# V. *Ecology, Bionomics and Evolution of the Torrential Fauna, with Special Reference to the Organs of Attachment.**

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[PLATES 15–18.]

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## CONTENTS (continued).

## INTRODUCTION.

IN studying the life and characters of the animals inhabiting the torrential streams of India and elsewhere, one thing has become quite clear to me—that evolution is no more than the adaptation of organisms to environment. "Adaptation" signifies correlation of an animal with its habitat, and therefore the study of animal organisation, however detailed, cannot by itself lead to the proper understanding of this phenomenon. Environment with its unlimited gradations plays an important part in the making and re-making of the characters, and sometimes the resultant forms are of such totally different types that genetic relations can hardly be discerned (*vide infra*, pp. 190, 237, 246). This fine adjustment of an organism to the external conditions of its existence is the result of a series of gradual changes *induced* by the environment.

Since the publication of DARWIN's epoch-making work more attention seems to have been paid to the study of animal morphology in its various aspects than to the habitats of animals. In fact, it is only in recent years that the importance of animal ecology as a subject for investigation has come into prominence. Several workers in recent years have denied the existence of "adaptations," and the idea of utility in evolution, which is a necessary complement of the process of adaptation, is being considered of no importance. For example, one reads "that characters have arisen at variance with the innate tendencies of 'Heredity,' and persisted without the aid of 'Natural Selection'" (KYLE, 1926, p. vii), or that evolution is predetermined and in the unfolding of characters "selection" plays no part (BERG, 1926). Again, NOBLE and JAECKLE (1928) remark as follows: "Many other so-called highly adaptive structures in the Amphibia are as fortuitous in their occurrence as the large digital discs. Adaptation in these cases is a chance relationship, not a progressive modification towards particular habitat requirements." In fact, there is a strong trend of feeling at the present day that evolution is not coherent, but is fortuitous, and such conclusions are based on assumptions such as the following: "In whatever direction we look, in the coastal region or in fresh water, we find many diverse forms living under precisely the same conditions, yet with quite different shapes and structures" (KYLE, 1926, p. 250), and according to some others, animals possessing similar adaptive modifications are found living under widely different conditions. Undoubtedly different forms of animals are found living in the same place within a few feet of one another, but have the gradations in the environment been studied so thoroughly that there is justification for saying that these different animals are " living under precisely the same conditions " and that they do not occupy definite " niches " in the environment ? Again, has the modification of a structure been correlated with one or more factors in the environment, and has it been established that the same factors do not influence life in another environment where the same modification is found ? The present study is mainly directed towards the elucidation of such problems.

The groundwork of DARWIN's theory of evolution was that the " variations " selected by Nature are of a beneficial character, but he was unable to demonstrate the truth of it. The utility of a structure can be judged only by reference to its function in relation to the environment, and when a progressive modification of a structure can be shown to be the direct outcome of some factor or factors of increasing strength in the environment, the utility of the modification becomes obvious. Again, it is found that when highly evolved animals revert to a primitive condition of life they assume a mask of apparent simplicity. I have purposely said " apparent simplicity," for, though the animals return from a complex to a simple organisation, they never assume a truly primitive or ancestral condition (*vide infra*, pp. 190, 237, 246). It is generally admitted that the path of retrogression is different from that followed by the original progressive evolution. This is so because evolution, progressive or retrogressive, takes place only through modifications of the pre-existing structures, by a simple change of functions.

I have remarked above that evolution takes place by a series of gradual changes. This is a conclusion reached both from taxonomic work as well as from studies in the field. I agree with REGAN (1924) " that evolution has been a slow and gradual process, that in its main lines it has been adaptive, and that changes of structure have been intimately related to, and even determined by, changes of function ; further, that as a rule the first step in the origin of a new species is the formation of a community with a new and restricted environment, or with new habits ; in other words, that some form of isolation, either localisation or habitudinal segregation, is the condition of the development of a new species." How true all this is will be shown in the subsequent parts of my paper.

My greatest debt of acknowledgment is due to my late chief, Dr. N. ANNANDALE, whose encouragement and advice were always helpful and are still an inspiration. I also gratefully recall the facilities given to me by Lieut.-Col. R. B. SEYMOUR SEWELL, Director, Zoological Survey of India, for carrying out this work in the field. My colleagues, Drs. B. PRASHAD, B. n. CHOPRA, H. S. PRUTHI, have helped me in various ways, and my best thanks are due to them. I am especially indebted to Dr. B. PRASHAD for the great trouble he has taken to supply me with the micro-photographs of my preparations.

The work was finished in the Department of Zoology of the University of Edinburgh,

and I have great pleasure in offering my sincerest thanks to Prof. J. H. ASHWORTH, F.R.S., for his valuable criticisms and helpful suggestions. For the courtesies so kindly extended to me by the entire staff of the Department of Zoology I am specially grateful. I have consulted many specialists, and from all of them I have received the fullest measure of assistance, which has been gratefully acknowledged in suitable places in the text or in footnotes.

I take this opportunity to express my thanks to my assistant, Babu D. N. BAGCHI, who very ably helped me in the field, and with his usual skill and care has drawn some of the figures illustrating this paper. My friend Mr. M. SAYEEDUDDIN has drawn some of the text-figures under my supervision, and for his help in this matter my best thanks are due to him.

At the end I have given a list of the papers referred to in the text, but no attempt has been made to draw up a complete bibliography.

## ECOLOGICAL FACTORS AND CLASSIFICATION OF HABITATS.

### *Ecological Factors.*

HUBAULT (1927, p. 366), from a detailed study of the torrential fauna, has concluded that " Il y a une faune torrenticole, il n'y a pas à proprement parler de faune rhéophile." According to this author, the animals live in the rapid waters because of certain advantages provided by the physico-chemical composition of the water, and in spite of the mechanical effects of the swift currents. He admits, however, that being obliged to submit to the current, the animals stem it by means of well-marked adhesive devices. There is no doubt that the swift-flowing water is well aerated, and the current carries food to the sessile animals, but " it has the disadvantages that come with the impact of moving water and the objects that it carries along; also those that are due to the great difficulty that attends locomotion or the maintenance of constant spacial relations with the environment " (PEARSE, 1926, p. 190). I shall show later how, by gradual perfection of the organs of attachment, animals have been able to colonise the swift currents. It was after this invasion that further modifications occurred in the build of these animals.

When the entire organisation of an animal is taken into account (after all, the study of a structure, however thorough, cannot be substituted for the study of an " organism as a whole ") it becomes clear that the changes have been induced by the direct effect of the current. For example, the oxygen content of the water (see HUBAULT, 1927, pp. 192–224), which is another main factor in the environment, is dependent to a certain extent on the rate of flow of the current. If one were only to take into account the modifications of the respiratory organs in the fauna of the torrents, he would undoubtedly find that these animals cannot exist without a high percentage of oxygen. It is known, however, that the respiratory organs tend to be greatly reduced in well-oxygenated waters (DODDS and HISAW, 1924), and once the organs are reduced the animals can only exist in waters with a large quantity of oxygen. This can be verified by keeping hill-stream animals in captivity : they die after a short time. Some of the hill-stream animals, such as *Rhithrogena,* funnel-mouthed tadpoles of *Megalophrys,* and certain species of *Glyptosternum,* have secondarily taken to life in slower waters, and consequently have either gradually re-developed their respiratory organs or have enlarged the existing ones.

It may, however, be remarked that the current at the bottom and the sides is much less than that in mid-stream where the maximum velocity occurs at about 0·4 of the depth from the surface, and probably there is a corresponding deficiency in the percentage of the oxygen both at the bottom and at the sides. The shallowness and low temperature of the water are other physical factors which influence the fauna. The salts dissolved in the water may have considerable bearing on the nature of the fauna, but I have not studied this in detail.

Among the biological factors attention may specially be directed to the nature of the food available in the hill-streams. It consists of algæ and slime, covering rocks and stones, or of micro-planktonic organisms in the current. Special modifications of the mouth-parts have been induced by the necessity of feeding on both these types of food. The encrusting food has either to be scraped away from the substratum or the animal has to gather micro-organisms from the currents. Some insect larvæ—*Hydropsyche,* for example—manufacture web-like structures to strain organisms out of the current. There are very few predaceous animals in the torrent fauna. Certain insect larvæ, Perlids and Caddis-worms, and fish feed on insect larvæ, chiefly Ephemeroptera, Chironomids, etc.

As regards protection, the narrow crevices among rocks and stones provide enough shelter. Most of the animals live under stones or in vegetation ; all of them are positively statozoic, and most of them are negatively heliozoic in their behaviour (see HUBAULT, 1927, for tropisms, pp. 223–278). Only a few forms live on the upper surface of rocks, and are thus exposed to a strong light in shallow and clear waters.

In general the eggs of these animals are relatively large, and are laid in sheltered places in the water, and the larvæ gradually invade the swift part of the current. The larvæ from large eggs hatch out at a fairly advanced stage, so that they are capable of resisting the adverse effects of the environment to a certain degree. In an environment which is unfavourable for the free development of the young ones, the animals have responded by increasing the size of the egg. I have given these details because recently NOBLE (1927, p. 39) has denied that the large size of the egg is of any advantage to the swift-water dweller.

### *Classification of Habitats.*

PEARSE (1926, p. 17) has classified the animals of rapidly flowing streams into two associations—animals of springs and animals of brooks ; but since he " feels that from a biological point of view streams are more naturally distinguished as swift or sluggish " (p. 188), it appears to me that his classification is arbitrary. I think it is better to divide the animals of this environment according to the strength of the current which they inhabit. PEARSE has classified the animals of the brooks into seven "strata,"* but in view of my observations I propose to modify them as follows: –

REALM. FRESHWATER ANIMALS.
  PROVINCE. ANIMALS OF FLOWING WATER.
    FORMATION. ANIMALS OF RAPIDLY FLOWING STREAMS.
      ASSOCIATION (*a*).—Animals of pools and sides of streams.
      ASSOCIATION (*b*).—Burrowing animals.
      ASSOCIATION (*c*).—Swimming animals.
      ASSOCIATION (*d*).—Swift-current inhabitants.
        SUB-ASSOCIATION 1.—Plant-inhabiting animals.
          *Stratum* (i).—Root-inhabiting animals.
          *Stratum* (ii).—Animals entangled in the plants.
          *Stratum* (iii).—Animals on the plants.
        SUB-ASSOCIATION 2.—Rock-inhabiting animals.
          *Stratum* (i).—Animals on exposed surfaces.
          *Stratum* (ii).—Animals on underside of rocks.
          *Stratum* (iii).—Animals among pebbles and shingles at the bottom.

It should be remembered that there are no hard and fast lines between these divisions, and that generalised animals are sometimes found in more than one habitat. In the case of the highly specialised animals, such as the Blepharoceridæ, the habitat is absolutely fixed, and such animals cannot exist in any other environment.

I have divided the animals of the rapidly flowing streams into four associations, mainly on the nature of the current affecting them. The fauna of the pools and the sides of the stream lives in a gentle flow of water, or in some cases in almost stationary water, but in this environment it has the advantage of a cold and well aerated medium. Food is carried to the animals by the current, or in a gentle flow of water the dead organisms tend to settle down at the bottom and form the food of the majority of the pool-dwellers. The second association comprises burrowing animals such as dragonfly larvæ (Gomphinæ) and Mayfly larvæ (*Palingenia* and *Polymitarcys*). These are not affected by the swiftness of the current, but possess all the advantages of life in rapidly flowing water, such as abundance of oxygen and food, and security from enemies.

There are few animals that can swim against a swift current, and except for a few species of fish I do not know of any other animal that could be included in this association. After travelling for a certain distance these animals get into deep pools, and then they can be considered as members of the first association.

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* While discussing brook-inhabiting animals on p. 191, PEARSE gives wrong references to the various "strata." He seems to have confused this habitat with the one preceding it, for his references agree with those of the "strata" of the animals of the springs.

It is with the permanent inhabitants of the swift currents that I am mainly concerned in this paper. Most of them are provided with means to stem the current, and I have classified these animals into various " strata " according to the nature of their adhesive devices. The bed of a hill-stream consists of loosely placed stones resting on a bottom of pebbles and shingles (in some cases there is a sandy bottom). On the leeward side of larger rocks aquatic vegetation is found, in the form of tufts of mosses or flowering plants of various kinds. The inhabitants of the swift currents can be divided into two sub-associations, namely, the plant-inhabiting animals and the rock-inhabiting animals. This division is very natural, and a collector is greatly impressed by it. For instance, in the two photographs on Plate 16, superficially the environmental factors appear to be more or less similar, but in the case of the Pun-Wa-Sherra stream (lower) the rocks in the stream-bed and forming the lips of falls are bare, while the rocks in the neighbourhood of the sacred fall of Dhud-Dhara (upper) are covered with a carpet of mosses. Consequently, in the former habitat the lips of falls harboured Blepharocerid larvæ and nymphs of *Iron* and *Bœtis*, while in the latter habitat the fauna was richer and more varied and chiefly consisted of clinging larvæ of the Chironomidæ and the Ephemeroptera. No flattened larvæ of the *Iron* type were found here. This shows how the distribution of the fauna is influenced by the nature of the bed.

The vegetation in the stream-bed consists of mosses and flowering plants, such as *Eriocaulon miserum*, *Hydrobryum lichenoides*, *Dierœa wallichii*, etc. (common in the Khasi Hills); the latter have thin and elongated leaves, and offer little resistance to the current. By the impact of the current the plants are bent in the direction of the flow: they are thicker near the root-end and taper towards the free end. Thus a stream-line form is presented to the current. All the animals living in plants have one character in common, and that is, the torpedo-like shape of the body. Since the current flows on all sides of these animals, such a form is well adapted to offer minimum resistance (p. 253). There are three types of animals living among plants. There are animals—such as the funnel-mouthed tadpoles of *Megalophrys* and Tipulid larvæ—which live securely entangled among roots and bases of stems. They lie free in such habitats, and are probably not affected by the swiftness of the current. They are not provided with any elaborate devices for fixation. They possess hydrostatic organs, so that when disengaged from their habitat, they are lightly carried by the current and their buoyant bodies save them from injury. The second category includes animals, such as *Nephelopteryx*, *Helodes*, *Phalacrocera*, *Gammarus*, etc., that live entangled among the leaves and stems of plants. These organisms are provided with hook-like processes on their bodies and limbs which serve to anchor them among plants. The third type comprises those animals that live on the exposed surfaces of plants, such as the larvæ of *Simulium* and Chironomids.

The rock-inhabiting animals can be divided into three " strata " according to whether they live above or below the rocks or at the bottom of the stream among pebbles and shingles. Those animals that live on the exposed surfaces of rocks are of two kinds, readily recognised by their form, which depends upon their mode of attachment. Those that cling to the rocks by means of claws on the legs (*Bœtis* larvæ), by the grappling-hooks at the posterior end of the body (larvæ of *Simulium*, Chironomids, etc.), or by both of these (Caddis-worms), swing about freely in the current anchored by these points of attachment, and consequently they have a torpedo-like, stream-line body; whereas those that adhere to rocks by means of the frictional pads on their ventral aspect are flattened and scale-like (*Iron, Psephenus*, etc.). The animals of the bare rocks can be further divided according to their power of resistance to the current. For example, the Blepharoceridæ and certain species of *Iron* and *Bœtis* are capable of living in very wild waters, while most of the other fauna inhabits moderately strong current. The animals living on the under side of rocks are all flattened (*Perla, Iron, Psephenus*, etc.). They adhere to the rocks by closely applying their ventral surfaces to them; the depressed form of these animals further enables them to seek shelter in narrow crevices. In the case of the bottom-inhabiting animals the current is a negligible factor, and consequently the animals possess the same type of form as their allies of the sluggish waters. They show adaptations to the high percentage of oxygen and the type of food available in these streams.

Properly speaking, there is no surface fauna or planktonic fauna in this environment. A large number of micro-planktonic organisms are found helplessly drifting with the current, and constitute a great portion of the food supply of the torrential fauna.

## BIOLOGY OF THE TORRENTIAL FAUNA, with special reference to the organs of attachment.

In studying the animal life in torrential streams of India, special attention has been paid to the insects and the vertebrates.

### INSECTA.

There are nine orders of insects whose representatives in some stage are found in water, and it is worthy of record that all of them are met with in greater or lesser numbers in clear and rapid-flowing waters. These insects belong to the orders Plecoptera, Odonata, Ephemeroptera, Hemiptera, Neuroptera, Trichoptera, Lepidoptera, Coleoptera and Diptera.

### *Plecoptera.*[*]

During the course of my extensive touring I have found that nymphs of the *Perla* type (probably *Neoperla*) are quite common in the swift-flowing Himalayan streams.

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[*] Prof. J. A. LESTAGE has very kindly read through the section, and for this my best thanks are due to him.

Their elongated and greatly flattened body is modified to present a stream-line form to the current, and to offer as little resistance as possible. The movably articulated paired claws help the animal to hook itself on the substratum. Besides these devices the nymph is further provided with a series of strong, backwardly directed spines in the various regions of its body, and these enable it to maintain its position in narrow crevices among stones. The nymphs usually lie with their heads pointing upstream, their broad femora directed obliquely backwards and their tibiæ pointing forwards and lying for a part of their length in the grooves on the femora, to be noticed shortly. To follow the arrangement and utility of these spines, I propose to describe them as they are distributed on the different parts of the body.

*Ventral Surface of Head and Body.*—The ventral surface of the head and of the three thoracic segments is smooth, except for irregular patches of fine, black, hair-like processes. But along the posterior borders of all the abdominal segments strong, chitinous, and backwardly directed spines are present. On the first abdominal segment they are restricted to the lateral borders, but their extent progressively increases towards the median line in the posterior segments. On the last two or three abdominal segments they occupy the entire posterior border. The lateral spines are the longest and strongest, but towards the median line they become gradually shorter and weaker. This, however, does not apply to the last few segments, where the spines are of a more or less equal length throughout except for those that are situated at the extreme ends ; these are better developed than the others. The whole of the ventral aspect of the abdominal segments is covered with fine hairs and bristles which are directed backwards. The intensity of growth of these structures increases with the distance from the anterior end. The margins of the podical plates are provided with long spines, and their general surface is thickly covered with bristles.

In all the hill-stream animals there is a strong tendency to apply their ventral surfaces to the substratum as closely as possible, and this would necessitate the perfect smoothness of the parts of the body that come in close contact with the rocks. The arrangement of the spines described above affords clear indication as to how much of the ventral surface of the animal is closely applied to the rocks. The backwardly directed spines in the other region would naturally prevent the animal from slipping backwards. It is also obvious that the nymph cannot move backwards with its body closely pressed to the substratum, though a movement in the anterior direction presents no difficulty. Usually the nymphs raise their bodies on their legs well above the substratum when making their quick movements.

*Dorsal Surface of Head and Body.*—On the dorsal surface of the head and the thoracic segments is a characteristic pattern which is partly formed by areas of black, short, hair-like spines. As a general rule these spines are directed backwards, but here and there are patches in which the spines are directed laterally. Along the margin of the head and the thoracic segments, and also on any prominences on these parts, the hair-like spines are replaced by strong, chitinous spines. In the region of the head they are present along the lateral borders and along the posterior ridge of the orbit. Besides the spines on the lateral and the posterior borders of the thoracic segments, the anterior borders of the second and the third segments are provided with a row each of these strong spines which is interrupted in the middle. On the lateral flaps of the thoracic segments the " hairs " are longer, and there are also backwardly directed spines which do not show any definite arrangement. The posterior borders (Plate 17, fig. 1) of the abdominal segments are provided with long, chitinous, strong spines, and all of these are sharply directed backwards. They are continuous along the dorsal surface, and laterally with those that have already been noticed on the ventral surface. When an animal is examined either from above or from below, the spines are seen projecting laterally and backwards along the sides of the body. The general surface of the tergites is covered with long bristle-like structures.

The dorsal surface is better equipped with anchoring devices than the ventral surface. The necessity for this becomes obvious when it is remembered that these nymphs live on the under side of stones, which lie superposed on one another in the stream bed, and provide narrow channels for the water to flow, and in this position their dorsal sides are directed towards the bed of the stream, and have therefore to withstand the rapidity of flow. The under surface has, moreover, to be smooth, so that the animal can adhere firmly and closely to the substratum. In narrow crevices the utility of the spines along the lateral borders is obvious.

*Legs.*—The coxa and the trochanter are short and stumpy, and are immovably joined together, and the latter is fused to the femur, an arrangement which makes this portion of the leg rigid. The femur is greatly flattened and is very stout and well developed. The ventral surface of the coxa is smooth except for a few fine hairs ; the trochanter possesses a row of backwardly directed spines along its anterior border. The ventral surface of the femur in its proximal half is covered with short and delicate spines which are directed backwards and outwards ; at its extreme distal end there is a crown of strong, backwardly directed spines, and both its borders are provided with long, backwardly directed spines, those along the mesial border being longer and stronger. The tibia is also flattened and is smooth on the ventral surface ; it possesses a row of distally directed spines along its mesial border and a crown of spines at the distal end ; of the latter, two are specially modified and claw-like. The tarsus is smooth and ends in a pair of strong, highly chitinised and movably articulated claws. When the leg is examined from above it is found that the coxa, trochanter and femur are provided with fairly strong, backwardly directed spines on the general surface ; there is a crown of spines at the distal end both of the coxa and of the trochanter. On the femur the spines are better developed in the lateral regions (Plate 17, fig. 2), and it is worth noticing that in this aspect there is no crown of spines at the distal end of the femur. The tibia possesses a row of spines, along the mesial border, and there are a few at the distal end also. Besides the strong spines, the position of which is indicated in the above description, the dorsal surface is densely covered with black, hair-like growths which are directed backwards. The whole of the posterior border of the appendage is covered with long natatory hairs.*

The femur is grooved on the under side along the distal half, near the outer border, for the reception of the tibia, which in the natural position is directed forwards. It is a device to present a solid structure to the current and to expose as little of the surface as possible. Along the border of this groove strong backwardly directed spines are present. The complicated arrangement of the spines on the leg indicates the direction of the flow of the current, and their direction in the various parts indicates the positions of the different parts of the body as they rest in nature. There appears to be a close adjustment between these spines and the flow of the current.

*Anal Cerci.*—Each segment of an anal cercus telescopes into the one preceding it, but at the exposed posterior border of each there is a crown of backwardly directed strong spines. In the proximal region these spines are present only on the dorsal surface, but they encircle the whole of the segment in the distal region.

I have here described in detail the organs of attachment of the nymph of the *Perla* type, which is a very highly specialised organism for life in torrents. In somewhat slow-running streams are found small stone-fly nymphs of the *Leuctra* type which are not so greatly flattened. In these forms the anal cerci and the antennæ are greatly elongated, and are provided with circlets of spines which help to anchor the animal.

Among Plecoptera, as is also seen among the other animals inhabiting torrents, the body is either greatly depressed or has become cylindrical. Both forms appear to be equally well adapted to present a stream-line to the rushing water. The former type is represented by the *Perla*-like nymphs already discussed, the latter by the nymphs of *Nephelopteryx*.

The nymphs of *Nephelopteryx* live among mosses growing over rocks and boulders in a rushing torrent. Such growth is usually present on the leeward side of the rock, and is being constantly swayed from side to side by the eddies of the current flowing over it. The nymphs live in such situations by taking hold of the plants with the help of their powerful claws, which are denticulated. As a reaction against the constant tearing-away force of the water the legs are thin and long. They enable the animal to sway from side to side without actually loosing its hold on the moss. The most characteristic feature of these nymphs is the series of backwardly directed carinate processes on the back. These structures have been used by some authors to distinguish species of the genus, but their true biological significance has only recently been understood. LESTAGE (1920) at first thought them to be functionless structures secondarily acquired, but HUBAULT and LESTAGE (1925) referred to the true function of these structures for the

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* IMMS, in his 'Text-book of Entomology,' gives a sketch of a nymph of *Perla* sp. (p. 246, fig. 257), in which he shows the natatory hairs as situated along the posterior border on the first leg and along the anterior border on the other two pairs of appendages. This is obviously incorrect. A similar wrong figure of *Perla abdominalis* is published in Dr. E. ROUSSEAU'S 'Les Larves et Nymphes Aquatiques des Insectes d'Europe,' p. 293, fig. 80A (1921).

first time. HUBAULT, in his more comprehensive work (1927), makes the following interesting remarks about the adaptations of these larvæ: " *Nephelopteryx,* avec ses pattes assez grêles, ses longues antennes, ses cerques développés, les dents prononcées de sa forte carène dorsale, présente avec l'Hypnacée un certain mimétisme, semblable à celui des Caprelles dans les Floridées marines." Indeed, the presence of similar hooking structures in *Caprella* and in *Nephelopteryx* shows how similar structures are sometimes developed by widely different animals in response to certain common factors in their environments. This problem is discussed later (p. 264).

The adult stone-flies do not go under water for the purpose of egg-laying, though some are known to sit at the edge of water and dip their hinder end, from which they shake off the egg masses. Generally the eggs are dropped in water by the insect half-running, half-flying over its surface. The eggs are mucilaginous and stick to stones in swift currents. Eggs of certain species are provided with rope-like structures, which are shot out when the egg comes in contact with water (SCHOENEMUND, 1924, pp. 29, 30). These structures become entangled in stones and weeds and help to anchor the eggs. Eggs of certain other species, such as *Perla maxima* (SCHOENEMUND, *op. cit.*), are provided with spine-like outgrowths which have been termed " canals " by SAMAL (1923) and SCHOENEMUND. These spines are re-curved and are found in pairs in small pits, or are arranged in a single row in the middle of the egg. Their arrangement varies in different species. SAMAL (1923, p. 244) remarked: " Quel rôle jouent ces canaux ? Peutêtre, pourrait-on les considérer comme des appareils respiratoires de l'œuf ? " I believe that these spines enable the mucilaginous eggs to anchor themselves more firmly to rocks in rapid-flowing water. In swift currents a reduction of the respiratory organs takes place on account of the richness of the oxygen in the water,* and it is hardly possible that these tiny eggs have developed these spines for the purpose of respiration.

### *Odonata.*

According to TILLYARD (1917, p. 328), larvæ of the Epallaginæ, Megapodagrioninæ and Protoneurinæ are commonly met with on rocks in swift currents, while those of Aeschninæ, Corduliinæ and Calopteryginæ are less frequently met with in such situations. To this list may be added *Ictinus* (Gomphinæ) and *Zygonyx* (Libellulinæ), which are actual waterfall dwellers in India. About the habitat of the latter, FRASER (1927, p. 763) remarks as follows: " They deposit their eggs in the deeper pools occurring in the course of their parent streams, and not even the terrific scouring of the monsoon waters dislodges the larvæ from their original birthplaces. I have seen exuvia clinging to rocks beneath high waterfalls, where a week before it seemed inconceivable that any living organism could survive the rush and weight of water." In the typical larvæ of this habitat the body is broad, short and thickset, and the legs are muscular. The Corduliinæ are bottom dwellers in slow-running waters, and are consequently flat-

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* DODDS and HISAW, ' Ecology,' vol. 5, pp. 262–271 (1924).

bodied. Some representatives of this family have invaded the bare rocks in swift currents, and they resemble the typical, limpet-shaped inhabitants of this region. The Aeschninæ and Calopteryginæ are commonly found among weeds and possess long and slender bodies and legs. Those that have taken to life on bare rocks possess the same general form, and cling to rocks by means of their strong grappling claws, their long and slender legs permitting a certain amount of swaying movements caused by ripples in the current. These larvæ can be compared with the Ephemerid larvæ of the *Bœtis* type in their general form and the mechanism of attachment (p. 192).

Through the kindness of Lieut.-Col. F. C. FRASER, I have examined the larvæ of *Ictinus* and *Zygonyx*. They belong to two different families, but owing to the similarity in habitat they have converged so much as regards their general build that it is difficult to distinguish them readily, and even an expert Odonatologist may be deceived. Both of these are representatives of bottom-dwelling families. According to FRASER (*op. cit.*), these larvæ are adapted to live in strong currents on account of their shape (Plate 18, fig. 5), " the ventral surface being very flat and broad, the dorsum sharply keeled and stream-lined, and rising steeply like the ridge of a tent. Apparently by applying the flattened ventrum to rocks, and possibly contracting the ventral plates, they exert a vacuum, limpet-like suction, which holds them firmly anchored." I have not seen these larvæ in a living condition, but the examination of the preserved material shows that no vacuum can be created on the ventral aspect of the animal. The abdominal region has assumed an oval, disc-like form, and most of the segments are provided with a pair of transversely elongated and narrow pads on their ventral aspect (Plate 18, fig. 5). When magnified each pad is seen to consist of short, stout and backwardly directed spines. Undoubtedly the spines help to increase friction, and under the pressure of the current, which is advantageously utilised on account of the stream-line form of the dorsal surface, provide the animal with an efficient non-slipping device. The strong claws on the legs are also very useful for fixation.

As has been indicated above, the weed-dwelling larvæ of fast currents are generally of a slender build and are elongated; they are also characterised by the possession of long, spidery legs. According to TILLYARD, the Aeschninæ and the Synlestinæ are the commonest inhabitants of this environment, though the larvæ of Calopteryginæ, Lestinæ and Agrioninæ are also met with in such situations. Attention may here be directed to two different looking larvæ, *e.g.*, *Macromia ida* (Libellulinæ) and *Matrona basilaris* (Calopteryginæ). The Libellulinæ are bottom inhabitants, and consequently possess a greatly flattened body. In *Macromia ida* the depressed form of the body is further modified so as to offer less resistance to the current, and for the purpose of attachment the legs are greatly elongated and strong claws are developed. In *Matrona basilaris* the body is long, thin and attenuated, resembling a stick-insect in form, a shape which is admirably adapted for offering small resistance to the current. The long, spidery legs of both the forms are developed for anchoring the animals in weeds, where they are constantly swayed from side to side with every eddy of the current. The long legs are well adapted to bear the force of the current by bending before it without either breaking or loosing hold of the substratum.

## *Ephemeroptera.**

I propose to discuss the nymphs of the three families, of which two—Heptageniidæ and Bætidæ—are well represented in the fauna of India, while the remaining family, Prosopistomidæ, is known to me only through examination of preserved material.

Most Mayflies drop their eggs on the surface of pools in the course of a rapid current, and only once have I noticed the females under submerged stones in a gentle flow of water at Benhope, in the Nilgiris. Several instances of the females entering water for the purpose of laying eggs have, however, been recorded (EATON, 1865, SLADE, 1904), and among hill-stream insects it does not appear to be a rare occurrence.

The eggs of the Ephemeroptera are of various shapes and sizes, and are provided with peculiar devices by which they can anchor themselves in flowing water (BENGTSSON, 1913, PERCIVAL and WHITEHEAD, 1928). All the eggs are viscid. "When laid in dishes they adhere to the bottom, so do those of Bætis to stones. When twigs or algæ are introduced, they become attached to them. There are two kinds of structures found upon them—micropylar structures and knob or thread-like extensions of the chorion—both of which are important to the egg, and there is also a variety of chorionic sculpturings which have no apparent significance" (Miss MORGAN, 1913, p. 398). The thread-like extensions of the chorion, which originally lie coiled up, are shot out as soon as they come in contact with water, and by entangling themselves in pebbles or weeds securely anchor the eggs in flowing water. In certain eggs the threads at their terminations carry viscid discs for attachment. The hook-like projections and different types of chorionic sculpturings of certain other eggs are useful for increasing friction, and thus they materially contribute to the ultimate fixation of the eggs to the substratum.

### *Heptageniidæ.*

In the nymphs of this family the body is dorso-ventrally flattened, the ventral surface is flat and the dorsal profile is arched gently in stream-lines. The head is broad and ellipsoid and more or less spatulate. The outline of their profile is thus admirably adapted to afford little resistance to a rapid flow of water so long as they remain with their heads pointing upstream, the habitual attitude of all when at rest. The legs are robust and flattened, and can be closely applied to the substratum. They are provided with powerful terminal claws. The gill lamellæ are modified in certain genera to form organs of attachment. The anal cerci are well developed, and in some species are utilised for increasing friction.

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* I am greatly indebted to my friend and colleague Dr. B. N. CHOPRA for the identification of the Ephemerid nymphs. Prof. J. A. LESTAGE has very kindly read through this section and has made valuable suggestions; my best thanks are due to him.

In the hill-streams of India I have collected nymphs of *Ecdyonurus*, *Epeorus* and *Iron*,* and have examined a few specimens of *Heptagenia* and *Rhithrogena*, kindly given to me by the British Museum and by Mr. E. Percival, of the University of Leeds

The members of this family are usually divided into two subfamilies (Lestage, 1917), Rhithrogeninæ, including *Rhithrogena* and *Iron*, characterised by the great development of the first pair of gill lamellæ, which are dilated and continuous on the ventral surface of the body, and Heptageninæ, including such forms as *Heptagenia*, *Ecdyonurus*, *Epeorus*, etc., characterised by the first pair of gill lamellæ being simple and placed widely apart. Hubault (1927, pp. 111–118) has doubted the validity of such a classification, and by a series of convincing arguments has demonstrated that *Epeorus* and *Iron* are intimately related,† and that the classification that aims at keeping these two closely allied forms in different subfamilies must be considered as faulty. Hubault, in his turn, has re-arranged the genera of this family on the basis of the number of caudal setæ. He proposes a subfamily Epeorinæ for *Epeorus* and *Iron*, in which the median tail seta is absent, and a subfamily Ecdyonurinæ for *Arthroplea*, *Heptagenia*, *Ecdyonurus* and *Rhithrogena*, in which three well-developed caudal setæ are present. According to this author, *Rhithrogena* affords a connecting link between the two subfamilies in so far as it resembles *Ecdyonurus* in its general aspect and *Epeorus* in the structure of the mouth-parts.

According to Eaton (1883, p. 8), "Much diversity is exhibited in the number and relative proportions of the caudal setæ." The same author (p. 17), while discussing characters which have been used as bases of classifications but which are not fundamental, points out that the number of caudal setæ is a very unreliable character even for distinguishing genera very intimately related to each other. It varies with sex as in *Polymitarcys*, and even with individuals of the same species, for example, *Atalophlebia australasica*. It is clear from above that even Hubault's classification is open to criticism, for it is possible to show that the gill lamellæ and the caudal setæ are adaptive characters liable to be greatly influenced by the factors in the surrounding medium. The variations in them are due to the strength or slowness of the current. Before discussing further the relationships of the various genera of the family *Heptageniidæ*, I propose to give biological notes on them.

The nymphs of the genus *Ecdyonurus* are found in the hill-streams of India under stones in clear and moderately rapid-running waters. The adaptations for maintaining their hold in swift currents are similar to those exhibited by the nymphs of the *Perla* type (p. 179). The nymphs of *Ecdyonurus* are, however, better fitted to live in torrents than the Perlid nymphs. The body is more flattened, the ventral surface is perfectly smooth, and the spines along the posterior border of the dorsal surface of each abdominal

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* In the 'Rec. Ind. Mus.,' vol. 25, p. 598, fig. 3, I published a figure of a species of *Iron* and erroneously called it a Perlid nymph. This figure is, however, the first record of the occurrence of *Iron* in India. It is a very widely distributed genus in Indian waters.

† Prof. J. A. Lestage informs me that the "*Iron*" of Hubault is an *Epeorus*. This would explain the difficulty in distinguishing between the larvæ of these two genera.

segment, so characteristic of the Plecoptera, are represented by small distally directed processes. The femora are blade-like, with their ventral surface smooth and the dorsal surface covered with numerous backwardly directed spines. The spines are better marked along the outer or anterior border of the femur, while from the posterior border issue long, bristle-like hairs. The femur is grooved along the outer border for the reception of the tibia, which is long and slender, and is armed with a few backwardly directed spines. The tarsus, which is similar in form to the tibia, terminates in a strong claw. The anal cerci are well developed, and are provided with circlets of distally directed spines.

The gill lamellæ recline obliquely at the sides so that their ventral surfaces touch the substratum. Each gill lamella is somewhat thickened along the inferior margin. By the application of this additional callous surface to the substratum the area of adhesion is increased. These callosities are better marked on the median lamellæ, which are longer and broader than the others.

The nymphs of *Heptagenia* are similar to those of *Ecdyonurus*, and in certain cases the resemblance is so close that they can be hardly distinguished. In the former the lamellæ are narrowly lanceolate and do not help to support the animal on the substratum. So far as the form of the body and the legs is concerned, *Heptagenia* shows an advance on the *Ecdyonurus* type, as also in the fact that the spines on the posterior border of the segments on the dorsal surface are still further reduced. The nymphs of *Heptagenia* have failed to utilise their gill lamellæ for the purpose of adhesion, and thus the advantage gained in the flattening of the body and the legs is counterbalanced. The *Ecdyonurus* and the *Heptagenia* nymphs have been modelled along slightly different lines to withstand an equally swift current. *Heptagenia* appears to have reached the climax of modification along its line, while the gill lamellæ of *Ecdyonurus*, by further modifications, have been instrumental in the production of the highly modified genera of Heptageniidæ. It will be shown presently that the function of attachment is being gradually shifted from the legs to the gill lamellæ. Such a change of function is a common phenomenon among living organisms.

I have collected large numbers of the nymphs of the genus *Epeorus* in different parts of India, notably in the Kangra Valley (Western Himalayas), at Pashok (Eastern Himalayas), at Dumpep (Khasi Hills), and in a rapid stream below Silver Cascades in the Palni Hills, South India. These insects are usually found under stones in rapid-running current, but at Dumpep I found them to occur in great numbers in deep water on the bare surface of boulders. They are very agile in their movements, and it was difficult to catch them in deep water. On the least disturbance they seek shelter under rocks. Their ventral surface is flat, and can be closely applied to the substratum. The dorsal surface is of the same colour as the rock on which they rest. They were only observed to crawl on rocks, and were not noticed to swim. Out of a great variety of these insects in my collection, I select for reference the nymphs collected in a small, clear and rapid-running stream below Dumpep, Khasi Hills.

The body and legs are moderately depressed, the ventral surface is smooth, but the dorsal surface bears the usual spines. In the mid-dorsal region each abdominal segment bears two posteriorly directed spines. The dorsal surface of only the femur and tibia possesses short, backwardly directed spines, while the entire ventral aspect of the leg is covered with fine, needle-like, backwardly directed spines. The anal cerci are also covered with distally directed spines. All these spines help in increasing friction between the animal and the substratum. The surface of contact of the animal with the substratum is increased by the close application of the inferior borders of the gill lamellæ, which recline obliquely at the sides and are more or less broadly ovate or sub-acute in form, each overlapping the one behind it. The lamellæ of the first pair are of a different shape, and are situated widely apart. The lamellæ are so arranged in *Epeorus* that they form complete borders at the sides and prevent the water from going under the animal; but the water can get in at the anterior end on account of the gap between the lamellæ of the first pair. The lamellæ of the seventh pair are laterally placed so that there is a channel for the water at the posterior end also.

The outer or the inferior border of each lamella, except the first, is thickened, and for a greater part of its length bears a spinous pad (Plate 17, fig. 3). Each spine consists of a long and strong basal portion and of a sharp, hook-like curved apical portion. In the anterior region of the pad the basal portions of the spines are directed forwards, but their apices are turned backwards, thus enabling the animal to withstand the push from the anterior end. In the posterior region of the pad, as also along its inner border, the spines are directed outwards and their curved apices point inwards. This is a device to withstand the rush of water from the sides. The direction of the spines in the intermediate region is different at different places, but on the whole the arrangement of the spines is such that the tearing-away action of the current on the stream-line form is resisted from all sides. The backward push of the current at the anterior end is resisted by the backwardly directed spines, and the lateral force of the current is resisted by the inwardly directed spines. Along the outer margin of the pad there are simple, backwardly directed stout spines. The spinous pads of these insects thus form a marvellous friction device.

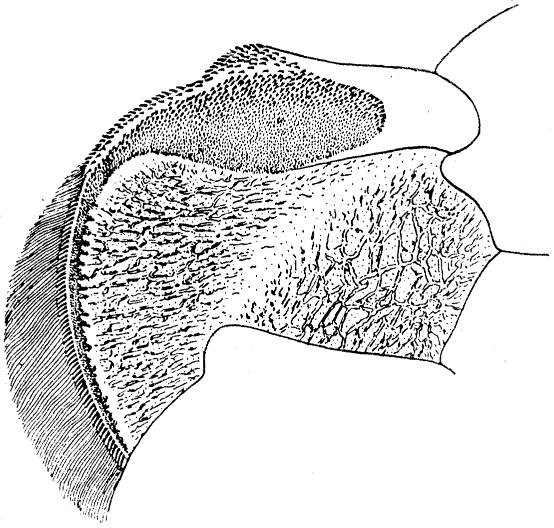
The first gill lamella (Plate 17, fig. 4) differs both in shape and in function from the rest. At the anterior end it is produced into a wing-like expansion which lies below the base of the third leg. At the base of this expansion lies a thickened band of chitin, which in form and position corresponds to the thickened spinous pads of the remaining lamellæ. It may be considered as a rudiment of the once spinous pad, and its position indicates the former anterior limit of the first lamella beyond which extension has taken place so as to form a barrier to the flow of water from the anterior end. The first lamella is thin, and bears a small pad of hooked spines on the inferior edge at the posterior end.

When this insect is examined in the living condition it is noticed that the thickened portion of the lamella is closely applied to the substratum, while the upper free portion is kept in a rapid to-and-fro motion. It is generally believed that this process facilitates respiration by shaking the gills; but from a study of the hill-stream fish, where an analogous movement is performed by the paired fins (p. 235), I have come to a different conclusion. It has already been pointed out that in *Epeorus*, water can enter from the anterior end beneath the animal, and there seems to me no doubt that the movements of upper portions of the gill lamellæ are for the purpose of expelling this leakage water. The convergence between the fish and the insect larvæ in this respect is remarkable. It is due to the flapping of the free parts of the structures involved, and their consequent increase in size that ultimately the complete rim is formed on the ventral surface of the animal.

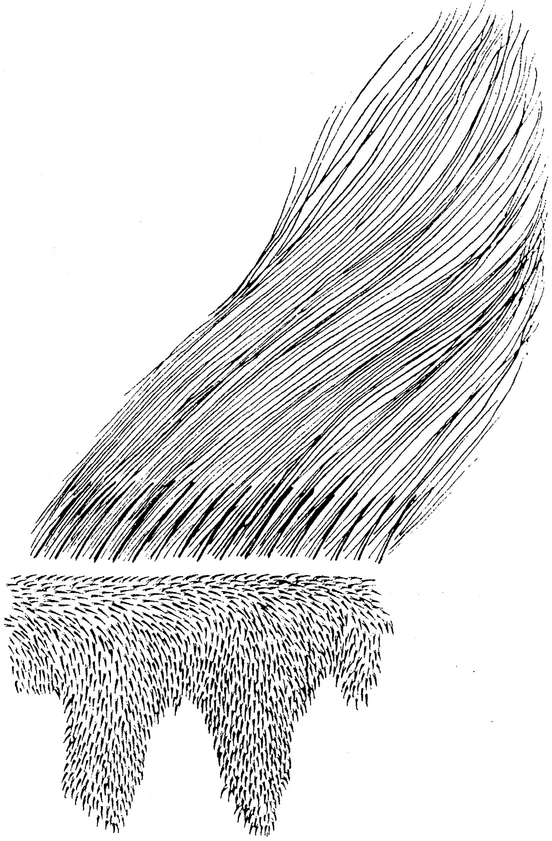
The difference between *Epeorus* and *Iron*, as has been shown by HUBAULT, is very small indeed. If a nymph of *Iron longimanus* (DODDS and HISAW, 1924, Plate 2, fig. 7) be examined, it seems rather difficult to judge whether it should be regarded as *Iron* or *Epeorus*. The nymphs of these two genera are separated on the relative positions of the gill lamellæ of the first pair; in *Iron* they meet in the median line, and in *Epeorus* they are widely apart. *Iron* (Plate 18, fig. 4) is a North American genus, but in recent years a couple of species have been recorded from Europe, one species from China, and one from Japan. It is a common genus in India, especially throughout the Himalayas and the Khasi Hills. The insects are found under stones in swift currents, though on occasions I have found them encrusting the bare surface of rocks. In the Pun-Wa-Sherra stream near Dumpep a few specimens were collected from the neighbourhood of falls, but they were not noticed to frequent the lips of falls. DODDS and HISAW have shown that the effectiveness of the species of *Iron* to withstand the current is determined by the differences in the formation of the so-called " sucker " on the ventral surface of the animal. They have indicated a definite correlation between the rate of flow and the " sucker " of *I. longimanus* and of an undetermined species of *Iron*.

The frictional pads of *Iron* (fig. 1) are more extensive than those of *Epeorus* and have assumed a very characteristic form and structure On the first gill lamella the pad is in the form of a narrow strip more or less coextensive with the hairy fringe along the outer border, from which it is separated by a distinct narrow channel. Along the inner border the pad is produced at intervals into finger-like prominences (fig. 2). The nature of the spines is the same as described for *Epeorus*. Their sharply curved terminal hooks are directed either backwards or inwards, but their direction at different regions of the pad is different. The direction is determined by the physical action of the current, and everywhere the spines are so placed as to effectively withstand its action. The terminal portions of the spines on the finger-like projections are directed inwards and those in the basal region of the pad backwards. Along the outer border there are strong and simple spines directed posteriorly.

The pads on the remaining gill lamellæ are of a somewhat different nature. Each pad can be divided into an anterior broad and thickened portion lying obliquely in the transverse plane of the animal and the posterior part trailing along the inferior border of the lamella. The latter is similar in structure to the pad on the first gill lamella. With the formation of the adhesive pads on the gill lamellæ the legs are modified and only their claws serve as clinging organs. They are consequently thin and elongated when compared with the legs of *Heptagenia* and *Ecdyonurus*. They are somewhat flattened to offer less resistance to the current. The femur is covered on the dorsal surface with a sparse growth of spines and posteriorly terminates in a dagger-shaped process. The caudal setæ are also provided with backwardly directed spines. All these are accessory devices for increasing friction.



Text-fig. 1.—One of the 2nd to 5th gill-lamellæ of *Iron* (*in situ*). × 8. Note the spinous pad along the border.



Text-fig. 2.—The finger-like prominences on the adhesive pads of the gill-lamellæ of *Iron*. × 250.

The nymphs of *Rhithrogena* are believed to be more highly specialized for life in torrential streams than those of *Iron* or *Epeorus*, on the ground that the gill lamellæ are better developed and form a complete adhesive disc on the ventral surface of the animal. According to Needham and Lloyd (' Inland Waters,' p. 371), "*Epeorus*, *Iron* and *Rhithrogena* form an adaptive series." I am not familiar with the conditions in which the nymphs of *Rhithrogena* live, but an examination of preserved material and a study of the published descriptions and figures have convinced me that *Rhithrogena* is in no way more specialized than *Iron*. A comparison between Eaton's figures of the ventral surface of *R. aurantiaca* (Plate 54, fig. 2) and of *Iron sp.* (Plate 55, fig. 2) clearly indicates in which of the two the disc is better formed on the ventral surface. In *Rhithrogena* the lamellæ are narrower, so that they overlap one another at their distal ends only and are not provided with any spinous pads on their ventral aspect, which is perfectly smooth. The fibrils of the abdominal tracheal branchiæ are more extensive in *Rhithrogena* than in *Iron,* and this fact indicates that the former inhabit less oxygenated waters than those in which the latter are found.* Moreover, as is discussed further, the presence of three caudal setæ in *Rhithrogena* is an indication that these insects live in gentler currents; the general facies of the animal also points to the same conclusion.

There is no doubt that in the family Heptageniidæ evolution had proceeded along adaptive lines, but hitherto the significance, the causes, and direction of such a course have not been properly understood. Having discussed the chief characters of the various genera in relation to environment, it is now possible to correlate them with the flow of water, the chief factor in the environment. The development and the consequent modifications of the gill lamellæ have already been pointed out. The caudal setæ under normal conditions help the animal in progression and act like the tail fin of a fish. The inner margins of the two lateral cerci and both the margins of the middle cercus are beset with long hairs, which meet and overlap to form an oar-like structure. Such is the condition in the nymphs of *Siphlonurus, Ameletus,* etc. In the sluggish water Heptageniid genus *Arthroplea* there are three subequal cerci, the inner borders of the lateral and both the borders of the median are ciliated. The Heptageniid nymphs are not powerful swimmers, but they belong to the crawling type, and therefore the natatory organs are not so well developed in them as in *Siphlonurus.* In *Heptagenia* the three cerci retain the same arrangement of cilia as in *Arthroplea.* In *Ecdyonurus* the ciliation is less marked, while the cerci of *Epeorus* and *Iron* have become glabrous. In *Epeorus* and *Iron* the median seta disappears. In swift currents the caudal setæ cannot be spread out like a fan, but they must be held together so as to carry back a stream-line revetment to the extreme posterior end. In this process it is easy to conceive that the median seta will be pressed out of existence, metaphorically speaking, by the pressure of the lateral setæ. Moreover, all ciliation along the inner borders of the lateral setæ will also tend to disappear. *Rhithrogena* is an inhabitant of moderate currents, and the third caudal seta has appeared again to aid in locomotion. To me it seems probable that *Rhithrogena* is derived from *Iron.* Some individuals of the latter genus took to living in pools and regions of moderate currents of the torrential stream. Such a reversion of habitat with a corresponding reversion of structures is fairly common in the hill-stream fauna, and the resultant animals have so far been a source of great confusion.

It is clear, therefore, that the Heptageniidæ should be treated as one homogeneous

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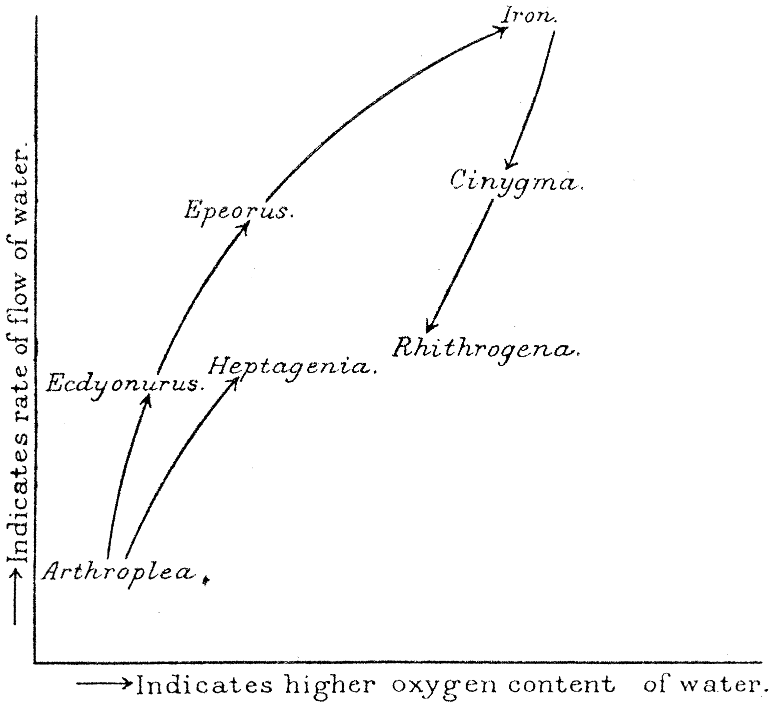
* In swift and well-oxygenated waters the respiratory organs show a tendency towards reduction; see DODDS and HISAW, 'Ecology,' vol. **5**, pp. 262–271 (1924).

family and any attempt to subdivide it on adaptive characters is likely to lead to great confusion. The probable development and evolution of the various genera under the influence of the rapid current is represented in the accompanying diagram (fig. 3).



TEXT-FIG. 3.—Diagram illustrating the probable evolution of the Heptageniid nymphs as induced by two of the main factors in their environments.

## *Bœtidœ.*

The family is divided into several subfamilies whose habits and habitats are very diverse. In the swift currents of the Indian hill-streams I have so far collected the representatives of Bætinæ and Ephemerellinæ only, and as the modifications exhibited by these two types of nymphs are of a different nature I propose to deal with them separately.

*Bœtinœ.*—The Bætinæ are abundantly represented in the torrential fauna of India by the genus *Bœtis*, whose small and shrimp-like nymphs are to be commonly found in mosses growing in rapid waters. Some have invaded the bare rocks, but the number of such nymphs in a particular locality decreases with the increase in the rate of flow of the current. Besides the Blepharoceridæ, these are the only insects that can maintain their hold on the lips of falls ; but their number in such situations is very small. These insects are of active habits, and when disturbed they move sideways, rarely forwards and backwards, with great agility, with their heads always directed upstream so as to present a stream-line form to the current. The adaptations exhibited by certain species of *Bœtis* for life in swift currents are discussed by DODDS and HISAW (1924) and I am in full agreement with their views and interpretations.

*Bœtis* is as much a genus of calm waters as of rapid-running currents. In the sluggish waters they are active swimmers and possess a torpedo-shaped stream-line body for cutting through water. The cilia on the three caudal setæ are well developed and form an oar-like organ of progression. In swift currents, especially in the species that live in mosses, the torpedo-shaped body is retained, for this form is admirably adapted for offering small resistance to the current when it acts with equal force on all sides of the animal. The legs are elongated and modified for clinging. The tibia and tarsus are provided with backwardly directed spines on their ventral surfaces and the leg terminates in a strong and pectinated claw. In certain species the dorsal surface is provided with a series of backwardly-directed hooks, which enable the animal to anchor itself in mosses. These modifications are similar to those found in the Plecopterid genus *Nephelopteryx* (p. 181). In those species of *Bœtis* which live on bare rocks the body is slightly depressed and the ventral surface is flattened. The femora are also flattened and can be closely applied to the substratum.

The three caudal setæ, so characteristic of the sluggish water forms, are reduced to two in the swift-current forms. There exists a direct correlation between the swiftness of the current and the degree of reduction of the median caudal seta. I shall illustrate this point by referring to the three species of *Bœtis* investigated by DODDS and HISAW (1924). In sluggish waters the caudal setæ are richly provided with cilia. In *B. tricaudatus*, DODDS, " The caudal cerci have very scant hairs, which do not overlap to form a swimming organ " (p. 141, Plate 1, fig. 2); this species lives in currents flowing at the rate of 5 feet per second. *Bœtis intermedius*, DODDS, (p. 142, Plate 1, fig. 6), lives in waters flowing as much as 8 feet per second, and in this form the middle caudal cercus has become decidedly shorter as compared with that of *B. tricaudatus*, DODDS. In *B. bicaudatus*, DODDS, the middle caudal cercus is still further reduced and is represented by a small vestige at the anterior end; this species lives in places where the water flows at the rate of 10 feet per second. The reduction of the median seta is accompanied by a tapering of the posterior end of the body, so that in swift currents a stream-line revetment of the body may be carried to the extreme posterior end of the animal. I have shown a similar series of changes in the Heptageniidæ (p. 190).

*Ephemerellinæ.*—The nymphs of this subfamily, so far as I am aware, have not hitherto been recorded from India. In my collection they are represented by a few specimens from the Krelnu Giri Nallah at Dalhousie and the Ravi River at Chamba in the Western Himalayas. They possess a depressed and elongate form, and on this account it is easy to distinguish them from the rest of the mayfly larvæ. It has, however, not been possible to assign them definitely to any genus, though they look like *Ephemerella*. The specimens were collected from underneath stones in swift currents. The body is depressed with the ventral surface flat. The femora of the first pair of legs are greatly flattened and are provided with tubercles on the dorsal aspect. The tibia and the tarsus are slender and are serrated along the ventral edge.

The terminal claws are strong and sparsely denticulated. The lateral edges of the abdominal segments are pectinated with backwardly directed spines. All these are devices by which the nymphs are enabled to maintain their hold in swift currents.

LESTAGE has recently (1925) discussed the salient features of this type of nymph in relation to its bionomics. The most remarkable nymphs of this group are those of the genus *Drunella,* which are said to possess " a sucker on the ventral side of the abdomen, formed by the hairy sterna of seven of the abdominal segments. Each of these segments bears a dense growth of fine hairs, which are shorter on the median portion and become longer laterally, where they are situated on a low ridge. The sucker is completed anteriorly by a similar hairy ridge, which follows the curved anterior margin of this segment to form a crescent-shaped area, while on the last two segments of the sucker the hairs are of about uniform length, and distributed over the entire surface of the sternum. This is an adhesive organ of considerable power, as shown by the strength with which nymphs adhere to rocks or aquaria, strongly resisting efforts to remove them " (DODDS and HISAW, 1924, p. 146).

I have carefully studied the published figures of the nymph of *Drunella grandis* (DODDS and HISAW, 1924, Plate 2, fig. 11, and EATON, *Monograph,* Plate 39), but am not able to make out the mechanism by which a vacuum can be created on the ventral surface so as to convert it into a sucker. Before a vacuum can be formed the water below the animal must be pressed out, and there does not appear to be any device for accomplishing this. The arrangement of the spines, on the other hand, suggests that adhesion is effected by increasing friction on the under surface. There is a tendency towards reduction of the spines at the anterior end, and this would permit the front end to be kept as close to the substratum as possible in order to prevent the water from flowing underneath the animal. The low ridge at the sides and along the anterior border of the abdomen is developed for the same purpose. In short, a disc of a somewhat similar nature to that of *Iron* (p. 188) is formed, but the chief point of difference is that the gill lamellæ, which in *Drunella* are situated on the dorsal surface, are not used to increase the surface of adhesion. The disc of *Iron* is more extensive and elaborate, and is, therefore, capable of resisting a very rapid current. Adaptation of the same kind has been achieved by the nymphs along two different lines, and it is interesting to note that regular series exist showing the various steps in the gradual transformation of the animals. *Ecdyonurus, Epeorus* and *Iron* form one series in which the gill lamellæ form adhesive organs, and the second series consists of the diverse species of *Ephemerella* leading up to *Drunella.* In the latter series the gill lamellæ do not take any part in the formation of the adhesive disc, which is formed by the flattening of the body alone.

Remarkable and diverse types of modifications are found in the Ephemerellid nymphs, but unfortunately their adaptive significance is little realized. For example, LESTAGE (1925) says : " Pourquoi un milieu identique, un même genre de vie, un même régime, ont-ils modelé tel type autrement que tel autre ? Comment peut-on concevoir le processus de cette évolution ? Voilà une question qui restera longtemps encore sans réponse." The whole confusion seems to have arisen by neglect of the study of the various factors in an environment. I have indicated in the beginning how an apparently "milieu identique" can be shown to consist of different regions having different sets of conditions in so far as they affect the animal life (p. 176). I shall further illustrate this point here by referring to the form of legs and the disposition of the tracheo-branchiæ in the various species of *Ephemerella.*

It has been noticed by Miss MORGAN (1913) and LESTAGE (1925) that among the *Ephemerella* nymphs the denticulation on the claw is inversely proportional to the depressed form of the femur. For instance, the femur of *E. deficiens,* MORG., is simple, but the claw is strongly pectinated, whereas in *E. tuberculata,* MORG., the femur is flattened, but the claw is simple. It has been shown in several cases that long and slender legs provided with strong and pectinated claws are an adaptation for life in aquatic plants in swift currents. The animal resists the constant pulling and swaying movements by bending and stretching its legs and by securing a firm grip with the pectinated claws. In those nymphs that live on bare rocks the necessity is to keep the legs as closely pressed to the substratum as possible, and consequently the femora are greatly flattened. The tubercles on the dorsal surface of the femur probably enable the animal to secure a hold in narrow crevices or they help in reducing resistance (p. 255). On rocks the tip of the claw is the only part that can be used effectively for gripping, and consequently the teeth along its inner margin tend to disappear. Thus it is possible to correlate the structural differences with variations in environments.

The tracheo-branchiæ are dorso-lateral in position, and in nymphs living in narrow crevices or among mosses they are apt to be injured. In these forms a protective covering is developed for the delicate gills. This tendency towards cover-formation has been considered to be of great taxonomic importance, and it is on this character, in spite of other fundamental differences, that the Ephemerellinæ and the Cæninæ have been considered to be close allies (LESTAGE, 1925). In the two types of nymphs the elytroid covering is developed under entirely different environmental conditions; in Cæninæ it is probably for the avoidance of silt, as in *Asellus,* whereas in Ephemerellinæ it is produced in clear waters to save the gills from mechanical injury. Such a covering is developed in widely separated Ephemerid nymphs (NEEDHAM and MURPHY, 1924), living in diverse environmental conditions, but with the sole purpose of saving the gills from injury of any kind. Such a convergent evolution has often baffled the taxonomist, and there is no doubt that the true relationships of the Ephemerellinæ and Cæninæ will become clear only when the mode of life of these animals is better understood.

### *Prosopistomidæ.*

The most remarkable nymphs are those of the genus *Prosopistoma,* which appear at first sight to be small *Apus*-like Crustaceans, and, in fact, were referred by their discoverer to the Branchiopoda. Through the kindness of Mr. L. BERLAND, of Museum

National d'Histoire Naturelle, Paris, I have been fortunate to examine a few specimens of these curious animals. With the exception of the tail region, the head and body are broadly oval in appearance and are greatly depressed. The dorsal surface is convex and the ventral is somewhat concave. The slender legs terminate in powerful claws and are concealed underneath the body. The organism is thus admirably adapted to present a stream-line form to the current (compare its form and position of legs with Psephenid larvæ, p. 204). Forming the margin of the body there is a strong and narrow chitinous band, which can be closely applied to the substratum. Internal to the band, the surface is covered with small papillæ on the ventral aspect, which probably help the animal in adhesion.

The small Coccid-like nymphs of *Prosopistoma* are found in clear and rapid streams generally near the shore and in fairly deep waters (40 to 150 cm.). They live on the underside of rocks, hiding in narrow crevices. It is evident, therefore, that these animals are not adapted to live in very swift currents. With the help of their fan-like tail setæ they are able to swim from one place to another with great speed, but their crawling movements on stones recall those of bed-bugs. When placed in clear water they apply themselves to one another by coiling and curling in various ways and thus form small masses. When alarmed they seek shelter under stones with great agility (see Psephenid larvæ for similar habits, p. 203). The nymphs are known to adhere to stones with considerable force and it is difficult to dislodge them (see LESTAGE, in ROUSSEAU's 'Les Larves et Nymphes Aquatiques des Insectes d'Europe,' pp. 179–181).

It has hitherto been supposed that these animals "possess the faculty of adhering firmly by suction, like a limpet, to stones" (EATON, 1883, p. 13). I am, however, unable to understand how a permanent vacuum can be created on the ventral surface of the animal. It seems to me probable that a true sucker is not formed and that the adhesion is effected, firstly by the close application of the margin of the body to the substratum so that no water can get beneath the animal; secondly, by the stream-line form of the animal, which helps to keep the nymph pressed down to the substratum by the force of the current, and, lastly, the movements of the retractile caudal cerci, which, by pumping out the leakage water from underneath the animal, help to create a negative pressure in that region (p. 259). The last suggestion, here advanced for the first time, requires further consideration.

The retractile movements of the caudal cerci (mouvements d'invagination ou d'évagination) have been observed by earlier writers, who attributed to them an important *rôle* in the respiratory mechanism of the animal. According to them, these movements are instrumental in creating a respiratory current through the gill-chamber. VAYSSIÈRE (1882), however, showed the futility of this theory by demonstrating that these movements had nothing to do with the respiratory current, which had a definite entrance and exit. Up to the present no other hypothesis has been advanced to account for the characteristic movements of the caudal cerci. It is from analogy, and not from a study of the living organisms, that I have inferred the utility of the movements for pumping out the leakage water from underneath the animal.

### *Hemiptera.*

My colleagues, Dr. B. N. Chopra and Dr. H. S. Rao, directed my attention to certain creeping water-bugs of the family Naucoridæ, which they had collected in the hill-streams of Northern Burma (Myitkyina District and Northern Shan States). The insects were found living under stones in swift currents; they are greatly flattened dorso-ventrally, are oval in outline and scale-like in appearance (Plate 18, fig. 2). The smooth dorsal surface is greatly arched, and is admirably adapted to present a stream-line form to the current and to offer only a little resistance. The legs of the first pair are modified to form grasping organs; they are greatly flattened and can be closely applied to the substratum. The middle and the hind pair of legs are suited for crawling, and it is on these appendages that special frictional pads are developed to prevent the animal from slipping. Of the two pairs, the hinder pair is better developed and is densely provided with frictional devices.

Each crawling leg (Plate 17, fig. 6) arises from a socket-like depression in which the well-developed coxa can be rotated freely. This movement enables the animal to use the legs for crawling at one time and fixing itself on rocks at other times. At the distal end in the mesio-ventral region of each coxa there are many long and stiff hairs directed backwards. There are rows of short, backwardly-directed spines along the borders of the femur, which is grooved at the distal end to accommodate the proximal part of the tibia. The tibia is richly provided with strong, backwardly directed spines, especially along the mesial border; the spines increase in length posteriorly. In the distal third of its length the tibia is broadened and bears a pad of well-developed spines on its ventral aspect. The spines are slightly curved, elongated and directed distally. The tarsus is highly chitinised; its proximal segment bears a few strong backwardly-directed spines. The tarsus ends in a pair of strong, recurved claws. The pads on the tibiæ are well marked, and in most cases they appear black on account of the thick deposition of a chitinous material. There is no doubt that they are very efficient in stemming the rapid flow of water.

On the ventral surface (Plate 18, fig. 2), in the middle line, there is a series of short and strong hooks directed posteriorly, and each segment is produced into a backwardly directed process at the margin. Each half of an abdominal segment on the ventral surface bears an oval patch of lighter colour, and towards its outer limits there is a patch of short, backwardly pointed spines. Each segment also bears a pair of small rounded depressions, from which tufts of strong bristles seem to arise. To me these structures appear to be remnants of once well-developed organs of attachment. The increased flattening of the body and the development of adhesive pads on the legs have brought about the smoothening of the ventral surface.

My colleague, Dr. H. S. Pruthi, collected a large number of Naucorid bugs from the algal mats and aquatic vegetation in the head-waters of the Narbadda River in moderate current. In these insects the lateral margins of the body are serrated and the legs are provided with long spines, which are directed posteriorly (Plate 17, fig. 7). The dorsal surface is smooth, but the ventral surface is covered with backwardly directed hairs. Along the mid-ventral region the body is slightly elevated and the hairs in this part are longer and stronger. These are small bugs, and in their appearance and mode of attachment to plants closely resemble the onisciform larvæ of *Helodes* (p. 205).

### *Trichoptera.**

As a class the caddis-worms are enabled to progress in rapid waters by means of the anal hooks and the powerful claws on the legs; these structures show a definite correlation between their form and the strength of the current. The animal is but slightly modified, because it is the case more than the insect itself that is subjected to the effect of the environment. Only in the free-living forms the body deviates slightly from the normal type.

The caddis-worm fauna of the swift currents can be roughly divided into two categories according to the habits and habitats of the animals and without any reference to their systematic position. Firstly, the free-living larvæ that do not build a case or a web-like structure, and, secondly, those that manufacture some kind of shelter; there are no rigid lines of demarcation. As a rule these animals are met with in all kinds of situations, but, so far, I have not found them on the brinks of the falls or on the upper surface of bare rocks in *very* swift currents. The free-living forms are obviously the best adapted for life in rushing torrents, because in these situations the tube, instead of being advantageous in providing shelter and safety, would be an encumbrance.† Attention may here be directed to a similar state of affairs found in the torrent-inhabiting Chironomidæ (p. 210). The convergence in this instance is evidently due to the similarity of environment.

In the larvæ of the first category the abdominal hooks (see Hubault, 1927, p. 334, for figure) are greatly developed and the claws on the legs are of a relatively larger size. By means of these grappling organs the larva is enabled to fix itself effectively at both ends. They are found on exposed surfaces of rocks and on aquatic vegetation in moderate currents. The abdominal hooks have their inner curved surface sharply denticulated.

The free-living larvæ are of a small size and belong to the family Rhyacophilidæ. The body is depressed and the ventral surface is somewhat flattened; the body is thick in the middle and pointed towards both ends (fig. 10*b*). All these are modifications due to life in strong currents.

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* My best thanks are due to Prof. J. A. Lestage for reading through the account of the Trichoptera and to Mr. D. E. Kimmins for identifying the material.

† Lloyd (1921, p. 23) observed that the normally tube-inhabiting larva of *Neuronia postica* abandons its case when entering submerged trash, where the case probably proves cumbersome.

The larvæ of the second category can be classified into those that manufacture fixed shelters and those that build portable cases. According to my observations, the former are better adapted for life in rapid waters. There are certain larvæ that live on the underside of stones, where they construct a barricade of pebbles, holding them together by their strong silken secretion. These are sluggish in their habits and on provocation they leave their shelter and seek refuge among small stones in the bed of the stream. These larvæ are in a sense free-living, and thus provide a connecting link between the larvæ of the two categories.

Certain larvæ manufacture a shelter of thin-spun silk, which becomes covered with mud or silt, and fasten it on the upper surface of rocks in rapid-flowing water. I have found this type (genus *Philopotamus*) in a small stream near Peebles, and such a type of larval shelter is perhaps only to be found among the Philopotamidæ (NOYES, 1914). The case is analogous to the larval cases of the torrent-inhabiting Lepidoptera (p. 201) and of *Antocha* (Tipulidæ, p. 209). The larval shelters of these widely separated groups of insects afford an instructive case of convergence.

Of the caddis-worms with portable cases there is a great variety of form found in rapid-flowing water. I have collected certain larvæ of the family Leptoceridæ, which fasten their cases to rocks in swift currents and spread out their legs in order to receive the organisms which the current may sweep to them. The case is elongated and always found with the head directed upstream, thus presenting a stream-line form to the current. These animals are found in masses in suitable places.

Generally, however, the portable case is dorso-ventrally flattened, the upper surface being slightly arched and the under surface flattened so that it can be closely applied to the substratum. The cases are formed of small bits of stone and are, therefore, heavy, enabling the animal to remain near the bottom. Some tubes are elongated and rectangular in form, while others are oval and limpet-shaped. In all cases the form is so modified that the pressure of the current is used for keeping the animal close to the substratum. The limpet-shaped forms are so closely applied to stone that they adhere to it even when the stone is taken out of water and held in such a way that the animals are directed vertically downwards. According to ULMER and THIENEMANN (see HUBAULT, 1927, pp. 335, 336), the attachment is effected by the formation of a sucker. ULMER has observed it in *Lithax obscurus*, HAG., and THIENEMANN in *Drusus dicolor*, RAMB.

According to these authors, the silky lips of the orifice of the tube are closely applied to the substratum and by a backward contraction of the larva in the tube a vacuum is created. If it were really so the animal would hang from the stone with only the portion of the orifice applied to it; but actually the whole of the ventral surface remains in contact with the rock. This observation clearly indicates that the sucker-theory of attachment has to be abandoned. The fixation is effected thus: the flattened tube is closely applied to the substratum, and when a stone harbouring these is taken out of water, a thin film of water is caught between the case and the rock. It is partly due to the capillary action of the water that the object sticks to the stone. The most important factor, however, is the atmospheric pressure, which acts only on the exposed upper surface and is prevented from exerting any influence on the underside of the tube on account of the presence of a thin film of water. It is observed that when the stones are held out of water for a long period the animals drop off. This is due to the evaporation of water, which binds the animal to the rock. The same action can be observed by applying the broad side of a piece of rubber to a glass slide under water and then lifting the two together. The rubber will stick to the slide so long as the surface is wet.

The most remarkable are the *Ancylus*-shaped cases of certain species. These are found sticking to rocks in fast currents. The tube is formed of small particles of sand agglutinised by an abundant secretion of the animal. Such are the cases of the European species, *Thremma gallicum.* A similar type of larval shelter, scale-like in form and with flexible margins, I have figured in ‘ Journ. Bombay Nat. Hist. Soc.,’ p. 124, fig. 9*b*, 1927. The upper surface is arched and stream-lined and the attachment is effected by means of adpression. Superficially these forms resemble the Psephenid larvæ.

At the time of pupation *all* the caddis-worms manufacture a pupal shelter*, which is cemented to the substratum. The place selected is such that the insect can readily escape from the current ; they usually occur on the upper surface and sides of a rock in shallow water. Thus masses of pupæ are usually found at one place. Pupal cases of thick spun silk were found on the vertical faces of rocks over which the water fell in the Pun-Wa-Sherra stream, near Dumpep. These cases were fastened to the substratum by means of adhesive pads and resembled the pupal shelters of the European species, *Oxyethira tristella* and *Agraylea pallidula.* Their superficial resemblance to the pupal cases of rapid water Lepidoptera may also be noted.

“ The eggs of the caddis-flies are dropped in various ways and places. Some are dropped in the surface of still pools while in flight. The females of some of the Hydropsychidæ crawl beneath the water and spread their eggs in a single layer over the lee side of stones in the gentler currents. The big form of *Phryganea* fasten their pretty green eggs in a gelatinous ring on the stem of some aquatic plants ” (Needham, 1918, p. 902). Lestage (1922) has described the immersed egg-masses of a species of *Micrasema* from flowing water. He observes that “ Les pontes étaient disposées, les unes à côté des autres, à la *face inférieure* des pierres immergées en plein courant.” While working at Dalhousie in May-June, 1927, the brinks of small waterfalls in the course of the

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* Lloyd (1921, p. 5) remarks that “ Trichoptera are the only insects, possibly excepting a very few Diptera (of the genera *Simulium* and *Chironomus*), with aquatic pupæ. In several other orders one finds a few species with submerged pupæ, but they all tap the stems of a few aquatic plants, entrap air in dome-like covers, or in some other way breathe free air. The pupæ of Trichoptera are as much aquatic as are their larvæ.” In the hill-stream insects there is a tendency to have purely aquatic pupæ, for example, in Blepharoceridæ, *Antocha* (Tipulidæ), *Maurina* (Psychodidæ), *Psephenoides* (Dryopidæ, Coleoptera), *Elophila* and *Aulacodes* (Lepidoptera), etc., etc.

Punjpul Stream were found literally covered with gelatinous egg-masses. So far as I am aware, no animal has ever been recorded as depositing its eggs in such perilous situations. Simuliidæ, Blepharoceridæ and some other insects are known to lay eggs on the wet sides of a fall, but not actually in a swift current. Quite a number of insects enter water for egg-laying, but they seek the undersides of stones in gentler currents, and even then they frequent the leeward sides of stones.

The egg-masses were at first noticed about the full-moon period, and about a week after a Trichopterous fly* was observed to visit the lip of the fall. The water was rushing down with great force, and only after exercising much patience were we able to secure three females in the process of egg-laying and to capture several on the wing. The females were observed hovering over the small falls. They alighted on the wet surface of rocks, wrapped themselves with their wings, and hurriedly entered the rushing water with the head pointing upstream. They carried with them a film of air, which made them appear silvery, and so their progress under water could be easily watched. When disturbed, the insect rose to the surface and flew away.

Except for a small portion in the middle, the whole of the lip of the fall was covered with small gelatinous masses. This was not surprising, because at this time of the year there were thick swarms of caddis-flies at Dalhousie. The position of the eggs showed that some of the insects must have penetrated into the water for a considerable distance before depositing eggs. The egg-masses† looked like algal growths, and it was only after a careful examination that their true nature was discovered. Each egg-mass (Plate 17, fig. 8) is broadly oval in outline and is similar to the ring-like mass of *Phryganea*, except that it is more compact and that the central portion is also filled up. The egg-masses were hanging from the rocks and were swayed from side to side with every eddy of the current. The eggs when freshly laid were of a dull white colour, but they turned brown after a short time and then became dusky. In the preserved material each larger egg-mass is about 2·7 mm. long and 2 mm. broad, while a smaller egg mass is 2 mm. long and 1·6 mm. broad. The numbers of eggs in three masses were 220, 280 and 296 respectively. The eggs are enclosed in a thick gelatinous and transparent bag. Each egg is oval in shape, 0·27 mm. long and 0·24 mm. broad.

The adult insect is provided with frictional devices by which it is enabled to stem the current when under water. The long and slender legs terminate in grappling claws. The coxæ are greatly flattened and applied to one another in the mid-ventral line in such a way that a keel is formed to cut through the water. At the junctions of the various divisions of the legs strong brushes of spines are developed and some are

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* The insect was sent for determination to Prof. J. A. LESTAGE, but he and Dr. G. ULMER are unable to determine the female generically. They consider it to belong to the subfamily Lepidostomatinæ (Fam. Sericostomatidæ).

† The gelatinous egg-masses provided shelter and food for several types of organisms. Chironomid larvæ were found in great abundance, while the young of Blepharoceridæ and Trichoptera were not uncommon. There is no doubt that the Chironomidæ and the caddis-worms feed upon these egg-masses.

present on the tibia. The spines are directed distally and by fixing themselves into the unevennesses of the rocks anchor the animal in swift currents.

### *Lepidoptera.*

In fast-running water the larvæ of Lepidoptera live beneath sheets of silk spun over exposed surfaces of current-swept boulders. Those found by me two miles below Pashok, in the Eastern Himalayas, were living on huge rocks forming lips of falls; while those collected from the Narbadda River were found on stones covered with growths of filamentous algæ and forming the bed of a rapid. They were also found on bare rocks, and especially in places where the river bed was formed by one rock the silken houses of these larvæ were quite common. When the cases were preserved in spirit, the liquid turned greenish owing to the presence of chlorophyll in the plants, such as algæ, etc., that had become entangled in the silk and on which the insect probably feeds. About the habit of *Aulacodes simplicalis*, MUIR and KERSHAW (1909, p. xl) remark as follows: "In several spots where the water was most rapid we found the larvæ of a species of Hydrocampinæ living on the surface of rocks, sometimes under 18 to 24 inches of swiftly flowing water, at other times under a few inches, or where the rocks were continuously covered with a shower of spray."

When disturbed the larva readily moves from one part of the case to another, but is very reluctant to leave its shelter. When forced to come out it moves fairly quickly on the bare rocks by grappling on to the substratum by means of the crotchets on its abdominal prolegs. The sharply hooked and highly chitinised crotchets are directed towards the middle of the "planta," and therefore to disengage them the centre of the disc is completely inverted by the muscles attached in the middle of the disc. The prolegs are situated on segments 3 to 6 and 10.

The three pairs of thoracic legs are short and stumpy and at their terminations bear short but strongly chitinised and recurved claws. The claw resembles in form the hooks on the posterior appendage of a rapid-water Chironomid larva. The body of the larva is somewhat depressed so that it offers less resistance to the rushing current. The anchoring devices are distributed along the entire length of the animal so that no free portion is presented to the current. The larva is further protected by its silken shelter from being swept away.

Each larva at the time of pupation manufactures a dome-shaped pupal shelter under some portion of the larval cover and this it fastens securely to rocks leaving rows of openings on the anterior and the posterior sides of the case for the free circulation of water through it. When the pupal case is completed, the unoccupied portion of the larval shelter is washed away. The pupal case shows a remarkable similarity to the limpet-shaped shelters of so many of the rapid-running forms.

I have no direct observations to offer on the bionomics of the imagines. According to MUIR and KERSHAW (1909, p. xli), "The adult moth readily takes to water when frightened, diving below the surface, and using its legs for swimming. The wings are appressed to the body and the whole insect more or less covered with air bubbles. They were capable of remaining 30 minutes or more below the surface, clinging to plants and submerged weeds. It is possible that in suitable situations the female enters the water to oviposit, but this would be impossible where the stream runs swiftest, and in such places it is possible that they lay eggs on the wet rocks along the edge of the water."

### *Coleoptera.**

I have devoted some time to the study of the bionomics of the beetles of the two families—the Dryopidæ and the Helodidæ. The former are found in great abundance in the torrential streams of India and the latter were studied in a small, clear, rapid-running stream near Peebles (Scotland).

*Dryopidæ* (*Parnidæ*)†.—The small beetles of the family Dryopidæ live under logs and stones and in mosses in clear flowing water. In these forms the tarsal claws are very strong and in the several species of *Elmis* from South India they are toothed near their bases. In *Helichus tenuis*, from the Haldwani Division of Kumaon, the body is covered by hair-like processes and the legs are long and slender. *H. tenuis* probably lives clinging to water weeds, where the animal is swayed from side to side with every eddy of the current, and its long and slender legs armed with terminal grappling claws are of great assistance for anchorage in these circumstances.

Certain Dryopid beetles, such as *Psephenus* and *Psephenoides*, possess scale-like rounded or ovoid larvæ which have been termed by COMSTOCK "Water-pennies." These are found in great abundance in the Western Himalayas (Kangra Valley), in the Eastern Himalayas (Darjiling), in the Khasi Hills and in the Head Waters of the Narbadda River, Central Provinces. The only detailed account of the Indian larvæ of this type is that of BÖVING (1926), who has recently described the immature stages of *Psephenoides gahni*, from material collected in the Nandhaur River, Haldwani Division of Kumaon. He has described the habits of the larva by inference from its anatomical structure. I made observations on the habits of the *Psephenus*-like larvæ in a small stream, below Dumpep, in the Khasi Hills. Both the types, *viz.*, with abdominal gills and with anal gills, were fairly common in this stream.

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* Mr. K. G. BLAIR has read through the account of the Coleoptera, and for this my best thanks are due to him.

† Beetles showing diverse affinities have been grouped in the family Dryopidæ and by recent authorities they are split up into three distinct families. BÖVING (1926) has discussed the probable relationships of the beetles of this assemblage, but in view of the fact that my collection has not yet been determined, I refrain from referring to them by their distinctive names. The *Psephenus*- and *Psephenoides*-like larvæ that I have collected in great numbers from several places in India are found living together in the same stream. The former are characterized by the presence of free branchial filaments on the ventral side (IMMS, fig. 480), and the latter by the presence of a group of retractile anal gills (figured by BÖVING). According to BÖVING, Psephenidæ and the Dryopidæ (including Elmidæ) are distinguishable only on the character of the gills.

The larvæ (Plate 18, fig. 1) were found in great abundance on the underside of stones in rapid-flowing water about 6 to 7 inches deep. When the animal was crawling, the body appeared to be flat; but when it rested on the substratum the body was greatly arched. In the former position the body was carried on the legs and the margins were raised so as to obviate friction during locomotion, whereas in the position of rest the flaccid margins of the larva were closely pressed against the substratum, and it was rather difficult to dislodge it with fingers. The anal gills were thrust out and withdrawn with great force at regular intervals; in their fully extended condition the gills presented a flower-like pattern.

A larva was placed on a wet slide and observations were made to test the sucker action of the body. It was noticed that so long as the slide was wet the animal could be moved about in all directions with slight force, but as the slide dried it became increasingly difficult to move or lift the larva. A number of larvæ were left in water in a finger-bowl. After a time it was found that all of them had come together and had formed a mass by applying their ventral surfaces to one another. A piece of stone was placed in the bowl close to them. After an hour or so all the larvæ were reposing on the underside of the stone. This indicates positive statozoic and negative phototropic habits of these animals.

When a larva was dropped in a bowl of water it sank to the bottom very slowly, and meantime moved its margins in all possible ways, ultimately coiling itself up like an Isopod. In nature probably it adopts this device when forced from its hold by the current; it coils and rolls.

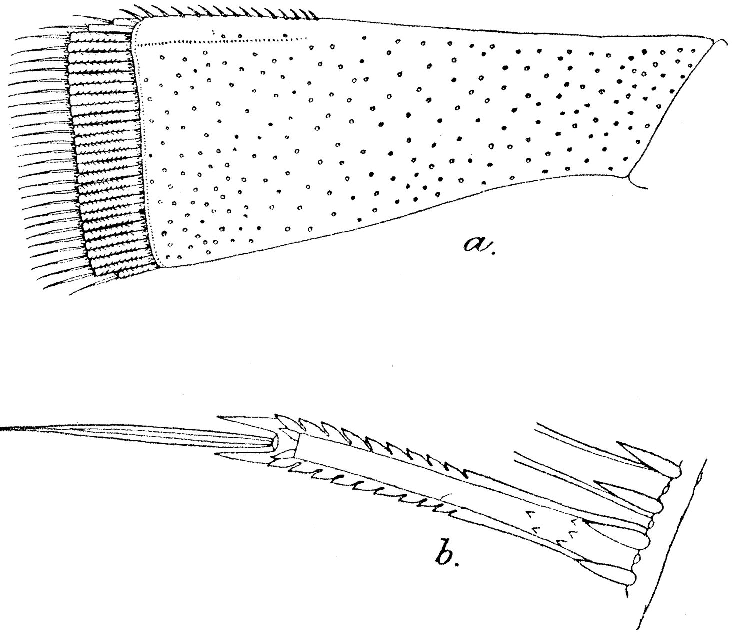
Previous to pupation, a number of mature larvæ were observed to seek small, shallow, oval or circular depressions on the under surface of the stones and pebbles. At first the dorsal surface of the larva became flat and the margins of the disc were cemented to the substratum by a sticky secretion. After a while the body became arched again and closely resembled the larva when viewed from above, except that it was provided with long, hair-like processes. As I have indicated in an earlier paper (1927, *b*) the margin of the attachment of the puparium leaves a black mark on the stone.

Respiration is carried on by abdominal branchiæ in *Psephenus*, and KELLICOTT (1883) observes that "These long white organs are seen waving to and fro continually while the animal is alive. This motion appears to be due to the up-and-down stroke of the last segment, which repeatedly strikes the water, as the tail of a crayfish does when swimming." It is obvious that with a continuous flow of water to bathe the branchial filaments, no sucker can be formed on the ventral surface of the animal. The sucker theory of the attachment of these larvæ has, therefore, to be abandoned.

Attention may here be directed to the fact that the larvæ of the Dryopidæ show a progressive series of adaptations for life in swift currents. It has been pointed out by NEEDHAM and LLOYD ('Life of Inland Waters,' p. 371) that in the larvæ of *Elmis*, *Dryops* and *Psephenus* there is a "close correlation between the degree of flattening of the body and the rate of flow of the water inhabited." This series could be made more imposing by including the larva of *Helichus* before *Psephenus* and that of *Psephenoides* after it. It is in the last genus that the entire margin of the body is closely applied to the substratum.

Having indicated that no sucker is formed in these larvæ, I shall now attempt to show how attachment is actually brought about. When the animal crawls, the muscular legs with their powerful tarsal claws are its main organs of anchorage. There are strong bristles immediately above the claw and a tuft of them on the inner side a little distance away from it on the proximal side. Along the mesial border of the leg there is a row of thorn-like, backwardly directed processes. All these chitinous outgrowths help to increase friction and impart greater security to the movements of the larva. The flat scale-like body is also advantageous, for it offers very little resistance to the flowing water.

When at rest the body is arched and is so shaped in streamlines that the resistance offered to the current is the least possible, and the resultant pressure, instead of dislodging it, holds it down firmly to the substratum. Near its free edge each of the lateral and radially extended expansions of the thoracic and abdominal tergal shields is furnished with a dense continuous fringe (Plate 17, fig. 9 ; fig. 4*a*). This fringe can be divided into two parts, the distal part consisting of long hair-like setæ situated at short distances from one another, and a proximal part of flat rod-like structures which are denticulated along their margins and lie close to one another, forming a continuous flaccid rim at the margin. Distally each rod terminates in a pair of strong spines, from the middle of which a seta arises (fig. 4*b*). At the base of these rods, but ventral to



Text-fig. 4.—The marginal area of a *Psephenus*-like larva. *a* = lateral and radially expanded tergal shield. × 50 ; *b* = a portion of the distal part of the same. × 300.

them in position, is a series of strong spines directed towards the periphery. On the ventral surface of each rod near the proximal end there are a few short spines directed outwards. The arrangement of the spines described above is such that they enable the animal to stem the current flowing in the same direction in which they are placed. It is obvious, therefore, that only the structures of the side of the animal opposing the current are in use at one time. The advantage of the superficial radial symmetry is also clear, for in whichever position the animal rests there are sufficient spines to prevent it from slipping. If the animal be lifted vertically upwards (this never happens in nature) from its centre, then theoretically, according to the direction of the spines, they should offer no resistance, but by this pull a temporary sucker will be created which would resist the upward lifting of the insect. The animal, however, is so small that I could not perform this experiment successfully.

The accompanying figures (Plate 17, fig. 9 ; Plate 18, fig. 1, and text-fig. 4) clearly show the complicated structure of the margin of the larva. BÖVING (1926, p. 381) also referred to the structure of this region, but had not appreciated the significance of the various parts.

A study of the marginal region of a young larva of the Psephenid type shows that the entire complicated apparatus of the adult is due to the modification of the cilia* usually present in aquatic larvæ. It is possible to trace all the stages in the evolution of the mature structure. Along the distal end of the anterior border of the lateral expansions are rows of spines followed posteriorly by a narrow area of lighter chitin. The spines are directed towards the periphery and provide movable articulations between the various shields. The lighter areas of chitin indicate where the lateral expansions telescope one into another. This arrangement enables the larva to coil itself like a Trilobite.

*Helodidæ.*—The onisciform larvæ of a species of *Helodes* (probably *H. minutus* LINN.) were found living in mosses and in accumulations of dry leaves and twigs in the course of a small, rapid-running, clear stream near Peebles (Scotland). The larva, when removed from its hold, partially coiled itself.

The margins of the segments are laterally extended and the animal closely resembles a Trilobite in appearance. The legs are very muscular and are provided with groups of strong distally directed spines, which undoubtedly prevent the animal from slipping. All along the margin of the body there are strong bristle-like spines directed posteriorly. On each segment the spines increase in length towards the posterior end and the last two spines on each side of the segment are greatly elongated. It is by means of these chitinous prolongations that the larvæ are enabled to entangle themselves in mosses growing in swift currents. HUBAULT'S figure of *H. minutus* shows all the salient features to which reference has been made above.

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* I have examined a *Psephenus* larva in the collection of the Zoology Department of the University of Edinburgh and have found that its marginal region is provided with long, stiff hairs which are not differentiated like those described above in the Indian Psephenid larvæ. This indicates that *Psephenoides* is better adapted to live in torrents than *Psephenus*.

## *Diptera.**

I have made personal observations only on the larvæ and pupæ of the Simuliidæ and the Blepharoceridæ, and to a limited extent on those of the Chironomidæ. In the case of some of the other families I give below a brief summary of our knowledge regarding the torrent-inhabiting forms. Attention may be directed here to the habits of the Empid flies, of which several species were collected at different places at Dalhousie and in the Chamba Valley. The flies were found clinging to the edges of rocks over which the water was rushing, or to the damp, moist surfaces of rocks and crevices, placed so close to the main rush of water that they were drenched with the spray. Several pairs were seen *in copulâ* in such localities.

The behaviour of the Empid flies that I observed at Dalhousie is similar to that of the Blepharoceridæ.† It is probable that they belong to the sub-family Clinoceratinæ, the members of which are known to "frequent running water, some resting beside waterfalls or on water-splashed rocks in swift streams, or even amphibiously entering the water" (MELANDER, 1927, p. 7). *Clinocera* is known from Western Himalayas, and it is probable that my specimens belong to this genus.‡ These insects moved sideways in fits and starts, but their movements were very quick. They always preferred the shady side of the rock and were quite common towards the evening. In the earlier part of the night they were found in abundance and were strongly attracted to artificial light. The flies sometimes rested at one place for quite a long time, taking to flight when disturbed.

The convergence in outward form between the Blepharoceridæ and the Dalhousie Empids is still further remarkable. The latter have long thin legs, provided with spurs and spines on different parts to enable the animal to anchor itself on rocks. They bend on their flexible legs when hit by the spray of water, but instantly regain their former position without having lost their hold in the interval.

### *Psychodidæ.*

Of this family, HUBAULT has given a short account and has referred only to the larva of *Pericoma*, which he found among mosses in rapid waters. This larva is found entangled among mosses by means of chitinous spines with which the body is densely covered. MIALL and WALKER (1895, pp. 141–143) have very clearly indicated the function of these spines as follows: "It seems probable that these long and stiff hairs, all pointing backwards, like those which project from the dorsal shields, save the larva

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* Mr. F. W. EDWARDS has read through the section on Diptera and has made valuable suggestions. My sincere thanks are due to him for his kind help.

† TILLYARD, 'Australian Zoologist,' vol. 2, pp. 166, 167 (1922).

‡ Mr. F. W. EDWARDS has very kindly informed me that the Empids I collected at Dalhousie belong to the genus *Clinocera*. In his experience *Clinocera* "are usually very active and difficult to catch, taking alarm very easily."

from being swept away by a sudden rush of water. Buried, as it commonly is, in well-rooted, filamentous algæ, the larva has only to keep its head upstream to offer a most effective resistance to the current, while it will not be seriously hindered in travelling head-first through the weeds." This description applies with but little modification to most of the animals that live in similar situations in the hill-streams

The larva of *Ulomyia* lives in clear running water; it is similar to the larva of *Pericoma* except that it is provided with "two rows of acute, lanceolate, foliaceous, branchia-like appendages" down the back (MIALL and WALKER, p. 152).

The most remarkable Psychodid larvæ are those of the genus *Maruina* described and figured by MÜLLER (1895) from Brazil. These occur in company with the Blepharocerid larvæ of the genus *Curupira*; but their habitat is somewhat different. The larvæ of the Belpharoceridæ are found in the course of a swift current on bare rocks, while those of *Maruina* "live on rocky walls, covered with a slippery carpet of algæ, and kept moist by the spray of the waterfalls or by the drops of water running down from above" (p. 479). The larvæ are greatly flattened and ovoid and their ventral surface is provided with eight suctorial discs, the last of which is placed on the penultimate segment. MÜLLER's figures of the disc of *Maruina* show a close similarity between its structure and that of the disc of a very young Blepharocerid larva. In both the circular disc is provided with radially arranged spines in the peripheral region, followed towards the centre by a series of small blocks of chitin of various shapes and sizes (see fig. 6). The centre of the disc is a plane surface of undifferentiated chitin. From the figures alone it is not possible to discuss the structure of the disc of *Maruina* in any great detail, but its general similarity with the disc of a Blepharocerid larva is remarkable and provides an illustration of convergence.

### *Tipulidæ.*

Several genera of Crane-flies include aquatic species. HUBAULT (1927) discusses the representatives of the following that have been found in torrential streams—*Dicranomyia, Phalacrocera, Pedicia, Dicranota* and *Tipula*. According to ALEXANDER (1920) there are three categories of the aquatic larvæ of Tipulidæ, namely (1) *Phalacrocera* and *Triogma,* which live on submerged vegetation; (2) *Dicranomyia, Pedicia, Triogma, Dolichopeza,* etc., which live in very rapid water on or in submerged mosses; and (3) *Elliptera* and *Antocha,* which live in silk cases under water on bare rocks in cascades. These groups are arranged according to the degree of modification they exhibit for aquatic life as well as for life in rapid waters. By a study of the various forms named above it is possible to trace almost all the steps of the adaptation which have enabled the larvæ to live in torrential streams.

Larvæ of *Phalacrocera* and *Triogma* are provided with elongate leaf-like or spine-like projections, with a thick cuticle, which is denticulated or serrated in various ways for enabling the animal to hook itself to weeds in case of a sudden rush of water. The

*Phalacrocera* larva is further enabled to " cling to a moss-stem by its large anal hooks, and, thus secured, it may at times be observed to sway its body from side to side, as if to promote respiration. It creeps from stem to stem by grasping with the mandibles and the anal hooks alternately. When alarmed, it curls itself up like a caterpillar " (MIALL and SHELFORD, 1897, p. 344). The larvæ of *Dolichopeza* and *Tipula* are provided with backwardly directed spines on their bodies, while in the larvæ of *Dicranomyia* the abdominal and the thoracic segments are armed with dorsal and ventral transverse ridges on the basal annuli. The larvæ of *Dicranota* and *Pedicia* are characterized by the presence of definite pseudopods bearing adhesive spines. In *Dicranota* " the 6th, 7th, 8th, 9th and 10th segments* bear paired retractile processes, which resemble the pseudopods of caterpillars, and end in triple crowns of chitinous hooks. Beneath these are many regular rows of still smaller hooks, which form transverse rings. The terminal surface, enclosed by a circle of hooks, is inclined a little backwards in the two foremost pairs of pseudopods, a little forwards in the others. The pseudopods can be retracted completely by means of their attached muscles " (MIALL, 1893, p. 238). MIALL's excellent description and figures of the pseudopods of *Dicranota* correspond closely with the structure and mechanism of the so-called lateral suckers of the larvæ of *Deuterophlebia* (p. 227). The convergence between the two structures is noteworthy.

The arrangement of the spines in several transverse rings on the pseudopods has a biological significance. The distal row of spines contains the longest spines, which decrease in size in proximal rings. After every ecdysis probably the upper whorl of spines is discarded and the lower one takes on its function. Even in the case of accidental injury to the distal whorl the proximal whorls are more or less ready to take on its function. In animals living in torrential streams the necessity of such a mechanism is obvious. In the disc of the sucker of Blepharocerid larvæ a similar arrangement is found (p. 222).

The larva of *Pedicia* differs from that of *Dicranota* in the position of its abdominal feet. Besides the abdominal appendages on the body, the hair-like outgrowths enable the animal to entangle itself among weeds, as described by MIALL and WALKER for the larva of *Pericoma* (1895, p. 143).

The larvæ of the genus *Elliptera* live in elongated and somewhat flattened cocoons of mud and silk which are placed with the current on dripping rocks near waterfalls and rapids. These are arranged in longitudinal rows with short spaces between. When nearly full-grown, the larva crawls to a less exposed place and spins its cocoon, and when ready to emerge as an adult the pupa makes its way through the end of the cocoon away from the current. The third to the ninth abdominal segments of the larva are provided with ridges on the dorsal as well as on the ventral surfaces ; the dorsal ridges are provided with spines.

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* There is a discrepancy in IMMS's 'Textbook of Entomology' regarding the position of the pseudopods of *Dicranota*. On page 611, he says, " In *Dicranota* five pairs are evident on segments 7 to 11," but on page 616 he describes the same structure on segments 6 to 10. The latter is right.

The most remarkable among the Tipulid larvæ are those of the genus *Antocha.* ALEXANDER (1920) says: " Both larvæ and pupæ spend their entire lives in cases on stones in water—usually in running, well-aerated water, and often in the most rushing torrents " (p. 800). ALEXANDER further remarks that, " As a rule, the larval cases are made on rubble or rounded stones, a crevice or a groove caused by inequalities of the rock surface covered over being the simplest and commonest place chosen. The inequalities in the rock are bridged over by a silken mud- or silt-covered case, which is very delicate and laterally fimbriated with the young larva, but become much firmer, thicker and more compact with the older larva and pupa. . . . The pupa has two powerful hooks at its caudal end, enabling it to fasten to the case. In most cases the pupa hangs with the current, head downstream, like the pupa of *Blepharocera* and unlike the somewhat similar appearing pupa of the Simuliidæ, which rests with the head upstream* against the current, the pupa case being open at the cepahlic end only " (p. 801). It may be noticed that in its habitat and its habits of case building the larva of *Antocha* shows great convergence to certain Lepidopterous and Trichopterous larvæ of torrential streams. " Dr. NOYES found larvæ of Antocha in a small rapid-flowing stream near Ringwood Hollow, and there the cases were covered with tiny pebbles, and it was quite impossible to distinguish them superficially from associated caddis-worm cases " (ALEXANDER, 1920, p. 802). Indeed, it is a fine illustration of the effect of environment in moulding to a common form the shelters of these two widely different groups of insects.

ALEXANDER has described in detail the arrangement of the setæ on the body of the larva and of the pupa of *Antocha.* These setæ enable the animal to hook itself both to the substratum below and to the silken covering above.

### *Chironomidæ.*

The larvæ of the midges offer several interesting examples of adaptation for life in rapid waters. Their bionomics and modifications have been studied by THIENEMANN (1926). They are provided with two pairs of pseudopods: the anterior pair is situated on the prothoracic and the posterior pair on the anal segment. Both pairs are provided with chitinous claws.

In all the typical hill-stream forms the anterior prolegs are less strongly developed

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* So far as I am aware the Simuliid pupæ are found with the head pointing downstream. I have shown them in their natural position in my fig. 7, *b*, in the 'Journ. Bombay Nat. Hist. Soc.,' vol. 32, p. 121 (1927). The pupal case of the Simuliidæ is open at the cephalic end only, and if the head were to be directed upstream the rush of water would disturb the pupa and interfere with the emergence of the fly. The arrangement and form of the hooks on the body of the pupa also indicate that it lies in the case with its head pointing downstream. HUBAULT (p. 338) observes, " Ainsi que l'indique TONNOIR sur une des figures de son travail, les nymphes de Simulies, comme celles de Blépharocéridés présentent, dans leurs cocons, un rhéotropisme négatif qui facilite la sortie de l'imago." The matter was referred to Mr. F. W. EDWARDS, who has confirmed my observations about the position of the Simuliid pupæ.

and are capable of being entirely retracted, especially in the Tanypinæ. The posterior prolegs are, however, more strongly developed, longer, and furnished with claws of greater length than those of the sluggish water forms. In certain species the curved ends of the claws are strongly pectinated (HUBAULT, 1927, fig. 35*c*) and provide the animal with a better grip.

There is another point to which attention may be directed. The Chironomid larvæ that live in swift currents have acquired the habit either of living without a case or of living in silken nets, *e.g.*, *Tanytarsus*. *Diamesa*, *Prodiamesa*, *Orthocladius*, *Tanypus*, etc. are without tubes, probably because in rapid waters, instead of the tube being advantageous in providing shelter and safety it would be an encumbrance. The reduction of their anterior pair of prolegs can be correlated with the loss of cases in these forms, for according to LEATHERS (1922) these appendages are mainly used in a Chironomid larva for building the tube or any other type of silk net. Reference may here be made to the Trichopterous larvæ living in swift currents which are either free-living or have secreted silk nets. The convergence in these respects between the representatives of these two groups may be noted.

Although these hill-stream Chironomids do not secrete material used in forming cases, nevertheless they are provided with well-developed salivary glands. LEATHERS (p. 47) makes the following observation regarding the larva of *Orthocladius*: "The larvæ apparently do not make use of their well-developed silk glands for the purpose of building tubes. It seems probable that they would not be so well developed unless they had some important function." He considers that their development is correlated with the nature of the food. The larvæ of most of the genera named above either live on rocks or on plants in a swift current and are thus comparable in their mode of life to the larvæ of *Simulium*. From analogy it appears to me probable that the development of extensive salivary glands in the two groups of animals is correlated with a common mode of life. In the case of the *Simulium* it is known that the secretion of these glands provides a substratum into which the hooks on the prolegs are fixed, and possibly the secretion of the salivary glands of *Orthocladius* and other hill-stream Chironomidæ is used for the same purpose.

Mr. F. W. EDWARDS has very kindly directed my attention to the two characteristic Chironomid genera of the torrents—*Cardiocladius* and *Charadromyia*. The larvæ of the former are free-living on rocks and plants in waterfalls and swift currents and pupate in strong cocoons spun on rocks, stones and waterweeds (SAUNDERS, 1924). JOHANNSEN (1905, p. 183) has referred to the habits of the American species (*Thalassomyia*=*Cardiocladius*), as follows: "The larvæ of the two species of which they are known live in rapidly-flowing water. Here the larva spins upon the surface of the rock a cocoon so loose, transparent, and open that it is not hidden by it, though it prevents the larva from being washed away." The larvæ of the *Charadromyia* "construct tough silken galleries over the rock or other submerged surfaces, preferably where the water rushes over the rock ledges with greatest force. These whitish silken galleries are quite noticeable in these situations, and it is astonishing that they are not often beaten to pieces after a heavy mountain shower" (TERRY, 1913, p. 294).

Chironomid larvæ have been found associated with other aquatic insects on several occasions, and without much consideration such occurrences have been recorded as instances of commensalism. HUBAULT (1927, pp. 161, 311) may be consulted for references on the subject. It may be remarked that the torrent-inhabiting animals have acquired sedentary habits to a marked degree, for in rapid-flowing waters moving about is a dangerous pastime and the animals show a tendency to lie as closely as possible to the substratum which they grip by means of several types of ingenious devices. This statozoic habit, to use WILLEY's term,* is so well marked that the animals will cling to any object that furnishes them with proper support: *Psephenus* larvæ have been found on bivalve shells† and Ancyli have been found adhering to water beetles.‡ Pupal cases of *Simulium* larvæ are often found superposed on one another.§ In a small collection from the stream flowing near the Chamba Hydro-electric Power Station, three Blepharocerid pupæ harboured Simuliid pupæ. All such instances of an accidental nature should not be confused with commensalism or any other kind of animal association.

### *Simuliidæ.*

The Simuliidæ have received considerable attention in recent years and a great deal of knowledge has accumulated regarding the bionomics of these insects. Very little work has so far been done on the Indian forms, though they are found in great abundance in all the hill-streams that I have visited. In a clear, rapid-running, small stream below Dumpep, in the Khasi Hills, the larvæ and pupæ were found in masses on the water-plant *Eriocaulon miserum* and also on the upper surface of the bare rocks situated in the shallow and rapid-running current. Whether on plants or on rocks the larvæ selected a situation as close to the surface of the water as possible, and the pupæ in this attempt were often found to be superposed on one another. The larvæ were common on mosses encrusting the slanting rocks of a rapid, but were never found on bare rocks forming the lips of falls. Usually there is little vegetation in the mountain torrents of India, and the larvæ of the black flies are found in groups on bare rocks in moderate currents. In February and March, 1927, the whole of the stream bed of the head-waters of the Narbadda River, near Pharisemar (Rewa State), in places where there was a rapid, was found literally covered with the larvæ and pupæ of the Simuliidæ. In such places the rocks were covered with long filamentous algæ. The pupæ were found along with the larvæ, but the larvæ appeared to have been very particular about the choice of the places where they made the cocoon, for I found the pupal cases

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* WILLEY, 'Convergence in Evolution,' p. 37 (London: 1911).

† KELLICOTT, 'Canadian Entomologist,' vol. 15, p. 192 (1883).

‡ JOHNSON, 'Nautilus,' vol. 17, p. 120 (1904).

§ PURI, 'Parasitology,' vol. 17, p. 330 (1925).

generally on the apices of weeds or on small protuberances of rocks. Some were even found on the pupæ of the Blepharoceridæ. This position probably helps the insect at the time of eclosion.

As regards the normal mode of progression of the larvæ I fully agree with PURI'S observations (1925, p. 297). The movements are characteristic and can be readily made out by watching a larva on a glass slide in a drop of water. It must, however, be observed that when the larva detaches its anterior or posterior appendage from the substratum there is a violent contraction of the animal and a sudden sharp pull is noticeable. Besides the normal mode of progression I have studied the movements of an animal when it crawls on a dry surface (a glass slide was used for the purpose). In these circumstances the movements are slow and all the details of the mechanism can be properly made out. After a quivering movement of certain parts of the head a " drop " of secretion is poured out from the salivary slit. The front part of the head is now applied to the substratum immediately in front of the secretion and the body is pulled up into an arch. The thoracic proleg is bent forwards so as to grip the sticky secretion with its crown of hooks. With the proleg as pivot the body is pulled up so that for a short time the body forms an arch on the thoracic appendage, which itself is vertical in position. An instant later the leg is bent anteriorly and the body is dropped forwards. By repeating these movements the larva is able to progress slowly, and it was observed that after a dozen paces the animal was unable to secrete the sticky juice, in spite of the efforts it made by shaking its head. Sometimes the larva was so exhausted that it could not pull its leg from the sticky secretion and in such cases the gripping action of the hooks and their relation to the salivary secretion could be seen very beautifully under a microscope. On a wet surface, however, the larva could travel a much longer distance in the same way, and when a number of them were allowed to crawl on a slide the tracks of their movements were clearly indicated. A photograph of these tracks was published in 'Nature' of April 23, 1927.

Up till quite recently it had been considered that a *Simulium* larva was provided with definite suckers, which enabled it to cling to rocks and weeds in swift currents. TONNOIR (1923, *a*, pp. 163–172), in his work on the modes of fixation and the progression of these larvæ, made it abundantly clear that no sucker-action was involved in the fixation of either the anterior or the posterior appendage; but he made one mistake in an otherwise excellent chain of reasoning. He observed that, " La dissection montre, d'ailleurs, qu'il n'existe pas de faisceaux musculaires destinés à la formation de cette coupe." PURI (p. 311) observed " that there are fairly strong muscles connected with the centre of the disc (Plate 8, fig. 10) and that they contract when the larva fixes itself by its posterior end. But in spite of the presence of these muscles the larva cannot fix itself effectively without the further help of the sticky salivary secretion; a fact which may mean that the saliva helps to fill up the spaces between the hooks and thus to form a complete rim all round. There is no doubt, however, that a larva remains fixed to the substratum mainly by means of the hooks which firmly grip the salivary secretion, but it is not possible to say how far the sucking action of the appendage helps the larva at the moment when it first attaches itself to the support. The first-stage larva has a pair of long hairs arising from the middle of the circular area surrounded by the rows of hooks, and it is therefore very improbable that this appendage functions as a sucker, at least in the first-stage larva."

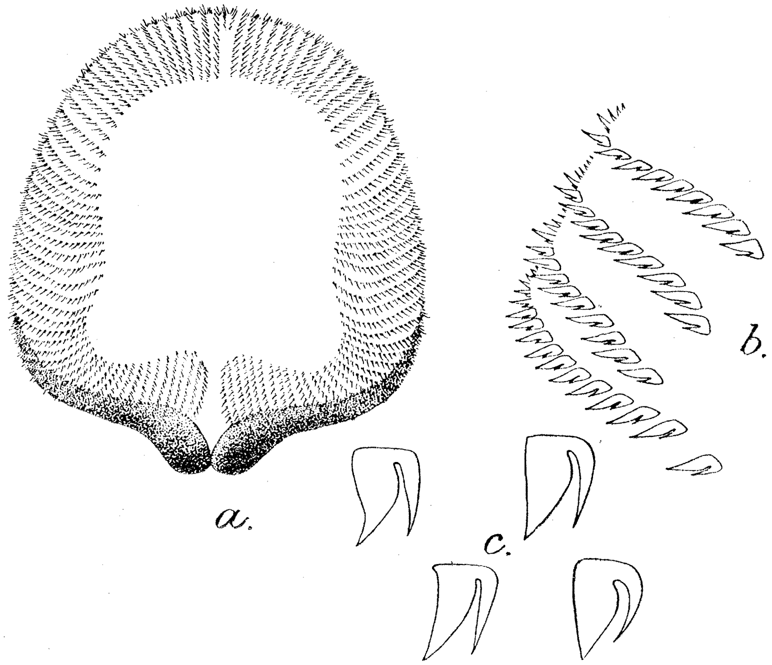
The above passage clearly shows that PURI had a vague idea regarding the function of the posterior appendage and that he had not understood the action of its muscles. I made extensive observations on this point in nature and came to the conclusion that TONNOIR'S explanation of the mechanism of the so-called " suckers " of the *Simulium* larva was correct, but the action of the various muscles described by PURI and the elucidation of the nature of the salivary secretion which according to PURI " helps to fill up spaces between the hooks," required further consideration. It was with this object in view, and not with the intention to lay claim to a discovery (as misunderstood by TILLYARD, ' Nature,' July 30, p. 154, 1927), that I communicated a short note to ' Nature ' on this subject.

The fixation of the *Simulium* larva to the substratum is effected by means of the sticky salivary secretion and the hooks of any one of the following structures : the posterior appendage, the thoracic proleg and the labrum. The posterior appendage is the chief organ of attachment, but when the animal is not feeding, it curls itself up in a loop and takes hold of the silk threads by means of the hooks on the thoracic proleg (HORA, ' Journ. Bombay Nat. Hist. Soc.,' vol. 32, p. 121, fig. 7*b*, 1927). It is possible that the hooks on the outer face of the labrum assist the animal while it rests in this position ; but the hooks on both the labrum and thoracic proleg come into play when the larva looses its hold on the substratum and hangs by means of the silk threads in the rushing current. In these circumstances the animal hauls itself up by alternately using the hooks on these two structures (HORA, *op. cit.*, fig. 7*c*).

*Posterior appendage* (fig. 5*a*).—The body of the larva is greatly dilated posteriorly and at the extreme end is flattened into a disc-like area, which bears several rows of radially arranged, strongly chitinized hooklets in the peripheral region. The arrangement of these hooks is markedly interrupted in the mid-dorsal region and slightly so in the mid-ventral line. There are from 11 to 17 hooks in each of the rows (fig. 5*b*) except the first three or four on each side of the medio-dorsal line. All the hooks are directed towards the periphery.

The nature of these chitinous hooks has not been understood so far. I shall here describe their structure, reserving discussion of the probable mode of their evolution for another place (p. 262). In Canada balsam preparations each " hook " (fig. 5*c*) appears to consist of a flat base externally produced into two spine-like outgrowths, one of these being much longer and stronger than the other. The whole of this structure is so arranged on the appendage that the two processes are directed towards the periphery of the disc. The relative form and length of the spines differ somewhat with their distance from the centre of the disc. When magnified each hook is seen to consist of a stout basal portion and a more slender hook. The two components of each hook diverge from each other like the two arms of the letter " V." In the angle between the two components is a notch into which the thread of secretion readily slips; the thread is then more securely held by the hook. Of the two arms of the hook, the outer sickle-shaped one is free and is the one that functions, while the other lies against the body wall of the animal, partly embedded in it, to give support to its working partner. The mechanical principle involved is that of the lever of the third type (p. 262).

The muscles of the posterior appendage are described by PURI (*loc. cit.*, p. 321) as follows: " The posterior sucker with its circlet of hooks is provided with numerous muscles, originating chiefly in the eighth abdominal segment, though a few are attached to the seventh. Arising from the lateral and the ventral surfaces, they stretch to all points in the circle except the medio-dorsal, which is devoid of hooks. A pair of slender muscles arises from the lateral wall of the eighth segment and is inserted upon the middle of the disc. A very stout muscle, originating dorsally from the anterior end of the seventh segment, and dividing into two strands, is also attached within this space. The arrangement of these muscles of the posterior appendage is very complicated and can best be followed by reference to Pl. VIII, fig. 10."



TEXT-FIG. 5.—The posterior appendage of a *Simulium* larva. *a* = posterior appendage laid flat on a slide. × 150; note the medio-dorsal (lower) and the medio-ventral regions where the rows of spines are interrupted; *b* = a portion of the appendage showing arrangement of spines in rows. × 500; *c* = the different forms of spines. × 1,000.

In determining the function of the posterior appendage it seems to me that undue importance has been attached to the presence or absence of muscles in the centre of the disc, and I fail to see why the presence of the muscles in the centre should lead to the conclusion that the organ functions as a sucker. When a larva fixes its posterior disc in the salivary secretion, it is observed that the various parts of the disc are moved slightly. This movement is, in all probability, caused by the numerous slender muscles inserted in the various parts of this structure, with the object of enabling the larva to fix its hooks in the secretion. The strong muscles that are attached in the centre of the disc are certainly meant to enable the animal to detach its so-called " sucker " from the secretion. I have already pointed out that these movements are violent and can be readily noticed. Both the prongs of the hook are directed towards the periphery, and to disengage them a pull in the opposite direction is needed. It is by the action of the strong muscles in the centre that this pull can be given. The crotchets on the abdominal appendages of a Lepidopterous larva have their hooks directed towards the centre of the disc and the muscles perform quite a different function there. A typical abdominal leg of a Lepidopterous larva " is a fleshy, more or less conical, retractile projection whose apex or *planta* is rounded and flat. The latter is provided with a series of hooks or crotchets which aid the larva in locomotion, and to the centre of the *planta* is attached a muscle by means of which it can be completely inverted " (IMMS, p. 403). The points of similarity and dissimilarity between the functioning of the disc of a *Simulium* larva and of the abdominal leg of a Lepidopterous larva may be noted.

There are two other points in the arrangement of the hooks on the posterior appendage which require further elucidation. These are, firstly, the presence of the hooks only in the peripheral region of the disc, and secondly, the interruption of the rows both in the mid-dorsal and mid-ventral lines. The presence of hooks only in the peripheral region makes it possible to pull them out of the secretion by contraction of the centre of the disc. For the proper fixation of the hooks into the salivary secretion it is essential that the disc should be brought as close as possible to the substratum. This would necessitate the expulsion of water by adpression, and the two regions where the rows are interrupted allow the passage of water. Once the fixation is effected the larva hangs from the silk threads and the water freely flows under its posterior disc. These interrupted regions recall the valvular gateway to be seen in the sucker of a Blepharocerid larva (p. 222); the former allows the water to pass both ways, whereas in the latter the water can pass from the cavity of the sucker (a true functional sucker), but is prevented from entering it. The posterior disc is strengthened along its dorsal border by the posterior limbs of an X-shaped sclerite, and there are a few simple scales lying external to the anterior limb of this structure.

*Thoracic proleg and labrum.*—The prothorax is produced on the ventral surface into a median appendage known as the thoracic proleg. This consists of a proximal and a distal portion; the latter is capable of being retracted into the former and at its extremity bears radial rows of small hooks. Behind the crown of hooks there is a triangular chitinous plate lying latero-dorsally, with its anterior border produced into pointed processes arranged in groups of three to five. The proleg is supplied with a number of fairly strong muscles. The labrum is almost semicircular, is directed downwards and overhangs the mouth, and on its dorsal or anterior surface in the median line is an elongated patch of strong distally directed hooks. The hooks on the thoracic proleg and on the labrum are of the same kind as those found on the posterior appendage, but those on the labrum are very much shorter.

The thoracic proleg and the labrum work in opposition to haul up a larva along the silk thread to its former support. PURI (*loc. cit.*, p. 297) noticed that for this purpose the larva uses the proleg and the mouth-parts "like a hand to hand" rope-climb. According to my observations, of the mouth-parts only the labrum functions in this process. In an earlier paper (1927*b*, p. 121, fig. 7*c*) I have given a diagrammatic representation of the progression of the larva during this process. In the first position the animal is seen to be fixed to the thread by means of the hooks on the labrum and on the proleg when these two structures are wide apart. The proleg slides forwards and its apex comes to lie close to the labrum. Now the labrum slides forwards and the two structures separate again. It should be noticed that both the structures remain constantly in touch with the thread, and that a sliding movement of only one of them takes place at a time. The various movements described above can be watched by jerking the larva from a support, when it will hang by a thread in the same way as a spider does, and then keeping it in the middle of a tube full of water. In these circumstances it was observed that the larva continuously moved its hinder end from side to side, and when by chance the posterior appendage came in contact with the thread, the larva adopted the characteristic looping movements for progression along the thread.

The thoracic proleg is strengthened in the dorso-lateral region by a chitinous plate, which is produced anteriorly into pointed processes arranged in groups of three to five. When this appendage works in opposition to the labrum the area of greatest stress will be the dorso-lateral region. The structure of the chitinous plate shows that it gives rigidity to the area, combined with a certain amount of flexibility at the anterior end (the region of the pointed processes).

*Salivary Secretion.*—The salivary glands are well developed and occupy the greater part of the abdominal cavity. They are filled with a thick secretion which coagulates in water and is not soluble in spirit. It is poured out on the substratum in the form of two flattened threads applied side by side, which are very sticky and very strong. I have indicated their nature in a former paper (1927*b*, p. 122). The salivary secretion furnishes a substratum for the attachment of the hooks and plays as important a rôle in the fixation of the larva as the hooks on the various appendages. At the point of attachment these fine silk threads are spread out into a flower-like pattern by the close application of the appendage.

*Pupa.*—The pupa is more or less enclosed by the cocoon manufactured by the larva from its sticky salivary secretion. The pupa lies loose in the cocoon, except for the fact that the spines on the ventral side are entangled in a number of fine silk threads arising from the posterior end of the floor. In preserved specimens the pupa can be easily taken out of the cocoon, but under natural conditions, where the current strongly presses the dorsal wall of the cocoon against the pupa, the forwardly directed hooks on the dorsal surface of the pupa become fixed in the dorsal wall of the cocoon and anchor the animal. PURI (*loc. cit.*, pp. 330–333) has described in detail the arrangement of the spines on the body of the pupa. The function of these becomes evident when it is remembered that the pupa is always found with the head pointing downstream (p. 209), which condition is essential for the emergence of the fly in a rushing stream. The head and the wing-sheaths on the ventral surface are covered with chitinous papillæ which help to increase friction.

### *Blepharoceridæ.*

According to KELLOGG (1907, p. 3), the larvæ and pupæ of the Blepharoceridæ, " like the lip of a fall, the rocks of cascades, and the sides of a pot-hole in which the water, is ever whirling and boiling." TONNOIR (1924, p. 8), in his account of the Tasmanian Blepharoceridæ, states that " L'habitat des larves est naturellement différent suivant les espèces ; on peut les ranger, sous ce rapport, en deux catégories : (*a*) la première, comportant *E. tasmaniensis* et *E. similis,* a des larves qui exigent une eau très oxygénée et, par conséquent, très rapide et écumante, comme celle d'une cataracte ou au bas d'une chute ; ceci fait que l'on ne trouve guère ces larves que sur le roc, toutes les autres pierres étant emportées par le courant violent d'un tel cours d'eau ; (*b*) les larves de la seconde catégorie, celles de *E. ferruginea* et *E. fluviatilis* (et probablement aussi celles de *E. montana* et *E. confinis*, s'il faut en juger d'après l'habitat de l'imago), se contentent d'une eau beaucoup moins rapide, bien que, dans certains cas, j'ai rencontré la larve de *E. ferruginea* avec celle de *E. similis* : d'ordinaire on les trouve fixées sur les pierres du fond, en compagnie des larves de *Simulium*, d' Ephémères, de Plécoptères et de Trichoptères."

In the course of my field-work I have been greatly impressed by the peculiar habitat selected by the larvæ and pupæ in different parts of India. In November, 1926, I made observations on the animals inhabiting a small torrential stream below Dumpep, in the Khasi Hills (Plate 15, fig. 2). It is a clear swift-running stream with rapids and falls in its course. After a great deal of search only two Blepharocerid larvæ were found on the upper surface of a stone, lying in a narrow channel through which water was flowing with a tremendous rush. A couple of miles away from Dumpep is another stream, known as Pun-Wa-Sherra (Plate 16, fig. 2) which flows in a series of falls and rushes down with great speed to join the Nong-Priang stream below Cherrapunji. Here masses of Blepharocerid larvæ were found on the lips of falls or on steep bare rocks. Very few specimens were present on the rocks forming the general bed of the stream. In December, 1926, I was working on the fauna of small streams in the neighbourhood of Pashok, Darjiling Himalayas, where the pupæ and larvæ of the net-winged midges were only found on the rocks of the rapids and were absent from the immediate neighbourhood of falls. They were found in small groups on the upper surface of stones in the swiftest current and were consequently more widely distributed in the stream-bed than those of the former category. In May–June, 1927, I noticed at Dalhousie, in the Western Himalayas, that the Blepharocerid larvæ were neither present on the lips of falls, nor on the rocks of the rapids, but were present in great number on rocks and stones at the base of falls over which water fell with a tremendous crash. It may be remarked that occasionally larvæ and pupæ are found in other places in the same stream, but the habitats described above are very characteristic.

The young larvæ are usually found in moderate currents,* either at the sides of rocks near a fall where they are kept moist by the intermittent splashing of water or on the lower sides of rocks over which the water is falling. In both situations it is possible to correlate the size of the larvæ and the rapidity of the flow in which they live. The flies lay their eggs either on wet rocks at the sides of the falls, where they are kept moist by spray or on the under surfaces of stones. Hatching out in these situations the larvæ gradually make their way into the swiftest part of the current. Several other authors have also noticed that the eggs are laid in currents of moderate strength.

Usually it is mentioned that pupæ are found in similar situations, and according to HUBAULT the pupæ actually prefer swifter currents than those in which the larvæ live. He observes: "Arrivée à maturité, la larve bien souvent change une seconde fois de place et choisit un nouvel endroit, où le courant est encore plus fort: par exemple le rocher sous la lame d'eau de la cascade elle-même, ou bien celui qui, placé sous la chute, la reçoit de plein fouet" (p. 304). This may be true for those species that live in rapids; their behaviour will correspond to that of the *Simulium* larvæ that are found in company with them in such situations. My observations on those forms that live on the lip of a fall or on a rock at its base are different. About the time of pupation the larvæ seek comparatively sheltered places. They often choose small pits on the rocks or retreat to the banks of a stream. In the Khasi Hills they were found on vertical rocks over which the water trickled down from a fall and kept them moist. At Dalhousie they were usually found on the sides of the rocks and not on their upper surfaces.

KELLOGG found the pupæ in the same places as the larvæ "with heads pointing downstream" (1907, p. 3), whereas KOMÁREK and WIMMER remark that "the pupa is found in the same places as the larva. The pupæ are apt to occur like the larvæ closely clustered together with the heads pointing upstream" (1922, p. 66). HUBAULT found the pupæ with the heads pointing downstream. I have always found the pupæ with the head pointing downstream and this has a marked biological significance, namely, the facilitating of the emergence of the adult insect. It may, however, be

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* Regarding the larvæ of *Phænocladius*, a Chironomid, HUBAULT (p. 352) makes similar observations. He says: "Il faut noter la migration des larves de *Phænocladius*: jeunes, on les rencontre massées sur places de ponte, dans les algues qui couvrent certain rochers des rives, mouillés par les eaux; développées, elles vivent accrochées aux pierres des cascades."

remarked that in this position the pupa presents an inverted stream-line form to the current and, as will be shown later, the animal is absolutely fastened to the substratum by a sticky secretion.

Of all the animals that inhabit torrential streams the larvæ of the Blepharoceridæ are the best adapted to hang on to bare rocks in the most tumultuous situations. In most of the larvæ the body is slightly depressed, and it is only in a few that a regular limpet-like form is attained. By virtue of half-a-dozen ventral suckers, each of which is capable of powerful and independent attachment to the stones, these larvæ manage to live in the swiftest part of the current. The suckers have become so important that the body has become segmented secondarily, so that the major divisions of the body conform to the suckers and not to the original body segments. I shall have occasion to discuss this point at some length later (p. 230). With the help of these suckers, used as feet, the larva walks over the stones under the swiftest water by its characteristic lateral undulating movements. Besides the suckers the larvæ are provided with certain accessory organs of attachment which mechanically help the animal to stem the current. In order to study these devices I propose to divide my entire collection into two groups, irrespective of the taxonomic position of the various forms in each group, namely (1) those larvæ which possess well-defined lateral appendages and in which the body is constricted between each division, (2) those in which the body has assumed a chiton or limpet shape and the lateral appendages are not well defined.* The body is marked into six divisions, but is not constricted between these divisions. I shall first describe the structure and mechanism of a sucker, which is common to both the forms and which is by far the most complicated and efficient organ of attachment that I have to deal with in this paper. It may be remarked that the occurrence of true suckers is very rare in the fauna of the torrential streams.

*Sucker*.—The most conspicuous organs of attachment are the ventral suckers. These have received considerable attention at the hands of several workers. KELLOG (1903, p. 204) was the first to describe the structure of a sucker and the manner of its working, but his description is meagre and is of a general nature. It is to KOMÁREK (1914, pp. 1–28) that we are indebted for a detailed account of the various parts of the

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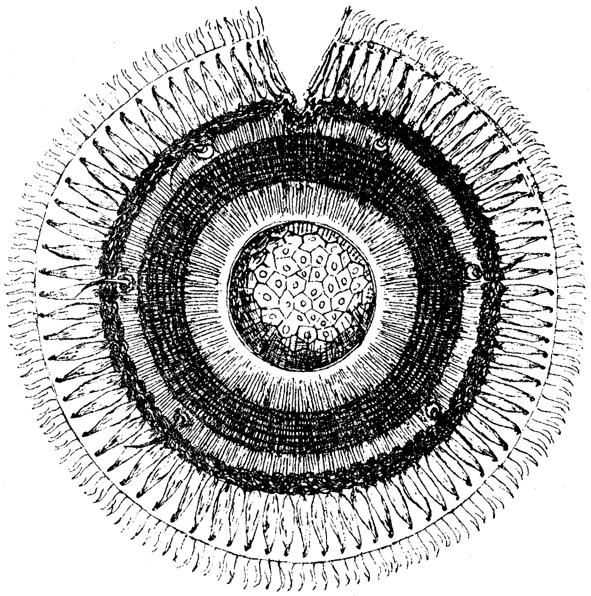
* Mr. F. W. EDWARDS, in a letter to me dated May 4, 1928, writes as follows : " In my holiday in Corsica I searched specially for Blepharocerid larvæ and obtained four species. I remembered what you said about the chiton-like larvæ being found especially in places where the water was falling on to them, and sure enough in such places I found small black larvæ something like the one in your photograph. However, these larvæ were not confined to such places, nor did they always have the ' chiton ' shape ; some which certainly belong to the same species have the normal body-constructions, and I am led to believe that the chiton-like larvæ have simply contracted themselves, either in preparation for pupation, or because of the force of the water compelling them to take the firmest possible hold. My larvæ seem to be those of *Apistomyia elegans,* which is rather nearly related to *Hammatorhina*." These observations are very interesting in showing the direct effect of environment in the moulding of the form. I have observed that *all* young larvæ are constricted between the divisions and it is only in grown-up animals living in fiercest currents that the chiton shape is developed.

apparatus and for an attempt to explain the rôle of each in the harmonious working of the entire structure. In several cases I am not in agreement with KOMÁREK's description and with his explanation, but to avoid unduly lengthening the following account I have purposely refrained from discussing the points of difference in detail. It should, however, be understood that where my conclusions happen to differ upon any point, it is not due to my overlooking the observations of previous workers on the subject. A brief reference may, however, be made to the recent observations of HOFENEDER (1928). His account of the morphology and physiology of the sucker agrees with that of KOMÁREK in most respects, but he gives a better description of rod-like structures in the outer layer, and his interpretation of their function is more correct. He considers the valvular gateway at the anterior end of the sucker as an inlet for the flow of water into the sucker to disengage it, but with this view I do not agree. In the Indian species only one type of rod is found in the outermost layer, whereas HOFENEDER and KOMÁREK found two types of rods alternating with each other.

Each sucker, as seen in lateral view in a fully distended condition, appears as a vase-shaped structure, of which the base is represented by the general cuticular covering of the body at the base of the sucker. It originates as a tube which widens gradually towards the distal end and terminates at the apex in a broad, sloping rim. Two black bands are visible in this view, one near the apex representing the black margin of the disc and the other near the base of the tube representing the rim of the chitinous piston which works the sucker. When seen from the ventral surface a sucker (fig. 6) appears as a rounded and radial structure with a series of concentric bands lying at different levels of the sloping sides of the vase-shaped structure. Generally there are three light yellow and two dark rings, besides the outermost delicate and dull white fringe and the rounded web-like sculptured disc forming the centre of the disc. In some cases I have observed three dark bands enclosed by four light rings. In my preparations the outermost layer forms a continuous fringe round the sucker and consists of a delicate chitinous sheet. The chitin is thickened along radial strands, so that on superficial examination a fringe of hairs seems to surround the sucker. This delicate structure is liable to shrivel in various ways and may appear as shown by KOMÁREK in his figure. A close study of this structure shows that it is in reality a continuation of the outer chitinous layer that forms the outside of the vase-shaped sucker. Internal to this is the broad, light yellow ring. Under a high-power magnification it is seen to consist of a series of rods lying flat, side by side, at short intervals. All my preparations show rods of only one kind (fig. 6). At the distal end each rod is curved inwards forming a crotchet at the extremity. Internal to the rods is the first black band; it consists of three or four layers of small, deeply pigmented, chitinous blocks of various sizes and shapes. Immediately following these blocks towards the centre is the second light yellow ring. It consists of a series of rods more or less similar to those described in the first light ring, with this difference that the rods are here continued right to the bottom of the sucker as chitinous strands. In the middle of their lengths, or slightly more in the distal half, the chitinous strands are deeply pigmented, forming the second dark ring, and then the remaining proximal portion of the strands forms the third or the innermost light yellow ring. Forming the centre of the disc is the circular piston; the polygonal markings represent the attachment of the muscles or the tendons of the muscles on the inner surface.

As on the outside, the inner surface of the vase-shaped sucker is covered by a delicate thin and transparent chitinous layer. The area of this membrane that covers the outermost layer of rods (the layer does not extend to the tip of the rods) is provided with small spines on its ventral surface; all the spines are directed towards the centre and literally cover the whole of the surface.

The radial symmetry of the disc of the sucker is interrupted (fig. 6) on the anterior side and a V-shaped space is left blank in that region; the apex of the V is directed towards the centre of the disc. Forming the two arms of the V are two rods of the outermost light layer; they support membraneous flaps concave outwards and convex towards the centre of the disc. In this region the arrangement of the chitinous blocks and of the other layers is interrupted. Near the apex of the V the chitin is arranged into concentric circles, the centre of which is formed by the apex of the V.



TEXT-FIG. 6.—Sucker of a Blepharocerid larva as seen from the ventral surface. (Diagrammatic, modified after KOMÁREK.)

In the central light yellow band there are six funnel-shaped depressions (fig. 6) which appear on superficial examination as clear spaces; these are placed on the anterior-lateral border of the disc and are absent from the posterior part. They are radially arranged. In some of these I have found long pointed sickle-shaped spines, as figured by KOMÁREK, and in some short tube-like structures, as figured by CAMPBELL (1921, fig. 130).

Generally speaking, the disc of the sucker as seen from the ventral surface appears to consist of threads of chitin radially arranged and lying side by side. They appear to originate from the bottom of the cup, and after passing through various pigmented regions terminate at the apex forming a fringe of " hairs." This is all that is shown in the figures of the structure of the disc by most authors. I have indicated above the structure of the various regions and will now discuss the functions of the various morphological units.

*Rim.*—The outermost layer forming a fringe to the whole structure is very flaccid. By the pressure of the current it spreads out evenly on all sides of the sucker and is closely pressed against the substratum, thus preventing the entrance of water into the cavity of the vase-shaped structure. In young specimens this layer is not so clear, and I have been unable to find it in my preparations.

*Outer layer of rods.*—In young individuals the structure of this layer can be easily made out. Each rod is a flattened rib-like structure, broader at the base and gradually tapering towards the distal end, where it forms a crotchet. When a sucker is applied to the stone, these rods lie flat on the substratum and grip the stone by their terminal hooks. In this way they prevent the flexible walls of the tube from collapsing when a vacuum is created inside the tube. It may also be noted that the minute spines on the ventral surface of the membrane covering the under side of these rods are also used for the same purpose.

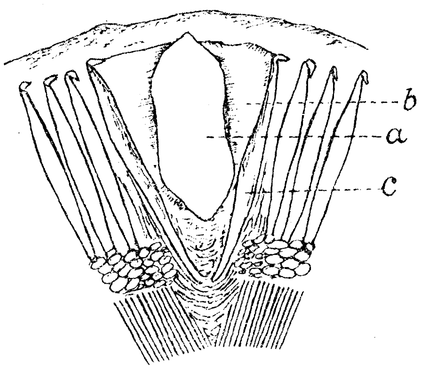
*Layer of chitinous blocks.*—The function of these chitinous blocks seems to be to give mobility and strength to the layer of rods described above (*cf.* the carpal and tarsal bones in vertebrate limbs). The rods may be deflected under the pressure of a strong current, but they do not break and ultimately they readjust themselves in their old positions.

The structure of the disc inner to these blocks shows only the above described two layers in the process of development. From the base issue strands of chitin, after a short distance these become deeply pigmented, and beyond this region they exhibit the structure of the rods with developing hooks at their apices. The pigmented region ultimately breaks up into a series of blocks, and the ends become differentiated into rods. As soon as the outer layer is cast at the time of ecdysis, the inner layers are ready to replace it and thus the efficiency of the sucker is never impaired. It is also evident that these hooked rods must play a very important rôle in the formation of the sucker, because ample provision is made to replace them as soon as they are cast off.

*Valvular gateway* (fig. 7).—It is evident that before a vacuum can be created, the water filling the tube of the sucker must be expelled. The valvular gateway allows the exit of water from the cavity of the sucker, but the arrangement of its membraneous flaps is such that no water can get in. It has been pointed out above that at the apex of this V-shaped structure the neighbouring chitin is arranged in concentric half-rings. This shows the direction of the force with which the water is ejected and the lines of the flow of water before it is finally pushed out. CAMPBELL terms it "Valve gateway of sucker" and shows all the salient points in its structure in his fig. 127 (p. 283).

*Funnel-shaped depressions.*—The position and nature of these depressions has already been noticed, but little is known of their function. It appears to me probable that they are used to let in water when the animal begins to disengage its sucker. The hollow spines or tubes that are found inside them prevent the sudden inrush of water; each structure acts like a valve that allows the water to flow in only.

The presence of these funnels along the lateral borders only of the sucker can also be explained. These have such narrow apertures that on account of the capillary action, it will not be possible for water, unless forced, to pass through them. This is done in two ways, firstly the pressure of the current pushes in the water, and secondly, the vacuum inside the tube sucks in the water. When it is remembered that these larvæ lie in the current, with their longitudinal axes at right angles to the direction of the flow, it will be seen that these small valvular apertures are on the lateral borders of the disc to take advantage of the current. It is also evident that the three funnels on the leeward side of the sucker will be of less use. It is also obvious that one big aperture to let in the water would have been distinctly harmful to the animal, for a sudden rush of water inside the sucker might tear away the larva from its support.



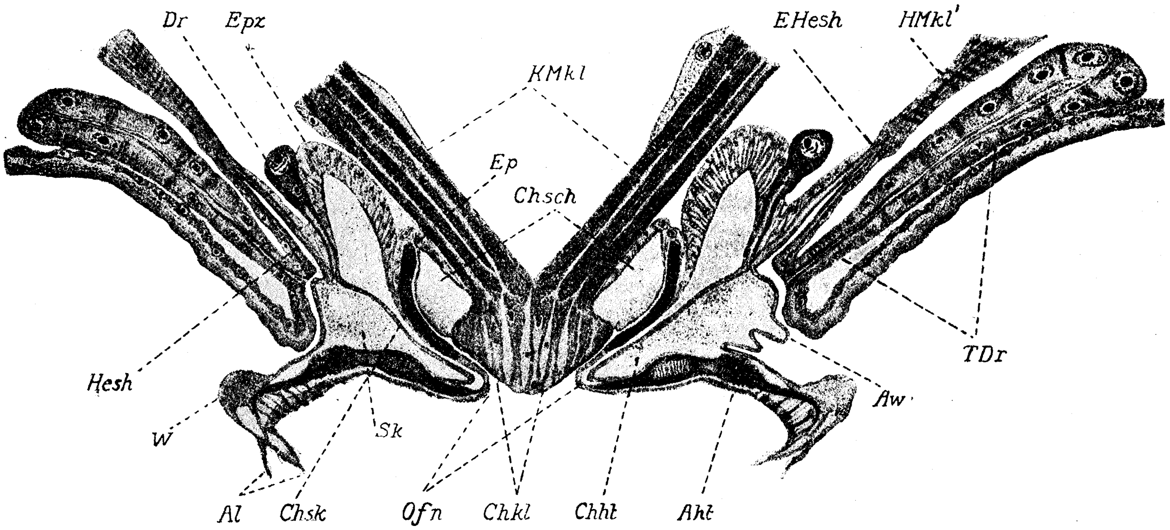
TEXT-FIG. 7.—The valvular gateway of the sucker of a Blepharocerid (highly magnified, diagrammatic). *a* = opening; *b* = membranous flap; *c* = rod supporting the membrane.

My explanation of the action of these apertures is as follows: when a sucker is applied to a stone the outer rim lies flat on the substratum, the dorso-ventral muscles push the piston down (not upwards as remarked by all other workers) and the water is expelled from inside the tube; the piston then comes back to its position and a vacuum is created. The rim then lies flat on the stone and the funnel-shaped apertures are now closely applied to the surface of the stone. When the insect begins to loosen the hold of its sucker the tube of the sucker is pulled up by certain dorso-ventral muscles that lie lateral to the muscles of the piston. In this action the inner portion of the rim is lifted from the substratum, and the funnel-like apertures now free from the surface let in the water. The whole of the action becomes clear from a study of the figure which I reproduce here from KOMÁREK (fig. 8).

*Piston.*—In very young specimens I have not been able to trace any structure corresponding to the piston which is so characteristic of the suckers of the mature larvæ. Strong muscles are attached on the inner surface of the piston, the edge of which is strongly chitinized and deeply pigmented. Two great muscle bundles run dorsally and diagonally from each sucker, and after traversing the body cavity are attached to the dorsal walls. These muscles are responsible for the creation of the vacuum. There are other weaker muscles which act in the way described above to disengage the sucker.

Komárek has described a number of large glandular cells and glands radially arranged and very closely connected with the sucker. These are, in my opinion, the mother-cells of glands of the chitinous secretion, which ultimately forms the rods, blocks, and other characteristic structures of the disc.

*Probable evolution of the sucker.*—According to Komárek the sucker was probably evolved as follows: "Ursprünglich waren wahrscheinlich an der betreffenden Stelle nur Drüsen vorhanden und die Tiere lebten am Boden der Bäche. Dort wo sich die Ventralseite mittels Drüsesekretes an die Steine klebte, lag die Insertionsstelle, an welcher sich die divergierenden dorsoventralen Muskeln vereinigten. Durch Kontraktion der letzteren konnte die weiche Haut der Ventralseite eingestülpt werden; rings um dieses Centrum bildete sich eine wallartige Hautausstülpung und dies war schon eine primitive Saugvorrichtung, die man als Anlage der hochorganisierten Haftscheibe ansehen kann." I have studied the probable development of the sucker in a series of young specimens in my collection. In the earlier stages each sucker corresponds to an abdominal leg of a Lepidopterous larva whose apex is provided with a series of



Text-fig. 8.—Median section through the sucker of a Blepharocerid larva transverse to the body axis (after Komárek). *Aht* = the outer skin of the disc rings; *Al* = free margin of the disc; *Aw* = the outer wall of the sucker; *Chht* = chitinous support; *Chkl* = chitinous piston; *Chsch* = the chitinous ring round the piston; *Chsk* = the chitinous sac; *Dr* = bicellular gland; *EHesh* = the end of the skin layer; *Ep* = epithelium of chitinous ring round the piston; *Epz* = epithelial cell layer; *Hesh* = the skin layer; *HMkl* = muscles of the skin layer; *KMkl* = muscles of the piston; *Ofn* = central opening of the sucker; *Sk* = secretion of glands; *TDr* = the tubular gland; *W* = marginal rim.

Note.—The above is a translation of Komárek's explanation of his lettering.

crotchets of equal length arranged in a " uniserial circle " (Uniordinal type of arrangement). All the hooks are turned towards the centre of the " planta " and can therefore be disengaged only by the muscles attached to the centre of the disc, by means of which the latter can be completely inverted. In the earlier stages these muscle attachments do not show a web-like pattern on the outside. Life in rapid waters demands a close application of the ventral surface of the animals to the substratum, and in this process the crotchets will gradually come to lie flat on the disc and will be greatly compressed in the dorso-ventral plane. At a very early stage the valvular gateway makes its appearance. It is now possible to conceive that the muscles used for the inverting of the disc will help in the circumstances to drive away the water from the centre of the disc and to create a vacuum in the manner indicated above. The funnel-like depressions are represented by triangular spaces which no doubt help by letting in the water to destroy the vacuum. It has been pointed out that the young larvæ are found near the edge of the stream on wet rocks and gradually invade the swift part of the current. There is a marked correlation between the behaviour of the larvæ to the current and the development of the sucker. In both these cases it is clearly seen that certain stages in the evolution of these insects are represented in their ontogeny.

*Accessory organs of attachment.*—Under this heading I propose to describe a variety of structures that assist the larva to anchor itself on rocks in swift currents. They are of the nature of mechanical devices similar to those described for the other groups of insects. It will be convenient to deal with the larvæ of the two categories separately.

*Larvæ with well-marked lateral appendages* (Plate 17, fig. 10).—According to KELLOGG (1903, p. 203), " The larva is footless ; but each body part (not body segment) bears a pair of small, unsegmented, pointed projections, situated on the ventral aspect of the lateral margin. This projection may be of slight use to the larva in locomotion, but, at best, only of slight use." I am not familiar with the larvæ of the American Blepharoceridæ, but in the case of the Indian larvæ, in which these appendages are well developed, there is no doubt that they help the larva in locomotion and fixation. In young individuals a lateral appendage is narrow at the base and is expanded at the distal end into a circular disc. From the dorsal and a part of the lateral surface of the disc issue tufts of long hair-like processes. The ventral surface of the disc is covered with innumerable small hooked spines (Plate 17, fig. 11) ; the whole structure appears as a well-defined pad of orange-yellow colour. When highly magnified each spine is broad, strongly chitinized, and sharply hooked, the hooked tip being directed mesially and posteriorly. But at the distal margin of the appendage the spines are stronger and are directed outwards.

The animal moves by lateral movements with its longitudinal axis at right angles to the current. In these circumstances the spines on the pads of the appendages are of great use to the animal for holding on to the substratum, while the spines on the side are of little use. In the case of the long spines at the end of the pad the order of utility is reversed. Those on the leeward side prevent the animal from slipping, while those on the side on which the current impinges are of little use. So in this unidirectional current it is obvious that organs of one side of the animal only can be used at one time. In young larvæ groups of strong spear-like spines are present along the lateral borders at the base of the lateral appendages. These spines are driven into the unevenness of the rocks when the animals are pushed back by the current and help to anchor the larvæ.

*Larvæ with Chiton-like form* (Plate 18, fig. 3).—In the larvæ belonging to this category the lateral appendages, situated in small notches, are greatly reduced in size and are very strongly chitinized. They appear as dark blunt projections along the lateral borders and are provided with bristle-like hairs at their apices. Along the lateral borders the body is provided with strong and sharp spines, which enable the animal to anchor itself on the substratum (Plate 18, fig. 3). There are a few bristle-like spines on the ventral surface but these are very sparse. Forming the entire border of the ventral surface, with the exception of the region of the mouth, there are variously arranged rows of the tubercles. Under high magnification each of these tubercles appears as a comb-like structure, with the spines directed towards the centre of the animal (Plate 17, fig. 12). With the help of these setose processes the larva is enabled to grip firmly the apparently smooth surfaces of rocks in torrential streams. At the posterior end the chitin is arranged in regular strands and forms a semicircular pad. This broad rim can be strongly pressed against the substratum and the whole animal sticks to the rock like a limpet. The entire organisation of this type of larva shows remarkable adaptation for life in swift currents and, so far as I am aware, this larva is unparalleled by any other creature living in similar environmental conditions.

Attention may here be directed to the dorsal armature of certain Blepharocerid larvæ. It has long been known to the students of net-winged midges that in certain larvæ the integument of the dorsal surface is produced into wart-like or spine-like outgrowths, the nature of which differs in different species. These structures have been very usefully employed by some authors in distinguishing species, though their true significance has never been realized. From a study of the principles of hydraulics and in view of the fierce currents inhabited by these larvæ, it seems clear that the dorsal armature is a device to reduce resistance to the current (p. 255). Their growth seems to depend on the nature of the current inhabited, and gradations exist between a nearly smooth dorsal surface and one with highly developed armature.

In the European larvæ the gradual evolution of these structures may be traced from the descriptions of KOMÁREK and WIMMER (1922). For instance, the larvæ of *Liponeura* from Zchenes-Zchali (p. 72), of *L. platyfrons* (p. 68), of *Blepharocera armeniaca* (p. 76), of *Liponeura* of Betscho and of *L. caucasica* (p. 70) form a series, showing the progressive reduction of the dorsal armature.

Even where the integument of the larva appears to be smooth, an examination under the binocular microscope shows the remains of the warts here and there (Plate 3, fig. 13), and the thick chitin of the dorsal surface appears to be broken up into a series of channels and ridges. The channels, by roughening the surface, probably enable the animal to offer less resistance in tempestuous waters (p. 255).

*Pupa* (Plate 17, fig. 16).—The pupa of the Blepharoceridæ is strongly convex on the dorsal surface and flat on its ventral aspect by which it adheres. The dorsal body wall is highly chitinized and is generally of a dark brown colour. Each pupa is fastened to the rocks by six pads, three on each lateral margin of the ventral aspect of the abdomen; these pads are not like the suckers of the larva, whose hold can be voluntarily loosened, but they permanently attach the pupa to one spot. The attachment of the pupa is effected by a very sticky substance, and when a pupa is forcibly detached from the substratum three whitish pads can be seen on each side; the remains of the hardened sticky secretion can be seen on each of these.

The dorsal skin of the pupa, when magnified, shows a number of papillæ which cover the whole of the surface (Plate 17, fig. 15). These papillæ appear to be studded with spines and warts of different kinds. When a pupal skin is examined while still enclosed within the larva, these papillæ are seen to be covered with spines of definite nature (Plate 17, fig. 14). Each papilla bears a strong spine in the centre with a crown of shorter spines all round it. It is evident that these structures must be of immense service in reducing resistance to the current. As the pupa becomes firmly attached to the substratum the spines are reduced and the smoothening of the contours is brought about by the rushing torrent.

### *Deuterophlebiidæ.*

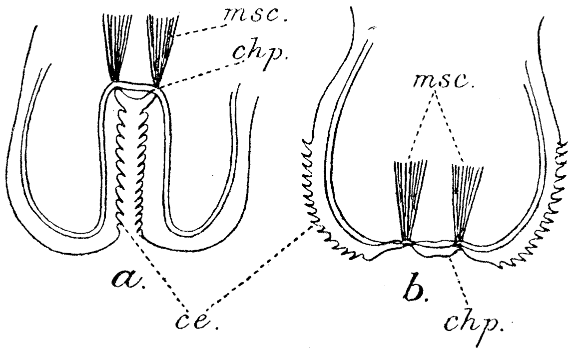
The family Deuterophlebiidæ was proposed by EDWARDS (1922) to accommodate certain remarkable Dipterous insects of doubtful affinity, but said to be allied to the Blepharoceridæ. EDWARDS had only two male insects from Kashmir, which he described as *Deuterophlebia mirabilis*. Since then, Miss PULIKOVSKY (1924) has described the larvæ and pupæ of this genus from the Altai Mountains in Siberia. BRODSKY and BRODSKY (1926) have quite recently extended the known range of the genus to Turkestan in Central Asia. Through the kindness of Mr. F. W. EDWARDS I have examined the Siberian larvæ and pupæ in the collection of the British Museum.

The larvæ and pupæ of *Deuterophlebia* are said to inhabit swift-running, clear streams, where they have been found in company with the Blepharoceridæ. They cling to smooth rocks by means of seven pairs of grappling organs borne on the ventral aspect of the lateral abdominal outgrowths. " The larvæ turn continually the anterior part of their body from side to side and move by stretching in and out their pediform abdominal outgrowths " (PULIKOVSKY, p. 46).

Each lateral disc of attachment is in the form of a thick rounded pad, the centre of which is smooth, while the periphery bears 10 to 13 rows of peculiar hooks. These hooks are so arranged on the disc that when the proleg is fully extended (fig. 9, *b*) they point towards the periphery, just like the crotchets on the posterior appendage of a

*Simulium* larva (p. 213). In this position they are capable of grappling on to the rock and effecting an attachment to the substratum. At the time of loosening the hold the centre of the disc is pulled upwards by a set of muscles, in such a way that the claw-bearing surface is invaginated so as to form a narrow canal (fig. 9, *a*). The entire mechanism of relaxation and fixation is similar to that of the posterior disc of a *Simulium* larva (p. 213) or of the abdominal appendages of the *Dicranota* larva (p. 208). In *Simulium* the functional portion of each spine gets support from its greatly developed basal portion, while in *Deuterophlebia* the same end is achieved by a rather complicated mechanism (see PULIKOVSKY's description).

Miss PULIKOVSKY has, however, explained the mechanism of attachment in a different way. According to her (p. 52), "special muscles draw in pads, though what muscles are used when the larva relaxes its hold is not evident; possibly those inserted at the outside of the prolegs. The sucking by drawing in the pad must be relaxed by the presence of the claw at the sides of the sucker. The comb-like plates form in conjunction a surface parallel to the surface of the proleg with only small intervals between them. The sucking, however, is effected after the claws are all drawn in. The combs point downwards when the pad is drawn in, and evidently can hook to the substratum only by the drawing out of the pad and the claw-bearing surface. Special muscles moving separate claws or the full set of them were not detected." It seems to me that Miss PULIKOVSKY has misunderstood the physiology of the entire structure. As I have indicated above, no sucker-formation takes place, and the attachment is effected by the hooks which are inserted into small unevennesses of the apparently smooth rock. I have reproduced in fig. 9 two diagrams from Miss PULIKOVSKY's paper, illustrating the mechanism of motion of the larval proleg, which show my point clearly and at the same time refute Miss PULIKOVSKY's theory of attachment.



TEXT-FIG. 9.—Diagram illustrating the mechanism of motion of larval proleg of *Deuterophlebia* (after Miss PULIKOVSKY). *a* = position at the time of detachment (contracted); *b* = position at the time of fixation (extended); *Chp* = chitinous pad; *cl* = claws; *msc* = muscles.

The pupa is more or less similar to that of the Blepharoceridæ, except that in the former the uniformly oval outline of the body is caused by the lateral chitinous extensions of the body and not by the flattening of the entire body. Like the

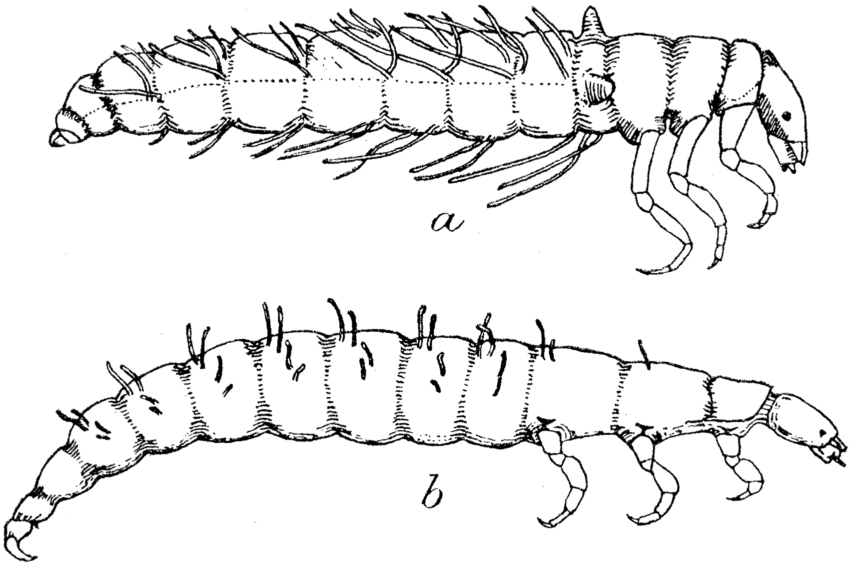
Blepharocerid pupa it is attached to the substratum by means of a sticky secretion, which is applied on the ventral aspect on three pairs of pads.

### *Some Observations on the Phylogeny of the Blepharoceridæ and the Deuterophlebiidæ.*

Mr. F. W. Edwards, in a letter dated January 10, 1928, has informed me that " The affinities of the Blepharoceridæ and Deuterophlebiidæ are very doubtful, but the two families are probably somewhat allied. The latest opinion is that they are probably as nearly related to the Anisopodidæ (Rhyphidæ) as to any other family, although they have been placed near the Simuliidæ. They are certainly among the oldest families of Diptera, and though we have no definite evidence, they probably originated as far back as the Jurassic." Crampton (1926) writes on this point as follows : " The origin and affinities of the Blepharocerids are still a mystery, and the Blepharocerids form such an isolated group, that it is preferable to consider them as constituting a distinct superfamily, the Blepharoceroidea. It is extremely probable that the Blepharocerids arose from ancestors allied to the Anisopodid-like common ancestors of the Culicoids and Bibionoids."

In classifying Diptera some authorities have attached great importance to the larval and pupal characters, while others ignore them altogether and base their divisions on the characters of the adult alone. Edwards (1926) has recently advocated that " a close study of the whole structure of the species is essential. Nor must such a study be confined to the structures of the adult, since the early stages can often provide most valuable information." The value of embryology in the study of phylogeny has long been recognized by zoologists, and here I propose to discuss the evidence afforded by the study of the Blepharocerid larvæ towards an elucidation of their probable ancestry. These larvæ are so highly specialized that hitherto no attempt has been made to investigate them with a view to ascertain their affinities with the more common Dipterous insects. The imagines have so far provided no clue to the phylogeny of the family. In these insects, where the adult state lasts for a short time and the greater part of life is spent in the larval condition, there seems to me no doubt that modifications in the larvæ are recognizable long before any significant modification makes its appearance in the adult. This is shown by the great variety of larval forms, though the resulting imagines are similar (Tonnoir, 1924, Lestage, 1925). It is also clear that the modifications in the adult can be traced back to the specialization of the larva, and that the former are the direct outcome of the latter. In short, here literally " the child is the father of the man." The Blepharoceridæ and the Deuterophlebiidæ are characterized by a secondary venation in the wing, and this feature is directly correlated with the habit of the larva and pupa of living in torrential streams and the consequent sudden eclosion of the imago. It seems probable that a Blepharocerid-type of larva has evolved from the worm-like ancestral form common to all dipterous insects under the direct influence of life in flowing waters.

It is known that the six body divisions of a Blepharocerid larva have been secondarily acquired, and that they mask the original segmentation of the insect which makes its appearance at the time of pupa-formation under the larval skin. Tonnoir (1923) has shown that the cephalic division (first division) " contains the thorax and the *two first abdominal segments*; each of the four following divisions contains one abdominal segment and the anal division the three last abdominal segments; thus the nine abdominal segments are represented." So the peculiar Blepharocerid larva reveals its ancestry at the time of pupation, when it consists of a head, a thorax, and nine abdominal segments. It appears to me probable that in such an ancestral form the median suckers were present on the second to the seventh abdominal segments. This arrangement of the organs of attachment would leave the anterior and the posterior ends of the animal free to be swayed by the eddies in the current. Such a state of affairs is not conducive to life in rapid waters, and consequently the torrential animals either spread out their organs of attachment uniformly all over the surface or the free parts of the body are reduced so that the entire body is centralized round the organs of fixation. These two principles are beautifully illustrated by the modifications undergone by the free-living Trichopterous larvæ (p. 197). The thorax, bearing legs, is increased in size and the abdomen is reduced, so as to bring the posterior pair of hooks as close to the anterior organs of attachment as possible (fig. 10, *b*). In the Blepharoceridæ something of a similar nature has happened. The anterior free segments became telescoped in the first segment of the body bearing an adhesive device, *i.e.*, second abdominal segment, while the last two free segments merged themselves into the seventh abdominal segment. In the least specialized Blepharocerid genus *Edwardsina* there is sometimes a deep



Text-fig. 10.—" Drawings showing form of caddis-worms. *a* = Case-bearing larva; *b* = Caseless species from Rhyacophilidæ " (after Dodds and Hisaw, ' Ecology,' 1925).

incision between the seventh and eighth abdominal segments and a very distinct demarcation between the eighth and ninth abdominal segments. In *Blepharocera* and *Hapalothrix* this latter is missing, that is to say, the eighth and the ninth segments have completely fused; but this compound segment is somewhat distinct from the seventh, and in *Apistomyia* even this constriction is but faintly indicated (Tonnoir, 1923). In the chiton-shaped larvæ all indications of the former segmentation have disappeared.

The Psychodid larvæ show a series of forms which recall the probable stages through which the ancestors of Blepharocerids must have passed. I do not believe that any genetic affinity exists between the two families; the resemblances are the result of convergence. The larva of *Psychoda minuta* exhibits the ancestral worm-like form (Malloch, 1917, Plate 39), that of *P. cinerea* is somewhat flattened dorsoventrally, and that of *P. superba* is still further modified in the same direction. A larva figured by Malloch as *Psychoda sp.*? shows this flattening to a marked degree, and then the final form so far known is reached in the larvæ of the genus *Maurina* from California (Kellogg, 1901) and Brazil (Müller, 1895). In *Maurina* (*Pericoma*) the ventral surface is provided with adhesive discs, but no suckers. Consequently, in spite of the presence of eight broad discs the larvæ of *Maurina* were observed by Kellogg not holding so fast to the substratum as the larvæ of the Blepharoceridæ.

The larvæ of the Deuterophlebiidæ have not departed to any great extent from the general plan of the Dipterous larvæ, though the head has been partly telescoped into the first thoracic segment and the third thoracic segment is greatly reduced. Unfortunately we do not know the exact composition of the abdominal divisions. It seems to me probable that whereas the ancestors of Blepharocerids had flattened larvæ to start with and ultimately developed median suckers (compare Psychodid larvæ), the ancestors of the Deuterophlebiidæ had larvæ with seven pairs of abdominal prolegs which they used for locomotion, just as the larvæ of *Atherix*, *Dicranota* and others do at the present time. The indications are that the Blepharoceridæ and the Deuterophlebiidæ have been derived from totally different stocks, and that any resemblances which they exhibit are due to convergence.

There is no doubt that the Blepharoceridæ are one of the oldest families among the Diptera. The transition from a worm-like ancestral larva to the present larval form of the Blepharoceridæ must have been brought about by a series of gradual changes extending over a long period, and it is, therefore, likely that the ancestors of Blepharoceridæ must have taken to life in running water at a very early period.

## Pisces.

In dealing with the taxonomy of hill-stream genera I have included extensive biological notes on fishes, and an attempt has been made to correlate structural peculiarities with factors in the environment. Annandale and I (1922) gave a short summary of the adhesive devices of fishes in our article on "Parallel Evolution in the

Fish and Tadpoles of Mountain Torrents"; while certain aspects of this problem were later dealt with more fully by ANNANDALE (1924). Since then a notable contribution on the adhesive sucker of *Garra* (= *Discognathus*) has been published by RAUTHER (1928), who apparently was not aware of the work done in India.

Reference may here be made to KYLE (1926) regarding the organs of attachment in freshwater fishes. He says (p. 269): "Another form of attachment is the adhesive disc on the belly of the fish, and this would seem to be the almost natural apparatus for the purpose of stemming a current. And if structures arose and developed on account of their utility we should expect to find it (*sic*) in the freshwater forms, but it (*sic*) is only found in marine forms. The nearest approach to the condition in freshwater is Gastromyzon of North Borneo, in which the whole ventral surface of the belly, with the pectorals at the sides in front and the ventrals behind, form a large sucker, and is used by the fish to adhere to stones in the mountain torrents. Another freshwater form, Pseudecheneis, lives in the rapids of the Himalayas and is provided with a transversely plaited disc between the pectoral fins. But apart from these examples, freshwater fishes manage to keep their places without sucking-discs." KYLE has used this as an argument to prove that structures do not arise and develop on account of their utility. In the following summary I shall indicate that all the hill-stream fishes that live on rocks in rushing waters are provided with adhesive discs, and the obvious utility of these devices is clearly indicated by the fact that the degree of development of an adhesive apparatus is directly correlated with the rate of flow of the current. Indeed, it seems impossible that any animal should be able to keep its place in tempestuous waters without an adequate means of fixation.

KYLE (p. 269) has observed that "In the rapid streams of the Himalayas the Anabantoids use their movable spine to anchor themselves to stones." So far as I am aware the Anabantoids are either found in estuarine waters or in the sluggish waters of the plains. The Anabantoids are labyrinthyform fishes provided with accessory organs of respiration. These fishes come to the surface often for their supply of oxygen, and if prevented from doing so they are "drowned." It seems to me highly improbable that the Anabantoids live in rapid waters anchored to stones with their spines, for they must rise to the surface for air, and in this act they would be liable to be swept away.

Roughly speaking, the hill-stream fishes can be divided into four groups. (i) The first group comprises small species, such as *Danio rerio*, *D. æquipinnatus*, etc., which are found in pools and pot-holes in the beds of streams. Here they are not affected by the swiftness of the current and their form is of the ordinary type. On the rush of water they seek shelter under rocks and stones at the bottom of the pools. They are good swimmers and can make their way against a gentle current. (ii) The second group contains strong migratory fishes such as *Barbus tor*, *Salmo salar*, etc., and powerful fishes such as Trout and the various species of *Orienus*, *Schizothorax*, *Labeo*, *Barilius*, etc., that live permanently in the course of swift streams. The members of this group are cylindrical in form and possess a powerful, muscular tail. They are generally found in deeper pools, but are capable of progressing against the current by a sheer muscular effort, *e.g.*, the leaps of salmon. After travelling a certain distance these animals get into deeper pools and take rest. Specimens of *Barbus tor* have been taken by me along with species of *Orienus* in the Western Himalayas in rapids about a foot or so deep. In such situations the fish shelter themselves among rocks or large pieces of stone, and in some of them the posterior lip is hypertrophied to act as an adhesive organ. (iii) To the third group I assign the small loaches which are so common in the hills of India, and the " Darters " of America (Etheostominæ, Percidæ). They are found in all situations in a rapid stream and their elongated, cylindrical form enables them to live among shingles in a rapid ; they are usually of small size and are very quick in their movements. The readiness with which they seek shelter among pebbles is simply marvellous. Some of them closely adhere to rocks and the body is somewhat flattened. The lips are thick and fleshy, and the paired fins are more or less horizontally placed. (iv) To this last group belong all the flattened fish which either live on the upper surfaces of rocks or are found skulking under stones. They are provided with well-developed means of attachment either in the form of definite suckers or as frictional devices. They crawl about on rocks in various ways, either by using alternately their lips and suctorial disc, the lips and the fins, or the pelvic and the pectoral fins. Some fishes are known to climb vertical faces of rocks for a considerable distance, for example, *Garra* in India, and *Arges* in the Andes (S. America). All of them are, however, capable of darting from one place to another with great speed, and this is due to the muscular action of their whip-like tails.*

The formation of a true vacuum-sucker has been studied in two instances only, namely, in *Garra* and in *Sicyopterus*. They belong to widely separated families—the Cyprinidæ and the Gobiidæ respectively. *Garra* is abundant in the hills of India and other countries of Asia and Africa ; while the other genus was studied in its native habitat in the Andamans by the late Dr. N. ANNANDALE. In outward form and appearance the two fishes are very much alike and their mode of life is also similar. *Garra* adheres by means of a disc formed by the modification of the skin on the ventral surface. The morphology, histology, physiology and the probable evolution of the disc have already been dealt with, and recently RAUTHER (1928) has given more particulars. In the development of *Garra* the various stages in the probable evolution of the disc are represented (HORA, 1921, pp. 639–643), and the earlier stages in the

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* In most of the hill-stream fishes the lower lobe of the caudal fin is distinctly longer and better developed than the upper. The powerful stroke of such a fin would result in raising the anterior end of the fish towards the surface. When darting from rock to rock in shallow rapid-running waters, the fish actually moves with its head pointing towards the surface and thus obviates encountering any obstructions in its path. It is also remarkable that in certain Homalopterid fishes the marginal rays of the caudal fin are fused together to form a compact plate-like structure, which enables the fish to give a powerful stroke during progression.

development of the disc are found as permanent stages in the more primitive species of the genus. A close study of the fishes of this genus has revealed a definite correlation between the rapidity of the flow and the development of the disc, and in the case of *G. gravelyi* and *G. mullya* I have been able to indicate that individuals of the same species living in lakes and in adjacent streams are differently modified. Indeed, this extreme plasticity of the organism is a great difficulty in defining the precise specific limits of the various species of the hill-stream genera.

The genus *Garra* is probably derived from sluggish-water fishes of the genus *Cirrhina*, by a series of gradual modifications induced by life in swifter and swifter currents. The differences between *Garra* and *Cirrhina* are bridged over by such forms as *Lissochilus* and *Crossochilus*. The latter genus in its highest development is similar to the primitive species of *Garra*; for example, ANNANDALE'S *G. adiscus* from Seistan is as much a *Crossochilus* as a *Garra*, and it is only for the sake of convenience that I regard it as *Garra*.

Besides having sucking-discs papillated peripherally the fishes of the genus *Garra* are provided with fringed and papillated lips. The papillæ are beset with retroverted spines, which help in adhesion. In the highly specialized members of the genus *Garra* the outer rays of the paired fins are provided with adhesive pads and the disc is considerably reduced, as in *Garra kempi* from the Naga Hills. This transfer of the adhesive organ from the centre of the animal to the extremities is a remarkable feature of all the hill-stream animals. The disc of *Sicyopterus*, as in other members of the family, is formed by the union of its ventral fins. This modification appears to have been originally induced for life in the breakers on the seashore, but *Sicyopterus garra* from the Andamans appears to have perfected it while taking to life in swift currents.

In all other hill-stream fishes the organs of attachment consist of papillated or striated pads of skin, which are beset with retroverted spines for clinging to stones. Such structures may be developed on any part of the ventral aspect of the animal that comes in contact with the substratum. The lips are usually hypertrophied and covered with papillæ. The barbels are short and stumpy, and at their bases possess adhesive pads, as in *Glyptosternum labiatum*, or are covered with papillæ, as in *Pseudecheneis sulcatus*. The chest and the outer rays of the paired fins are, however, the most suitable places for the development of the "discs," and in the following account attention will be directed chiefly to the modifications of these regions. A short series of forms showing gradual development of the adhesive apparatus induced by the swiftness of the current is here considered, but for a detailed treatment of the subject my earlier work may be consulted.

It has been supposed that the greatly enlarged lips of the hill-stream fishes, such as the Loricariidæ, form a sucker in conjunction with the mouth. It has been assumed that the lips are laid flat on the substratum and serve as the border of a sucker formed by a vacuum created by the mouth. In the highly specialized fishes of the Indian torrents, I have shown (**1923**, *b*) that the process of respiration continues even when the fishes are closely applied to the substratum. In the circumstances it is impossible to conceive that a sucker can be created by the lips. Moreover, most of these fishes feed on the algal slime, which they scrape off the rocks by their specially modified jaws and teeth, and in ingesting this material advantage is taken of the current entering through the mouth. Even in such fishes as *Gyrinocheilus* (Cyprinoidea) and *Arges* (Loricariidæ), in which the respiratory current is not taken through the mouth but is inhaled and exhaled through separate passages in the gill opening, the gill chamber is in direct communication with the oral cavity and it is not possible that the lips can form a sucker. The adhesion is, however, effected by the spinous papillæ on the lips and by the low pressure induced by the rapid-flowing respiratory current through narrow channel and passages (p. 259).

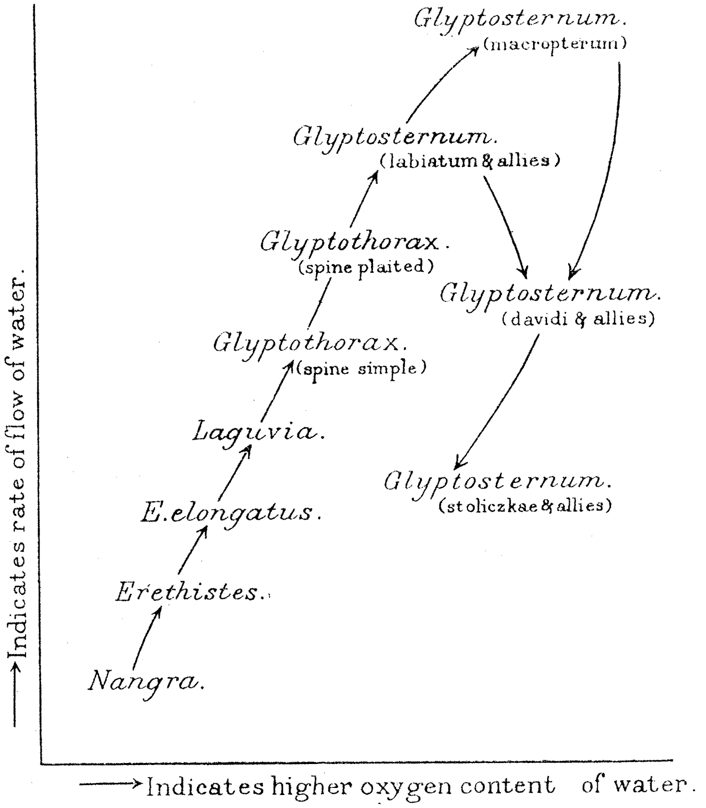
It has been pointed out above that some of the loaches (*Nemachilus,* etc.) living in fast currents are somewhat flattened, and the paired fins in them are more or less horizontally placed. This increase of the adhesive surface by a close application of the outer part of the paired fins to the substratum is better marked in the Homalopteridæ, some of the primitive members of which, such as *Glaniopsis* and *Crossostoma,* are similar in form and behaviour to the flattened species of *Nemachilus.* Superficially, the line of demarcation between the families Cobitidæ and Homalopteridæ is very faint indeed. They have been separated from each other on the characters of the paired fins which are more horizontally placed in the Homalopteridæ and in which some of the outer rays (at least in the pectoral fins) are simple. Such a change is evident among all the fishes that cling to rocks by means of the lateral fins, and even among the Homalopteridæ a gradual broadening of the fins and an increase in the number of rays, both simple and branched, have been induced by life in stronger and stronger currents. These modifications are further correlated with the increased flattening of the body. *Glaniopsis* and *Crossostoma* are more or less cylindrical, and among the species included in the genus *Homaloptera* all kinds of body-form occur. Some are like *Nemachilus*, whereas others are greatly flattened.

From these depressed species a regular series of gradations can be traced through such genera as *Parhomaloptera*, *Balitora* and *Hemimyzon* to the most specialized genus of the family, *Gastromyzon,* in which the fins overlap one another and with the greatly flattened ventral surface of the animal convert the under surface into a disc-like structure. When the body is so depressed that the fins come in contact with the substratum, the outer extremities of these fins are used for adhesion and consequently specialized skin-pads are developed on their ventral aspect. The outer rays become more and more specialized for the function of attachment and are brought closer to the body. This results in the inner rays being directed upwards. In living fishes this inner portion of the fins is constantly in motion, and in this way helps to pump out leakage water from the ventral surface of the animal when closely applied to the rock. The negative pressure thus produced on the under surface keeps the animal fixed to the substratum. This constant flapping of the inner rays leads to the greater development of the fins, till ultimately they overlap and form a complete disc on the ventral aspect of the animal, which now becomes so closely applied to the rock that no water can enter on its under side (*cf.* the description of same process in the Heptageniid nymphs of mayflies, p. 188). It is usually considered that by this arrangement of the fins a sucker is formed on the ventral surface. A sucker could be created only by the middle part of the animal being raised, but this would not be possible in the rapid current where the animals lie flat, closely pressed to the substratum. Moreover, I have not been able to find any mechanism by which the centre of the animal could be arched upwards. Nevertheless, there is no doubt that when lifted by the hand a vacuum-sucker is created. Under normal conditions I believe that adhesion is not the result of sucker-formation but is due to the action of the current produced by the fins, that is, to adpression, and to the adhesive pads on the fins.

A parallel series of modifications is exhibited by the Siluroid fishes inhabiting the torrential streams of the Oriental Region—Sisoridæ; of Africa–Amphilidæ, and of South America—Loricariidæ. Notes on the habits of the Sisoridæ have already been published (HORA, 1923), while an acquaintance with the members of the other families was recently made by a study of the preserved material in the collection of the British Museum. I have here to express my sincere thanks to Mr. J. R. NORMAN for giving me facilities to study this material.

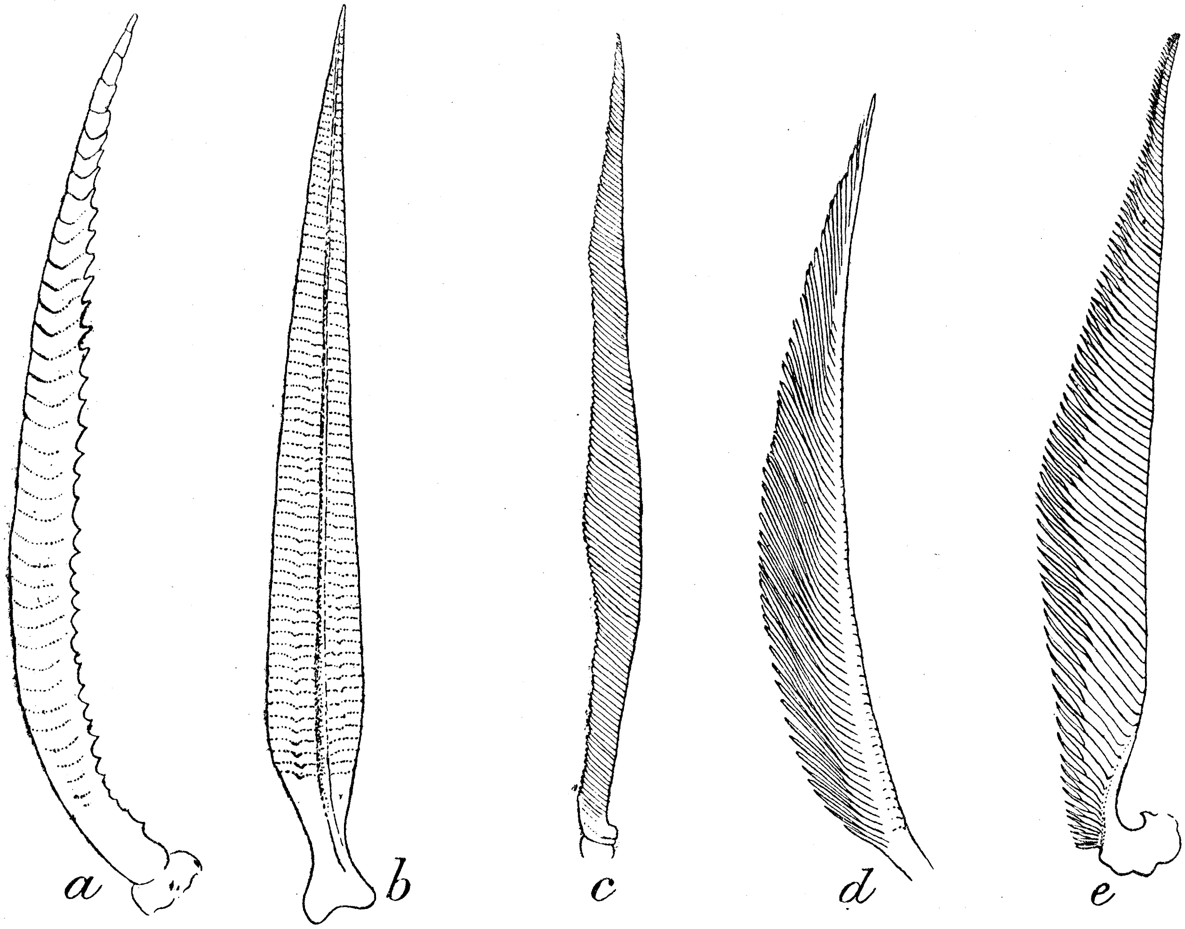
The Sisoridæ furnish a remarkable series of forms, which in the degree of their modification clearly illustrate the direct effect of the environment. For example, the small fishes of the genus *Nangra* live at the bottom of rivers of the Indo-Gangetic plain. Life at the bottom has induced a heavier build and a reduction of the air bladder. Thus modified they were in a better position to invade the swifter current where bottom-life is more or less a necessity. The next genus in the series is *Erethistes*, most of the species of which live at the bottom, in deep but rapid-flowing waters, at the base of the hills. One species, *E. elongatus*, has invaded smaller streams and is found below the Darjiling Himalayas and in the Garo Hills. The whole of the ventral surface between the pectoral and the ventral fins is thrown into longitudinal folds which undoubtedly help the animal in adhering to the substratum. It may be remarked that in a cylindrical fish this is the part that first comes in contact with the substratum and is consequently modified for adhesive purposes. Now the flattening of the animal commences and the adhesive disc becomes more and more restricted to the chest region of the fish. My genus, *Laguvia*, from the base of the Darjiling Himalayas, shows an advance on *E. elongatus* and leads to the genus *Glyptothorax*, in which there are two types of fishes, (i) in which the thoracic disc is extensive and the outer ray of the paired fins is not provided with an adhesive surface, (ii) in which the thoracic disc is relatively much smaller, the form is greatly depressed and the outer ray of the paired fins is furnished with an adhesive surface.

All possible gradations occur between such forms as *Laguvia* and *Glyptothorax pectinopterus* (HORA, 'Rec. Ind. Mus.,' xxv, Plate 4, 1923), and from the habitats of the different species it is clear that modifications have been induced by the direct effect of the swifter and swifter current. By a further reduction of the thoracic disc and its ultimate disappearance, and by perfecting the adhesive pads on the outer rays of the paired fins, the fishes of the genus *Glyptosternum* can be derived from those of the genus *Glyptothorax*. In the former genus evolution has proceeded along different adaptive lines. Those that continued to live on bare rocks in swift currents perfected the adhesive devices along the same line as indicated for the Homalopteridæ, till ultimately the wing-like pectorals overlapped the ventrals, as in *G. macropterum* from Burma, and formed a water-tight disc on the ventral aspect of the animal. Others on reaching the highlands of Central Asia found less strenuous conditions in the relatively calm and placid waters of the deep rivers, discarded their specialized garb and assumed a simplicity which made me believe at first that they were genuinely primitive species of the genus. This retrograde evolution (fig. 11) can be followed through such forms as *G. davidi* from China, *G. hodgarti* from Nepal to *G. maculatum* from Tibet, and *G. stoliczkæ* from Kashmir and the adjacent regions. A similar series exhibiting retrograde evolution has been indicated among the Heptageniid nymphs of mayflies.



TEXT-FIG. 11.—Diagram illustrating the probable evolution of the Sisorid Fishes as induced by two of the main factors in their environment.

Among the Amphilidæ of Africa the form is greatly depressed and the paired fins, which are horizontally placed, undoubtedly help the animal in clinging to rocks. The fishes of the genus *Phractura* (*Ph. fasciata*, for example), are characterized by a flat body and a whip-like tail. In *Doumea* the form is similar to that of *Homaloptera*. In *D. typica* the mouth is small and is surrounded by thickly papillated lips and tentacles which help in adhesion. The paired fins are broad and the outer adhesive ray is soft and flat. The highest development in this family is reached in the genus *Amphilius*, the members of which are superficially similar to *Glyptosternum*. The skin on the ventral aspect of the adhesive ray is well-thickened and is covered with microscopic spines. On removing the enveloping skin the ray is seen to consist of a spine, broad and bony at the base, but segmented in its distal portion. Along its outer border it gives off soft, pointed, cartilaginous rays (fig. 12, *d*). In this connection the close convergence of the spine of *Amphilius* and of *Glyptosternum* may be noted. Such a segmented structure is useful for adhesion in current of varying rapidity in the hill-streams, for it easily bends before pressure. This would be impossible for a bony



Text-fig. 12.—Outer pectoral rays dissected from fin-membrane to show the segmented nature of spine in widely separated Siluroid genera. *a* = Glyptothorax; *b* = *Arges*; *c* = *Glyptosternum vinciguerræ* (Regan); *d* = *Amphilius*; *e* = *Glyptosternum stoliczkæ* (Day). *a*, *c* and *e* are after Annandale (1923).

structure. In this instance it may be noted that the production of similar structures has been induced by similar factors in the environment.

The Loricariidæ of South America constitute a family of remarkable Siluroid fishes, which are found only in the clear waters of the hill-streams. The various subfamilies and genera show a series of gradual modifications by which these fishes have managed to establish themselves in swift currents. Unlike the other Siluroid fishes they are covered with a bony armour of scutes, which are spinose, with the spines directed posteriorly. In narrow crevices among rocks there is no doubt that these spines help the animal in fixation. The form is depressed and the paired fins are horizontally placed. The outer ray of the lateral fins is flattened and is provided on the ventral surface with strong retroverted spines for grappling on to the substratum. The mouth is on the ventral surface, considerably behind the tip of the snout, and is bordered by extensive lips, which are closely studded with adhesive tubercles.

In the Loricariidæ the entire surface is covered with scutes, but life in swift currents demands a closer application of the ventral surface to the substratum and consequently the scutes on the under surface are gradually reduced. The function of fixation is thus shifted from the middle of the fish to the extremities, and in response to this the outer ray of the paired fins is greatly flattened and is segmented. In the specialized forms it becomes very flexible, at least in its distal portion.

In the Hypoptopomatinæ the chest is covered with thin scale-like scutes, and among the Plecostominæ the scutes on the ventral surface of *Chætostomus* (*Ch. marginatus*) are thin and smooth ; while in *Pseudacanthicus* (*P. serratus*) and *Ancistrus* (*A. cancanus*) the ventral surface in front of the anus is naked and can be closely applied to the substratum. In *Neoplecostoma* (Neoplecostominæ) the body is naked on the ventral surface in front of the anal fin, except for a squarish patch on the chest. This is covered with numerous backwardly directed spines, and these no doubt function in the attachment of the animal just in the same was as the thoracic discs of the Sisoridæ. The most highly specialized Loricariid fishes are those of the subfamily Argiinæ, which are naked and resemble the Amphilidæ and Sisoridæ in general form and build. There is no doubt that the nakedness of the body is secondarily acquired by *Arges*, by a further modification of such forms as *Plecostoma*. It is worthy of remark that in some species of *Arges* the skin in the region corresponding to the rectangular plate of *Neoplecostoma* is granular, indicating the last stages in the reduction of the scutes.

The Argiinæ have been observed to climb vertical rocks in rushing water by using alternately their lips and the ventral fins for adhesion (JOHNSON, 1912 ; EVERMANN and KENDAL, 1905). EVERMANN and KENDALL observed that these fishes can progress on land by using alternately their pectoral and pelvic fins. In *Arges* the lips are so closely applied to the substratum that the normal mode of respiration is obstructed and the fishes " breathe " by taking in and expelling the respiratory current through the inhalent and exhalent apertures formed by the modifications of the gill opening.

Attention may here be directed to the observations of EIGENMANN (1912) on

*Rivulus waimacui* (= *R. holmiæ*). He writes that "*R. waimacui* showed remarkable powers of climbing the high steps in the creek bed. One would spring out of the water and remain attached by its tail to the side of the rock, whence it would leap to a still higher point." I have examined one of EIGENMANN'S specimens of this species in the British Museum. There is no adhesive structure in the caudal region of the fish, and how it could stick to rocks by its tail I am unable to explain. Most of the freshwater fishes have the habit of leaping out of the water occasionally, and this is especially true of the family to which *Rivulus* belongs. EIGENMANN says that "At the time of my visit the water was confined to cracks in the long rocky steps forming the bed of this creek," and it seems probable that the *Rivulus* in jumping out of the water fell on a dry rugged rock, where its mucous secretion would help it to adhere for a short time till it jumped up again and reached another dry and rugged rock.

## BATRACHIA.

In 1922, ANNANDALE and I gave a short survey of the organs of attachment of the brook-inhabiting tadpoles, pointing out that in general the modifications undergone by the Batrachian larvæ are similar to those exhibited by the fish of mountain torrents. NOBLE (1927) has recently described the probable adaptations of the tadpoles of swift currents at some length. Through the kindness of Mr. H. W. PARKER I had an opportunity of examining the highly modified forms of Amphibian larvæ in the collection of the British Museum, and through the generosity of Dr. MALCOLM A. SMITH I have received some interesting material for study. My sincere thanks are due to these gentlemen for their kind help.

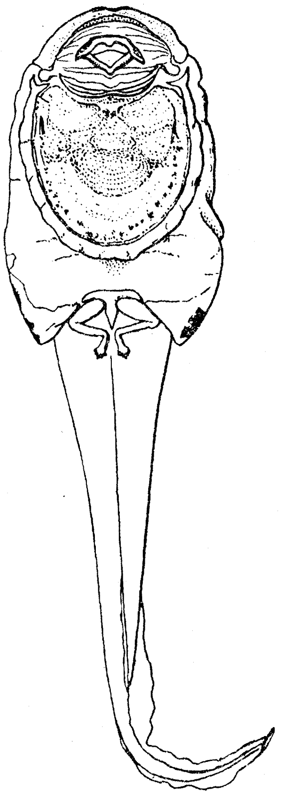
It has already been pointed out (ANNANDALE and HORA, 1922, p. 506; HORA, 1923, *b*, p. 582) that the hill-stream tadpoles can be divided into three categories according to their habitats. Tadpoles of *Rana alticola* and *R. malabarica* are found in large pools where the current is a negligible factor and consequently the animals are not provided with any kind of adhesive apparatus. They are large and stout, with powerful tails, and are endowed with strong swimming powers. The second group comprises tadpoles of the section Ranæ Formosæ of the subgenus *Hylarana* of the genus *Rana*, and all other tadpoles in which one or both the lips are greatly developed to form a "sucker" round the mouth. These tadpoles are usually found sticking to the sides of rocks or skulking under stones in rapid waters. They can be observed to crawl by the muscular action of the lips. In the flat form of the body and the stream-line curve of the dorsal profile the animals exhibit marked specialization for life in swift currents. The tadpoles of this group show different stages of evolution of the so-called "oral-sucker," and this can be correlated with life in waters of stronger and stronger current. The third category includes the funnel-mouthed tadpoles of *Megalophrys*, which are found in sheltered places in the course of swift currents or in pools and puddles in the bed of an intermittent hill-stream. The funnel mouth of these tadpoles has perhaps caused more discussion than any other single tadpole feature, and even now naturalists are not agreed as to its probable functions. I (1928) have critically reviewed the various suggestions and have tried to interpret the mechanism and functions of this peculiar structure from observations on the living tadpoles.

The tadpoles of the swimming type require no further consideration here. Those of the second type can be subdivided into two groups, firstly, those in which a definite sucker exists behind the mouth, and secondly, those in which the lips alone form the requisite organ of attachment. The morphology and histology of the true ventral sucker of the tadpole of *Rana afghana* and its allies have already been described and the mechanism of the sucker explained (ANNANDALE and HORA, 1922). So far, we are acquainted with the peculiar structure of *R. afghana* only in its fully formed condition, but it seems highly improbable that such a structure could have arisen *de novo*. It seems likely that either the earlier stages have not yet been discovered or perhaps have been eliminated during ontogeny. To me it seems probable that the line of evolution of the sucker will prove to be similar to the development of the sucking-disc of the fishes of the genus *Garra* (HORA, 'Rec. Ind. Mus.,' xxii, pp. 639–643, 1921). The efficacy of the sucker has been demonstrated already (HORA, 1923, *b*, p. 588) by showing that a tadpole could lift out of water an object about 60 times its own weight.

The disc of *Rana afghana* is very extensive ; it is almost as broad as the body and a little more than half its length ; it is provided with a free border, except at the anterior end, where the border is replaced by the posterior lip, which is fimbriated along the posterior border and is notched in the middle. The anterior and the posterior lips are continuous and at the corners of the mouth are thrown into folds, which fit into socket-like depressions at the anterior terminations of the free borders of the disc. The anterior lip is well developed, and is provided with series of tooth-rows all over its surface ; even its free border is provided with a row of teeth. When the lip is expanded the teeth are directed forward, but they are recurved at their tips and are pointed with a series of backwardly directed spines along their ventral aspect, which help in adhesion. The complicated arrangement of folds at the corners of the mouth is probably for the purpose of respiration. I have made no direct observations on this point, but it seems probable that by means of these folds the respiratory current is so managed that neither the efficiency of the sucker is impaired nor the mouth lifted from the substratum when a current of water is sucked in through the corners of the mouth.

In preserved specimens the central portion of the disc presents the form of a saucer. Along its sloping sides the skin is hardened in places (fig. 13), and numerous patches of spines are developed, which undoubtedly help in the adhesion of the disc. In the centre the skin is thin and smooth, and through it the muscles of the disc are seen clearly.

As has been indicated above, these tadpoles live on rocks in swift currents, and under these conditions they have never been observed to swim. They crawl about on rocks with the head always pointing upstream, and the progression is effected thus : A tadpole, quietly lying at the bottom, holds on to the substratum both by means of its disc and by means of the broad anterior lip. During progression the anterior lip is detached from the substratum by means of a pair of strong muscles originating from the posterior border of the orbit and inserted on the maxillæ; they pass below the eyeball and occupy the whole of the floor of the orbital region. By a contraction of these muscles the maxillæ supporting the broad upper lip are pulled upwards and backwards, and it seems probable that in this action the nasal region of the skull is also moved. On the relaxation of the muscles the anterior lip is thrust forward and takes hold of the substratum. Now the sucker is disengaged and brought as close to the anterior lip as possible. By repeating these movements the animal is able to progress fairly rapidly in the fiercest currents. Sometimes, when alarmed, these tadpoles were noticed to dart from one rock to another, and in this movement advantage is probably taken of the powerful muscular tail, but the movements were too rapid to allow me to study the mechanism.

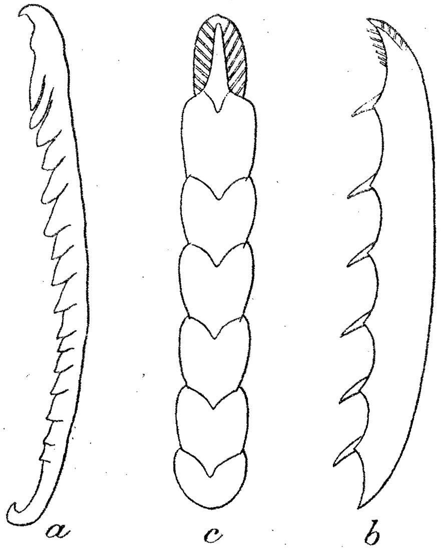


TEXT-FIG. 13.—Ventral aspect of the tadpole of *Rana hainensis* (diagrammatic).

About the habits of the frogs of this type (*Rana larutensis*, for example) LAIDLAW (1900) remarks as follows: "These handsome frogs are extremely common along the banks of the rapid jungle torrents running about the foot of Gunong Inas. They sit on the great boulders strewn along the course of the stream, and when one approaches them, spring boldly into the water, no matter how fiercely it may be pouring down. Soon after being disturbed they will again take up their station on the rock which they had quitted, and in such a position their colouring renders them well-nigh invisible." These frogs are provided with broad discs on their toes, which are studded with spinous outgrowths for increasing friction (HORA, 1923). From a study of the digital pads of the tree-frogs, NOBLE and JAECKLE (1928) have concluded that these structures are fortuitous in their occurrence, and, therefore, no adaptive significance should be attributed to them. So far as I can judge their main argument for this view is that the digital discs are not only found in tree-frogs, but among others also that frequent rocks, etc. The point for consideration in such a study is whether in both these habitats frictional devices are necessary, or not, to prevent the animal from slipping. It is likely that a frog living on rocks needs these pads as much as a frog living on trees. It seems to me probable, however, that the development of these pads was originally induced by a habit of living on rocks, and it was afterwards that the frogs became arboreal in their habits, and adapted themselves for such habitat by a further modification of their body and by perfecting the discs. The exceptionally long hind-limbs of these animals enable them to swing before the current with its eddies without loosening their hold.

It is clear from the above account that in *R. afghana* and its allies the lips and sucker share equally the function of attachment, but in most of the other hill-stream tadpoles adhesion is effected by the help of the lips alone. It has been hitherto considered that the broad lips provide a rim round the mouth which, acting as a sucker, creates a vacuum. This is not so, because the tadpole continues to "breathe" when it is attached to the substratum, and this necessitates a respiratory current flowing in from the mouth or from the nasal openings and passing out through the spiracle. In the case of the tadpoles of *R. afghana* and its allies, I have indicated that at the corners of the mouth the folds of the lips form respiratory channels, and the same is true regarding most of the tadpoles that adhere by means of their lips alone. But when the lips are so closely applied to the substratum that no water can enter into the mouth, the respiratory current enters through the nasal openings. In some tadpoles, for example *Ascaphus truei*, these openings become specially modified for this function (see NOBLE, 1927, for description and figures). It must be borne in mind that the respiratory current is also the food current of the animal. In most of the species with which I am acquainted (no direct observations on the living animals have been made) more or less well-developed channels exist at the corners of the mouth, and in this region the teeth are either feebly developed or are altogether absent. In certain tadpoles, such as *Rana beddomei*, finger-like processes are developed in these grooves, probably to test or filter the food particles entering the buccal cavity.

The adhesion is brought about by means of the rows of teeth or papillæ that are present on the enlarged lips, and in the case of the tadpoles of *Hyla* of Santo Domingo, NOBLE (1927, Plate 9) has been able to indicate a definite correlation between the tooth-row number and the speed of the current. The known tadpoles of Ranidæ and Bufonidæ could be arranged in similar series. It is evident, however, that the progressive evolution of these structures is to be accounted for on the principle of change of function. For example, in *Rana liebigii*, a slightly modified hill-stream animal, the form and structure of the horny teeth on both the lips are more or less similar. Each tooth is a rod-like structure, flattened and spatulate for a short distance near the free end. This flattened portion is probably used for rasping off slime, and is serrated, with a series of distally directed teeth along its borders. The ventral aspect of the remaining part of the tooth is provided with strong recurved spines which are directed posteriorly. Thus, the distal portion of the tooth is used for scraping and the proximal for fixation. In the highly specialized tadpoles of *Helophryne* the teeth on the anterior lip are further modified and are used for the purpose of attachment only. Each tooth resembles a slightly curved rod, sharply pointed at its apex, and along the ventral border of each tooth is a series of powerful spines directed posteriorly (fig. 14, *a*). The teeth on the posterior lip are similar to those of *Rana liebigii*, but are much better developed (fig. 14, *b*, *c*), and these rows of saw-like teeth present so many sharp points which hold on to the substratum. The respiratory current entering the mouth will carry with it the food scraped away from the substratum, but it is clear that the lips in conjunction with the mouth cannot form a sucker. The soft papillæ with which the extremities of the lips are sometimes studded, are not provided with spines, but they undoubtedly serve to increase friction.



TEXT-FIG. 14.—Teeth of *Helophryne rosei* (highly magnified). *a* = grappling tooth of anterior lip, side view; *b* = partly scraping and partly grappling tooth of posterior lip, side view; *c* = same as seen from ventral surface.

In some tadpoles only one lip (posterior) is developed, while in others both lips are equally developed. These differences in the growth of the lips are probably due to the relative position of the mouth in the ancestral forms. For example, when a species with an anterior or a slightly inferior mouth takes to life in rapid waters, by holding to the rocks by means of its "teeth," those on the lower or posterior lip will be greatly affected, and consequently this lip will become larger and larger under the influence of the stronger and stronger currents. Sometimes it so happens that the teeth do not keep pace with the growing lip, which consequently becomes studded with soft papillæ for adhesive purposes. On the other hand, when a tadpole with a distinctly inferior mouth takes to life in rapid water it can employ both the lips for adhesion, and consequently both the lips are equally developed. The tadpole of *Bufo penangensis* (STOL.) may be taken as the type of the first group; in it the anterior lip is small and bears only two series of teeth, while the posterior lip is greatly developed and besides bearing a series of teeth is thickly studded with short rounded papillæ. These tadpoles, according to FLOWER (1899), "live in the swift-flowing hill-streams, and are to be found where the torrent is rushing fastest, fixed to the face of granite boulders which obstruct the stream; a favourite place of theirs was a perpendicular wall of rock which the water fell over in a small cascade; they hold on so fast with their mouth that they cannot easily be pulled off, but have to be plucked away between one's finger and thumb. They move upstream and about the face of the rock by means of their mouth; when placed in a glass bowl they never lay on the bottom (as most tadpoles do), and seldom swam about, but fixed themselves to the glass sides. In captivity they died in a few hours, the still water probably not suiting them." As an instance of the second type, the tadpole of *Helophryne* may be taken. In this animal both lips are equally developed and are provided with several series of teeth. Short, thick papillæ are situated on the posterior lip near its hinder end.

Two distinct types of *Megalophrys* larvæ are known. One type is heavily built and is provided with broad adhesive lips similar to those of *Rana beddomei* and *R. liebigii*, while the second type includes slim-bodied larvæ provided with a curious umbrella-like structure surrounding their mouth. Of the known tadpoles of *Megalophrys*, two species belong to the former type, and six or seven to the latter. Regarding the habitat of the two heavily built species of *Megalophrys*, SMITH (1917, p. 273) remarks as follows: " In general characters these two tadpoles are alike, and on my visit to the hill I found them both inhabiting the same stream. While *M. pelodytoides* was at a higher level, where the water was shallow and the current swift, *M. hasseltii* lived lower down, in deep pools of nearly still water. The flat, rounded, body of this latter tadpole was in marked contrast to the flattened shape of the former, that lives continually in running water " (the correlation between the build of the body of these two tadpoles and their corresponding habitats may be noted). The habitat of the second type of larvæ has so recently been discussed by me (1928) that it is unnecessary to recapitulate it here. Unfortunately our knowledge of the environmental factors is very backward, and though ANNANDALE was fully aware of the differences in the habitats of the two types of larvæ, he assumed that they lived under similar conditions.

As early as 1906, ANNANDALE (p. 292) compared the habitat of *Rana liebigii* with that of " *Megalophrys montana*," and observed that the tadpoles of *R. liebigii* " frequent the upper surface and sides of submerged stones, under which they hide themselves when alarmed; but the larvæ of *M. montana* remain, at any rate during the day, in corners of the extreme edge of the same pools, generally among the vegetable debris which collects in such places." Again, in 1924, he wrote as follows (p. 17): " Generally speaking, the two types of tadpoles have a rather different habitat, those of slender shape and with an umbrella-like mouth inhabiting rapid-running streamlets, the other rather slower waters; but this is not always so. In hill-streams in Tenasserim I have found the two types together, that is to say, within a few feet of one another, those of the heavily built type skulking under stones, those of the other type in corners of the little pools." In spite of such a clear distinction ANNANDALE considered that the two types " exist in the same environment." I have elsewhere (p. 176) indicated that these apparently similar environments harbour totally different types of fauna, in correlation with the different conditions prevailing for existence.

I have given these details because NOBLE, in a recent paper (1927, p. 76), relying on the similarity of habitat of the two types of tadpoles, has stated that " the expanded mouth may appear sporadically and suddenly in different groups of Salientia." A hypothesis which takes for granted that such complicated structures " may appear suddenly " will not carry us very far towards understanding the true relationships of the various types.

A somewhat modified " umbrella-mouth " occurs among the tadpoles of certain species of *Phyllobates*,* *Microhyla* and *Phyllomedusa*. As the differences in the habitat in which most of these larvæ and their close allies live have not been properly recorded, it is not possible to indicate the origin of the umbrella-mouth of these genera. A consideration of the probable conditions under which the funnel of the *Megalophrys* tadpoles may have been evolved may throw some light on the origin of the umbrella-mouth in others.

There is no doubt that the tadpoles of *Megalophrys pelodytoides* and *M. hasseltii* are primitive, as compared with the funnel-mouthed tadpoles of the other species, and in fact they differ very little from the larvæ of the western genus *Pelobates*. It has also been pointed out that the build of these animals is directly correlated with the rapidity of the current. It is easy to conceive that under the action of the stronger and stronger current the two lips became broader and developed an increasing number of tooth-rows. Thus modified they would superficially resemble the present-day tadpoles of *Helophryne* and *Ascaphus*. These types of lips when not fully expanded take a crenular form, and this condition is better marked in spirit specimens. NOBLE'S (1927, p. 61) figure of *Ascaphus truei* illustrates my point very clearly. I believe that these supposed highly developed ancestors of the funnel-mouthed tadpoles took to life in quieter waters or in sheltered places in swift currents. Under changed conditions the lips were no longer necessary for adhesion and were consequently held free from the substratum, and under the pressure of the water assumed the folded form so characteristic of the umbrella-mouthed tadpoles of *Megalophrys* under water. Even the disc of a lamprey, when not in action, is folded in a vertical wedge-shaped fashion (DAWSON, 1905, p. 91).

The so-called changed conditions require further explanation. The continuous increase in the size of the lips must have been brought about by a continuous flow of water of increasing swiftness. Now suppose that on account of some change in the meteorology of the place the perennial streams become intermittent, liable either to break up into a series of pools and puddles which may dry up altogether or become rapid torrents generated by a single shower (such is the habitat of the funnel-mouthed larvæ). The tempestuous waters of torrents contain a high percentage of dissolved oxygen and it is known that animals tend to reduce their respiratory organs under such a condition. In fact, DODDS and HISAW ('Ecology,' V, pp. 262–271, 1924*a*) have been able to show a "definite correlation between gill area and oxygen content of the water." So when these tadpoles with reduced gills were left in pools and puddles with an ever-decreasing quantity of oxygen dissolved in the water, they would naturally come to the surface for inhaling the atmospheric air, and this habit would ultimately lead to the lungs becoming once more functional for respiration.

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* Regarding the habitat of the two types of tadpoles of *Phyllobates*, DUNN (1924, p. 11) remarks as follows: "These two sorts of tadpoles were common in the stream at La Loma. Those of *latinasus* were similar to Rana tadpoles in appearance and in actions. The tadpoles of *talamancæ* seemed to remain in the deepest parts of the pools and were very active and darter-like in their movements." So there is a close similarity between the habitats of the funnel-mouthed tadpoles of *Phyllobates* and *Megalophrys*.

In the tadpoles of *Xenopus lævis* the same thing happens as has been pointed out by BLES (1905, p. 812). He remarks that "the tadpoles are constantly rising to the surface for air, and do so more frequently the warmer the water is; it follows that the lungs are not only hydrostatic in function but also respiratory. Reducing the quantity of water has the same effect as raising the temperature." In the course of a swift current *Megalophrys* tadpoles have never been observed to rise to the surface, but when taken out and kept in a bowl of water it was "observed that the tadpole could not lie at the bottom for an indefinite period, but after every ten to fifteen minutes it came to the surface, remained there with its funnel expanded for a short time and then sank under water with the funnel folded. When the funnel was expanded the tadpoles were observed to give out fairly large bubbles of air" (HORA, 1922, p. 9). When kept for a longer time in captivity they came to the surface more frequently, and the specimens kept in captivity by SMITH in a large bath with bricks and water-weed in it were found constantly hanging from the surface film. Thus, there appears to be a direct correlation between the quantity of oxygen in the water and the hanging of the tadpoles from the surface film.

It is well known that the hill-stream animals die after a short time in captivity, because in still waters they do not find enough dissolved oxygen to sustain their activities, and the very fact that SMITH (1926, p. 985) was able to rear the *Megalophrys* tadpoles in a bath tub shows that they must be using their lungs for respiration. The *Xenopus* larvæ have to rise constantly to the surface to effect an exchange of gases because they are not provided with any mechanism by which they can hang from the surface film indefinitely. The case of the *Megalophrys* tadpoles is different. Their broad lips, originally developed for the purpose of attachment, would expand at the surface under the influence of the surface tension (also partly by their own muscular action) and the rows of teeth by breaking through the surface film would form a mechanical support for the larva to hang from. It is clear, therefore, that under the changed environmental conditions a corresponding change in the form and function of the structures has taken place.

Considerable attention has been paid to the feeding mechanism of the umbrella-mouthed larvæ of *Megalophrys*. The process is exactly similar to that described by BLES (p. 813) for the tadpoles of *Xenopus*. He says: "They thrive best in water which is thick with the Flagellates. In this they float almost vertically in mid-water, rapidly undulating the posterior third of the tail and at the rate of 40 to 50 a minute take in gulps of the water. The water passes out through the spiracle; the *Chlamydomonas* are retained by the filters in the buccal cavity and drawn into a ciliated groove on either side of the pharynx. . . . When the water is clear they swim restlessly about like fish, as though searching for food, taking a gulp every now and then, as if to test the water, and then swimming on. As soon as fresh culture is poured in they immediately suspend themselves in mid-water and commence gulping regularly." The noteworthy point about this tadpole is that it possesses no horny teeth on the lips, which are not employed for scraping away food from the substratum. The *Megalophrys* tadpole, like the *Xenopus* larva, feeds on mirco-planktonic organisms and consequently does not use the lips for scraping. The characteristic horny teeth of the normal type of larva are absent, but the inner surface of the funnel is covered with radiating rows of horny projections. It is well known that in still waters the micro-planktonic organisms tend to collect in the surface layers of the water, and that is the reason why *Megalophrys* tadpoles continue to feed at the surface. In this position they have the double advantage—plenty of food and access to atmospheric air.

It is to be noticed that the lungs of the *Xenopus* tadpole are not such efficient hydrostatic organs as those of the *Megalophrys* larva, for the posterior third of the tail of the former tadpole continues to undulate rapidly to secure equilibrium and stability in mid-water, whereas the larva of *Megalophrys* achieves the same result by a slight bend of the body (HORA, 1922, p. 9, fig. 1, *b*). As I have indicated in previous papers, the *Megalophrys* tadpole is capable of feeding at all levels in the water, probably more efficiently under water because a current of water can be sucked in more easily. At the surface the rows of teeth form regular channels through which water flows to the mouth, the teeth serving two functions in the circumstances: firstly, of hanging from the surface film, and secondly, of allowing currents of water to enter the mouth. There is no doubt that they prevent larger particles of food from entering the buccal cavity.

NOBLE (1927, p. 106) believes that "life-history frequently does not change when adult structures are modified, but remains as a good indication of relationship." This is true in the case of those animals which continue to live in their earlier stages in the same or similar type of environment; adults living under different conditions may diverge, but the larvæ living under similar conditions remain alike. The reverse is equally true as pointed out by DUNN (1924, p. 12); larvæ living under different conditions become dissimilar, whereas the adult remaining under more or less similar conditions look alike. The variety of larval types found in the genus *Rana* is to be correlated with a similar type of frog in all instances. Again, the two distinct types of *Megalophrys* tadpoles produce adults which can hardly be divided into two genera, and the same is true of the other genera in which an umbrella-mouth has appeared in some of the species. I have shown a similar state of affairs among the insect larvæ (p. 229). These instances clearly "support the precedence in time of function over form, and the possibility of apparent reversal of the biogenetic law, owing to different larval habits and similar adult habits" (DUNN, 1924, p. 12).

It will not be out of place to refer briefly to the modifications undergone by the Caudata for life in rapid waters (see NOBLE, 1927, for detailed account). The form is greatly depressed and the tail is muscular and powerful. The most remarkable point is that recurved claws are developed on the digital tips. These modifications are well-marked in such animals as *Onychodactylus japonicus*; this species differs from the larvæ of all other Amphibia in having a fin on the outer edge of both fore and hind limbs. No observations have hitherto been reported on the utility and action of these limb-fins, but from an analogy with fishes (p. 235) and certain insect larvæ (p. 188) it seems probable that by the continuous flapping of these membranes the animal pumps out the leakage water from underneath its ventral surface when adhering to the substratum. In this action a negative pressure is created on the ventral surface and the animal adheres closely to the substratum.

## PHYSICS OF THE MECHANISM OF ATTACHMENT.

The means whereby the animals of the torrents are enabled to live in the swift currents are, firstly, the devices which enable the organisms to offer less resistance to the current, secondly, the increase in the specific gravity, and lastly, the mechanical means by which fixation to the substratum is effected.

### *Resistance-reducing Devices.*

"A body in steady motion through any real fluid, or at rest in a moving current, experiences a resistance whose magnitude depends upon the relative velocity, the physical properties of the fluid, the size and form of the body, and, at velocities above the critical, also upon its surface roughness" (GIBSON, 1923, p. 183). Throughout the preceding sections attempt has been made to indicate the close correlation that exists between the relative velocity of the current and the build of the animals. The rate of flow of water is subject to considerable variations in hill-streams, but probably the minute organisms living at the bottom are not greatly affected by it, since the greatest velocity of a stream is at a point which is about 0·6 of its depth from the bottom.

*Size of the animal.*—When discussing the adaptations of torrent-inhabiting animals, STEINMANN (1907, p. 141) directed attention to their small size, but HUBAULT (1927, p. 325) has dismissed it by saying that "Mais cette petite taille est-elle réellement une adaptation ? N'est-ce pas plutôt, comme l'aplatissement dorso-ventral, une circonstance antérieure à l'entrée des organismes en eaux vives ?" This is true to a certain extent, because from the very nature of the hill-streams it is evident that animals of large size cannot find enough space to move about in them. But leaving aside this consideration, one finds that the size of an organism is governed by the rapidity of the current; for example, among mayfly nymphs the small shrimp-like animals of the genus *Bœtis*, and among Diptera the small larvæ and pupæ of the Blepharoceridæ and of the Deuterophlebiidæ, have been able to establish themselves in very swift currents. The large apple-snails (*Pila*) of India are replaced in the hill-streams of the Western Ghats by *Turbinicola*, which is considerably smaller in size. Again, among fishes I have indicated that *Garra* is derived from *Cirrhina*-like ancestors (p. 234); the former is much smaller than the latter. The species of *Garra*, such as *G. rupeculus*, *G. lissorhynchus* and *G. kempi*, that live in swift currents are considerably smaller than the others, such as *G. mullya* and *G. jerdoni* that live in relatively moderate currents.

The reverse is equally true. *Glyptosternum stoliczkæ* and *G. maculatum*, which have secondarily taken to life in the deep and sluggish waters of the Highlands of Central Asia, are much larger than their relatives of the Himalayan slopes, from which they are undoubtedly derived (p. 237).

It may be asked what utility the small size confers on the organism, for life in torrential streams. It is known that " at velocities below the critical, where the flow is ' stream-line,' the resistance is due essentially to the viscous shear of adjacent layers of the fluid. It is directly proportional to the velocity, to the viscosity, and, in bodies of similar form, to the length of corresponding dimensions. Thus, the resistances to the motion of small spheres at such velocities are proportional to their diameters " (GIBSON, 1923, p. 183). It is clear from the above that any animal entering a swift current can reduce its resistance by decreasing its dimensions, the form remaining more or less unchanged.

It must, however, be borne in mind that the animal, unlike an inanimate object, is also being influenced by the biological factors in its environment. For example, it is well known that food has a considerable effect, not only on the size of the animal, but also on the size of its progeny. In hill-streams the food is scarce and has to be collected by elaborate devices. Those animals that feed on the micro-planktonic food or on the slime covering rocks or stones (this is the source of food of the majority of the fauna) are smaller in size than those, like the nymphs of *Perla* and the large-sized larvæ of Trichoptera, that feed on animal food, consisting of insect larvæ, etc. These larger animals live on the under side of rocks or form barricades with small pebbles at the bottom and are thus not affected by the swiftness of the current to any serious extent. It is evident, therefore, that small size is advantageous for torrent-inhabiting animals and is, therefore, a distinct adaptation.

*Form of the body.**—Though the advantage of a " stream-line form " for rapid locomotion through a fluid is well recognized by biologists, it appears that its true significance has not been realized, since the mechanical principle involved has not been applied to the study of this type of form of the organisms.

Suppose an object *O* is obstructing a stream flowing from A to B (fig. 15). The water is displaced at the front end of the body and will tend to flow at a greater speed over the body (p. 259) to converge at the hinder end a short distance away from the object. Thus, there will be an area of " dead water " which will have a low pressure. This would tend to pull the body in a backward direction. It is to minimise this " dead water " area at the hinder end that a tapering form is useful, for it allows the water to glide over smoothly in gentle curves and lessens the tendency towards eddy-formation.

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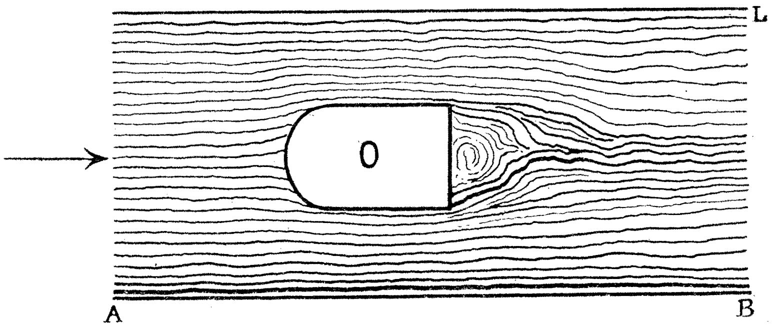
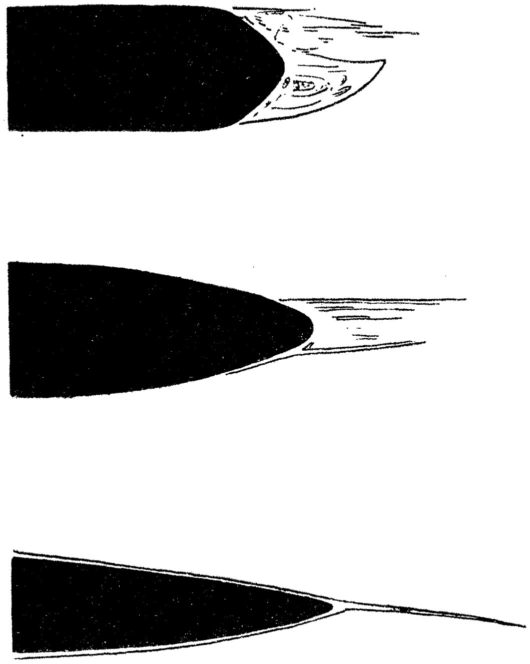
* Reference may here be made to GREGORY'S (1928) recent paper on the " Studies on the Body-forms of Fishes." He has described the body form with reference to certain partly inscribed rectilinear figures and in his account has explained the utility of the stream-line forms. The paper contains a comprehensive bibliography.

STANTON (1923, p. 82) has been able to demonstrate the usefulness of the tapering form experimentally, by using small model balloons of varying fineness of tail. In fig. 16 a representation is given of his results. "It will be seen that in each case there is a dead-water region at the tail, the extent of which increases with the bluntness of the tail, and since it also increases with the speed of the flow, it is probable that the region will be large even in the case of a fine-tailed balloon of normal size at normal speed" (STANTON, 1923). In the case of the hill-stream animals, for example, a *Bœtis* larva (fig. 18, *c*), this stream-line revetment of the body is carried backwards



TEXT-FIG. 15.—Showing lines of flow of water over an obstruction placed in its path. AB = bottom; L = surface level; O = object obstructing flow.

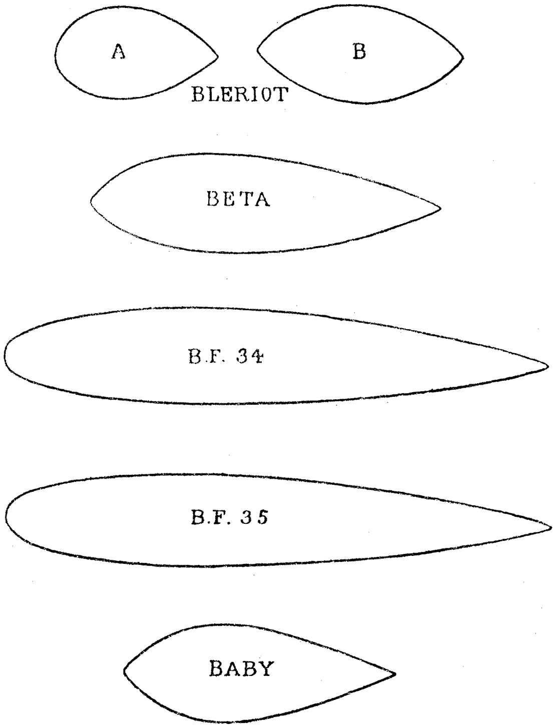


TEXT-FIG. 16.—Models of balloons, showing usefulness of tapering form in lessening the tendency towards eddy formation (modified from STANTON'S photographs).

over a long distance to a point. The long, whip-like tails of some of the torrent fishes have a similar significance; by this device the animals obviate all tendencies towards the formation of "dead-water" area.

It has been experimentally shown in the case of the struts of aeroplanes that the stream-line form offers less resistance to a fluid medium. The following table and figures, reproduced from Gibson (1923, pp. 208, 209), show the correlation between the form of the strut in section and the resistance.

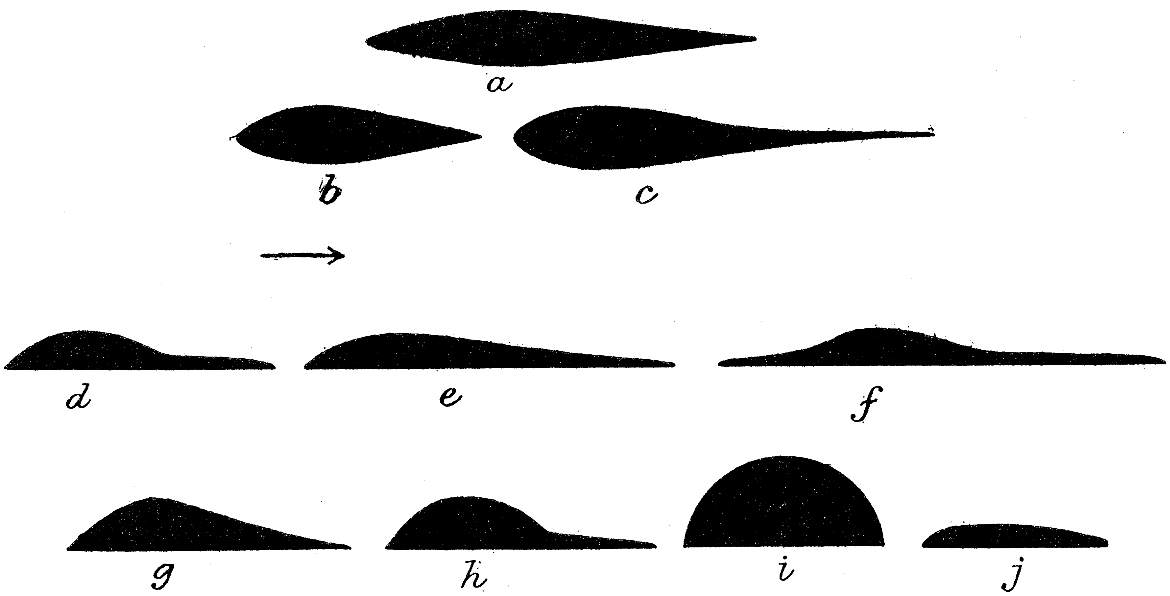
| Type of Strut. | Resistance of 100 feet of Strut in Pounds at 60 feet per sec. |
|---|---|
| Bleriot A ... ... ... | 23·7 |
| Bleriot B ... ... ... | 24·5 |
| Baby ... ... ... | 7·9 |
| Beta ... ... ... | 6·9 |
| B.F. 34 ... ... ... | 7·2 |
| B.F. 35 ... ... ... | 6·3 |



Text-fig. 17.—Cross-sections of various types of struts of aeroplanes (after Gibson).

It is clear from the above table and figure that the resistance offered by a tapering body, such as B.F. 35, is considerably less, and also in the form shown by the type of strut known as "Baby." In the hill-stream animals the form is still better adapted and the resistance that these animals offer to the current must be very small indeed.

The brook inhabitants are either greatly flattened dorso-ventrally or are cylindrical in form, with a long tapering body in all cases. In the flattened organisms the tail is sometimes long or whip-like, or the body is shortened and the animal assumes a limpet shape. From the diversity of the forms of animals met with in the torrents it has been assumed that there is no adaptation as regards body-form in this fauna. For example, HUBAULT says, regarding the dorso-ventral flattening, "Mais enfin l'aplatissement dorso-ventral est-il réellement une adaptation, une accommodation de l'organisme à la vie torrenticole ?—C'est douteux à mon avis ; ce fut surtout pour l'animal une circonstance heureuse qui lui facilita l'entrée et la vie dans les eaux rapides." This explanation is, in fact, no explanation. Animals with different forms live under different conditions, and in every case there is a fine adjustment between external form and the environmental factors. For example, the animals that dangle freely in the current, such as the larvæ of *Simulium,* the nymphs of *Bœtis* or the Æschninæ living on bare rocks and among plants like *Nephelopteryx,* have a cylindrical tapering form. The current flows freely on all sides of these animals, and therefore on every side they must present a stream-line form, and this is only possible by assuming the cylindrical tapering form which they possess. As soon as they begin to rest on the substratum, the ventral surface is not influenced by the current and, therefore, the stream-line form is replaced by a



TEXT-FIG. 18.—Body-forms (diagrammatic) of torrent-inhabiting animals. *a, b, c* = forms of animals that dangle freely in the current ; *d, e, f, g, h, i, j* = forms of animals that lie closely pressed to the substratum. *d, e, f* = showing progressive modification towards tapering of the form (compare strut types B.F. 34 and B.F. 35). *g, h, i* = showing progressive modification towards limpet-like form (compare strut type Baby). *a* = Rhyacophilid Trichopterous larva ; *b* = form of free-swimming fish such as *Barbus tor ;* *c* = *Bœtis* nymph ; *d* = a *Balitora* fish ; *e* = a *Phractura* fish ; *f* = a *Farlowella* fish ; *g* = a *Gastromyzon* fish ; *h* = nymph of *Iron ;* *i* = a *Psephenid* larva, and *j* = a Planarian.

flattened surface. In those animals that lie closely pressed to the substratum, the ventral surface becomes flat and the dorsal stream-lined. The change from one form to the other is induced by the habits of the animal of resting on the substratum, as is shown in the case of the Sisoridæ (p. 236).

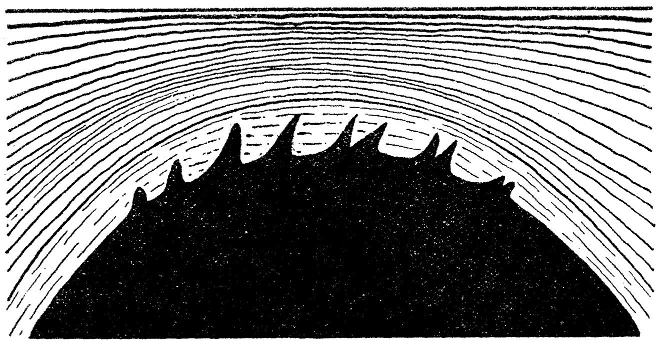
The dorso-ventrally flattened animals assume several forms. The most conspicuous and usually the most abundant of these is that in which the lower surface is quite flat; the head is broad in comparison with its length and often more or less spatulate, as a rule rather lower in front than behind. For offering less resistance two types of modifications take place, firstly the tail is elongated, as in *Balitora* (fig. 18, *d*), *Phractura fasciata* (fig. 18, *e*, Amphillidæ) and others, to carry back to the posterior end the revetment of the stream-line form. In some individuals the snout is also produced into a long process, as in *Farlowella amazonum* (fig. 18, *f*) of the Loricariidæ, to reduce the pressure exerted by the force of water at the anterior end. These modifications would correspond with the " B.F. 35 " type of strut section. Certain other animals shorten their tail and develop a more or less arched body, so that they take on the limpet shape, as in *Gastromyzon*, *Iron*, *Psephenus*, *Prosopistoma*, *Ancylus* and others. In this modification the form is that of the " Baby " type of strut section. This allows the currents to flow over the surface gently and uniformly. There is probably a further advantage in this form—it presents a stream-line on all sides, so that it can resist pressure from all sides. That is probably one reason why the animals of the rocky sea-shore, which adhere to the substratum, also develop a limpet-like form.

There are certain animals in the hill-streams, such as the Planarians, which lie absolutely flat on the rock and are very thin. Such forms certainly offer little resistance to the current. The same can be said of the silken sheets of Lepidoptera and *Antocha*. As most of the hill-stream fauna lives in crevices among rocks it is evident that the dorso-ventrally flattened form is more useful. Some of these, such as *Iron* and the Blepharocerid larvæ, live on the upper surface of bare rocks along with the cylindrical animals; only the mode of attachment in the two cases is different (p. 178). It is worthy of remark that the larva of *Simulium*, that hangs in the currents with its posterior end directed upstream, is broader at the posterior than at the anterior end (this is unusual with animals) in order to present a stream-line form to the current.

*The surface roughness.*—So long as the velocities remain below the critical, " with stream-line motion there is no slip at the boundary of solid and fluid, and the physical characteristics of the surface do not affect the resistance " (GIBSON, 1923, p. 183). But " at velocities above the critical, where the motion as a whole is definitely turbulent, there would still appear to be a layer of fluid in contact with the surface in which the motion is non-turbulent. The thickness of this layer is, however, very small, and any increase in the roughness of the surface, by increasing the eddy formation, increases the resistance. At such velocities the resistance is due in part to the viscous shear in this surface layer, but mainly to eddy formation in the main body of the fluid. This latter component of the resistance depends solely on the rate at which kinetic energy is being given to the eddy system, and is proportional to the density of the fluid and to the square of the velocity " (GIBSON, *loc. cit.*).

Among fishes it is noticeable that the scales are reduced in those forms that live in swift currents ; ANNANDALE and I (1920, pp. 154, 155) directed attention to this in the case of the fish of Seistan. In fact, all Cyprinoid fishes, the Schizothoracinæ and the Cobitidæ, that inhabit the Highlands of Central Asia, are characterized by small scales or by the total absence of them. There is no doubt that these fishes have been derived from normal Cyprinoid fishes with large scales. Similarly in the Andes at great altitudes the Loricariidæ are represented by *Arges* (p. 239) in which the body is naked. Attention may also be directed to the reduction of the chitinous spines that occurs in most of the insect larvæ living in rapid waters (p. 179).

There is no doubt that the waters of the hill streams are turbulent in their flow, and in these circumstances a rounding-off of the contours of the animals living therein is a great necessity, since it enables them to offer less resistance to the current. But there are some animals which live in the fiercest currents and still possess spines on the surface (Blepharoceridæ, p. 226). These structures under ordinary circumstances would be considered not only useless but distinctly harmful to the animals in rushing torrents. Though it may seem a paradox, it is nevertheless true that these processes help to decrease resistance. For instance, it is known that " in some such bodies as spheres and cylinders the law of resistance may change widely with comparatively small alterations in the conditions ; thus, for example, at certain speeds the *resistance of a sphere may actually be reduced by roughening the surface* " (GIBSON, *loc. cit.*, p. 207. The italics are mine.) The body of a Blepharocerid larva may be compared with a half-cylinder split longitudinally, and it is probable that the amazing variety of chitinous armature on the backs of these larvæ (p. 226) is developed to reduce the resistance to the tempestuous currents in which they live. The spines obstruct the current and make it flow at a lower velocity in the neighbourhood of the body (fig. 19). The very



TEXT-FIG. 19.—Diagrammatic representation of a chiton-shaped Blepharocerid larva with dorsal armature showing the efficacy of the spines in reducing resistance in tumultuous currents. Broken lines indicate the area where water flows relatively slowly on account of the obstruction caused by spines. The swift current (full lines) glides over this area of slow-moving water and thus the animal actually lives in a medium where the tearing-away action of the current is reduced.

swift current then glides smoothly over this area of relatively calm water. This instance shows how ignorant we are of the physical factors in the environment which ultimately shape the organisms, and how difficult it is to understand the utility of a structure without knowing the requirements for which it is produced. The spines on the body increase resistance at certain velocities, but they decrease resistance at some higher velocities. The correlation of the production of the spines and the rate of flow of water will make it possible to understand properly the adaptations of animals which are provided with such devices and which inhabit torrential streams.

### *Specific Gravity.*

Since the sinking or the floating power of an animal depends on its specific gravity, it is clear that those animals that live constantly near the surface (floating organisms), such as Globe-fishes, the Siphonophora, etc., must of necessity be lighter than the water; those that move up and down through the various depths of water possess hydrostatic organs to facilitate their movements (the air-bladder and lungs of vertebrates), and lastly, those animals that have taken to life at the bottom must possess heavier bodies than the water, so that they may not have to spend energy in counteracting the upward lifting action of water; this is true of all aquatic organisms, whether marine or freshwater. Most of the freshwater animals, especially of streams, are positively statozoic in their habits; for to establish themselves permanently in fresh water they must either be fixed, or else be strong enough to withstand and make headway against the currents of the streams and rivers they inhabit, otherwise they will, in the long run, be swept out to sea.

The same argument applies with greater force to the fauna of the torrents, and consequently it is found that with a few exceptions, such as the funnel-mouthed tadpoles of *Megalophrys*, *Ranodon*, *Tipulid* larvæ, etc., the *permanent* inhabitants of a swift current are bottom-dwellers and are consequently of a heavier build than their allies of sluggish waters. The specific gravity is increased by the reduction of such organs as the air-bladder of fish (HORA, 1922*a*), the lungs of Batrachians (NOBLE, 1927, p. 38), and by a reduction of the abdominal cavity, partly induced by a change in the form and partly by the development of strong muscles both in the dorsal and ventral walls. In all cases, this change, either in the build of the animals or in its habits, is produced by the necessity of remaining as close as possible to the substratum. The reverse is equally true. For example, when an animal modified for life in hill-streams takes secondarily to life in deep and calm waters the hydrostatic organs become a necessity once more, and consequently either the old reduced structures are enlarged (lungs of *Megalophrys* tadpoles) or new structures are developed, and a direct correlation is thus established between the animal organisation and the environmental conditions.

Can these modifications be considered as adaptations for life in rapid waters? They undoubtedly are, but the critics must be satisfied on two points: firstly, why certain animals living in rapid waters possess hydrostatic organs, and secondly, why certain animals living in calm waters exhibit similar modifications, such as have been considered above in the torrential fauna ? It has been pointed out above (p. 177) that the funnel-mouthed tadpoles of *Megalophrys* and the Tipulid larvæ live in such situations where they are securely sheltered from the effect of the current, and when dislodged from their sheltered positions their buoyancy helps them to be lightly carried by the current. When in the dry season the stream breaks up into pools and puddles, the hydrostatic organs help the *Megalophrys* tadpole to tide over the unfavourable condition by enabling it to make use of the atmospheric air for respiration (HORA, 1928).

The answer to the second question is obvious. In animals living at the bottom, either in still waters or in rushing torrents, the necessity of lying close to the substratum is the same, and in both cases the end is achieved by an increase in specific gravity. For example, similar modifications have been induced in the brook-dwelling Sisoridæ (p. 236) and the mud-fishes of India, such as *Saccobranchus* and *Clarias*. In these Siluroids the air-bladder is greatly reduced and is divided into two lateral chambers which are enclosed in bones. Similarly the caddis-worms that live at the bottom of deep lakes, and probably never visit the upper strata, build their cases of heavy material. Thus, it is seen that similar, complicated modifications take place in animals living under dissimilar conditions, *but the purpose of the change in the two cases is the same.* I discuss this purposeness in evolution further on (p. 264).

### *Mechanical Devices for Fixation.*

The mechanical devices whereby the animals secure adhesion to the substratum are many and are of diverse kinds. I propose to deal with them under the following main headings : (i) sticky secretions, (ii) vacuum-producing devices, (iii) seizing devices, and (iv) hooking devices.

*Sticky secretions.*—The secretion, by which the pupæ of insects, such as *Psephenoides* (p. 203), Blepharoceridæ (p. 227), Deuterophlebiidæ (p. 228), etc., adhere, must be different from that by which a mollusc or a Planarian can progress on the rock and adhere at the same time. The animal surface coming in contact with the substratum may pour out the secretion, as in Protozoa, Polyzoa, Mollusca and Turbellaria, or the secretion may be formed in an internal organ (*e.g.*, the salivary glands) and poured out through special ducts on the substratum to which the animal applies its body, as in Blepharocerid and Deuterophlebiid pupæ. In *Simulium* and certain Chironomids the secretion is poured out on the substratum, so as to form a network of silk threads into which grappling hooks are inserted for attachment. In the *Simulium* pupa and in certain caddis-worms the secretion is used in the manufacture of the tube which the animal inhabits. In some cases this pupal tube is fixed to the substratum. Various modifications of this type of attachment occur. (For an account of these modifications reference may be made to the preceding sections.)

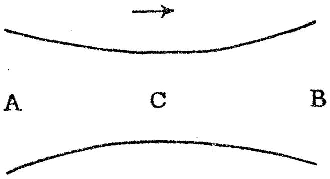
*Vacuum-producing devices.*—Under this heading are to be dealt with true " suckers " and other mechanical devices by means of which a reduced pressure is created on the ventral surface of the animal, so that it is closely adpressed to the substratum. The sucker, as I understand it, consists essentially of a disc which can be laid flat on a plane surface. In order to produce a " vacuum " its central part must be capable of being raised without disturbing the margin, which must remain in close contact with the surface to which it is applied. In the cavity produced by raising the central part a complete or a partial vacuum is created. Neglecting the pressure due to the layers of water, a complete sucker can resist a pull equal to the atmospheric pressure. So far as I am aware, suckers are not the normal modes of attachment in the fauna of the torrents. They are found in lampreys, in *Garra* (p. 233), in the tadpoles of the section Ranæ Formosæ (p. 241), in the larvæ of the Blepharoceridæ (p. 219), and possibly in *Sicyopterus garra,* Hora, from the Andamans (p. 233). With the exception of the tadpole and the lampreys, in which the sucker is of a considerable size, the adhesion to the substratum is augmented by accessory organs of attachment, such as the pads on the outer rays of the paired fins of *Garra* and *Sicyopterus*, the papillated lips and the various kinds of spines found in Blepharoceridæ. In swifter and swifter currents even the sucker of *Garra* is reduced and is replaced by pads on the fins.

After discussing the structures of attachment in fishes in general, Kyle states that they are to be found more commonly in the marine than in the torrential fauna. He explains this as follows : " The origin of these discs must be referred, therefore, simply to the habit of resting on the bottom, and the necessary condition of their development appears to be the suitable position of either the ventral or pectoral fins. The sucker is only developed on the anterior half of the belly, that is, when the ventral fins are anterior. The absence of suckers in the freshwater fishes is thus accounted for by the fact that in most of them the ventrals are posterior." Except that the suckers have developed in response to bottom life in strong currents none of Kyle's other conclusions is borne out by the facts adduced here. In my previous papers (1923*b*, 1925, 1927), I have indicated the main reasons for the absence of suckers in the majority of the torrential fauna, but it is necessary to summarize here the main points.

The currents of the sea and the breakers of the sea-shore are different from the flow of a torrential stream in two respects. Firstly, in the case of the latter the flow is always in one direction, whereas the marine currents flow in various directions. Secondly, the marine currents may attain a considerable swiftness, but they never rush at the rate of a mountain torrent. Under such conditions a sucker is more useful in marine organisms, because in the first place it can resist pressure from all sides, and secondly, because the pressure is not very great, and a relatively small sucker is capable of holding on. In torrents, on the other hand, there is a considerable pull in one direction, and to resist this the animal must have either a large sucker (tadpoles) or a series of them (Blepharoceridæ). In the brook inhabitants, therefore, more advantageous means are employed for adhesion.

The hydraulic principle involved in the formation of a vacuum on the ventral surface of flattened organisms, when they rest on the substratum, is the same as that which governs the flow of water through pipes, and this can be illustrated as follows :—

Suppose a constant current of water is flowing through a tube A B in the direction indicated by the arrow in fig. 20. Let this tube vary in diameter so that it is much narrower at the point C. It is evident that the water will be flowing at a greater speed at C than at A, since the same amount of water passes through A and C in a given time. Now suppose $p_1$ = pressure at A, $v_1$ = velocity at A, $p_2$ = pressure at C, $v_2$ = velocity at C, $w$ = weight of 1 cubic foot of water, $g$ = force of gravity. By the principle of the conservation of energy, and neglecting frictional losses, the sum of the pressure energy and the kinetic energy of a given quantity of the flowing water must remain constant. Therefore, by equating the energy we get—



TEXT-FIG. 20.—Diagram illustrating the principle of flow of water through a pipe of varying diameter.

$$\text{Pressure energy at A, } \frac{(p_1)}{w} + \text{velocity energy at A, } \frac{(v_1^2)}{2g}$$

$$= \text{pressure energy at C, } \frac{(p_2)}{w} + \text{velocity energy at C, } \frac{(v_2^2)}{2g}$$

$$\text{or} \quad \frac{p_1}{w} + \frac{v_1^2}{2g} = \frac{p_2}{w} + \frac{v_2^2}{2g} \text{ (per pound of water).}$$

Now, since the velocity at C must be greater than the velocity at A (since the diameter is less at C), $p_2/w$ must be less than $p_1/w$. This means that a "partial vacuum" is produced at C.

Let this principle now be applied to the case of the flattened organisms such as those shown in fig. 18, *d-j*. The water entering below an animal at the anterior end would tend to spread under its broad ventral surface and consequently its rate of flow would be reduced and the pressure increased. This tendency is obviated by shooting out this water with considerable force, with the help of the inner rays of the pectoral fins in the fishes (p. 235), by the gill-lamellæ in the Heptageniid nymphs (p. 188) and by the tail in *Psephenus* (p. 203) and *Prosopistoma* (p. 195). The currents thus produced result in lowering the pressure on the ventral surface and the animal is enabled to stick to the substratum. As a consequence of the increased flattening of the body the water is prevented from flowing underneath it. It has been shown that the lateral appendages, by overlapping one another and by meeting in front and behind on the ventral surface of the animal, convert it into a broad disc, which when applied to the substratum is probably water-tight. When such an animal begins to adhere, the water from the under side is expelled with a few vigorous strokes, and then the margins of the disc prevent any further water from flowing underneath it. In this process a vacuum is formed and the animal adheres without much exertion on its part. The ventral surface, however, lies flat on the substratum and there is no sucker-formation whatsoever.

In hill-stream fishes and tadpoles the lips are usually hypertrophied, and it has been assumed that in conjunction with the mouth they form a sucker. In the preceding section I have indicated that this is not the case (pp. 234, 243). While studying the mechanism of respiration in the highly specialized Indian hill-stream fishes, I observed (1923*b*, pp. 591–596) that only a small upper portion of the gill-opening is used for the exit of the water. It has also been shown above that the inspiratory current enters through the channels at the corners of the mouth. Thus, a flow through a narrow tube is established, and by increasing the rate of flow in this tube the fish can lower the pressure in the buccal cavity, and make the broad lips adhere to the substratum.

Attention may here be directed to the interesting experiments performed by CUNNINGHAM (1893–95) to test the mechanism of attachment of *Zeugopterus punctatus*. " The fish are seen in aquaria to be nearly always adhering to the vertical sides, remaining in one place for a long time, and keeping themselves suspended in this way in a vertical position without any difficulty. . . . It was evident that the adhesion of the fish was not produced by ordinary sucker action—in other words, by hydrostatic pressure—because the space beneath the body was freely open to the outside water in front dorsally and ventrally to the head. The posterior parts of the fin-fringes were in constant motion, moving in a series of vibrations from before backwards, together with the part of the body to which they are attached, and the effect of this motion was to pump out the water from the space between the body and the glass, its place being supplied by water which entered in front. The subcaudal fin-flaps were perfectly motionless, and tightly pressed between the base of the tail and the surface of the glass, so that any movement of them was impossible." With the help of carmine powder CUNNINGHAM was able to demonstrate that the current flowed with a greater speed below the animal than above it. This means a lower pressure on the under surface, which enables the fish to adhere. CUNNINGHAM was, however, unable to show any use for the subcaudal prolongations, for he noticed that the fish could adhere even when these structures were removed.

In all hill-stream animals in which this method of vacuum production is employed, a saucer-like disc is formed on the ventral aspect (*Gastromyzon*, *Iron*, etc.). By closing the disc at the posterior end the animal is enabled to restrict the area for the exit of water, so that the current flows through it with great velocity and consequently the pressure is reduced. In *Zuegopterus* the low pressure created, even after the removal of the subcaudal prolongation, was probably sufficient to support the weight of the fish. No experiments were, however, performed to test whether the efficiency of adhesion was in any way affected by the removal of these structures, but it would seem obvious that their absence would be detrimental in flowing water.

*Seizing devices.*—In the preceding sections it has been indicated that spines or scales on the ventral surface of the organisms inhabiting rocks in swifter and swifter currents tend to be reduced, till ultimately the ventral surface becomes smooth and flat and can be closely adpressed to the substratum. In this action advantage is taken of the principle of " seizing " for holding on to the substratum. When two surfaces, well fitted to one another, are brought together and the fluid separating them is expelled (either by the vacuum-producing devices already noticed or by the mechanical means to be presently described), they " adhere strongly together, or *seize*, partly on account of the vacuum between them, but more, since the effect takes place even in a good vacuum, on account of molecular forces of attraction being brought into play. Seizing takes place more readily with bodies of the same than with those of different materials " (DUNCAN, 1904). The animals that apparently seem to adhere by means of sucker-formation, such as *Gastromyzon* and Trichopterous larvæ of the type of *Lithax* and *Drusus* (p. 198), in reality lie flat on the substratum, and adhesion is such cases is due to the power of seizing.

Attention may be directed to the ridge-and-groove pattern found on the adhesive pads of most of the hill-stream animals, especially in fish, *e.g.*, the thoracic discs of *Glyptothorax* and *Pseudecheneis* and the fin-ray pads of *Glyptosternum.* At first I considered that these pads function in the same way as the ridge-and-groove patterns on motor tyres ; but it now seems to me that there is a considerable difference in the mechanism of the two. Motor tyres are grooved to increase their tractive effort, and this is effected by the flattening of the solid rubber ridges, the consequence of which is that the edges become sharp and are therefore rendered more efficient in taking hold of the unevennesses of the roads. In fishes, however, the grooves on the pads serve as channels for the exit of water from underneath the structure, so that it can be brought into intimate contact with the substratum and " seizing " can take place. The same is true of papillated surfaces.

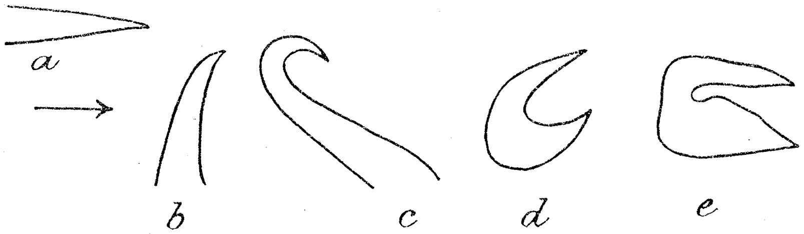
The ridges and grooves on the pads are either transversely placed, as in *Pseudecheneis,* or more often are situated obliquely in a longitudinal direction, as in *Glyptothorax* and *Glyptosternum.* Where the adhesive apparatus consists of a series of pads, they are placed obliquely in a longitudinal direction, as in *Balitora,* and in the Heptageniid nymphs. Probably the latter type is more useful, for it will not only resist the push backwards but will also be able to stand the side-to-side push due to the eddies in the current.

*Hooking devices.*—Animals living among plants possess strong gripping claws, which are denticulated along their inner borders to provide a firmer grip. Some, such as *Phalacrocera, Nephelopteryx,* etc., are beset with backwardly directed chitinous hooks on their bodies, which entangle them in the mosses or mats of algæ when they lie with the head pointing upstream. Certain insect larvæ and *Onychodactylus japonicus* (p. 248) are found on bare rocks, which they grip by means of strong recurved claws.

Those animals that lie flat on the substratum have retroverted spines developed on their adhesive pads. Since these pads are developed on the surface that lies in close contact with the substratum it is obvious that the spines would help to prevent the animal from slipping by interlocking with roughnesses on the surface of the rocks. Moreover, as these animals lie at one place for a fairly long time, this type of mechanical interlocking arrangement would be very effective.

Throughout the preceding section it has been noticed that there is a tendency in the hill-stream animals to transfer the adhesive pads from the centre of the animal to the extremities. This enables the animals to bring a large surface in contact with the rocks and thus increases the seizing power. Further, gripping by the extremities gives the animals a more stable equilibrium in the current. The former, however, appears to me to be the more important factor.

Much variation in form and structure is exhibited by the spines on the adhesive pads, and in some cases it is possible to trace their gradual specialization. On the adhesive pads of fish (HORA, 1922*b*) they are simple, with a somewhat broader base and a slightly curved tip (fig. 21, *b*). The terminal hooks are directed posteriorly, and by digging into the substratum prevent the animal from slipping. In the Heptageniidæ and others the main body of the spine (fig. 21, *c*) is directed against the current, but it is hooked at the tip, so that the terminal point acts in the same way as the fish spine. An interesting series of modifications is found in those spines that hook on to a loose surface, such as vegetation or a silken network of threads. In Chironomids (fig. 21, *d*) the hooks on the posterior appendage are in the form of forks with two prongs. One of these functions for gripping, while the other lies embedded in the body wall and gives support to its partner. With the increased work on the outer prong the inner becomes considerably enlarged, till in the larva of *Simulium* it is better developed than the sickle-shaped portion of the spine that holds the thread (fig. 21, *e*). The principle on which such a spine functions is that of the lever of the third type, in which the fulcrum is at one end (the basal portion of the spine), the work is at the other (the sickle-shaped portion of the spine), and the force is in the middle. Thus, in this spine the strain of breaking is resisted by the broad base from which the two portions spring. The mechanism is similar to that of a tin-opener.



TEXT-FIG. 21.—Form of spines found on the adhesive pads of torrent-inhabiting animals. *a* = lateral spine of a Blepharocerid larva; *b* = spine on the adhesive pads of fish; *c* = spine on the gill-lamellar pads of Heptageniid nymphs; *d* = spine on the posterior proleg of a Chironomid larva; *e* = spine on the posterior appendage of a *Simulium* larva.

In this part of my work I have had the privilege of consulting Dr. J. B. TODD, Lecturer in Hydraulics in the Engineering Department of the University of Edinburgh, and I have great pleasure in offering him my sincere thanks for his valuable help.

## EVOLUTION: DIVERGENT AND CONVERGENT.

It may be indicated at the very outset that our conception of the relative importance of the two principles—Divergence and Convergence—has undergone a considerable change since the publication of the *Origin of Species.* According to DARWIN, "species are multiplied and genera are formed" by the application of the principle of "Divergence of Character," while his reference to the opposite principle is only a passing one. BERG (1926), on the other hand, says, "DARWIN represents evolution as a process of *divergence* of characters. As a matter of fact, predominative importance belongs to convergence of characters." There is hardly any doubt that since DARWIN's time extensive study of characters has shown that quite a number of apparently homogeneous genera and families are in reality polyphyletic in origin. Thus, in evaluating the relative importance of characters the problem of the morphologist has become very complicated indeed. In fact, a certain number of biologists have given up all ideas of useful adaptation and explain the variations or divergence in characters as due to some innate tendencies of heredity.

"Divergence of Character" is a simple principle, for there is no doubt that as a general rule "the more diversified in structure the descendants from any one species can be rendered, the more places they will be enabled to seize on, and the more their modified progeny will increase" (DARWIN). Our present conception of classification, represented as the branches of the great "Tree of Life," is based on this principle. OSBORN in 1902 treated this subject from a physiological aspect and termed it "The law of Adaptive Radiation." DARWIN had emphasized the variations in characters, without giving any definite cause, beyond attributing to the organism a tendency to vary by chance, while OSBORN in his law expresses "most clearly the idea of differentiation of habit in several directions from a primitive type."

The principle of divergence is simple and obvious and is of a wide applicability. It may, however, be remarked that the force with which DARWIN launched this principle led subsequently to some unjustifiable conclusions, for most instances of divergence came to be regarded on *a priori* grounds as indicating distant relationship and most instances of convergence to denote close affinity. It was under such a misapprehension that GASKELL came to believe in the relationships of the fish *Cephalaspis* and the trilobites *Paradoxides* and *Olenellus.* BIDDER (1927) has shown that the apparent similarity between the trilobites and the fish is due to the fact that both were shaped to resist destruction from the torrential currents of the Silurian Seas. Similar forms are met with to-day among the fauna of the torrential streams, and I need only refer here to the larvæ of the insects *Prosopistoma* (p. 194) and *Psephenus* (p. 202), both of which were at first regarded as Crustaceans of the *Apus* type. The tergal and sternal shields of the Psephenid larvæ so overlap that a certain amount of movement of one segment over the other is possible. Thus, when a larva is disengaged from its mooring, it coils and rolls, reminding one of the habits of the trilobites. Several animals have adopted this method of taking glancing blows lightly in the torrential currents. The Bornean fish *Gastromyzon* is superficially not unlike the Silurian fish *Cephalaspis*.

This apparent similarity in structure or habits, which animals living under similar conditions exhibit, is popularly known as "convergence in evolution." But recent work on correlation between animal habitat and structure has brought out a number of facts which are supposed to indicate that convergent evolution may occur in animals living under totally different conditions; and *vice versa*, animals living under identical conditions exhibit divergent characters. This is a misapprehension. Convergence is the result of "independent functional adaptation to similar ends" (WILLEY, 1911). I wish to direct special attention to the phrase, "similar ends," for it may happen that animals living under different environments may have to respond in a similar fashion to a common factor in the habitats, and this would lead independently to "functional adaptation to similar ends" resulting in the convergence of characters. For example, in the case of a strong swimming fish in stationary waters and of another fish which leads a more or less sedentary life in rushing torrents, the habitats of the two are totally dissimilar, yet in both cases the body is gracefully stream-lined to offer less resistance to the current. Whether the fish moves through the water, or the water glides over the fish, the physical principles involved in the reduction of resistance to the fluid medium are the same. It is also known that as a rule larger eggs are characteristic of both the stream-breeding and the terrestrial as against pond-breeding Amphibia. The large egg is not an adaptation to the stream or terrestrial habitats, but is a provision which gives the progeny a better start under unfavourable conditions (p. 175). In all the hill-stream fishes the air-bladder is greatly reduced and in specialized forms it is enclosed in two bony capsules. Similar modification of the bladder takes place in the mud-inhabiting Siluroids of India, such as *Clarias* and *Saccobranchus*. These two habitats are very dissimilar, but the reduction of the air-bladder increases the specific gravity of both types of animals, so that they can remain near the bottom in their respective habitats.

Again, an interdigital web may develop in animals living under different conditions. It is developed in the Cormorant, *Phalacrocorax carbo*, living in water, in the lizard, *Palmatogecko rangei* living on sand, and in the frog, *Rhacophorus volans*, and in bats living in the air at times. In all these cases the end in view is the same, *viz.*, to offer great resistance to the medium, aquatic, terrestrial or aerial, in order to obviate slipping or to aid in propulsion. Among torrential populations it is noticed that several larvæ of Trichoptera (p. 197) and Chironomidæ (p. 210) are not provided with sheltering cases but lead an open life on rocks in rushing currents. In these circumstances the tubes, which are characteristic of a majority of species of these families, are not manufactured, because these, instead of being advantageous in providing shelter and safety, become encumbrances. Among Chironomidæ the larvæ of the genus *Metriocnemus* (LEATHERS, 1922, p. 33) are found only in the leaves of the pitcher-plant, *Sarracenia*. They pass their entire larval stage without manufacturing any tube. The animal burrows in the closely packed débris composed of the chitinous remains of insects at the bottom of the pitcher ; in these circumstances the tube would undoubtedly be an encumbrance and is, therefore, no longer formed.

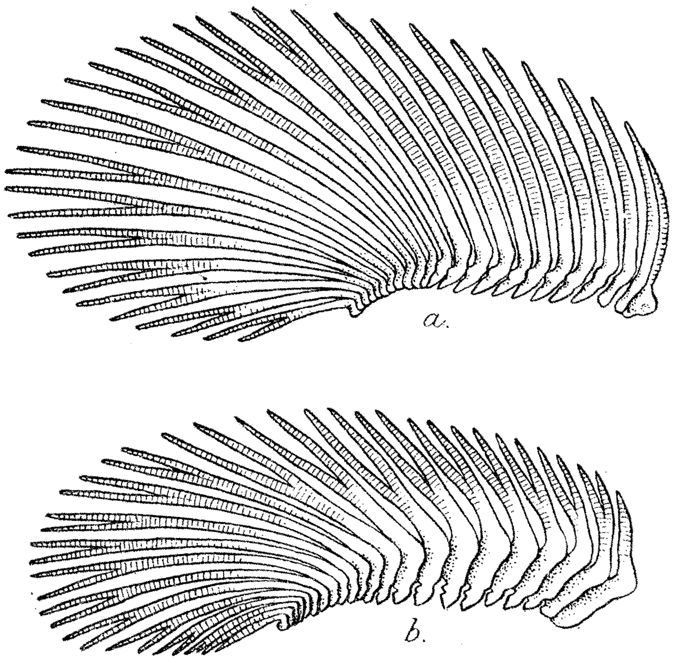
The habits of the caddis-worm, *Neuronia postica*, are of great interest (p. 199). Normally it is provided with a tube, but when entering submerged débris it abandons the tube, and under these conditions it is as free-living as the larvæ of the Rhyacophilidæ —the torrent-inhabiting Trichoptera. It is clear, therefore, that the convergence in the habits of both the sluggish-water forms and the brook-inhabiting animals has resulted from independent functional adaptations to similar ends. From the above it is clear that in all cases where similar structures or habits have originated under apparently dissimilar conditions, a thorough study of the habitats and bionomics of the organisms would probably reveal that these adaptations fulfil similar ends.

The statement that different types of structures are found in the same environment is, according to my experience, merely superficial. The more one realizes the gradations in the environment, the more clear it becomes that animals of different kinds occupy definite " niches " in the same habitat.

Convergence of single characters is well recognized in all taxonomic studies, but the principle of Communal Convergence requires further consideration. In 1911, WILLEY remarked: " How far this community of habitats leads to structural convergence is not clear, because the anatomical characters of the associated forms have not been worked out in sufficient details from this point of view." ANNANDALE and I have shown in a series of papers the remarkable evolutionary complex that has resulted in the fauna of small streams in the Himalayas and elsewhere. As an illustration of communal convergence, attention may be directed to the body forms of brook-inhabiting animals. Those that lie closely pressed against the substratum possess a flat ventral surface, and the dorsal surface is arched in gentle stream-lines. In quite a number of animals of this habitat the body assumes a limpet-shaped or chiton-shaped form ; indeed, have not the limpets and the chitons assumed this form in order to meet the rushing of the waves ? One may also refer to the insects of brooks (Plate 18). The Psephenid larva (Coleoptera) ; the Naucorid bug (Hemiptera) ; the Blepharocerid larva (Diptera) ; the nymph of *Iron* (Ephemeroptera) and the nymph of *Ictinus* (Odonata) illustrate convergence towards a limpet-shaped form in different orders of insects living under similar conditions in torrents, and one could very easily add a number of examples from other groups of animals to this large series.

It is clear from what I have stated above that divergence is the result of habitudinal segregation, or isolation, or some kind of " Adaptive Radiation," and that divergence has to be attributed to differences in the environment. It may seem a paradox, but convergence is also the result of some kind of adaptive radiation, and the cause of this is the similarity of an individual factor or factors in the environment.

In 1924, ANNANDALE discussed certain instances of a peculiar type of evolution which he termed " Divergent Evolution." Though as we have seen above, divergent evolution has acquired a well-established meaning, I shall for the present denote this peculiar type of evolution by the term used by ANNANDALE. Thus, " Divergent Evolution " (ANNANDALE) may be said to have occurred " when organisms related in general structure exhibit in the same or similar environment different modifications in structure or form or instinct, and these modifications are correlated with the same element in the environment." For instance, the freshwater sponges living in muddy waters prevent their ostia from being blocked up and rendered ineffective by solid particles held in suspension in the water which enters them; the ostia in some are reduced, as in *Tetilla dactyloidea* var. *lingua*, while in others, as *T. limicola*, they are distinctly enlarged. In the former the reduction prevents the particles from entering into the channels, while in the latter their enlargement renders it possible for the animals to take in and expel the particles through the broad passages. These differences, it seems probable, are due to individual variations in the ancestral forms of these sponges that migrated to the muddy waters. The forms with relatively smaller pores evolved along the line of further reduction in the size of the pores, while the opposite course was adopted by those that had larger pores to start with. Here, again, it is seen that the best use is made of whatever initiative or bias an organism possesses



TEXT-FIG. 22.—Divergent modifications of fin-rays of the pectoral fins in two highly specialized genera of Homalopterid fishes. *a* = *Balitora brucei*, GRAY; *b* = *Gastromyzon borneensis*, GÜNTHER.

in the beginning, and the two apparently contradictory adaptations actually solve the same problem by different methods.

The highly specialized Cyprinoid family of Homalopterid fishes is characterized, among other things, by the position and structure of its paired fins, which are horizontally placed and are provided with a number of simple rays. The structure of these fins (fig. 22) in two highly modified genera—*Balitora* and *Gastromyzon*—is very different. In *Balitora* there are a number of simple rays, apparently produced by the coalescence of the branches of an ordinary ray; whereas in *Gastromyzon* there is only one simple ray, the neighbouring rays, although appearing simple superficially, being in reality forked. In this case the primary branching is retained and each of these is then modified into a simple ray. The simple rays in the paired fins bear on their ventral aspect adhesive pads of skin, which enable the animals to stem tempestuous currents. So far as the adhesive efficacy of these two types of fin-rays is concerned, there can hardly be any doubt that both are equally efficient. In both cases I have been able to trace regular series by which these divergent modifications have occurred under the influence of the same factor in the environment.

## ORIGIN AND EVOLUTION OF THE TORRENTIAL FAUNA.

In 1922, I briefly alluded to the origin of the hill-stream fauna and indicated that it had been derived from the fauna of the sluggish waters of the plains by a step-by-step colonisation of the higher reaches. To support this hypothesis the evidence afforded by the distribution, comparative morphology, and embryology of the various forms of brook-inhabiting fish was adduced. HUBAULT (1927), from a study of the invertebrate fauna of torrents, has come to a different conclusion. According to him the cold- and oxygen-loving animals of the brooks are a relic of the glacial period. He concludes as follows: "j'ai essayé de donner quelques indications sur l'origine de la faune torrenticole actuelle, fille de la faune des glaciations, qui s'est largement propagée dans les cours d'eau par l'intermédiaire des rives des nappes d'eau froide" (p. 366).

In recent years I have studied the invertebrate fauna of torrents in detail, and in every group of animals discussed in the preceding pages I have found evidence of step-by-step colonization. The animals have become gradually modified under the direct effect of the current, which appears to me of paramount importance in their habitat. Unfortunately, most of the invertebrates in my collection have not yet been determined and, therefore, I have to rely on vertebrates, especially fish, for a further treatment of this subject.

EIGENMANN (1912) discussed the probable mode of population of the Guiana Plateau by fish, and came to the conclusion that "The evidence seems, then, to favour the conclusion that the larger part of the fauna of the upper Potaro has been more or less recently acquired, and that the smaller part is composed of relicts of the original fauna of the Guiana Plateau." Most of the species he found inhabiting the plateau were identical with those in the plains below, and only three species, *Helogenes marmoratus*, *Pœcilocharax*, and *Lithogenes villosus*, were more or less endemic in the streams of the plateau. *Lithogenes* is a highly specialized Loricariid fish and must have reached the plateau by climbing over rocks in the rushing torrents. The others resemble sluggish-water forms and have probably ascended by small rivulets or through backwaters at the edges of the streams. I believe, therefore, that even these endemic species have been derived from ancestors living in streams below the plateau.

For some years I have been interested in the fauna of the Cherrapunji Plateau (Khasi Hills, Assam). The ascent to this plateau is precipitous from all sides and the heavy rainfall (458 inches per annum) is drained off by rushing torrents flowing in deep gorges. In the swift currents are found highly evolved hill-stream fishes, such as *Balitora, Glyptothorax, Pseudecheneis* and *Garra*, but at the edges and in pools the sluggish-water forms of the plains occur. The fish-fauna of the plateau (HORA, 1923*b*, p. 582) comprises *Ophicephalus gachua, Danio æquipinnatus*, and *Barbus tor*. The Snake-headed *O. gachua* is a marsh-loving fish, and is known to wander from pool to pool in the dry season. This species must have ascended the steep slopes by frequenting the pools and puddles at the edge of the streams, and even on the plateau it is commonly to be found in such situations. *D. æquipinnatus* is a small fish which lives in pot-holes and deep pools and is capable of swimming against feeble currents; it has possibly reached the plateau by ascending small rivulets into which a stream breaks up in a dry season. *B. tor* is a muscular fish which, like the salmon, can swim against swift current. These three species are common in the plains, and there is no doubt that the fish of the plateau are derived from those of the plains; in fact, *B. tor* ascends every year for breeding purposes. As other instances the peculiar fish of the group Schizothoracinæ, Cobitidæ, Sisoridæ, etc., of the Highlands of Central Asia may be cited. There is no doubt that all these fish have been derived from those that frequent the slopes of the Himalayas. They have been greatly modified secondarily, but they still retain certain impressions of their former environment. Indeed, there is no indication in this fauna which shows that it is indigenous and that it has not been derived from the fauna of the low-lying lands of the neighbouring countries.

From TILLYARD's table of the different habitats of the dragon-fly larvæ (p. 328) it is possible to trace the gradual evolution of the hill-stream forms and ultimately of those that are found in strong currents. Take, for example, the Gomphinæ, which are commonly found either buried in sand or in débris in rapid waters. A small number of these are found at the bottom in still waters, but in running waters they seek safety by burrowing or by hiding themselves in the débris. The bottom form is retained by the débris dwellers, while the burrowing larvæ have become greatly modified. It is from the inhabitants of the débris that forms like *Ictinus* are ultimately to be derived. Take again the Æschninæ, Lestinæ and Agrioninæ; they are found among weeds both in still water and in running water. The long and slender body becomes greatly elongated under the direct influence of the rapid flow and the legs are greatly stretched. The Corduliinæ and the Libellulinæ are bottom inhabitants with flat and depressed bodies.

Under the action of the current the body is still further depressed and the ventral surface is flattened. The above consideration indicates that nature models the existing material and shapes it in such a way that, without any big jump, the animal gradually becomes adapted for life in a particular environment.

It is believed that primitive life originated and flourished in the sea, while fresh waters were secondarily invaded by those forms which could either lead a fixed life or else were strong enough to withstand and make headway against the currents of streams and rivers. The same argument applies with considerable force to the fauna of torrents. Just as it is possible to trace the various steps in the gradual colonization of the fresh waters by marine animals in the estuarine areas, so the actual origin of the torrential fauna can be traced by studying the animals of a stream, from the plains to its source in the hills. Indeed, the study of evolution in such abnormal habitats is not hindered by the absence of geological data, etc. To a naturalist these habitats are like open books in which he can read the process of evolution for " Verily storm and stress are the mothers of evolution " (MACBRIDE, 1927, p. 70). The importance of evolutionary factors can be realized more easily by a study of abnormal habitats, such as estuaries, swamps, torrents, etc., where environmental factors undergo considerable changes and the animals in accommodating themselves to these changes undergo striking modifications.

What causes have impelled the animals to migrate into rapid-flowing waters ? To understand these properly reference has to be made to the principle of " Divergence of Character " of DARWIN, of " Adaptive Radiation " of OSBORN, and " Opportunity Dispersal " of ROBSON (1928). Necessity and opportunity may be considered as the two causes which impelled the organisms to seek abode in swift currents. Of the necessities of animal existence there are mainly three—food, shelter from enemies, and propagation of the race. Considering only the individual requirements, the first two are of the greatest importance. Experience shows, however, that an animal often risks its life to attain food. Just as " national life is chiefly controlled by the desire to capture markets," so " animal life is chiefly concerned with the occupation of feeding grounds " (WILLEY, 1911, p. 114). The slime on the rocks may provide enough food for certain animals, while the swift current enables plankton feeders to strain large quantities, though brook water is usually poor in plankton. The rapid-flowing water continually stirs up sediment. There is no competition for space in this habitat; those that can withstand the current will share in the booty. They will have the further advantage of cold and highly oxygenated water. It is thus clear that the search for food must have induced the animals to enter into swift currents.

Opportunity has been another great factor in the population of the hill-streams. Only those organisms could take possession of these rich feeding grounds which could withstand the current in one way or another. For instance, the flat, leaf-like form of the Planarians enabled them to crawl along the surface of stones at the bottom and to seek refuge in narrow crevices; the bottom-inhabiting Sisoridæ by virtue of their higher specific gravity could with advantage enter into rapid-flowing waters;

*Sicyopterus garra*, with its modified ventral fins, could hold on to rocks in swift currents, and the insect larvæ, provided with grappling organs for terrestrial locomotion, adapted the same structures for clinging to the rocks; and lastly, the powerful swimmers negotiated swift currents by their muscular efforts, while some of these finding the flow too much for them took to bottom life and modified their skin into adhesive organs of different types. In some, silk-secretion evolved for the manufacture of tubes, etc., was used for the purpose of attachment.

In short, the fauna of the torrents at every step provides ample illustrations of DOHRN's "Theory of the Change of Functions" (DOHRN, 1875, pp. 60–76; MARSHALL, 1894, pp. 53–62), which helps to explain the most serious objection against the theory of Natural Selection. On this point GOODRICH (1924, p. 141) writes as follows: "Of what use can a complex organ be before it is completed? But this objection loses its force when it is remembered that organs rarely, if ever, can be said to 'begin.' Entirely new functions and entirely new organs are not suddenly developed. All are evolved by the gradual transformation of, addition to, or subtraction from, something already there." The paired fins of fishes, evolved as balancing organs, take on the function of attachment; the gill lamellæ of the Heptageniid nymphs become modified for attachment; and the broad-lips of *Megalophrys* originally evolved for attachment take on a totally different function in the funnel-mouthed tadpoles. In the case of the disc of *Garra*, it is clear that it starts as a callosity of the skin in the region where it touches the rock, but in the more highly evolved forms it is gradually perfected under the direct effect of the current. The short, hair-like, chitinous outgrowth on the body of the torrent-inhabiting insect larvæ becomes transformed into strong spines to enable the animals to stem the current. The torrential fauna is full of such instances, though it must not be forgotten that it is not only the parts that are modified, the organism is modified as a whole.

The fact that structural modifications are produced through change of functions seems to have led to a great confusion in the study of animal adaptations; for example, HUBAULT (1927, p. 339) observes, "Cet aplatissement, cette petite taille ne sont-ils pas au contraire deux états préexistants, qui ont facilité à ces organismes l'accès des eaux courantes?" Quite recently POPOVICI-BAZNOSANU (1928) has come to similar conclusions from a study of the insect larvæ inhabiting the torrents. Adaptation means the adjustment of an organism to the conditions of its existence; whether the animal was favourably shaped when it entered a particular habitat, or was secondarily modified in response to environmental factors, matters little. Those of the former category would become adapted more easily than those of the second type. But the process of adaptation is soon realized when it is seen that small animals become still smaller and the dorso-ventrally flattened animals become still more flattened by taking to life in stronger and stronger currents. "With whatever initiative organisms may have been endowed at their origin, *they have not escaped continuous moulding by their surroundings* during their evolution" (BORRADAILE, 1923, p. 375).

What part has natural selection played in the evolution of the torrential fauna? I wish to make it clear at the outset that natural selection is not a *force*, but a *method*, and "that the rôle of natural selection is to keep the organism in direct adaptation to its environmental relations, so that as these latter change the organism changes with them" (KERR, 1926, p. 193). Suppose an animal capable of stemming a current flowing at the rate of $x$ feet per second in a dry season, takes on a habitat where the current flows at the rate of $x + y$ feet per second, in the rainy season. If $x + y$ is only slightly greater than $x$ then the animals may be able to stem it by efforts on their part which would result in the increased efficiency of their organs of attachment. But if, on the other hand, $x + y$ is considerably greater than $x$, the result would be that there will be a wholesale destruction of the animals, and there is no possibility of selection being made. The former case is nicely illustrated by the fishes of the genus *Garra* in their development, in their individual variability and specific differentiation. It has been indicated that hill-stream animals lay their eggs in places where water flows gently, and that the individuals of each generation gradually invade the swifter and swifter currents, which can be correlated with the increasing efficiency of their organs of attachment. During the monsoons, when the streams are in flood in India, there is a very great destruction of the hill-stream animals and particularly of those in unfavourable situations. Under such stresses the animals are being continually improved and become more and more adapted to the environment.

Thus, in the origin and evolution of the hill-stream fauna it is seen that divergent evolution is the starting-point, and the animals which are more favourably placed than others are the first to invade the swift currents. Under these new conditions a continuous adjustment is made by the organism and natural selection keeps it in direct harmony with its environmental factors. I have purposely refrained from discussing, (i) what causes animals to vary, and (ii) how the modified characters are transmitted; but, as an ecologist, I have attempted only to explain how animals become adapted.

## SUMMARY.

In the course of this work I have attempted to treat the ecology, the bionomics and evolution of the torrential fauna, with special reference to that of India. In studying the adaptations, attention has been mainly directed to the means whereby organisms manage to stem the rapid flow of the currents.

Of the physical conditions (pp. 174, 175) that influence the ecological distribution of the torrential fauna the principal one is the rate of flow of the current. The high percentage of oxygen in the water is another important factor, but it is dependent on the current to a very great extent. Shallowness and low temperature of the water are also of some importance.

Among the biological factors (p. 175), food is the most important. The majority of the animals feed on the algæ and slime that cover rocks and stones, but some

strain microplanktonic organisms out of the current. Only a few torrential animals are predaceous in their habits.

In classifying the habitats (pp. 175–178), I have adopted PEARCE's nomenclature, but have modified it considerably in view of direct observations in the field. The entire classification is based on the swiftness of the current, and the reasons for the proposed classification of the habitats are fully discussed.

In studying the bionomics of the torrential fauna attention has been specially directed to the insects and the vertebrates, but a few observations on other animals are also recorded. In the account of the Plecoptera (pp. 178–182) the bionomics and the organs of attachment of the nymphs of the *Perla*-type are fully dealt with. Attention is also directed to the nymphs of the *Nephelopteryx*-type (p. 181), which are cylindrical in shape and are furnished with hooking devices.

Among Odonata (pp. 182–184) the torrent-inhabitants are of two types. Those that lie flat on the substratum are flattened dorso-ventrally, while those that grapple on to the rocks by means of their claws and swing before the current are cylindrical in form. The probable adaptations of the nymphs of three families of Ephemeroptera—Heptageniidæ, Bætidæ and Prosopistomidæ—are discussed. A reference is also made to the adhesive and anchoring devices found on their eggs.

The genera of Heptageniidæ have been differently grouped into two subfamilies (p. 185) by LESTAGE and by HUBAULT. The former based his classification on the character of the gill-lamellæ; the latter on that of the caudal setæ. The adaptive significance of these characters is discussed and their gradual evolution and modification, as induced by the swiftness of the current, are indicated in *Ecdyonurus, Heptagenia, Epeorus, Iron* and *Rhithrogena.* The members of this family form a homogeneous assemblage, and a graphic representation of the relationships of the Heptageniid genera is given.

Of the Bætidæ (pp. 191–194), members of the two subfamilies—the Bætinæ and the Ephemerellinæ—are discussed. Nymphs of *Bœtis* cling to rocks and weeds with the help of their powerful claws and are met with in all kinds of habitats. In swift currents the stream-line form is better developed by a reduction in the number of the caudal setæ from three to two, so that the stream-line revetment of the body is carried to the extreme posterior end. In the Ephemerellinæ the structural modifications of the claws and the tracheo-branchiæ of *Ephemerella* are discussed, and it is indicated that the differences can be correlated with variations in the environmental factors. Reference is made to the supposed relationships between the Ephemerellinæ and the Cæninæ, and it is concluded that the gill chamber is polyphyletic in origin and does not denote genetic affinity.

The nymphs of *Prosopistoma* (pp. 194–196) adhere to rocks by creating a reduced pressure on their ventral surface, but no sucker formation takes place, as is commonly believed.

In the account of the Hemiptera (pp. 196, 197) two types of Naucorid bugs are referred to. Differences in the anchoring devices of the plant-inhabiting and rock-inhabiting bugs are indicated. The attachment is chiefly effected by the spinous pad on the tibia and by the claw.

The Trichopterous larvæ of the swift currents (pp. 197–201) are of two kinds—free-living and those that manufacture some kind of shelter. The abdominal hooks and the claws are the organs of fixation. A detailed account is given of the eggs and oviposition of a species of Trichoptera (Lepidostomatinæ) from Dalhousie. The fly lays its eggs on the lips of falls, a unique situation so far as is known at present.

Lepidopterous larvæ (pp. 201, 202) of the genera *Aulacodes, Elophila,* etc., live on rocks in swift currents under thin sheets of silk. The crotchets on the prolegs and the terminal claws on the thoracic legs enable the animal to stem the current.

Of the Coleopterous larvæ (pp. 202–205), direct observations were made on the Dryopidæ and Helodidæ. *Psephenus-* and *Psephenoides*-like larvæ are abundantly represented in the torrential fauna of India, and a detailed account of their bionomics and the organs of attachment is given. It is concluded that adhesion is not the result of a sucker-formation.

Certain Empid flies of the genus *Clinocera* (p. 206) were found in great abundance at Dalhousie. Their habits were studied in detail and their behaviour was found to be similar to that of the Blepharoceridæ.

The Psychodid larvæ (pp. 206, 207) of the genera *Pericoma* and *Ulomyia* live in moss, in which the backwardly directed processes on their bodies become entangled and prevent them from slipping. The larvæ of *Maruina* are dorso-ventrally flattened and are provided with a row of eight "suckers" on the ventral surface; the pupæ are cemented to the rock and are similar in appearance to those of the Blepharoceridæ.

The larvæ of the Tipulid genera *Triogma* and *Phalacrocera* anchor themselves in moss by their long leaf-like processes, which are denticulated and serrated in various ways (p. 207). The larvæ of *Tipula* live among roots of plants where they are not affected by the current, while those of *Dicranota* and *Pedicia* are provided with pseudopods which end in rows of chitinous hooks (p. 208). The larvæ of *Antocha* (p. 209) live under a shelter of thin-spun silk, and the pupa fixes itself to the case with two powerful hooks at the caudal end and lies in the current with the head pointing downstream.

In the Chironomidæ (pp. 209–211) the hooks on the posterior pair of pseudopods serve as the chief means of attachment. The tube, so characteristic of the sluggish-water forms, is discarded, because, instead of being advantageous in providing shelter and safety, it proves an encumbrance. Larvæ of *Cardiocladius* and *Charadromyia* live under sheets of thin-spun silk, and are thus protected from being washed away.

A general account of the biology of the Simuliidæ is given and the mode of fixation and progression of the larvæ is discussed (pp. 211–217). In a *Simulium* larva the attachment to the substratum is effected by the salivary secretion and the hooks on the posterior appendage, the thoracic proleg and the labrum. The morphology of these structures is described and the exact mechanism of gripping by the hooks is explained. The function of the various muscles connected with the posterior appendage is also discussed (p. 214).

Special attention has been paid to the study of the larvæ and pupæ of the Blepharoceridæ (pp. 217–227). The chief organs of attachment are the suckers, but there are other mechanical devices also which enable the animal to stem the current. The morphology and physiology of the sucker are discussed in detail.

The remarkable larvæ of *Deuterophlebia* (pp. 227–229) possess seven pairs of grappling organs. It has been hitherto believed that they act as suckers, but it is indicated that they take hold on the substratum by means of the claws. In the mechanism of their attachment the so-called suckers of *Deuterophlebia* correspond with the pseudopods of *Dicranota.*

Observations are made on the probable phylogeny of the Blepharoceridæ and the Deuterophlebiidæ (pp. 229–231) as deduced from a study of their larval structure. The conclusion is reached that the members of the two families have evolved along two independent parallel lines and that the resemblances between them are due to convergence induced by life under similar environmental conditions and not to any genetic affinity between the two. The probable mode of evolution of the Blepharoceridæ is indicated by referring to the various forms exhibited by the larvæ of the Psychodidæ. It is pointed out that the Blepharoceridæ constitute one of the oldest families of the Dipterous insects.

In fishes attachment to the substratum is effected either by the formation of a sucker, as in *Garra* and *Sicyopterus,* or more often by means of a reduction of the pressure on the ventral aspect by various devices. The corrugated adhesive pads are provided with spines which prevent the animal from slipping. It is indicated that the broad lips do not form a sucker in conjunction with the mouth, as has been believed hitherto (p. 234). Evolutionary series showing gradual modifications induced by environmental factors are given in the case of the Homalopteridæ (p. 235), the Sisoridæ (p. 236) and the Loricariidæ (p. 239).

The brook-inhabiting tadpoles can be classified into three ecological associations, and the chief characteristics of these groups are discussed. In the larvæ of Batrachia adhesion to the substratum is effected either by the formation of a definite sucker, as in the tadpoles of the section Ranæ Formosæ, or by the hypertrophy of the lips, which on the ventral aspect are covered with rows of teeth or papillæ, as in the tadpoles of *Helophryne.* The structure and mechanism of the teeth are explained (p. 243) and reasons are given why in some tadpoles only one lip and in others both the lips are hypertrophied (p. 244). The probable mode of evolution of the funnel-shaped mouth of the *Megalophrys* tadpoles is indicated, and it is concluded that the broad lips developed for the purpose of adhesion became modified into a funnel-shaped apparatus when the tadpoles took to life in sluggish waters. The reversion of the biogenetic law is discussed (p. 248) and a brief reference is made to the modifications of the Caudata for life in swift currents.

In dealing with the physics of the mechanism of attachment attention is directed to the resistance-reducing devices to the specific gravity, and to the mechanical means by which fixation to the substratum is effected. It is indicated that the resistance has been diminished by a reduction in the size (p. 249), by assuming stream-line forms (p. 250), by smoothing of the surface at a certain velocity (p. 254), and by roughening the surface at a different velocity. The adaptational significance of these modifications is discussed and examples are given in each case.

The mechanical devices for fixation are (i) sticky secretions (p. 257), (ii) vacuum-producing devices (pp. 258–260), (iii) "seizing" devices (p. 260), and (iv) hooking devices (pp. 261–262).

In the course of this work numerous instances of parallel evolution are cited, and it is suggested that community of habitat has led to structural convergence. Convergence implies resemblances "which result from independent functional adaptation to similar ends"; this basic idea of convergence is explained by citing several instances (pp. 264–265). Attention is also directed to a peculiar type of evolution ("Divergent Evolution" of ANNANDALE) and to the causes that produce it.

It has been supposed by certain workers (*e.g.*, HUBAULT) that the torrential fauna is of glacial origin, but evidence is adduced to prove that this fauna has colonized the torrents by means of a step-by-step migration from lower levels (pp. 267–269). The causes of this migration are studied (p. 269) and the part played by change of function, the principles of which were set forth by DOHRN ("Theory of the Change of Functions"), is indicated with the help of several examples (p. 270).

In the course of this work no attempt has been made to study the causes of variations or the mode of their transmission, but an effort has been made to show, from a purely ecological point of view, how animals become adapted to their surroundings.

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## EXPLANATION OF PLATES.

### PLATE 15.—*Torrential Streams in India.*

FIG. 1.—Ravi River below Chamba, Western Himalayas. The series of Ephemerellid nymphs (resembling *Drunella*) referred to on p. 192, were collected here.

FIG. 2.—Small Stream below Dumpep Dak Bungalow flowing through a small creek over a series of steps. Most of the field-work was done in this place.

### PLATE 16.—*Torrential Streams in India.*

FIG. 1.—Dud-dhara fall in the course of the Narbadda River, Central Provinces.

FIG. 2.—Series of falls in the course of the Pun-Wa-Sherra Stream, Khasi Hills, Assam.

The two photographs illustrate a similar type of environment, but the fauna on the lips of the two falls was different, owing to the fact that in the Pun-Wa-Sherra Stream the rocks were bare while those of the Dud-dhara fall were covered with moss (p. 177).

### PLATE 17.—*Devices for Reducing Resistance and for Adhesion.*

FIG. 1.—A portion of the tergum of a Perlid nymph (prob. *Neoperla*) showing arrangement of spines (p. 180). × 35.

FIG. 2.—Dorsal surface of the femur of same showing arrangement of spines (p. 180). × 15.

FIG. 3.—Third gill-lamella of *Epeorus* (p. 187). × 26.

FIG. 4.—First gill-lamella of same (p. 187). × 26.

FIG. 5.—A portion of the spinous pad on the gill-lamellæ of *Iron* showing finger-like projections from the basal region. The basal parts only of the marginal setæ are shown (p. 188). × 185.

FIG. 6.—Crawling leg of a Naucorid bug of the rock-inhabiting type (p. 196). × 12.

FIG. 7.—Crawling leg of a Naucorid bug of the plant-inhabiting type (p. 197). × 12.

FIG. 8.—An egg-mass of the Trichopterous fly (Lepidostomatinæ) from Dalhousie (p. 200). × 10. Note the gelatinous strand by which the mass is fixed to the substratum.

FIG. 9.—A portion of the peripheral region of a Psephenid larva showing arrangement of spines on rod-like structures (p. 204). × 215.

FIG. 10.—A Blepharocerid larva with well-marked lateral appendages (p. 225.) × 13.

FIG. 11.—A portion of a pad of the same, showing arrangement of spines (p. 225). × 1800.

FIG. 12.—Papillæ on the ventral surface of a chiton-shaped Blepharocerid larva, showing the comb-like arrangement of their spines (p. 226). × 670.

FIG. 13.—A portion of a Blepharocerid larval cuticle from the dorsal surface, showing cracks in the thick cuticle and wart-like processes distributed irregularly (p. 226). × 260.

FIG. 14.—A portion of a Blepharocerid pupal cuticle from the dorsal surface of a pupa still enclosed within the larval cuticle, showing spinous papillæ (p. 227). × 350.

FIG. 15.—A portion of the cuticle from a pupa of the same species which had been for some time living free in the torrent. The spines on the papillæ have been rubbed off by the rushing current (p. 227). × 550.

FIG. 16.—A Blepharocerid pupa (p. 227). × 11.

All the figures are from direct microphotographs of my preparations. Figs. 13, 14 and 15 illustrate devices for reducing resistance, while the others indicate the nature of adhesive surfaces.

PLATE 18.—*Illustrating Convergence towards a Limpet-shape in different orders of Insects living under the conditions found in Torrents. In each case the ventral aspect is shown.*

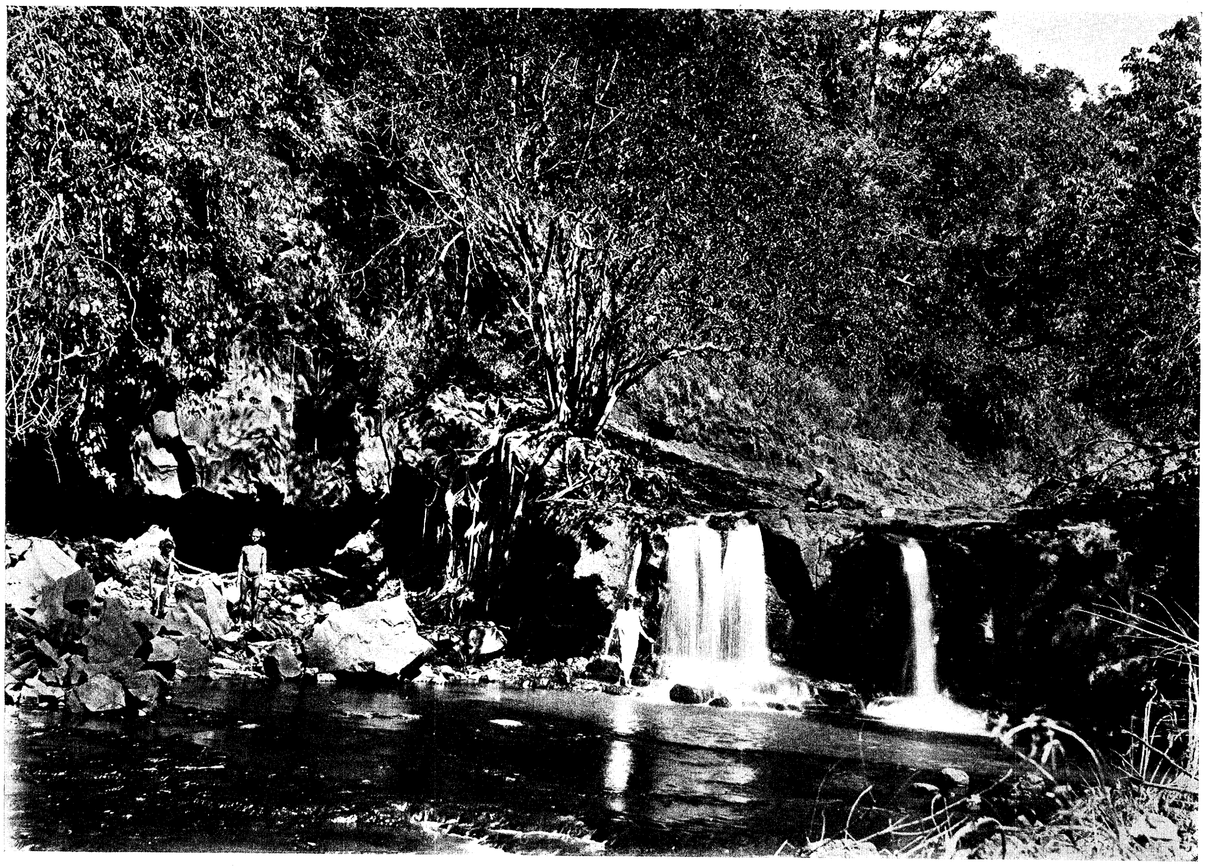
FIG. 1.—Coleoptera, a Psephenid larva from the Kangra Valley (p. 203). × 8. The marginal fringe and the legs are the chief organs of attachment.

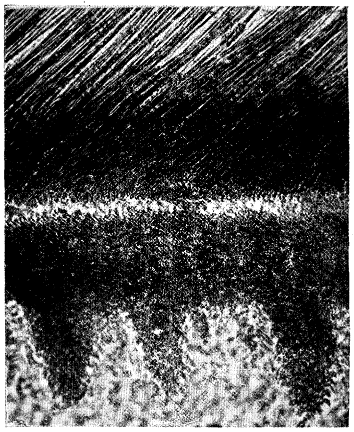
FIG. 2.—Hemiptera, a rock-inhabiting Naucorid bug from Northern Burma (p. 196). × 4. The spinous pads and the central row of backwardly directed spines are indicated.

FIG. 3.—Diptera, a Blepharocerid larva from Dalhousie, Western Himalayas (p. 226). × 33. Showing the central row of half-a-dozen suckers, the lateral spines, the papillæ in the peripheral region and the semicircular, striated, chitinous pad at the posterior end.

FIG. 4.—Ephemeroptera, a nymph of *Iron* from the Kangra Valley (p. 188). × 3. Showing the gill-lamellæ forming a rim round the ventral surface of the body and the positions of their spinous pads.

FIG. 5.—Odonata, larva of *Ictinus rapax* from S. India (p. 183). × 2. Showing the six pairs of spinous pads.

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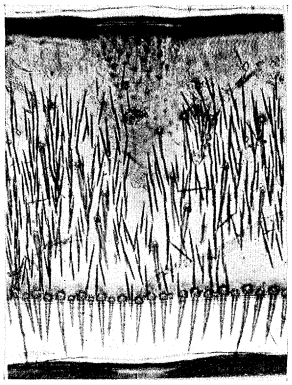
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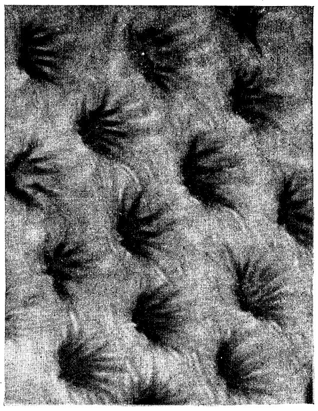
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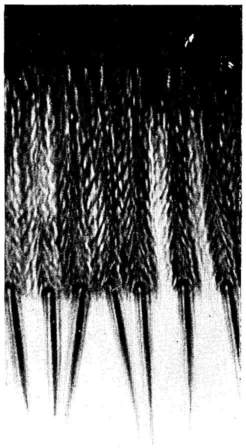
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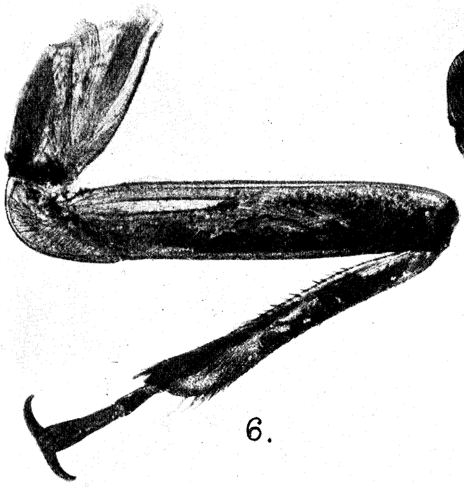
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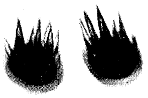
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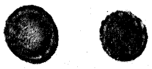
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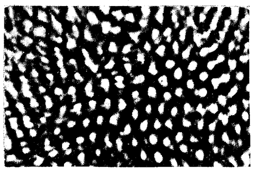
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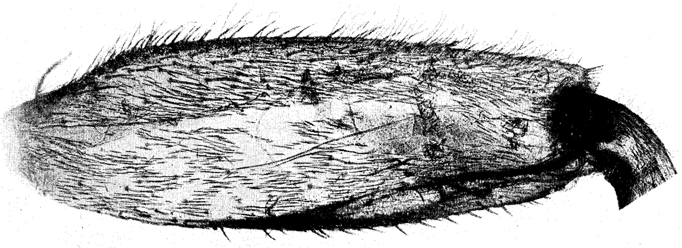
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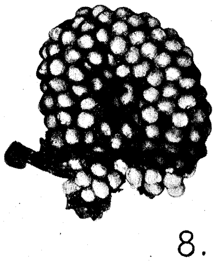
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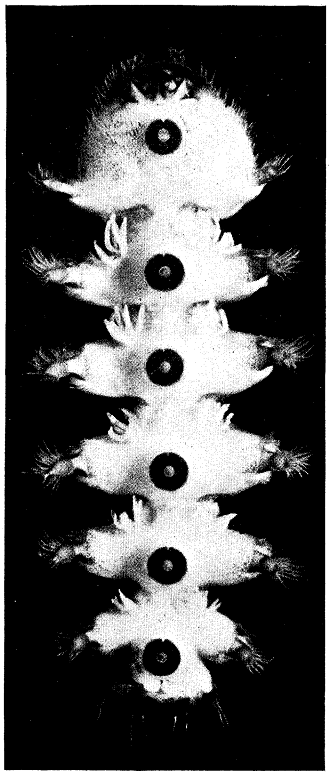
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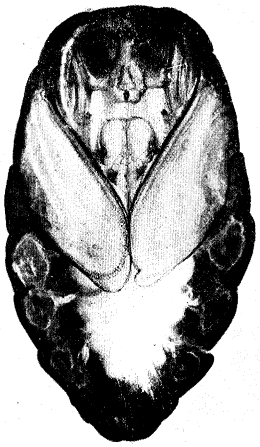
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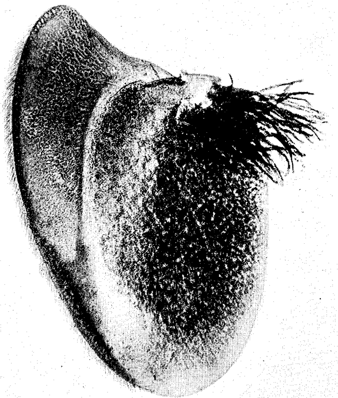
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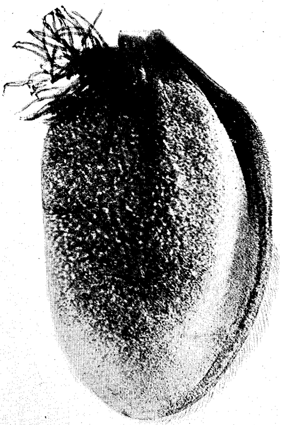
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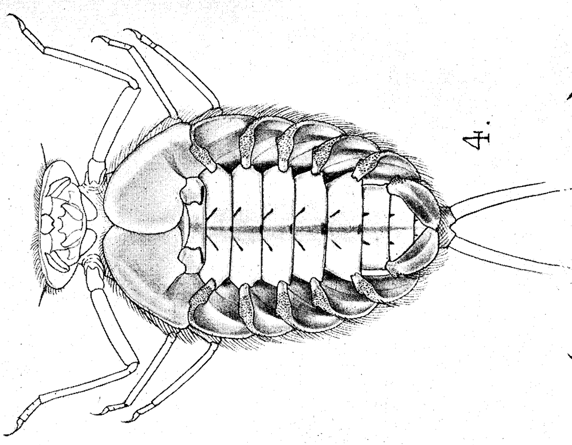

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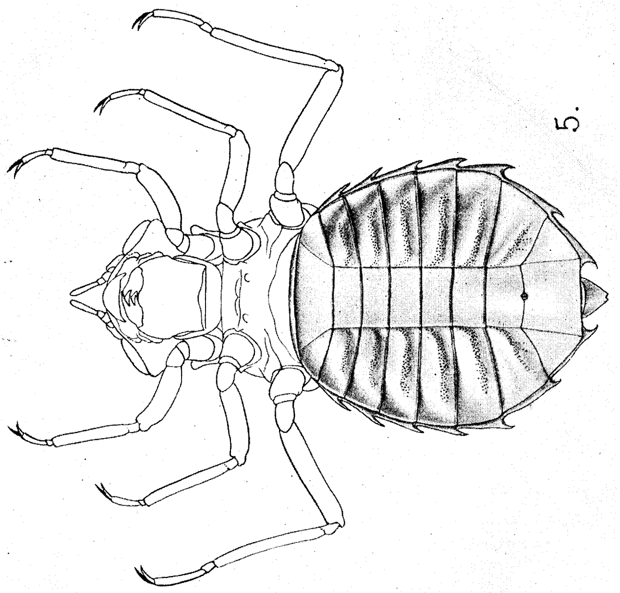

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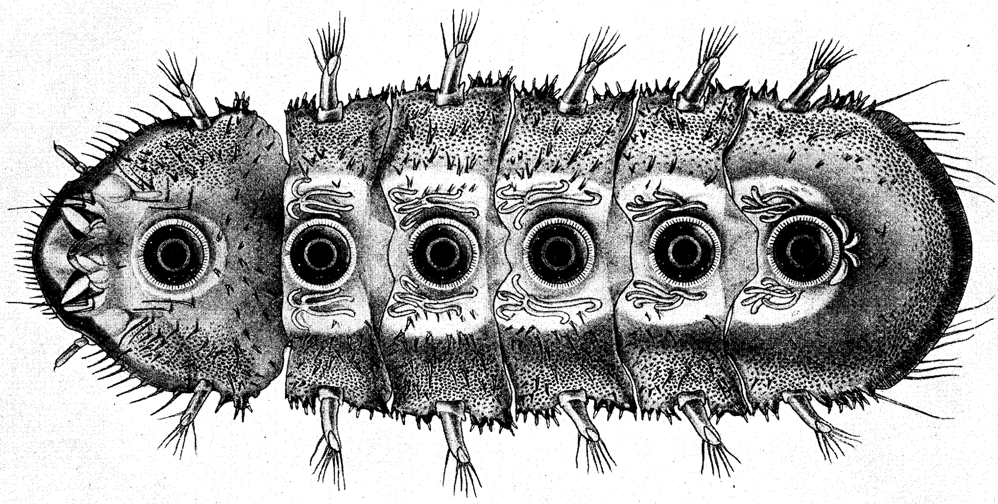

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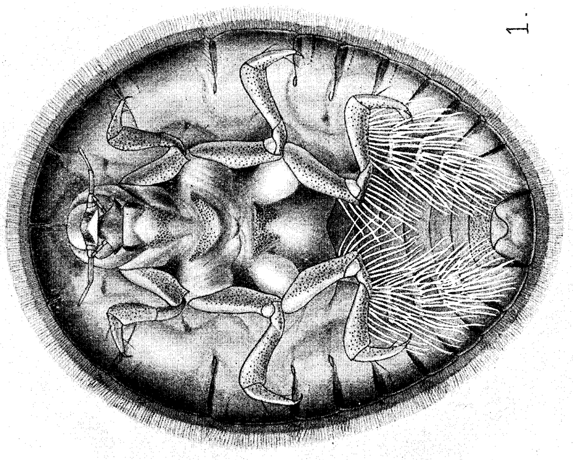

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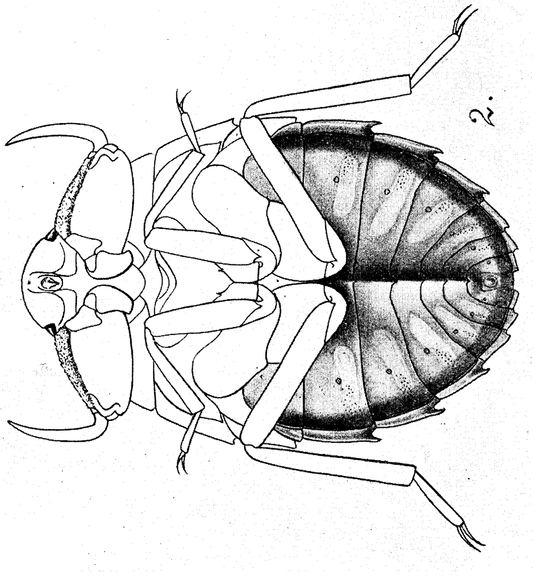

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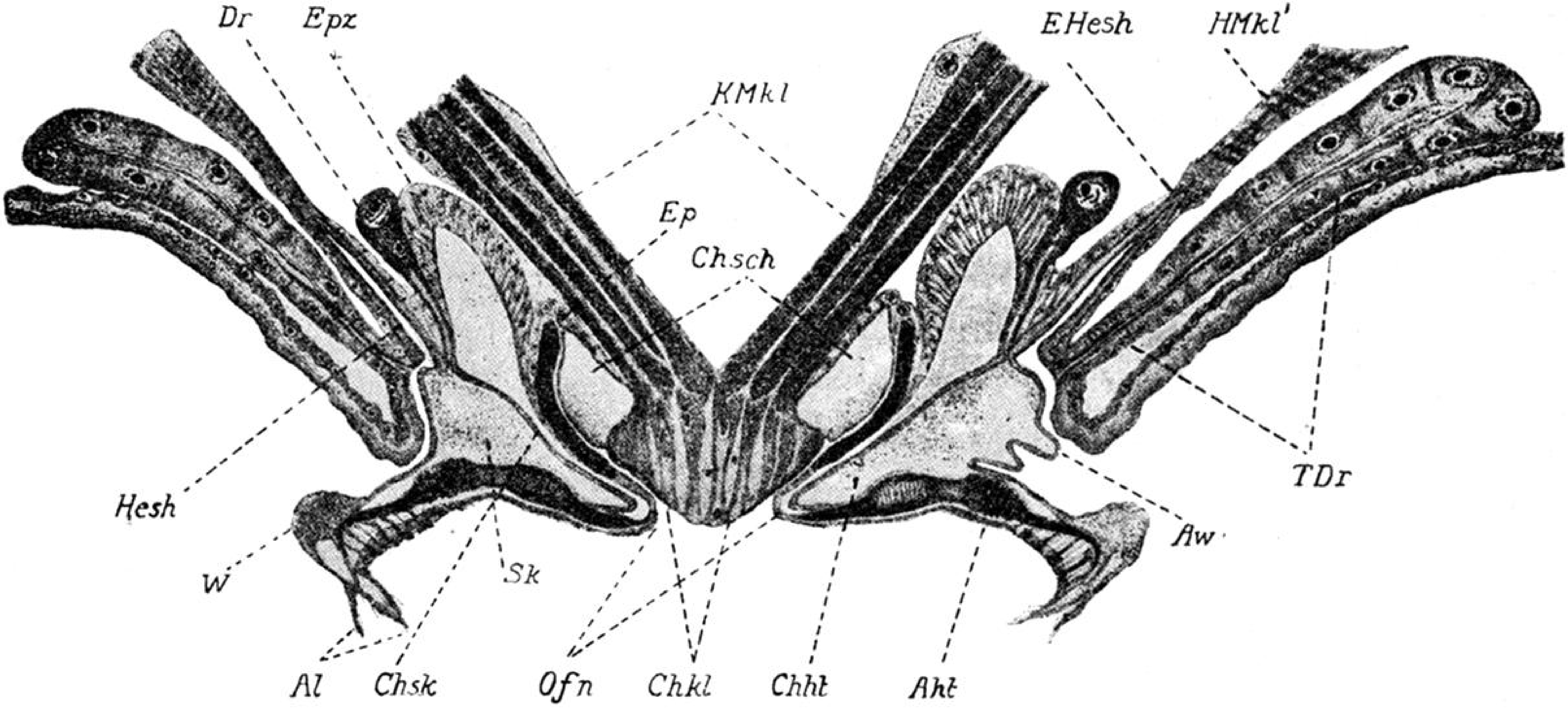

TEXT-FIG. 8.—Median section through the sucker of a Blepharocerid larva transverse to the body axis (after KOMÁREK). *Aht* = the outer skin of the disc rings ; *Al* = free margin of the disc ; *Aw* = the outer wall of the sucker ; *Chht* = chitinous support ; *Chkl* = chitinous piston ; *Chsch* = the chitinous ring round the piston ; *Chsk* = the chitinous sac ; *Dr* = bicellular gland ; *EHesh* = the end of the skin layer ; *Ep* = epithelium of chitinous ring round the piston ; *Epz* = epithelial cell layer ; *Hesh* = the skin layer ; *HMkl* = muscles of the skin layer ; *KMkl* = muscles of the piston ; *Ofn* = central opening of the sucker ; *Sk* = secretion of glands ; *TDr* = the tubular gland ; *W* = marginal rim.

PLATE 15.—*Torrential Streams in India.*

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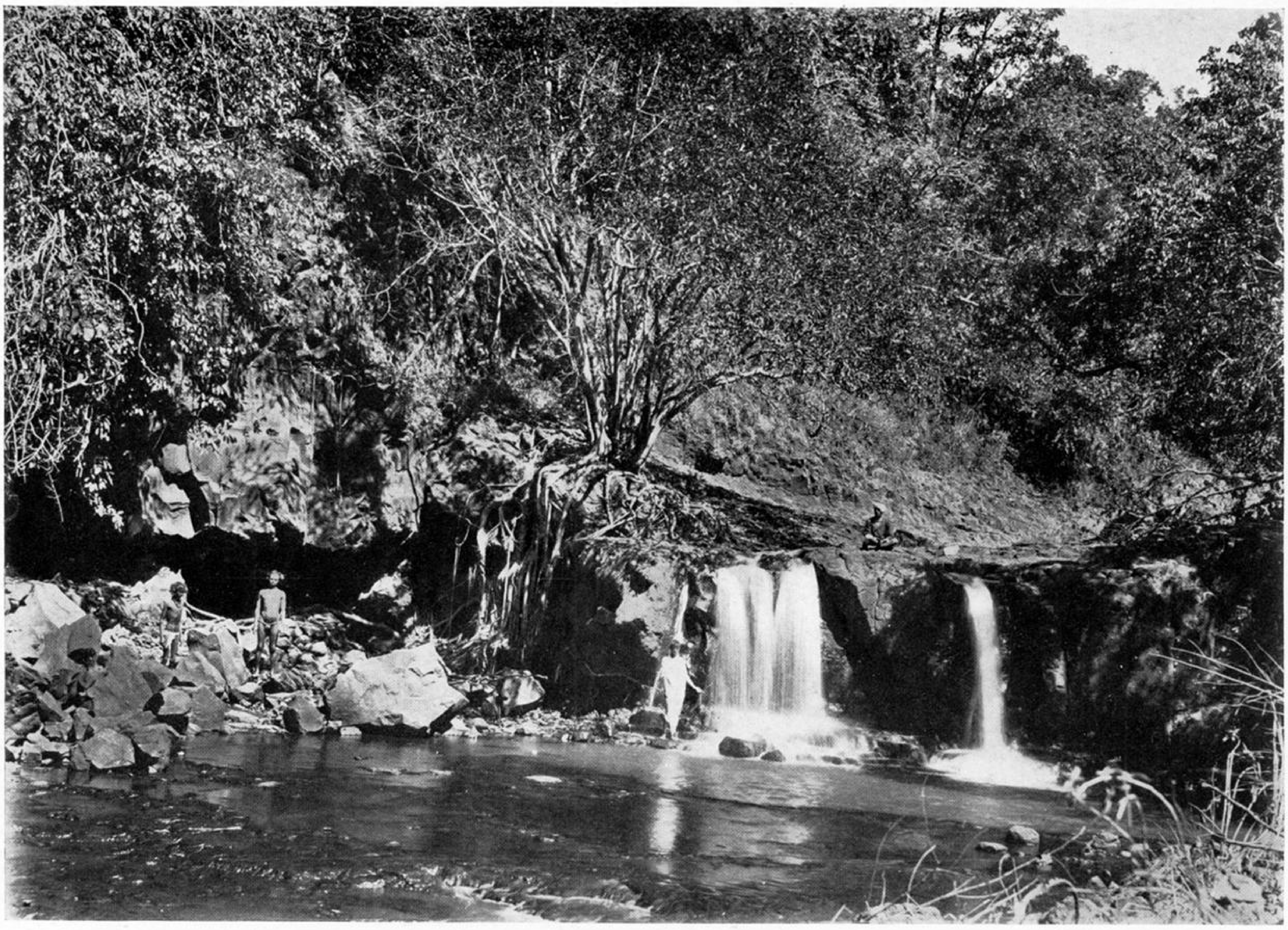

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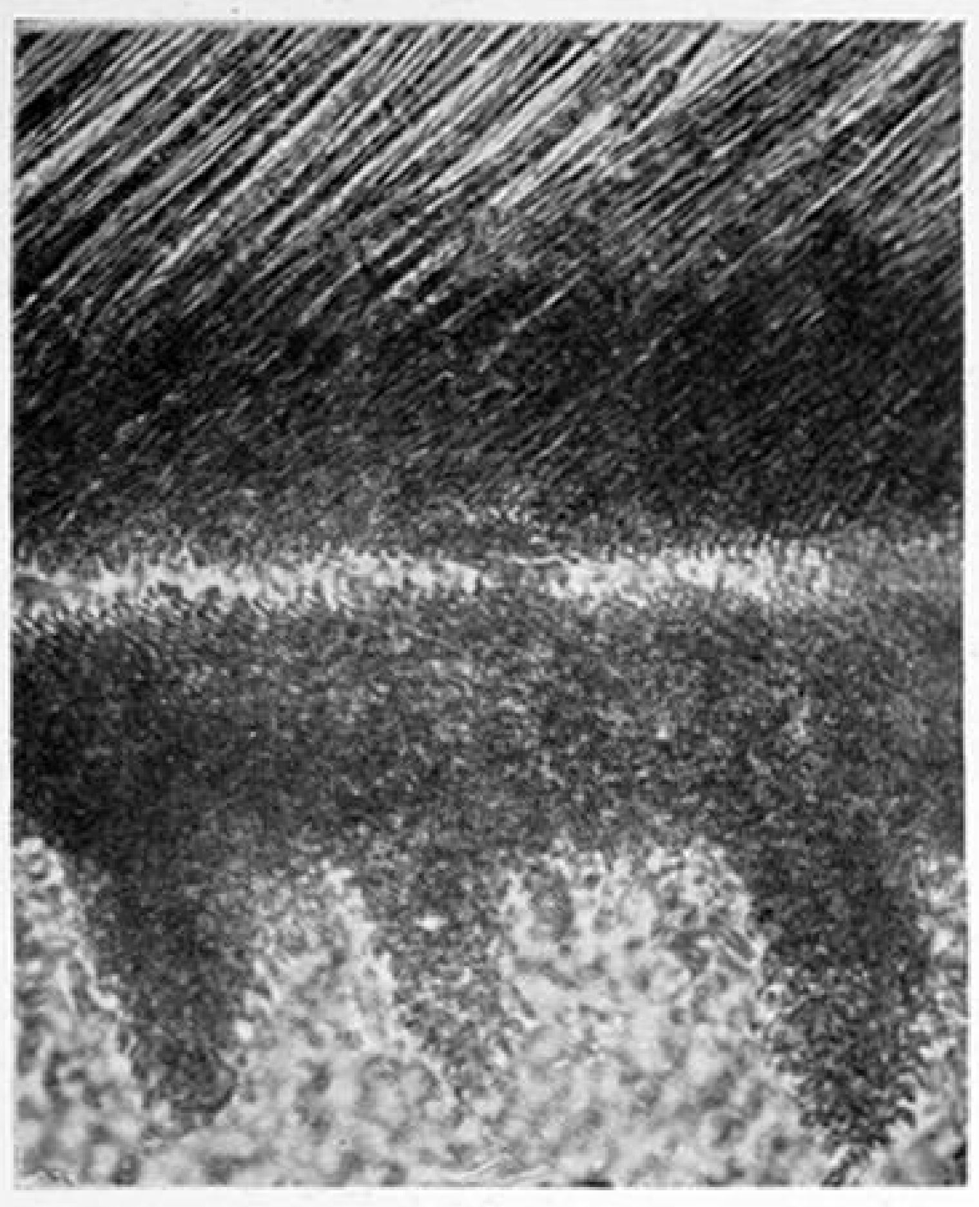
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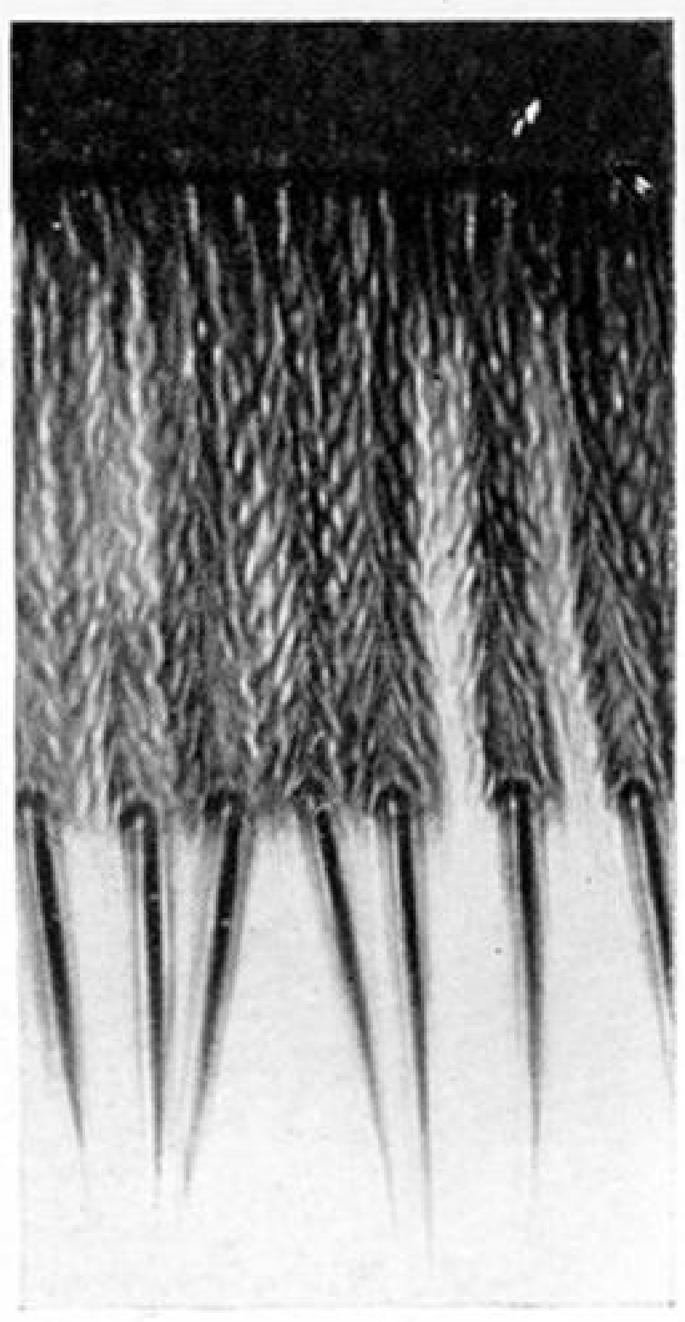
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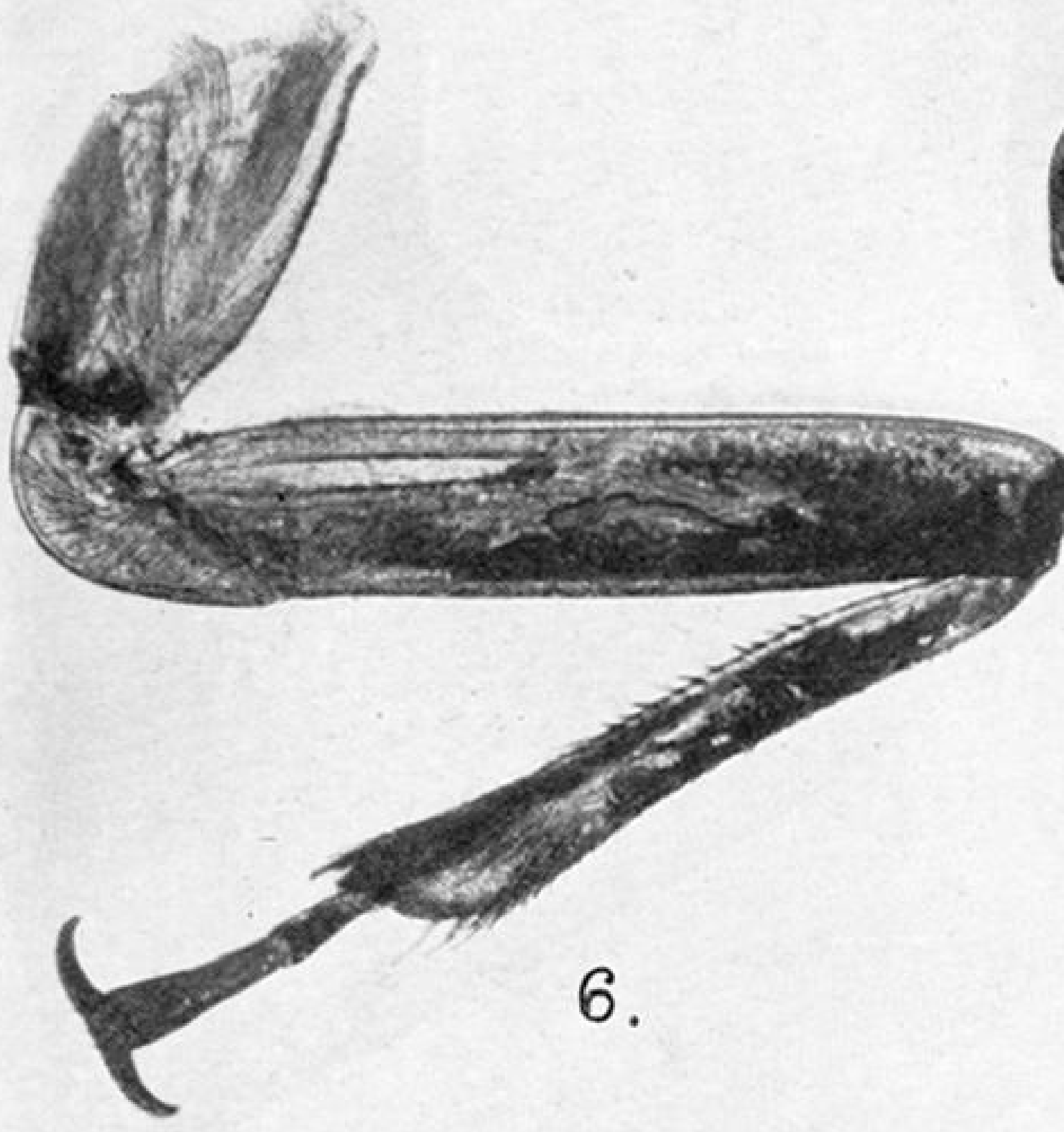
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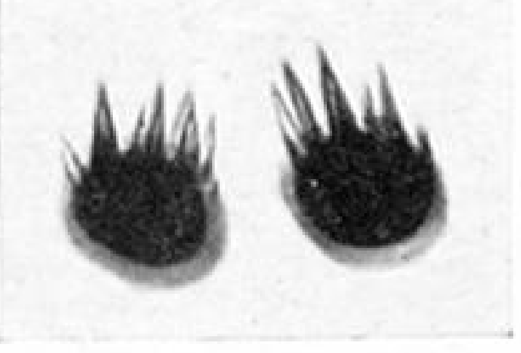
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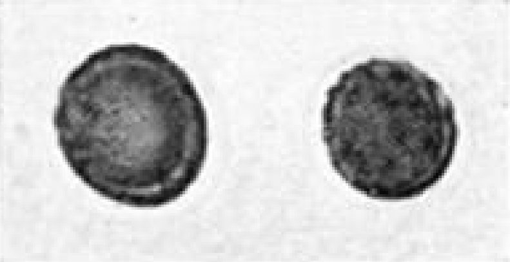
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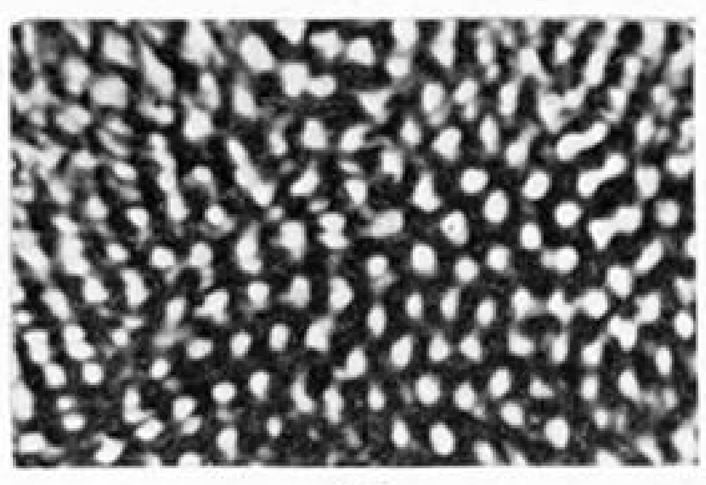
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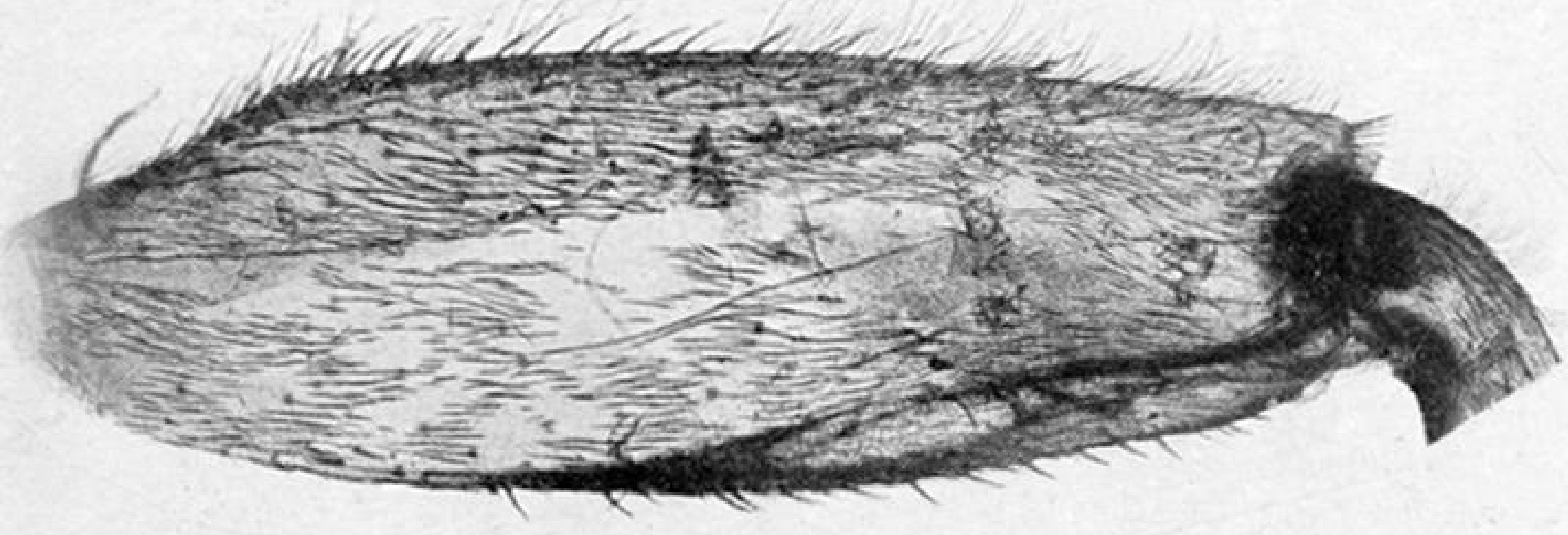
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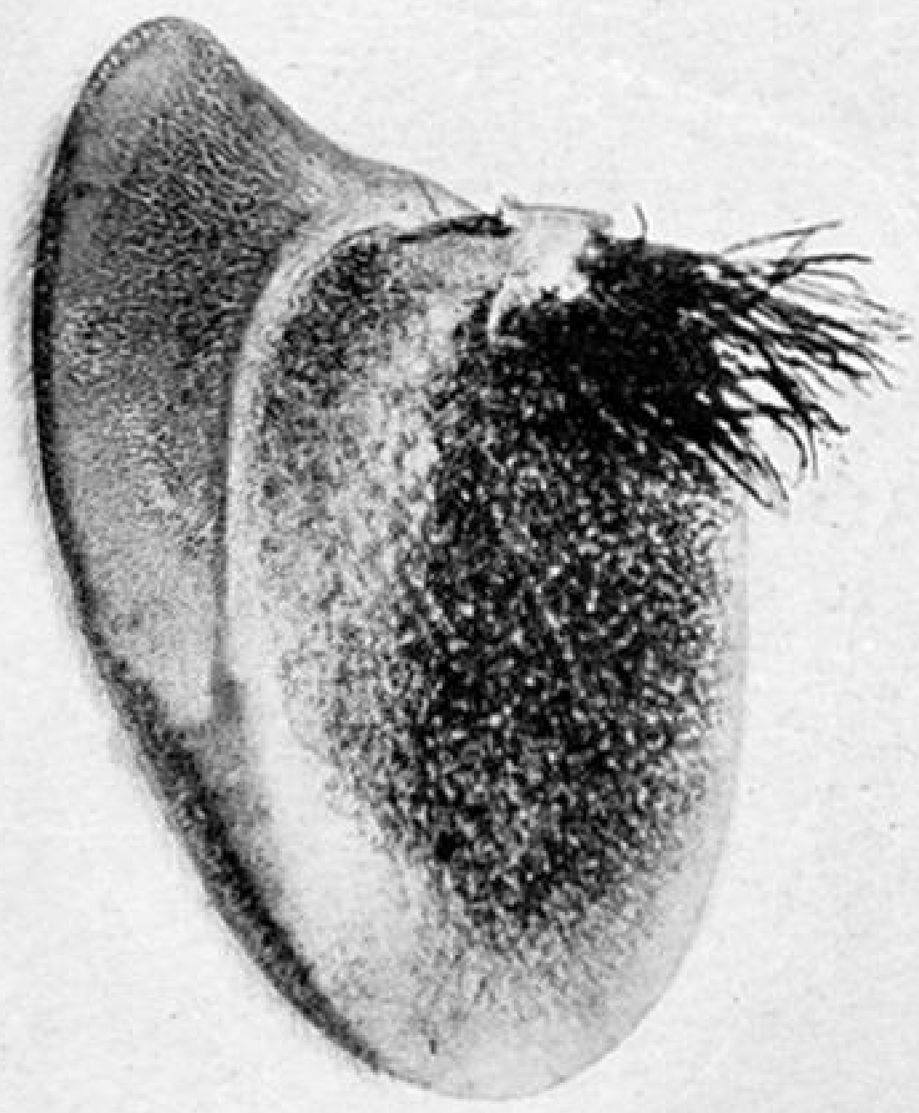
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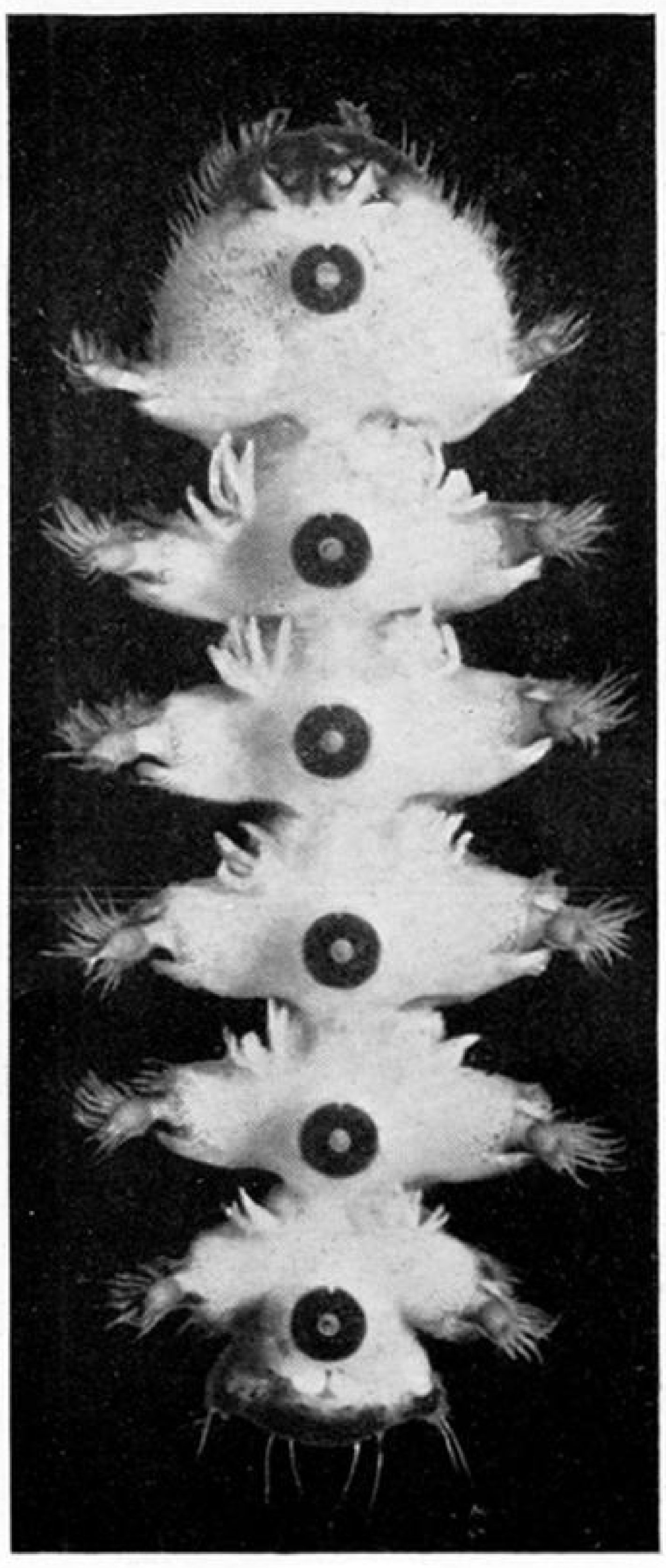
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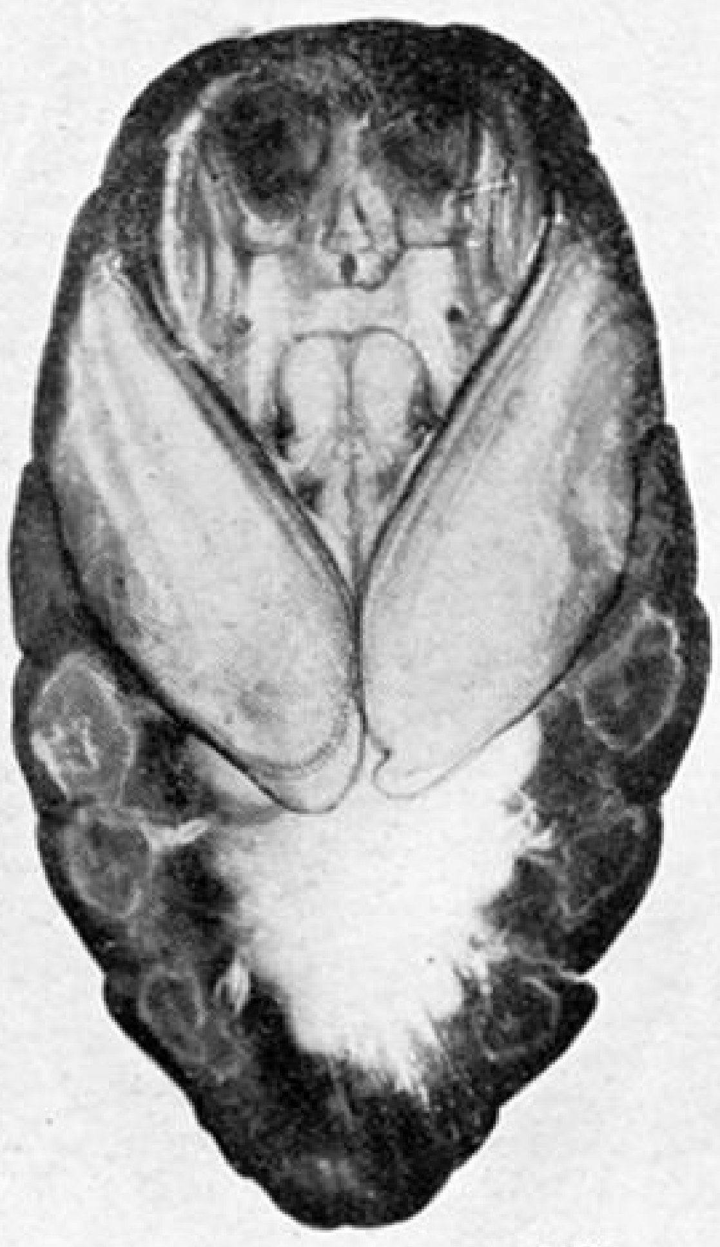
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PLATE 17.—*Devices for Reducing Resistance and for Adhesion.*

FIG. 1.—A portion of the tergum of a Perlid nymph (prob. *Neoperla*) showing arrangement of spines (p. 180). × 35.

FIG. 2.—Dorsal surface of the femur of same showing arrangement of spines (p. 180). × 15.

FIG. 3.—Third gill-lamella of *Epeorus* (p. 187). × 26.

FIG. 4.—First gill-lamella of same (p. 187). × 26.

FIG. 5.—A portion of the spinous pad on the gill-lamellæ of *Iron* showing finger-like projections from the basal region. The basal parts only of the marginal setæ are shown (p. 188). × 185.

FIG. 6.—Crawling leg of a Naucorid bug of the rock-inhabiting type (p. 196). × 12.

FIG. 7.—Crawling leg of a Naucorid bug of the plant-inhabiting type (p. 197). × 12.

FIG. 8.—An egg-mass of the Trichopterous fly (Lepidostomatinæ) from Dalhousie (p. 200). × 10. Note the gelatinous strand by which the mass is fixed to the substratum.

FIG. 9.—A portion of the peripheral region of a Psephenid larva showing arrangement of spines on rod-like structures (p. 204). × 215.

FIG. 10.—A Blepharocerid larva with well-marked lateral appendages (p. 225.) × 13.

FIG. 11.—A portion of a pad of the same, showing arrangement of spines (p. 225). × 1800.

FIG. 12.—Papillæ on the ventral surface of a chiton-shaped Blepharocerid larva, showing the comb-like arrangement of their spines (p. 226). × 670.

FIG. 13.—A portion of a Blepharocerid larval cuticle from the dorsal surface, showing cracks in the thick cuticle and wart-like processes distributed irregularly (p. 226). × 260.

FIG. 14.—A portion of a Blepharocerid pupal cuticle from the dorsal surface of a pupa still enclosed within the larval cuticle, showing spinous papillæ (p. 227). × 350.

FIG. 15.—A portion of the cuticle from a pupa of the same species which had been for some time living free in the torrent. The spines on the papillæ have been rubbed off by the rushing current (p. 227). × 550.

FIG. 16.—A Blepharocerid pupa (p. 227). × 11.

All the figures are from direct microphotographs of my preparations. Figs. 13, 14 and 15 illustrate devices for reducing resistance, while the others indicate the nature of adhesive surfaces.

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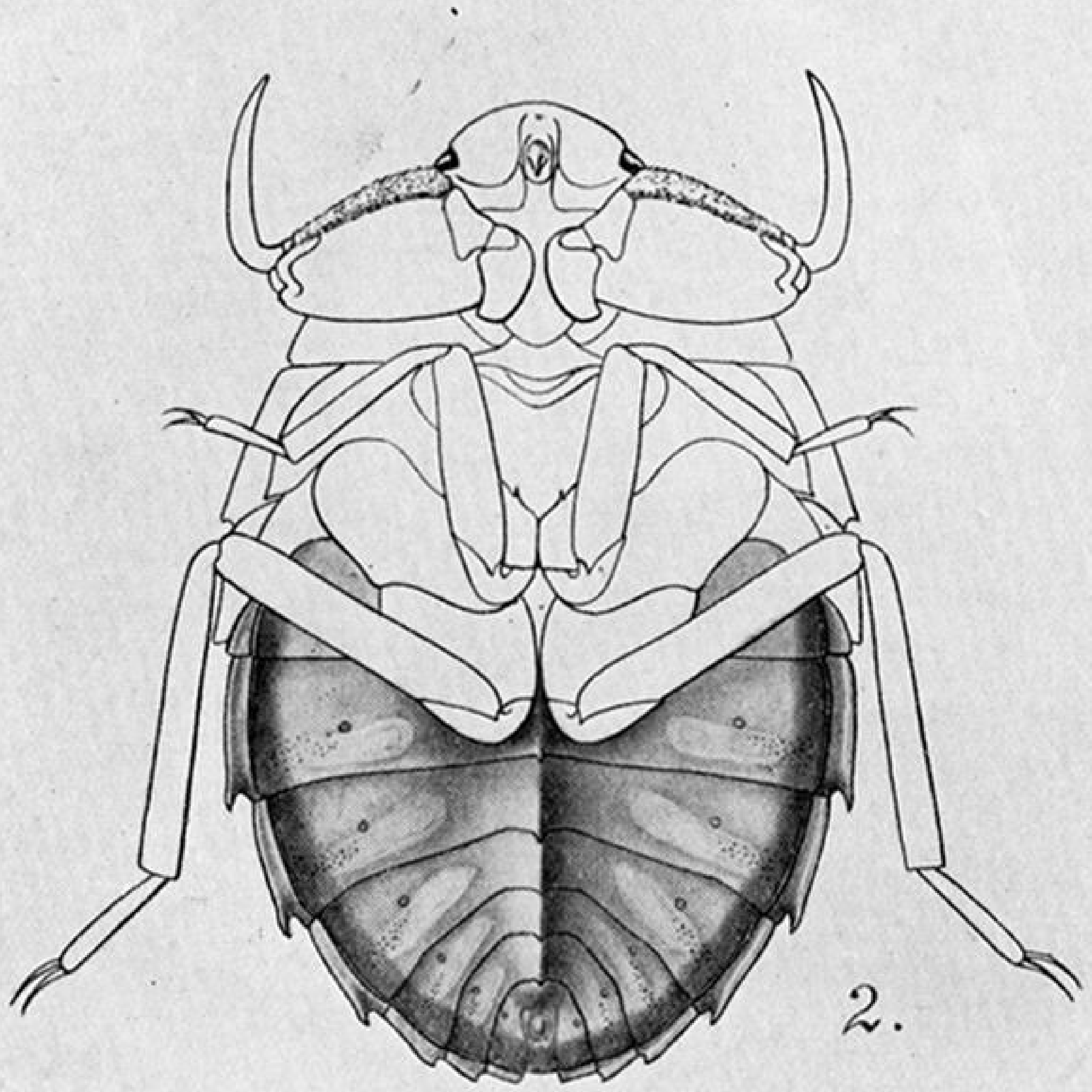

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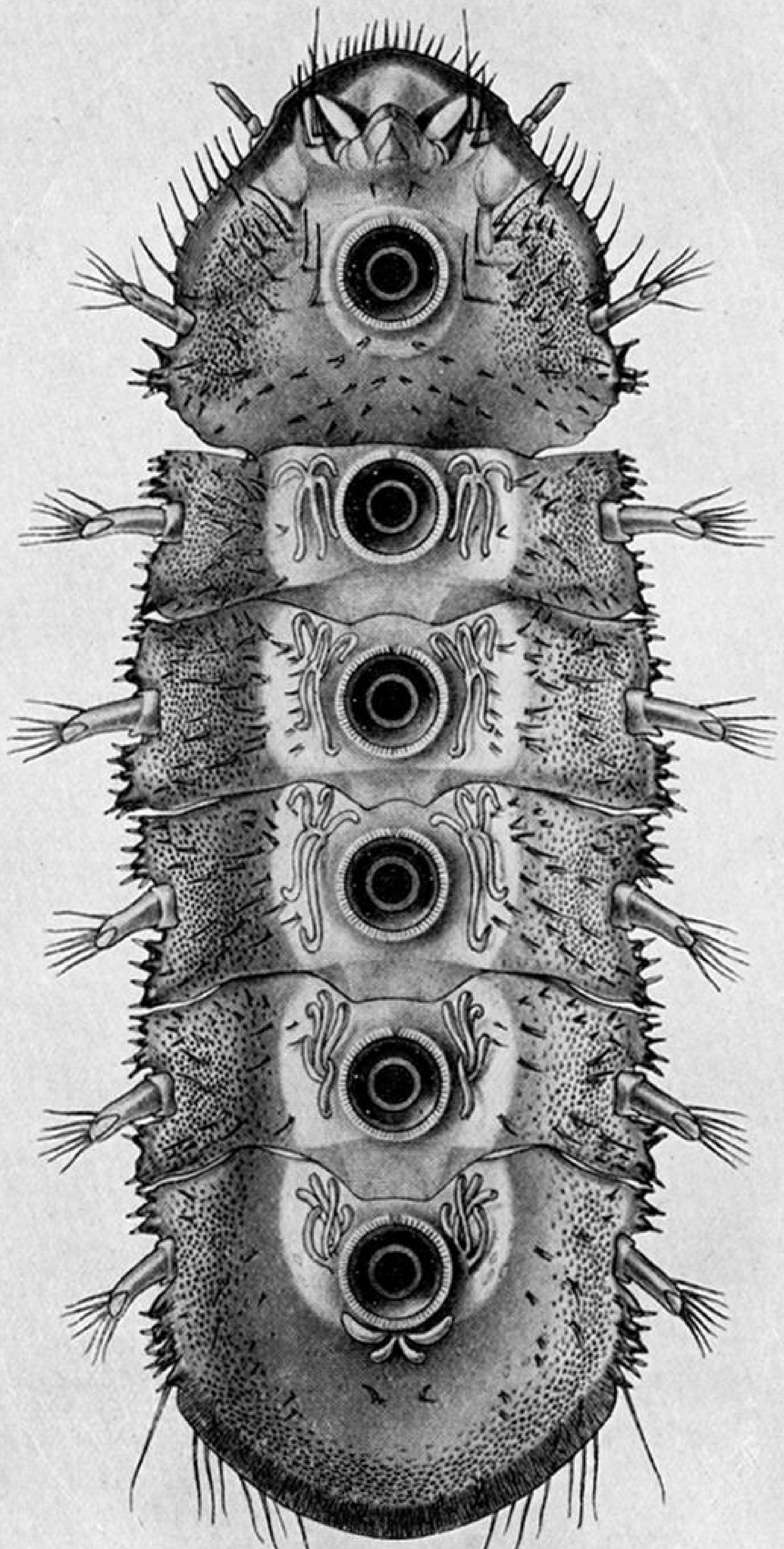

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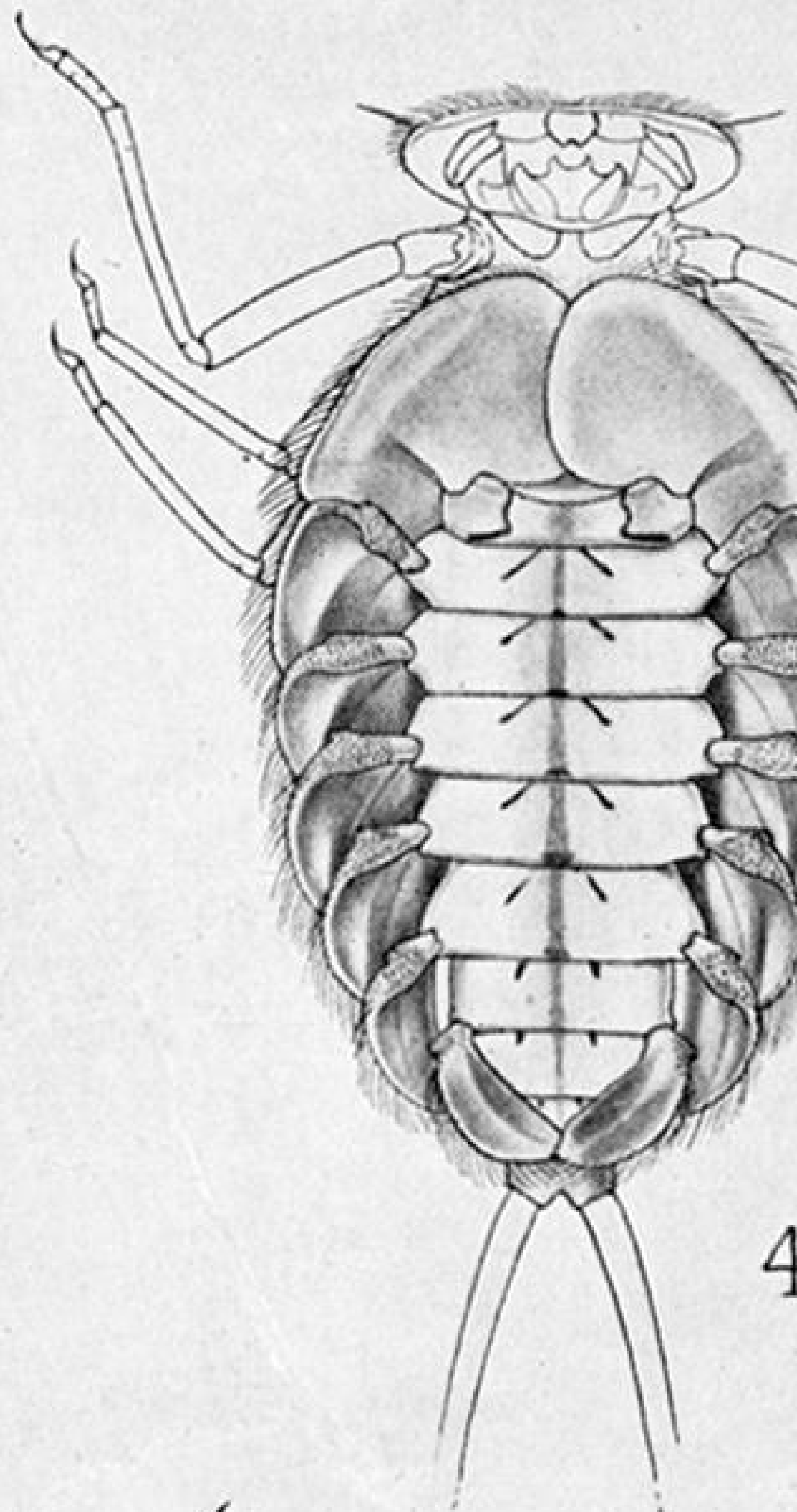

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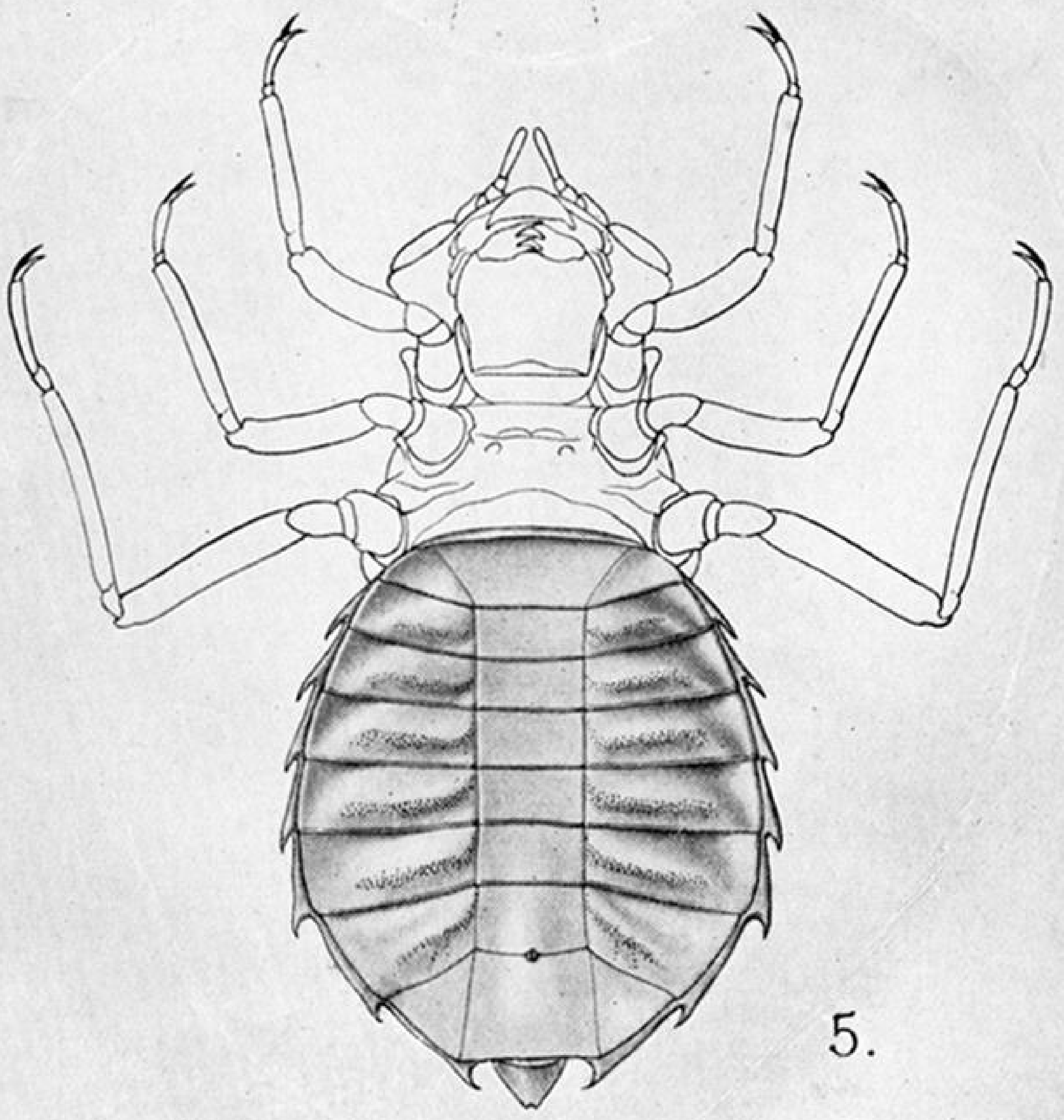

5.

Plate 18.—*Illustrating Convergence towards a Limpet-shape in different orders of Insects living under the conditions found in Torrents. In each case the ventral aspect is shown.*

Fig. 1.—Coleoptera, a Psephenid larva from the Kangra Valley (p. 203). × 8. The marginal fringe and the legs are the chief organs of attachment.

Fig. 2.—Hemiptera, a rock-inhabiting Naucorid bug from Northern Burma (p. 196). × 4. The spinous pads and the central row of backwardly directed spines are indicated.

Fig. 3.—Diptera, a Blepharocerid larva from Dalhousie, Western Himalayas (p. 226). × 33. Showing the central row of half-a-dozen suckers, the lateral spines, the papillæ in the peripheral region and the semicircular, striated, chitinous pad at the posterior end.

Fig. 4.—Ephemeroptera, a nymph of *Iron* from the Kangra Valley (p. 188). × 3. Showing the gill-lamellæ forming a rim round the ventral surface of the body and the positions of their spinous pads.

Fig. 5.—Odonata, larva of *Ictinus rapax* from S. India (p. 183). × 2. Showing the six pairs of spinous pads.