Differentiation and Commensalism in the Hydroid *Proboscidactyla flavicirrata*[1]

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Proboscidactyla IS A GENUS of two-tentacled hydroid that has been found only on tubes of sabellid polychaete worms. The polychaete species whose tubes support the hydroid vary in different parts of the world; in any particular locality only one or two polychaete species apparently support the hydroid. In the Puget Sound area, only one species of this hydroid, *Proboscidactyla flavicirrata* (Fig. 1), has been reported, and it is found only on the tubes of the polychaetes *Schizobranchia insignis* and *Pseudopotamilla ocellata.*

A mature colony of *P. flavicirrata* forms a dense ring around the open end of its host's tube. Only the gastrozooids actually come into contact with the radioles (tentacles) of the worm, however. The gonozooids of the hydroid form a concentric ring just below that of the gastrozooids. Aberrant gonozooids are sometimes found at scattered locations on the worm tube, but gastrozooids are restricted to the rim of the tube (Campbell, 1968 *b*). In the absence of the worm (*i.e.,* if the worm is removed from its intact tube or if the tip of the tube with its attendant colony is excised and maintained thereafter apart from the worm) the hydroid gastrozooids dedifferentiate and are resorbed. Upon reintroduction of a host worm, dedifferentiated colonies will redifferentiate. Aspects of this peculiar morphogenetic behavior are examined. I would like to thank Dr. A. T. Newberry for his help in the preparation of this article.

METHODS

Sabellid worms of the two host species, and also of *Eudistylia vancouveri* and one other similar, but unidentified, polychaete were taken from their tubes and put in glass tubes (Fig. 2). These tubes were anchored in paraffin and submerged in running seawater. About 90 percent of the worms adapted readily to these tubes, which then served as easily accessible substrates upon which *Proboscidactyla flavicirrata* could be planted. All experiments were done in seawater at 13° C.

To plant a colony of *P. flavicirrata* on one of these glass tubes, the distal 15 mm of a sabellid tube supporting such a colony was excised, split longitudinally, wrapped around the end of the glass tube (rather in the fashion of a cigar band), and secured with cotton thread (*arrow,* Fig. 2).

As controls, hydroid colonies were thus planted on the ends of glass tubes containing either of the normal host polychaete species.

In the experiments, hydroid colonies were placed either (*a*) on empty glass tubes, (*b*) on tubes that contained a sabellid worm of a nonhost species, or (*c*) on paper tubes in which the host species was separated from direct contact with the hydroid by a single layer of filter paper (Whatman no. 1) or by a Millipore filter (pore size, 0.2 μ).

On one occasion stoppered Erlenmeyer flasks were provided with incurrent and excurrent tubes to the tips of which colonies were fitted. A slow flow of seawater (simulating the feeding current normally maintained by the worm) passed through the flasks via these tubes.

A few hydroid colonies were mounted on the tips of glass tubes through which a large air bubble was passed every 15 seconds. This provided the gastrozooids with a mechanical disturbance similar to that of a worm emerging at the end of the tube.

RESULTS

In the controls, functional and differentiated colonies remained alive and active for the duration of these experiments.

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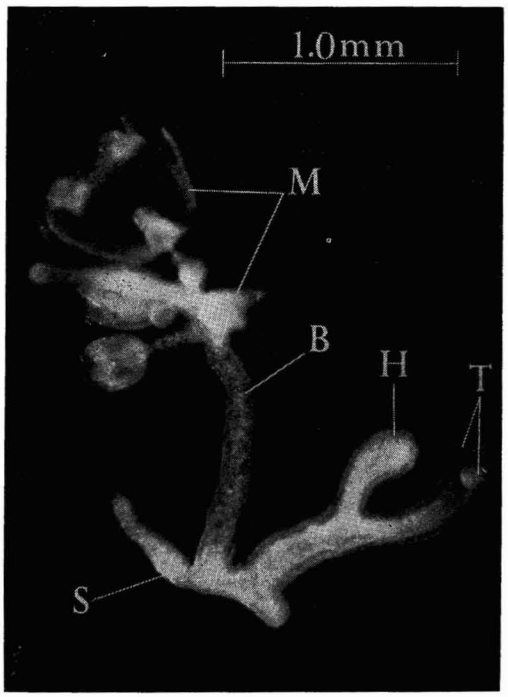

FIG. 1. Gastrozooid and gonozooid of *Proboscidactyla flavicirrata*. *M*, Medusae and *B*, blastostyle of the gonozooid; *T*, tentacles and *H*, hypostome of the gastrozooid; and *S*, stolon.

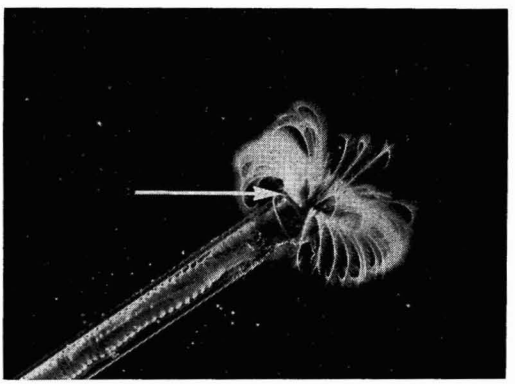

FIG. 2. The sabellid worm *Pseudopotamilla ocellata* in a glass tube; arrow indicates the position of a transplanted colony of *Proboscidactyla flavicirrata*.

Colonies planted on empty glass tubes invariably dedifferentiated: within 24 hours the gastrozooids moved off of the excised sabellid tubes and began to migrate, via stolonic growth, upon the glass tubes. After 48 hours the gastrozooids began to disappear, and by 72 hours only creeping stolons remained. These stolons continued to migrate upon the glass for several days, frequently branching and anastomosing.

The gonozooids of the colonies on empty tubes (in contrast to the gastrozooids of such colonies) moved little but remained differentiated and active for weeks after observable feeding by gastrozooids had ceased.

These degenerate colonies could be made to redifferentiate gastrozooids (up to 10 days after they had disappeared) merely by placing a worm of either of the two host species into the hitherto empty glass tube. Wherever a stolon contacted the worm (*i.e.*, at the rim of the tube) a gastrozooid developed. This regeneration usually was detectable 3 to 4 days after a worm was introduced; by the seventh day the gastrozooids had proliferated and reestablished themselves around the rim of the tube.

Colonies planted on glass tubes inhabited by host polychaete species, but separated from these worms by paper or Millipore filters, migrated and dedifferentiated as if on empty tubes. It appears that at least occasional direct contact with the body of the worm is necessary to maintain a stable, differentiated hydroid colony.

Colonies planted on the incurrent and excurrent tubes of the Erlenmeyer flasks, and those planted on tubes through which air was bubbled, showed no marked difference from the behavior of colonies on undisturbed empty glass tubes; gastrozooids were resorbed, and migrating stolons moved out onto the tubes.

Sabellid worms other than the two normal host species would not support a differentiated colony, nor would they induce redifferentiation in a degenerate colony.

DISCUSSION

Proboscidactyla flavicirrata exhibits some striking parallels to the situation Braverman (1960) found in the colonies of the hydroid *Podocoryne carnea*, a species with a differentiating system that requires, for the existence of part of its hydranth constituency, the presence of another organism. In the case of *Podocoryne carnea* that other organism is a hermit crab; for *Proboscidactyla flavicirrata* it is a sabellid worm. In the absence of a crab, *Podocoryne carnea* loses its spiral hydranths (dactylozooids), while its

feeding gastrozooids and gonozooids remain active, supporting the colony. However, the loss of gastrozooids in degenerating *Proboscidactyla flavicirrata* colonies deprives the colonies of any means of feeding. While *P. flavicirrata* gonozooids may remain active for almost 4 weeks after the gastrozooids of the colony have disappeared, they most probably derive nutrients from the resorption of other parts of the colony. In the persistent absence of the host worm, however, the entire hydroid colony eventually disappears. Unlike *Podocoryne carnea,* then, *Proboscidactyla flavicirrata* appears to require a host to maintain itself as a viable colony; it is an obligatory commensal.

The gastrozooid of *P. flavicirrata,* once reduced to merely a migrating stolon, differentiates only upon contact with a worm of the "right" species. The mechanism whereby this is accomplished is as yet undetermined. Mechanical stimuli such as currents or bubbles are apparently not sufficient morphogenetic inducement. Chemical stimulation probably plays an important role. But if an inducer is involved, it is apparently an indiffusable one bound to the surface of the worm. The abnormal zooids described by Uchida and Okuda (1941) encourage this hypothesis. They reported *Proboscidactyla* zooids with as many as seven tentacles, all asymmetrically located on the side of the zooids closest to the worm, suggesting that actual contact with the worm fosters the differentiation of tentacular tissue. Campbell (1968 *a*) has also shown that contact with the worm is required to induce metamorphosis of the planula of *P. flavicirrata.*

SUMMARY

In Puget Sound the colonial hydroid *Proboscidactyla flavicirrata* is found on the tubes of two species of sabellid polychaetes, *Schizobranchia insignis* and *Pseudopotamilla ocellata.* This two-tentacled hydroid appears to be an obligate commensal. Only in the presence of one or the other species of worm does a colony maintain differentiated gastrozooids. Mechanical stimuli and water currents similar to those created by host worms are unable by themselves to maintain a differentiated colony. Direct contact with the worm is demonstrably necessary to sustain a fully differentiated colony. Nondiffusable chemical inducers are indicated.

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