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THE TROPHOTAENIAE[1] OF THE GOODEIDAE, A FAMILY OF VIVIPAROUS CYPRINODONT FISHES

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FOUR PLATES (TWENTY-FOUR FIGURES)

AUTHOR'S ABSTRACT

The embryos of twenty-one species of the family Goodeidae have extensive rectal processes (trophotaeniae) which serve as absorptive organs, by means of which the embryos while they are retained in the ovarian cavity absorb substances dissolved in the ovarian fluid. Embryos of three species have not been available for study. No trophotaeniae are present in one species Ataeniobius toweri. There are three general types of trophotaeniae, rosette, sheathed and unsheathed. The structure of the trophotaeniae is sufficiently constant in each species to be used in species determination.

INTRODUCTION

In a recent paper (Turner, '33) the writer gave an account of the discovery of some unique absorbing structures found in the embryos in some species of the family Goodeidae, found in the Mexican plateau and in some adjacent streams. The structures were found in five species belonging to as many genera, and it seemed likely, because of the constancy of their occurrence, that the embryos in the remaining genera and species might also be equipped with the processes. Fortunately the writer has been able to study embryos of all the remaining species except three. In 1905 Dr. Seth Meek made an extensive collection of Mexcian fishes for the Field Museum and gravid females of most of the species of the Goodeidae were found in the collection. Alfred C. Weed and the officials of the Field Museum kindly permitted the writer to secure ovaries from the gravid females and to study the embryos. Much of this material was in an excellent state of preservation and not only the gross structures of the rectal process but the histology also could be studied. In addition,

[1] The term trophotaeniae, 'growth ribbons,' was introduced by Hubbs and Turner ('37).

gravid specimens of Xenoophorus erro and of Characodon lateralis from the collection at the museum of zoology at the University of Michigan were examined with the permission of Dr. C. L. Hubbs. Another species formerly classified as Ilyodon paraguayensis was examined at the National Museum by Hubbs and was found to be identical with the Mexican Ilyodon (Characodon) furcidens. Later a specimen was loaned to the writer by Dr. George S. Meyers, Curator of Fishes. This paper is written, therefore, with first-hand or indirect information on the condition in all the species except, Alloophorus zonistius, Goodea gracilis and Balsadichthys xantusi.

During the examination of the embryos some very noticeable variations in the character of the ovary also came to light. When alignments of the various species were made on the basis of these ovarian peculiarities and of those existing in the rectal processes of the embryos, it became apparent at once that a natural classification of the members of the family constructed on these characters did not agree with the classification that had been made previously, using peculiarities of teeth, fin position, length of intestine, etc. After an examination of the material Hubbs agreed with the writer that a complete reclassification of the family was necessary. Such a revision has been made and the generic and specific names used in this paper are the ones appearing in the revision (Hubbs and Turner, '37).

The reader is referred to the writer's first paper ('33) for an account of the peculiar reproduction of the Goodeidae, the nature of the embryonic rectal processes in some species, the relation of the embryos to the ovary in which they are retained, the gross and histological structure of the processes themselves, and finally for some speculations as to the evolutionary relations of this family to some other families of the order. The species for which the trophotaeniae were first described (Turner, '33) were as follows: Lermichthys multiradiatus, Balsadichthys whitei, Girardinichthys innominatus, Zoogoneticus cuitzeoensis and Goodea bilineata. In the revision by Hubbs and Turner the first four names remain un-

changed but 'Neotoca' bilineata replaces 'Goodea' bilineata of the writer's paper ('33).

It is the purpose of this paper to describe the general features of the trophotaeniae in each genus and species of the Goodeidae in which they were found, to give an account of the histology of the processes in all cases in which the state of preservation permits and to draw a few conclusions concerning the phylogeny of the various genera on the basis of similarity and dissimilarity in the processes.

ASSUMED ORIGIN OF THE PROCESSES

It is likely that the immediate ancestor from which all the Goodeidae were derived was a form in which viviparity had already been established. It is probable also that embryos of this form secured nutrition and oxygen from the fluid of the intra-ovarian cavity by absorbing them through the skin. There is a probability that this absorptive function was especially emphasized in the region about the proctodaeum and that there may have been some rectal imbibition. A slight enlargement and extension of the proctodaeal lip would give rise to an incipient absorptive membrane encircling the posterior orifice of the gut. The interior of the membrane would be composed mostly of reticular connective tissue which has already been shown to be continuous with the sub-mucosa of the gut and the sub-epithelial connective tissue of the skin. An increase in the surface of the absorptive membrane would focus the absorptive function here. Such an increase in surface has apparently been accomplished in several ways: 1) The development of numerous short blunt lobes; 2) the elongation of the posterior part of the membrane with the lateral margin divided into finger-shaped or ribbon-shaped processes; 3) the development of very long ribbon-like processes without any noticeable extension of the membrane. With the exception of the 'rosette' type of process all elongations have arisen from the lateral and posterior margins of the membrane.

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The trophotaeniae show a high degree of specificity as regards arrangement about the posterior end of the gut, number of branches, sub-division of branches and length of processes in each species. A degree of variability exists within each species but it is within such narrow limits that the specific features of each species may be recognized easily.

Another feature which constitutes a fundamental difference in the types of processes is a wide tissue space. This space separates the external epithelium from the connective tissue mass of the interior and in extreme instances the external epithelium has the appearance of a sheath. It occurs in the 'rosette' type of process and in the group that will be referred to as 'sheathed.'

In the description of the processes the different types will be divided into three groups: 1) rosette type; 2) the 'sheathed' type or those having a wide internal primary tissue space; 3) the unsheathed type in which there are no primary tissue spaces.

1. The rosette type

a. Gross morphology. A typical rosette type is found in Goodea luitpoldi and in Goodea atripinnis, a slightly modified type in Neoophorus diazi and Allotoca dugèsii and a more highly modified type in Xenoophorus captivus and Xenoophorus erro.

In Goodea luitpoldi and Goodea atripinnis (figs. 1 and 2) the system of trophotaeniae is in reality a much thickened, flattened, lobulated and somewhat folded membrane which is deeply incised at the margins forming a series of blunt processes united at their bases and attached to the posterior end of the gut. There are eight or ten such processes in each system. The individual processes are slightly cleft at the ends forming a series of minor branches. All branches are swollen at the ends and constricted at intervals forming bulbous swellings between the intervals. Most of the processes arise from the anterior and lateral margins of the terminal portion of the

gut and the processes in this region are not very constant except in approximate number and length. A pair of processes arising from the postero-lateral position is much more constant in its position and shape and is usualy longest. The greatest length of any process in an embryo of maximal size before birth (16 mm. in Goodea luitpoldi and 13 mm. in Goodea atripinnis) is about 1½ mm. Although these processes are short, their large number and breadth produce an extensive surface.

The processes in these two species differ from all others somewhat in their relation to the folds of the ovary. They are so tightly pressed against the ovigerous folds of the ovary that they appear to be partially embedded forming a shallow 'plug and socket' relation.

Gravid females of Goodea gracilis have not been available and consequently no description of the trophotaeniae can be given.

The trophotaeniae of Neoophorus diazi (fig. 3) differ from the two first described in being more compact and somewhat more regular in form. In a 5-mm. embryo the processes are in the form of short irregular cylinders slightly swollen at the ends. A posterior pair is somewhat longer than the others. At this stage the longest processes are about 1½ mm. in length. In an embryo 13 mm. long, the total surface of the processes has considerably increased but the processes have not elongated. There has been a general increase in the diameter of all processes; all have become more bulbous and some have terminal bifurcations and lateral bulbs.

Allotoca dugèsii. Only one stage of this species was available, one in which the embryos were 3 mm. in length. The processes as seen in thirty-three specimens were constant in form and arrangement although they were very small (fig. 5). Two pairs of blunt rounded processes were present, one anterior and one posterior to the gut opening. The individual processes were rounded at the ends and constricted at intervals to produce bulbous swellings. The system resembles that of the earlier stages of Neoophorus diazi. No short lateral

processes were present as in Xeoophorus diazi but there is a possibility that these might have developed later. In the 3 mm. embryo each pair of processes was about ½ mm. in length.

In Xenoophorus captivis (fig. 7) the lateral and posterior margins of the rectal lip give rise to the processes. In a 5 mm. embryo the processes are rather slender and longer than in the three species already described, and there is little resemblance to the typical rosette. Bulbous swellings are slightly developed. The arrangement of the processes is not symmetrical. On the right side there are usually three processes more or less joined at their bases; on the left two short ones joined anteriorly and a wide flat one which sometimes gives rise to one or two branches. This latter is the longest.

As the embryo grows the relations just described are maintained and the only change is an elongation of all the processes. In a 9-mm. embryo the longest processes reach a length of 5.5 mm.

In Xenoophorus erro the system of trophotaeniae resembles that of Xenoophorus captivus, in being variable and in lack of symmetry. The 9-mm. specimen illustrated in figure 4 shows the arrangement most commonly found. In this specimen four processes, each about 1 mm. in length, emerge from the membrane at the anterior and lateral margins. Two longer ones of unequal length emerge in a posterior lateral region, the longer one always appearing on the left side. The longer of these last two has a single short branch. Variations, especially in slightly older and larger specimens, are so common that the entire systems of processes are not identical in any two specimens. Five, instead of four, short processes sometimes occur at the lateral and anterior margins and they are frequently longer than those shown in the figure and of unequal length. The two postero-lateral processes are quite variable as to length and number of short branches. One or two short branches may be found on the left and from one to three on the right process.

There is rather little resemblance of the Xenoophorus type of process to the rosette type of process at any stage, but the classification of the Xenoophorus type is made with considerable assurance for two reasons: 1) Histologically the processes are like the rosette type; 2) the structure of the ovary bears a strong resemblance to that of Goodea atripinnis, Neoophorus diazi and Allotoca dugèsii. But for these features the processes might be classified with the sheathed type which they superficially resemble.

b. Histology. In locating different portions and surfaces of the trophotaeniae the term proximal will be used for the point of attachment at the lip of the hind gut and distal for the apical or free end. The dorsal surface will be the surface nearest the embryo while the ventral surface will be that part that is pressed against a fold of the ovary.

There is little difference in the microscopical anatomy in the trophotaeniae of the four species just described. Sections of the processes (figs. 19, 20 and 21) will illustrate the salient points. The internal stroma of the trophotaeniae is composed of a lower dense and an upper diffuse layer of connective tissue. The larger blood vessels are carried in the dense layer and these large blood vessels give rise to a rich capillary network located at the surface of the diffuse layer. There are spaces between the cells and fibers to which the term secondary tissue space is applied. The basal layer of the stroma tends to become much thicker and denser at the proximal end of the processes (fig. 21) where it merges with the submucosa of the gut. The diffuse connective tissue of the upper layer does not resemble any tissue in the gut. A wide primary tissue space exists between the external epithelium and the stroma. This space does not resemble any similar space in either skin or gut and so is probably a specialized feature associated with absorption. It disappears altogether at the proximal ends of the processes but becomes very extensive at the distal ends. The external epithelium can be divided into two sharply contrasting parts.

Wherever the primary tissue space separates the epithelium from the stroma the cells of the epithelium are cuboidal or columnar and are arranged so as to form a definite palisade. Near the distal end of the processes this epithelium usually contains a single layer of cells (fig. 20), otherwise it contains from two to four layers (fig. 19). Some of the cells contain fine granules and are evidently glandular. That part of the external epithelium in contact with the stroma contains a single layer of simple flat cells.

The trophotaeniae of Goodea luitpoldi and of Goodea atripinnis are almost identical histologically. In Neoophorus diazi the processes contain much less primary tissue space and the stroma, especially the lower compact layer, is in some instances practically non-existent, being confined to areas beneath bulbous elevations of the free epithelium. In the trophotaeniae of Xenoophorus captivus the primary tissue space is still more reduced. The free epithelium is separated from the stroma to such a slight extent in some of the processes that the space is reduced to a cleft. The histological structure of the processes of Xenoophorus erro is almost identical with that of Xenoophorus captivus.

Since the palisade-like portion of the external epithelium is in contact with the ovarian fold during gestation it may be assumed that absorption is accomplished through this membrane. Some of the cells being glandular are in a position to change the chemical character of the substance absorbed from the epithelium of the ovarian fold and discharged into the primary tissue space. From the primary tissue space substances in solution would be absorbed either directly by the capillaries lying at the surface of the stroma or temporarily by the secondary tissue spaces of the spongy upper layer of the stroma. The trophotaenial veins enter the circulation of the embryo through two vessels. One extends dorsally from the process and joins the caudal vein. Another joins a plexus located in the walls of the gut.

2. The sheathed type

The trophotaeniae of the following genera will be described under this division: Skiffia, Ollentodon, Neotoca, Girardinichthys, Lermichthys and Balsadichthys. The processes of Ilyodon probably belong in this division also, but no critical histological examination could be made because of the poor state of preservation of the material available for sectioning. The trophotaeniae of Skiffia lermae, Skiffia variegata and Ollentodon multipunctatus are referred to this group with some reservation for the same reason. An abundant supply of living laboratory-bred specimens of Neotoca bilineata has been available, however, and there is little doubt that the other three species will show the same basic features.

In this group the processes are long and ribbon-shaped. They are attached to the rectal membrane at the lateral and posterior margins only. The trophotaeniae are not pressed against the ovarian folds as in the rosette type of process but lie within the intra-ovarian cavity completely surrounded by the fluid of the cavity. The presence of a wide primary tissue space separates this group from the 'unsheathed' type.

a. Gross anatomy. The trophotaeniae in the genera Skiffia, Ollentodon and Neotoca have been reduced to three. They occur always in the form of a single median posterior process attached to the rectal membrane on its posterior side, and a pair attached laterally. In Skiffia variegata (fig. 10) the posterior median process is shorter than the laterals, in Ollentodon multipunctatus (fig. 9) the three are practically equal in length while in Neotoca bilineata (fig. 8) the median process is always longer. In Skiffia lermae (fig. 11) the median process is shorter than its laterals and in about two-thirds of the cases observed the posterior end in bifurcated. An incipient bifurcation is sometimes noted in the median process of Neotoca bilineata and rarely a specimen is found in which all three processes may be fused into a single mass with only the terminal parts free. Single variations of this type are found within a brood which otherwise contains only

normal specimens. The typical arrangement of the processes is apparently already established in an embryo of 3 mm. length.

Girardinichthys innominatus and Lermichthys multiradiatus. These two species are much alike in the arrangement of their trophotaeniae (figs. 12, 13). Each has but four processes, one short pair attached to the rectal membrane laterally and a little anteriorly, and a longer pair attached posteriorly and laterally. This arrangement can be made out by the time the embryos are 3 mm. long, the longest process being not longer than 2 mm. at this time. In Girardinichthys innominatus (fig. 12) the posterior processes become flattened and ribbon-shaped and reach a length in a 13-mm. embryo of about 7 mm. The members of the anterior pair are slightly more than 1 mm. in length. In Lermichthys multiradiatus (fig. 13) the processes are rounded, blunt and finger-shaped with a tendency toward local swellings and short minor branches. In a 9-mm. embryo the members of the posterior pair are a little more than 2 mm. in length while the anterior pair reaches about half that length.

Because of the resemblance of the arrangement of the processes the two are assumed to be clearly related genetically and this view is further fortified by their histological resemblance and by peculiarities in ovarian structure.

Balsadichthys. This genus has a more elaborate system of trophotaeniae than any other genus in this subdivision. In Balsadichthys whitei there is considerable variation in the details of the branches of processes but in general the arrangement is a bilateral one (fig. 6). All processes have the shape of elongated and slightly flattened cylinders with the ends rounded and a little dilated. An anterior pair arises from the lateral portion of the anterior wall of the rectal membrane. Each member of the pair is about 3 mm. long and has from one to three branches. A second pair is attached to the membrane lateral to and behind the membrane. Each member is from 8 to 11 mm. long and may have as many as four lateral and terminal branches between 1 and 2 mm. in

length. Finally, a shorter process about 7 mm. in length emerges from the membrane in a median posterior position. This branch may contain one or two sub-branches. There are a great many minor variations in the branches even within the members of the same brood but the basic arrangement of two lateral pairs and a single median posterior process does not vary. Whatever the minor variations may be, the terminal endings number from twelve to fourteen.

Balsadichthys xantusi. No gravid females were available and hence no statement can be made concerning the trophotaeniae.

Ilyodon furcidens. This species has been known formerly as Characodon furcidens. The holotype collected by Eigenmann, was reported to have come from Paraguay and bore the name Ilyodon paraguayensis Eigenmann. A recent examination of a gravid female of the holotype at the National Museum brought to light the fact that the embryos had the typical goodeid nutritive processes. A further study by Hubbs demonstrated that Ilyodon paraguayensis was identical with the Mexican Characodon furcidens. Assistant Curator of Fishes, George S. Meyers, makes the following statement concerning the embryo studied. "The embryo examined is one taken from the holotype of *Ilyodon paraguayensis* Eigenmann (U. S. National Museum Catalogue Number 55642), which is now considered to have been erroneously reported from Paraguay and to be a synonym of the Mexican *Ilyodon furcidens.*"

The embryo available has been in preserving fluid for a long time and the arrangement and character of the processes can be determined only approximately. There are two long slender processes about equal in length. These probably constitute one pair. In addition there are at least six processes less than half the length of the long pair. In an embryo 8 mm. long the longest pair of processes measures 6 mm. On the basis of the processes alone it would be impossible to classify the type as 'sheathed' because of the poor state of preservation. There are, however, peculiarities of the ovary

which always accompany the 'sheathed' type of process and these features were clearly seen. The processes of Ilyodon are therefore classified with those of other genera having the sheathed type, but an accurate description of the processes must be postponed until better material is available.

The trophotaeniae of Characodon lateralis (fig. 14) are represented by a single pair of flattened ribbons which emerge from the side of the rectal membrane. The two members, 5.5 mm. long, are approximately equal in length.

b. Histology. Balsadichthys whitei. The histology of the trophotaeniae in this species is typical for the group (fig. 22). The stroma is relatively sparse, is composed principally of loose connective tissue comparable to the spongy stroma in the rosette type of process and is uniform throughout the process. There are numerous small secondary tissue spaces. Larger blood vessels course through the stroma and give off numerous branches which reach the surface of the stroma where they break up into capillaries. The external epithelium is attached to the stroma along a narrow band that extends from the base to the apex of the process but is otherwise free from the stroma. Along the narrow band where stroma and epithelium are in contact the epithelium is composed of flat cells. Where free from the stroma the epithelium is composed of a single layer of cuboidal or columnar cells. Between the free epithelium and the stroma is a wide primary tissue space. These trophotaeniae resemble those of Girardinichthys more than any other.

The sheathed type of trophotaenia is retained at its maximal stage of development almost up to the time for birth of the embryo and resorption then begins. Immediately after birth the resorptive process is accelerated and within a few hours after birth the processes have entirely disappeared. As the resorption begins the free external epithelium shrinks down upon the stroma and the primary tissue space is obliterated. The secondary tissue spaces within the stroma also shrink and the entire stroma becomes condensed (fig. 23). In the final stages the external membrane disappears and the

stroma loses its structure, becoming reduced to a condition in which only a few of the larger blood vessels remain surrounded by remnants of connective tissue and undifferentiated cells.

The histology of Neotoca bilineata, Lermichthys multiradiatus and Girardinichthys innominatus has been described and compared in the writer's previous paper. The principal features resemble those of Balsadichthys whitei.

In the cases of Ollentodon multipunctatus, Skiffia variegata and Skiffia lermae it is assumed that the processes do not differ greatly from the condition described in the writer's previous paper for Neotoca bilineata. No adequate histological examination of the trophotaeniae was possible, however, because of the poor state of preservation.

3. Unsheathed type

This type of trophotaenia differs from the sheathed type in several important histological features: 1) The stroma is spongy and contains many secondary tissue spaces. The epithelium is in direct contact with the stroma at all points. 2) The epithelium is very irregular. The cells are of irregular shape and varying heights and the nuclei are located at different levels.

As in the case of the sheathed type of trophotaeniae, the processes are not pressed against any part of the wall of the intra-ovarian cavity, but are freely suspended in the intra-ovarian cavity.

a. Gross anatomy. The bilateral symmetry exhibited by most genera having the sheathed type of trophotaeniae, especially Neotoca, Girardinichthys and Lermichthys, is lacking here. The processes are arranged in the form of flat extensions of the rectal membrane principally from the lateral and posterior margins.

Alloophorus robustus. There is considerable variation in arrangement of the processes of this species (fig. 16). The single posterior process is sometimes divided once or twice, the branches being unequal in length. The divided lateral

branches may be more deeply divided than is the case in the specimen represented in the figure, or even subdivided at the ends. Rarely in large specimens an additional pair of processes appears attached to the anterior wall of the rectal lip.

All processes are flat, pointed and ribbon-shaped. The long posterior process in a 14.5-mm. embryo is 13 mm. in length.

Xenotoca variata. The trophotaeniae in this species (fig. 18) greatly resemble those of Alloophorus robustus in their arrangement, variability and shape. In extreme cases the trophotaeniae of the two species are scarcely distinguishable. The posterior process is more often divided than in Alloophorus robustus and the two lateral branches are usually divided to about the same extent. Variations occur in the form of extensions of the branching of the processes even within members of the same brood.

Chapalichthys encaustus. All the tissues of this delicate lake fish are inclined to be thin and transparent as compared to those of the two preceeding species and this condition is reflected in the structure of the trophotaeniae (fig. 17). The arrangement of the processes is much like that in Alloophorus robustus and Xenotoca variata. However, the processes of Chapalichthys are longer, thinner, more narrow and much more delicate in texture.

The processes arising from the posterior margin of the rectal membrane are always two in number and of unequal length. The shorter one is usually branched. The two processes arising from either lateral margin of the rectal membrane are of about equal length and in nearly every case one or the other is branched. The longest process in an 11-mm. embryo is 10.5 mm. in length.

Zoogoneticus quitzeoensis. The unsheathed type of trophotaeniae reaches its most elaborate development in this species (fig. 15). Laboratory-bred specimens were available and it was possible to secure embryos with processes in different stages of development. In a 3-mm. embryo in which

the yolk sac is still quite large the system of processes is already about 2 mm. long. The flattened membrane at the posterior end of the gut extends rapidly at the posterior margin and finger-like extremities become budded off as it grows. Four such laterally placed processes arise from the membrane and by the time the embryo is 8 mm. long the membrane terminates posteriorly in a single finger-shaped process. At the same time the four budding processes have greatly elongated also. In addition to the extension just described a series of three shorter pairs also arise from the lateral margin of the rectal membrane. As the embryo approaches its maximal size before birth these six anterior laterally placed processes grow rapidly.

In a typical specimen there are eleven termini arranged as illustrated in figure 15. Variation in the number of the five posterior extensions is seldom found although there is frequently some variation in their relative lengths. Variation in the anterior six is common and takes the form of reduction in number, partial fusion of two or more at their bases and more rarely a fusion of one or both of the posterior pair with the processes lying just behind them.

b. Histology. The peculiarities of the tissues and their relative arrangement in the trophotaeniae of Zoogoneticus quitzeoensis have been described in the writer's previous paper and the description will not be repeated here. The histological structure of the trophotaeniae in embryos of Alloophorus robustus and Xenotoca variata seems to be almost identical with that of Zoogoneticus quitzeoensis. In Chapalichthys encaustus the same general arrangement of tissues is found (fig. 24). The stroma consists of very delicate connective tissue with fibers relatively fewer in number and much thinner than in the three other species. The secondary tissue spaces are relatively larger and more abundant. Larger blood vessels run through the interior of the stroma and ramify to produce capillary branches which lie just below the basement membrane of the external epithelium. The external epithelium of the trophotaeniae in this species resembles that already

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described for Zoogoneticus quitzeoensis but it is somewhat more regular in Chapalichthys.

The case of Ataeniobius toweri

In this species trophotaeniae seem to be lacking. Gravid females obtained from the Field Museum collection were examined and embryos 3 mm. long had no processes. In embryos of this length in other species the processes are already developing and are quite conspicuous. Unborn embryos 13 mm. long also had no processes. Hubbs examined specimens from the National Museum collection and likewise was unable to find any processes. On the basis of these findings it is assumed that processes do not exist in this species and that it is able to secure its nutritive substances and oxygen from the ovarian fluid without their assistance.

The absence of the trophotaeniae may be accounted for either by assuming that the species has never developed the processes or that they have been developed and have become atrophied secondarily. Since no trace of processes has been seen in the embryos at any stage, the writer inclines to the opinion that they have never been developed and that Ataeniobius toweri is therefore genetically separated from the other Goodeidae.

Phylogeny of Goodeidae based upon the character of the trophotaeniae

It is taken for granted that the evolution of the trophotaeniae in the Goodeidae has not been dependent upon any factor in the external environment. The immediate environment of the embryos of all genera and species is the interior of the maternal ovary and while there are some differences in ovarian structure among the various species, these structural peculiarities cannot account for the origin of the different types of trophotaeniae.

If the origin of the trophotaeniae in the first place and the development of many specific types, each characteristic of a

species, in the second place, are not to be attributed to environment it follows that no particular type of trophotaenia has any peculiar survival value for the species possessing it. Any attempt to account for the basic likenesses and differences in the trophotaeniae would then turn to a genetic interpretation. The variations would be regarded as fortuitous ones which had become genetically fixed and basic resemblances would indicate close phylogenetic relationship. A classification based on the peculiarities of the processes should, therefore, express actual phylogenetic relationships. Such a classification would recognize, first, the absence of trophotaeniae in Ataeniobius and the division of the other members of the family into three principal groups as already indicated.

1. The rosette type. The relations of this group to the sheathed and unsheathed type can be arrived at only approximately. If only the peculiarities of the processes were considered it would not be difficult to assume that the rosette is the primitive type and that the other two were derived from it. However, there are basic peculiarities in the ovary indicating that those species having the rosette type of processes are much more nearly related to those species having the unsheathed type of process than they are to those bearing the sheathed type. The sheathed type might easily have arisen from the rosette type by the reduction of some of the processes and the elongation of the others. The most fundamental histological features of the sheathed type of trophotaeniae are already incorporated in the rosette type.

Within the group of species having the rosette type Goodea atripinnis seems to represent the most unspecialized form with Goodea luitpoldi bearing a close resemblance to it. The processes in Neoophorus diazi represent a somewhat more specialized form with a tendency toward reduction of the anterior and lateral processes and an elongation of the posterior pair. In Allotoca dugèsii there has also been an evolution in the direction of a reduction in number and an elongation of the remaining processes. The climax has been reached

described for Zoogoneticus quitzeoensis but it is somewhat more regular in Chapalichthys.

The case of Ataeniobius toweri

In this species trophotaeniae seem to be lacking. Gravid females obtained from the Field Museum collection were examined and embryos 3 mm. long had no processes. In embryos of this length in other species the processes are already developing and are quite conspicuous. Unborn embryos 13 mm. long also had no processes. Hubbs examined specimens from the National Museum collection and likewise was unable to find any processes. On the basis of these findings it is assumed that processes do not exist in this species and that it is able to secure its nutritive substances and oxygen from the ovarian fluid without their assistance.

The absence of the trophotaeniae may be accounted for either by assuming that the species has never developed the processes or that they have been developed and have become atrophied secondarily. Since no trace of processes has been seen in the embryos at any stage, the writer inclines to the opinion that they have never been developed and that Ataeniobius toweri is therefore genetically separated from the other Goodeidae.

Phylogeny of Goodeidae based upon the character of the trophotaeniae

It is taken for granted that the evolution of the trophotaeniae in the Goodeidae has not been dependent upon any factor in the external environment. The immediate environment of the embryos of all genera and species is the interior of the maternal ovary and while there are some differences in ovarian structure among the various species, these structural peculiarities cannot account for the origin of the different types of trophotaeniae.

If the origin of the trophotaeniae in the first place and the development of many specific types, each characteristic of a

species, in the second place, are not to be attributed to environment it follows that no particular type of trophotaenia has any peculiar survival value for the species possessing it. Any attempt to account for the basic likenesses and differences in the trophotaeniae would then turn to a genetic interpretation. The variations would be regarded as fortuitous ones which had become genetically fixed and basic resemblances would indicate close phylogenetic relationship. A classification based on the peculiarities of the processes should, therefore, express actual phylogenetic relationships. Such a classification would recognize, first, the absence of trophotaeniae in Ataeniobius and the division of the other members of the family into three principal groups as already indicated.

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for the present at least in Xenoophorus captivus and Xenoophorus erro in which the trophotaeniae are much elongated.

2. The sheathed type. Within this group three diverging lines have been established: 1) Balsadichthys and Ilyodon have departed least from a primitive condition in which there were numerous and somewhat irregular trophotaeniae. 2) The genera Skiffia, Ollentodon and Neotoca have moved in the direction of the elimination of some of the processes and retention of three, two laterals and a median posterior one. The relative lengths of these three processes have become fixed as a specific feature in each species. 3) Lermichthys and Girardinichthys have also become specialized in the direction of a reduction in the number of processes but both have retained a short anterior and a longer porterior pair. Characodon lateralis possesses only a single posterior pair of trophotaeniae but the geographical ranges of Characodon and Girardinichthys are far apart and the resemblance in the processes of their embryos may represent a case of parallelism rather than close phylogenetic relationship.

3. The unsheathed type. In the ovaries of species having the unsheathed type of nutritive processes the ovigerous tissue is embedded in the dorsal and ventral walls and in the thick and much folded median septum in lens-shaped masses. These same features are found in species having the rosette type of process. In the species having the sheathed type of processes on the other hand, the ovaries of all are alike in having a thin unfolded median septum. Ovigerous tissue is not found in either the ovarian walls or in the median septum but is confined to a pair of thick dorso-lateral folds suspended in the intra-ovarian cavities on thin membranes. Because of the resemblances in ovarian structures in the two it is assumed that the group having the rosette type of process is closely related to the group having the unsheathed type of trophotaenia.

Of the two types the rosette type seems to be more primitive and it is quite possible that the unsheathed type of process was derived from the rosette type by an elongation of the solid portion near the base.

Within the group, the resemblance in the processes of Alloophorus robustus, Xenotoca variata and Chapalichthys encaustus is apparent and they are assumed to be closely related. The peculiarities of the processes of Zoogoneticus quitzeoensis separate this species into a subdivision removed from the other three. If the larger number of processes is considered as evidence for the retention of a primitive condition, Zoogoneticus quitzeoensis should be regarded as more primitive than the other three.

Species having no processes. The lack of any trophotaeniae in Ataeniobius toweri is considered adequate grounds for genetically separating this species from all others. There is no doubt whatever that the species belongs in this family as the modification of the anal fin characteristic of the males of all species in the family is very prominent in this species. If it be assumed that trophotaeniae have been developed and secondarily lost, its position in the phylogenetic scheme of the family cannot be fixed. If, on the other hand, it is assumed that trophotaeniae have never been developed in this species it would be fair to assume that this species represents a relic, resembling in its reproductive process the ancestral form of all the Goodeidae in the embryos of which trophotaeniae had not yet developed.

Similar absorptive structures in embryos of Brotulid fish

In 1933 A. E. Parr published an account of some deep sea explorations and figured the embryo of a viviparous Brotulid fish, Parabrotula dentiens, in which there were processes similar in position to those described for the embryos of the Goodeidae. The writer secured two of the embryos from Parr and studied the relations of the processes to the body of the embryo and also the microscopic structure of the processes themselves. The processes in the Brotulid embryo were found to be attached to the body in the region of the anus and the urogenital pore. They apparently serve the same purpose as in the Goodeid embryos, namely absorption of substances in solution from the fluid of the ovarian

cavity. They differ from any of the trophotaeniae in the Goodeids, however, in their microscopical anatomy and in the fact that there is no extension of the gut endoderm upon their surfaces. The vascular supply in the Goodeid and the Brotulid trophotaeniae is similar.

The occurrence of somewhat similar structures in the embryos of these two widely separated orders of fishes furnish an interesting case of parallelism. Both types of embryos respond to the similar environment and the necessity of absorbing substances in solution from the fluid of the ovarian cavity by developing similar absorbing structures in the same part of the body.

SUMMARY

1. The embryos of twenty-one species of the family Goodeidae have extensive rectal processes (trophotaeniae) which serve as absorptive organs, enabling the embryos to absorb substances dissolved in the ovarian fluid while they are retained in the ovarian cavity. Embryos of three other species have not been available for study.

2. The embryos of Ataeniobius toweri do not have trophotaeniae and it is assumed that this species represents an archaic type in which the trophotaeniae had not yet developed.

3. There are three principal types of trophotaeniae designated as rosette, sheathed and unsheathed.

4. The structure of the trophotaeniae is sufficiently constant in each species to be used in species determination.

5. The Goodeid type of trophotaenia is similar in topographical relations and vascular supply to that in the Brotulid fish, Parabrotula dentiens, but differs in microscopical anatomy.

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———— 1936 The absorptive processes in the embryos of Parabrotula dentients, a vivparous deep-sea Brotulid fish. J. Morph., vol. 59, pp. 313–325.

* The publication of this paper has been delayed. The paper from which the characterizations for the various genera and species are taken will be published in the near future.

PLATE 1

EXPLANATION OF FIGURES

Magnification is indicated in each figure by 1 mm. drawn to same scale.

1 Trophotaeniae of 16-mm. embryo of Goodea luitpoldi.

2 Trophotaeniae of 13-mm. embryo of Goodea atripinnis.

3 Trophotaeniae of 5-mm. embryo of Neoophorus diazi.

4 Trophotaeniae of 9-mm. embryo of Xenoophorus erro.

5 Trophotaeniae of 3-mm. embryo of Allotoca dugèsii.

6 System of trophotaeniae of 11-mm. embryo of Balsadichthys whitei.

7 Trophotaeniae of 5-mm. embryo of Xenoophorus captivus in an embryo of 9 mm.; the processes keep their relative positions but triple their length. The diameter of each process is also increased.

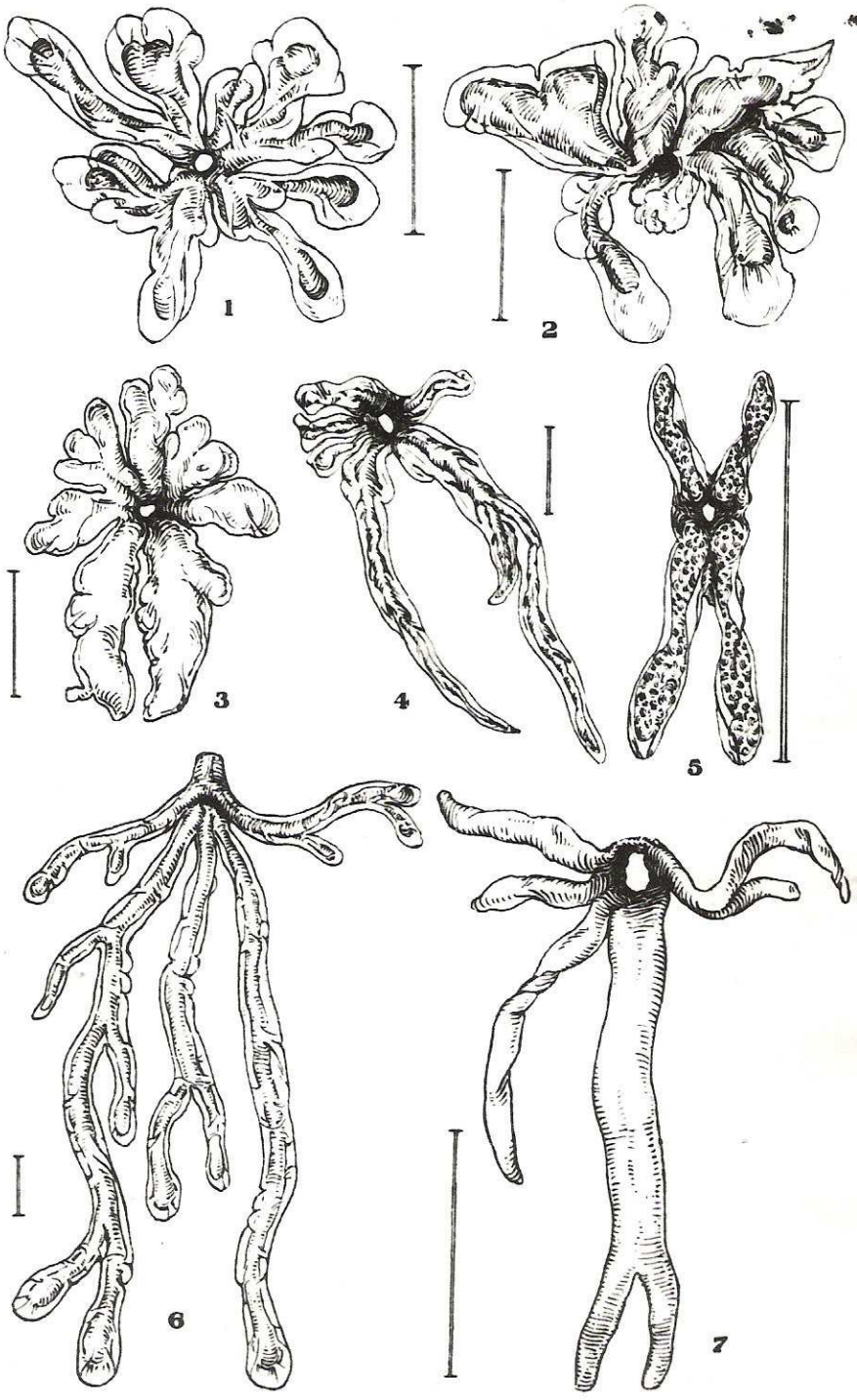
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PLATE 2

EXPLANATION OF FIGURES

8 Trophotaeniae of 11-mm. Neotoca bilineata embryo just before birth.

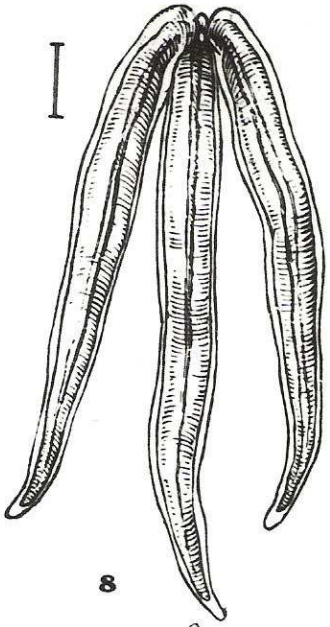
9 Trophotaeniae of 9.5-mm. embryo of Ollentodon multipunctatus.

10 Trophotaeniae of 9-mm. embryo of Skiffia variegata.

11 Trophotaeniae of 4-mm. embryo of Skiffia lermae.

12 Trophotaeniae of 13-mm. embryo of Girardinichthys innominatus a few days before birth. The anterior pair becomes resorbed to some extent just before birth.

13 Trophotaeniae of 9-mm. embryo of Lermichthys multiradiatus.



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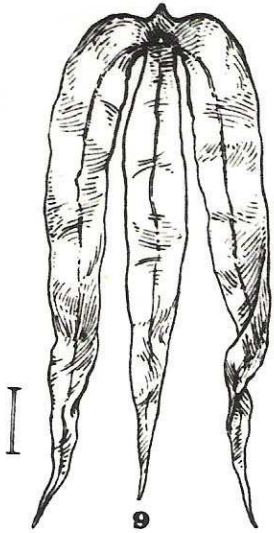

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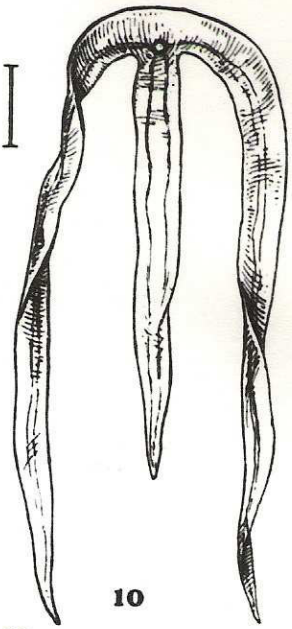

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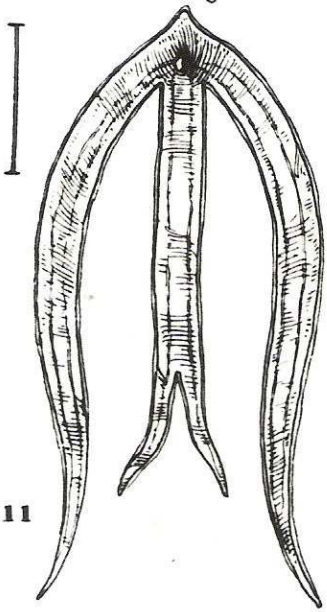

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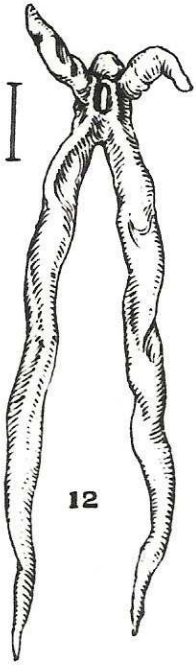

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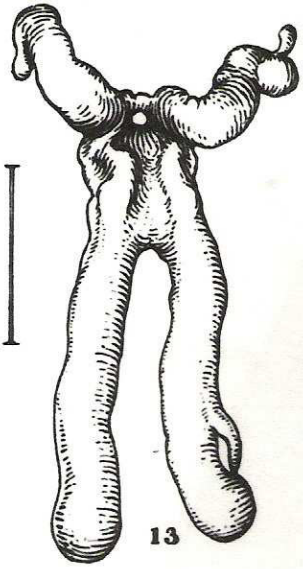

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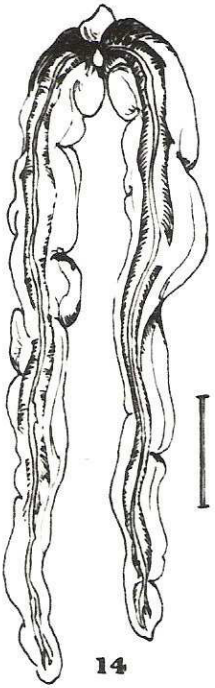
PLATE 3

EXPLANATION OF FIGURES

14 Trophotaeniae of 9-mm. embryo of Characodon lateralis.
15 Trophotaeniae of 8-mm. embryo of Zoogoneticus quitzeoensis.
16 System of trophotaeniae in 13-mm. embryo of Alloophorus robustus.
17 Trophotaeniae of 11-mm. embryo of Chapalichthys encaustus.
18 Trophotaeniae of 10-mm. embryo of Xenotoca variata.



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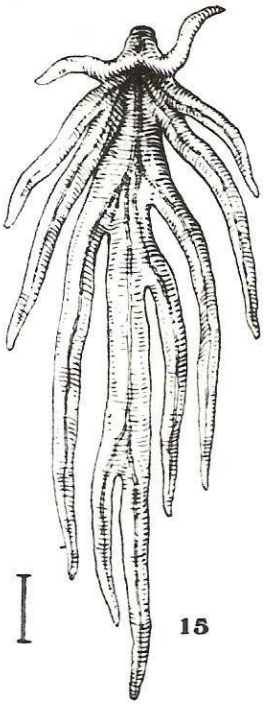

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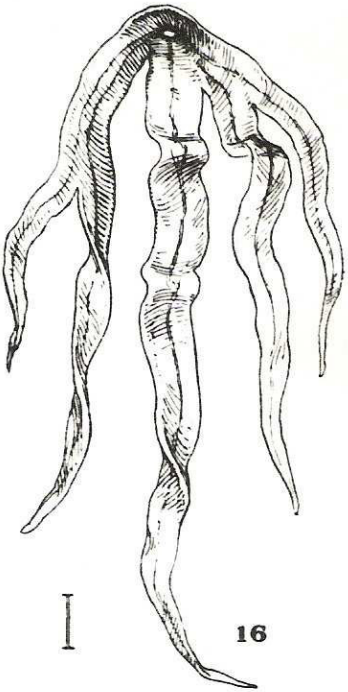

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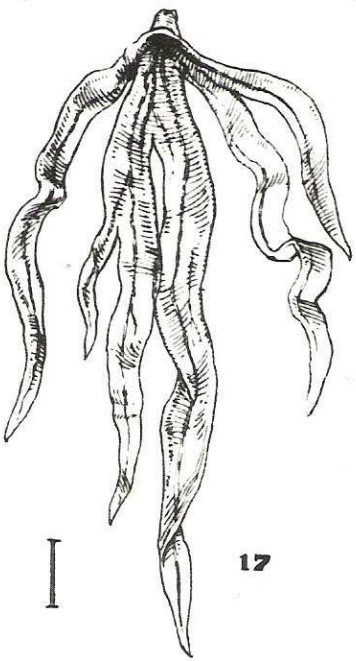

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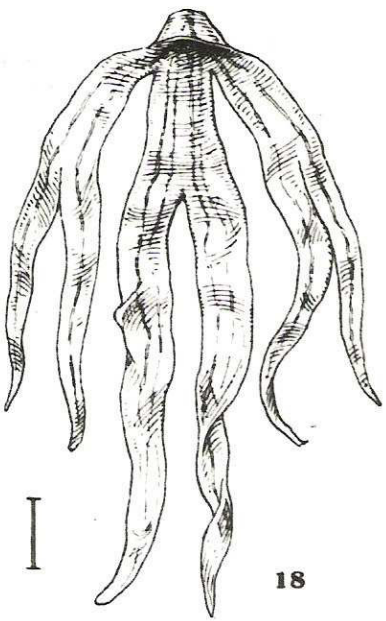

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PLATE 4

EXPLANATION OF FIGURES

19 Section through trophotaenia of 16-mm. embryo of Goodea luitpoldi at a point midway between basal and distal ends.

20 Section through distal end of a process of a 13-mm. embryo of Goodea atripinnis. The terminal portions of the processes of Neoophorus diazi and Goodea luitpoldi have almost identical structures.

21 Section through base of a process in 13-mm. embryo of Neoophorus diazi. The spongy layer of stroma is thin and the primary tissue space is shallow. Structure of the process at a more distal point is like that of Goodea luitpoldi (fig. 19).

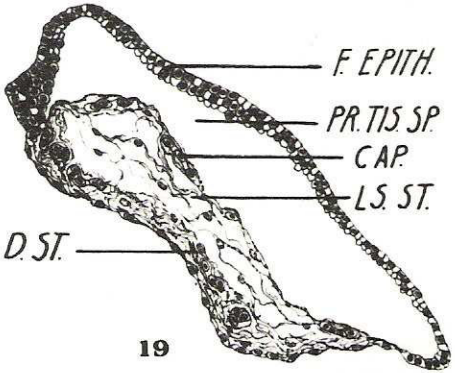
22 Cross section of trophotaenia of Balsadichthys whitei.

23 Section of process of Balsadichthys whitei during its resorption. The external epithelium has disappeared, the primary tissue space has been lost and the stroma has condensed and lost its characteristic structure.

24 Cross section of trophotaeniae of Chapalichthys encaustus.

ABBREVIATIONS FOR ALL FIGURES

Bl. V., blood vessels
Cap., capillaries
D. St., dense stroma
Epith., epithelium.
F. Epith., free epithelium
Ls. St., loose stroma
Pr. Tis. Sp., primary tissue space
S. Tis. Sp., secondary tissue space



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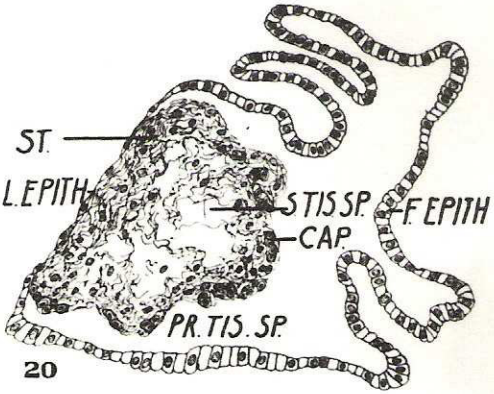

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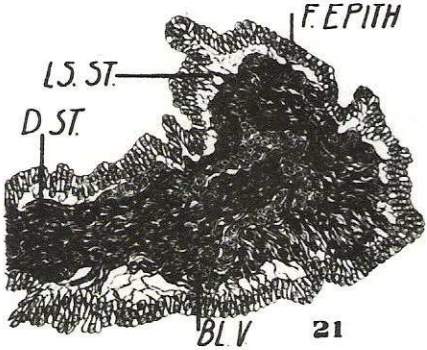

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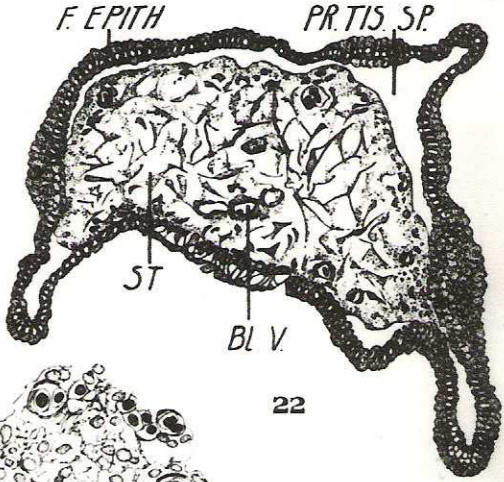

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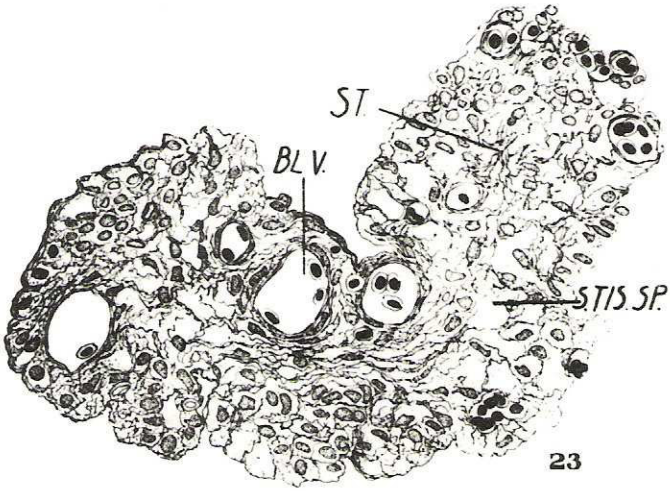

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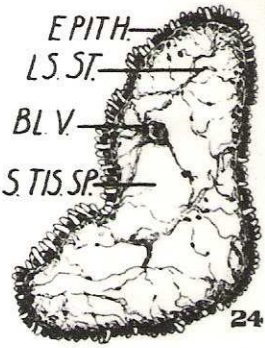

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