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Allogeneic and xenogeneic interactions in reef-building corals may induce tissue growth without calcification

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ABSTRACT: Tissue growth without the deposition of calcium carbonate skeletons was recorded in 2 Red Sea hermatypic cnidarians during competitive interactions. Tissue contacts between allogeneic colonies of the hydrocoral *Millepora dichotoma* resulted in unilateral overgrowth. In 39% of the assays the overgrowing tissue did not secrete a skeleton for up to 10 wk. These tissues were loosely attached to the overgrown branch, and rapidly advanced by up to 25 mm within the first 2 wk. Thereafter, tissue growth slowed down or stopped and calcium carbonate was deposited over the subordinate branch, starting at the original contact area. In xenogeneic interactions between the scleractinian coral *Cyphastrea chalcidicum* and the cirriped barnacle *Savignium dentatum*, tissues of the coral always overlaid the plates of the barnacle without depositing calcium carbonate as long as the barnacles were alive (up to 5 yr). Calcium carbonate was deposited by the coral's tissue on the barnacle's plates only following barnacle death. In both cases, the non-calcifying overgrowing tissues lacked polyps but appeared normal in histological sections and contained typical cnidarian cells and endosymbiotic zooxanthellae. This type of tissue growth without calcification is a newly described allogeneic/xenogeneic response elicited by hermatypic cnidarians.

KEY WORDS: Coral · Cirripedia · Growth · Calcification · Competitive interactions · Histocompatibility

INTRODUCTION

Hermatypic cnidarians are the most important framework builders in modern tropical reef communities (Fagerstrom 1987). Tissue growth in this group of organisms is considered to be closely associated with calcification, the deposition of aragonitic calcium carbonate by the overlying calicoblastic, ectodermal layer (Barnes & Chalker 1990). Moreover, the most frequently used methods to estimate coral growth rates, such as alizarin red staining (Barnes 1970, Lamberts 1978), buoyant weight measurements (Bak 1973, Jokiel et al. 1978, Davies 1989) and incorporation of the radioactive isotope ^{14}C (Rinkevich & Loya 1984), are related to the deposition of skeletons rather than to the growth of tissues. Tissue growth without calcification in hermatypic cnidarians or free tissue movements above already deposited skeletons have only rarely been documented, although Brown et al. (1994) observed periodical withdrawal of coral tissues into the calices as a response to air exposure during low tides.

Hard substratum for settlement and growth is probably a limited resource for sessile reef invertebrates such as hermatypic corals, which are known to compete for space during their growth (Jackson & Buss 1975, Sheppard 1985, Lang & Chornesky 1990). This competition is expressed as a complex array of antago-

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nistic responses against conspecifics, as well as against unrelated organisms. During these interactions, various competitive processes, some of which are still poorly understood, occur on the morphological, cellular and biochemical levels (e.g. nematocyst discharge, development of mesenterial filaments and sweeper tentacles, allelopathic interactions, unidirectional translocation of photosynthates, unilateral and reciprocal overgrowth: Bak et al. 1982, Rinkevich & Loya 1983, Chornesky 1991, Salter-Cid & Bigger 1991, Chadwick-Furman & Rinkevich 1994, Frank & Rinkevich 1994, Rinkevich et al. 1994). Overgrowth during both allogeneic and xenogeneic interactions is one of the most common and well-documented competitive mechanisms. In calcareous cnidarians, such overgrowth has always been marked by simultaneous tissue formation and skeleton deposition as in the regular growth pattern (e.g. Potts 1976, Bak & Criens 1982, Rinkevich & Loya 1983, Chornesky 1991, Chadwick-Furman & Rinkevich 1994).

Tissues and skeletons of living hermatypic cnidarians also serve as substrata for a variety of parasitic and commensal sessile invertebrates (Patton 1976, Morton 1983). Several groups of invertebrates, such as serpulid tubeworms (Strathmann et al. 1984, DeVantier et al. 1986, ten Hove 1989, Marsden et al. 1990, Frank & ten Hove 1992), cirriped crustaceans (Ross & Newman 1973), molluscs (Morton 1983) and sponges (Wulf & Buss 1979), are known to inhabit the living surfaces of hydrocorals and madreporarians. These epibionts exhibit a variety of mechanisms to avoid overgrowth by the coral's tissue and skeleton (Hiro 1938, Gohar & Soliman 1963, Ross & Newman 1973, Morton & Scott 1980, Anderson 1992, Brickner 1994).

Here we describe the phenomenon of tissue growth without calcium carbonate deposition in 2 Indo-Pacific hermatypic cnidarians, *Millepora dichotoma* (Hydrozoa) and *Cyphastrea chalcidicum* (Anthozoa), which develops following allogeneic and xenogeneic interactions, respectively. Allogeneic contacts between *M. dichotoma* colonies are usually followed by rapid overgrowth of one colony over the other (Frank & Rinkevich 1994). In some cases, however, we observed allogeneic overgrowths which were not associated with calcification. Xenogeneic interactions between the scleractinian coral *C. chalcidicum* and the barnacle *Savignium dentatum* occur in about 84% of all coral colonies near Eilat, in the Red Sea (Brickner 1994). The barnacle bases are embedded within the coral skeleton and their plates are covered by the coral's tissue up to the rims of the barnacle aperture (Ross & Newman 1973). This coral tissue covering the barnacle's plates does not deposit calcium carbonate as does normal tissue (Brickner 1994).

MATERIALS AND METHODS

All field work was carried out by SCUBA diving in the shallow-water (3 to 6 m) coral reef adjacent to the H. Steinitz Marine Biology Laboratory at Eilat, Israel (29° N, 35° E) on the Red Sea. The fringing reefs of the northern Gulf of Eilat are characterized by high coral coverage and species diversity (Loya 1972).

Branches (ramets), about 10 cm long each, were removed in the field from 9 large *Millepora dichotoma* colonies (identified as A to I) using wire cutters. The isolated ramets were secured to plastic clothespins that had been pre-glued to 5 × 20 cm Plexiglas plates. Ramets from 6 colonies (A to F) were arranged in pairs, in 2 replicates each of all 15 possible pairwise combinations. Ramets from 3 colonies (G to I) were paired in 8 replicates each of all 3 possible pair combinations. The tips of adjacent branches in each allogeneic pair were carefully put in gentle direct contact. This procedure minimizes injury to contacting tissues, as indicated by *in situ* follow-up observations on allogeneic pairs, which displayed healthy tissue with extending polyps as in other branch tips. One isogeneic control assay was set up for each of the 9 studied colonies. Interacting branches were observed *in situ* every 10 to 14 d for up to 12 wk following the first tissue-to-tissue contact. A pair of branches was vitally stained with alizarin red S dye *in situ* every 3 to 4 wk (10 to 15 mg l^{-1}, 24 h: Lamberts 1978). Plexiglas plates bearing the pairs of interacting colonies were put into 30 l transparent plastic bags, into which 30 mg of dissolved powdered dye was injected. For histological studies, contacting pairs of branches were fixed in 2.5% glutaraldehyde in sea-water at room temperature for 3 to 4 h. Non-calcifying overgrowing tissues, which were loosely attached to the overgrown branch, were then removed using fine forceps, rinsed in double distilled water (DDW), dehydrated with increasing concentrations of ethanol and embedded in glycol methacrylate plastic. Sections (1 to 2 µm) were prepared using glass knives and stained with hematoxylin and eosin (Bancroft et al. 1990). Control sections were prepared from naive *M. dichotoma* branches after decalcifying the skeletons in a formic acid/sodium citrate solution (Rinkevich & Loya 1979).

Ten colonies of the scleractinian coral *Cyphastrea chalcidicum* infested by the pyrgomatide barnacle *Savignium dentatum* were marked *in situ* with plastic tags along a 10 m transect and used for 2 experiments. In the first, 5 coral colonies were stained with alizarin red S dye as described above. Immediately thereafter, coral tissues were removed using a jet of tap water. Newly calcified zones were visualized under a stereomicroscope as pink-reddish areas (Lamberts 1978). Plates of 5 barnacles were taken from 2 of these

colonies in order to record coral calcification on the plates. Tissue residues were removed by soaking the plates in concentrated household bleach (sodium hypochlorite) for several hours. Subsequently they were rinsed in DDW, mounted on aluminum stubs using conductive glue, coated with gold palladium and observed with a JEOL JSM 840 scanning electron microscope (SEM). In the second experiment, 30 barnacles of various sizes from the other 5 coral colonies were killed without harming their shells, by inserting a sharp metal needle into their apertures. After 14 d the alizarin red staining protocol was carried out on the 5 coral colonies, and the barnacles were observed under the stereomicroscope. SEM preparations were made from several plates of the previously killed barnacles. Histological sections from *C. chalcidicum* tissues overgrowing the plates of live barnacles, and from regular coral tissue, were prepared following decalcification as described.

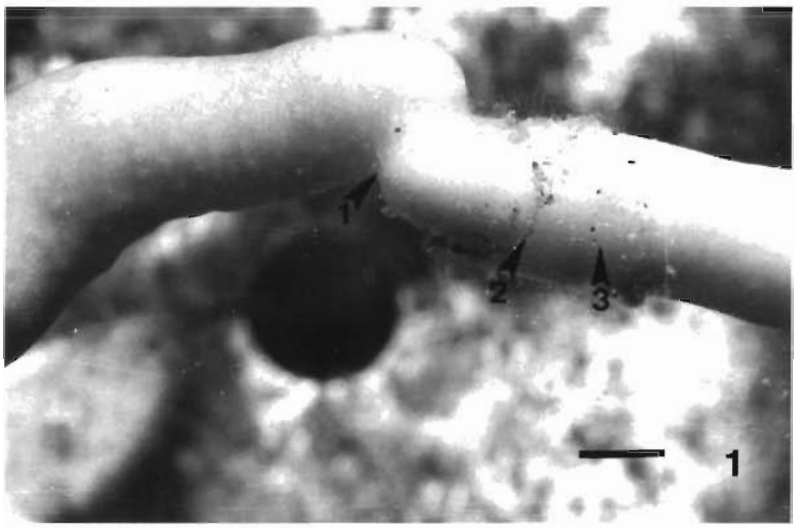
RESULTS

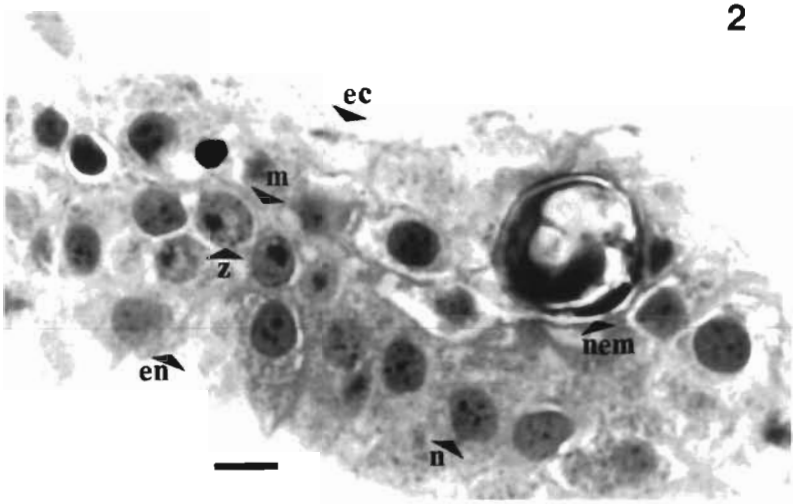
Allogeneic interactions in *Millepora dichotoma*

Tissue fusion was evident in all *Millepora dichotoma* isograft assays within 1 to 3 wk after initial tissue-to-tissue contact. Allogeneic combinations did not reveal any tissue fusion (cf. Frank & Rinkevich 1994). Primary incompatible allogeneic responses (Frank & Rinkevich 1994) in all 18 *M. dichotoma* colony-combinations were recorded as unilateral overgrowths, starting only a few days following tissue-to-tissue contacts (Table 1). Most (83.3%) outcomes of replicate pairs were consistent in terms of type of response and the directionality of overgrowth. In 7 pair combinations (17 assays, 38.9% of all combinations), the overgrowing tissues of 6 of the 9 studied colonies (all except colonies B, G and H; Table 1) started to develop without any sign of a simultaneous calcification process. In the field they were recognized as loosely attached, delicate sheets of tissue over the subordinate (= overgrown) branches (Fig. 1), which could be peeled off easily with a fingernail. These non-calcifying sheets of tissue advanced on the other colony's branch by up to 25 mm from the contact area within the first 15 d (combination BD: Table 1). This was 12 times faster than the most rapid calcifying pair (2 mm; combination CF: Table 1). After 2 wk, the average extent of growth of non-calcifying tissues (13.4 ± 8.2 mm) was significantly higher than that of normal calcifying tissues (1.1 ± 0.31 mm, $p < 0.001$; *t*-test). After 6 wk, non-calcifying tissues still covered a significantly greater portion of the subordinate branch than did calcifying tissues (15.4 ± 7.5 and 1.6 ± 7.86 mm, respectively; $p < 0.001$). After 10 wk, all overgrowing tissues which had started as non-calcifying tissues had already deposited calcium carbonate, and the rapid advancement of these tissues slowed down or stopped. Still, these tissues occupied a significantly greater part of the overgrown branch as compared to those that had started as calcifying tissues (16.4 ± 7.86 and 2.5 ± 0.97 mm, respectively; $p < 0.001$). Polyps were not observed in non-calcifying tissues. Histological sections revealed, however, that the overgrowing

Table 1 Primary allogeneic responses between *Millepora dichotoma* conspecifics as recorded after 2, 6 and 10 wk following initial tissue-to-tissue contact. Numbers of replicates are given; numbers in parentheses (only for colonies A to F) indicate the average overgrowth distance in mm. < and > indicate overgrowth directionality; Ca: calcification; NCa: no calcification

Combination	After 2 wk	After 6 wk	After 10 wk
AB	2 A>B, NCa; (5)	2 A>B, NCa; (7)	2 A>B, Ca; (7)
AC	2 A>C, Ca; (<1)	2 A>C, Ca; (<1)	2 A>C, Ca; (1)
AD	2 A>D, Ca; (1)	2 A>D, Ca; (2)	2 A>D, Ca; (3)
AE	2 A<E, Ca; (<1)	2 A<E, Ca; (1)	2 A<E, Ca; (2)
AF	2 A<F, NCa; (6)	2 A<F, NCa; (9)	2 A<F, Ca; (10)
BC	2 B>C, Ca; (<1)	2 B>C, Ca; (2)	2 B>C, Ca; (3)
BD	2 B<D, NCa; (25)	2 B<D, NCa; (25)	2 B<D, Ca; (25)
BE	2 B<E, Ca; (<1)	2 B<E, Ca; (2)	2 B<E, Ca; (3)
BF	2 B<F, Ca; (<1)	2 B<F, Ca; (<1)	2 B<F, Ca; (3)
CD	2 C<D, Ca; (<1)	2 C<D, Ca;(2)	2 C<D, Ca; (3)
CE	2 C>E, NCa; (17)	2 C>E, NCa; (20)	2 C>E, Ca; (23)
CF	2 C<F, Ca; (2)	2 C<F, Ca; (4)	2 C<F, Ca; (4)
DE	2 D<E, NCa; (14)	2 D<E, NCa; (16)	2 D<E, NCa; (17)
DF	2 D>F, Ca; (1)	2 D>F, Ca; (1)	2 D>F, Ca; (2)
EF	2 E<F, Ca; (<1)	2 E<F, Ca; (1)	2 E<F, Ca; (1)
GH	6 G>H, Ca; 2 G<H, Ca	6 G>H, Ca; 2 G<H, Ca	6 G>H, Ca; 2 G<H, Ca
GI	2 G<I, NCa; 6 G<I, Ca	2 G<I, NCa; 6 G<I, Ca	2 G<I, Ca
HI	5 H<I, NCa; 3 H<I, Ca	5 H<I, NCa; 3 H<I, Ca	3 H<I, NCa; 5 H<I, Ca



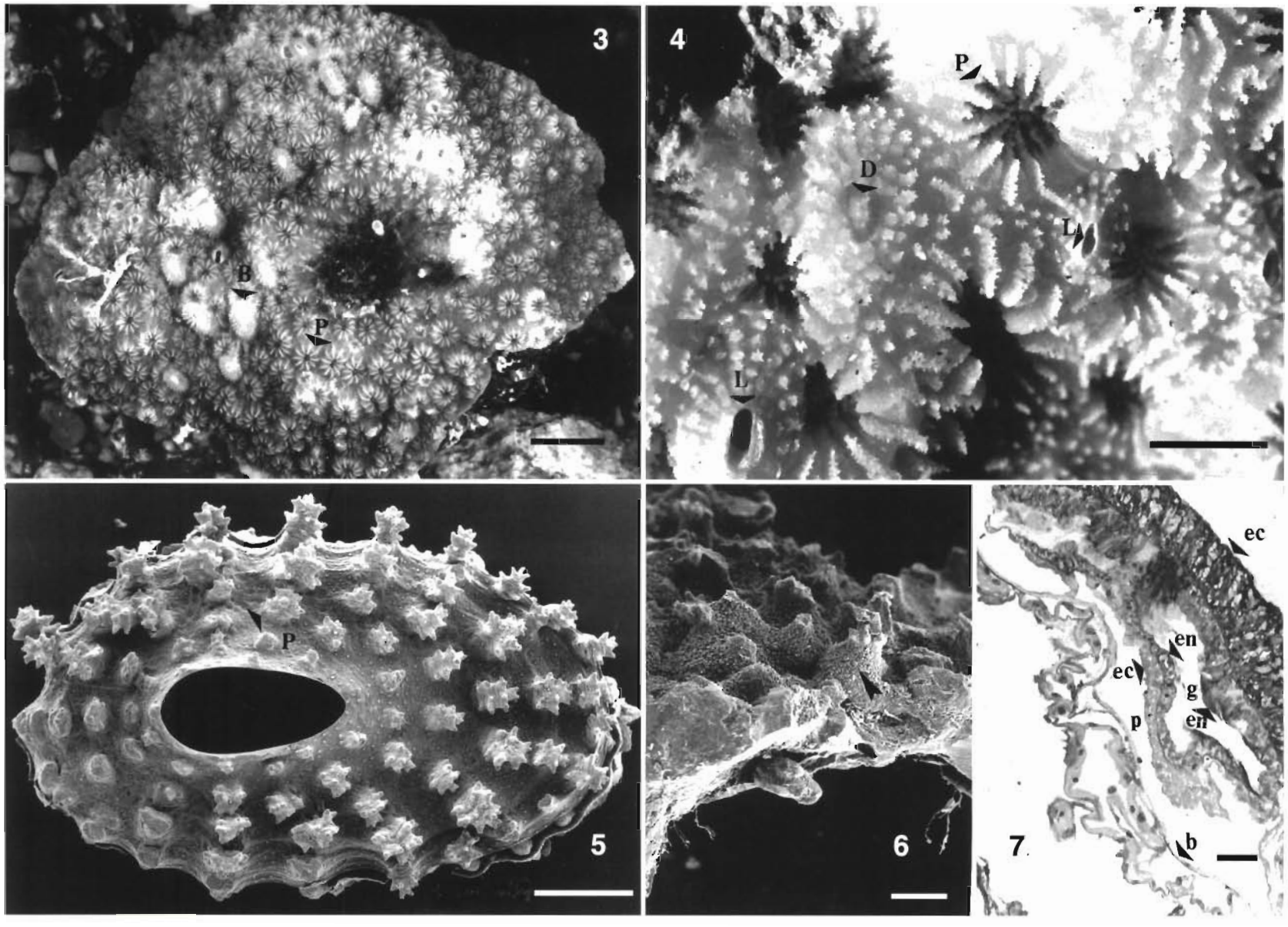


Figs. 1 & 2. *Millepora dichotoma*. Fig. 1. Allogeneic overgrowth, 4 wk following initial tissue-to-tissue contact. Tissue growth without calcification has been followed by calcification, starting from the original contact area. Arrowheads indicate the original contact area (1), edge of calcifying overgrowing tissue (2) and non-calcifying tissue (3). Scale bar = 10 mm. Fig. 2. Cross section (2 µm) through overgrowing tissue without calcification (hematoxylin and eosin). ec: ectoderm; en: endoderm; m: mesoglea; n: nucleus of endodermal cell; nem: nematocyst; z: zooxanthella cell. Scale bar = 10 µm

tissues contained endosymbiotic zooxanthellae, nematocyts and other cell types, arranged in ectodermal and endodermal cell layers as in regular *M. dichotoma* tissue (Fig 2). The skeletons of the subordinate branches below the non-calcifying allogeneic sheets of tissue did not stain with alizarin red, indicating that no new calcium carbonate was deposited there. In contrast, other branch termini, including those which were overgrown by tissue and skeletons (37 assays; Table 1), stained weakly pink-reddish. The primary allogeneic responses in the non-calcifying overgrowth assays were usually completed within 2 wk. Thereafter, the rapid advancement of the 'superior' colony's tissue slowed down significantly or even stopped, and calcium carbonate was deposited, starting at the tip area of the original tissue-to-tissue contact. This result was then confirmed by *in situ* observations (Fig. 1) and by alizarin red staining (pink-reddish color on the overgrown tips of the subordinate branch).

Xenogeneic interactions between *Cyphastrea chalcidicum* and *Savignium dentatum*

The plates of all living *Savignium dentatum* inhabiting *Cyphastrea chalcidicum* colonies were found to be covered by homogeneous zooxanthellate coral tissue without calcification when observed under the stereomicroscope. Polyps were absent on the plates of all living barnacles (Figs. 3 to 5). The coral tissue advanced up to the barnacle's aperture, and was tightly attached to the barnacle's plates. This type of overgrowth differs, therefore, from the loosely attached non-calcifying *Millepora dichotoma* tissue envelopes that arise during allogeneic encounters. All studied colonies of *C. chalcidicum* stained well and evenly with alizarin red, as expected for a hemispheric colony. However, the plates of all living barnacles remained white and did not stain at all, indicating that no calcium carbonate was deposited by the overlying coral tissue. SEM preparations from plates of living *S. dentatum* revealed only a few, limited spots of calcified material of coral origin (data not shown), which might explain the tight attachment of the coral tissue to the plates. Even limited coral calcification over the barnacle plates can be easily seen because the radial strands and projections which are characteristic of the plates for *S. dentatum* are not visible if covered by coral skeleton (Figs. 3 to 6). Plates from dead individuals, on the other hand, were always covered by calcium carbonate of coral origin (Figs. 4 & 6) and stained well with alizarin red. Their apertures were almost completely sealed by coral skeleton already 3 wk after their death (Fig. 4). Histological sections of *C. chalcidicum* did not reveal any significant difference between calcifying and non-



Figs. 3 to 7 *Cyphastrea chalcidicum* and *Savignium dentatum*. Fig. 3. Overview of *C. chalcidicum* colonized by *S. dentatum*. B: barnacle; P: coral polyp. Scale bar = 6 mm. Fig. 4. Exposed skeleton of *C. chalcidicum* colonized by *S. dentatum*. D, barnacle which was killed 21 d before this photograph was taken: aperture sealed by coral skeleton; L, live barnacle; P, coral polyp. Scale bar = 3 mm. Fig. 5. *S. dentatum*. SEM preparation of a plate from a live barnacle (upper view). P: projection on barnacle's plate. Scale bar = 1 mm. Fig. 6. *S. dentatum*. SEM preparation of a plate from a barnacle which was killed 14 d before sampling. Arrowhead indicates projection on the plate, now covered with calcium carbonate of coral origin. Scale bar = 200 µm. Fig. 7. *C. chalcidicum* and *S. dentatum*. Cross section (2 µm) through decalcified barnacle and the overgrowing coral tissue (hematoxylin and eosin). b: barnacle's tissue; ec: ectoderm; en: endoderm; g: gastric cavity; p: location of decalcified plate. Scale bar = 30 µm

calcifying tissues, except of the lack of polyps in the latter (Fig. 7). Cross sections of coral tissue overgrowing living *S. dentatum* plates clearly demonstrated the typical structure of the inter-polyp madreporarian tissue, consisting of 2 body walls separated by a gastric cavity (Fig. 7). Typical cnidarian cells were arranged in ectodermal and endodermal cell layers in each body wall. Symbiotic zooxanthellae were observed within endodermal cells, which had a normal appearance, like those of the control sections.

DISCUSSION

We have documented here the occurrence of growth without calcium carbonate deposition in 2 hermatypic cnidarians, *Millepora dichotoma* and *Cyphastrea chalcidicum*, engaged in allogeneic and xenogeneic interactions, respectively. These species represent 2 distinct classes of the Cnidaria: *M. dichotoma* belongs to the Hydrozoa, *C. chalcidicum* to the Anthozoa. The phylogenetic distance between these 2 species within the Cnidaria suggests that growth without calcification is not a unique phenomenon, and may be expressed by other reef-building corals as well.

Unilateral overgrowth by tissue without calcification or polyp development in allogeneic encounters of *Millepora dichotoma* was a temporary phase during the establishment of primary allogeneic responses. It was always followed by development of regular calcifying tissue and polyps, usually within the 4 to 10 wk following initial tissue-to-tissue contact. The non-calcifying tissue advanced rapidly over the subordinate branch and was loosely attached to it until calcification began. Overgrowth by non-calcifying tissue extended for significantly greater distances over the subordinate branches, as compared to the regular calcium-carbonate-depositing tissue (Table 1). The absence of polyps is probably attributable to the extremely rapid growth. This rapid tissue advancement, without calcification or polyp development, may therefore be regarded as a newly described allogeneic effector mechanism that evolved for rapid occupation of substratum. The efficiency of this type of growth is well demonstrated by the significantly greater areas occupied on the subordinate branches by non-calcifying tissues as compared to normal calcifying tissues. Similar responses involving rapid growth without calcification are also found in other hermatypic corals in cases of rapid regeneration after tissue lesions, and produce features referred to as 'lip of tissue' (Bak et al. 1977, Bak & Steward-Van Es 1980). The overgrowing tissue slowly eliminates the tissue of the subordinate branch by the expression of unknown effector mechanisms, or indirectly by drastically reducing light and nutrient supply, as has been suggested by Ivker (1972) for allogeneic interactions between *Hydractinia echinata* conspecifics. Calcium carbonate is probably deposited by the overgrowing partner only on clean areas of the subordinate colony's skeleton. Rapid overgrowth without calcification was displayed in at least 1 combination by only 6 colonies out of the 9 studied (Table 1). The occurrence of non-calcifying tissue in only some of the combinations, and its high degree of reproducibility within repeatable assays of the same combinations (except for GI and HI; Table 1), suggest that a specific genotype-combination is required for this effector mechanism to be expressed. Similar specificity has also been recorded for other effector mechanisms in the scleractinian corals *Stylophora pistillata* and *Acropora hemprichi* (Chadwick-Furman & Rinkevich 1994 and Rinkevich et al. 1994, respectively).

Overgrowth of *Savignium dentatum* plates by *Cyphastrea chalcidicum* tissue without skeleton deposition and polyp development is probably the result of a different mechanism. The non-calcifying coral tissue above the barnacle's plates, which probably provides protection against predation (Patton 1976), was found to be a long-term situation, lasting as long as the barnacle lives (up to 5 yr: Brickner 1994). Death of the barnacle was immediately followed by calcium carbonate deposition by the overgrowing coral tissue and eventually by appearance of coral polyps above the plates. On living barnacles, calcium carbonate deposition by the overgrowing coral tissue may prevent the barnacle's growth by cementing the sutures between plates and bases (Ross & Newman 1973), and eventually may reduce food and oxygen supply by sealing the aperture. *S. dentatum* presumably possesses some physiological-biochemical mechanisms to prevent skeleton deposition by the overgrowing *C. chalcidicum* tissue.

We suggest that tissue growth without calcification, as observed in the 2 hermatypic species studied here, reflects 2 similar end products of 2 different biological processes with unlike ecological backgrounds. Growth without calcification in *Millepora dichotoma* was probably triggered in the superior partner as a result of tissue contact with a specific allogeneic colony. In *Cyphastrea chalcidicum*, on the other hand, growth without skeleton deposition was induced by the overgrown barnacle *Savignium dentatum*. The non-calcifying tissues were histologically indistinguishable from regular tissues overlying skeleton in both studied species. One may therefore assume that the calcification-inhibiting agent directly prevents the precipitation of calcium carbonate at the biochemical level and not by obstructing the development of a normal calicoblastic layer. The rapid calcification of *C. chalcidicum* tissue immediately following the barnacle's death supports this hypothesis. Rapid overgrowth without skeleton

deposition is an allogeneic effector mechanism in *M. dichotoma*, and the inhibition of calcium carbonate deposition in *C. chalcidicum* by *S. dentatum* is a xenogeneic effector mechanism, induced by the barnacle. As such, neither phenomenon has been described previously. They should be taken into account in future coral growth and competition studies.

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