REMARKS ON TONNOIR'S THEORY OF THE EVOLUTION OF THE VENTRAL SUCKERS OF DIPTEROUS LARVAE.

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After studying the early stages of the remarkable Indian Psychodid insects of the genera *Horaiella* and *Neotelmatoscopus* discovered by me in the Teesta Valley, Tonnoir [1] has tentatively proposed a new theory of the evolution of the ventral suckers of Dipterous larvae. His views are at such great variance with our knowledge of the form of hill-stream animals that, after a perusal of his manuscript, I wrote to him about the weak points in his chain of arguments. To this I have received no reply, and as the article is now published, I avail myself of the opportunity to show how faulty his explanation is.

Tonnoir traces the evolution of the sucker from very flattened forms, in which the ventral surface is horizontal and can be closely applied to the substratum. The dorso-ventral muscles of such a Dipterous larva would be able to convert the entire ventral surface into one large sucker. In the next stage, according to him, a fringe of hairs is developed round the margin "to facilitate the retention of the suction or vacuum." "In order to allow more mobility" the fringe now migrates towards the axis of the body, where, during the course of further evolution, it becomes discontinuous and forms a series of oval, more or less complete discs, which ultimately become perfected into powerful suckers, such as are to be found in the larvae of the Blepharoceridae. Tonnoir explains his theory with the help of a good diagram and states that in accordance with his theory the organs of attachment of the larvae of *Sycorax*, *Horaiella*, *Maruina*, *Neotelmatoscopus* and the Blepharoceridae would form an evolutionary series.

For a critical study of Tonnoir's views, noted above, it seems desirable to direct attention to the form of the body and the organs of attachment in the torrential population as a whole. As an adaptation to life in swift currents, the representatives of several groups of animals have evolved suckers or sucker-like adhesive devices to withstand the tearing away action of the rushing waters. A fairly detailed comparative study of these devices, in different groups of animals that have taken to living in torrential streams, is contained in my paper [2] on the "Ecology, Bionomics and Evolution of the Torrential Fauna, with special reference to the organs of attachment." In the same paper an account is given of the body-forms of these animals, and the physical principles involved in the mechanisms of attachment are also discussed. For a comprehensive study of the problem reference should, therefore, be made to this paper.

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[1] Tonnoir, *Rec. Ind. Mus.*, XXXV, pp. 73, 74 (1933).

[2] Hora, *Phil. Trans. Roy. Soc. London*, (B) CCXVIII, pp. 171-282, pls. xv-xviii (1930).

The brook inhabitants are either greatly flattened dorso-ventrally or are cylindrical in form. The latter shape is suitable only for those animals that dangle freely in the current which flows on all sides of the animals, and, therefore, presents a stream-line form on every side. In most of the torrential animals the ventral surface is flat and horizontal, and this flattening becomes more and more pronounced as the animals invade swifter and swifter currents. The object of this modification is to enable the animal to cling to the substratum as firmly as possible, and this is secured by lessening the pressure on the under surface of the animal. Let us suppose that the water flows beneath an animal living in a torrential stream. Naturally the speed of the water will be retarded in this region and it will mean that the rate of flow of the current above the animal will be greater than that of the current below it. According to the principles of hydraulics, the pressure on the dorsal surface will thus be lowered and this will naturally tend to lift the animal from the substratum. A number of animals obviate this tendency by shooting out this water from beneath them with considerable force. Fishes do so with the inner rays of the pectoral fins, the Heptageniid nymphs (Ephemeroptera) by their gill lamellae and the larva of *Psephenus* (Coleoptera) and the nymph of *Prosopistoma* (Ephemeroptera) with the help of their tails. In the most highly adapted forms, such as the nymph of *Iron* (Ephemeroptera) and a number of Sisorid and Homalopterid fishes, the entire ventral surface becomes converted into a broad disc which when applied to the substratum is probably water-tight. According to Tonnoir's theory this useful process of increased flattening and the ultimate conversion of the entire ventral surface into a broad disc is reversed, for he supposes that in the evolution of the suckers the marginal adhesive fringe of forms like *Horaiella* shifted from the margins to the middle of the body. For purposes of adhesion there cannot be any advantage to the animal in the reverse process and to me it seems full of dangers, for frolicking about is a dangerous pastime in swift currents and, therefore, the inhabitants of brooks develop more and more statozoic habits, and there seems no desire on their part to secure "more mobility." From the evidence afforded by the modifications of the body-forms of brook inhabitants, it would appear that the larvae of *Sycorax* and *Horaiella* are more highly adapted for life in swift currents than are the larvae of *Maruina* and *Neotelmatoscopus*, in spite of the fact that the latter are provided with series of adhesive discs on their ventral surface. In fishes, a group of animals about which I am less ignorant, a regular series exists among the Sisoridae showing the shifting of the adhesive pad from the central part of the body to the periphery. I (*loc. cit.*, p. 236) refer here to the forms represented by the genera *Erethistes*, *Laguvia*, *Glyptothorax*, *Pseudecheneis*, *Glyptosternum*, etc. As I have already explained, when a fish begins to rest with the head pointing up-stream and the front part is pressed against the substratum, the thoracic part of its body comes in contact with the rocks, and consequently rugose adhesive pads appear in this region first of all. When the form becomes greatly flattened, these adhesive pads are replaced by similar pads that develop on the ventral surface of the outer rays of the paired fins. Even in species of *Garra* (*loc. cit.*, p. 234) that live in very swift currents, the sucker becomes reduced and pads are developed on the rays of the paired fins. So far as I have been able to ascertain, the suckers of the chiton-shaped Blepharocerid larvae are proportionately smaller in size than those of the deeply segmented larvae. The reduction of the suckers in the broad larvae is compensated both by the form as well as by the spines and adhesive papillae that are developed on the ventral surface round the margin. It would thus appear that from the knowledge we possess Tonnoir's supposition cannot be correct.

The probable mode of origin and evolution of the powerful suckers of the fish *Garra* [1] and of the tadpoles of *Rana afghana* [2] have been studied from the developmental series of these animals. In both of them the sucker starts as a callosity of the skin which, by stages, becomes differentiated into the various structures of the discs of the respective animals. It is thus seen that in the fish and the tadpole the sucker develops as a totally new organ, and does not replace any pre-existing organ of attachment. The case of the Dipterous larvae, as well as of several other insect larvae, is different. Some of these possess pseudopods for progression on land, for burrowing or for crawling about in vegetation. When, by competition or some other impelling force, a number of them are obliged to invade flowing waters, these very pseudopods help them in fixation. Under the stress of stronger and stronger currents, the pseudopods become more and more perfected as organs of adhesion till in the Blepharoceridae, that live in the fiercest currents, they assume the form and function of perfect vacuum suckers. Tonnoir admits that in the sucker of the very young larvae of the Blepharoceridae "the number of rods is not as large and that the valvular gate is not yet present." It may also be pointed out that at this stage the structure of the funnel-like depressions is also different; they are represented by triangular spaces. In the earlier stages the characteristic piston of the Blepharocerid suckers is also in a nebulous condition. I have shown already that before the development of the valvular gateway, the discs of the Blepharocerid larvae cannot act as vacuum suckers, and that at this stage they can be compared with the pseudopods of insects. In order to give an idea of the working of the discs of the young Blepharocerid larvae, I compared them with the pseudopods of the Lepidopterous larvae.

My view regarding the evolution of the Blepharocerid sucker receives support from the fact that the body of the larva has become segmented secondarily round these points of fixation. From this consideration I advanced the view that in the ancestral form of the Blepharoceridae the pseudopods were probably present on the second to the seventh abdominal segments. The discovery of the larvae of *Neotelmatoscopus*, in which the pseudopod-like discs are present on the second to the seventh abdominal segments, is very significant and deserves more than casual attention. Feuerborn [3] and Tonnoir (*loc. cit.*) have already referred to this character in connection with the affinities of the Blepharoceridae. I am not in a position to discuss the relationship of the Blepharoceridae

[1] Hora, *Rec. Ind. Mus.*, XXII, pp. 639-643 (1921).
[2] Hora, *Trans. Roy. Soc. Edinburgh*, LVII, pp. 469-472 (1932).
[3] Feuerborn, *Arch. Hydrobiol.*, Suppl.-Bd. XI, pp. 55-128 (1932).

and the Psychodidae, but I hope some other student will make an unprejudiced study of this point. Whatever light the discovery of the *Neotelmatoscopus* larvae may shed on the probable ancestry of the Blepharoceridae, it is abundantly clear to me that *Maruina* and *Neotelmatoscopus* cannot be closely related. I do not agree with Tonnoir that the presence of eight 'suckers' in the larvae of *Maruina* represents a more primitive character than the six-sucker condition found in the larvae of *Neotelmatoscopus*; to my mind the variation in the number of suckers in the two forms denotes that *Maruina* and *Neotelmatoscopus* are evolved from different ancestors, the larvae of which possessed eight and six pseudopods respectively. It has been pointed out by Tonnoir that the larvae of the Psychoidae are eminently plastic in their faculty of adaptation. It is little wonder then that diverse types of larvae first developed pseudopods on various segments of the body, and that in those larvae that took to life in flowing waters, the pseudopods became transformed into sucking discs. The great diversity of form in the larvae would also explain the evolution of the very peculiar larvae of *Horaiella*. *Horaiella* is probably derived from an ancestral stock in which the larvae were greatly flattened dorso-ventrally. This form became still further accentuated under the stress of swift currents. It would thus seem that *Horaiella*, *Maruina* and *Neotelmatoscopus* are evolved from entirely different ancestral forms and whatever similarity they now possess is due to convergence in response to the similar special habitat.