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Fusion or non fusion of coral fragments in *Acropora*

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ABSTRACT. Corals inhabit high energy environments where frequent disturbances result in physical damage to coralla, including fragmentation, as well as generating and mobilizing large sediment clasts. The branching growth form common in the *Acropora* genus makes it particularly susceptible to such disturbances and therefore useful for study of the fate of large sediment clasts. Living *Acropora* samples with natural, extraneous, broken coral branches incorporated on their living surface and dead *Acropora* skeletons containing embedded clasts of isolated branch sections of *Acropora* were observed and/or collected from the reef flat of Heron Reef, southern Great Barrier Reef and Bargara, Australia respectively. Here we report three different outcomes when pebble-sized coral branches became lodged on living coral colonies during sedimentation events in natural settings in *Acropora*: 1) Where live coral branches produced during a disturbance event come to rest on probable genetic clone-mate colonies they become rapidly stabilised leading to complete soft tissue and skeletal fusion; 2) Where the branch and underlying colony are not clone-mates, but may still be the same or similar species, the branches still may be stabilised rapidly by soft tissue, but then one species will overgrow the other; and 3) Where branches represent dead skeletal debris, they are treated like any foreign clast and are surrounded by clypeotheca and incorporated into the corallum by overgrowth. The retention of branch fragments on colonies in high energy reef flat settings may suggest an active role of coral polyps to recognise and fuse with each other. Also, in all cases the healing of disturbed tissue and subsequent skeletal growth is an adaptation important for protecting colonies from invasion by parasites and other benthos following disturbance events and may also serve to increase corallum strength. Knowledge of such adaptations is important in studies of coral behaviour during periods of environmental stress.

KEYWORDS: scleractinian coral, coral reef, biomineralisation, skeletogenesis, clypeotheca, disturbance.

1. Introduction

Modern reef-building corals inhabit high energy environments near sea level where waves and currents commonly cause physical damage to colonies, including fragmentation, and generate and mobilize large sediment clasts that may come to rest on in situ colonies. Hence, corals in shallow reef environments frequently undergo sedimentation and clearance (re-suspension) of fine and coarse sediment. Many corals have apparently adapted to frequent disturbance and increase their distribution through vegetative reproduction and dispersal of broken fragments (Tunnicliffe, 1981; Bothwell, 1981; Highsmith, 1982). However, although fragmentation is a useful strategy for dispersal in some corals, many shallow reef corals have developed defensive mechanisms to adapt to sedimentation events, including both morphological and behavioural adaptations (e.g., Hubbard & Pocock, 1972; Hubbard, 1973; Barnard et al., 1974; Bak & Elgerschuizen, 1976; Lasker, 1980; Stafford-Smith & Ormond, 1992; Stafford-Smith, 1993; Riegl, 1995). Most studies of coral responses to sedimentation have involved the reaction of corals to finer sediment (mud-sand-granule size ranges), and in some cases that sediment is incorporated into the skeleton (e.g., Davies 1992). The effects of deposition of coarse clasts on corals are more poorly documented despite the common occurrence of coral communities in high energy settings, including gravel-cobble-dominated environments (e.g., Braga et al., 1990; Perry & Smithers, 2009). In particular, very little research has been conducted on the incorporation into scleractinian coral skeletons of coarse foreign material that cannot be dislodged from the coral colony, despite such occurrences presumably being common in nature. Cases of fused, broken branches have been observed in nature in some corals (e.g., *Acropora*, Collins, 1978; *Madracis mirabilis* and *Oculina diffusa*, Logan, 1985), but such interactions have rarely been documented in detail. Experimental work on reactions between mature coral branches from different colonies has been undertaken mostly to investigate competitive interactions and histocompatibility behaviour (Potts, 1976; Collins, 1978; Neigel and Avise, 1983).

Most of the gravel-sized sediment produced in clean reef environments consists of broken skeletal material, including live or dead coral branches. Such branches may be difficult to dislodge from a particular corallum by biological means or by subsequent physical energy (e.g., wave action), especially where the in situ corallum has irregular surface and branching morphology (e.g., Stafford-Smith & Ormond, 1992), such as is common in *Acropora*. Coral debris deposited on a living colony can represent one of four classes of relationships with the underlying colony: (1) dead coral fragment possibly encrusted by other biota (live-dead relationship of Fagerstrom & West, 2011); (2) living fragment from the same colony or clone (conspecific and isogenic); (3) living fragment from another colony of the same species (conspecific but anisogenic), or (4) living fragment from a different species or genus (heterospecific and anisogenic) (see West et al., 2011 figure 1). Here we report three different observed outcomes when pebble-sized coral debris became lodged on living coral colonies during sedimentation events in natural settings.

2. Materials and methods

Two field sites were chosen to allow observation of biological interactions in both live collected and dead coral skeletons so as to evaluate preservation potential in fossil material. Living *Acropora* samples with natural, extraneous, broken coral branches incorporated on their living surface were observed and/or collected from the reef flat of Heron Reef, southern Great Barrier Reef (~E151º55.53', S23°26.07'). Dead *Acropora* skeletons containing embedded clasts, including isolated branch sections of *Acropora*, were collected from beach cobbles at Bargara, central coast of Queensland, Australia (~E 152°27'22.56"; S 24°48'17.30"). Heron Reef is a clean carbonate environment ~70 km off shore, whereas the Bargara corals occur in a rocky-pebble shore setting with abundant, shore-worked carbonate and fluvial-derived siliciclastic gravel.

Samples were analysed using x-ray computer tomography (µCT) and then cut for microstructural analysis on polished and etched sections and blocks using scanning electron microscopy (SEM). The corals were scanned with a micro computed tomography scanner (µCT 40, Scanco Medical, Brüttisellen, Switzerland), at an energy of 70 kVp and intensity of 114 µA with 200 ms integration time. The scans resulted in an isotropic nominal resolution of 30 µm. The reconstructed cross sectional images were exported as stacks of TIFF images with 1024 x 1024 pixels for further visualisation with DRISTI©. Polished sections were etched in 2% formic acid for approximately 20 s. Samples for observation using SEM were gold coated and were analysed on either a FEI QUANTA 200 Environmental scanning electron microscope (SEM) or a FEI QUANTA 3D SEM.

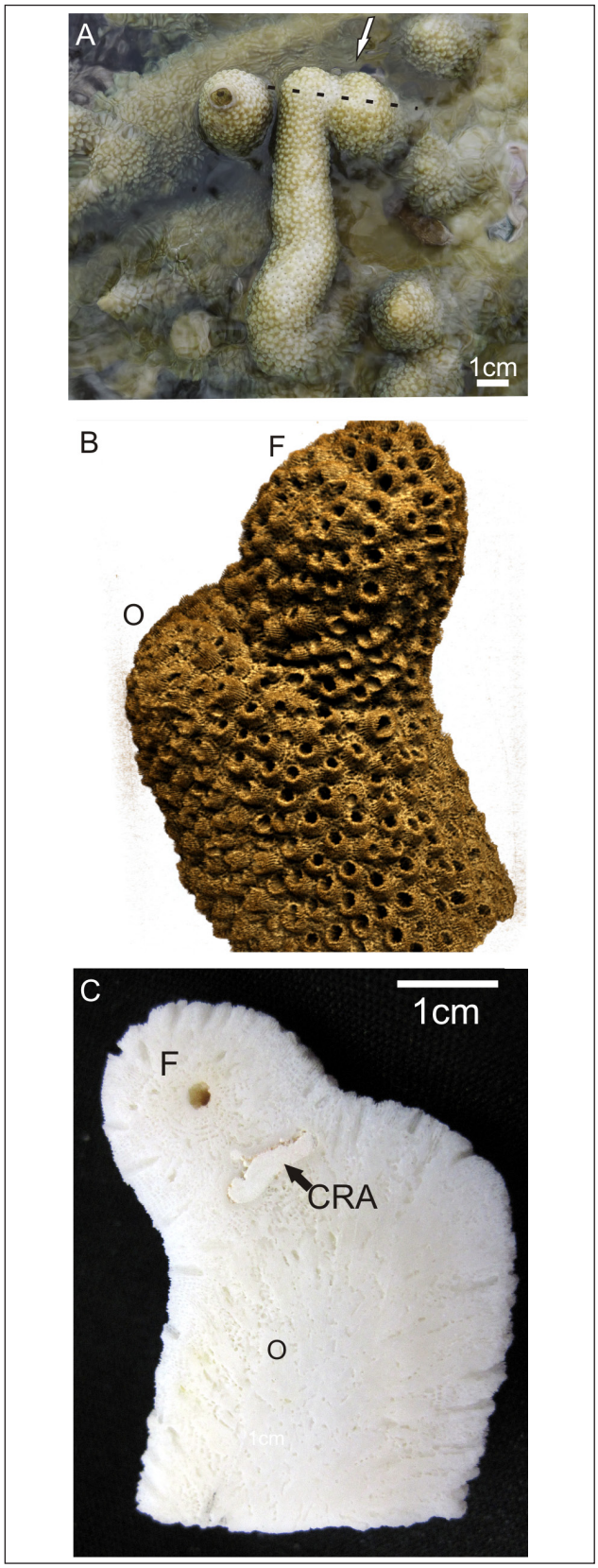

Figure 1. A: Fused branch of *Acropora sp*. on the reef flat of Heron Reef, Southern GBR. The dashed line represents a vertical line of section for Fig. 1C. The arrow shows the direction of view of µCT image (upper right) in Fig. 1B. B: 3D reconstruction of µCT images of the outer surface of the fused branch of *Acropora*. C: Photograph of the cut surface of the fused branch. The fused branch is shown by the letter F and the original in situ branch by the letter O. The cut section contains a grain of coralline red algae (CRA) at the junction between the branches.

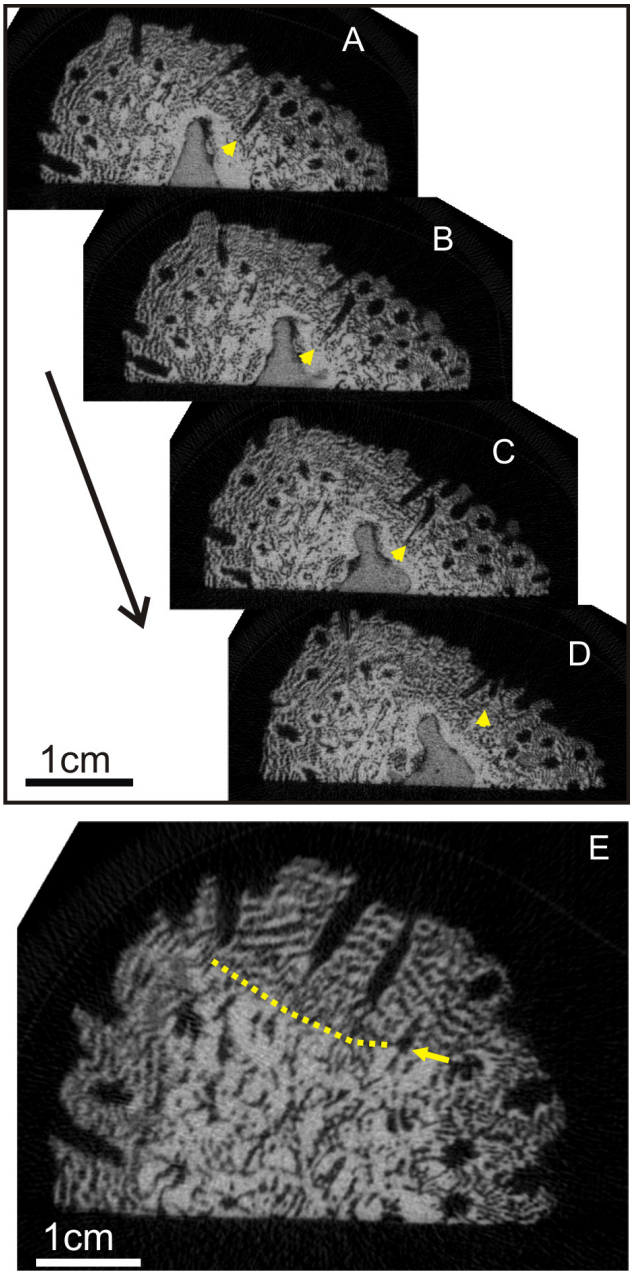

Figure 2. X-ray images of slices collected during µCT analysis. A to D: Sections through the junction between the two *Acropora* branches in Fig. 1. The yellow arrows track the location of an individual corallite through the section. The corallite, which initiated from the broken branch, had a straight growth direction initially, but the trajectory changed around a neighbouring corallite from the other branch. This competition for space resulted in a high density of corallites on the surface and changes to their size and shape. E: X-ray section through the broken branch. There is a large density difference between the inner and outer areas. The junction on the upper side of the image (dashed yellow line) is an apparent fracture surface on which the coral has been able to regenerate. No corallites are continuous through this surface and the yellow arrow shows the apparent initiation point of one corallite on the upper side of the junction.

3. Results

Pebble sized *Acropora* branch sections were observed enclosed within the skeletons of subfossil *Acropora* coralla from Bargara (Plate 1A). They are encased within the skeleton in the same way as other - non-carbonate clasts, which include basalt and quartzite. The clasts range in size from 3 to12 mm. In all cases (i.e., both for coral clasts and for siliciclastic pebbles), the cavities were lined by obvious clypeotheca (see Nothdurft & Webb, 2009), thus separating the clasts from living coral tissues as the clasts were incorporated (Plate 1B-D). Clypeotheca surrounding the *Acropora* branch is stained dark in appearance, but the source of the staining is unknown. Otherwise, the clypeotheca developed around the clast is constructed in the same way as clypeotheca previously reported on external corallum surfaces around the external bases of branches (Nothdurft & Webb, 2009). Hence, it represents a surface produced by the amalgamation of flanges

produced from near the tips of coenosteal spines with centripetal growth (Plate 1E), and covers over corallite apertures much like upside-down dissepiments. The clypeotheca completely sealed off coenosteum and corallites alike from the cavity containing the entrapped clast. The extent to which polyps beneath the clast were able to deflect and grow around the clast or rather ceased growing to be abandoned and covered by clypeotheca is still somewhat unclear because it is very difficult to track an individual corallite through its entire trajectory of growth. However, some corallites certainly appear to have been abandoned and sealed over.

In samples from the reef flat on Heron Reef, clearly broken and redeposited *Acropora* branch fragments were found to have been incorporated onto existing colonies (Fig. 1, Plate 2). In one example, a clearly broken and displaced coral branch consisting of a broken end and distal tip came to rest more or less horizontally on top of in situ, predominantly upright branches on the underlying colony. The branch was then fused into place by continued skeletal growth, both from the underlying colony and from the displaced branch itself. The axial corallites of the horizontal clast and the upright branches to which it became fused are perpendicular to each other (Fig. 1A). Both ends of the broken branch were completely covered with living polyps of similar architecture and colour to those in the rest of the underlying colony. Corallites over the top of the fused branch appear to originate both from the branch and from the underlying colony with no discernable juncture and the broken end of the branch has been completely overgrown by new coral growth. At the depressed junction between the fused branches, closely-spaced smaller corallites occur with no lips (Fig. 1B; Plate 2A, B). Underlying and overlying corallites directed toward the junction of the branch and corallum do not appear to change direction and must terminate, but the exact nature of the process is not clear.

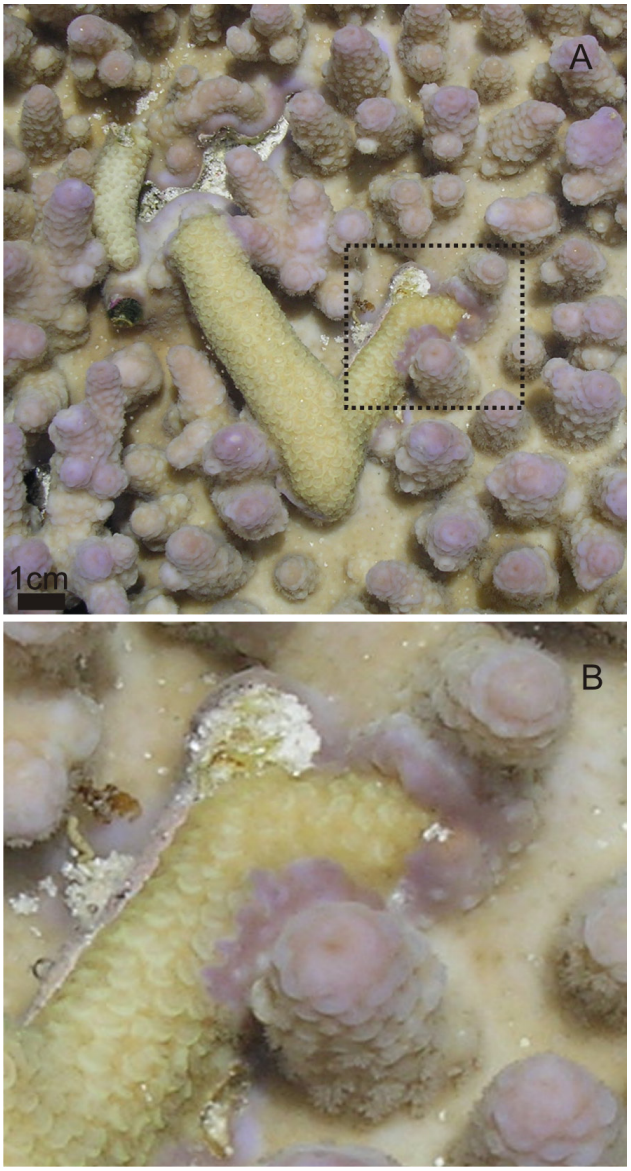

Figure 3. Photograph of probable anisogenic interaction between the host colony of *A. hyacithus* and an incorporated branch of *Acropora sp*. The location of the higher magnification image in B is shown on A with a dashed box.

The polished and etched sections (Plate 2B, C) show that there is no obvious skeletal junction between the branches, but several coarse clasts of coralline red algae (CRA) have lodged between the opposing branches and become incorporated at the approximate location of the junction (Fig. 1C). Embedded clasts that are visible in section include an elongate pebble approximately 7 mm long and 3 mm wide adjacent to numerous other loosely packed grains of mixed carbonate origin, including CRA, mollusc and coral fragments ranging in size from 100 to 500 µm. The coral skeletal has encased the clasts with new skeletal growth not in contact with the grains in some places and with coral skeleton moulded to the surface of the grain in intricate detail in other places (Plate 2F).

Within the broken branch and the *in situ* branch to which it fused, there appears to be a large amount of skeletal thickening deposits where synapticulae have completely filled areas between septa, costae and ceonosteum (Fig. 2, Plate 2E). This thickening occurs in areas of the branches that initially formed prior to the fusion. The skeletal formation on the outer 2.5 to 3 mm of the branches is much less dense where septal and costal structures rarely exceed 50 µm in thickness.

In another example where an *Acropora sp.* branch fragment was deposited more or less horizontally on a colony of *A. hyacithus* (Fig. 3A) The branch also became fused to the underlying corallum, but in this case, the polyps of the branch and the host colony are different in colour and there is a clear junction between the live polyps of the branch and those of the underlying colony (Fig. 3B). The junction is irregular in outline and is white, apparently with a thin region of dead tissue. The margin stands higher in relief on the in situ colony side of the junction. A purple pigmentation was observed in the tissue of the underlying *A. hyacinthus* and is consistent with the colour of new tissue growth at the ends of branches. The internal characteristics of the junction are unknown as the sample could not be collected.

4. Discussion

In the case of the incorporated coral branches found within *Acropora* coralla at Bargara, Queensland, the branches are interpreted to have been dead when deposited on the living coral surface because they are moderately abraded (Plate 1A, C) and must have been abraded before being embedded in the living colony. The living coral colony treated them as foreign clasts that could not be dislodged passively or by means of soft tissue manipulation, and they were simply grown around and incorporated into the corallum. If the dead branches of an adjacent colony were grown over and encrusted *in situ*, Fagerstrom & West (2011) would have termed it quasi-fusion. Regardless, in the case of the clasts, they apparently served as irritants, and the colony withdrew soft tissues from the area immediately beneath and adjacent to the foreign clast and secreted a clypeotheca to isolate living coral tissues from the cavity containing the clast. The sealing off of individual polyps beneath the clast, rather than their diversion around the clast, may suggest that they were damaged by abrasion or it may simply reflect normal resorption of non-viable polyps consistent with the high levels of colonial integration in *Acropora*. In other cases of clypeotheca production individual polyps appear to have been readily 'sacrificed' and sealed over in order for the overall colony to have protection, apparently from invasion where soft tissues were stressed by adjacent sediment (Nothdurft & Webb, 2009) or in this case damage from an individual clast. This is consistent with the previous interpretation of clypeotheca as a protective skeletal adaptation to a localised stress (Nothdurft & Webb, 2009).

Although coral branch clasts observed in coralla at Bargara appear to have been dead upon deposition, clypeotheca also apparently was observed at the junctions between non-clone branches of *A. formosa* in allograft (anisogenic) experiments

(Collins, 1978, his figure 30). Collins (1978, p.108) noted the formation of 'epithecal morphology, a consistent feature noted at all mature allogeneic interfaces' where non-clonal branches were forced to interact with each other. Potts (1976, p. 84) also may have referred to clypeotheca in describing the formation of 'a growing edge similar to the expanding edge of the basal disk of a colony,' developing where two non-clonal branches of '*A. palifera*' (now *Isopora palifera,* Wallace et al., 2007) grew against each other without fusion of soft tissues. Clypeotheca was described at the junction between two colonies of *I. palifera* by Nothdurft &Webb (2009). Hence, clypeotheca production may in some cases also be a response to stress from interactions with more aggressive coral species.

The broken branch that fused seamlessly to the underlying colony on Heron Reef developed no clypeotheca and demands a different interpretation. In this case, the polyps on the branch were still clearly alive at the time of deposition, and they remained alive when collected, well after fusion took place. We interpret the fused branch as most likely representing a clone-mate (i.e., the same genotype - isogeneic) of the underlying colony. Although no genetic analyses have so far been carried out to test that hypothesis, previous studies of interspecific aggression (Lang, 1971; Shepard, 1979) and soft part and skeletal fusion (Hildemann et al., 1975; Logan, 1984; Neigel & Avise, 1983; Frank et al., 1997) in scleractinian corals suggest that it is unlikely that two mature non-clone mates would have fused so readily at both the soft tissue and skeletal levels. Although allogenetic fusion occurs in some very young coral colonies where spats settle very close to each other (Hidaka, 1985; Hidaka et al., 1997), presumably owing to delayed development of the histocompatability mechanism (Frank et al., 1997; Raymundo & Maypa, 2004), allogeneic fusion of mature colonies is rare (Chornesky, 1991; Fagerstrom & West, 2011). Significantly, the coral branch did not appear obviously to have been broken off of the host colony, although that possibility exists. The branch differs from the underlying colony in that it has significantly thickened skeletal structure, but that could represent a stress response wherein polyps limited their own extension, so as to reduce interference with other proximal polyps while continuing to deposit skeletal aragonite. Some of the polyps appear to have changed their growth trajectories (Fig. 2). It is difficult to track an individual corallite through its entire trajectory, but interestingly, some may have stopped growing and entire corallites were abandoned where they interfered with opposing polyps. This observation differs from that of Collins (1978) who suggested that all polyps survived at the sites of experimental fusions between *Acropora* branches, but that they diverted significantly away from the contact zone. However, polyp abandonment apparently occurred in an example illustrated by Neigel & Avise (1983, their figure 1A) and polyp abandonment is consistent with the stress reaction of *Acropora* where clypeotheca is formed (Nothdurft & Webb, 2009).

Regardless, of the morphological response, the apparent clone-mate branch may have been transported laterally from a different, but clone-mate colony. Fragmentation is an important mode of reproduction for branching corals, such as *Acropora* (Tunnicliffe, 1981; Highsmith 1982), in shallow reef settings and large storm events can break and distribute corals over 100s of meters of reef surface. Hence, clone-mates can be distributed over a wide area of reef flat and then come into contact again with lateral transport of broken branches during subsequent disturbance events. The likelihood of such a process depends on the morphology of the colony and recurrence rate of the disturbance events that cause physical damage to the colonies.

Irrespective of the exact source of the branch, it was not washed off of the colony subsequently. As its position was not particularly obstructed by underlying morphology, it is interesting to speculate that it may have been in some part anchored initially by soft tissues, perhaps partly by interaction between the polyps in the underlying corallum and the branch. That soft tissues responded relatively quickly to the clast is suggested by the fact that the broken end of the branch was not colonised by other benthos before being overgrown by new coral skeleton. Hence, soft tissue from the larger colony may have expanded over the broken branch end relatively quickly and this may have helped anchor the branch into place before full soft tissue and skeletal fusion occurred. Such ability would aid fragile colonies in these high energy settings by fostering rapid development of rigid buttresses where colonies were damaged and branches fell into contact with each other. The relatively fragile *Agaricia tenuifolia* developed the ability to fuse with non-clone-mates as a possible means to produce such buttresses and increase strength across adjacent colonies (Chornesky, 1991). Rapid response of polyps to anchor to a clone-mate fragment could serve the same purpose. However, some branching corals (e.g., *Stylophora pistillata*) appear to have a chemical response between adjacent branches that signals their proximity and limits their mutual interference and presumably fusion during normal growth (Rinkevich & Loya, 1985). That type of response would be at odds with any active role for polyps in anchoring a fragment to the colony. Regardless, Fagerstrom & West (2011) highlighted the importance of processes involving clone interaction in the formation and rigidity of skeletal reef framework and early interaction and or fusion of soft tissues could be an advantageous adaptation for framework forming corals.

Finally, there is the third case, also from Heron Reef, wherein a transported branch was actively being overgrown by the underlying colony. In that case, the apparent fusion was clearly the result of competitive overgrowth (Neigel & Avise, 1983; Hidaka et al., 1985) wherein the underlying colony was dominant. Such reactions have been observed in cases of anisogenic fusion (Hidaka, 1985; Rinkevich & Loya, 1985; Chadwick-Furman & Rinkevich, 1994; Frank et al., 1997) and suggest that the transported branch was not a clone-mate of the underlying colony. A variety of stressful interaction circumstances are associated with discoloured tissues pink, purple or blue. This cellular inflammation and the melanin-producing signalling pathway are two mechanisms employed by invertebrates to remove foreign organisms (e.g., Palmer et al., 2008; Willis et al., 2004 and references therein). No discoloured tissue was observed in the example of clone mate interaction (Fig. 1A). Although the sample was not collected, it is unlikely that any skeletal fusion would be observed, but as with the previous example, there may have been early interaction of soft tissues before the overgrowth reaction began. It is unknown if the host colony deposited a clypeotheca around the branch like that observed by Nothdurft & Webb (2009) between two colonies of *Isopora palifera*. Regardless, continued growth of the underlying colony would eventually encapsulate the branch entirely within the corallum and produce an embedment similar to those documented above from Bargara, but in this case as a live-live ecological association.

In summary, we have demonstrated three different behaviours regarding the interaction between coral colonies and broken coral branches that become lodged on their surfaces in natural settings. Where live coral branches produced during a disturbance event come to rest on probable genetic clone-mate colonies they become rapidly stabilised leading to complete soft tissue and skeletal fusion. Where the branch and underlying colony are not clone-mates, but may still be the same or similar species, the branches still may be stabilised rapidly by soft tissue, but then one species will overgrow the other. Where the underlying colony is dominant, the smaller branch will eventually become embedded within the host corallum. Where branches represent dead skeletal debris, they are treated like any foreign clast and are surrounded by clypeotheca and incorporated into the corallum.

The retention of branch fragments on colonies in high energy reef flat settings may suggest an active role of coral polyps to recognise and fuse with each other. This ability may represent an adaptation to help heal damaged colonies where branches were broken, but not removed from the host colony, so as to increase corallum strength. Many reef framework forming invertebrates have developed the ability to fuse with clone-mates and non-clonemates to provide rigidity in high energy settings (Fagerstrom & West, 2011). Where non-clone-mate branches are involved, they do not become fused with the underlying colony at both soft tissue and skeletal levels, but the corals may compete at the site of contact and the branch may be engulfed forming a quasi-fusion. In such cases, the encrustation formed by new skeletal growth may still be very firm. Where dead coral branches

come to rest on a colony, the colony isolates the clasts in cavities lined by clypeotheca. Such an adaptation may be important for protecting colonies from invasion by parasites and other benthos following disturbance events. In both cases, individual polyps may be abandoned and resorbed by the colony. This provides strong evidence of the very high level of colonial integration in *Acropora*.

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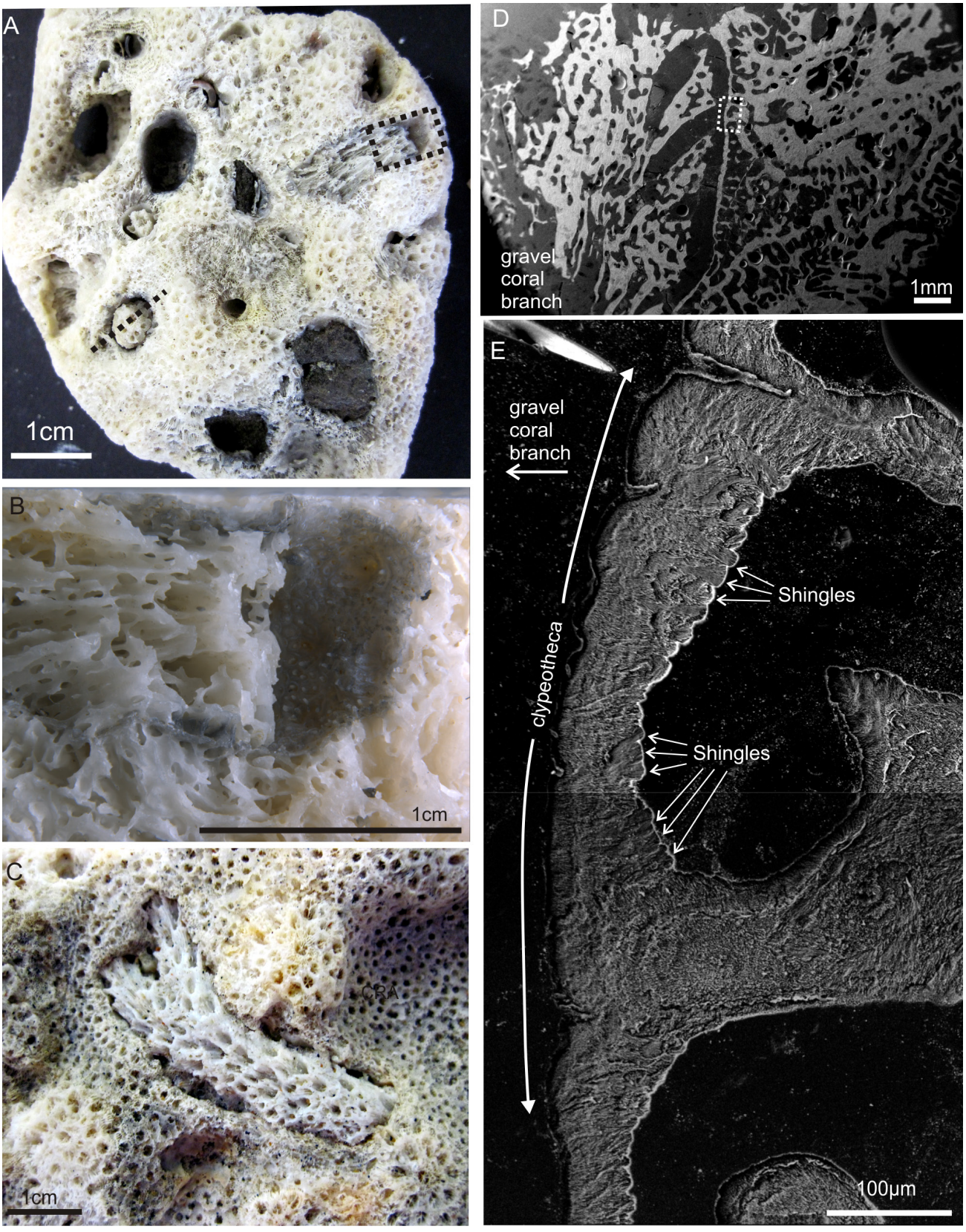

Plate 1. Photographs and SEM images of coral rubble washed up on a beach around the rocky headlands at Bargara, Queensland. A: *Acropora* fragment containing encased gravel fragments including coral branches and noncarbonate clasts. B: Photograph of a gravel clast consisting of an *Acropora* branch contained within the larger corallum. The branch was encased in clypeotheca (stained area). The location of this image is shown in Plate 1-A by the dashed box. C: Photograph of another example of sediment (*Acropora* branch) that was incorporated into the larger skeleton. Note how the skeleton is modified to wrap around the sediment grain. D: SEM image of a branch from Plate 1-A (sectioned vertically at the location of the dashed line) that is surrounded by clypeotheca. The embedded clast is on the left side. E: Higher magnification stitched image showing typical clypeotheca in cross section (location shown by dashed box in Plate 1-D). The walled structure has a shingle microstructure on the surface away from the grain (to the right) indicating clypeotheca growth away from the grain into the living coral tissue.

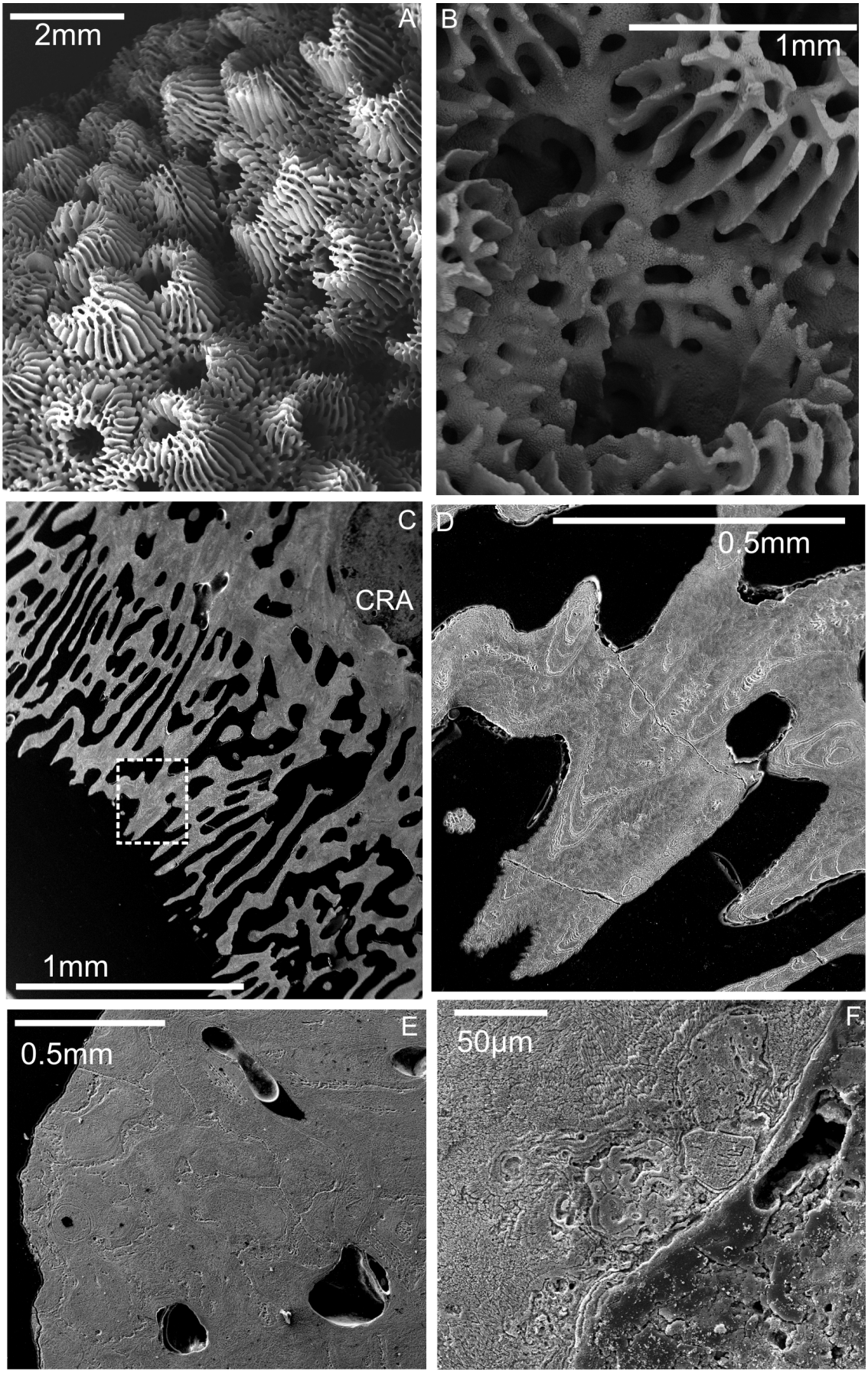

Plate 2. SEM images of external surfaces and polished and etched sections of junction between the two branches in Figure 1. A and B: External surfaces of the junction between the two branches showing complete skeletal fusion, but variability between corallite size, shape and orientation. C: Image of polished and etched section at the approximate junction between the branches illustrating an essentially seamless skeletal fusion. Note the difference in thickening of skeletal material prior to the fusion compared to post fusion skeletal deposition and the grain of coralline red algae (CRA) at the junction between the branches. D: Close-up view of Plate 2-C (dashed box) showing no skeletal demarcation at site of fusion between branches. E: Polished and etched section of part of original broken branch that has a large degree of skeletal thickening deposits. F: Polished and etched section of the contact between coral and encased sediment grains of mixed carbonate material showing the intricate contouring of the skeletal surface by what is presumably clypeotheca around and against the sediment grains.