JOURNAL

OF

MORPHOLOGY.

THE EMBRYOLOGY OF THE UNIONIDAE.

A STUDY IN CELL-LINEAGE.

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mesodermic cells (myocytes ; products of the larval mesoblast), some of which show a paired arrangement (Strangzellen of authors). Stretching across the primary body cavity from one shell valve to the other, nearer the anterior than the posterior end, is the larval adductor muscle, likewise a product of the larval mesoblast ; dorsal to this, and running parallel to the hinge-line from the posterior end of the primary body cavity to open anteriorly between the five large cells already noticed, is the large unicellular thread-gland.

The accompanying text figures (3, 4, and 5) will make the relations of the areas more readily referable to the cleavage stages. It of course goes without saying that the areas in the second and third figures are only approximately correct in outline. The first figure is an actual reproduction of Fig. 47 (Pl. IV).

(b) *Transformation of the Young Larva into the Glochidium.*

Perhaps the simplest way of describing the transformation into the glochidium will be, first, to describe the glochidium, and then to ask how this form is derived from that of the young larva already described. Figs. 92 and 93 illustrate this description.

The glochidium larva of Anodonta possesses two triangular shell valves joined by their bases at the hinge-line. The valves are quite thick, strong, and brittle, and pierced by numerous fine pores. At the apex of each valve is a strong hook (provided with numerous teeth), which is quite different in appearance in Unio and Anodonta, being much stronger in the latter form, which I have figured. These hooks are joined to the valve proper by a hinge, and are moved by special muscles (myocytes). Each valve is somewhat spoon-shaped, and the cavity is lined by the larval mantle, consisting of large, flat vacuolated cells. The curve of the anterior edges of the valves is considerably greater than that of the posterior edges; the hinge-line straight, and of considerable extent. The valves are united by a strong internal ligament. The adductor muscle is very powerful, and, as in the young larva, is nearer the anterior than the posterior end. The larval mantle bears four paired

tufts of stiff, sensory hairs, arranged in a very characteristic manner. Three pairs lie just beneath, and within the powerful hooks ; these three form the angles of a right-angled triangle, the base of which is parallel to the transverse plane of the larva, the apex being directed anteriorly. The fourth pair lie on either side of the opening of the thread-gland. These are, undoubtedly, the four tufts described for the young larva ; but how different in their relative positions ! As in the young larva, each tuft is borne by a single cell, the base of which is elongated in a peculiar manner, to be described more fully later on.

Near the posterior angle of the valves are two ectodermal pits—the lateral pits. Between them, beneath the ectoderm, is the entodermal sac. Behind this lie the lateral wings of mesoderm cells. The ventral plate occupies the whole of the posterior median region as far forward as the oral plate, which has now assumed the form of a stomadeal invagination. Just in front of the oral plate is the opening of the thread-gland, from which the long, much-tangled larval thread has been extruded.

The transformation of the young larva into the glochidium is attended by a series of shiftings and displacements of cells and groups of cells, which make this part of the development extremely difficult to follow. Flemming is the only author who has described these processes in detail; and indeed his description leaves little to desire in some ways. But Flemming was so uncertain as to the morphological meaning of the larval parts that he gave them all special names: "Wimperschild" = ventral plate ; "Vorderwulst" = entodermic sac ; "Mittelschild" = oral plate. It is due to this failure on the part of Flemming to recognize the homologies of these various parts that the apparent neglect of this part of his work is due.

The early appearance of the four paired tufts of hairs is of great assistance in following these changes. The arrangement of the sensory hairs on their first appearance has already been described. Their final arrangement may be seen in Fig. 93. To recapitulate: At first they are arranged in a row on each side, as follows : one tuft to the side of the thread-gland aperture, and a second tuft a little below this; the third lies just above the oral plate, and the fourth to the sides of the ento-

dermic sac.[1] During the metamorphosis the first two pairs move backwards with the thread-gland nearly to the oral plate. They thus come to be associated with the third pair of sensory hairs, which lie near the oral plate. When the invagination of the larval mantle takes place it is these three tufts which lie beneath the shell-hooks on each side. By this time the oral and ventral plates have grown together, and the fourth pair of sensory hairs now lies a little in front of the oral plate, and to the sides of the aperture of the thread-gland.

From the posterior angle of the valves of the shell to the oral plate—which is now assuming the character of a stomadeal invagination (in February glochidia of Anodonta)—the whole median surface is formed by cells of the ventral plate. The further growth forward of this plate is what causes the anterior displacement, in parasitic glochidia, of the oral plate to its definitive position. The foot—which is formed in this region—is then derived from cells of the ventral plate. It of course goes without saying that during these shiftings the larval mantle has invaginated. Having thus outlined the metamorphosis, it now remains to treat of each stage in detail.

The most striking difference between the young larva and the glochidium is the bifid condition of the mantle in the latter as contrasted with its unpaired condition in the former. It has been known since the time of Flemming's paper that the difference is established by the invagination towards the dorsal line of the whole ventral surface of the young larva along the median plane. But while this has in general been known, the histological changes which must accompany such a stupendous transformation have never been described. These are illustrated in Figs. 83 to 91. The preparation consists, first, in the establishment of a line of suture-cells (Figs. 80, 82, and 86) which divides the basis of the larval mantle into two halves, from the thread-gland to the oral plate; and, second, in the vacuolation of the cells which are to invaginate. Invagination

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[1] This differs from Schierholz's description of their original position. It may be, however, that he overlooked their earliest appearance, when they are seen with difficulty. Schierholz described three pairs as lying near together, just beneath the edge of the shell, at the transverse level of the oral plate. This is not their original position in Unio.

commences, as might be expected, along the line of the suture-cells, and is at first most active near the thread-gland (Fig. 82). It is accompanied by very pronounced changes of form on the part of the invaginating cells. The greater mass of the proto-plasm migrates to the inner end of the cells (Fig. 85); the nucleus accompanies it — a very usual appearance in large invaginating cells ; the cells then roll up and in towards the shell, which thus comes to be lined by two layers on each side (Figs. 87 and 90): first, the protoplasmic layer already spoken of (which is very intimately attached to the shell); and, second, the cells of the invaginated mantle. Beginning, as I have said, in front, the invagination passes backwards, in proportion as the oral plate travels towards the ventral plate, which, on its part, moves forward to meet the former. *The rest of the mantle rudiment is thus divided into lateral halves and invaginates under the same appearances, carrying with it the median ventral and oral plates, which have now met and occupy the whole of the posterior region.*

The vacuolation of the larval mantle cells begins in quite an early stage—about the stage of Fig. 79. Flemming has figured and described the appearance of these cells at this time. The vacuolation, which is not at first very marked, soon becomes more and more exaggerated (Fig. 85). Indeed, it seems as though there was an active effort on the part of the cells in question, with a given amount of protoplasm, to cover the greatest space possible. The transition from the compact columnar cells of Figs. 76, 77, and 78, to the flat, much-vacuolated cells of Figs. 84 and 93 is most striking.

The suture-cells are well seen in Fig. 90 and in section in Figs. 85, 86, and 87. They are long, spindle-shaped, deeply staining cells, with rod-like nuclei ; in cross section they are wedge-shaped (Pl. VI, Fig. 85).

During the invagination of the mantle, the thread-gland has shifted its position backwards along the line of the suture-cells, and now lies just in front of the oral plate. Although the displacement of the thread-gland takes place along the line of the suture-cells, yet I should hesitate to attribute any active share to these cells. They seem rather to be the preformed

path of displacement, and serve to separate the halves of the larval mantle as well. Schierholz has figured a muscle-cell connecting the thread-gland with the oral plate, and attributes to it the function of causing this displacement.

The ventral plate goes through some interesting changes (to which I have already referred) about this time. Figs. 83 to 89, representing sections in various planes through the stage of Fig. 82, illustrate the description. The ventral plate grows past the posterior margin of the larval mantle (which represents the anterior end of the blastopore) and towards the oral plate (Figs. 83 and 84), which is at the same time moving backwards through the larval mantle. At this time the oval plate can be recognized only as a cluster of deeply staining nuclei (Fig. 84), all traces of its previous pit-like condition being obliterated by the great expansion of the cells of the larval mantle. A tongue of cells of somewhat similar appearance to the ventral plate at the opposite end of the embryo might lead to the belief that similar processes of development were responsible for the two structures; and hence that the appearance of free, forward growth of the ventral plate was illusory. But that this is not the case is proved by horizontal sections (Figs. 86 and 87). These show that at the anterior end of the embryo (*i.e.,* directly opposite the ventral plate) there is a protrusion of the cells of the larval mantle without the shell, caused of course by the violent contraction of the adductor muscle on the addition of killing reagents. There is nothing of this sort to be seen at the posterior end. It is the section of the protruding cells which is seen in sagittal section at the anterior end. (*Cf.* lines of section in Figs. 84 and 87.) I have hence been forced to conclude that there is an actual growth forward of the ventral plate above the cells of the larval mantle. The oral plate has been moving backwards through the larval mantle at the same time. During the invagination of the mantle the two structures meet and unite (Fig. 88).

The mantle cells have rolled away to the side; and hence the whole of the median portion of the glochidium, from the oral plate to the posterior angle of the shell, is formed from the ventral plate (Fig. 93). According to the united testimony of

those who have studied the post-embryonic development, the anterior part of this area is the basis for the formation of the foot and pedal structures.

Schierholz derives the rudiment of the foot from the median portion of the cells of the larval mantle lying between the oral plate and the anterior end of the ventral plate. That I am unable to agree with him goes without saying.

It is practically certain that the anus forms behind the anterior limit of the blastopore, but still within the limits of the area originally occupied by its posterior portion.

It will suffice to merely mention the lateral pits (cf. Figs. 89 and 93 to 97) lying at the sides of the foot-fold, as we may now call the area of the ventral plate. They are covered with active cilia, which are in direct continuity with the cilia of the foot-fold (Fig. 93). The structure of the walls is shown in the sections (Figs. 94 to 97). Schierholz and Schmidt derive the gill-filaments from the outer walls of these pits. Within the pits, according to Schierholz, lie two or more rounded cells which he regards as the basis of the otocysts. I have sometimes seen such cells in the stage of Fig. 79 lying on the surface near the anterior end of the ventral plate, but it seemed to me that they did not persist. In any case it is difficult to see how they could represent the otocysts.

The cerebral ganglia have begun to form in some glochidia of Anodonta in February. A section through their rudiment is shown in Fig. 94, which is taken about 22 μ. in front of the stomodaeum.

The bristles which lie on each side of the thread-gland and beneath the hooks of the shell have been considered sensory by all authors who have mentioned them. I found that when the glochidia were left for some time in a weak solution of methylene blue the cells bearing these bristles were the only ones in the embryo which took the stain. After fixing with picrate of ammonia, long, stained protoplasmic processes of these cells could be traced for some distance beneath the larval mantle. In Fig. 86 I have shown the course of the processes of the lateral bristle-bearing cells. In no case was I able to make out any coördinating structure with which the processes

were connected, though one can hardly doubt that such a structure exists. Flemming and Rabl have figured somewhat similar but shorter protoplasmic processes to the bases of these cells. Their reaction to methylene blue seems to me fresh evidence of their sensory nature.

I do not include a detailed description of the cells in question ; for that has already been done by Flemming and Rabl. I shall merely call attention to the conical form of these cells and their elevation above the surrounding surface (Fig. 92). They are supposed to transmit to the adductor muscle the stimulus which causes its contraction. The necessary stimulus might of course come from contact with the prospective host, in which case the contraction of the muscle would force the hooks into its skin, thus securing the requisite attachment (Schierholz).

Mesoblast.

In the stage of Fig. 82 and presumably somewhat later, the teloblasts of the primary mesoblast are still recognizable. The remainder of the primary mesoblast has fallen into a clump of small cells, which take up a position behind the entodermic sac as the latter moves forwards (Fig. 84). In the glochidium the mesoblast is very distinctly paired and lies in contact with the posterior walls of the lateral pits (Figs. 89, 94, and 97), stretching to the posterior end of the embryo on each side. A special wing of the mesoblast may be seen on each side behind the lateral pits. In well stained specimens this portion of the mesoblast shows but few clear nuclei with distinct nucleoli (Fig. 93). According to Schmidt, these cells are the fundament of the organ of Bojanus (the nephridia).

Some of the myocytes are specially modified as retractors of the hooks (Schmidt). The others are attached to the larval mantle and shell, and serve to keep the former in varying degrees of approximation to the latter.

Entoderm.

In embryos of Unio of the stage of Fig. 82 the entoderm no longer forms a sac, but has become a mass of cells (Figs. 83

and 84).   It is already beginning to stretch forward towards
the oral plate above the cells of the larval mantle.   It is
no doubt the mechanical cause of the splitting of the larval
mantle, which permits the ventral plate to come in contact
dorsally with the entoderm sac and to fuse anteriorly with
the oral plate.   In the glochidia of Unio, which do not as
such reach so advanced a stage of development as those of
Anodonta, the entoderm remains in this state till the post-
embryonic development begins (*cf.* Fig. 89).   In those glochidia
of Anodonta, however, which have wintered in the maternal
gills, the entoderm has already begun its differentiation.   It
has taken on the form of a sac which in one case ran through
seven sections of $7\frac{1}{2}$ mm. each (Figs. 95–97).   Lateral expan-
sions in the middle of its course I took for the liver diverticula
from comparisons with Schmidt's sections of parasitic larvae
(Fig. 96 *l.c.*).   Anteriorly it was connected with the stomo-
daeum (Fig. 95) and posteriorly the end-gut was indicated
(Fig. 97).

General Remarks.

One cannot view such a remarkable and unusual series of
phenomena as accompanies the transformation of the young
larva into the glochidium without asking one's self what is
the reason of it all?   Why, for instance, should the thread-
gland be formed so far from its definitive position?   The most
natural explanation is that the primitive function of the organ
in question has changed, and that a new position seemed more
favorable for the discharge of the new function.   On such an
hypothesis there is nothing wonderful in such phylogenetic
changes of position being repeated in ontogeny.   We can
easily apply this to the explanation of the displacements of
the thread-gland.   In its definitive position practically in the
centre of the ventral surface, it manifestly occupies the best
position for the discharge of its present function, which, as we
have seen, is probably to assist the glochidium in attaining
parasitic attachment to its host.   For if the thread becomes
attached, for instance to a fish's fin, the larva is pulled on to
the fin ventral surface down ; when the muscle contracts the

hooks are forced into the tissue of the fin. Now were the original position of the thread-gland to be retained, *i.e.*, at the anterior angle of the valves of the shell, the larva would not be likely to "land" on the fin in so favorable a position for attaining a secure footing. We have seen before that the primitive function of this gland was probably excretion ; the change in function, then, has brought about a corresponding change in position.

I should not attempt to apply such an explanation to the movements of the oral plate and ventral plate, but would rather explain them as caused by the necessities of precocious segregation which must often isolate organs which later are intimately related.

Two factors are responsible for the redistribution of the sensory hairs in the glochidium, *viz.*, the backward motion of the thread-gland, and the invagination of the larval mantle. I have just considered the movement of the thread-gland; now as to the larval mantle. I call this the larval mantle because all authors who have described its later history state that it does not form (or does in part only) the mantle of the adult, but degenerates, giving us the so-called "fungus-like bodies" of Braun. The larval mantle is established certainly in a very curious way, and yet I think that a little consideration will convince us that at bottom it is not much different from the mantle of other forms. Its borders are formed by the evaginated edges of the shell-gland to which the shell remains attached. Practically the same thing is true for the embryonic mantle of all Molluscan forms. The difference is simply that the cavity is so enormous in this larva; and instead of being a groove-like cavity above the foot, deeper at the (primitive) posterior end, here the cavity is so great that the embryo lies within it at one end. Schmidt has attributed this concentration of the embryonic area to the immense development of the adductor muscle. It seems to me, however, an unnecessary assumption to make, for the parts in question no doubt occupy all the space they require. We should expect the embryonic material to assume a compact form, and its position at the posterior end is the natural one. The posterior end is always the growing zone of the embryo.

But why these parts are so small is a different question. We can recognize in this the degrading influence of parasitism. It would, indeed, be strange if this mode of life, which can so profoundly influence animals which have become adapted to it, as to render it a matter of speculation in what corner of the animal kingdom to classify them, had not left a deep imprint on the organization of this larva. The effect of parasitism is to exaggerate all organs essential, and to eliminate all that are inessential, to the parasite. This is precisely what has taken place in the glochidium. The larval thread, the strong muscle, the heavy shell with its hooks, and the larval mantle, are all essential to its peculiar mode of parasitism. The foot, the mouth, the intestine, the heart, *etc., etc.*, are all inessential. The former have thus been enormously exaggerated, becoming precociously impressed on the cleavage of the ovum ; the latter have been reduced to mere rudiments, the reduction also leaving its imprint on the segmentation ; but they have not been eliminated, because they are functional organs in the adult.

This is one of the most interesting of all cases of parasitism, because we have an animal fully equipped as a larva for parasitic existence, and later leading an independent life. It shows us how far parasitism can go without eliminating the possibilities of a higher evolution. It seems strange that the parasitism should finish with the larval life ; but that it does so, and that, despite its short duration, the preparation therefor should so profoundly alter the characters of the larva, is one of the best examples of the oft-emphasized fact that natural selection deals no less with the larva than with the adult. We might search the animal kingdom through without finding a better example. What a bountiful supply of transitory organs of offense and defense has nature supplied to this larva ! and all that a passing and purely larval condition should be ensured in the greatest possible number of cases !

Another important question which suggests itself, is : Why has this brief parasitic period been intercalated in the life history of this animal ? I think that Schierholz answered the question very satisfactorily when he said that it was to avoid the injurious action of the fresh water on the delicate shell of

the young animal. As parasitism gradually became the fixed habit of the species, the adaptation to the requisite conditions became more and more perfect, until the parasitism became a necessary consequence of the structure, and an indispensable condition of development.

The parasitism of the glochidium is but one way of securing protection against the injurious effects of fresh water on delicate larvae. The same protection is assured other forms (turbellarians, Cyclas, gasteropods) by a foetal development, which takes place either in the body of the mother or in impervious capsules. The mode of securing this end among the Unionidae is evidently correlated with the enormous number of young produced. Not that the enormous number of the young made actual viviparous reproduction such, *e.g.*, as in the Cycladidae, impossible, and hence forced, so to speak, the species to devise another means of protection. It is more logical to hold either that the parasitic habit preceded the production of such a multitude of larvae, or else that both evolved *pari passu*. We cannot, at any rate, suppose that a species could be thus perpetuated if only a few young were produced, so precarious and uncertain is the attainment of the necessary conditions of higher development.

If we suppose the Unionidae to have been derived ultimately from a marine form, we are offered a hint as to the possible mode of evolution by the present condition of Dreissena, which is evidently undergoing a similar change of habitat. The development of this form is a metamorphosis with a free-swimming larva, which hardly differs from the marine larvae of the same class. It is easy to picture two or three possible courses of evolution open if it becomes completely adapted to life in fresh water (in which case, as all our experience tells us, the larva would be lost). In the one case it might become purely viviparous like Cyclas, and produce but few young ; or the ova might be deposited in impervious capsules (as, *e.g.*, pulmonates) ; or, again, the larva might in some way become adapted to parasitism, with consequent protection to its delicate structure. It is practically certain that in this last event the larva would change in two ways: First, so as to make it an

efficient parasite ; and second, so as to be protected, as far as possible, during its brief but necessary contact with the fresh water.   To ensure the continuance of the species an enormous number of young would have to be produced.   With the aid of some such an hypothesis the curious ontogeny of the Unionidae becomes more comprehensible.

(c) *Axial Relations.*

I have left till the last the consideration of the trochophore stage, and the axial relationships of the larva in the Unionidae, because it seemed better to have the whole course of develop-
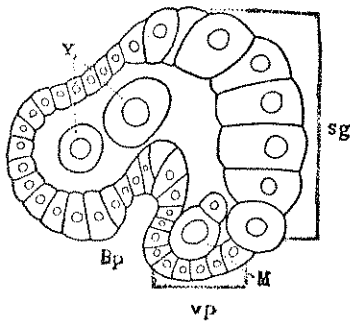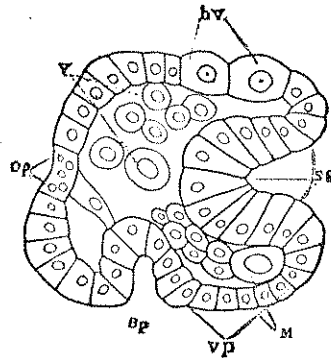
FIG. 6. — Gastrula of Unio.
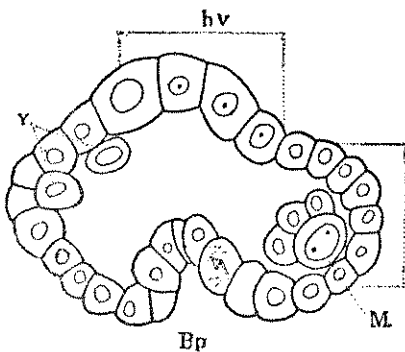
FIG. 7. — Slightly older Gastrula of Unio.

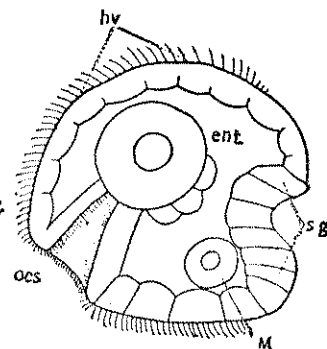FIG. 8. — Cyclas (after Stauffacher).

FIG. 9. — Teredo (after Hatschek).

Bp. Blastopore.
h.v. Head-vesicle.
o.p. Oral plate.

v.p. Ventral plate.
Ent. Entoderm.
M. Mesoblast.

oes. Oesophagus.
s.g. Shell-gland.
Y. Larval Mesoblast.

ment in mind in such considerations. The accompanying text
figures (6 to 9) require but little explanation; they show that
there is no real difficulty in recognizing the homologous areas
in Unio, Cyclas, and Teredo. The latter is one of the most
typical of the marine veligers; that is to say, approaches most
nearly the trochophore in its structure.

Of the typical trochophore organs, the apical plate with its
tuft of cilia, the praeoral and postoral rows of cilia and the
head kidney are missing in Unio. These are of course among the
most characteristic organs of the trochophore and most essential
to the free life of the larva. It is these organs which always
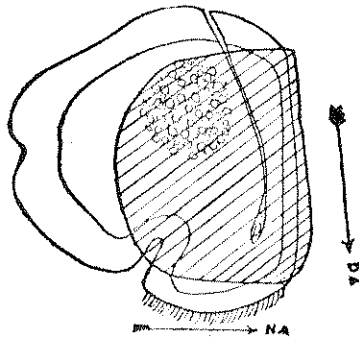degenerate more or less subsequent to the giving up of the

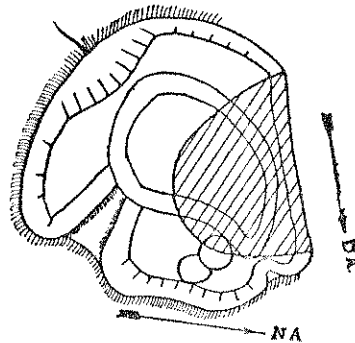FIG. 10. — Young Larva of Unio.
N.A. Neural Axis.   D.A. Dorsal Axis.

FIG. 11. — Teredo (after Hatschek).
[N.A. Neural Axis.   D.A. Dorsal Axis.

free life. A complete series can be traced through the various
degrees of degeneracy of the organs in question to their com-
plete absence in the Unionidae, where we can recognize only
the homologous areas. The swollen cells of the head vesicle
are the only remaining differentiation of the apical area which
can be interpreted as rudimentary trochophore organs.

It is important to notice that in the veliger stage of all
Mollusca the long axes of the shell or shell-gland and of the
foot, which in the adult are parallel, are inclined at an angle of
nearly 90° to one another. The figures 10, 11, and 12 in the
text illustrate this in Anodonta, Ostrea, and Teredo. Even the
most cursory examination of Gasteropod larvae will show that
the same thing occurs there. This is due to the fact that the
dorsal and ventral surfaces of the trunk are independently

established in these forms.   The two most important factors in establishing the adult relations are the growth of the shell-gland, *i.e.*, dorsal region, and of the foot respectively.   The shell-gland assumes the adult relations first owing to its early importance; the foot or neural axis is established later; this is in adaptation to its lack of function in the trochophore.

These axial shiftings have often been referred to.   It will, nevertheless, be useful to review shortly the clearest accounts of them.   Fol (No. 44) gives a remarkably straight-forward account of the axial shiftings in the pteropods and heteropods.   His statement in his pteropod paper is so concise
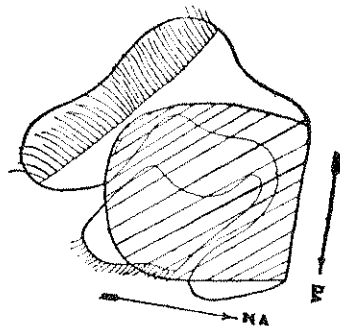

FIG. 12.—Ostrea (after Horst, from Korschelt and Heider).

N.A. Neural Axis.   D.A. Dorsal Axis.

that it may be quoted entire (l.c., p. 202).   "En effet, aussitôt que les deux feuillets primitifs de l'embryon sont formés, le feuillet externe se met à croître et à s'étaler beaucoup plus rapidement d'un côté que de l'autre.   Ce côté à croissance rapide répond à la région ventrale et postérieure de la larve, à celle où se trouve, on se le rappelle, la sphérule primitive protoplasmique, à celle qui donne naissance au pied et au manteau.   Le tissu ectodermique qui occupait dans l'origine le pôle formatif subit de la sorte un déplacement relatif et paraît remonter le long du dos de l'embryon pour arriver enfin à la région céphalique."

" La sphérule primitive protoplasmique " to which Fol refers is the posterior macromere.   The mantle and the foot, the whole trunk in fact is traced back to the posterior macro-mere.

In his heteropod work Fol is, if possible, even more explicit. He shows that the region of the shell-gland is at first posterior, and that gradually it comes to lie above the mouth, *i.e.*, dorsally; at the same time the upper pole, as marked by the polar globules, is pushed around anteriorly until finally it lies at the anterior end of the body. The foot area has expanded at the same time. Thus there is a change of axis which has been accompanied by the formation of new regions, viz.: the shell-gland (dorsal surface), and the foot (ventral surface). Where these two regions meet posteriorly there must be a stationary area, a zone of growth. This region of growth corresponds in position to the first somatoblast of Unio.

Later authors describe a stationary area in the region indicated. Conklin (No. 40) says, " The cells of the posterior arm (of the cross) enlarge greatly and are carried forward until they lie over or even anterior to the cross-furrow, while the point at which the polar bodies are attached (the centre of the cross) is carried forward through an angle of about 90° so that it finally lies at the anterior end of the long axis of the embryo. The position which the polar bodies first occupied (immediately over the cross-furrow) coincides with the middle of the dorsal area, while the ectoderm cells which immediately surround the ectoderm pole are carried forward until they lie at the cephalic pole of the embryo. The endoderm seems to take no part in this shifting, and the ectoderm on the posterior side of the ovum is not shifted forward, but grows around in the opposite direction. There is thus a stationary point in the ectoderm on the posterior side of the ovum in front of which the ectoderm cells are shoved forward, and back of which they are shoved backward and downward. This stationary point coincides very nearly with what is later the region of the shell-gland."

This stationary point coincides also very nearly with the region of the first somatoblast. It must be a region of proliferation, anteriorly and posteriorly.

Heymons (No. 47) has witnessed the same phenomena in Umbrella. He says, p. 26 : " Hieran sind lebhafte Wucherungs-processe im Ektoderm betheiligt. Dieselben schliessen sich im wesentlichen an die neuerdings auch von Conklin be-

schriebenen Erscheinungen an.   Im hinteren Theil des Ekto-
dermfeldes beginnen sich die Zellen mehrfach zu theilen, und
nach vorn fortzuschieben, während gleichzeitig das durch die
Richtungskörper gekennzeichnete Centrum des animalen Poles
allmählich an das Vorderende gelangt.   Nur der hinterste
Theil des Ektodermfeldes nimmt an dieser Verschiebung keinen
Antheil, sondern wuchert weiter nach hinten, d. h., nach dem
vegetativen Pol hin.   Die beiden Urmesodermzellen wurden
dadurch gewissermassen vom Ektoderm entblösst, oder doch
nur von sehr wenigen plattenförmig ausgebreiteten Ektoderm-
zellen an ihrer dorsalen Fläche bedeckt.   Letzere stellen damit
die Grenze zwischen der nach vorn und der nach hinten
wachsenden Partie des Ektoderms dar.   Unmittelbar vor ihnen
macht sich später, wenn die geschilderten Vorgänge beendet
sind, weiter eine starke Vermehrung und Anhäufung von Ekto-
dermzellen bemerkbar, die sich später in das Innere einsenken,
und die Anlage der Schalendrüse bilden."

*If this region of proliferation were traced further back it
would probably be found that it was referable to a single cell,
viz.: the first somatoblast.   This is what I have done in the case
of Unio.   The whole ectodermal trunk region is thus traceable to
the first somatoblast, the second product of the posterior macro-
mere.   The mesodermal elements are traceable to the same macro-
mere.   The whole trunk region behind the mouth can thus be
traced back step by step to the posterior macromere.*   Dr. Whit-
man showed that this was true of Clepsine as far back as 1878,
and Wilson has shown essentially the same thing for Nereis.

It seems to me that these facts afford a new basis for com-
parison of the trunk of Annelida and the postoral shell- and
foot-bearing region of Mollusca.   They correspond in position
and in their relation to the germinal layers ; it seems also that
they can be traced back to identical blastomeres.   I must con-
fess that Unio is a form but little adapted to place this question
beyond dispute.   I have, however, the utmost confidence that
in less highly modified forms this position will be sustained.

EXPLANATION OF PLATE VI.

FIG. 82. Embryo slightly older than Fig. 79 ; seen from the ventral surface. Invagination of larval mantle begun.

FIG. 83. Obliquely sagittal section of stage of Fig. 82 ; *v.p.*, ventral plate.

FIG. 84. Median sagittal section of same stage.

FIG. 85. Ventral half of transverse section through stage of Fig. 82. Shell not drawn in.

FIG. 86. Horizontal section through ventral wall of same stage.

FIG. 87. Section slightly dorsal to Fig. 86 (*v.* Fig. 84 for plane of section).

FIG. 88. Median sagittal section of the young glochidium of Unio complanata.

FIG. 89. Transverse section of the same stage, passing through the intestine.

FIG. 90. Same series; three sections ($7\frac{1}{2} \mu$) in front.

FIG. 91. Horizontal section of same stage, showing opening of thread-gland into mantle cavity.

FIG. 92. February Glochidium of Anodonta, anterior view; only a mere fraction of thread drawn.

FIG. 93. Ventral view of same; shell gaping.

FIGS. 94-97. Four transverse sections from stage of Fig. 93. Sections asymmetrical, passing further forward on left side.

FIG. 94. Through cerebral ganglia.

FIG. 95. Three sections posterior to Fig. 94; *oes.*, rudiment of oesophagus.

FIG. 96. Five sections posterior to Fig. 94.

FIG. 97. Six sections posterior to Fig. 94.

(Sections 7.5 μ thick.)