

# STRUCTURAL MODIFICATIONS IN THE FISH OF MOUNTAIN TORRENTS.

By SUNDER LAL HORA, *M.Sc.*, Assistant Superintendent,  
*Zoological Survey of India.*

## CONTENTS.

	PAGE
Introduction	31
Conditions affecting fish in rapid waters	34
Modifications for life in hill-streams	35
The external form	35
The scale-covering, etc.	36
The paired fins and the skeletal and muscular structures connected therewith	36
The caudal fin and its peduncle	40
The mouth, its position and shape; the jaws; the barbels; the lips and their muscles	41
The eyes	42
The gill-opening, branchiostegal rays and membranes	43
The air-bladder	43
Special modifications of the skin	44
The minute structure of the adhesive apparatus	47
Cyprinoidea	47
Siluroidea	51
Conclusion	58
Origin of the hill-stream fauna	58
Means of dispersal	60
Methods of propagation	61

## INTRODUCTION.

Although in recent years considerable advance has been made in the study of animal adaptations to different types of environment, little attention seems to have been paid to the wonderful modifications exhibited by the fauna of mountain torrents. Except for a few casual remarks found in descriptions of hill-stream fishes, no detailed account, so far as I know, has been published of the subject. Nikolsky<sup>1</sup> in 1891 published a paper dealing with the correlation between the shape of the body of fishes and the strength of the current of streams and Annandale,<sup>2</sup> in two recent papers, has described some adaptive features in the fauna of hill-streams. Nikolsky's paper is unfortunately in Russian and is not available in Calcutta. From Annandale's papers I have received much help. Dr. Annandale has visited a large number of hill-streams in India and elsewhere, and was greatly impressed by the interesting adaptations exhibited by the various groups

<sup>1</sup> Nikolsky, *Rev. Soc. Nat. S. Petersb.*, pp. 137-139 (1891).

<sup>2</sup> Annandale, *Rec. Ind. Mus.* VIII, pp. 29-32 (1912), and *ibid.*, XVI, pp. 113-117 (1919).

of animals inhabiting these streams; it was at his suggestion that the work here published was undertaken.

Apart from their natural position in the animal kingdom, hill-stream fishes may be divided bionomically into two primary groups. The first group comprises those forms that migrate upstream at certain periods of their lives for spawning, etc.; these may be called the temporary inhabitants of these streams. Fishes of this group travel against the current by muscular effort and do not show, to any great extent, special modifications for life in rapid waters. The members of the second group are the permanent residents of the streams and of still smaller torrents and many exhibit extreme adaptations. It is with the latter group that the present paper is concerned.

The greatest handicap in dealing with the subject was the paucity of material available in the Museum or to be obtained from the streams. Species of many of the genera dealt with in this paper were not only poorly represented, but the specimens often consisted of old and badly preserved individuals quite unfit for detailed morphological investigation. In the hill-streams, on the other hand, there may be plenty of fish, but the readiness with which they seek shelter underneath stones or the swiftness with which they dart away makes it extremely difficult to obtain a good series of specimens. Most of the species are, therefore, known from very few individuals. Through the kindness of the Director, Zoological Survey of India, I was allowed to make tours in the Naga Hills, the Manipur Valley, the Khasi Hills, the Kumaon Hills, the Kharagpur Hills and the Darjiling Himalayas. Good collections were made at all these places. For histological investigation the material, wherever practicable, was fixed either in formol-alcohol or corrosive sublimate; haematoxylin and eosin have chiefly been used in staining sections of the adhesive apparatus.

The taxonomy of the Indian hill-stream genera has hitherto been involved in a state of great confusion and this factor greatly impeded the progress of my work. In a series of papers,<sup>1</sup> chiefly dealing with hill-stream forms, I have tried to elucidate the taxonomy of those genera of which sufficient material was present in the collection of the Indian Museum, and I have also worked out completely the collections made by myself in Manipur<sup>2</sup> in order to find out the correct names of the fishes with which this paper is concerned. Besides these I have published recently a paper on some rare and new forms kindly sent to us by Mr. G. E. Shaw from the base of the Darjiling Himalayas. In interpreting the generic position and specific limits of the various species assigned by Day to *Erethistes* and *Psilorhynchus*, I have derived great help from this collection.

---

<sup>1</sup> Hora, *Rec. Ind. Mus.* XXIX, pp. 195-215, pls. x, xi (1919); *ibid.* XXII pp. 13-19, *ibid.*, XXII, p. 633, pl. xxiv-xxvi (1921).

<sup>2</sup> Hora, *Rec. Ind. Mus.* XXII, pp. 165-214 (1921).

The figures illustrating this paper were drawn by me with the help of a camera lucida.

The types selected for the study of hill-stream adaptations belong to the two chief orders of Indian freshwater fishes, the Cyprinoidea and the Siluroidea. The genera on which observations have been made are the following :—

## Cyprinoidea.

*Balitora* Gray.  
*Bhavanaia* Hora.  
*Psilorhynchus* McClelland.  
*Parapsilorhynchus* Hora.  
*Garra* Ham. Buch.

## Siluroidea.

*Erethistes* Mull. & Trosch.  
*Glyptosternum*<sup>1</sup> McClelland.  
*Pseudecheneis* Blyth.  
*Glyptothorax*<sup>1</sup> Blyth.  
*Laguvia*<sup>2</sup> Hora.

All these genera are found only in small mountain torrents, with the exception of certain species of the genus *Garra* which descend into streams of fair size. All show special adaptations to this environment.

The Schizothoracinae and some of the species of *Nemachilus* which live in rapid-running rivers show similar but less well-marked adaptations. Some remarks on the nature of the adhesive apparatus of these forms are also included in this paper.

---

<sup>1</sup> While recently attempting to revise the species of the genus *Exostoma* Blyth, I have found that this generic name cannot be employed for the forms to which it is usually assigned. I propose the following changes in view of the facts given below :—

*Exostoma* Blyth = *Glyptosternum* McClelland.

*Glyptosternum* McClelland = *Glyptothorax* Blyth.

McClelland (*Calcutta Journ. Nat. Hist.* II, pp. 584-585, and 587-588, 1842) described five species, *Glyptosternon reticulatus*, *G. sulcatus*, *G. striatus*, *G. pectinopterus* and *G. labiatus* under the new generic designation *Glyptosternon*. Blyth (*Journ. As. Soc. Bengal* XXIX, pp. 153-155, 1860) split up these five forms into four distinct genera, *Glyptosternon*, *Pseudecheneis*, *Glyptothorax* and *Exostoma*. He regarded *G. reticulatus* from Afghanistan as the type-species of McClelland's *Glyptosternon*. According to McClelland this species is stated to be "without spines; the first ray of the pectoral and ventral fins soft and pinnate, giving off soft pointed cartilaginous rays along the anterior margin; which are enveloped in the membrane of the fin. The under surface and anterior portion of the body form a flat corrugated surface." Of the several species of *Exostoma* in the collection of the Indian Museum, all except *E. berdmorei*, possess the outer ray of the pectoral and the ventral fins similar to that of McClelland's *Glyptosternon reticulatus*; they ought, therefore, to be included in the same genus. *Exostoma berdmorei*, Blyth, which is known from a single specimen from Tenasserim, now in a very bad condition, is the type-species of the genus *Exostoma*. The pectoral spine of this species is totally different from that of the others and corresponds to those forms which were included by Blyth under his genus *Glyptothorax*. The absence of a "pectoral disk," which led Blyth to separate the genus *Exostoma* from *Glyptothorax*, is not a valid generic distinction, because the thoracic adhesive apparatus of almost all the species included in the genus *Glyptothorax* may become indistinct in specimens which are old or have been badly preserved.

The generic name *Glyptosternon*, McClelland was latinised into *Glyptosternum* by Günther (*Cat. Fish. Brit. Mus.* V, p. 185, 1864).

<sup>2</sup> In a paper published recently (*Rec. Ind. Mus.* XXII, p. 739, 1921) I have given reasons for separating *Erethistes asperus* (McClelland) (*Calcutta Journ. Nat. Hist.* IV, p. 404, pl. xxiv, fig. 2) along with the two new species from the base of the Darjiling Himalayas from the genus *Erethistes* and have placed them all in a new genus *Laguvia*. This genus is intermediate in certain respects between *Erethistes* and *Glyptothorax*.

## CONDITIONS AFFECTING FISH IN RAPID WATERS.

The conditions that influence the fauna of hill-streams are the following :—

(i) The chief factor is the strength of the current, and all the remaining conditions are due to it. The adaptations which are dealt with further on are all due primarily or secondarily to this one cause. The rate of flow of water varies considerably according to the season, but throughout the year its average flow is much higher than that of any stream in level country. This rapid flow of water would render life impossible to many animals if they did not possess special organs of adhesion or other appliances to counteract its influence. In places like Cherrapunji (Khasi Hills), where 458 inches of rain falls in a comparatively short time, the rate of flow of the water must at times be extremely rapid, and at such times some even of the most powerful fish cannot withstand it for more than a few minutes. It is unfortunate that I have not been able to collect any precise data to compare the rate of flow of water and the fauna inhabiting it. This is a case in which co-operation between a zoologist and a physicist is called for.

(ii) Next in importance are two factors on which the very existence of the animals depends—food and shelter. In a hill-stream there is always a sufficient quantity of food, but the only type usually available consists of algal slime covering stones and rocks. There is no opportunity for any other type of vegetation to grow, as it is liable to be uprooted and carried away by the strength of the current. In pools and ditches that are sometimes formed on the bank of the streams, there is generally a growth of water-weeds, but these cannot be referred to as rapid streams. Certain fishes such as the species of *Nemachilus* feed on May-fly and Dragon-fly larvae, but this type of food is usually scarce.

As regards shelter, there is plenty of it in a hill-stream for little fish. The species of *Nemachilus*, on the slightest provocation, hide themselves underneath stones. Those who have made collections in the hill-streams know how advantageous it is to run the net among small stones and sometimes to pick up stones in the net, because in this way all those forms which rest underneath stones are netted.

(iii) Hill-streams are never very deep, and their water is usually very clear. Consequently during the day-time the animals have to withstand intense light.

(iv) The water is well aerated as it is constantly in motion.

These conditions do not apply to pools that occur in the course of hill-streams, and the fish-fauna of these pools is very different from that of the rapid current. It is possible that those forms which live in rapid waters are sometimes carried into these pools, but I have never come across any instance in which the typical sluggish-water forms have been found in rapid waters. Species of *Danio*, *Lepidocephalichthys*, *Barbus*, *Barilius* are generally

met with in the pools. Of these genera only smaller forms like *Danio rerio* are usually found, for they alone are able to find during the flood season sufficient shelter underneath rocks and stones. The pools are, however, sometimes inhabited by large species of *Barbus* and *Barilius* which are sufficiently powerful to withstand floods.

#### MODIFICATIONS FOR LIFE IN HILL-STREAMS.

The modifications for life in hill-streams may be considered under the following heading:—

1. The external form of the fish and its size.
2. The scale-covering, etc.
3. The paired fins and the skeletal and muscular structures connected therewith.
4. The caudal fin and its peduncle.
5. The mouth, its position and shape; the jaws, the barbels, the lips and their muscles.
6. The eyes.
7. The gill-openings, branchiostegal rays and membranes.
8. The air-bladder.
9. Special modifications of the skin.

1. *The external form.*—Nikolsky (*op. cit.*) has dealt with this subject but as the text of his paper, which I have not seen is in Russian, I give my own observations in full. The fish with which this paper is concerned all live on the bottom, and the form is so modified as to offer the least resistance to the rapid current. The head and body are greatly flattened and in *Balitora*, *Glyptosternum* and in the most specialized hill-stream species of *Garra* and *Glyptothorax* the form is almost leaf-like. The ventral profile becomes straight and horizontal throughout and the dorsal profile is but slightly arched. The head is usually small and semicircular and the snout is trenchant. The Bornean genus *Gastromyzon* is in shape a typical hill-stream form.

The shape of the body depends upon the strength of the current and any deviation from the characteristic form of the fish is directly proportional to the rate of the flow of water. Thus the form of those fishes that live in places where the intensity of the flow is intermediate between that of a sluggish stream and of a hill-torrent is almost cylindrical, as in *Crossochilus latia*. Confining our attention to the members of the genus *Garra*, one can find all possible gradations in shape between such forms as *Crossochilus latia* and the most specialized hill-stream form such as *Balitora*. *Garra mullya*, one of the most widely distributed forms in the genus, lives in ponds, tanks and sometimes in rapid waters. The specimens collected from ponds and tanks are cylindrical, while those collected from rapid waters are sometimes flattened. Great modification in form is exhibited by *G. lissorhynchus*, *G. kempi* and *G. nasutus*, all of which are known from rapids

in the Eastern Himalayas. In dealing with the fishes of the Manipur Valley I have shown how the fauna of a stream changes within very short limits according to whether the bed is rocky or muddy. Small size is a distinct advantage in hill streams, firstly because the streams are small and secondly because small forms can find more shelter under pieces of rocks and stones during floods.

2. *The scale-covering, etc.*—In those Cyprinid fishes that take to hill-stream life, the lepidosis undergoes considerable modification. In the Schizothoracinae the scales are small and partly buried in the skin or are totally absent except in the anal and scapular regions. If in a normal Cyprinid genus in which the scales are large and imbricate, the hill-stream forms be compared with those from other types of environment, it will usually be found that the scales are greatly reduced on the under surface, and in some cases they disappear altogether. The region of the chest, which is to some extent employed in the process of adhesion, is the first to be modified, and then, with the increased rapidity of the flow of water, more and more of the under surface becomes naked. In two species of *Garra*, *G. abhoyai* and *G. rossicus*, the dorsal surface in front of the dorsal fin is also naked.

The reduction of scales on the lower parts is necessitated by the fact that a plain and smooth surface is necessary in order to allow adherence to rocks. I have not been able to understand why the scales should be reduced on the dorsal surface in *Garra abhoyai* and *G. rossicus*. Both possess a subcylindrical shape and are not among the most specialized hill-stream forms.

3. *The paired fins and the skeletal and muscular structures connected therewith.*—The fins are very plastic structures in the anatomy and they have been employed for various functions by diverse groups of fishes. The modifications of the pectoral fins in Flying-fishes, of the first dorsal fin in Sucking-fishes and of the ventral fins in Gobiidae and Gobiesocidae are a few instances among many. In hill-stream fishes the paired fins are used as organs of adhesion or of locomotion and for both these functions powerful muscles are required. In certain cases they are probably used also for respiration.

The outer rays of the paired fins are employed for the function of adhesion and the number of the inner rays is consequently increased. In *Gastromyzon borneensis* there are as many as 26–28 rays in the pectoral and 20–21 in the ventral fins. In an allied Indian genus, *Balitora*, there are 21 rays in the pectoral and 11 in the ventral fins. The outer rays of these fins are greatly thickened and much flattened.

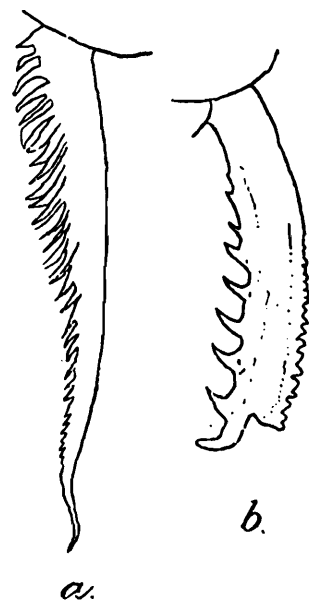
Besides an increase in the number of fin-rays of the paired fins, their position and shape undergoes considerable change. The fins, instead of being situated on the under surface of the fish, are pushed outwards and ultimately are placed horizontally on the sides of the body. This change is brought about for two reasons, firstly to allow the ventral surface to be firmly applied to rocks, and secondly to enable the fins to act as organs of adhe-

sion. As regards the shape of the fins, some of the inner rays are directed upwards against the sides of the body, so that when the outer rays are used for the purpose of adhesion, the inner rays can be kept constantly in motion, probably for the purpose of respiration. I have embodied my observations on this point in an immature specimen of *Psilorhynchus* in a former paper.<sup>1</sup> In the genus *Glyptosternum* (fig. 8) only a few rays of the paired fins are visible from the under surface, while the remainder are reflected upwards. I have not observed these fishes in nature, but on a recent tour to the base of the Darjiling Himalayas, I was able to verify the observation that I had previously made on the immature specimens of *Psilorhynchus* from the Naga Hills, by keeping a half-grown specimen of *Garra annandalei* in an artificial pond of water in the course of the Mahanadi River. In *Parahomaloptera microstoma*<sup>2</sup> the shape of the fins is somewhat less modified than is the case in *Glyptosternum*.

The greatest specialization as regards fin-structure is found in *Gastromyzon borneensis*. The pectorals begin with a long base, vertically below the eyes: the ventrals possess long curved bases, which are united posteriorly. Between the bases of the ventral and the pectoral fins there is a lateral extension of the abdominal skin. "By this arrangement the whole flattened abdominal surface, together with the fins and the flattened lower surface of the head forms an enormous suction disc."<sup>3</sup>

I have already pointed out that the outer rays or the spines, as the case may be, of the paired fins are greatly flattened. Interesting modifications take place in the outer ray of these fins in the genus *Glyptosternum*, "soft pointed cartilaginous rays" are given off along the anterior margin (fig. 1a) to support the striated skin which forms the adhesive apparatus. This is described in detail below when dealing with the modification of the skin in the formation of the adhesive apparatus.

The pectoral and the pelvic girdles are modified in certain hill-stream fishes, owing to the acquisition of new functions by the paired fins. It is unfortunate that I have not been able to study these structures in *Psilorhynchus*, *Bhavaniana*, *Balitora* and *Homaloptera*, on account of the paucity of



TEXT-FIG 1.—Pectoral spine of *Glyptothorax* and *Glyptosternum*.

- a. Outer pectoral ray of *Glyptosternum labiatum*.  
 b. Pectoral spine of *Glyptothorax berdmorei*.

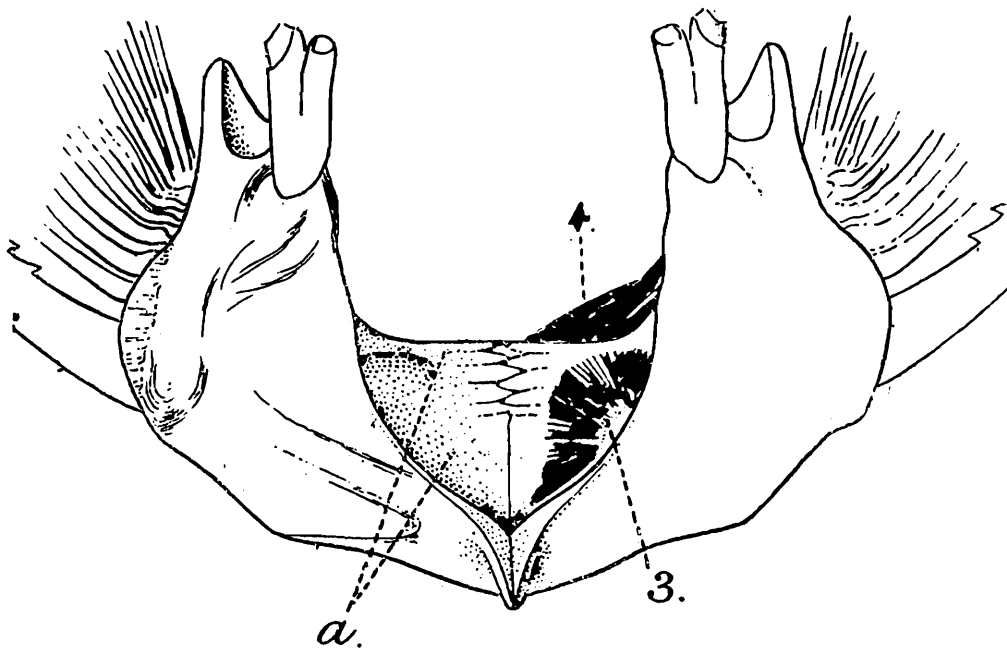
<sup>1</sup> Hora, *Rec. Ind. Mus.* XIX, p. 212 (1920).

<sup>2</sup> Weber and Beaufort, *Fishes Indo-Austr. Arch.* III, p. 20, fig. 5 (1916).

<sup>3</sup> Weber and Beaufort, *ibid.*, p. 2 (1916).

material; but even in those Cyprinid genera of which material was available in sufficient quantity, I am unable to find any striking modifications. In *Garra*, for instance, the whole structure is more or less similar to that found in *Labeo*, except that the adductor and abductor systems of muscles are better developed. At the same time it must be remembered that the fins do not form the chief organs of adhesion in this genus.

In the Siluroids, *Glyptothorax* and *Pseudechencis* in which the chief adhesive organ is situated on the chest, the only modifications consist in the fusion of the various bony elements for strengthening of the girdle. On account of the horizontal position of the fin, the shape of the girdle is considerably changed (fig. 2).



TEXT-FIG. 2.—Dorsal view of the pectoral girdle in *Glyptothorax madraspatanus*.

*a* = interclavicle; 3, 4 = muscles of the pectoral spine.

Great difficulty has been experienced in adopting suitable terms for the description of the various structures. I have followed Parker<sup>1</sup> in preference to McMurrich<sup>2</sup> in drawing up my descriptions.

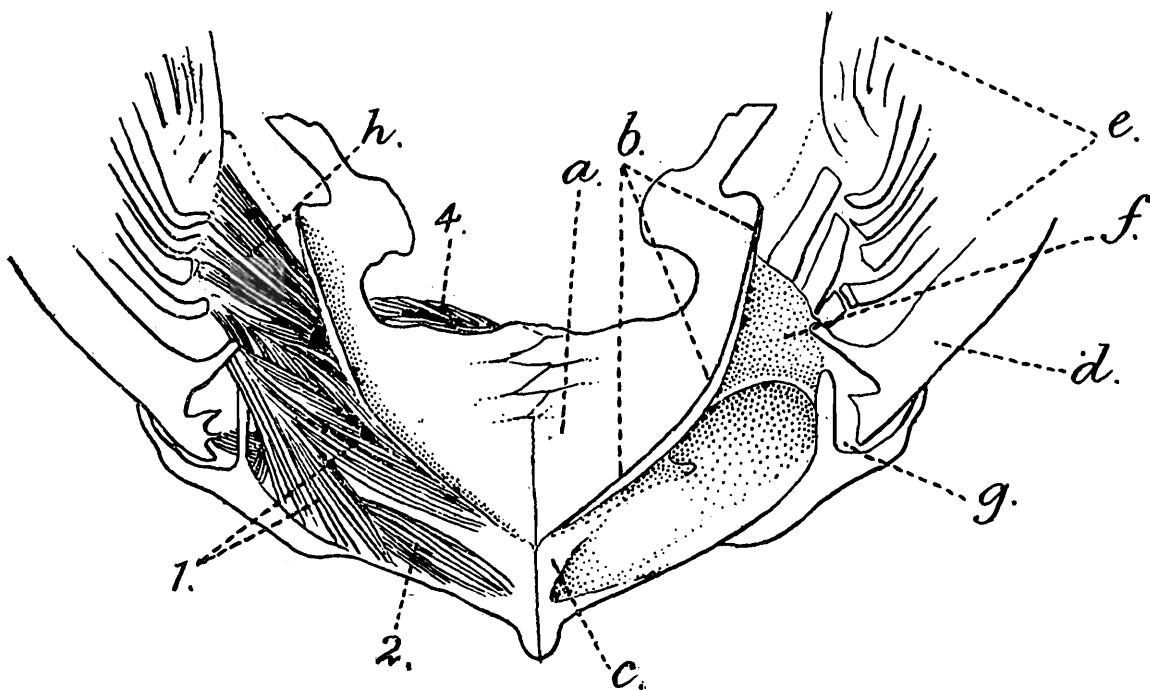
Besides the modifications enumerated above, other characteristic specializations are also found in *Glyptothorax* and *Pseudecheneis*. On the ventral aspect of the interclavicular bones (fig. 3) there are keel-like ridges (fig. 3*b*) for the attachment of the muscles. These ridges are greatly elevated posteriorly and end in spine-like processes; but they slope down anteriorly and meet each other in the mid-ventral line close to the union of the clavicles and the interclavicles.

<sup>1</sup> Parker, *A Monograph of the structure and development of the Shoulder girdle and Sternum in the Vertebrata* (1868)

<sup>2</sup> McMurrich, *Proc. Canadian Inst. (n.s.)* II, pp. 301-306 (1884).



The muscles controlling the movement of the pectoral fin (figs. 2, 3) in *Glyptothorax* are also interesting. Besides the abductor



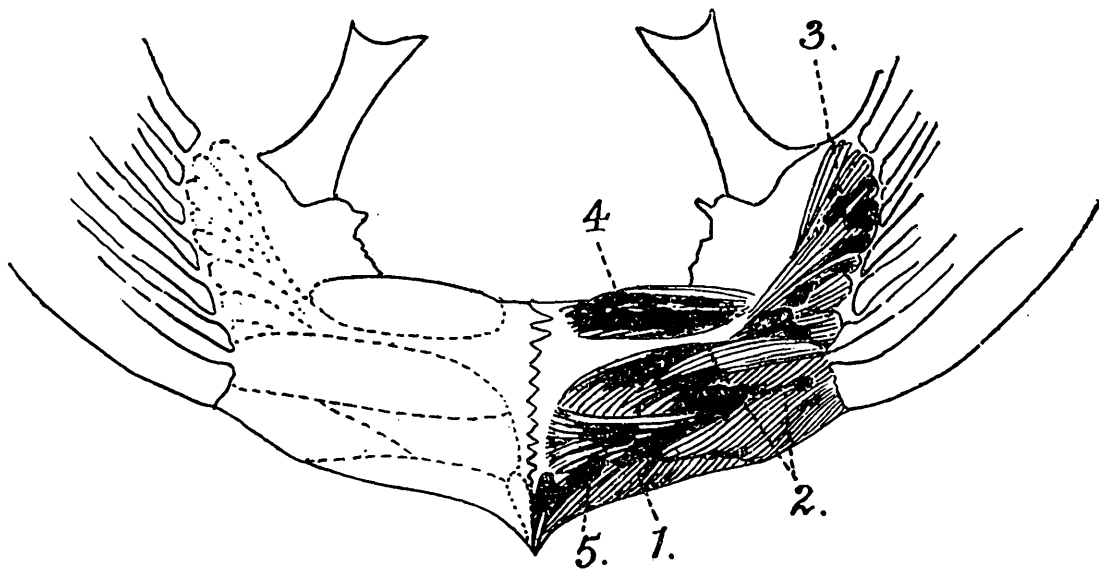
TEXT-FIG. 3.—Ventral view of the pectoral girdle in *Glyptothorax madraspatanus*.

*a* = interclavicle; *b* = interclavicular ridge; *c* = clavicle; *d* = pectoral spine; *e* = pectoral fin rays; *f* = groove for the attachment of abductor muscles; *g* = groove in the cubito-humeral process; *h* = abductor muscles; 1, 2 and 4 refer to the muscles of the pectoral spine.

and the adductor systems, there are four special muscles to move the spine. Muscle 1 arises from the anterior grooved and thickened border of the clavicle and also from along its posterior border near the base of the interclavicular ridge against the sides. Its action is to pull the spine towards the body and fold the rays. Muscle 2 takes its origin from the anterior border of the clavicle, further forward than muscle 1. In its course, it passes underneath muscle 1 and its function is that of expanding the fin. Muscle 3 is very extensive and fan-shaped. It arises along the whole of the surface of the clavicle and the interclavicle on the dorsal side and in its course passes through a bony canal. Its action is the same as that of muscle 2. Muscle 4 is very strong and passes through a passage in the bone. The muscle takes a curved course and its action is somewhat like that of a rope passing over a pulley. Its function is that of folding the fin. It arises from the grooved and thickened posterior border of the clavicle.

The actions of the various muscles were studied by moving the muscles and by watching their effect upon the fin. It is clear that muscles 1 and 4 are stronger than 2 and 3, because it is in the action of folding of the fin that the adhesive function of the outer rays is involved. In those species of *Glyptothorax* in which the adhesive apparatus is present on the under surface of the pectoral spine, muscle 1 is the better developed.

In the genus *Glyptosternum*, where the fins act as organs of adhesion, the modifications in the musculature are more marked (fig. 4) and the arrangement is different. The muscle labelled 2 in *Glyptothorax* correspond to 5 in *Glyptosternum*; muscle 4 is the same in both cases. Muscle 1 arises close to the mid-ventral suture of the clavicle and is inserted in the form of a glistening tendon on the anterior border of the pectoral spine. Its action is to expand the fin. Muscle 2 arises near the mid-ventral line and is inserted on the bases of the spine and the first few rays. Its function is, in all probability, to keep the spine and the few outer rays closely pressed against the substance on which the fish may be resting. This muscle is large and is not found in any other genus that I have studied; it has no other muscles to counteract its action.



TEXT-FIG. 4.—Muscles of the pectoral fin in *Glyptosternum labiatum*.  
Numbers 1, 2, 3, 4 and 5 indicate the muscles referred to in the text.

As regards the skeleton of the pectoral girdle in *Glyptosternum*, there are no bony ridges for the insertion of muscles. Otherwise it is very similar to that of *Glyptothorax*.

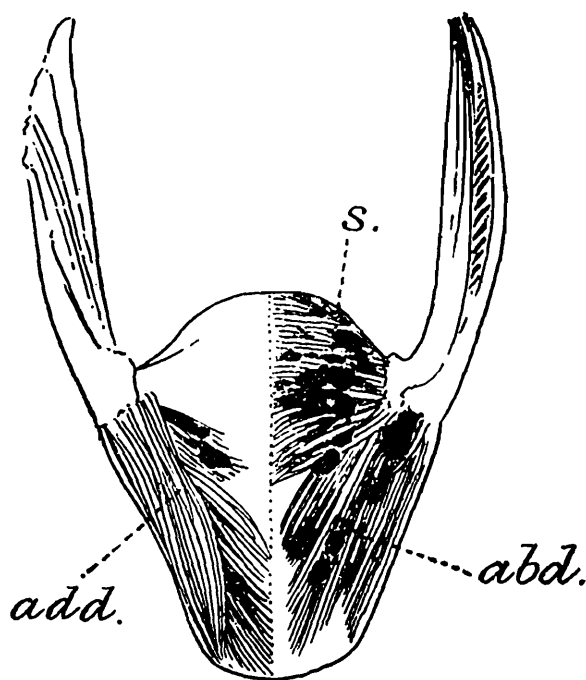
The pelvic fins also possess a special muscle (fig. 5) beside the abductor and adductor systems. This keeps the fins closely pressed against rocks, when the fish is resting, thus enabling it to adhere to rocks by means of striated skin on the under surface of some of the outer rays of the pelvic fin.

4. *The caudal fin and its peduncle*.—There is a general tendency amongst hill-stream fishes to possess a long, narrow, band-shaped caudal peduncle. For example in *Nemachilus tenuis* and *N. lhasae* the caudal peduncle is more narrow and elongated than in any other species of the genus that I have seen. These two species resemble the Central Asiatic forms figured by Herzenstein<sup>1</sup> and it is possible that these features are correlated with high

<sup>1</sup> Herzenstein, *Wiss. Res. Przewalski Central. As. Reis.*, Theil III (2), pls. i-vii (1888).

altitudes and rapid running streams. Similarly in the genus *Glyptothorax*, two species, *G. striatus* and *G. saisii*, from the Khasi and the Parasnath Hills respectively, have a different form of caudal peduncle from the remaining species. It is long and narrow. In almost all species of *Homaloptera*, *Bhavana* and *Balitora* and in the most specialized species of the genus *Garra* the caudal peduncle is similarly modified.

As regards the fin, the chief modification consists in the inequality of its lobes. In most cases the lower lobe is somewhat longer than the upper, as in *Balitora brucei*, *Bhavana australis*, *Glyptothorax striatus*, *Glyptosternum labiatum* and *Garra nasutus*. In *Gastro-*



TEXT-FIG. 5.—Muscles of the pelvic fins in *Glyptosternum labiatum*.

The right side of the figure shows the ventral view and the left side the dorsal view of the pelvic girdle. *add* = adductor muscles; *abd* = abductor muscles; *s* = special muscle.

*tromyzon borneensis*, though the caudal fin is not deeply forked, the lower portion is longer and stronger than the upper.

I was not able to follow the true significance of these modifications, because the movements were too rapid for detailed analysis.

It may be pointed out in this connection that in Elasmobranch fishes, where the mouth is on the under surface considerably behind the tip of the snout, the lower lobe of the caudal fin is much shorter than the upper. I hope to make further observations on this point on another occasion.

5. *The mouth, its position and shape; the jaws; the barbels; the lips and their muscles.*—The mode of life and the nature of food in mountain-rapids necessitates a change in the position of the mouth and the structure of the jaws. The mouth, instead of being a transverse cleft at the anterior end of the fish, is situated on the under surface considerably behind the tip of the snout. It is usually crescentic or semicircular in outline. The jaws are greatly strengthened and their edges become sharp and cutting. In most cases, *Oreinus* for example, the jaws are covered with a strong horny covering. This is due to the fact that hill-stream fishes have to strip algal slime from stones for their food.

Barbels in rapid-waters would be a source of great encumbrance and, therefore, they are much reduced. In most of the hill-stream species they can only be made out after a careful examination.

In *Balitora* they are short and stumpy and liable to be overlooked. In the remaining hill-stream genera discussed in this paper they are short and thread-like. In *Parapsilorhynchus*, however, they are short and cylindrical.

In *Nemachilus* and the Homalopterid genera the lips are so modified as to form a sucker with the help of the mouth, and consequently they exhibit diverse modifications and specializations. In the genus *Nemachilus* the lips are divided in the middle and are greatly swollen, so that when they are pulled outwards away from the mouth, their divided parts form a continuous ring-like sucker. In most cases the skin of the swollen region is plicated, but I have not been able to find any trace of definite spines such as will be described later in the structure of the adhesive apparatus of other genera. I have already described in a previous paper<sup>1</sup> the way in which, by the action of certain muscles, the lips of *Bhavanaia annandalei* are converted into a sucker. In *Balitora* the thick lips are cut up into several tentaculate processes and when pulled apart they form an effective sucker. In most of the species of the genus *Glyptosternum* the lips are "reflected and spread continuously round the mouth, so as to form a broad flat sucker." Similar modifications occur in certain of the most specialized forms of the genus *Glyptothorax*.

6. *The eyes*.—With the flattening of the form in hill-stream fishes the eyes are more and more pushed towards the upper surface. In forms like *Balitora brucei*, *B. maculata* *Glyptothorax saisii*, *G. striatus*, *Pseudecheneis sulcatus* and in almost all species of the genus *Glyptosternum* the eyes are situated on the dorsal surface and are placed close together. Besides this change in position, they are much reduced in size. To what cause this reduction is due, I do not know; but it is quite probable that the intensity of the light in the clear shallow waters of the hill-streams may have something to do with it.

7. *The gill-openings, branchiostegal rays and membranes*.—With the employment of the under surface for the purpose of adhesion to rocks and stones, the gill-openings are generally restricted to the sides. Except in the genera *Glyptothorax* and *Laguvia*, the gill-openings, in almost all the genera dealt with in this paper, do not extend beyond the base of the pectoral fin on the under surface. In certain species of *Garra* the openings are somewhat wider, but even in them they are separated from each other by a considerable distance. The greatest modification as regards this character has taken place in two species of *Glyptosternum*. In these the gill-openings are situated above the base of the pectoral fin and there is a short narrow passage from the interior of the gill-chamber to the exterior.

With the restriction of the gill-openings to the sides, it is natural to suppose that respiration will suffer to some extent. Moreover, when a fish is feeding on the algal slime, the under

<sup>1</sup> Hora, *Rec. Ind. Mus.* XIX, p. 203, pl. x, fig. 2.

surface of the head and body are firmly and closely applied to the rock to which it may be clinging at the time, and this also will make respiration difficult. In all probability the following factors help hill-stream fishes in respiration :—

(i) The water in the hill-stream is better oxygenated and is purer than that of a sluggish stream in a flat country.

(ii) By reducing the gill-openings, the fishes are enabled to retain water in their gill-chambers for a comparatively longer time.

(iii) The inner rays of the pectoral fins in fishes of rapid streams are held in constant motion when the fish rests against a piece of rock. The movements of these rays may help respiration in two ways :—

(a) The blood may be oxygenated in the rays themselves, or (b) they may force water in and out of the gill-opening.

The following quotation from Mr. Chapin's notes given by Nichols and Griscom<sup>1</sup> on the mechanism of respiration in *Enchilichthys dybowskii* (Vaillant) when clinging to rocks is very interesting :—“ Two examples were brought alive in a basin where they stuck fast to the smooth enamel surface. When thus attached, the water for respiration enters by the back of the mouth, and the movement of the gills often makes the whole fish quiver or move slightly back and forth. Natives say they cling to rocks and eat algae. They can swim rapidly. The mouth is here drawn as though slightly extended, while sucking, it of course contracts.” The above observations were made on fishes in a state of captivity and require confirmation. The sucker by means of which the fish adheres appears from the figure to surround the mouth completely and it is probable that the fish uses both lips for adhesion as in the Indian hill-stream forms. The posterior jaw is in almost all cases more highly specialized for rasping the algal slime from the rocks than the anterior jaw and under the circumstances detailed above, it seems highly improbable that water can enter the gill cavities from the back of the mouth when the fish is either feeding on algal slime or clinging to a rock.

With the reduction of the gill-openings and the backward shifting of the mouth on the under surface considerably behind the tip of the snout, the branchiostegal rays and membranes are greatly reduced. Usually these structures on the two sides of a fish such as *Labeo rohita* meet and overlap on the under surface, but in hill-stream fishes, with the exception of those belonging to the genera *Glyptothorax* and *Laguvia*, they form an obtuse angle on the under surface, if they meet at all.

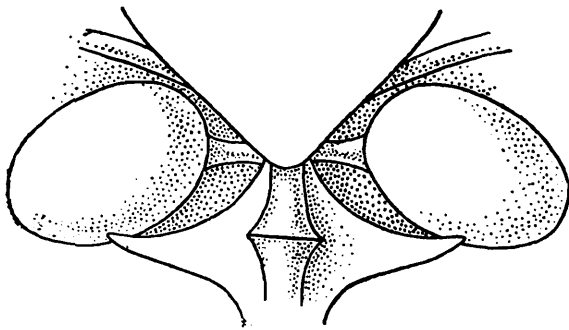
8. *The air-bladder.*—The bladder in the hill-stream forms shows considerable degeneration and in 1893 Bridge and Haddon<sup>2</sup>

<sup>1</sup> Nichols and Griscom, *Bull. Amer. Mus. Nat. Hist.* XXXVII, p. 720, pl. lxxvi, fig. 3 (1917).

<sup>2</sup> Bridge and Haddon, *Trans. Phil. Soc. London*, vol. 184, part I (B), p. 305 (1893).

attributed the reduction to the following causes, which bear repetition even to-day. They say:—"The causes that have led to the degeneracy of the air-bladder in so many forms are in many instances not difficult to trace, and, as in so many Physoclist Teleostei, the assumption of a purely ground habit of life is probably the most important one. Not a few of the genera of Siluridae abnormales inhabit the comparatively shallow waters of rapidly flowing mountain streams and torrents often living at a considerable altitude, and in general habit are not unlike our common English Loaches. Many are provided with an adhesive apparatus on the ventral surface of the body between the pectoral fins for attachment to stones, so that they may be enabled to withstand the force of mountain torrents. Such fishes when not in motion by the exercise of their fins probably rest upon, or attach themselves to, the river bottom, and the utter uselessness and probable harmfulness of an air-bladder as a hydrostatic organ under such conditions is no doubt the cause of its degenerate and rudimentary conditions in such Siluroids as *Sisor*, *Pseudecheneis*, *Glyptosternum*, *Eucliptosternum*, *Exostoma*, *Amblyceps*, etc." I have dealt with this interesting organ at some length in my previous paper and have shown in the case of the genus *Garra* that the reduction in the organ is directly proportional to the strength of the current of the streams in which the fish live.

In almost all the highly specialized hill-stream forms such as certain species of Loaches, Homalopterid fishes and the forms



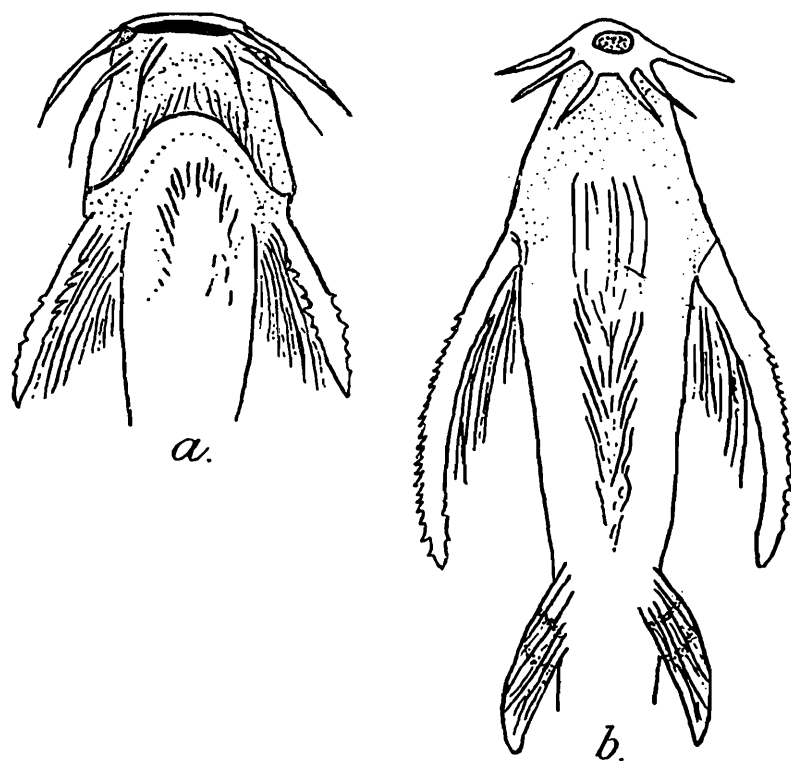
TEXT-FIG. 6.—Air-bladder of *Glyptothorax madraspatanus*.

included under the Silurid genera, *Glyptothorax*, *Glyptosternum* and *Pseudecheneis* the bladder is, divided into two lateral chambers (fig. 6) which are more or less connected with each other by a short, narrow transverse tube. Moreover the bladder is wholly or partially encapsuled by a bony case in almost all cases.

9. *Special modifications of the skin.*—Under this heading I include the diverse forms of modifications exhibited by the skin in the formation of adhesive organs. The simplest form of specialization occurs in Cyprinid fishes, where the skin covering the under surface of the few outer rays of the paired fins is greatly thickened and becomes cushion-like in places. By these cushion-like pads the fishes are enabled to cling to rocks and hold their own against a rapid flow of water. In the Silurid genera the skin instead of being plain is thrown into grooves and ridges. Such striated portions of skin may occur anywhere on the under surface of the fish but are generally found in the anterior third of the body. I have found such striated surfaces on the barbels, on the sides of the mouth,

on the chest between the bases of the pectoral fins and lastly on the under surface of the pectoral and pelvic spines, and I have been able to make out a series showing the gradual specialization of the adhesive apparatus in the Silurid genera.

The genus *Erethistes* comprises small hill-stream forms in which the under surface of the body is smooth and greatly flattened. In one member of the genus, *E. elongata*, the structure is, however, somewhat different. The whole of the chest and the belly (fig. 7, *b*) is rugose and shows low, but well-marked striations. In the forms which I have assigned to my new genus *Laguvia*, these corrugations are restricted to the chest and the belly is quite smooth (fig. 7, *a*). This feature is still further marked in the



TEXT-FIG. 7.—Under surface of head and chest of *Laguvia* sp. and *Erethistes elongata*.

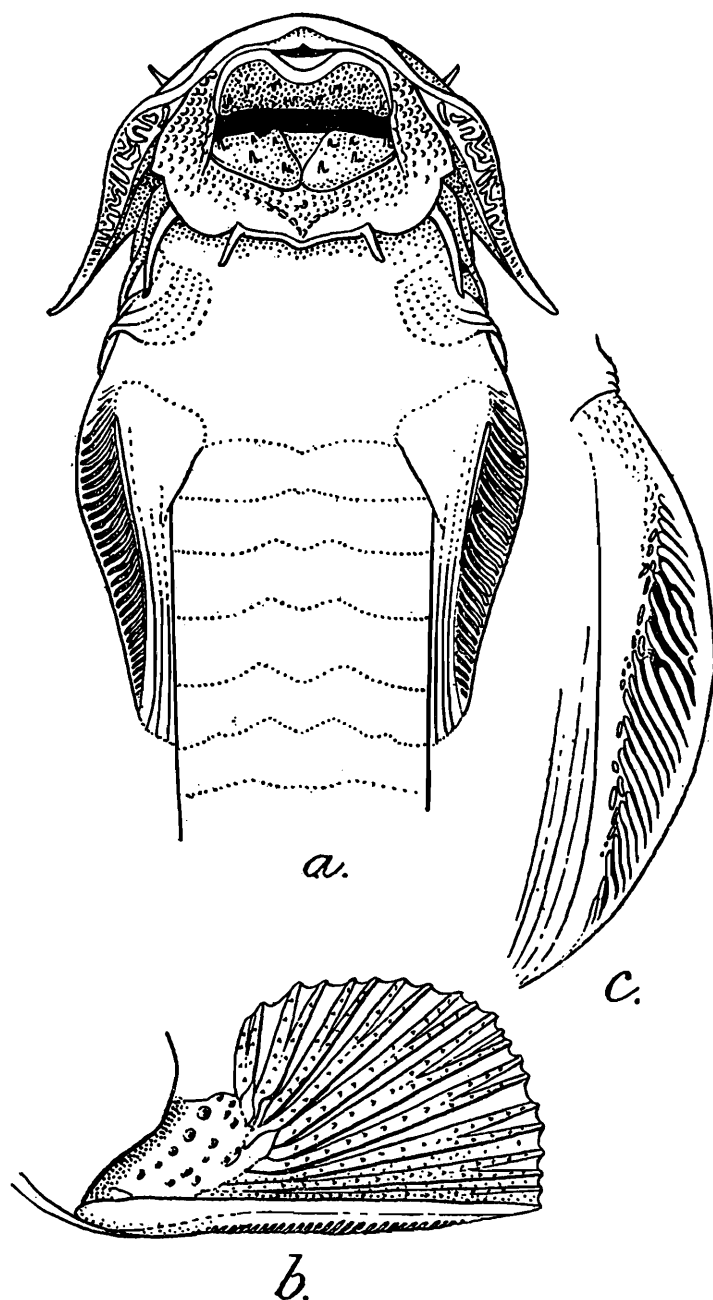
*a. Laguvia* sp.

*b. Erethistes elongata*.

members of the genus *Glyptothorax*, where a definite U-shaped or V-shaped adhesive apparatus consisting of folds of skin is present on the chest between the bases of the pectoral fins. In certain species of the last genus, from very rapid waters an adhesive apparatus of a similar nature is also present on the under surface of the pectoral and pelvic spines. In *Pseudecheneis sulcatus* the skin is somewhat differently modified on the chest, but the striations on the spines of the paired fins are of a similar nature to those of the preceding genus.

Specialization has proceeded along another direction in the genus *Glyptosternum*. Here the skin on the under surface of the spines (figs. 8*a* and *c*) is striated and each ridge is supported by a short, pointed, cartilaginous ray given off from the outer side

of the first pectoral and pelvic rays (fig. 1, *a*). Besides this the striated region is supported by a definite, highly specialized tissue (fig. 16, *s.t.*). The chest is absolutely devoid of any adhesive apparatus. In certain species of the same genus the under surface of the barbels and the skin near their bases is striated (fig. 8*a*).



TEXT-FIG. 8.—Structure and form of the pectoral fins and the position of the adhesive apparatus in *Glyptosternum labiatum*.

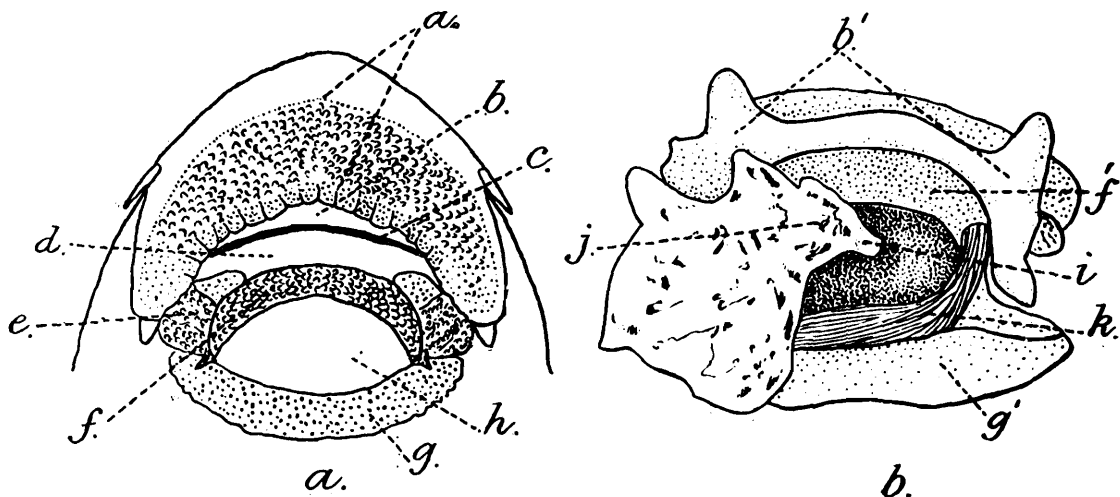
- a.* Under surface of head and chest showing striated skin on pectoral spines and on maxillary barbels.
- b.* Pectoral fin showing reflected inner rays.
- c.* Under surface of pectoral spine highly magnified.

The disc of *Garra* (fig. 9*a*) with its associated structures is an efficient type of adhesive organ. The disc consists of a central callous portion (*h*) and of free tuberculated lateral and posterior borders (*g*). Its anterior border is formed by the posterior labial fold (*f*) which in its development has replaced the



posterior lip. The anterior labial fold (*a*) is fringed and tuberculated and helps the fish in adhering to rocks. A rudimentary form of disc has recently been described by me<sup>1</sup> in *Parapsilorrhynchus discophorus*.

The disc of *Garra* works on the suction principle. In the middle of the under surface of the callous portion, a strong tendon (fig. *gb, i*) is inserted and attached to the urohyal (*j*), so that when the urohyal is elevated, the callous portion of the disc is drawn in and thus a cavity is produced which is surrounded by fringed borders. These fringed and tuberculated borders are provided with efficient organs of adhesion as will be seen later when dealing with the minute structure of the adhesive organs.



TEXT-FIG. 9.—The disc of *Garra* and its associated structures.

*a.* Disc as seen from the under surface.

*b.* Dissection of disc from the dorsal surface to show the mechanism for suction.

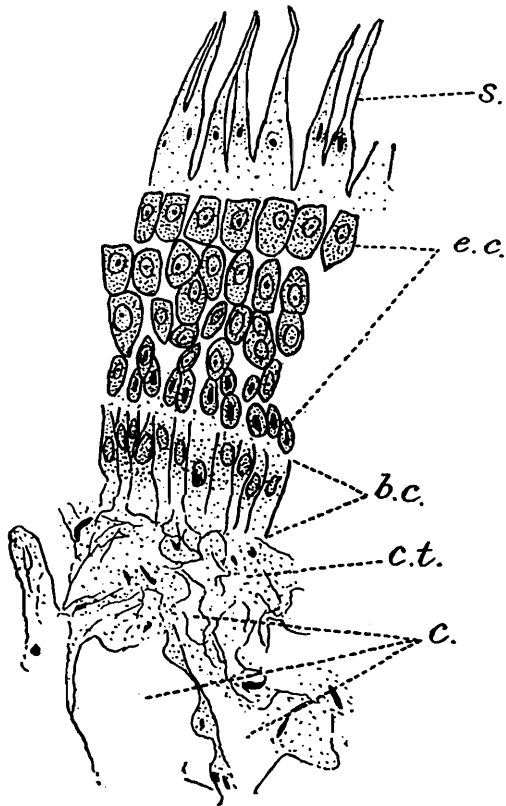
*a* = anterior labial fold ; *b, b'* = anterior jaw ; *c* = mouth opening ; *d* = posterior jaw ; *e* = connectives ; *f, f'* = posterior labial fold ; *g, g'* = free tuberculated border of the disc ; *h* = callous portion of the disc ; *i* = tendon joining the centre of the callous portion of disc with urohyal ; *j* = urohyal ; *k* = muscle joining the two sides of the anterior jaw.

### THE MINUTE STRUCTURE OF THE ADHESIVE APPARATUS.

The simplest form of adhesive apparatus is found among hill-stream fishes of the order Cyprinoidea. It consists of the thickened skin covering the under surface of the few outer rays of the paired fins. In a transverse section of such a structure in *Bhavana annandalei* (fig. 10) the following arrangement may be seen:—The epidermis consists of several tiers of cells, varying in shape and size with their depth and resting on a loose connective tissue (*c.t.*), which constitutes the dermis. The outer epidermal layer is modified into stiff and strong spine-like processes (*s*), which are somewhat curved near their extremities. The inner limit of these processes is not well-defined and they appear to rest

<sup>1</sup> Hora, *Rec. Ind. Mus.* XXII, pp. 13-19, figs. (1921).

upon a homogeneous layer of protoplasm, they occupy as much as one-third of the total thickness of the epidermis and their inner ends are broad. The nuclei of the spines are somewhat oval in outline and are placed in the proximal half; each is surrounded



TEXT-FIG. 10.—Transverse section through a portion of the adhesive pad on the outer rays of the pectoral fin in *Bhavanaia annandalei*.

*s.* = spine; *e.c.* = epithelial cells; *b.c.* = basal epithelial cell; *c.t.* = connective tissue; *c.* = cavities for blood vessels.

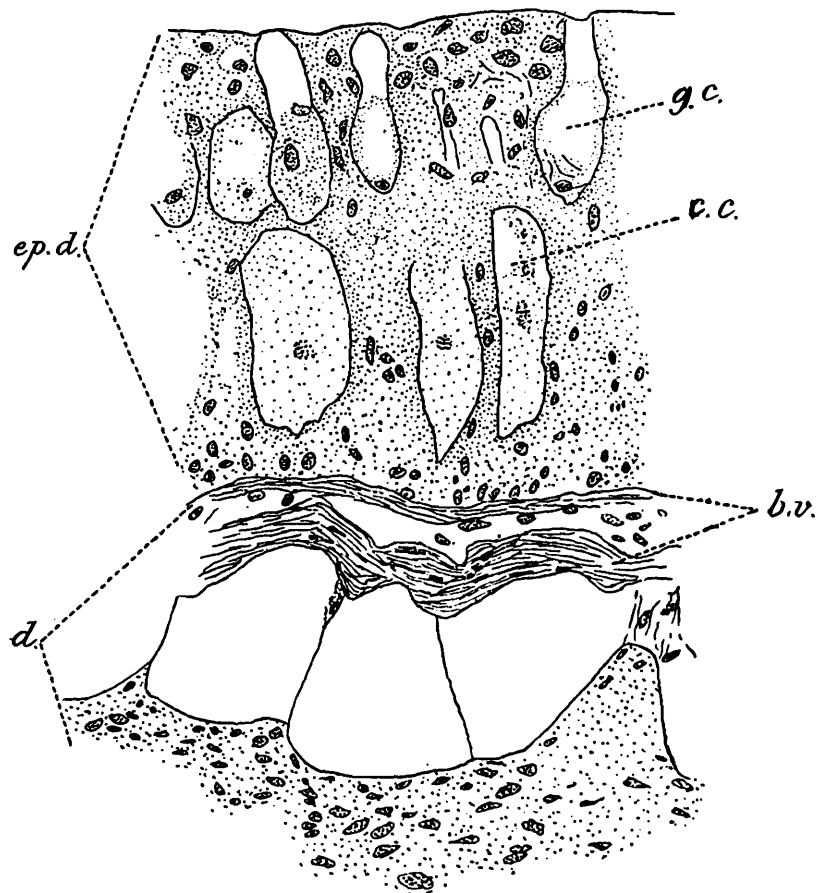
by a whitish halo. The protoplasm of the spine and of the basal homogeneous layer stains lightly with hematoxylin, eosin and borax carmine. The deeper tissue takes up the stain readily. Below the homogeneous protoplasmic layer, the tissue consists of several layers of almost rectangular cells (*e.c.*) each with a distinct nucleus in the centre. The cells diminish in size with the depth of the tissue and become more and more irregular in form and arrangement. The interspaces between them become broader and in certain cells two nuclei are present. Below these and immediately above the basal epidermal layer (*b.c.*) there is a tier of small, more or less regularly arranged cells, the nuclei of which are solid, deeply staining ovoidal bodies. The basal layer of epidermal cells is made up of columnar tissue, the nuclei are oval and lie almost in the middle of the cell, or nearer its upper than its lower ends. The upper as well as the lower limits of the basal cells are hardly distinguishable and both these ends stain lightly. The nuclei appear to be in a state of mitotic division as the chromatin substance in them is greatly diffused.

The connective tissue (*c.t.*) below the basal layer of the epidermis is very loose and is richly interspersed with cavities (*c.*) of the nature of blood-spaces. The nuclei are greatly elongated and stain deeply. The cell-limits in this tissue are not marked and the whole of the tissue is not so deeply stained as the middle layer of epidermal cells.

In the genus *Garra* this form of adhesive apparatus is supplemented by the presence of the characteristic disc behind the posterior jaw on the under surface. Before dealing with the structure of the adhesive disc, I propose to give a short account of that of the integument in this genus.

The deeper tissue takes up the stain readily. Below the homogeneous protoplasmic layer, the tissue consists of several layers of almost rectangular cells (*e.c.*) each with a distinct nucleus in the centre. The cells diminish in size with the depth of the tissue and become more and more irregular in form and arrangement. The interspaces between them become broader and in certain cells two nuclei are present. Below these and immediately above the basal epidermal layer (*b.c.*) there is a tier of small, more or less regularly arranged cells, the nuclei of which are solid, deeply staining ovoidal bodies. The basal layer of epidermal

In a vertical section of the skin (fig. 11) covering the tip of the snout, where scales are of course absent, the epithelial region (*ep.d.*) is made up of a homogeneous mass of protoplasm with a large number of nuclei scattered in it. The nuclei are aggregated either near the base or near the apex of the epithelial region; some of them are surrounded by a white zone. Near the upper surface are present a number of large ampulliform gland-cells (*g.c.*). The protoplasm of the gland-cells is restricted to the periphery or to the base and the nucleus generally occupies the centre of the basal protoplasm. In the middle of the homogeneous epithelial mass

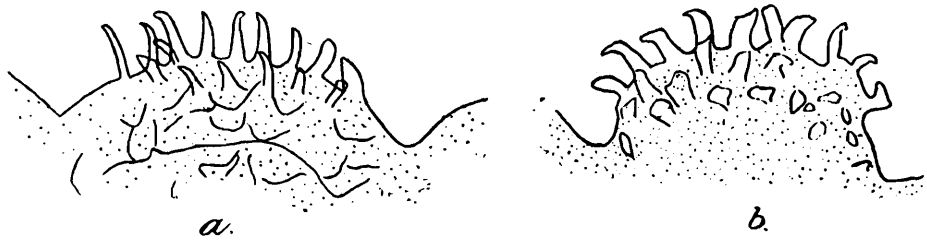


TEXT-FIG. 11.—Transverse section of the integument of *Garra annandalei* from the tip of the snout, x 435.

*ep.d.* = epidermis; *d.* = dermis; *g.c.* = gland-cell; *c.c.* = clavate cell; *b.v.* = blood vessel.

are found big "clavate cells" (*c.c.*) forming as it were a distinct row by themselves. Below the epithelium are blood vessels (*b.v.*) whose walls stain rather deeply with eosin. Underneath the blood vessels are a number of big cavities, which probably represent the adipose tissue. The adipose tissue is said to be present below the skin of most of the fishes, but its presence in this position between the epithelial and dermal regions, is interesting. Below the fat-cells is the connective tissue, which is marked by a large number of nuclei which are not surrounded by a white zone. The cell-boundaries in this region are not distinguishable.

The structure of the mental disc in *Garra* may be treated under two headings, (i) the structure of the central callous portion of the disc and (ii) the structure of its tuberculated borders and of the fringed tuberculated anterior labial fold (fig. 12). The structure of the former is very similar to that of the integument

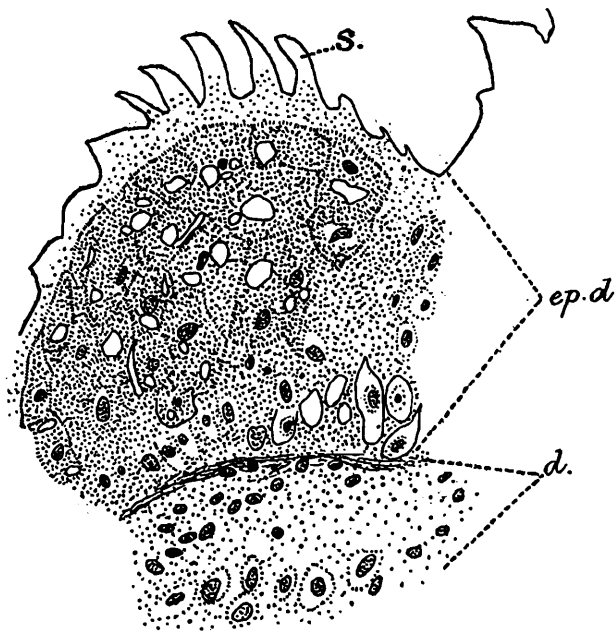


TEXT-FIG. 12.—Structure of tubercles on the disc and the anterior labial fold of *Garra annandalei*.

- a. Tubercle on anterior labial fold.
- b. Tubercle on lateral free borders of the disc.

described above. The following are, however, some salient points of difference:—

- (i) The epithelial cells are better defined and in certain places the ampulliform gland-cells are more numerous.
- (ii) The “clavate cells” are fewer in number and are situat-



TEXT-FIG. 13.—Transverse section through a portion of the tuberculated anterior labial fold of *Garra annandalei*, x 435.

s = spine; ep.d. = epidermis; d = dermis.

ed at great intervals. The protoplasm of these cells has receded inwards from near their upper cell-limits.

(iii) The dermis is chiefly composed of an adipose tissue, which is bounded both above and below by a thin layer of fibrous connective tissue.

The structure of the tuberculated region, on the other hand, is totally different. In a vertical section (fig. 13) of the fringed portion of the anterior labial fold, the superficial epidermal layer covering a tubercle is modified into spines (s). It is perhaps significant that I have not been able to find any nuclei in the spines; the spines are, otherwise, shorter, thicker and stouter than those described in *Bhavania annandalei*. On examining a large number of sections of this region and of the free tuberculated borders of the disc, I have observed that the spine is formed as a prolongation of the outer cell-wall of the superficial epidermal layer. Below the spinous layer, there are several tiers of polygonal cells (*ep.d.*) which are vacuolated. In the basal region the cell-limits are not well marked and the nuclei stand out prominently with haematoxylin stain. In some cells the nuclei are surrounded by a whitish halo. The dermis (*d*) consists of a compact connective tissue, with a large number of nuclei scattered just below the epidermis. The cell-boundaries in this region are not well-defined.

In the region of the posterior labial fold and also in that of the free border of the disc, the tubercles are provided with a dermal plug. The dermis consists of a large number of branched irregular cells, forming a primitive type of connective tissue.

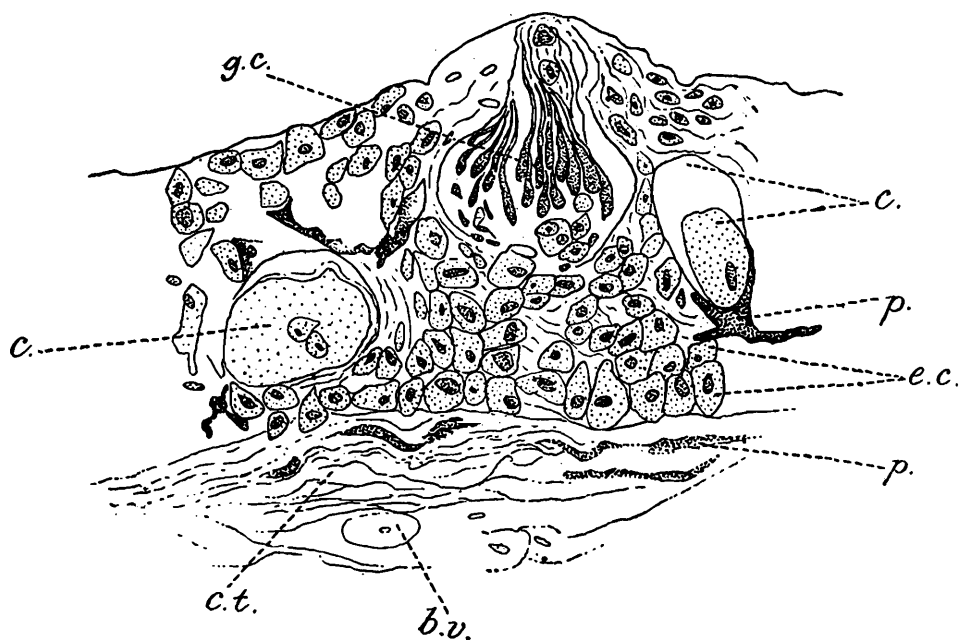
The structure of the tuberculated region in *Garra* differs from that of the integument and of the central callous portion of the disc in the following points:—

- (i) The gland-cells are absent.
- (ii) The "clavate cells" are absent.
- (iii) The superficial epithelial layer of cells is modified into spines which do not possess any nuclei.
- (iv) The adipose tissue is totally absent, and the dermis, therefore, presents a compact, solid structure.

In the order Siluroidea the modification of the skin to form an adhesive apparatus is very different. It is thrown into folds and ridges, which are characterized by a special structure. Any portion of the skin may thus be modified to serve the purpose of adhesion. To illustrate the structure of the adhesive apparatus in Silurid fishes, I will first describe that found in *Glyptosternum labiatum*.

The structure of the integument found in this genus may in the first place be considered. In a vertical section (fig. 14) of the non-striated skin covering the dorso-lateral surface of the pectoral spine, the epithelium consists of several layers of small, more or less flattened and rectangular cells which possess well-marked cell-walls and relatively large oval nuclei. The cells near the surface are smaller than those immediately below them. Their outline varies considerably according to the extent to which they may be packed together in a particular place. Black pigment (*p*) is present at certain places in the tissue. Most of the central space of the epithelium is occupied by a number of big "clavate cells" (*c*), which are distributed at regular intervals and form a distinct layer of their own. They are fairly well developed and

sometimes their nuclei may be as big as an ordinary epithelial cell. The "clavate cell" possesses a distinct cell-wall and in most cases it contains more than one nucleus. The contents of the "clavate cell" are very different from those of the surrounding epithelial cells, as it is only lightly stained with haematoxylin and eosin. The nucleus is surrounded by a whitish area. The most interesting point is the degree of vacuolation that is generally met with in these cells. The process of vacuolation sets in from the outer wall and the protoplasm gradually recedes towards the inner side. In extreme cases more than half of the cell is emptied of protoplasm. I have not been able to make out the structure of the contents of a vacuole. The nucleus is generally vesicular with a distinct membrane and in those cells, which contain only



TEXT-FIG. 14.—Transverse section through the integument of *Glyptosternum labiatum* x 435.

*e.c.* = small epithelial cells; *p.* = pigment; *c.* = clavate cell; *g.c.* = gland-cell; *c.t.* = connective tissue; *b.v.* = blood vessel.

one nucleus, its chromatin matter is diffused as if preparing for a mitotic division. I have not been able to observe distinct nuclear figures in any of these cells. If more than one nucleus is present in a cell, the nucleolus can also be readily made out. Ramsay Wright<sup>1</sup> described these cells in the integument of *Amiuris catus*. He observed, "there can hardly be any doubt that the clavate cells have an important physiological role to play. What that is remains still obscure." I have found these cells in the integument covering the tip of the snout in *Garra* and in the position described above in *Glyptosternum labiatum*; but am unable to understand their exact significance. It may, however, be pointed out that they are always absent in an adhesive tissue in fishes.

The gland-cells in *Glyptosternum* are not scattered as has al-

<sup>1</sup> Ramsay Wright, *Proc. Canadian Inst.* (n. s.) II, pp. 254-255 (1884).

ready been described in the integument of *Garra* ; but are aggregated to form definite structures. Each one of these structures is flask-shaped with the neck almost half as long as its total length. The mouth of the flask along with the adjoining tissue projects slightly above the surface of the integument. The body of the flask is occupied by a number of characteristic cells. The cells are elongated and are drawn out into long, fine processes which travel through the neck of the flask and open on the surface of the skin. The nuclei are very big and occupy almost the whole of the cell. The cells forming this characteristic structure do not begin at the same level and thus present an irregular bunch of cells hanging in the cavity of the flask by means of fine threads. Sometimes one or more epithelial cells make their way inside the flask and when seen they are usually found in the neck region.

It is after long hesitation that I have assigned to these cells the function of secretion. The following are the main reasons for holding this view :—

(i) The unicellular glands, usually present in the integument of fishes, are absent.

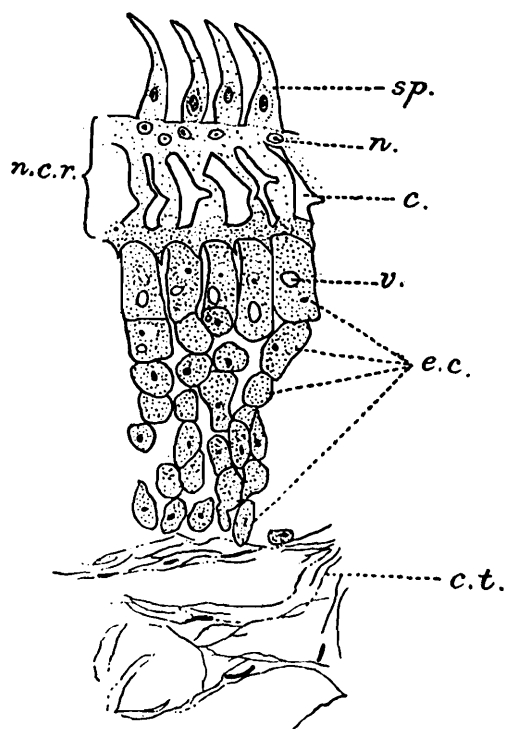
(ii) The mouth of the flask projects beyond the surface of the integument.

(iii) The cells have fine canals which open on the surface of the skin.

(iv) The cells are provided with big nuclei.

Such glandular structures are found at a considerable distance from each other, and I have not been able to find more than three in any one section.

In the structure of the adhesive apparatus (fig. 15) formed by the striation of the skin on the under surface of the pectoral and pelvic spines, a distinct advance is made upon that observed in *Bhavania* and *Garra*. The upper layer of epithelial cells is modified into curved spines (*sp.*), whose inner limits are not well defined. The spines are provided with definite nuclei, which are situated in their lower swollen portions. In the non-cellular region immediately below the spinous layer are a number of deeply staining bodies forming a definite row. What these bodies are, I have

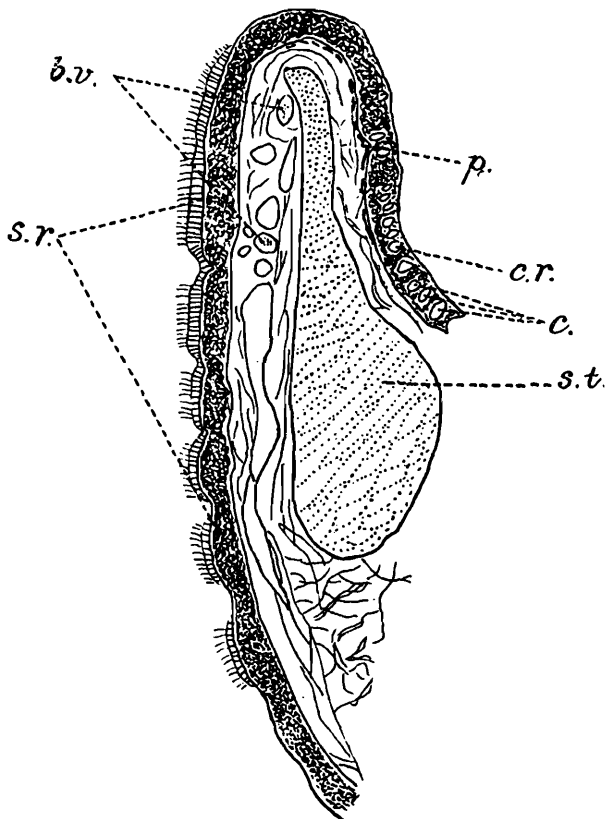


TEXT-FIG. 15.—Transverse section through the striated skin on the under surface of the outer ray of the pectoral fin in *Glyptosternum labiatum*, x 435.

*s. p.* = spine ; *n.* = nuclear bodies ; *n.c.r.* = non-cellular region ; *c.* = cavity ; *e.c.* = epithelial cells ; *v.* = vacuole ; *c.t.* = connective tissue.

not been able to determine definitely. Below the spines is a deep non-cellular layer (*n.c. r.*) in which are scattered a number of spaces (*c*) having a definite shape. They are almost crescentic in outline and possess a short spine-like process along their convex borders. The lower limit of the non-cellular region is formed by a regular wavy line. In the curves of this wavy line are situated a number of characteristic columnar cells. Each is provided with a nucleus, a distinct nucleolus and a small well-marked vacuole (*v*). Between two neighbouring cells there is generally a small chink-like cavity. Below these columnar cells, are a number of small epithelial cells which are irregularly arranged in four to five tiers. Usually they possess small, solid, deeply staining nuclei, but in certain cells the nuclei are altogether absent. Beneath the epithelial tissue is a loose connective tissue (*c.t.*) forming the dermis.

In the genus *Glyptosternum*, the adhesive apparatus is supported by a definite tissue as has already been remarked. The



TEXT-FIG. 16.—Transverse section through the thickened skin covering the pectoral spine in *Glyptosternum labiatum*, x 42.

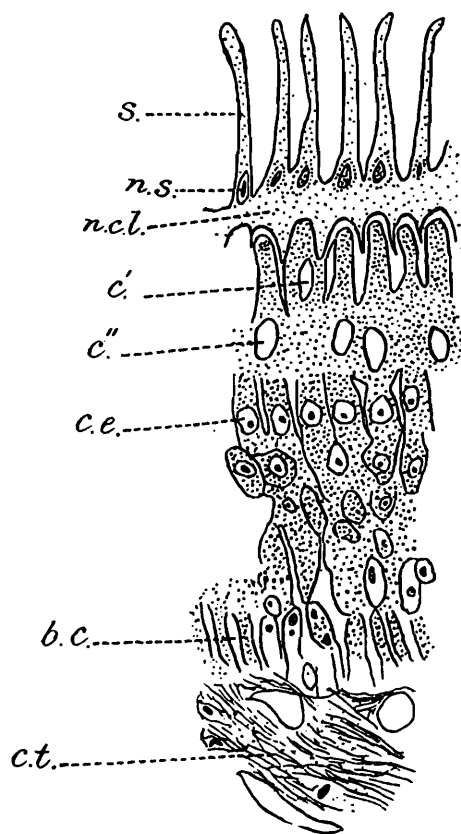
*s.t.* = supporting tissue; *c.r.* = clavate cell region; *p.* = pigment; *s.r.* = striated region; *b.v.* = blood vessel; *c.* = clavate cells.

supporting tissue (fig. 16) consists of a mass of polyhedral cells (fig. 17) which are very turgid and are closely packed together. The nuclei of these cells are fairly large and in certain cases there may be more than one nucleus in a cell. The cells vary in form and size to a considerable extent and towards the base they are so much pressed together that the cell-limits become almost obliterated and the nuclei become spindle-shaped. The supporting tissue (*s.t.c.*) is surrounded by a loose connective tissue (*c.t.c.*).

The structure of the thoracic adhesive apparatus of *Pseudecheneis sulcatus* is different from all the three types described above. The nuclei of the spines are situated in the non-cellular region and the cell-walls in the epithelial region are not well defined. In the cells of the first epithelial layer, immediately below the non-cellular region, there are ill defined vacuoles. The connective tissue is not so loose and is richly dotted with a large number of nuclei of various forms.



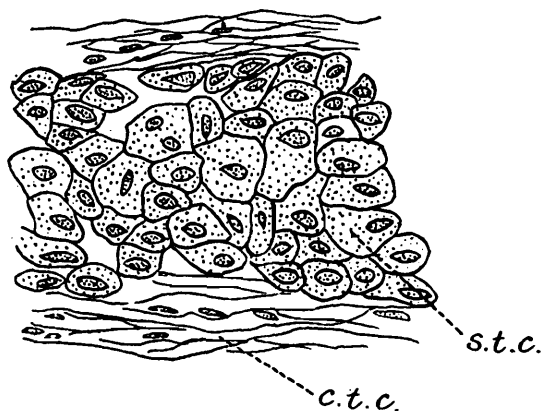
Within the genus *Glyptothorax*, the structure of the adhesive apparatus shows considerable variation. In *G. dorsalis*, a large number of specimens of which were collected in the sluggish and muddy streams of the Manipur Valley, the spines are small and the spinous layer as a whole is not well developed. The epithelium is composed of several tiers of small, squarish cells, of these the uppermost and the basal layers are highly vacuolated. The cell-walls are quite distinct and the basal layer is somewhat columnar. Below the epithelium is a dense sheet of connective tissue, in which are scattered



TEXT-FIG. 18.—Transverse section through a portion of the thoracic adhesive apparatus of *Glyptothorax madrasapatanus*, x 435.

s. = spine; n.s. = nucleus of the spine; n.c.l. = noncellular layer; c. = first row of cavities; c". = second row of cavities; c.e. = columnar epithelium; b.c. = basal cells of epithelium; c.t. = connective tissue.

kind of structure.



TEXT-FIG. 17.—Transverse section through the supporting tissue of the adhesive apparatus on the fins of *Glyptosternum labiatum*, x 435.

c.t.c. = connective tissue cells; s.t.c. = supporting tissue cells.

big cavities full of blood corpuscles. Underneath the connective tissue are fat-cells with eccentric nuclei. In *G. madrasapatanus* the structure (fig. 18) of the adhesive tissue is more advanced in so far as the cell-limits are not distinguishable. Immediately below the non-cellular region there are two layers of cavities (c'.c''); the upper is in the form of elongated spaces with intervening columns of protoplasm, while the second layer consists of rounded cavities in the substance of the protoplasm. Below this the epithelium consists of a row of columnar cells which are followed by a number of small, rounded cells. In the basal epithelial layer I have not been able to find any nuclear structures. The greatest specialization in the structure of the adhesive tissue within the genus is reached in those forms that possess an adhesive surface on the chest as well as on the under surface of the pectoral and pelvic spines. I take *G. sp.* from Madras as an example of this

In a vertical section of the striated skin covering the under surface of the pectoral spine of *G. saisii* (fig. 19, *a*) the structure in all essential points corresponds to that of the previous examples. The spines (*s*) are hooked and more regular; their nuclei (*n.s.*) are situated near the base and each of them is surrounded by a whitish halo. The nuclei project into the non-cellular region (*n.c.r.*). Underneath the non-cellular region there are two rows of cavities or open spaces. The cavities of the first row (*c'*) are greatly elongated, they are broader near the upper than near the lower end. On focussing, a part of the cavity is found to contain a lightly stained protoplasmic substance. The second row of spaces (*c''*) is similar to the first, but here the lower portion of the cavity is filled with protoplasm; the upper margin of each cavity is deeply stained and in the section there appears an interrupted band. Then follow large columnar cells (*c.e.*) which are provided with big nuclei. The nuclei are oval and possess a well-defined nucleolus, they are surrounded by a whitish halo. Below these there are several rows of small, rounded epithelial cells, some of which are devoid of any nuclear substance. The basal layer (*b.c.*) is represented by finger-like processes of protoplasm which do not possess any nuclei. It may be pointed out for the sake of clear understanding that the whole of the structure is one continuous mass and that the cell-boundaries are nowhere marked but in drawing up the description it has been convenient to treat the structure as if it were composed of a number of distinct layers.

It is interesting to note the changes in the structure as we pass from the ridge to the grooved portion of the striated skin. Attention may be drawn to the following points of difference in the grooved area (fig. 19*b*):—

(i) The spines become smaller and smaller till they are represented by small knob-like projections on the surface. In the middle of the groove the surface becomes entirely smooth.

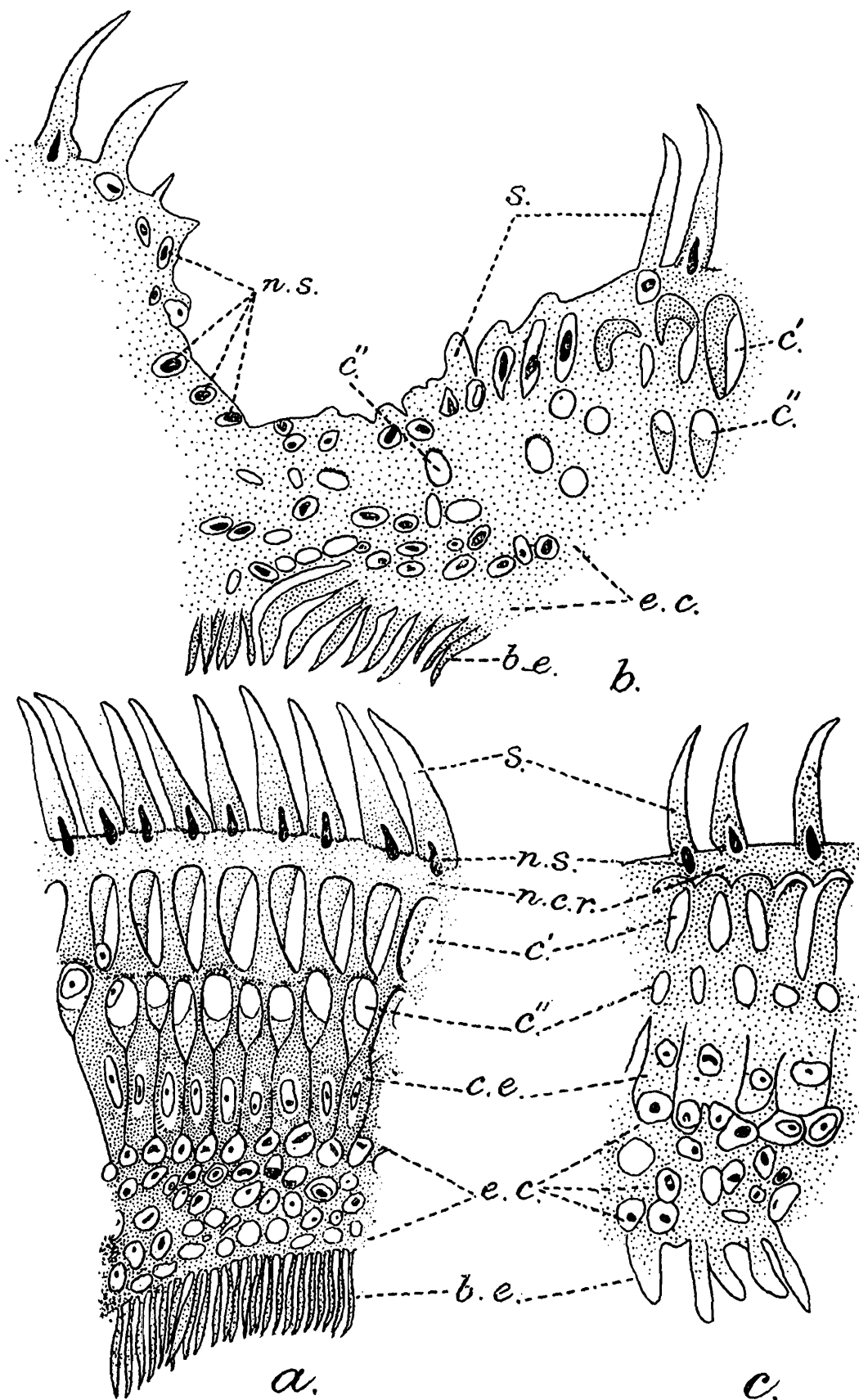
(ii) The nuclei of the spines recede inwards and ultimately form a continuous layer just below the surface of the skin.

(iii) The first layer of cavities is represented by small, oval or rounded spaces in the grooved region. In some cases this layer may be totally absent.

(iv) The second row of spaces is represented by small cavities; they are provided with a deeply staining upper margin.

The structure, on the whole, appears as a mass of protoplasm in which the nuclei are scattered either near the base or near the apex and a few cavities are present in the middle. The basal epithelium is represented by finger-like processes as described above.

In a horizontal section (fig. 19*c*) the structure of the adhesive tissue does not differ greatly from that seen in a vertical section. The chief difference lies in the form and extent of the various elements noted above. The non-cellular region is separated from the underlying tissue by a regular wavy line of demarcation. The



TEXT-FIG. 19.—Minute structure of the adhesive apparatus on the under surface of the pectoral spine of *Glyptothorax* sp.

- a. Transverse section through a portion of the ridge, x 650.  
 b. Transverse section through a portion of the groove, x 650.  
 c. Horizontal section through a portion of the ridge, x 650.

s = spine; n.s. = nucleus of the spine; n.c.r. = non-cellular region; c'. = first row of cavities; c'' = second row of cavities; c.e. = columnar epithelium  
 c.e. = small, rounded epithelial cells; b.e. = basal epithelial cells.

cavities are considerably smaller and do not show any protoplasmic elements within their limits. The so-called columnar epithelium is not well-marked. The underlying structure corresponds to that described for the vertical section.

Having described the structure met with in the different forms selected above, it will be advantageous to consider the lines along which evolution has taken place from the simplest to the most complicated structure. In the simplest type of adhesive apparatus the skin is thickened and its outer epithelial layer of cells is modified into curved spines; the gland cells and the "clavate cells" of normal skin-tissue totally disappear. Specialization proceeds along two lines, firstly there is an increasing tendency at every step towards vacuolation of the superficial epithelial cells and this ultimately results in the formation of definite cavities, and secondly the cell-walls of epidermal cells become indistinguishable. The final stage is reached in *Glypto thorax sp.* where the whole of the epidermal tissue appears as a syncytium. The adhesive apparatus of the Silurid fishes is distinguished from that of the Cyprinid forms by the fact that in the former the skin is thickened and striated, whereas in the latter it is only thickened and forms a plain cushion-like pad. I have not been able to understand the true significance of increased vacuolation or of the syncytium formation in the tissue of the adhesive apparatus.

There is, however, no doubt as to the function of the epidermal spines. All of them are curved in the same direction and probably they point posteriorly. As the fish sticks to a stone with the head pointed up stream, and the current of water tends to move it backwards, the spines when closely applied to a stone, fix it securely by taking hold of the unevennesses of the rock. In Silurid fishes the ridges are pulled outwards and a sort of vacuum is produced in the grooves which helps the fishes in adhering to rocks.

So far as I know, the type of structure described above is not met with in tissues of adhesion in any other group of animals. Dahlgren and Kepner,<sup>1</sup> who have given a summary of the subject, have not anywhere referred to a spinous structure. Even in a longitudinal vertical section through a small region of the grasping organ on the head of *Remora*, the characteristic structure that I have described above apparently is not found.

#### CONCLUSION.

In conclusion I wish to refer briefly to the origin of the hill-stream fauna and to the means of dispersal and propagation adopted by it. In the following discussion I take up these points one by one.

*Origin of the Hill-stream Fauna.*—There are two possibilities, firstly, that the forms now living in the mountain-rapids were once

<sup>1</sup> Dahlgren and Kepner, *Principals of Animal Histology*, pp. 409-417 (1908).

accidentally carried into them, and secondly that there has been a step by step colonisation of the hill-torrents from the sluggish-streams that flow in level country. As regards the first possibility it may safely be inferred that forms which have not previously acquired adaptive characters, cannot live in rapid waters because at every move they are liable to be swept away down stream. The second view is more probable and the following are some of the main points in its favour:—

(1) As a hill-stream changes into a sluggish stream in almost level country its fauna changes accordingly and intermediate forms, like *Crossochilus latia*, between the typical hill-stream fishes and the fishes of the slow streams are always met with in the intermediate regions where the water is neither flowing very fast nor very slowly.

(2) The very fact that the members of certain genera such as *Glyptothorax* and *Garra* can be arranged in a series according to the degree of modification they exhibit in response to the strength of the current of stream, shows that there has been a gradual colonisation of rapid streams.

(3) The hill-stream fishes in the course of their development pass through many different stages which clearly show, at any rate in the case of *Garra*,<sup>1</sup> that the evolution of such forms is from those that live in sluggish streams. Not only is this shown by the form of the body but also in the modifications of such organs as the air-bladder, the position and form of the mouth and the eyes, and in the reduction of the branchiostegal membrane and rays. In short, the developmental series of *Garra* as given in a previous paper recapitulates the history of the evolution of the genus.

Having subscribed to the view that the hill-stream fauna has originated by the process of gradual colonisation from the slow streams, it will not be out of place to discuss the causes that might have led to the migration of these forms. There are two chief factors which might compel such a migration:—food and safety. In the hill-streams there is always plenty of food in the form of algal slime on the exposed surface of rocks, but only those animals can make use of it which have their jaws specially adapted for rasping it off the stones on which it grows. As regards safety, it may be said that there is very little competition in the hill-streams among the fishes themselves. Moreover, they are practically safe from the ravages wrought by birds and large predaceous fishes, crocodiles, etc. Certain fishes like *Nemachilus* can find shelter underneath stones and the readiness with which they hide themselves is marvellous. Probably the fishes inhabiting slow-running waters originally ascended the hill-streams step by step in search of food and gradually acquired certain characters which made them specially suitable for living in the newly chosen environment.

---

<sup>1</sup> Hora, *Rec. Ind. Mus.* XXII, p. 639 (1921).

Annandale,<sup>1</sup> when discussing the evolution of the adhesive apparatus in hill-stream fishes, made the following remark about the genus *Garra*:—"Whereas the chief factor in the case of *Psilorhynchus* was rapid-running water in a rocky stream-bed, in *Discognathus* the primary factor was a peculiar mode of feeding." Quite recently I<sup>2</sup> also subscribed to this view, but a more detailed study of the adhesive apparatus has led me to modify my previous ideas. I believe that the mental disc of *Garra* has not primarily been evolved for the "peculiar mode of feeding," which is practically similar in all the genera of hill-stream fishes, but for securing adhesion to rocks in rapid running waters. The adhesive apparatus on the under surface of the paired fins is an additional organ of adhesion in species that live in very rapid waters. In certain highly evolved species of *Garra*, which have secondarily taken to live in lakes and pools, the peculiar pad-like structure on the under surface of the paired fins have disappeared though the characteristic mental disc is still present, as it is probably of use to the fish in its "peculiar mode of feeding" which was acquired as a direct response to a life in hill-streams.

I am, therefore, led to conclude that none of the hill-stream forms are ancestral forms, but that all of them are descended from migrants from the slow-running streams. The modifications that some of these forms exhibit are due to the physical conditions prevailing in mountain-rapids, and it is to this cause that we must ascribe the similarity in form and structure exhibited by the more advanced members of the genera dealt with in this paper.

*Means of dispersal.*—When dealing with the fish of Manipur it was pointed out by me that most of the new species from the hill-streams had a localised distribution. This is the case with almost all the hill-stream fishes and naturally it is difficult to imagine a wide range of distribution of these forms. The most highly modified forms are not capable of living for a long time in muddy channels, on account of the form of their bodies and the structure of their jaws. In cases where a very wide range has been attributed to a hill-stream species, it has always been found on comparison of material from different localities that several allied forms had been grouped together under the same name and that most of them are capable of specific separation. For example *Glyptosternum labiatum* which was described from the Mishmi Hills in Upper Assam, was recorded by Vinciguerra<sup>3</sup> from the Kachin Hills, Upper Burma. Regan<sup>4</sup> in 1905 separated the Burmese specimens from those collected in the Mishmi Hills under the new name *G. vinciguerrae*. A remarkably wide range of distribution was attributed to *Garra lamta*, but as

<sup>1</sup> Annandale, *Rec. Ind. Mus.* XIV p. 117 (1919).

<sup>2</sup> Hora, *Rec. Ind. Mus.* XIX, p. 213 (1920).

<sup>3</sup> Vinciguerra, *Ann. Mus. Civ. Stor. Nat. Genova*, (2), IX, p. 252 (1889).

<sup>4</sup> Regan, *Ann. Mag. Nat. Hist.* (7) XV p. 184 (1905).

has been shown elsewhere,<sup>1</sup> the forms from various localities are not specifically identical.

*Methods of propagation.*—All the hill-stream fishes with which I am acquainted are oviparous. The rapid current in these streams makes it impossible for them to lay their eggs loose in the rocky beds, as they are liable to be carried down stream and destroyed. In my tours to the hill-streams I have always found that the pools in the courses of these streams were full of young specimens of the genera *Nemachilus* and *Barilius* and of a few other small fish that are usually found in pools. In no case was I able to find young of *Garra* or of any other highly modified hill-stream forms. Dr. Annandale and Major Sewell, however, found *Garra* and *Psilorhynchus* in pools of hill-torrents in the Western Ghats. There appear to be two possibilities, (i) that the hill-stream fishes migrate to slow running waters to lay their eggs and that every generation has later on to ascend up-stream to its natural habitat or, (ii) that the eggs are tightly fixed to stones. I am unable to say at present which hypothesis can be accepted as correct.

---

<sup>1</sup> Hora, *Rec. Ind. Mus.* XXII, pp. 633-687 (1921).

