THE HELIOTROPISM OF ONCHIDIUM: A PROBLEM IN THE ANALYSIS OF ANIMAL CONDUCT.

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I.

Onchidium floridanum is a small naked pulmonate which lives in holes and crevices of the shore between tides. A description of the bionomics of this mollusk we shall present more fully in another connection,[1] omitting here those aspects not bearing directly upon the most curious puzzle propounded by its behavior, which in brief is this: under natural conditions the movements of *Onchidium* take place in the light, but without reference to photic control; yet when the animal is tested apart from its natural surroundings it is found always to be negatively phototropic.

In view of this apparent incompatibility, in reality very deep seated, one is led to inquire: Is the behavior of *Onchidium* an instance where "unnatural conditions" imposed in phototropism experiments vitiate attempted analytic explanation of normal activities and more especially what, fundamentally, is the *sense* of the state of affairs we have outlined, in terms of adaptation?

II.

1. Phototropism.—Exploration of the dome-shaped dorsum of the mantle of *Onchidium* with a light-beam 0.3 mm. in diameter and of moderate intensity showed that the movements of the mollusk, in the laboratory could be directed at will by even as small an illumi-

[1] A preliminary statement of certain of the results, utilized for different purposes than in the present connection, is found in the papers: Arey and Crozier (1918) and Crozier and Arey (1919*a*).

nated area as 0.3 sq. mm. To accomplish this result it was necessary to stimulate the anterior end of the mantle, which is more irritable, photically, than other regions of the mantle. The animal contracts on the non-stimulated side, and creeps away from the source of activation. The whole mantle dorsum is photosensitive, local areas puckering sharply into depressed pockets, secondarily extending as furrows across the animal's back, when one spot is illuminated. The anterior end of the foot, and the oral lappets, are more sensitive in this respect.

The tentacles, which in some *Onchidia* carry terminal eyes, are non-reactive to light, nor are the orienting movements of the animal interfered with in any way by the removal of the tentacles.

It therefore appears that although, as we have ascertained, this species of *Onchidium* does not possess differentiated mantle eyes (Semper, 1877; Stantschinsky, 1908), the physiological precursors, or perhaps the remnants, of such structures are actively functional in *Onchidium floridanum*.

Onchidium is quite unresponsive to increase of light intensity as such, but is very promptly and precisely oriented by incident light having a horizontal intensity component. There is found at all times and without exception a precise negative phototropism. That such orientation is in no way determined by "changes of intensity" is adequately demonstrated by the fact that these animals are at the same time conspicuously reactive to shading. When the light falling upon an *Onchidium* in air is suddenly decreased, the tentacles are forcibly withdrawn beneath the mantle, the head is retracted, locomotion stops, and the mantle is pressed into contact with the substratum. The distribution of this mode of irritability coincides with that evidenced in responses initiated by illumination. As with *Holothuria*, *Chiton*, and some other forms, the nature of the photic orientation of *Onchidium* is profoundly inconsistent with the differential sensitivity exhibited by the same animal (Crozier and Arey, 1918).

2. *In the Field.*—*Onchidium* lives during high-tide in "nests," cavities in the rock containing a number of individuals, from which the mollusks at low water emerge to feed upon exposed shore surfaces. The individuals emanating from any one nest return simultaneously to that nest before the tide rises again (Arey and Crozier, 1918).

The natural wanderings of the *Onchidia* while feeding upon the rocks take place without reference to the nature of the sunshine, whether brilliant or dull, and bear no relation whatsoever, at any time, to the direction of the incident light. The *Onchidia* creep out from their sheltering cavities only during daylight hours, however, and never at night, no matter how bright the moon.

In the laboratory, as far as our numerous experiments have shown, *Onchidium* moves away from a source of light under any conditions of temperature (15–32°), dryness (under water, or in air), and light (regardless of intensity) compatible with its active existence; whereas, on its natural substratum the same individual may creep directly into the horizontal rays of the setting sun, or away from them, with indifference. This state of affairs is well exemplified by the fact that, if an *Onchidium* is picked up from its natural substratum and a glass plate slipped between it and the rock, the animal orients immediately away from the sun, and with machine-like precision. Mere disturbance is not responsible for this phenomenon, because an equivalent handling of the mollusk, followed by its replacement on the rock, does not lead to the exhibition of negative heliotropism (provided the animal is restored to the rock within a certain radius of its "nest").

Similar results are obtained if an *Onchidium* creeping on the shore is shaded from the sun and then reilluminated from a new direction by light reflected from a mirror. Momentary "hesitation" may succeed such illumination, but the creature's path is not materially influenced.

3. Inhibition of Heliotropism.—We would emphasize the point that the natural movements of *Onchidium* cannot be viewed as "contrary to the dictates of the animal's heliotropism;" but that *during the creeping of the mollusk on the rock surface immediately surrounding its "home" this heliotropism is completely inhibited.* Proof of the correctness of this contention is seen in these facts, each of which has been verified upon a number of occasions.

(*a*) Removal of the oral lappets of an *Onchidium,* organs which normally are in constant contact with the substratum, or their anesthetization by $MgSO_4$, obliterates the normal directed homing of the animal; at the same time its negative heliotropism becomes a dominant factor in the control of creeping.

(*b*) An *Onchidium* removed to a strange section of shore moved about in a manner largely or entirely directed by the illumination. The same is true of any *Onchidium* which has been kept in an aquarium for 24 hours and is then returned to its native scene.

(*c*) In favorable instances, injection of *Onchidia* with strychnine (0.1 to 0.2 cc. of 1 per cent strychnine hydrosulfate), while not producing more than a moderate temporary contraction, succeeded by normal creeping, leaves the snail at the mercy of its heliotropism, although the animal may not have been handled at all, the injecting needle being simply inserted in its back and discharged.

These facts make it evident that in nature, as far as directed progression is concerned, the heliotropism of *Onchidium* is simply inhibited, or suffers central block, probably owing to those guiding impulses originating in the substratum and mediated through the oral lappets. Strychnine, while not necessarily "converting inhibition into excitation" (Cushny, 1919; Arey and Crozier, 1919), lowers the central threshold of solar activation impulses.[2]

It is improbable, furthermore, that the diurnal rhythmicity of *Onchidium's* appearance from its concealed rock cavities has any relation to heliotropism. The tidal rhythm of appearance is such, as we have learned by long observation, that even (as in summer) though two periods of low water may occur during daylight hours, the *Onchidium* colonies creep out to feed but once in the 24 hours. On the other hand, especially in winter,[3] several days may pass before a tidal period occurs in good daylight; the *Onchidia* then may make no appearance for several days. The brightness or dullness of the day has probably, as far as we can detect, no influence on emergence.

III.

With reference to the adaptation of habits to scene of life, the other activities of *Onchidium* are no less curious than its directed creepings ("homing") on the shore. It might be said that it is to the best interests

[2] "Reversals" of an analagous sort, but normally determined through feeding activities, are possibly involved in "homing" movements; this matter we shall treat separately.

[3] *O. floridanum* does not hibernate, as some other species appear to do (Hirasaka, 1912) in colder climates.

of this animal to come out into the sunlight; it must do so in order to obtain food; therefore, it disregards the dictates of its negative phototropism. This notion is sufficiently disposed of in the foregoing section; the negative heliotropism of *Onchidium* is not "disregarded" normally, it is centrally inhibited by other impulses competing for the nervous control of the body musculature. The further question remains: What is the rôle of the heliotropism of *Onchidium*? The mere existence of this type of response is sufficiently accounted for by the composition of the animal and the structural disposition of its parts. We have to inquire if this heliotropism is ever of "use."

Note in the first place our finding that the movements of an *Onchidium* on a rock substratum remote from its own "nest" are largely, and, in many instances, exclusively determined by the position of the sun. Might it not then be supposed that if an *Onchidium* should accidentally suffer displacement from its usual surroundings, its negative orientation by light would force it to enter some crevice or rock cavity, thus securing shelter and perhaps membership in a new colony? But the facts are different. The natural displacement of an *Onchidium* in this way is probably of very rare occurrence; these snails possess a well disposed system of repugnatorial glands (Crozier and Arey, 1919*a*), which makes such an event unlikely. Much more serious, however, is the fact that the animal withdraws sharply when shaded, as already stated. Furthermore, numerous instances we have carefully watched have yielded not one good case in which an *Onchidium* would enter a strange "nest" and remain there for more than a few minutes near the entrance (Arey and Crozier, 1918); they always crept out and away. These two kinds of response make it improbable that a "lost" *Onchidium* would seek refuge in a strange depression, and those which were purposely displaced in this way remained in fact creeping about on the rock until washed off by the rising tide.

IV.

We must refuse, then, to admit any obvious adaptive significance inhering in the photic behavior of *Onchidium*. Loeb has pointed out (1916) that positive heliotropism occurs in several arthropods "which have no opportunity to make use of it." Instances of this kind have drawn from some writers the curious comment that "these reactions are non-adaptive only under artificial conditions" (Mast, 1911), with the further assumption that "the reactions were inherited from ancestors in which they were adaptive." The normal inhibition of heliotropism in *Onchidium* is adaptive, if you like, but the further difficulty of finding some adaptive excuse for the existence of heliotropism at all remains all the more insoluble. The behavior of *Onchidium* is more curious than that of the crustaceans cited by Loeb, for there is physical opportunity to "make use" of their photic sensitivity, since they are exposed to light. Whether the mechanism for such a response is merely an "inheritance" from ancestors in which it was adaptive, one need not say, but the mechanism is fully present, though seemingly not used, and of obscure, if any, functional value—as far as concerns the movements of *Onchidium* on the rock surfaces.

BIBLIOGRAPHY.

Arey, L. B., and Crozier, W. J., 1918, The 'homing habits' of the pulmonate mollusk *Onchidium*, *Proc. Nat. Acad. Sc.*, iv, 319; 1919, The nervous organization of a nudibranch, *ibid.*, in press.

Crozier, W. J., and Arey, L. B., 1918, On the significance of the reaction to shading in *Chiton*, *Am. J. Physiol.*, xlvi, 487; 1919, *Onchidium* and the question of adaptive coloration, *Am. Nat.*, liii, 415.

Cushny, A., 1919, Note on strychnine tetanus, *Quart. J. Exp. Physiol.*, xii, 153.

Hirasaka, K., 1912, On the structure of the dorsal eyes of *Onchidium*, [Japanese], *Zool. Mag.*, Tokyo, xxiv, 20.

Loeb, J., 1916, The organism as a whole from a physicochemical viewpoint, New York.

Mast, S. O., 1911, Light and the behavior of organisms, New York, 1st edition.

Semper, C., 1877, Ueber Schneckenaugen vom Wirbelthiertypus, u. s. w., *Arch. Mikr. Anat.*, xiv, 117.

Stantschinsky, W., 1908, Über den Bau der Rückenaugen und die Histologie der Rückenregion der Oncidiiden, *Z. wiss. Zool.*, xc, 137.