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The structure and the fate of the test cuticle during the fusion-nonfusion reaction in colonies of *Botryllus schlosseri* (Tunicata)

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RIASSUNTO

Osservazioni al ME mostrano che in colonie a contatto di *B. schlosseri* si realizza una fusione e successivamente una dissoluzione delle cuticole con conseguente confluenza delle tuniche. Questo si verifica tanto con colonie fra loro geneticamente compatibili che incompatibili.

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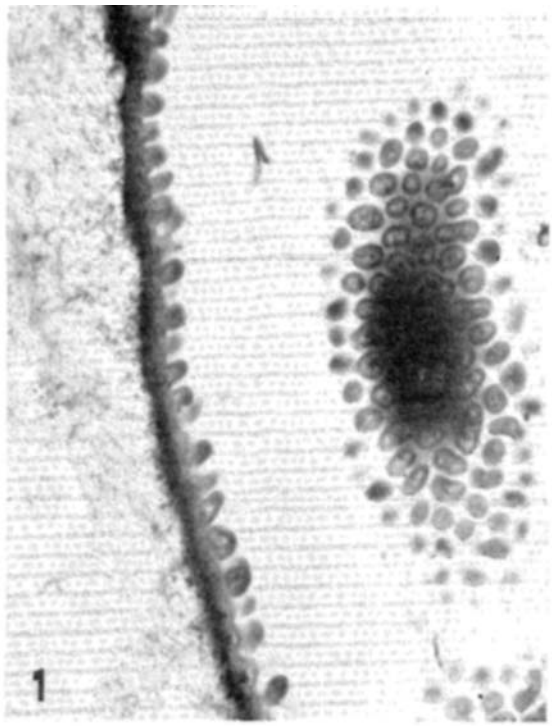
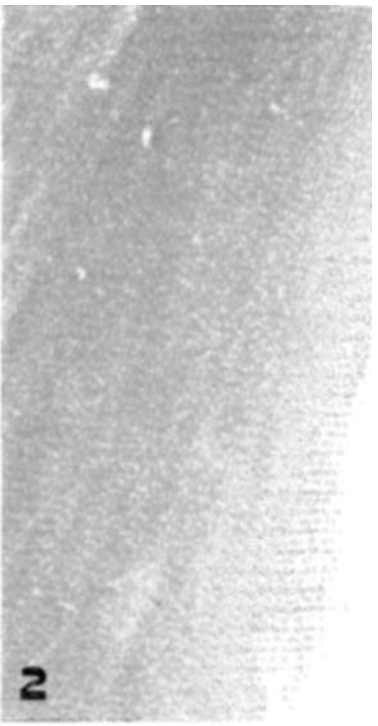
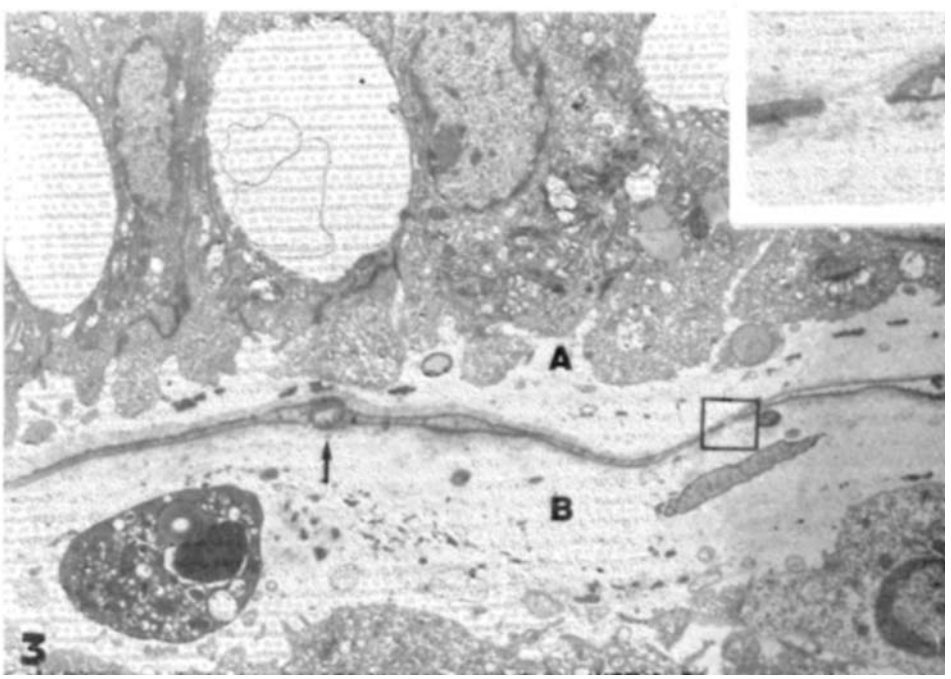
The colonies of *B. schlosseri* are composed of many zooids embedded in a common tunic. A network of blood vessels runs throughout the tunic and ends in numerous ampullae at the periphery of the colony. When colonies of *Botryllus* come into contact, they display either a " self- " or a " nonself- " recognition, in the form of a " fusion- " or a " nonfusion " reaction, respectively. The fusion reaction consists in the fusion of the tunics and the blood vessels so that a common circulation is established between the contacting colonies. The nonfusion reaction entails the formation of tissue necrotic spots in the area of contact. These phenomena are under a genetic control (OKA and WATANABE, 1957; SABBADIN, 1962; MUKAI and WATANABE, 1975). The processes and features of the nonfusion reaction in *B. primigenus* have been recently described and tentatively interpreted by TANAKA and WATANABE (1973) and TANAKA (1973).

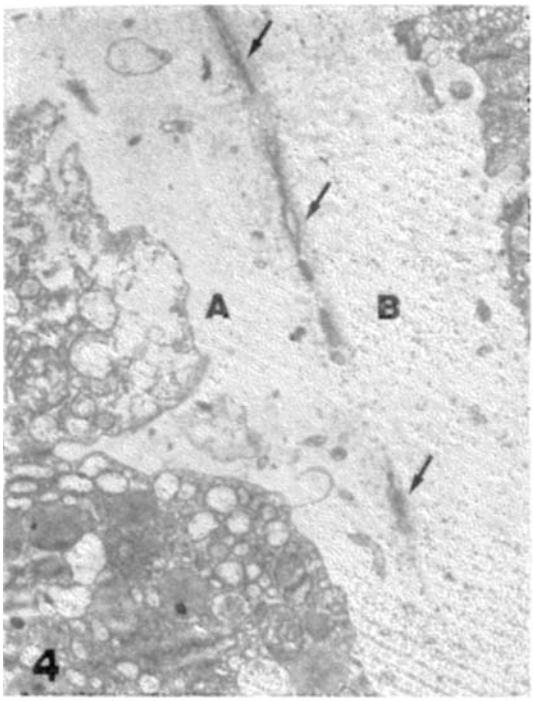
As a preliminary contribution to the problem, we have studied at the electron microscope (EM) the structures (test cuticle, tunic, test cells) which are involved in the fusion-nonfusion reaction in *B. schlosseri.* Pairs of colonies bred in laboratory and of known reciprocal compatibility or incompatibility were placed side by side, then fixed and embedded for EM at time intervals from the moment of contact. Areas of contact, selected with the aid of a dissecting microscope, were cut into thick sections for light microscopy or into thin sections for transmission electron microscopy (TEM) carried out with a Philips 300 EM. Isolated colonies, dried in a critical point apparatus, were observed at a scanning electron microscope (SEM).

At the EM the tunic turned out to consists of an amorphous ground substance crossed by variously oriented microfibrils (about 4-7 nm) running isolated or in bundles, and of scattered cells. The blood is constantly sequestered by an endothe-









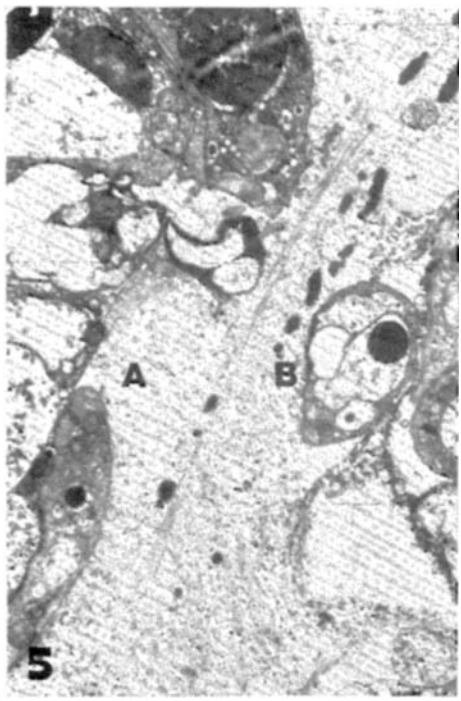


Fig. 1 — Test cuticle of *B. schlosseri* in longitudinal (at left) and tangential (at right) sections, showing the numerous papillae which arise from the electron dense layer. ×36,000.

Fig. 2 — Tunic of *B. schlosseri* seen at the SEM. A great number of small papillae (corresponding to those of figure 1) are distributed evenly on the test surface. ×9,500.

Fig. 3 — Contact and initial phase of dissolution of the cuticles of two (A and B) genetically incompatible colonies. A bacterium is entrapped between the confronting cuticles (arrow). The square delimits a region where the two test cuticles underwent dissolution. The same region is shown in the inset at higher magnification. Segments of the ampullar wall of the facing colonies are visible respectively above and below. ×5,000; inset ×25,000.

Fig. 4 — Cuticle dissolution and tunic fusion in the contact area of two (A and B) genetically compatible colonies. Residuals of test cuticle are still recognizable (arrows). ×9,000.

Fig. 5 — A still more advanced stage in the fusion of the tunics of two (A and B) genetically incompatible colonies. The test cuticles are completely dissolved and the original front of contact between the colonies is underlined by bundles of microfibrils. ×6,000.

lial wall both in the vessels and in the ampullae. At the periphery, the tunic shows an electron dense cuticle, which seems to represent a defensive barrier and which displays a great number of small papillae raised toward the outer surface. The papillae are recognizable both with TEM and SEM, as shown in Figs 1 and 2. The cuticle is of variable thickness and is constituted by a ground material more dense than that of the tunic and by densely packed microfibrils, mostly oriented normally to the surface.

In the contact area between the colonies, the confronting cuticles are compressed, loose their papillae and fuse into a single structure (Fig. 3). Later, this structure undergoes dissolution, which proceeds gradually starting from multiple sites (Fig. 4). At the end, the cuticle disappears, but the region where the cuticle dissolution occurred is still recognizable

by numerous bundles of microfibrils running along the original contact surface of the colonies (Fig. 5). Heterogeneous material (algae, bacteria, detritus, etc.) possibly entrapped at the beginning of the contact between the cuticles is finally phagocytized by the test cells or dispersed in the form of small electron dense masses. As a consequence of the cuticle dissolution, an actual continuity is established between the opposite tunics, which henceforth form a single unit. These phenomena occur equally whether the confronting colonies are genetically compatible or incompatible.

On the basis of the above observations, we are inclined to consider the dissolution of the confronting cuticles as a result of a remodelling of the contacting tunics rather than the effect of an enzymatic activity.

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