

Bud Movement in Hydra

Abstract. Buds in *Hydra viridis* moved upward in inverted budding regions although normally buds move downward. Their direction was not influenced by the orientation of the distal part of the bud. Bud movement, it would seem, proceeds independently of distal growth and basal attrition in the parent.

Invaginations and outpocketings are universally associated with morphogenesis of tissues. Budding in *Hydra* is reminiscent of these processes and has one feature that is not easily studied elsewhere: that is, normally buds are seen to move as they develop (1). Although the consequences of this movement are unknown, my results indicate that it is directed and active.

The bud's movement has been interpreted as an effect of the parent animal's growing distally and undergoing attrition basally (2). In this view, the bud only seems to move downward: the parent's base hypothetically moves toward it, while the parent's distal end grows away from it. Were this the case, buds would continue to move downward even if the polarity of the budding region were reversed. I have found, however, that buds move upward in animals in which the budding regions were inverted by grafting.

Animals were raised at room temperature in about 10 ml of artificial pond water in small petri dishes and were fed nauplii of *Artemia* sp.; the medium was changed daily. Green and white *Hydra viridis* were bisected above the position of the youngest buds, and distal green halves were grafted to proximal white halves. After several days, the border of the green and white halves of each animal had moved downward, and buds began to form as outpocketings in the green portion just above the border. Each of 12 animals with such buds was bisected above the bud and cut through a second time in the white region at about the lowest point occupied by buds prior to detaching. The excised piece, comprising the entire budding region, was turned upside down and reinserted into the parent by grafting (Fig. 1).

During the next 2 to 3 days the buds on 11 of these animals gradually shifted their attachments to the par-

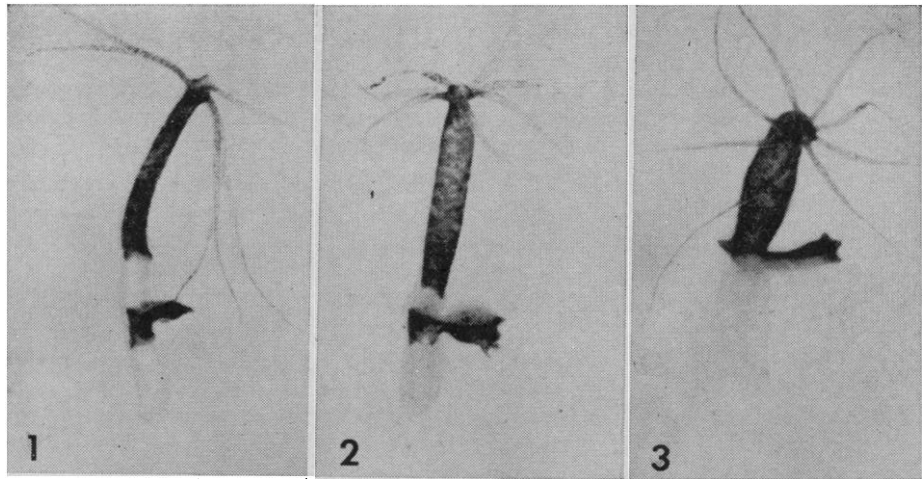


Fig. 1. Hydra in which the polarity of the budding region had been reversed about 1 hour previously. The developing bud is green and is confluent with the green section of the parental budding region. Fig. 2. Same hydra a day later. The bud has moved upward partially onto the white section of the inverted budding region and has taken on the color of this section. The reduced size of the white section of the budding region is probably due in part to the movement of parental cells onto the bud. Fig. 3. Hydra in which the bud on the right is developing over the border of green and white tissue.

ents from entirely within the green sections (Fig. 1) to positions overlapping the green and white sections (Fig. 2) and often to the white distal sections of the inverted budding regions. At the same time, the color of the parental tissue in contact with the buds was influencing the color acquired by the forming buds, presumably because of the movement of parental cells onto the buds (3-5). Thus, while the buds were initially all green (Fig. 1), they were later both green and white

(Fig. 2). As many as four buds subsequently initiated in the proximal green sections of the inverted budding regions were also seen to move distally. Later, buds were seen to move downward. The bud on the 12th animal did not seem to move.

As a control on the possibility that the buds moved upward as a result of wounding and grafting rather than of the inversion of the budding region, this region was cut out of three animals and reinserted without hav-

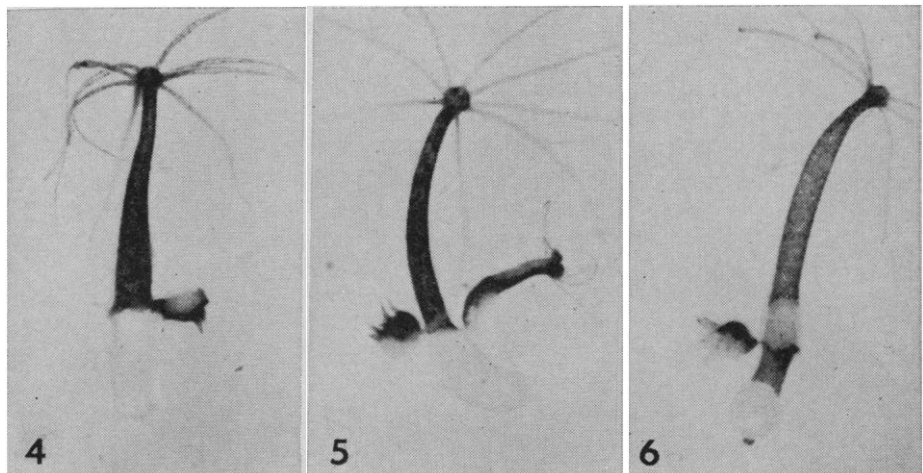


Fig. 4. Same hydra 3 hours after having had the orientation of the right bud reversed. The white portion of the bud is now seen facing upward. Fig. 5. Same hydra 2 days after grafting. The right bud acquired additional green and white areas after grafting. The bud has moved downward; its base is confluent with the white part of the parental budding region and is entirely white. The bud on the left of Figs. 3-5 is seen to have developed and, likewise, to have moved downward. This is the normal route for a bud. Fig. 6. The bud on the left of this hydra has the same orientation, with respect to its upper and lower surfaces, as it had prior to grafting 1 day earlier, but the polarity of the budding region has been reversed. The bud moved upward.

ing its polarity reversed. In one case, the bud did not move from the green, but in the other two cases the buds moved downward as usual onto the white part of the budding region.

Another possible explanation for the observed reversal in the direction of bud movement in inverted budding regions is that it was caused by an alteration in the orientation of the bud with respect to the long axis of the parent. The upper surface of the bud (facing the distal end of the parent) had, of course, become the lower surface (facing the basal end of the parent) at the same time that the polarity of the budding region was reversed. In order to determine whether reversing the upper and lower surfaces of the bud influenced the direction of the bud's movement, buds were cut off four parents, rotated 180° around their long axes, and grafted back at the points from which they had been removed. This was done with buds that had begun to form over the border of the green and white portions of the parent animals (Fig. 3). In the resulting grafts (Fig. 4), the white portion of a bud was more or less in contact with the green part of the parental budding region, and the green portion of a bud was in contact with part of the white region of the parental budding region.

In each case the area of contact of rotated buds and the distal green part of the budding region was reduced during the next 2 days, often to the point where the buds came in contact exclusively with the proximal white part of the budding region (Fig. 5). The color of the parent at points confluent with rotated buds was passed onto the buds giving rise to a checker-board appearance (Fig. 5); the distal portion of the bud was white and green, and the proximal portion was green and white.

Although these results excluded the possibility that the orientation of the upper and lower surfaces of the grafted portion of the buds influenced downward movement, it was still conceivable that the orientation of the bud influenced the upward movement of buds in animals in which the budding region had been inverted. To test this possibility, I reversed the orientation of a bud on each of two animals as above, but, when the bud had healed in place (about 1 hour later), the budding region of each parent was cut out, inverted, and reinserted into the parent. In these animals the polarity of

the budding region was opposite that of the remainder of the parent, but the bud was oriented as it had been originally. These buds moved toward the distal white section of the parental budding region (Fig. 6), as had the other buds on inverted budding regions (Figs. 1 and 2). Evidently the direction of bud movement is not influenced by the orientation of the grafted portion of buds irrespective of whether the buds are moving up or down.

The view that the movement of buds depends on growth and attrition at opposite ends of the parent is not supported by the present results. This view can also be challenged on the basis of Campbell's evidence that mitotic figures are present throughout the length of the hydra's body (3). This suggests that the distal end of the parent does not grow away from the buds. Furthermore, reports (3, 6) now indicate that the cell layers of the parental body wall can move downward at different rates. Since these layers in the parent are continuous with the corresponding layers of the developing bud, it is hard to imagine a mechanism through which the cell layers of the parent, moving at different rates, could move the bud as a unit at a single rate. Finally, buds generally move downward faster than the inner cell layer in the parent's budding region (4). Had the bud's movement depended on the movement of the parental body wall, the rate of the bud movement would scarcely have exceeded that of the inner cell layer of the parental body wall.

Another possibility not supported by my results is that the orientation of the upper and lower surfaces of the distal part of the bud influences the direction of its movement. The proximal part of the bud, which grows out of the parent after the distal part (4, 5), moves either upward or downward depending on whether the polarity of the budding region has or has not been reversed.

The only alternative explanation remaining is that something inherent in the polarity of the budding region governs the direction in which buds move. This influence is stable enough to withstand the grafting procedure and survives for several days with the polarity of the budding region reversed.

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References and Notes

1. W. Goetsch, *Arch. Entwicklungsmech.* **117**, 211 (1929).
2. P. Brien and M. Reniers-Decoen, *Bull. Biol. France Belg.* **83**, 293 (1949).
3. R. D. Campbell, *Science* **148**, 1231 (1965); ———, thesis, The Rockefeller Institute (1965).
4. S. Shostak and D. R. Kankel, *Devel. Biol.*, in press.
5. J. Kanajew, *Arch. Entwicklungsmech.* **122**, 736 (1930).
6. S. Shostak, N. G. Patel, A. L. Burnett, *Devel. Biol.* **12**, 434 (1965).
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Hampea Schlecht.: Possible Primary Host of the Cotton Boll Weevil

Abstract. *The boll weevil severely infests buds in natural stands of Hampea sp. in Veracruz, Mexico. The geography and ecology of these trees suggest that they may be the long-sought primary host of the boll weevil.*

The boll weevil (*Anthonomus grandis* Boh.) was described in 1843 from an insect collected in 1841 on an unidentified host plant in the state of Veracruz, Mexico. Many years later (1880) the weevil was reported to occur on cotton (*Gossypium hirsutum* L.), but it was not recognized as a serious pest of cultivated cotton until around the turn of the century. The subsequent history of its migration from Mexico to other cotton-growing areas is well known (1).

Its earlier history, however, has remained a mystery, the elements of which are as follows. The boll weevil has a narrow range of hosts, as it thrives only on plants of the genus *Gossypium* L. (the cottons) and, to a limited extent, on certain species of the related genera *Thespesia* Corr. and *Cienfuegosia* Cav. (2). The weevil is now well established on *C. affinis* (HBK.) Hochr. in Venezuela; it was first observed on plants of that species in 1949 (3). It occasionally infests plants of a few other malvaceous genera, but it is apparently unable to maintain populations on them.

Cotton has been cultivated in Mexico for several thousand years (4), but only in recent decades has the boll weevil expanded from a little-known oddity on this host into a major agricultural pest. Three hypotheses may account for this situation: (i) the insect was introduced into Middle America from elsewhere; (ii) the insect was indigenous to Middle America and occurred on cotton, but it only recently