bacterial community. Tang et al. (2011) indicated that invasion by *Terpios* onto corals initiates a shift in the coral bacterial community from one on healthy corals to that found on corals with black-band disease. Their results suggested that harmful bacteria weakening the coral might favor *Terpios*

outcompeting the coral for substratum (Tang et al. 2011).

As yet, only limited information briefly describing how *Terpios* invades victimized corals is available (Bryan 1973, Plucer-Rosario 1987, Rützler and Muzik 1993, Soong et al. 2009, Tang et al. 2011), and it is not clear how different coral species respond to an invasion by *Terpios* at the coral-sponge border under a fine scale. Therefore, the aim of this study was to examine the border between these 2 antagonists with scanning electron microscopy (SEM). Our findings provide insights into interactions between an aggressively invading sponge and its coral victims.

MATERIALS AND METHODS

Sample collection and maintenance

Field observations of coral-*Terpios* interactions were conducted at Gon-Guam and Chai-Ko, Green I., Taiwan (22°39'N, 121°29'E) from Aug. 2008 to July 2010. Due to the strong northeasterly monsoon in winter, observations were made more intensively during summer (May-Sept.). During the investigation, interactions between coral and *Terpios* were recorded with an underwater camera. To further examine the interaction border between corals and *Terpios*, 19 species of scleractinian coral and 1 hydrozoan coral with *T. hoshinota* invasion were collected by scuba diving from 3-5 m in depth at Gon-Guam and Chai-Ko on 28 July 2010 and examined by SEM. The 19 scleractinian corals included *Isopora palifera*, *Montipora aequituberculata*, *Mon. peltiformis*, *Hydnophora rigida*, *Favia stelligera*, *Psammocora digitata*, *Echinopora lamellose*, *Echinophyllia aspera*, *Goniastrea edwardsi*, *G. aspera*, *Pocillopora verrucosa*, *Acropora digitifera*, *Stylophora pistillata*, *Platygyra ryukyuensis*, *Leptoria phrygia*, *Favites chinensis*, *Cyphastrea microphthalma*, *Porites lutea*, and *Por. cylindrical*. The hydrozoan coral examined was *Millepora exaesa*. Every species was duplicated by collecting a sample from 2 different colonies, and the interactions were photographed before collection. *Terpios*-coral specimens were sealed in a plastic bag underwater when collected and preserved in fixative once the diver had left the water.

Terpios hoshinota on *I. palifera* was also collected and maintained in an aquarium (60 × 45 × 45 cm) equipped with illumination (12-h:12-h light dark regime and 70-90 $\mu\text{E}/\text{m}^2/\text{s}$ photosynthetically

active radiation, temperature control (25°C), filtration (EHEIM, Deizisau, Germany), and a protein skimmer. The seawater level in the tank was kept at only 20 cm deep, and 2 underwater pumps were used to create flow above the sponge. *Terpios hoshinota* could grow along the cut edge of the original coral substrata and also onto the shell debris at the bottom of the tank. Newly growing sponge on the shell debris was also examined by SEM for comparison of *Terpios* on a non-coral substratum.

SEM method

Freshly collected *Terpios hoshinota* was persevered in fixative (2.5% glutaraldehyde, 2% paraformaldehyde, and 5% sucrose in 0.1 M phosphate buffer at pH 7.0) overnight at 4°C. Subsequently, specimens were washed in phosphate buffer and post-fixed in 2% OsO₄/0.1 M phosphate buffer (pH 7.3) overnight. Standard procedures were used to prepare coated samples for SEM observations. Coral-*Terpios* samples were dried in a critical-point dryer (Hitachi HCP-2,

Tokyo, Japan), and coated with platinum in an ion sputter (Hitachi E1010). SEM observations were made on an SEM (Hitachi S-3500N) at a voltage of 5 kV.

RESULTS

After examining interactions of *T. hoshinota* with 19 species of scleractinian coral and 1 hydrozoan coral, the results indicated that there were 4 types of interactions between them, i.e., hairy tips, thick tissue threads, compact edges, and disintegrated tissues (Table 1). The 2 most common features at the coral-facing growth front of *Terpios* were hairy tips and compact edges, which were respectively found in 13 (totally 23 specimens) and 12 (totally 23 specimens) species of victim corals. Thick tissue threads were less often found at the coral-facing growth front of the sponge, and were found in only 7 (totally 8 specimens) species of coral victims, and only that on *Por. cylindrical* was found in both specimens examined. Disintegrated tissues were more rarely

Table 1. Morphological characterization of interactions between *T. hoshinota* and corals. “+” and “-” signs respectively represent the presence and absence of a character in the 2 replicates

Coral specimen	Sponge-coral border				
	<i>Terpios hoshinota</i>				Coral
	Hairy tips	Thick tissue threads	Compact edges	Disintegrated tissues	Disintegrate tissues
Scleractinian coral					
<i>Acropora digitifera</i>	++	--	++	--	+-
<i>Isopora palifera</i>	++	--	--	--	--
<i>Montipora aequituberculata</i>	++	--	--	--	--
<i>Montipora peltiformis</i>	++	--	--	--	--
<i>Porites cylindrical</i>	+-	++	++	--	--
<i>Porites lutea</i>	--	+-	++	--	--
<i>Pocillopora verrucosa</i>	++	--	--	--	--
<i>Psammocora digitata</i>	++	--	--	--	--
<i>Stylophora pistillata</i>	--	+-	++	--	+-
<i>Cyphastrea microphthalma</i>	+-	--	++	--	--
<i>Echinopora lamellosa</i>	++	--	++	--	--
<i>Favia stelligera</i>	++	--	++	--	--
<i>Favites chinensis</i>	--	--	++	--	--
<i>Goniastrea aspera</i>	++	--	--	--	--
<i>Goniastrea edwardsi</i>	--	--	++	--	++
<i>Hydnophora rigida</i>	+-	+-	--	--	+-
<i>Leptoria phrygia</i>	--	+-	++	--	--
<i>Platygyra ryukyuensis</i>	--	+-	++	--	--
<i>Echinophyllia aspera</i>	++	--	--	--	--
Hydrozoan coral					
<i>Millepora exaesa</i>	--	+-	+-	+-	+-

observed at the coral-facing growth front of the sponge, which was only found in 1 specimen of *Mil. exaesa*. On the coral side, disintegrated tissues were also rarely observed; only 5 (totally 6 specimens) coral species displayed disintegrated tissues at the coral-*Terpios* border. Eighty percent of specimens of the 19 species of coral displayed comparable color morphs and *Symbiodinium* densities with nearby corals in the same colony which had not been attacked by *Terpios* (see example photos in Figs. 1A, 2A, 3B). Table 1 also indicates that on *I. palifera*, *Mon. aequituberculata*, *Mon. peltiformis*, *Poc. verrucosa*, *Psa. digitata*, and *Eph. aspera*, the sponge displayed only 1 feature, hairy tips, at the coral-facing growth front; but the sponge on the other 14 species of coral displayed more than 1 feature.

Typical examples of detailed interactions between corals and *Terpios* are shown in figures 1-6. Figure 1 shows lots of hairy tips along the *Terpios* growth front on *I. palifera*. Hairy tips of *Terpios* touch the coral surface when it moves forward. As shown in figure 1A, the coral surface at the boundary next to *Terpios*

displayed no significant changes in the color morph or *Symbiodinium* density. Under SEM examination, hairy tips were found to be occupied by cyanobacteria, sponge tissues, and spicules (Fig. 1B-D). Nematocysts obviously from the victim coral were also found on the surface of the hairy tips (Fig. 1D). Direct exposure of internal cyanobacteria and spicules from the hairy tips (Fig. 1C, D) was caused by the loss of the fragile pinacoderm during SEM processing.

In figure 2, the compact edge and thick tissue threads at the *Terpios* growth front on *Pla. ryukyuensis* are shown. The thick tissue threads were obviously an extension of sponge tissues. However, the microscopic image of the compact edge of *Terpios* revealed only spicules but no sponge tissue or cyanobacteria extruding from the sponge front (Fig. 2B, C). Figure 2B and 2C also indicate that there was no direct contact between the sponge front and coral tissues, and no obvious disintegration was found on the coral surface. Sometimes, a clear border was also found at the coral-*Terpios* interface. As shown in figure 3A, the sponge seemed to hold its growth

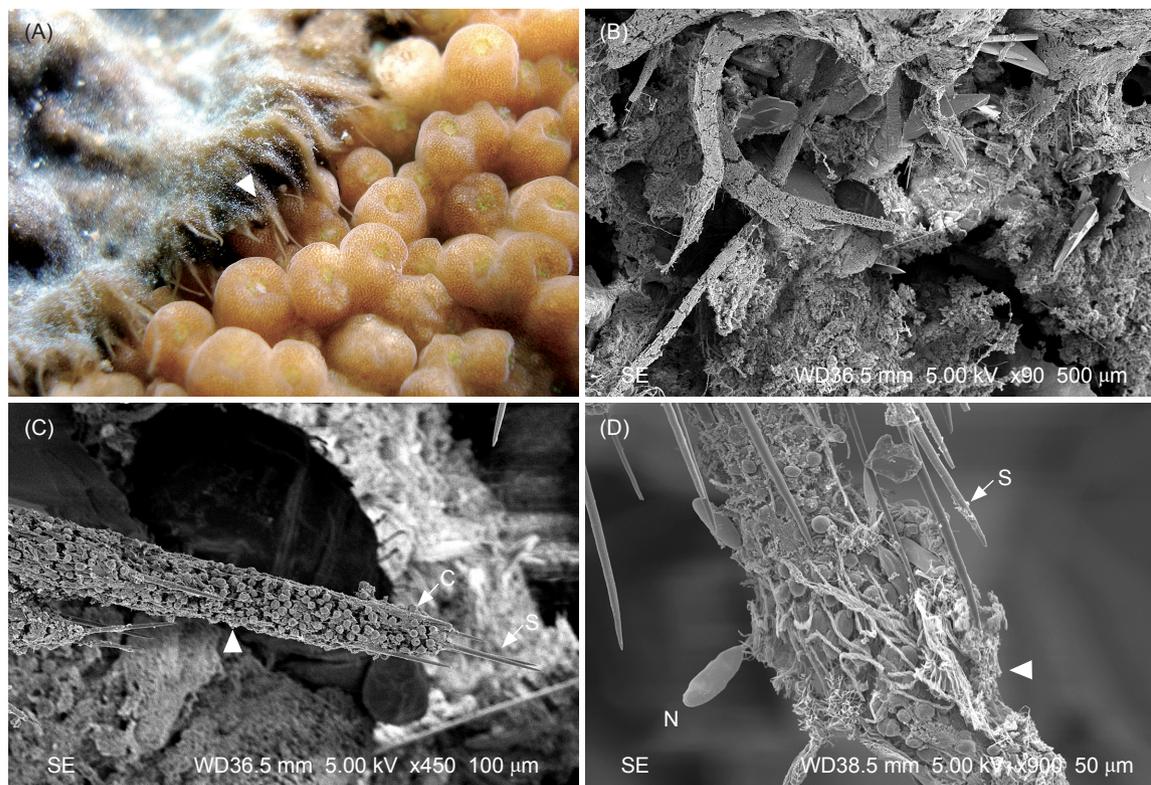


Fig. 1. *Terpios hoshinota* displaying hairy tips at the growth front in an interaction with coral. (A) An example from *Terpios* invading *Isopora palifera*; (B-D) SEM examination of the hairy tips found in (A) at different magnifications. The white arrowhead indicates the location of hairy tips. C, cyanobacteria; N, nematocyst; S, spicules.

by showing a compact edge at the boundary with disintegrated tissues of *S. pistillata*. This interaction was not prevalent throughout the entire *Stylophora* colony, because thick tissue threads derived from the sponge were also found to interact with the coral on different branches of the same colony (Fig. 3B). Under SEM examination, there was a 200-500- μm wide border without coral or sponge tissues between the 2 antagonists (Fig. 3C). When zooming into the *Terpios* front at the coral-interacting side, as shown in figure 3, many stinging nematocysts were found at the leading edge of *Terpios* tissues. Opposition against

Terpios growth was also found in an extreme case during our field survey: 1 *A. digitifera* colony had maintained the same boundary with *Terpios* for more than a year with no advance or regression.

Disintegration of coral tissues at the coral-*Terpios* border, even though very seldom, was also found. Taking *G. edwardsi* as an example, the coral tissue displayed disintegration and had disintegrated into filamentous residues along the border contacting *Terpios* (Fig. 4A). When examined at high magnification, the growth front of *Terpios* seemed to move forward by penetrating underneath the disintegrated coral tissue (Fig.

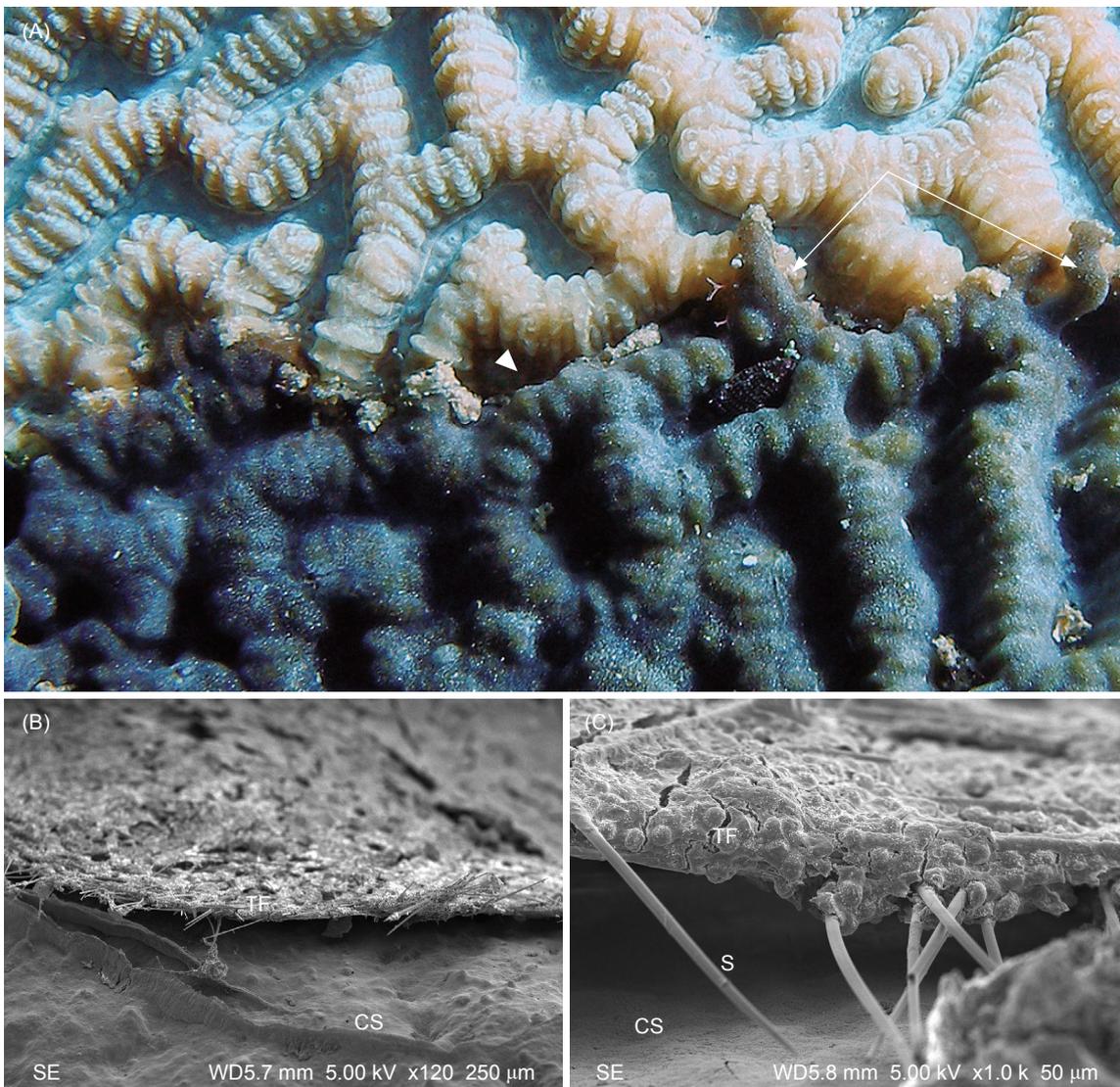


Fig. 2. *Terpios hoshinota* displaying a compact edge and thick tissue threads at the growth front in an interaction with coral. (A) An example of *Terpios* infecting *Platygyra ryukyuensis*; (B, C) SEM examination of the growth front with a compact edge of the sponge found in (A), indicated by a white arrowhead, at different magnifications. Thick tissue threads from the sponge are marked by white arrows. CS, coral surface; S, spicules; TF, *Terpios* front.

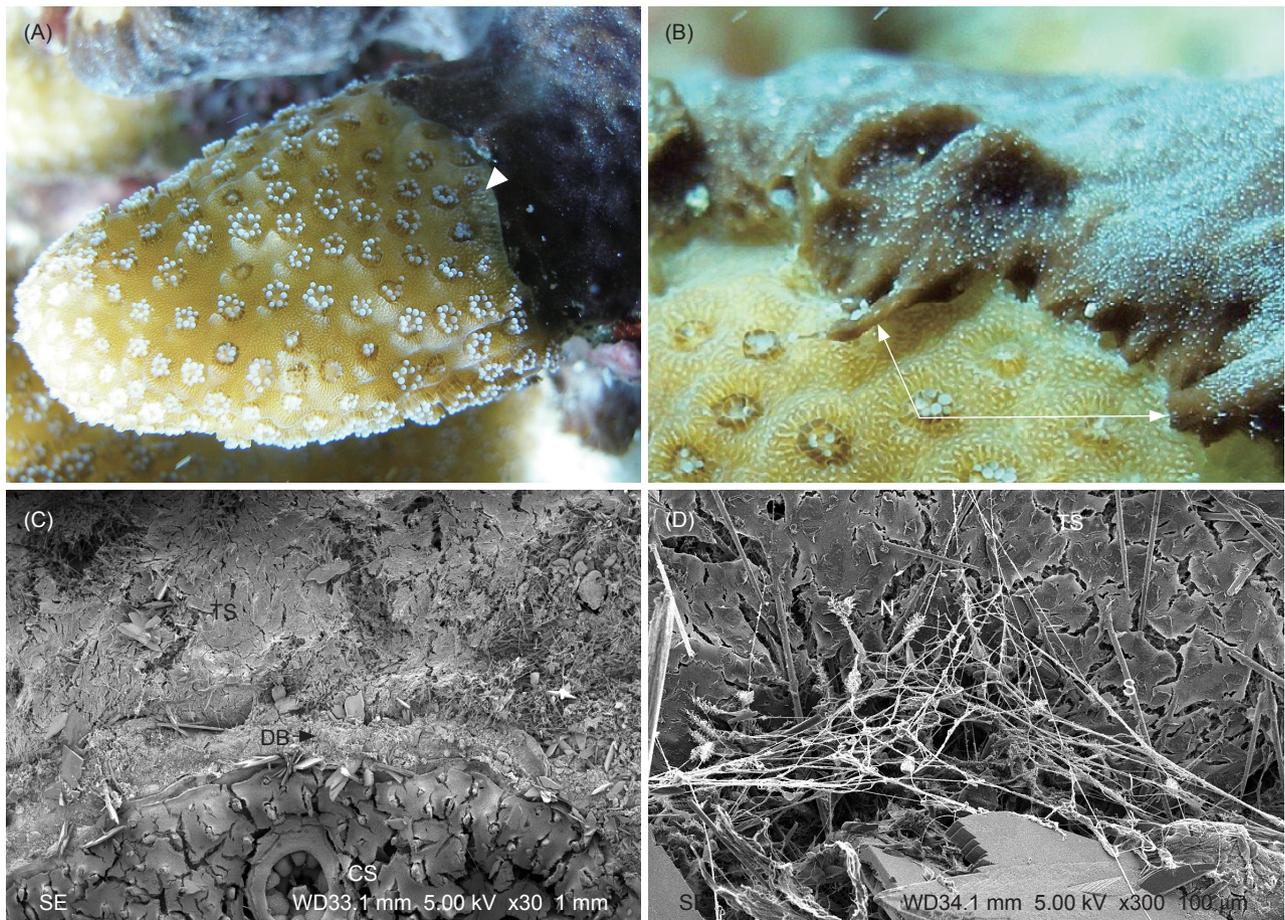


Fig. 3. Coral displaying both disintegrated and comparatively normal tissues along the growth front of *T. hoshinota* on different branches of the same colony. (A, B) Example from *Terpios* infecting *Stylophora pistillata* which displays (A) disintegrated coral tissues and (B) comparatively normal coral tissues at the coral-sponge interface. (C, D) SEM examination of the coral-sponge interface with disintegrated coral tissues at different magnifications. Disintegrated coral tissue is marked by a white arrowhead, and thick tissue threads from the sponge are marked by white arrows. CS, coral surface; DB, dead coral boundary; N, nematocyst; S, spicules; TS, *Terpios* surface.

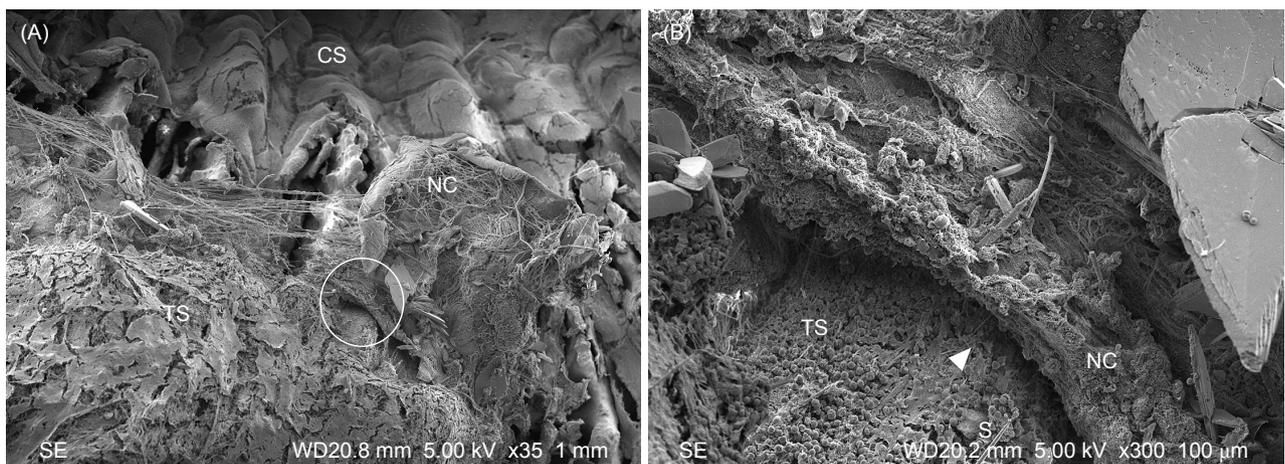


Fig. 4. SEM examination of the disintegration of *Goniastrea edwardsi* tissues at the growth front of *T. hoshinota*. (A, B) The same specimen at different magnifications; the white arrowhead indicates the growth direction of *Terpios*. CS, coral surface; NC, nematocyst; S, spicules; TS, *Terpios* surface.

4B). Disintegration was also found on the sponge side at the interaction of *Mil. exaesa* and *Terpios*. On *Mil. exaesa*, *Terpios* showed a retreat or curving-back of the sponge tissue at the coral-sponge front (Fig. 5A). However, at another part of the border between *Mil. exaesa* and *Terpios*, thick tissue threads of the growth front of *Terpios* had crossed over the coral tissue and touched down a certain distance behind the border (Fig. 5B). When examining the interaction found in figure 5A by SEM, there was a 100-300- μ m wide border with disintegrated *Terpios* tissues in which spicules were exposed (Fig. 5C). At the coral front interacting with *Terpios*, many spirocysts were found to be protruding from the coral surface (Fig. 5D). Along a disintegrated *Terpios* tissue zone (Fig. 6A), a piece of *Mil. exaesa* tissue at the coral-*Terpios* border also had spicules that had penetrated through the coral surface (Fig. 6B), suggesting retrogressive growth of coral on

Terpios.

In order to compare the growth of the *Terpios* on coral with a non-coral substratum, the sponge moving onto fragments of bivalve shells was also examined by SEM. As shown in figure 7A, *Terpios* had expanded its tissue onto the shell fragments by the 7th d of maintenance in the aquarium. The SEM examination indicated that rather than showing no direct contact between the coral and *Terpios* growth front, the sponge tissue had firmly attached to the surface of the shell fragments, and a group of protruding spicules was nearly completely free of sponge tissues and cyanobacteria (Fig. 7B).

DISCUSSION

By examining 20 species of coral with *Terpios hoshinota* invasion, it was found that

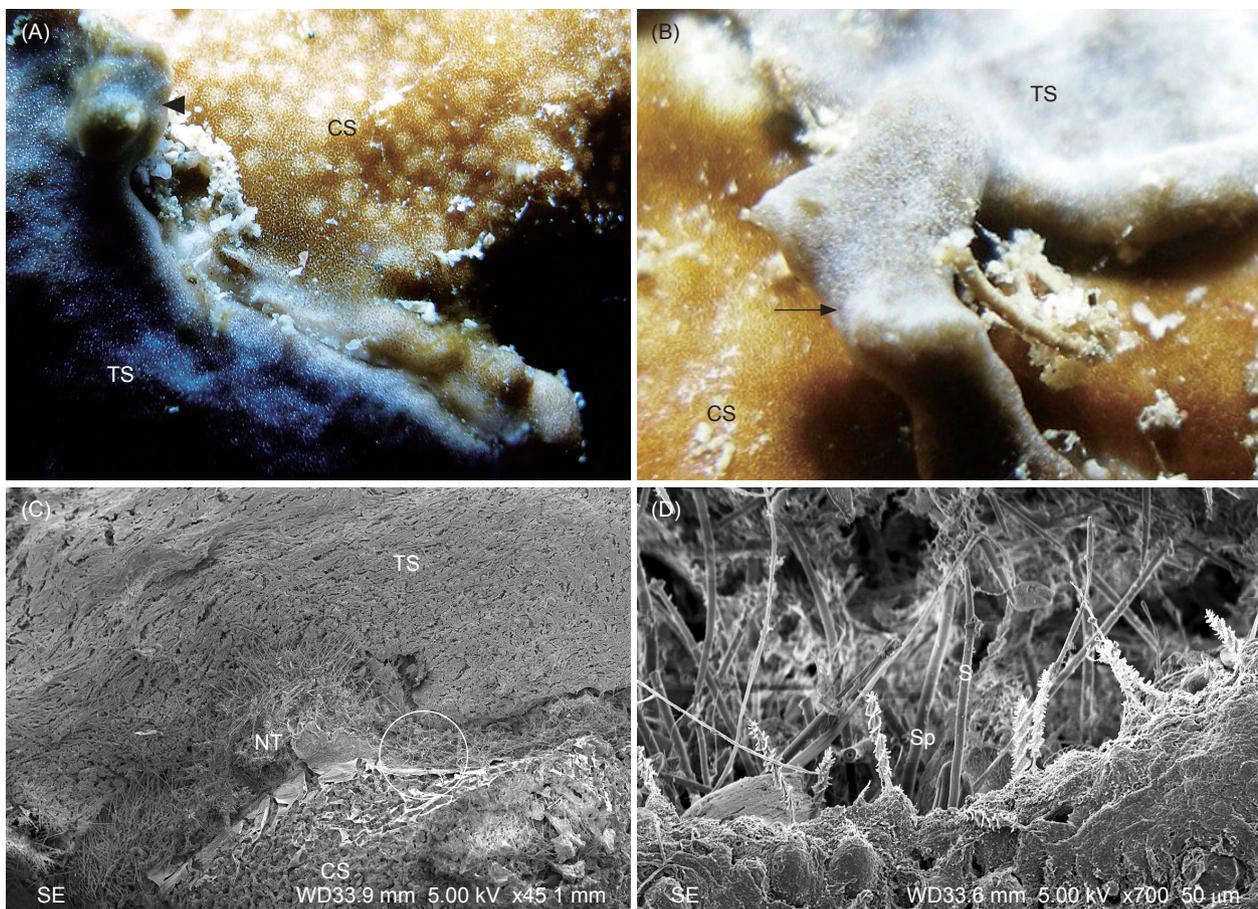


Fig. 5. *Millepora exaesa* fighting back against invasion by *T. hoshinota*. (A, B) The same specimen at different locations; the black arrowhead indicates a curving back of *Terpios* tissue; the black arrow indicates a thick tissue thread extending from the growth front of *Terpios*; and the white circle indicates the site from which (D) is amplified. CS, coral surface; NT, disintegrated *Terpios* tissue with exposed spicules; S, spicules; Sp, spirocyst; TS, *Terpios* surface.

features of the border between the 2 antagonists were not uniform among coral species or even within the same colony. These observations indicate that interactions between corals and *Terpios* are dynamic and also not species-specific as described in other coral-sponge interactions (Averts 1998 2000, McLean and Yoshioka 2008). Averts (2000) also indicated that the direction of overgrowth by the sponge might be attributed to the level of compactness of the coral, suggesting that the health status of the coral might also be a determining factor in *Terpios* infections. Overgrowth by the sponge when invading a coral was described as occurring by elevating the sponge's growing edge (McLean and Yoshioka 2007), but this was not the only feature found at the interface of coral-*Terpios* interactions. On the coral side, the growing edge of *Terpios* often displayed hairy tips, i.e., short, fine tendrils described by Rützler and Muzik (1993), which are full of sponge tissues, spicules, and cyanobacteria as found in the arm-like structure

(ALS) of Tang et al. (2011). But ALSs of *Terpios* were less often found in the field. We usually found ALSs when the growing edge of the sponge ran out of substratum of an invaded coral and tried to climb over an adjacent coral colony or perhaps faced strong defense by the coral victim (e.g., *Mil. exaesa* as seen in the inset of Fig. 1D). Another feature at the coral-*Terpios* border was the smooth and compact growing edge of *Terpios*, which is similar to the interaction in other crustose sponges, such as *Cliona caribbaea* and *Cli. lampa*, advancing on coral (Rützler 2002).

The observation of a several-millimeter-wide band of dead zooids paralleling the growing edge of the sponge usually indicates that allelochemical interactions are important in spatial competition

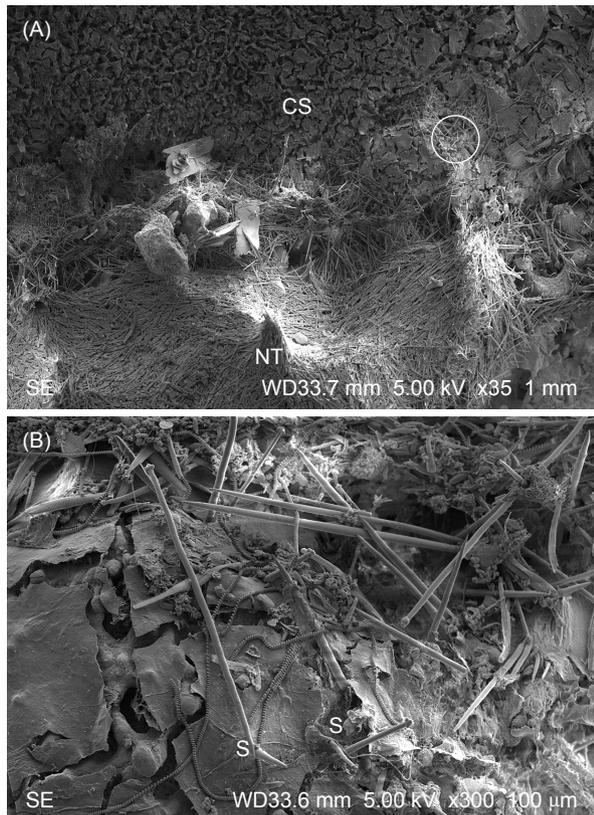


Fig. 6. *Millepora exaesa* growing over *T. hoshinota*. (A, B) The same specimen at different magnifications; the white circle indicates the site from where (B) is amplified. CS, coral surface; NT, disintegrated *Terpios* tissue with spicules exposed; S, spicules penetrating out of the coral surface.



Fig. 7. Growth of *T. hoshinota* on shell debris in an aquarium. (A) *Terpios* on *Isopora palifera* maintained in a laboratory aquarium; the white arrowhead indicates shell debris used for examination. (B) SEM examination of the shell debris with *Terpios*. S, spicules; SF, shell fragment; TS, *Terpios* surface.

on coral reefs (Jackson and Buss 1975). An allelochemical effect was also considered one of the mechanisms by which some aggressive sponges invaded corals (Jackson and Buss 1975, Porter and Targett 1988). In coral-*Terpios* interactions, both specimens from *G. edwardsi* and one of 2 specimens from 4 other coral species displayed disintegration at the coral-sponge border. Most of the coral specimens (80%) showed comparable color morphs and *Symbiodinium* densities between tissues closely contacting the sponge and those remote from the coral-*Terpios* border. Therefore, even though *T. hoshinota* was reported to produce chemicals, such as nakiterpiosin and nakiterpiosinone, with potent cytotoxicity (Teruya et al. 2004), allelochemicals might not be the major mechanism by which *Terpios* kills coral during its competition for substratum. It was more evident that *Terpios* kills corals by overgrowing them.

Scleractinian corals exhibit a wide variety of offensive and defensive mechanisms for acquiring and maintaining a living space (Connell 1973, Wahle 1980, McCook et al. 2001). One of the mechanisms is to use stinging warfare such as nematocysts or spirocysts. The 'stinging' mechanism includes the effects of polyps, sweeper tentacles, and mesenterial filaments. Several processes were documented in interspecific competition among corals (reviewed by Lang and Chornesky 1990) and also between corals and a range of other animals such as zoanths and gorgonians (Karlson 1980, Chornesky 1983, Chadwick 1987). During overgrowth by *Terpios*, some but not all victimized corals were observed to have ejected nematocysts at the contacting border. However, the defenses, including potential effectors not observable by SEM, such as chemicals, did not seem to be very effective in most cases. One successful case was found in the interaction between *S. pistillata* and *Terpios*, in which nematocysts at the surface of the growing edge of the sponge seemed to deter its advance. The most effective defense by coral's stinging warfare was found in *Mil. exaesa*, in which the coral not only caused disintegration of the *Terpios* growing edge but was also overgrowing the sponge in the reverse direction. Of course, chemical effects derived from *Mil. exaesa* cannot be excluded because it is a notorious toxin producer (Wittle et al. 1971, Shiomi et al. 1989, Radwan and Aboul-Dahab 2004, Iguchi et al. 2008). *Millepora exaesa* was further found to retrogressively grow on invading *Terpios* according

to findings of spicules protruding from the coral surface next to the coral-sponge border. This occurred only when the coral grew on un-degraded spicules left behind by disintegrated tissues of *Terpios*. When the soft tissues of coral moved over lobed tyrostyle spicules, the spicules were lifted up and penetrated through the coral tissue as shown in figure 6B.

Overgrowth by *Terpios* has caused substantial losses of coral coverage in Guam (Plucer-Rosario 1987), the Ryukyus, Japan (Rützler and Muzik 1993), and Green I., Taiwan (Liao et al. 2007). According to the experience in Guam, the coral coverage in Guam might recover (Plucer-Rosario 1987). A similar observation was also made in Japan (Reimer et al. 2011). Fortunately, the coverage of *Terpios* has not further expanded at Green I. since it was first noted in 2006 (Liao et al. 2007). The static situation of *Terpios* coverage might partly be due to a seasonal typhoon effect, but the dynamic interactive mode between the 2 antagonists, as revealed in this study, might be a crucial factor promoting the survival of invaded corals. If disturbance decreases, Connell (1978) suggested that coral recolonization is possible within a period of time. Therefore, it is our hope that we will see coral recovery from the *Terpios* invasion, if the environmental conditions of coral reefs can be protected from anthropogenic and natural disturbances.

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