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Colony Specificity in the Marine Bryozoan *Dakaria subovoidea*

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ABSTRACT—There is little information about colony specificity (allorecognition) in bryozoans. We examined the presence of colony specificity in the bryozoan *Dakaria subovoidea*, a common species on the Japanese coast. When two colonies made contact with each other at their growing edges, four types of reactions were observed: (1) overgrowth onto the opposing colony, (2) bilaminar erect growth, (3) nonfusion reaction, and (4) fusion reaction. When one of the growing edges was in poor condition, the first type of reaction was observed in both allogeneic and autogeneic combinations. The colony that was in poor condition was always overgrown with the good one. When both of the growing edges were in good condition, one of the other types of reactions was observed. In the second type of reaction, the colonies recognized the opposite colony as if it were a substratum and grew so as to form a standing wall. The third type of reaction exhibited the degeneration of zooids at the contact area. In this case, there were no fused zooids at the contact area. The fourth type of reaction was the fusion of colonies leading to the formation of contact border pores between zooids of the two colonies and sometimes to the formation of fused zooids at the contact area. The contact border pores exhibited unique morphology, which has not been reported previously. In this case, both colonies continued to grow harmoniously in direction in the same plane. These results suggest that colony specificity exists in *D. subovoidea*, as found in other sessile colonial marine organisms.

INTRODUCTION

In some colonial animals, when two colonies are brought into contact with each other, fusion or rejection occurs between them. This phenomenon of allogeneic recognition is called colony specificity. Studies on colony specificity lead to further understanding of the phylogeny of the immune system as it pertains to transplantation. For sessile colonial organisms, colony specificity may be thought to be necessary for survival in nature. Thus, this allorecognition system seems to have developed in many such animals.

In some compound ascidians, especially in the botryllids, many studies on colony specificity have been carried out [13, 19, 20, 23, 26]. In those animals, the complex systems of interaction between cells and humoral factors may play a role for recognition of self versus nonself [20]. Furthermore, it has been shown that colony specificity in botryllids is determined genetically by multiple alleles at a single locus, called fusibility alleles [19, 23, 26]. The nature of fusibility alleles resembles that of alleles at the major histocompatibility complex (MHC) of vertebrates [27].

In sponges [1, 2, 6, 7, 9–12, 24, 25] , hydrozoans [3, 8, 14, 15, 22], and corals [17, 18], studies on self-nonself recognition have been increasing. These studies have shown the presence of colony specificity or histocompatibility in these animals. In several species of both freshwater and marine sponges, there are reports describing the phenomenon of fusion or rejection among intraspecific colonies, but any genetic studies on colony specificity have never been performed.

Hauenschild [8] reported on a genetic system of histocompatibility in *Hydractinia* (a dioecious hydrozoan genus) somewhat similar to that of botryllids. There are only a few reports on histocompatibility in bryozoans [4, 5, 21], which are also sessile colonial organisms. Considering the taxonomic position of bryozoans, information about their histocompatibility is valuable to the study of phylogeny of transplantation immunity. In the present paper, we examine the presence of colony specificity in the cheilostome bryozoan *Dakaria subovoidea*, a common species on the Japanese coast.

MATERIALS AND METHODS

We used colonies of *Dakaria subovoidea* (Fig. 1). Most colonies were allowed to settle naturally on glass slides and cultured in boxes immersed in Nabeta Bay near Shimoda Marine Research Center, University of Tsukuba. Additional colonies were also collected from the seashore in Nabeta Bay.

When two colonies settled on a glass slide came into contact with each other at their growing edges, we observed the reaction processes under a binocular stereomicroscope. Here we called the combination of two different colonies, each of which is apparently derived from a single larva, allogeneic combination. Contact between growing edges of the same colony will be referred to as autogeneic combination, however, all of the contact of two colonies occurred in the way of colony growth. Colonies collected from the seashore were also used to help analyze the types of reactions between two colonies. Generally, the paired colonies (or parts of a colony) will be designated arbitrarily colony 1 and colony 2 in the following description (figure legends).

As most of animals were cultured in the Bay during study, we

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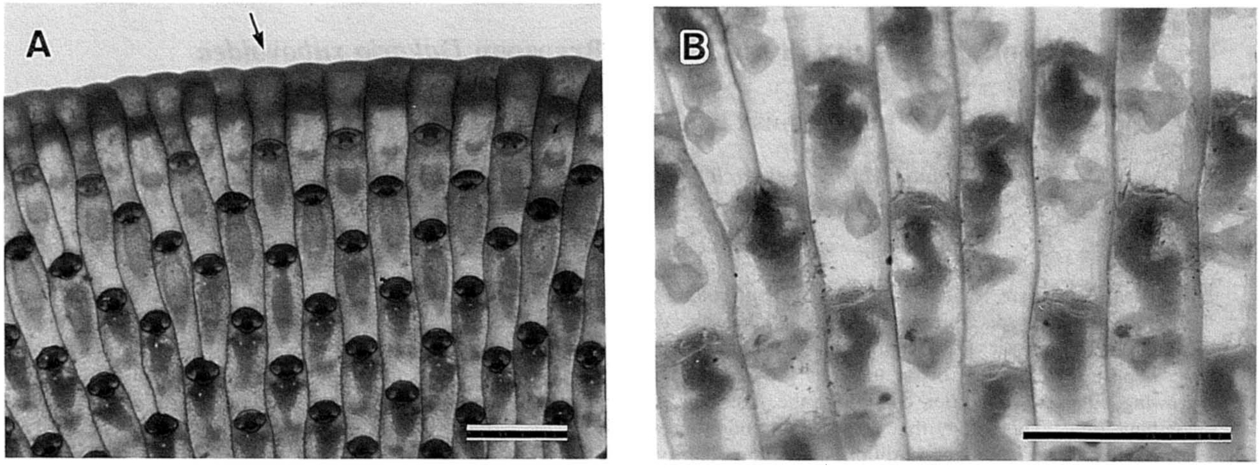

Fig. 1. A colony of *Dakaria subovoidea*. A: Ventral (frontal) view. B: Dorsal (basal) view. The arrow indicates the growing edge of a colony. Scale bars, 1 mm.

could not mention the reaction time obviously. We brought back the animals occasionally. The longest observation period was about three months.

The colonies were dissected and their interzooidal pores were observed under a binocular stereomicroscope. After the reaction between two contacting colonies had occurred, we also observed the contact border of two colonies.

RESULTS

Types of reactions

When two colonies came into contact with each other at their growing edges, four types of reactions were observed. The first type involved overgrowth onto the opposing colony (Fig. 2A). After contact between the growing edges of two colonies, the growing edge of one colony went onto the growing edge of the opposing colony. When one growing edge was in poor condition (poor condition involved the degeneration in the growing edge), this type of reaction was always observed in both allogeneic and autogeneic combinations. The colony that was in poor condition was always overgrown by the healthy one.

The second type of reaction resulted in bilaminar erect growth (Fig. 2B). Two colonies grew upward after making contact at their growing edges, and then the contact area became a bilaminar wall. Here, both colonies were in good condition and the growth rates of the colonies were almost

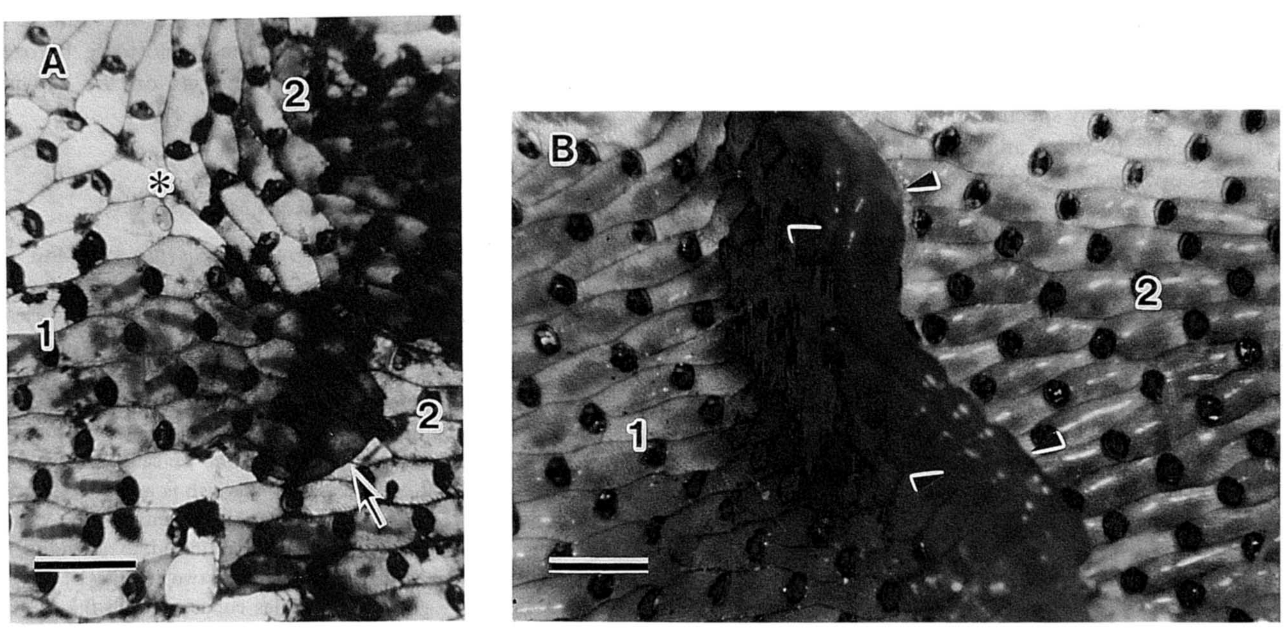

Fig. 2. Some types of reaction when two colonies make contact with each other at their growing edges. A: Colonies 1 and 2 were in contact with each other at their growing edges. In the area of the arrow, colony 1 overgrew colony 2 (overgrowth). In the area of the asterisk, both colony 1 and colony 2 changed their growth direction. Colony 2 grew from the right side of the figure and began to turn at the upper right of the figure. B: Colonies 1 and 2 were growing to make a wall with each other (arrowheads, bilaminar erect growth). Scale bars, 1 mm.

the same. They seemed to recognize each other as a substratum. This type of reaction was also observed in both allogeneic and autogeneic combinations.

The third type of reaction was nonfusion reaction (Fig. 3A). Both colonies stopped their growth at the contact area and changed their growth direction. At the contact area,

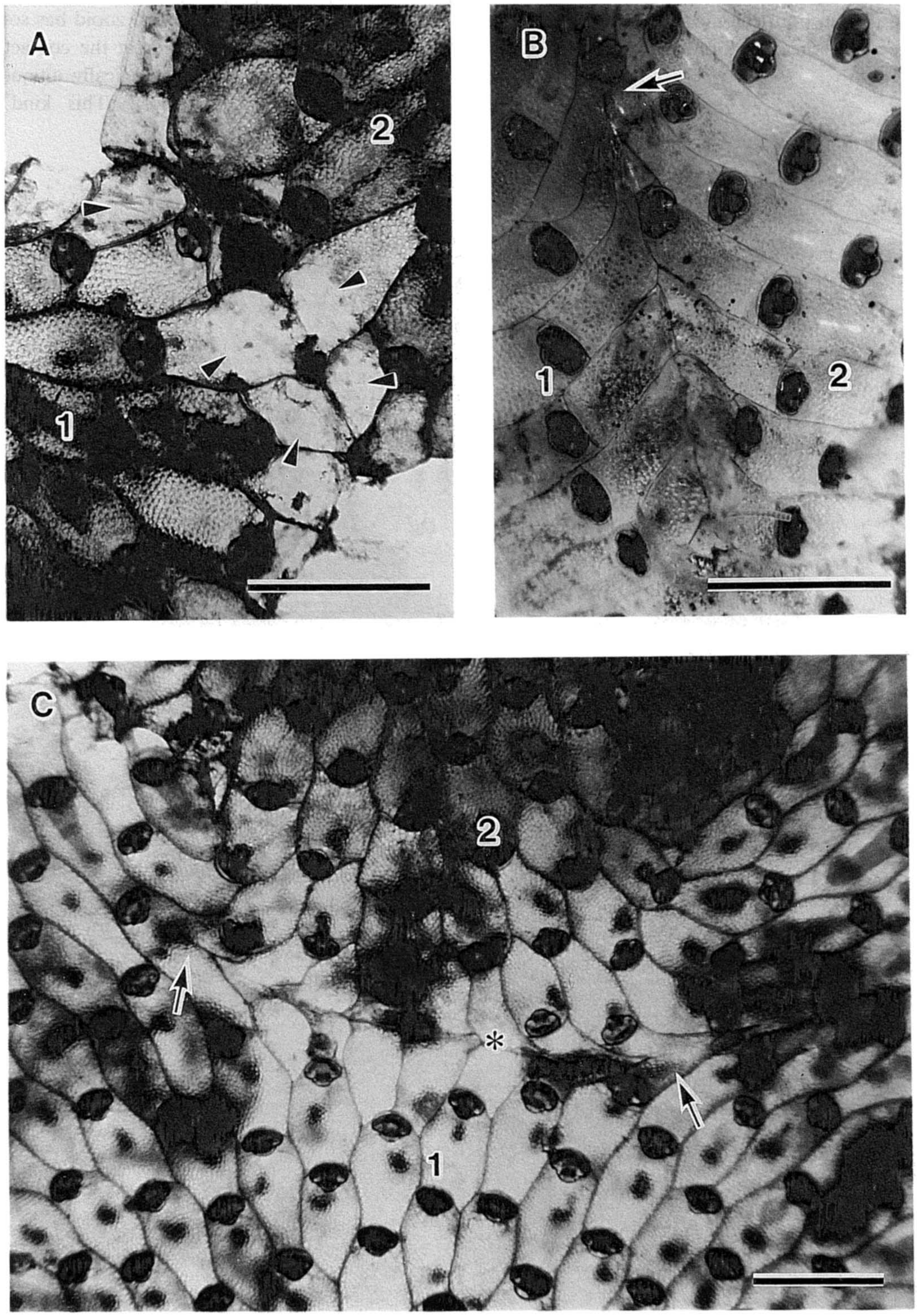

FIG. 3. Two types of reaction; nonfusion reaction and fusion reaction. A: Colonies 1 and 2 were in contact with each other at their growing edges and zooids of both colonies degenerated (arrowheads, nonfusion reaction). B: Colonies 1 and 2 were in contact with each other at their growing edges and changed their growth directions, and zooids of both colonies fused with each other (arrow, fusion reaction). C: Colonies 1 and 2 were in contact with each other at their growing edges (asterisk) and changed their growth directions, and zooids of both colonies fused with each other (arrows, fusion reaction). Scale bars, 1 mm.

degeneration of zooids occurred.

In the fourth type of reaction, fusion reaction, fused zooids (easily distinguishable by their special morphology) were formed by fusion of zooids at the contact area (Fig. 3B, C, arrows), without degeneration of zooids (Fig. 3C, asterisk). Following fusion, both colonies changed their growth direction and grew harmoniously forming a continuous sheet.

Pores on the interzooidal wall and contact border

In the second type of reaction (Fig. 4A), both colonies adhered together at their dorsal surfaces (adhesion surfaces). However, there was no sign of fusion or nonfusion between them. Contact border plates in the fusion case are shown in Figure 4B. Although a normal zooid has some pore plates in the transverse wall , zooids at the contact border in the fusion case formed a morphologically unique pore in their distal walls (Fig. 4B, arrows). This kind of pore was

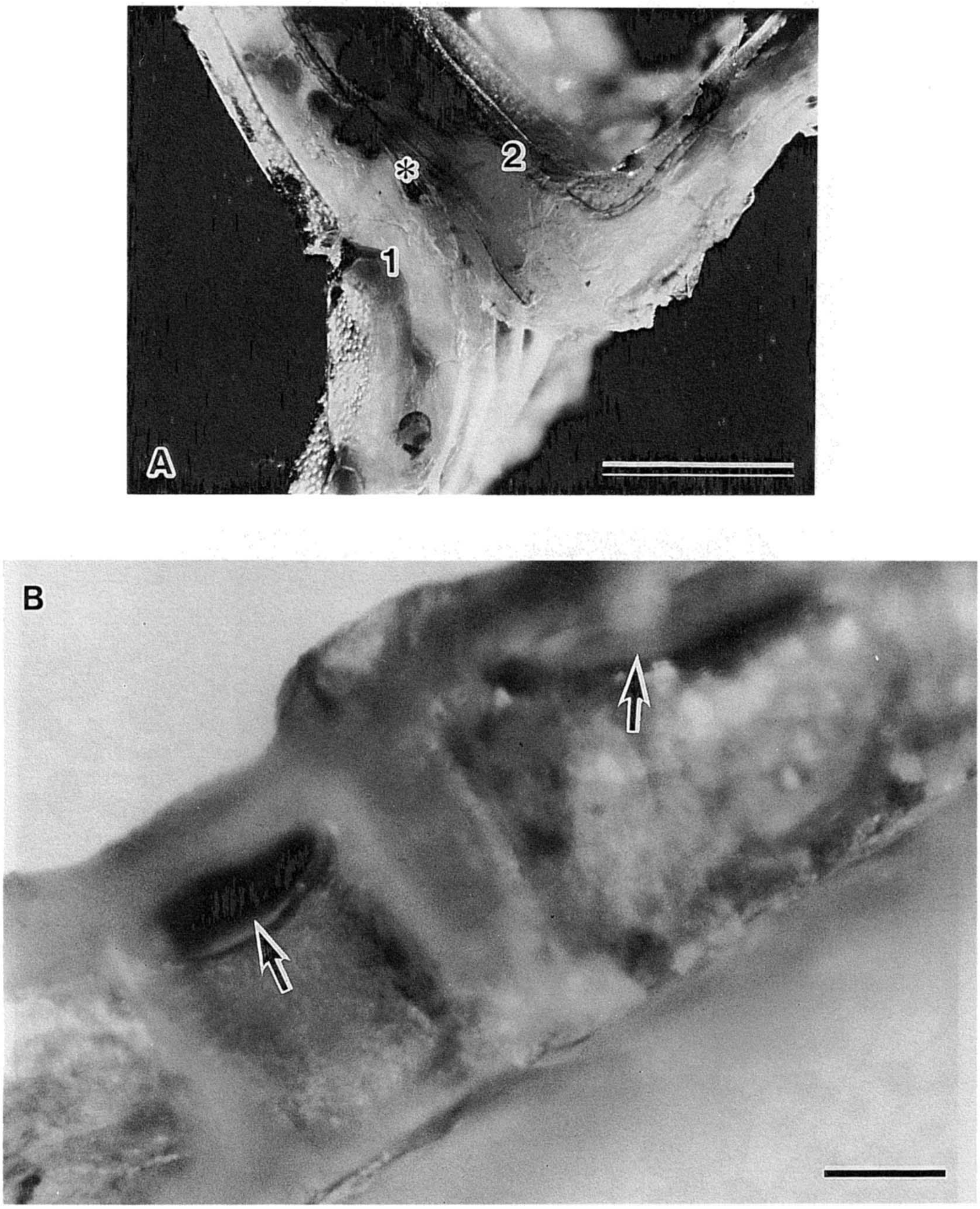

Fig. 4. Contact borders of two colonies. A: Colonies 1 and 2 which were cut perpendicularly to the contact border with a razor blade, are in the process of bilaminar erect growth. The asterisk indicates the contact border. Scale bar, 1 mm. B: Contact border plates in the fusion reaction. One of the fused colonies was removed from the other surgically and the distal (anterior) parts of two zooids of the remaining colony are shown. The arrows indicate unusual pores formed in the distal walls of the two zooids. The upper of the figure is ventral (frontal) of the colony. Scale bar, 100 μm.

observed only at the contact border in the fusion case.

DISCUSSION

When two colonies of *Dakaria subovoidea* made contact with each other at their growing edges, four types of reactions were observed (summarized in Fig. 5): overgrowth onto the opposing colony, bilaminar erect growth, nonfusion reaction, and fusion reaction. In the first type of reaction, there is no recognition of self or nonself because this type occurs between colonies of both allogeneic and autogeneic combinations. For the same reason, no recognition of self or nonself exists in the second type of reaction. However, recognition of self or nonself exists in the third and the fourth type of reactions. In the case of fusion reaction, we detected morphologically different zooids from ordinary ones that resulted from the fusion of two zooids at the contact border. In the case of nonfusion reaction, there was degeneration of zooids at the contact border, where a rejection reaction presumably occurred.

Chaney [4] reported histocompatibility in the cheilostome bryozoan *Thalamoporella californica*. In that species, fusion occurred only between zooids of the same colony that had grown apart or between sibling colonies. In *Dakaria subovoidea*, fusion occurred between zooids of the same colony and also between zooids of two different colonies, although we do not know whether the two different colonies were siblings or not. Furthermore, in this species, distinct rejections were observed between two different colonies. Therefore, our results strongly suggest that colony specificity exists in *D. subovoidea*.

In a few colonial ascidians, when two conspecific colonies are allowed to grow towards each other, they struggle each other for a substratum to overgrow [13]. The same reaction is seen even between subcolonies derived from the same colony [13, 16]. In these species, colony specificity is thought to be absent. That is, in colonial ascidians, overgrowth is seen only in the species lacking colony specificity. Although colony specificity may exist in *Dakaria subovoidea*, overgrowth was also seen in the struggle of the same or different colonies. There might be a certain difference in the feature of colony specificity between certain ascidian species and *D. subovoidea*.

There might be a certain relationship between allogeneic recognition, which involves the mechanism of genetical recognition of self or nonself, and the direction of colony

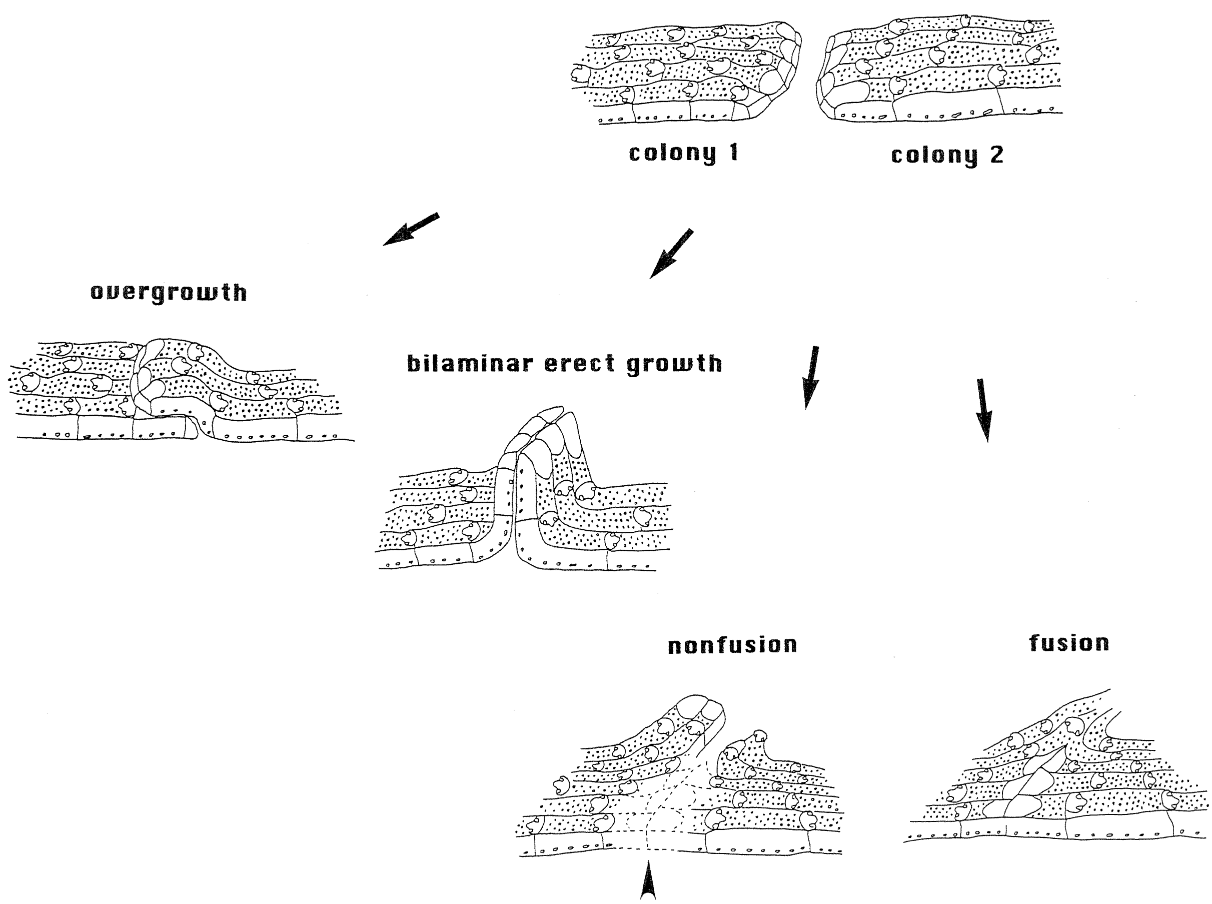

Fig. 5. Diagrammatic representation of four distinct types of reaction when two different colonies of *Dakaria subovoidea* make contact with each other at their growing edges. When colonies 1 and 2 are in contact with each other at their growing edges (top of figure), the result can be overgrowth, bilaminar erect growth, nonfusion, or fusion. The nonfusion reaction includes degeneration of zooids in the contact area (arrowhead), and the fusion reaction includes fusion of colonies without degeneration of zooids.

growth. In the first and the second types of reactions, both colonies grew three-dimensionally at the contact area (in the first type of reaction, the growing edge of one colony needed to grow vertically to overgrow the opposing colony). On the other hand, in the third or the fourth type of reaction, colony growth occurred only in two dimensions. A colony can grow both two- and three-dimensionally, however, only the case of two-dimensional colony growth showed the existence of allogeneic recognition. From these observations we have proposed two hypotheses concerning the mechanism of allogeneic recognition in the bryozoan *Dakaria subovoidea*: 1) Allogeneic recognition occurs only when two colonies grow two-dimensionally at the contact area, and three-dimensional colony growth shows no allogeneic recognition. That is to say, two-dimensional colony growth is essential for allogeneic recognition. 2) The absence of allogeneic recognition between two colonies leads to their three-dimensional growth, and the occurrence of allogeneic recognition leads to two-dimensional colony growth. In the latter hypothesis, the presence or absence of allogeneic recognition determines the form of colony growth. In any case, more studies are needed concerning the mechanism involved.

Chaney [4] was the first to examine the borders between sibling colonies of *Thalamoporella californica* and found fusion pore plates, resembling pore plates that exist in a colony. Shapiro [21] reported intercolony coordination of zooid behavior and a new class of pore plates in the cheilostome bryozoan *Membranipora membranacea*. Shapiro [21] reported "allocontact" pore plates between unrelated bryozoan colonies and suggested that the presence of morphological characteristics of intercolony rejection does not always imply a lack of physiological integration between colonies. Craig [5] also reported skeletal fusion in the cheilostome bryozoan *Fenestrulina* sp. derived from intraspecific contact. He reported the presence of pores in the skeletal walls between fused colonies and suggested that fused colonies are physiologically integrated. We found another type of contact border pore between fused colonies. This pore had a different morphology and had never been reported. It is unclear whether this new type of contact border pore implies a physiological integration between fused colonies. However, we think that the way of recognition of self versus nonself is somewhat different from that in *T. californica* or *M. membranacea* or *Fenestrulina* sp. and that the mode of intercolony communication is also different.

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