# Host Specificity, Settling, and Metamorphosis of the Two-tentacled Hydroid *Proboscidactyla flavicirrata*

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THE COLONIAL HYDROID *Proboscidactyla* has been found only on the leathery tubes of marine sabellid worms (Uchida and Okuda, 1941:433; Hand, 1954; Brinckmann and Vannucci, 1965: 367). Nothing is known about the means by which this specific commensal association arises. In this paper I present observations on planula settling and metamorphosis, which indicate that larvae are caught in the tentacles of the sabellid worm and transferred to the rim of its tube.

## METHODS AND MATERIALS

Medusae of *P. flavicirrata* (Brandt) were dredged in East Sound, Orcas Island, Washington at a depth of 15 meters, on August 16–18, 1964. Most specimens contained ripe gametes. Medusae kept in glass dishes without feeding shed and fertilized many eggs for three or four days at about 5 AM. Developing larvae were kept in sea water at 17°C, changed every 24 hours.

To test the influence of substrate on settling, five glass dishes of sea water were prepared with the following: (1) 3 sabellid worm tubes from which the worms had been removed; (2) 3 tubes with worms; (3) 3 worms in glass tubes; (4) some perisarc of obelia, and (5) sea water only. About 50 one-week-old planulae were pipetted into each dish. Observations were made during the following 8 hours, and at intervals over the next 8 days.

Studies on metamorphosis were made on planulae which had settled on a tube (see below), and which were transferred to a microscope slide where they completed metamorphosis.

## OBSERVATIONS

Planula settling and metamorphosis took place only on tubes containing sabellid worms, regardless of whether the tubes were natural or artificial. No settling occurred on tubes without worms, or on other surfaces.

Several hundred planulae were kept in clear glass dishes for 18 days. During this period none metamorphosed or settled.

Observations on the behavior of the planulae and sabellid worms during the settling process indicated the role of the worm. Initiation of the settling process began when a planula was caught in the ciliary currents of the sabellid's radioles (tentacles). In the vicinity of the radioles these currents are much swifter than the planula's swimming movement; therefore, the planula must be considered as a passive participant in initiating this association. However, when the planula does contact the worm, nematocysts discharge and anchor the planula (Fig. 1). The physical attachment is clearly indicated when a single planula binds to several adjacent pinnules, clumping them.

The next stage in the settling process involves the transfer of the planulae from the radioles to the rim of the tube. This is mediated through retractions of the worm into its tube, which

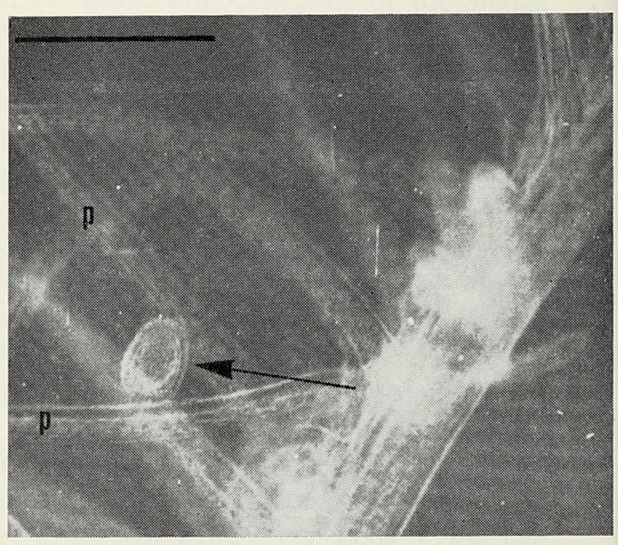


FIG. 1. *Proboscidatyla flavicirrata.* Planula (*arrow*) attached to two pinnules (*p*) of a sabellid worm. Printed from 16 mm film. Scale: 0.5 mm.

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scrape the planulae off onto the rim. This transfer was also made possible by a stickiness of the planulae, which developed after the contact with the worm. At least 20 minutes elapsed between attachment to the pinnules and transfer to the tube rim, and most retractions of the worm were unsuccessful in achieving this transfer. Probably the elapsed time represents the time required for secretion of an adhesive material.

Accidental contacts between the swimming planulae and the worm tube were refractile, and had no effect on the activity of the planulae. However, after a planula had been transferred normally to the tube it would undergo metamorphosis even if removed from the tube.

The visible onset of metamorphosis occurs about 6 hours after settling. Figure 2 shows the mature planula before attachment. Nematocysts are more abundant at the anterior end. The planula is characteristically spindle shaped. Figure 3 shows a planula several hours after attachment, as the first visible signs of metamorphosis become apparent. There is a loss of refractile quality of the endoderm at the future oral pole. This reflects the formation of a well delineated high columnar epithelium which is characteristic of the hypostome of the adult polyp. Also at this time the mouth has begun to form. The animal in Figure 4 shows a protrusion in the body wall below the hypostomal region. This evagination becomes a single tentacle, which elongates rapidly (Fig. 5).

Within several hours another protrusion is seen developing on the body wall (Fig. 5). It always develops after the tentacle has been initiated, and usually after the tentacle has elongated. It is always on the same side of the body as the tentacle, and is generally situated in the middle of the body. This protuberance develops into the "foot" (Campbell, 1967) which may be homologous with the stolon tip in other hydroids. The segment of polyp posterior to the foot adheres to the substratum, secretes a very fine perisarc, and becomes the stolon. The foot marks the anterior extent of the attachment to the substratum, and the distal portion of the polyp remains erect from the substratum.

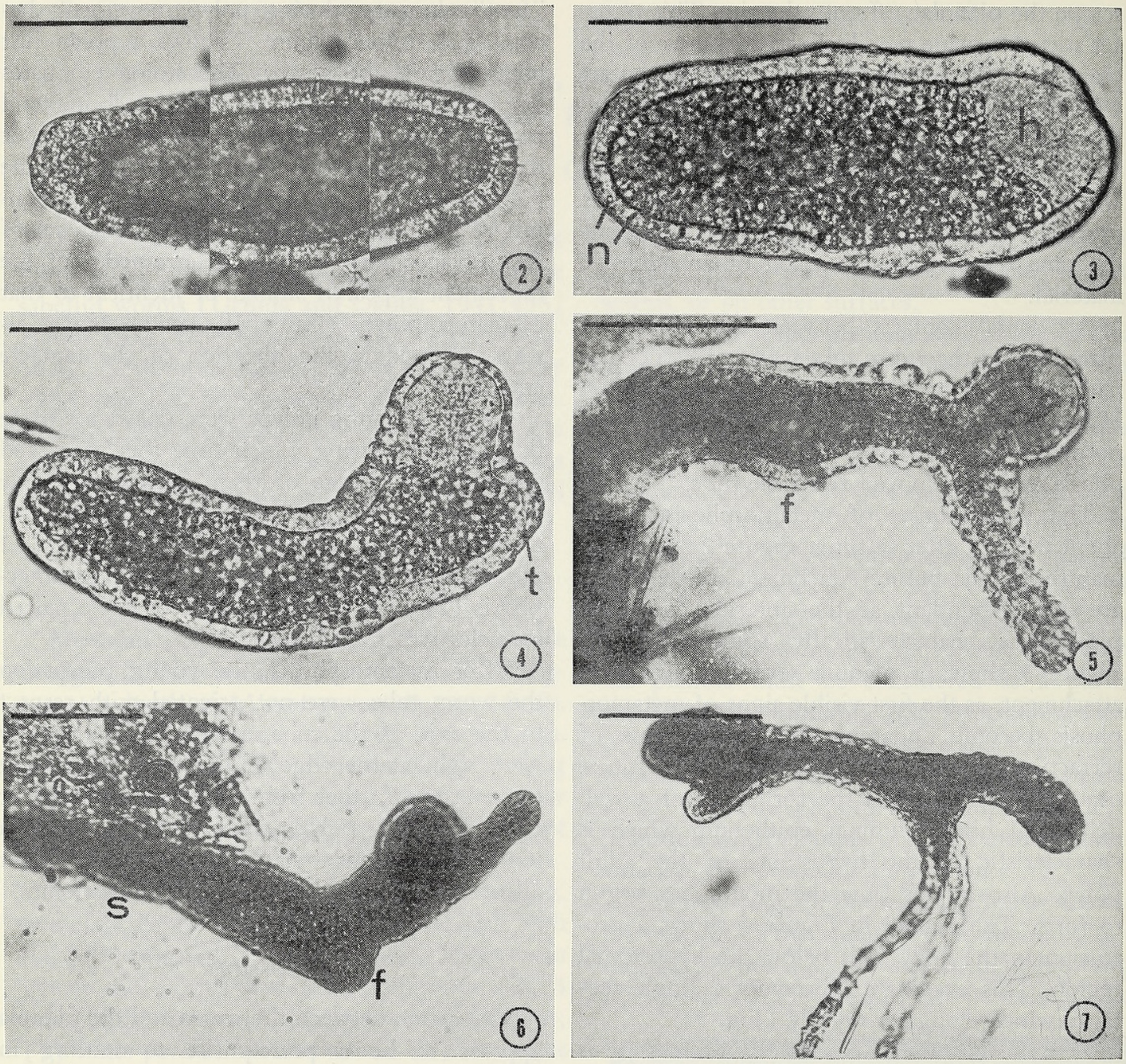
During the next 24 hours, the observed, single-tentacled polyps began to glide along the substratum. The polyp column posterior to the "foot" elongates during polyp movement, becoming a stolon. Figure 6 shows a polyp just beginning its movement. The stolon elongates not by terminal extension, for the aboral end remains fixed with respect to the substratum (or it may actually move in the direction of the polyp). Elongation is apparently due to stretching by the advancing polyp. The mechanism of this advancement was not determined, but the movement appeared similar or identical to that of mature polyps (Campbell, 1967). It was always oriented in the direction of the tentacle and foot.

About 30 young polyps were raised for more than a week during which time they were fed sabellid eggs. None of them during this time developed a second tentacle. Of about 250 metamorphosing polyps studied, however, 2 possessed two tentacles just after metamorphosis (Fig. 7). The formation of these paired tentacles was not observed.

After metamorphosis, the young polyps on the worm tube were not oriented with respect to the axis of the tube, although the majority were right at the edge of the tube. Movement carried some further from the rim. The behavior of these young polyps was not observed for a longer time, and so it is not known whether all of them were capable of forming colonies.

## DISCUSSION

Interaction between the worm and the planula appears to be a prerequisite to settling in *Proboscidactyla flavicirrata.* Since planulae deprived of contact with worms did not undergo metamorphosis during the more than 2 weeks of observation, the contact itself is probably a stimulus for metamorphosis. It is possible that nematocyst discharge is a direct part of this stimulation. These conclusions explain how the close association between the hydroid colony and worm tube, and the polyp's initial position on the rim of the tube, may arise. It would be interesting to know if other species of worms or other animals, which must also draw *Proboscidactyla* planulae into contact with themselves, similarly stimulate the planulae to settle and undergo metamorphosis. If there were a species specificity involved, this intricate interaction could present an explanation of the specificity




FIGS. 2–7. *Proboscidactyla flavicirrata.* FIG. 2. Mature planula; scale: 0.1 mm. FIG. 3. Planula metamorphosis, 3 hours after contact with sabellid worm; oral pole is to the *right;* the hypostomal endoderm (*h*) has differentiated; *n,* nematocyst; scale: 0.1 mm. FIG. 4. Planula metamorphosis, 4.5 hours after contact with worm; *t,* tentacle rudiment; scale: 0.1 mm. FIG. 5. Metamorphosis nearly complete, 7 hours after contact with worm; *f,* rudiment of "foot"; scale: 0.1 mm. FIG. 6. Beginning of migration; *f,* "foot"; tissue to the left of foot represents stolon (*s*), which in this case has stretched to about 3 times its original length; 12 hours after contact with worm; scale: 0.1 mm. FIG. 7. Newly metamorphosed polyp possessing two tentacles; small protrusion at *left* is the "foot"; scale: 0.1 mm.

of the *Proboscidactyla* colony for the sabellid worm tubes.

The initial attraction of the planula to the worm site, however, appears to be quite nonspecific, involving water currents set up by the branchial cilia. In this respect the commensal specificity resembles that of *Hydractinia* for shells inhabited by hermit crabs: Schijfsma (1935:290–302) and Cazaux (1958:2195), showed that there is no attraction of the *Hydractinia* planula by the hermit crab, but rather that settling is apparently stimulated by particular conditions of waterflow across a hard substratum, conditions which are frequently presented by a hermit crab shell in its habitat of swiftly moving water.