Memoirs of the College of Science, Kyoto Imperial University, Series B.
Vol. IV, No. 2, Article 4, 1929.

Notes on the Skin and the Cutaneous Sense Organs of some Cobitoid and Gasterosteid Fishes, with special reference to the Rudimentary Nature of the Lateral Canal System.

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With Plate XXIII.

(Received October 5, 1928)

It is the general rule in the development of the lateral canal that the head precedes the trunk ontogenetically as well as phylogenetically. One of the exceptions to this rule is, according to Plate, found in certain sticklebacks which have the canal on the trunk only. In my observations on a Japanese stickleback *Pungitius kaibarae* (Tanaka), however, the canal system is developed on the trunk as well as on the head, and ontogenetically the canal of the head appears earlier than that of the trunk. I also noticed some new examples of Cobitoid fishes in which the canal system is developed in the anterior portion of the trunk only, and not on the head. In the skin of *Misgurnus anguillicaudatus* (Cantor) I found various interesting figures, which I shall interpret as remnants and vestiges of the canal system.

Upon these observations, I base my opinion that the lateral canal of the Cobitoid fishes is of a rudimentary nature, and that Plate's exceptional case is more clearly explained by assuming the same degenerative process of the canal system in sticklebacks as in Cobitoid fishes.

It is my pleasure to express my hearty thanks to Prof. T. Kawamura

of the Kyôto Imperial University and to Assist. Prof. S. TANAKA of the Tôkyô Imperial University for their kind advice and encouragement during the entire course of my work.

I. Misgurnus anguillicaudatus (CANTOR).

Misgurnus anguillicaudatus is the most common Cobitoid fish in Japan. The materials for my investigation were obtained in part from a market in Tôkyô, but the majority were collected by myself in the Prefecture of Siga. The source of the material used is a matter not to be neglected, for fishes from different localities exhibited considerable variation, especially concerning the development of the neuromast canal.

The Skin.

Unlike many others, the present fish is covered head and trunk with an epidermis of nearly equal thickness, owing to the too weak development of the scales to affect the thickness of the epidermis. The epidermis consits of the epidermal, mucus and clavated cells, the last of which being, according to OXNER ('05) and others, the characteristic constituent possessed by the fishes of the suborder Ostariophysi and Apodes only, and with some questionable identies also by those of the order Hyperoartii and the family Gadidæ.

The mucus cells attain their full development in the upper half of the epidermis, and their distal end occupies the greater part of its surface area, scarcely leaving space for the epidermal cells. They are large and elongated often extending below the middle of the epidermis. In an early stage of the cell, there remains at the bottom of the mucus substance, which stains deeply with DELAFIELD's haematoxylin, a mass of eosinophile cytoplasma and a small nucleus of the cell. In advanced stages, however, the nucleus disappears in the mucous substance which now makes up the sole content of the cell. After the discharge of the mucus, the cell content appears alveolar, while the size of the cell diminishes gradually being replaced finally by other mucus

and epidermal cells. The clavated cells are spherical or elongate oval in shape, attaining their maximum size in or below the middle of the epidermal layer, and as they approach the surface, decrease in size till finally lost among the epidermal cells. In the middle layer, the clavated cells are found densely crowded together occupying an overwhelming proportion of it, leaving only narrow spaces for the epidermal cells. The cytoplasma of the clavated cell is homogeneous in appearance and stains clearly with eosin. Its nucleus rests at the center of the cell and is sometimes constricted into two or three segments, as OXNER has pointed out in the case of other fishes.

Concerning the mutual relation between mucus and clavated cells, it has often been the opinion of some students, since the time of LEYDIG, that they are merely two different phases of an identical cell. However as is to be proved in *Misgurnus anguillicaudatus*, there are no intermediate forms between these two sorts of cells. The different area of the skin for their distribution gives further support to this contention, as there are no clavated cells on barbels, lips, inner side of the operculum, and the mucous surface of the mouth cavity, while the mucus cells are abundantly found there. The reverse is true around the free neuromasts. The form, size and relative number of the mucus and the clavated cells differ remarkably according to life conditions. In a well-fed individual in summer time, the mucus cell usually exceeds the clavated cell in size, marking a contrast to the epidermis in most other Ostariophysous fishes, in which the latter is far larger than the former.

Since the other structural elements of the skin, such as the germinative layer, the basal membrane, the pigment cells, etc., do not exhibit any remarkable peculiarities, I may dispense with a description of them.

The Cutaneous Sense Organ.

There are two sorts of cutaneous sense organs in *Misgurnus anguillicaudatus*, i. e. the terminal bud, which is homologous with the taste bud on the mucous surface of the mouth cavity, and the neuromasts

of the lateral line system.

1) *Terminal Buds.* In general, terminal buds (Fig. 1) are flask or spindle shaped, about 0.045 mm. in height and 0.037 mm. in maximum diameter, and are imbedded among the epidermal cells. The bud consists of sensory cells, each being extremely attenuated above the level of its nucleus, which lies near the proximal end of the cell. The sensory cells are arranged regularly side by side, and are situated upon the papillar eminence of the dermis which projects among the epidermal cells. On the inside of the operculum, however, the epidermal cover is extremely thin and the sensory cells of the taste buds are sufficient in length to cover its entire thickness, so that the taste buds in this region rest directly upon the general base membrane of the epidermis.

I made a thorough examination of the skin in order to determine the distribution of the taste and terminal buds by a complete series of microtome sections. On the palatal organs, taste buds are found densely distributed on the mucous lining from the lip to the oesophagus and all over the gill region. Of the external skin, the barbels are most thickly populated by buds uniformly on all sides, the head is next, while the trunk has but few, the buds becoming rarer as we approach the caudal extremity. They are generally more numerous on the dorsal side than on the ventral, but there is no region where they are not to be found. Of the fins, these are most abundant on the dorsal and the caudal fins, the pectoral fin is very scantily provided, while on the ventral and the anal fins they are to be found in some fishes, and not in others. I do not know any groups of these terminal buds that can be defined as LANDACRE has remarked on the skin of *Amiurus melas*. In younger fishes, we often find twin and triplet terminal buds standing upon a common larger papilla and supplied by larger vessels.

2) *Neuromasts.* The neuromasts of *Misgurnus anguillicaudatus* are usually free and only exceptionally enclosed in a short incomplete canal, which will be described in detail as the remnant of the canal system. I also found many interesting structures among the scales as well as in the epidermis in the anterior portion of the trunk, which may

properly be called vestiges of the neuromast canal.

a) Free neuromast: The free neuromast is a decapitated cone, or is sometimes cylindrical in shape, having a height and a maximum diameter of about 0.07 mm. It is embedded in the epidermis, communicating with the exterior only by a small circular pore, and never stands upon a raised papilla as is the case with *Batrachus tau* and some other fishes. Each organ consists of two kinds of cells, the supporting and the sensory. The supporting cell is extremely long and distally attenuated, its nucleus being placed near the proximal bulge, is characterized by large size and a conspicuous nucleolus surrounded by a clear unstained area. The sensory cell is club-shaped and surrounded by supporting cells. It is only half as high as the neuromast, occupying the upper layer of the latter. Its distal end is drawn out to a fine bristle which, however, does not project beyond the level of the supporting cells as is sometimes the case with the neuromast in the canal (Fig. 1). The nucleus lies near the proximal end of the cell and is also characterized by a prominent nucleolus. Both the sensory and the supporting cells are generally arranged side by side, forming two well-defined layers according to their difference in height. The boundaries between the neuromast and the surrounding epidermal cells are very distinct and there is no firm connection as in the terminal bud.

The neuromasts are arranged in a definite pattern ef groups, though the number of organs possessed by each group exhibits considerable individual variation and often differs on opposite sides of the same specimen; but we can distinguish, among others, those which are found in every fish in a definite place. While alive, these neuromasts are easily detected with the naked eye as white spots, owing mainly to the absence of pigment cells under the epidermis at that place; but when the fish is killed with Bouin's fluid, the spot becomes more distinct because of the mucous secretion which covers the whole outer skin except the spot, and stains homogeneously yellow.

The free neuromasts attain their most luxurious development on the head, and their distribution pattern can be referred to the typical courses

of the lateral canal system in other fishes. In the trunk region, we see on each side two main lines and one branch line of free neuromasts, and as this arrangement may deserve some notice for the sake of comparison with that of other fishes, I shall describe it briefly. The middle body line commences at the dorsal ridge of the operculum, and running a short distance obliquely downward along its margin, soon turns its course, runs along the lateral furrow of the trunk, and reaches, but does not enter, the caudal fin. The neuromasts of this line are usually arranged segmentally, two or three being found situated closely side by side but rarely alone. Among the neuromasts of this line, those in the anterior portion are generally surrounded by a wall of epidermal projection, but this wall does not form a continuous groove with that of the neighbouring neuromast. As we proceed posteriorly, they become more superficial in situation. They do not seem to have any definite relation with the scales which are never pierced by the nerve fibers supplying the sense organ nor do they exhibit any deformities. The branch line starts at the common origin with the middle body line on its dorsal side, and runs parallel to the latter. It terminates near the posterior margin of the dorsal fin. The neuromasts of this line are arranged segmentally but are solitary. The dorsal body line begins just behind the occipital commissure group on the head, where the anterior limit of the scale insertion in the skin is marked. It runs closely along, and parallel to, the dorsal ridge of the trunk. The anterior end of this line on both sides may in some individuals so converge as to reach a single median neuromast. It terminates posteriorly at about the same level as the branch of the middle body line. This line is represented by a row of free neuromasts arranged at regular distances, and occasionally with sister sense organs side by side as is the case with the middle body line.

b) Remnant of the canal system: It was only by an unexpected chance during my study of the skin of *Misgurnus anguillicaudatus*, that I came upon the lateral canal organ in one specimen, and further careful search for this organ in more than twenty specimens bought from

a market in Tokyo failed to reveal it again, so that I was forced to interpret the circumstance as a very rare case. It was again a surprise, therefore, to discover among those specimens collected in the Prefecture of Siga more than half of the individuals possessing the lateral canal organs as is shown in the following table. The specimens were all full grown females with variable body length within the limits of 12 to 16 cm.

TABLE I.

Having the canal	on both sides	on one side	on neither side
Number of specimens	7	4	8

The neuromast canal lies just below the basement membrane of the epidermis, and extends in my specimens not more than 1 cm. parallel to the anterior portion of the middle body line of free neuromasts, the number of the pores of the canal varying from one to five. Anatomically, this portion is marked by the presence of the connective tissue of the lateral furrow, which is so massively developed here as to reach inwards to the air-bladder and separates completely the dorsal trunk muscle from the lateral, which are otherwise so close to each other as to meet forming the body wall of the longitudinal muscle. The presence of the canal does not seem to affect the distribution of the free neuromasts of this region; they are found in great numbers and are situated in the epidermis just at the opening of the canal.

The canal (Fig. 1) has a thick epidermal wall, composed of ordinary epidermal cells, and neither mucus nor clavated cells are distributed in it. It is not, however, a simple canal of uniform diameter throughout its entire extent, but consists of several shorter portions arranged end to end in a single line. Each of these portions communicates with the exterior by a pore (Fig. 2) near one end, and at the other end it may be connected with the neighbouring portion or may end blindly. The middle portion of each of these tubes is dilated, and therein usually rests a neuromast, this however being occasionally situated just under

the opening of the canal. The structure of this neuromast is essentially the same as that of the free neuromasts, only with these differences, that the former is a little larger than the latter, and the bristled ends of its sensory cells sometimes project conspicuously beyond the general surface of the supporting cells. The boundary between the sense organ and thd epidermal wall of the tube is tolerably intact and we find no discrepancy there as in the case of the free neuromast. The canal is surrounded either by the processes of the scale (Fig. 2) as numerous as the portions constituting the canal, or by well developed connecting tissue. Thus the canal is proved to have a definite relationship with the scales.

c) Vestiges of the canal system: In the anterior half of the trunk, dorsally as well as ventrally to the middle body line, there are some scales which carry each a small tube (Figs. 3 & 4). The tube is formed by the outgrowth of the scale, and may be situated either on the outer or the inner side of the latter, with its axis parallel to that of the body. It contains a structure of epidermal arrangement accompanied by a blood vessel and an irregular mass of cells and fibers. A minute examination of a series of sections convinces us that this is a vestige of the lateral canal, for in transverse sections these epidermal arrangements are generally circular with a hollow space in the center, having sometimes, however, a pore on one side (Fig. 3), or a swelling (Fig. 4) of the basal tissue of the canal, thus representing the opening or the neuromast of the canal respectively. In short it suggests in every respect a reduced figure of the remnant of the neuromast canal which was described in the foregoing section. The scales carrying these canals are not larger than the others and the length of each vestige is below 1 mm. in all cases examined, which is equal to the diameter of the scales in this region. It is wholly subcutaneous and communicates only with the connective tissue of the scale sac.

Of ten specimens collected in the Prefecture of Siga, seven had these vestiges, which were generally better developed in those which had the remnants of the canal. They are found near the anterior portion

of the trunk as far down as the region of the dorsal fin. The number of scales carrying these vestiges in one specimen may sometimes be counted by tens and, so far as I have a record, eight vestige-carrying scales appeared side by side in a single microtome section of the skin about 3 cm. posterior to the margin of the operculum.

d) Epidermal hollows: I have sometimes noticed in the epidermis of the same region of the trunk certain spherical hollows whose inner lining is made of small epidermal cells, not communicating with the exterior. The meaning of these figures could not be solved until the discovery of cases in which a small neuromast was found at the bottom of this hollow (Fig. 5). Thus it became clear that they also should be taken for vestiges of the canal system. In the epidermal hollows, I could not prove any definite relation with the scales.

From the above-mentioned observations on the neuromast system, I am inclined to think that *Misgurnus anguillicaudatus* once possessed a fairly well developed system of neuromast canals having intimate relations with the scales, but in later times they have undergone such degeneration that these canals do not appear at all in some individuals. The fact, however, that they may still be found in the anterior portion of the trunk in some specimens suggests to us the presence of influences, perhaps of a nervous nature, upon the building of the canal and its vestiges.

II. Cobitis biwæ Jordan & Snyder.

The following descriptions are based on the specimens obtained in Lake Biwa during the summer of 1925.

The skin. The epidermis of *Cobitis biwæ* consists of the epidermal and clavated cells (Fig. 6), but lacks the mucus cells, and this explains the fact that this fish is not at all slippery, and in this characteristic the present species is a remarkable exception among the Ostariophysous fishes, so far as I can judge from the literature of the subject and by my experience. The clavated cells occupy an overwhelming proportion of the epidermis in its middle layer, and the epidermal

cells are arranged in two layers; the germinative layer at the base and the exterior lining of the skin. No scales are found in the head region, and they are developed but weakly in the trunk.

The cutaneous sense organ: The terminal buds in this fish are distributed all over the head and the trunk, diminishing in number as we proceed towards the tail. The free neuromasts on the head are as in the foregoing species, arranged under a definite pattern, and in the trunk they are distributed in a single row along the middle body line.

The canal system (Fig. 6) is developed only at the anterior portion, ranging 0.8 to 1.3 cm. along the trunk. The number of the openings of the canal varied in my specimens from eight to twelve. Thus the canal of the middle body line seems to retain a wider range of distribution in *Cobitis biwæ* than in *Misgurnus anguillicaudatus*. The neuromasts enclosed in the canal are usually less numerous than the openings. The canal lies just below the epidermis, and is made of a thin layer of the epidermal tissue, guarded by incomplete tubes of scaly construction. Its lumen is not continuous throughout the course, so that we can recognize here too the vestigial nature of the canal. I could not, however, find any other vestiges of the canal as in the skin of *Misgurnus anguillicaudatus*.

III. Other Cobitoid Fishes.

1) *Barbatula oreas* (JORDAN & FOWLER).

Barbatula oreas is a common fish in Hokkaido. The skin of this fish consits of three sorts of cells as in *Misgurnus anguillicaudatus*, but the mucus cells are very small and scarce. The canal system is developed along the entire extent of the trunk as far as the base of the caudal fin, and also on the supraorbital, infraorbital, operculomandibular portion of the head. The structure of the canal exhibits no remarkable variation from that of the foregoing species.

2) *Misgurnus decemcirrosus* (BASILEWSKY).

I have examined several specimens of *Misgurnus decemcirrosus*

which were collected by Prof. T. KAWAMURA in China. The canal system of this fish is seen only in the anterior portion of the trunk, and the number of the openings of the canal is three or four. Thus in this fish the condition of the canal system is like that of the Japanese specimens of *Misgurnus anguillicaudatus*.

3) *Lefua echigonia* JORDAN & RICHARDSON and *Lefua nikkonis* (JORDAN & FOWLER).

I have examined many specimens of these fishes, but failed to find any trace of the canal system.

Discussion.

It is a general rule in the development of the canal system that the head region precedes the trunk either phylogenetically or ontogenetically. It is, therefore, an interesting fact that in *Misgurnus anguillicaudatus*, *Misgurnus decemcirrosus*, and *Cobitis biwæ* the system is represented by a short canal on the anterior portion of the trunk only, instead of the head only. In explanation of this fact there may be two theories, either that the case is an exception to the general rule as PLATE described in the case of a stickleback, or that, as I propose here, the canal system in these fishes has undergone degenerative processes, and there remains no trace of it in the entire region excepting in a small portion of the trunk.* The latter of these two alternatives, however, is supported by my observation on the vestigial nature of the canal in these fishes, and the presence of unmistakable vestiges and remnants of the canal system in *Misgurnus anguillicaudatus*.

It is suggested by COLLINGE, that the canal system in the Siluridæ was formerly more complicated in its structure as well as in its distribution than in the present fish. My observation on the Cobitidæ shows that such a degenerative process has been carried much further here than in the Siluridæ.

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* I shall discuss the former theory in a succeeding articles.

IV. Pungitius kaibaræ (TANAKA).

The following descriptions are based on specimens of eight spined stickleback *Pungitius kaibaræ* (TANAKA) collected in the vicinity of Kyôto by Prof. T. KAWAMURA, and the embryological materials are those presented to the Otsu Hydrobiological Station by Mr. J. KOBAYASHI, now Professor in the Hirosima Higher Normal School.

The skin. The epidermis of *Pungitius kaibaræ* consists of the epidermal and the mucus cells, but lacks the clavated cells (Fig. 7). The epidermal cells are relatively rich in cytoplasma as compared with those of the Cobitoid fishes, and the mucus cells are abundantly distributed near the surface as well as in the deeper portions. The scutum is a very large plate with irregular processes and hollows, thus exhibiting sometimes a reticular appearance (Fig. 8).

The cutaneous sense organs. One of the most remarkable aspects in the skin of this species is the lack of terminal buds on the external skin and on the inner lining of the operculum. Free neuromasts (Fig. 7) are arranged both on the head and on the trunk, being situated at the bottom of rather wide depressions or pits, none of which, however, is so confluent with those adjacent as to form a continuous groove. On the middle body line, they occur generally in dorsal-ventral pairs.

The system of neuromast canals is found both on the head (Fig. 8) and on the trunk (Fig. 7). The canal has a thin wall composed of epidermal and mucus cells and is guarded by processes from the scutum. In the head region, we can recognize the canal on the supraorbital, infraorbital and opercular regions, while on the trunk it appears as the middle body line.

In the young of *Pungitius kaibaræ*, the canal in the head is formed as early as when the fish is 1.5 to 2 cm. in length, while that of the trunk appears after it has grown to 2.5 cm. or more. Thus PLATE's description of the European stickleback that "Ausnahmen von der Regel, dass der Kopf in der phyletischen Entwicklung vorangeht, kommen vor. So hat der Stichling nur einen kurzen Kanal am Rumpfe,

während am Kopf und Schwanz die Sinneshügel frei liegen." is not applicable so far as the present species is concerned, for this has a system of neuromast canals on the head also, and in the ontogenetical development of the canal the head precedes the trunk.

From these observations on a Japanese stickleback, the exceptional situation of the European stickleback which has the canal on the anterior portion of the trunk only, seems to me more clearly explained by assuming a smilar degenerative process as in the Cobitidæ. Thus I trust I am not going too far when I propose a new law, "In both families, Cobitidæ and Gasterosteidæ, when the degeneration of the canal system takes place, it is in the anterior portion of the trunk that this process occurs last of all."

SUMMARY.

I. *Misgurnus anguillicaudatus* (CANTOR).

1) The epidermis consists of the epidermal, mucus and clavated cells.

2) Terminal buds are found on the entire outer skin of the fish, though not invariably on the ventral and the anal fins.

3) There are three trunk lines of free neuromasts.

4) The neuromast canal is found only exceptionally on the anterior portion of the trunk, and may be regarded as vestigial.

5) There are some singular structures among the scales as well as in the epidermis of the anterior portion of the trunk, and there are reasons for interpreting them as vestiges of the canal organs.

II. *Cobitis biwæ* JORDAN & SNYDER.

6) The epidermis is devoid of mucus cells.

7) The canal is found only at the anterior portion of the trunk as in the forgoing species.

8) There are no vestiges of a canal system in any region.

III. *Barbatula oreas* (JORDAN & FOWLER).

9) The canal system occurs both in the head and in the trunk.

IV. *Lefua echigonia* JORDAN & RICHARDSON and *Lefua nikkonis* (JORDAN & FOWLER).

10) The canal system is found neither in the head nor in the trunk.

V. *Misgurnus decemcirrosus* (BASILEWSKY).

11) The canal system is found for a short extent on the anterior portion of the trunk as in *Misgurnus anguillicaudatus.*

VI. *Pungitius kaibarœ* (TANAKA).

12) The epidermis consists of the epidermal and mucus cells, but lacks the clavated cells.

13) The terminal buds occur neither in the outer skin nor in the gill region.

14) The canal system appears equally in the head and in the trunk.

15) The canal system of the head appears earlier than that of the trunk.

16) The puzzling fact, that both in certain Cobitoid and Gasterosteid fishes the canal system is limited to the anterior portion of the trunk, can better be understood by assuming a special mode of the obliterating processes of the system in which degeneration takes place latest in the above-mentioned portion.

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EXPLANATION OF PLATE XXIII.

Fig. 1. A neuromast in the canal, and a terminal bud of *Misgurnus anguillicaudatus*.

Fig. 2. A canal and its opening in the skin of *M. anguillicaudatus*.

Fig. 3. A vestige of the neuromast canal with its opening, and a free neuromast in the anterior portion of the middle body line in *M. anguillicaudatus*.

Fig. 4. A vestige with a swelling at the base of the canal in *M. anguillicaudatus*.

Fig. 5. An epidermal hollow with a neuromast at its base in *M. anguillicaudatus*.

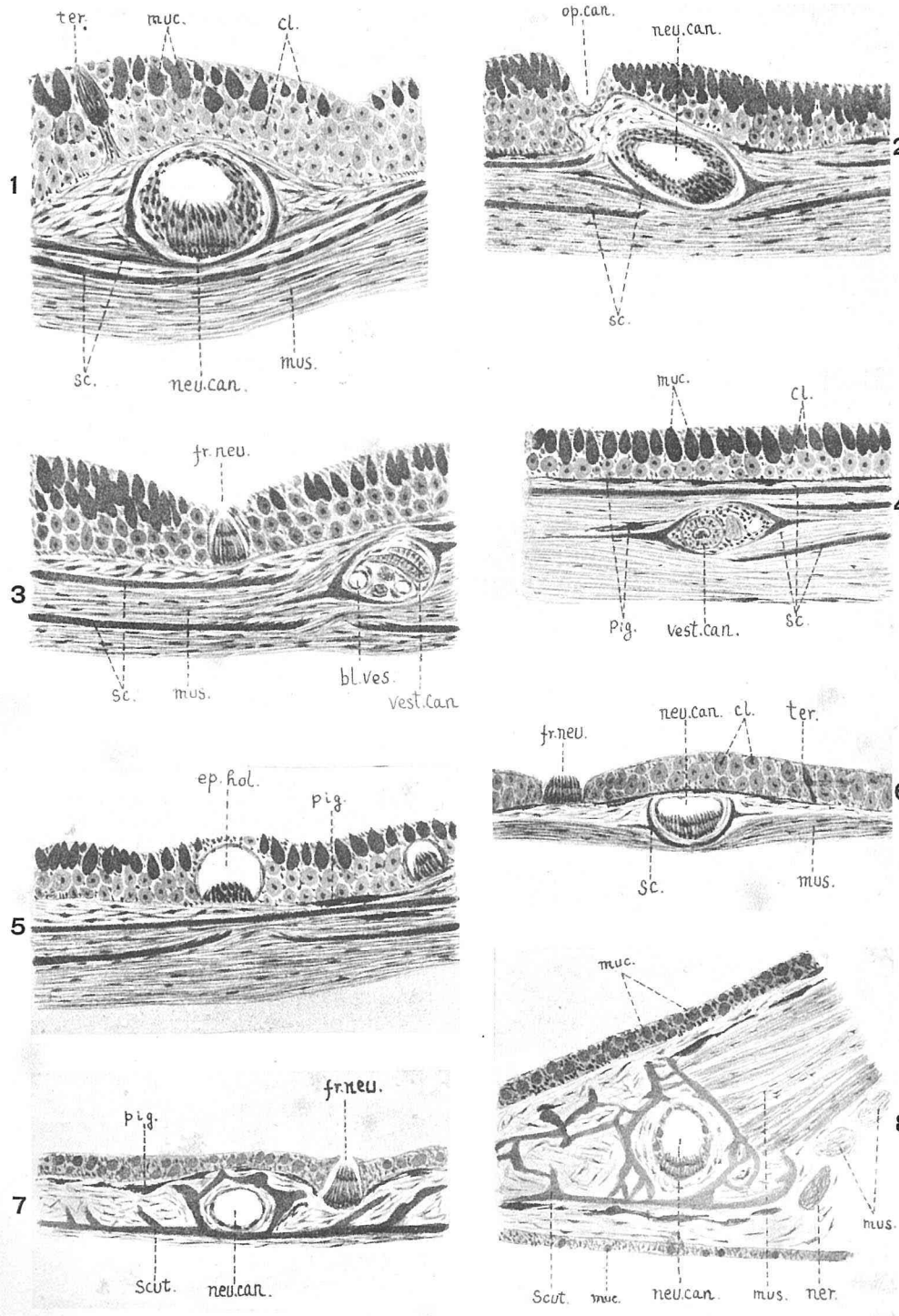
Fig. 6. A free neuromast and a neuromast in the canal in *Cobitis biwæ*.

Fig. 7. A free neuromast and the lateral canal in *Pungitius kaibaræ*.

Fig. 8. The neuromast canal of the opercular region in *Pungitius kaibaræ*.

ABBREVIATION OF LETTERS.

bl. ves ... ... blood vessel.
ep. hol ... ... epidermal hollow.
muc... ... ... mucus cell.
ner ... .nerve.
neu. can... ... ... neuromast canal.
pig ... ... pigment cell.
scut... ... ... scutum.
vest. can... ... ... vestige the ofcanal.
cl ... ... clavated cell.
fr. neu ... ... free neuromast.
mus ... ... muscle.
neu... ... ... neuromast.
op. can... ... ... opening of the canal.
sc ... ... scale.
ter... ... ... terminal bud.



D. Miyadi del.

Miyadi ; Cutaneous Sense Organs.