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The External Features in the Development of Lepidosiren paradoxa, Fitz

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V. *The External Features in the Development of* Lepidosiren paradoxa, Fitz.*

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[Plates 8–12.]

Introduction.

The following paper constitutes the first instalment of an account of the development of *Lepidosiren*. The material upon which it is based was obtained during a sojourn which I made for the purpose amongst the swamps of the Gran Chaco† during the years 1896 and 1897.

I should in some ways have preferred not to publish until in a position to give a fairly complete and rounded off account of the whole of the phenomena of development. This would, however, have meant very considerable delay, and I am induced to publish the set of drawings illustrative of the external features, both by the advice of my friends and by the fact that this will serve to make known those features in the development which are after all of the greatest general interest. It will be time enough when the research is completed to point out any conclusions that may be drawn from it as to the affinities of the group to which *Lepidosiren* belongs; but I may be allowed even now to draw attention to one point which seems to me to lend unusual importance to the features attending its development. That is the peculiar conditions under which the development will be found to take place—in a secluded retreat, in which, while able to hatch at a comparatively early stage, the larva continues to exist, performing only those vital processes necessary to all life, sheltered effectually from having to fight for itself amongst those ever recurring changes in environment, which bring in their train the hiding away under a veneer of adaptation of features due to long heredity and of phylogenetic importance. The development

* I am disposed upon the whole to regard the specimens of *Lepidosiren* obtained by me as belonging to a single species, though a very variable one, and to agree with Lankester's criticisms upon Ehlers' species *L. articulata* (*cf.* Ehlers, 'Nachrichten der K. Gesell. Wiss. Göttingen,' 1894, No. 2, and Lankester, 'Trans. Zool. Soc. Lond.,' vol. 14).

† For the discovery that *Lepidosiren* occurs in the Gran Chaco we are indebted to Dr. Bohls (*vide* 'Göttingen Nachrichten,' volume above cited.)

of *Lepidosiren* under such conditions of seclusion—conditions, too, which probably remain constant over very long periods of time—is enough, I think, to lend a very special interest to its developmental phenomena, quite apart from the interest they must have as belonging to one of the Dipnoi and to the first of the Dipneumona which has fallen under embryological investigation.

In this first contribution I confine myself pretty closely to external features, though in passing I take occasion now and then to mention some interesting point of internal structure. In the general remarks appended to the recital of observations I do not hesitate to draw attention to points in which the phenomena recorded seem to have a wider bearing, even though the full discussion of the questions involved must be left over to succeeding chapters dealing with the various organ systems in detail.

Before proceeding, it is a pleasant duty to acknowledge to what a very unusual extent the carrying out of my enquiry has been due to the co-operation of many friends.

In bearing the financial strain of the expedition I was aided by a grant of £200 from the Balfour Fund of the University of Cambridge, and another of £50 from Mr. J. S. BUDGETT, of Stoke Park.

For arranging transport, for providing us with a roof over our heads during the rainy season, for acting as interpreters of the Lengua language, and for help of the most varied kind in carrying out the research, I have to thank my two friends, Messrs. ANDREW PRIDE and R. J. HUNT. And Mr. HUNT I have to thank further for the careful way in which he collected and preserved additional material after the date of my departure.

Dr. MICHAEL FOSTER kindly obtained official recommendations for us from the Foreign Office, and this, together with the ungrudging help of H.B.M. Minister in Buenos Aires, the Hon. W. A. C. BARRINGTON, did much to smooth away difficulties in Argentina and Paraguay. To all these, as well as to other friends who helped the expedition in one way or another, I must express grateful thanks. Finally I must mention Mr. J. S. BUDGETT, of Trinity College, Cambridge, who was my companion throughout the expedition, and whose constant help and whose constant good comradeship during times of trouble and sickness were indeed such as cannot be adequately acknowledged.

The embryological material of *Lepidosiren* was all collected in the swamps about Waikthlatingmayalwa—in the Gran Chaco boreal (approximate latitude 23° 27′ S.; and longitude 58° 11′ W.). A small proportion was collected in the swamps by myself; the greater part was obtained by Indians. Of each batch of eggs as it was brought in to my temporary laboratory, some were at once preserved by a variety of methods, others were placed in dishes or tanks for further development. The larvæ lived pretty well in captivity; the young eggs were, on the other hand, very delicate. On this account, together with the poverty of the material of the very early stages, I am unable to give satisfactory *times* for the duration of the earlier phases of development. The working up of my material has been carried on in the laboratory of Mr. ADAM SEDGWICK—whose advice and teaching will, I hope, be visible enough through the course of this paper.

HABITS.

The interior of the Gran Chaco, about the level of the southern tropic, forms an almost dead level plain covered with tall coarse grass and dotted at intervals by fan palms (*Copernicia cerifera*, MART.). Otherwise almost imperceptible elevations are indicated by islands of dicotyledonous forest, a dense growth of such small trees as *Piptadenia quadrifolia*, N. E. BR., *Acacia præcox*, GRISEB., and various species of *Eugenia*, rising to a height of fifteen to twenty feet, while above these shoot up scattered taller trees, such as *Diplokeleba floribunda*, N. E. BR., *Quebrachia morongii*, BRITTON, *Cæsalpinia melanocarpa*, GRISEB., and a species of *Tecoma* (?) with large yellow flowers. Other wide spreading tracts lie somewhat below the mean level. For a large part of the year these are submerged and form swamps characterised by their own peculiar vegetation. The fan palms which dot the neighbouring plain cease near the margins of the swamps. These have the appearance of vast meadows, bounded in the far distance by a line of palm tops marking their further edge—and their otherwise uniform expanse varied occasionally by an isolated clump of palms indicating the position of an island. The greater part of the swamp is choked by a dense growth of tall Papyrus, or by coarse swamp grass bound together into an almost impenetrable mass by species of Convolvulaceæ and Asclepiadaceæ. The deeper parts of the swamp, where it may be, a sluggish stream creeps along, are mapped out by patches of a softer green foliage—the big leaves of a species of *Thalia*. In the swamp itself there are but seldom patches of open water, for where the larger swamp plants are absent the water's surface is still hidden under a floating carpet of *Pistia*, or *Azolla*, or a beautiful night-flowering *Nymphæa*.

During an ordinary rainy season the swamps have over most of their extent a depth of from two to four feet, though in places it may reach seven or eight. During the dry season the waters shrink up and the whole swamp may become dry.*

* The total rainfall for the year is about 60 inches, the rainy season being between September and April. There is little regularity, however, in the duration and extent of the rainfall; and in some years the rainy season is practically omitted.

As regards temperature the climate is one of considerable extremes. During the summer of 1897–98 the maxima of the various months taken in deep shade were as follows, in degrees Fahrenheit: November, 104·1; December, 104·0; January, 102·4; February, 104·0; March, 102·4. During the cold season the minimal temperature just touches freezing point.

It is these swamps which form the home of *Lepidosiren*. The creature is abundant, but one might expend much time in the swamps without ever getting more than the most fleeting glimpse of one. In habits it is normally sluggish, wriggling slowly about at the bottom of the swamp, using its hind limbs in irregular alternation as it clambers through the dense vegetation. More rapid movement is brought about by lateral strokes of the large and powerful posterior end of the body. *Lepidosiren* also burrows with great facility, gliding rapidly through the mud, for which form of movement the shape of the head, with the upper lip overlapping the lower and the "external" nares placed within the upper lip, is admirably adapted.

The diet of *Lepidosiren* is a mixed one. In the Chaco swamps, as BOHLS* has already pointed out, its favourite food is afforded by a large *Ampullaria*, which lives in enormous numbers in the swamps. Besides these masses of confervoid algæ are eaten. Young Lepidosirens, of 75 millims. in length, kept in a pool under fairly natural conditions, were found to have their gut full of the remains of the stems and other solid parts of Phanerogamous plants.

The gills being much reduced are quite unable to supply the respiratory needs of *Lepidosiren*. Even when the water is pure and in large volume the surface has to be visited at intervals. Owing to the want of suitable tanks, and the equally necessary fresh water at the only time of my stay in the Chaco when it was possible to get uninjured *Lepidosirens*, I am not able to say definitely what these intervals are. I have, however, aided by several sharp-sighted Indians, watched the surface of a pool in which I had half a dozen specimens for an hour on end without detecting one taking a breath of air. So that in all probability under such conditions the intervals may reach several hours in length.†

Two individuals contained in a small quantity of rather impure water were seen to take breaths of air at the following intervals in minutes :—

A ♂	5–2–3–3–3–4–4–2–3.
B ♀	$3\frac{1}{2}$–8–2–$1\frac{1}{2}$–$3\frac{1}{2}$–$8\frac{1}{2}$–2–$2\frac{1}{2}$.

Another individual which lay in thick mud preparatory to hibernation breathed at the following intervals—also in minutes :—

4–4–6–3–1–3–4.

The same Lepidosiren during other periods of observation appeared to breathe as continuously and rhythmically as a large Mammal.

So that on the whole the rate of pulmonary respiration appears to vary according to circumstance within very wide limits.

* Göttingen 'Nachrichten,' Jg. 1894.

† *Cf.*, GOELDI, 'Trans. Zool. Soc. Lond.,' vol. xiv., p. 419.

Both expiration and inspiration take place directly by the mouth. The tip of the head is pushed up above the water's surface, and the creature expires. The head is then usually withdrawn for a moment, and then pushed up again, the central parts of the lips separated, and an inspiration taken. After final withdrawal from the surface, a few bubbles are given off from the gill openings, probably the superfluous air left in the mouth and driven out on the recommencement of gill respiration.

The ordinary movements appropriate to branchial respiration may continue for a quarter of an hour, or even more, in a separated head. In the uninjured animal taken out of the water they are also continued, and the forcing of air, by this means, out between the soft and closely apposed lips of the gill openings gives rise to a very characteristic sound. Under normal conditions I have never heard a Lepidosiren make any sound other than a splash, and I have no evidence to support NATTERER'S assertion that it utters a cry like that of a cat.

Smell seems the best developed of the three ordinary special senses in *Lepidosiren.* Where there is a piece of food material one may see the creature with its head bent sharply downwards apparently sniffing about it. Sight appears to be very feebly developed in the adult, the eyes remaining very small while the rest of the body grows, and the great majority of individuals having the cornea white and unhealthy-looking. There is, however, a marked sensitiveness to light, and connected with this is a remarkable phenomenon, which may be suitably alluded to at this point. This is a change in colour induced by darkness. Every evening as dusk comes on the animals become paler in colour, the black chromatophores shrinking up to almost invisible dots, so that in the young animal the whole creature becomes practically white and semi-transparent, while in the adult, where the superficial epidermis is very thick, the change is not quite so striking, but still results in the general colour becoming markedly pale. At dawn the creatures are still pale, but gradually darken, until about sunrise the normal deep colour is re-attained. In unhealthy or badly wounded animals this reaction to light is much retarded; there the black chromatophores seem unable to push out their pseudopodia, and the general pale colour persists even under exposure to daylight.

During the rainy season, life being easy and food extremely abundant, the Lepidosirens eat voraciously; fat is stored up in great quantity in their tissues. This is especially the case in the tail region, where the large masses of lateral muscles become in great part replaced by orange-coloured fat.* As the dry season comes on, and progresses so far as to cause the area of water to greatly diminish in extent, a change comes, and the Lepidosiren ceases entirely to feed. The alimentary tracts of a large number of specimens which I examined at this period were completely empty. As

* The fat is actually deposited in the cells of the connective tissue septa between the muscles. This takes place to a special extent in the median longitudinal septum, which is so enlarged, especially in its ventral half, as to extend two-thirds of the way from the median plane to the side of the body, the inner portions of the myomeres having disappeared to make room for it.

the Indians put it, the Loalach now feeds on water. As the water shrinks more and more, and there is no longer enough to cover the gill openings, the Lepidosiren burrows down into the mud. As the water disappears he ceases his branchial respiration, but still keeps breathing by his lungs just as usual. As the mud stiffens, the opening in it made as he separates his lips to breathe, instead of being obliterated when the lips are closed and the snout withdrawn, remains patent. He gradually retires further down as the mud hardens sufficiently to keep the walls of the burrow from collapsing. Eventually* the Lepidosiren lies at the dilated lower end of a gallery closed externally by a kind of lid with a breathing aperture. In this portion he lies with his body sharply bent, and the tail folded over the face. Around the body is a copious secretion of mucus.† In the course of the tunnel there may be one or more lids like that closing the outer end. These are possibly due to occasional showers of rain during the dry season, the lower part of the burrow becoming filled with mud and the process of lid formation being repeated as at first.

In this retirement underground in the dry season *Lepidosiren* behaves like its African relative *Protopterus*.‡ The similar position assumed by the two animals in their dry season nest is very striking, as may be seen by comparing W. N. PARKER's figure of *Protopterus* with HUNT's of *Lepidosiren*.§

At the close of the dry season the Indians relate that the Loalach pushes out the door of its burrow, but remains in it for a time, till the water is deep enough for it to swim away.

The Lepidosirens, or Lŏálăchs, as the Lenguas call them, are hardly ever seen while the waters are up. The only thing to indicate their presence is a faint quivering movement of the grass as one moves along the bottom of the swamp. To the quite untrained eye this is almost imperceptible, but after a little experience with the Indians one becomes able to appreciate it, and the Indians themselves detect it at once. A small amount of wind suffices to hide the movement altogether, and consequently the Indians choose a time for hunting the Lepidosiren when the breeze is very light or when there is an absolute calm. The fishers usually start off about seven o'clock in the morning. They usually go alone. Large fishing parties, such as

* For details of the completed dry season burrow I am indebted to my friend, Mr. HUNT. *Cf.* 'Proc. Zool. Soc.,' 1898, p. 41.

† The mucous secretion of the skin of *Lepidosiren* appears to have a remarkable power of precipitating mud held in suspension by water. The mud of the Chaco is extremely fine and impalpable, and very muddy water required several hours of treatment with alum by the ordinary traveller's method before the mud was thrown down. A few live Lepidosirens put into a tank of the muddy water rendered it quite clear in a short time, the mud sinking to the bottom, and only a few flakes of mucus remaining floating about.

‡ *Cf.* STUHLMANN, 'Sitz. Akad. Wiss. Wien.,' vol. xxxii., 1888; and W. N. PARKER, 'Trans. Roy. Irish Acad.,' vol. xxx., 1892.

§ 'Proc. Zool. Soc.,' 1898, p. 41.

Bohls describes, I never heard of, except in cases where they were organised for my own benefit.

An Indian starting on a fishing expedition wears only an old garment round his waist, which is well tucked up when he gets to the fishing ground. Round his waist he has his string-work bag in which he carries his various little odds and ends. In his hand is his Loalach-kĭlyĭkthlŭkthlŭma or spear (fig. 1)—a piece of pointed $\frac{5}{16}$-inch iron rod, about three feet long, let into a piece of stick of about the same length to serve as a handle. In former days, as Bohls mentions, the spear was made of the hard Cascarandá wood, but with the introduction of iron rod by the missionaries as an article of barter, this has entirely supplanted the old material. From the edge of the swamp a journey of one to two miles has to be made through the swamp before a suitable fishing ground is reached. Here the water is from mid-thigh to waist deep and the vegetation is almost entirely coarse grass. The Indians *never*, so far as I can make out, fish amongst the "peguahó" (*Thalia*, sp.) as Bohls asserts. Nor do they fish amongst the Papyrus. The coarse thick grass growth is necessary for the track of a Lepidosiren to be obvious. As the Indian wades along, his spear over his shoulder, his eye constantly sweeps the growth of grass in his neighbourhood. At last he detects the faint quiver he looks for. It moves on for a few yards and he marks down the exact point at which it stops. He then, with spear poised, advances quickly, making as little disturbance of the water as possible, and arrived at the spot gives one prod after another until the violent shaking of his spear shows that he has transfixed his fish, or, as more often happens, the gentle quivering movement appears again in the vegetation as the Lepidosiren glides away through it. In this case he follows it up and repeats his efforts until he succeeds or loses track of his fish. For carrying about the Lepidosirens while still engaged in fishing, the Indians have devised a method as admirable as possible for saving trouble. Each Indian carries with him a large wooden or bone needle six or eight inches in length, through the eye of which is spliced a piece of stout string. On to this string each Lepidosiren is threaded as soon as it is caught and killed. The other end of the string is made fast to the Indian's waist belt, and in this way he is able to tow behind him a considerable number of these very slippery and also very weighty creatures with the least possible inconvenience. When he finishes fishing or when he leaves the swamp on his return home, he takes an elongated net that he has been carrying round him, laces together the opposite sides of this so as to make a cylindrical bag of it, lines it with plenty of grass to protect its sticky contents, and then places in it his Lepidosirens, and carries the whole home over his shoulder.

Fig. 1.

Loalach spear.

During the dry season, when the waters of the swamp have shrunk so that only in the deeper parts there are left pools a few inches deep, the Lepidosirens are obtained with greater ease. At this time the Indians go in parties. They take their spears, but, in addition, each cuts for himself a stout stick pointed at the end to be used as a rude digging implement. The party make their way to a suitable spot, where there is a fairly open space. The ground is covered with the collapsed swamp grass, which forms a mat, amongst which is perhaps four inches of water. The Indians scatter and proceed to probe the ground carefully with their spears in the search for the Loalach nests. The nests are situated especially along the margins of the papyrus growths, or close to a large tuft of grass. A nest is often discovered by the foot sinking into it. When this is the case the Indian probes the nest with his foot, and if he detects that the owner is at home, the other Indians come round and it is drawn out. It takes usually several men to ensure that the Loalach shall not escape—owing both to the extraordinarily slippery character of the skin and to the remarkable strength of the creature. When grasped in the hands, the Lepidosiren has a curious way of rotating its body about its long axis, which adds to the difficulty of holding it. The Loalach is of use to the Indian only as food. It is cooked either by roasting or boiling, and forms a thoroughly palatable dish.*

Breeding takes place within the first few weeks after liberation from the mud.† LANKESTER‡ has figured and described remarkable papillæ on the hind legs of male Lepidosirens, collected by Dr. BOHLS. During the greater part of the year these are comparatively inconspicuous. When the creature is set free at the beginning of the wet season, however, the papillæ begin to grow with extraordinary rapidity, and within a space of two or three weeks, may form slender filaments two to three inches in length (*vide* Plate 12 for male and female during breeding season), blood red in colour, from their intense vascularity. The main axis of the limb also appears to undergo a certain amount of enlargement. This extraordinary condition of the hind limb lasts only during the breeding season. Then the filaments rapidly disappear by atrophy—accompanied by the actual breaking off of fragments. Even after the papillæ have shrunk to their normal size they still, for a considerable time, bear a

* Amongst the adult specimens seen by me, females were more numerous, in the proportion of about 50 to 30, but this difference might, in part at least, be due to the greater size of the females, making them more likely to be detected by the fishermen; from the breeding habits one would expect there to be as many males as breeding females. Adult females averaged about 86 centims. in length, adult males about 77 centims. The largest female met with measured 102 centims. in total length, the largest male 98 centims.

† The exact time of this varies greatly from year to year in correlation with the extreme variability of the climate. In exceptionally rainless seasons, which are not infrequent, the swamps remain dry the whole year round. In 1896 the Lepidosirens were already free and spawning when I arrived on the scene—the first heavy rains having taken place three weeks before. In 1897 a careful watch was kept by the Indians, and Mr. HUNT reported the first eggs ten days after the first free Lepidosirens, on December 11. In the current season the swamps were still dry on February 12.

‡ Also referred to by EHLERS, 'Gött. Nachricht.,' Jg., 1894.

distinctive appearance from being crowded with black pigment cells—the pigment being, possibly, an excretory product associated with the intense digestive activity of the leucocytes concerned in the atrophic process. The appearance of the hind limb at various periods is shown in figs. A, B, C, and D on Plate 12.

What may be the object of the above modification of the hind-limb it is difficult to say. I am inclined to refer it to the category of modifications so often associated with the breeding season (*cf.* the newt's crest), commonly called ornamental, but which are perhaps more plausibly to be looked upon as expressions of the intense vital activity of the organism, correlated with its period of reproductive activity.

At the same time, as Professor LANKESTER has pointed out to me, the filaments from their rich blood supply, and the thinness of their walls, must serve as very efficient accessory organs of respiration.* Dr. HANS GADOW has also made the suggestion that the modified hind-limbs function as "spawning-brushes"—the mass of filaments becoming saturated with seminal fluid, and then being dragged over the eggs. Whether actually this function is performed can only be determined by future observations.

The eggs are laid in underground burrows† excavated in the black peaty soil of the bottom of the swamp. Each burrow has an entrance about four or five inches in width. This passes vertically down into the burrow, the bottom of which is nine inches to a foot beneath the surface of the ground. The burrow runs horizontally, and varies greatly both in shape and size. Sometimes it is nearly straight, sometimes curved or L-shaped in plan. One of these galleries I found to extend for about five feet, but the usual size is about two feet in length by about eight inches in width. After the eggs are laid the male remains in the nest with them—in a curled-up position from the size of the nest. Whether he remains after the young have escaped from the egg I cannot say.

I am not able to give any details as regards the act of spawning or fertilisation. The waters of the swamp are of a deep peaty brown colour, and this, together with the dense mass of vegetation pervading the water everywhere, effectually prevents all observation of *Lepidosiren* in its natural conditions. The Indians say that there is no copulation, the eggs being fertilised after they are laid, and this seems probably to

* Note added in correcting proof. Since writing the above, I am disposed to appreciate much more highly the respiratory capacity of the hind limb of the male during the breeding season. It is quite possible that with its aid the male may not be compelled to visit the surface at all during the time he is watching the eggs. There is a rich development of capillaries close to the surface of the filaments, forming an intra-epidermal network whose main function can scarcely be other than respiratory.

† This burrow is of course to be distinguished from the dry season burrow. The Lenguas apply to both the general name *thlankūk*, which means "house" or "nest." The breeding burrow is called *eltaanama* (the ordinary word for a bird's nest), the dry season burrow *etsāsa*. The two are quite different structures, the former being an actual excavation, the latter merely formed by the passage of the body through the mud.

be the case, although I failed to get direct evidence on which the statement might be based.*

THE CŒLOMIC EGG. (Plate 8, fig. 1.)

Only a single female was obtained by me with eggs lying loose in the cœlom. Each egg was enclosed in a colourless transparent capsule about 1 millim. in thickness.

The egg is spherical, and as a rule from 6·5 to 7 millims. in diameter, though it varies considerably, especially on the lower side of these dimensions. The egg is thus rather more than twice the diameter of the *Ceratodus* egg.

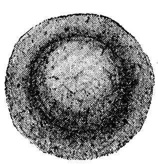
The larger part of the egg is of a very beautiful pale-salmon colour, this being the colour of the yolk granules. On the "animal" pole of the egg there is what I may be allowed to call a "germinal cap," white in colour, and covering about 100° of the surface.† The white colour here, and probably in other similar cases, appears to be due to the very fine sub-division of the yolk in correlation with the more intense metabolic processes taking place in its neighbourhood. A similar fine sub-division of the yolk granules seems very general where metabolism is active, and its object may be to make the yolk more easily and rapidly assimilable. The egg tends (up till the time when the segmentation cavity forms) to assume a position with the germinal cap downwards.

The Egg after Deposition.

The egg, as found in the nest, is surrounded by a thin, tough and horny capsule. This, I am inclined to think, is derived from the thick capsule of the cœlomic egg, the change in its consistency and thickness being a result of fertilisation; but this is mere conjecture, as the attempt to fertilise the few cœlomic eggs at my disposal did not succeed.

In addition to the horny egg capsule, I found in one batch of eggs a coating of jelly (*cf.* text fig. 2), evidently an oviductal secretion and corresponding with that found in Amphibia. In several other batches I found faint traces of the jelly, but in only the case mentioned was it well developed. The jelly coat in *Lepidosiren* appears to be vestigial, and this may not be unconnected with the conditions of comparative security under which the eggs develop in the nest.

Fig. 2.



Segmentation.

My account of the phenomena of segmentation cannot be very detailed, owing to the scanty nature of my material of the early stages, and to the great difficulty found in keeping the segmenting eggs alive. For the latter reason also I do not attempt to give data regarding the time elapsing between the various stages.

* It is impossible to look on the modified hind-limb, with its long, soft, non-erectile filaments, as of the nature of a copulatory organ.

† There is no trace of dark pigment in the egg.

The earliest stage of segmentation obtained by me is shown in Plate 8, fig. 2. Here, a single meridional furrow bisects the germinal cap without extending beyond its margin.

The second furrow appears in a plane perpendicular to that of the first. In the half-dozen eggs found in this condition there was, in each case, a displacement at the point of intersection of the furrows. In the egg figured (fig. 3), the first cleavage furrow had extended to the equator of the egg; the second had just begun to extend beyond the margin of the germinal cap.

In a slightly older egg (figs. 4 and 4B) the two first furrows have reached the lower pole, the second being considerably displaced where it intersects the first. Four new furrows have appeared, starting from one of the primary ones. These one may call vertical furrows, as they resemble those of the third cleavage in *Amia*. It is obvious that the furrows of the third phase, shown on the left side of the figure, when completed will intersect one of the primary furrows, showing how easy it would be for the set of furrows to become latitudinal. It is, in fact, common enough for the cleavage furrows of this phase to vary between vertical and latitudinal (*Petromyzon*—Eycleshymer; *Triton*—Eycleshymer; *Salamandra*—Grönroos). On the whole, a third cleavage phase of vertical furrows is especially characteristic of Ganoids; and without talking of "Homology" of the various furrows as some authors have done, the condition in *Lepidosiren* is of interest as pointing to a similar distribution of protoplasm and yolk in the eggs of the Ganoids and of the Dipnoi. In the egg figured (fig. 4) in illustration of the third phase of cleavage, a furrow has started in each quadrant. In another slightly younger egg one was present in only one quadrant, so that the four furrows of this phase do not necessarily appear synchronously. In fact, so early as this, marked irregularities begin to obscure the course of segmentation. These irregularities affect both the position of the various furrows and the time of their appearance. In fig. 5 an egg in the third phase is shown where the irregularity has become very marked, partly by displacement of the two primary furrows, and partly by the latitudinal character assumed by one (γ) of the third set of furrows.

The next stage obtained by me is illustrated by fig. 6. Here all trace of regularity has disappeared, and it is not possible to identify the various furrows. A comparison of the lower hemisphere of this egg with that of the much younger one in fig. 4 illustrates the time variation in the extension of the two primary furrows in different eggs, only one of these having surrounded the egg in fig. 6, while in fig. 4 both have.

The further stages of segmentation will be explained best by the figures (figs. 7–9). The blastomeres become smaller and smaller, those of the upper portion of the egg segmenting much more rapidly than those of the lower. In the lower portion of the egg one must note during stages 6 and 7* the predominance of meridional furrows. These begin at their upper ends, gradually extend downwards and finally run into

* By "stage 6" I would express more shortly "the stage represented in fig. 6," and I shall use this contraction in the remainder of this paper and those which are to follow it.

one of their neighbours. A similar phenomenon is well marked in Ganoids (*Acipenser ruthenus*—SALENSKY; *Amia*—WHITMAN and EYCLESHYMER), and it may be taken as leading on towards the meroblastic egg of Sauropsida, with its conspicuous radiating furrows round the periphery of the blastoderm.

The figures naturally indicate only divisions taking place by cleavage planes perpendicular to the surface of the egg, but as early as the stage of fig. 6, division planes parallel to the surface begin to appear, first in the portion of the egg corresponding to the germinal cap, and a little later in the yolk as well. The segments now go on dividing in all directions, the upper cells doing so most rapidly, and forming a cap thickest in the middle, of small cells, resting on the much larger lower cells.

Even in the second phase of cleavage the inner angles of the segments round themselves off so as to leave a slight space between them—the first beginnings of the segmentation cavity. As segmentation proceeds, the cells in the interior of the upper part of the egg round themselves off strongly from one another, and become separated by continuous chinks filled with fluid. This rounding off does not affect the superficial layer of cells except in their inner faces; laterally they remain closely apposed to their neighbours. The large yolk cells are but slightly affected, and only the upper ones become conspicuously rounded off. In a stage corresponding with fig. 9 a continuous segmentation cavity has appeared as a dark shadow (*seg. cav.*) in the middle of the upper hemisphere. The cavity is rounded, and at its upper pole approaches close to the egg's surface, being here roofed in by only a single layer of cells. The segmentation cavity rapidly spreads out all round under the superficial cell layer, and as it does so the small celled portion of the egg increases in extent, gradually spreading downwards over the surface of the egg. Its cells become fairly uniform, and the transition from them to the large yolk cells becomes more sudden, so that they come to be marked off from the latter by a more definite boundary. By the time the segmentation cavity has attained its maximum size, the boundary of the small cells has reached to a level about the equator of the egg. The cavity now shows conspicuously in the egg seen from above (*cf.* fig. 10A, *seg. cav.*).

In section the segmentation cavity is now seen to have the shape of a plano-convex lens resting directly upon the upper surface of the yolk. Its roof is formed over the greater part of its extent by two layers of closely apposed flattened cells, except at its lower edge, where it turns inwards to meet the floor of the cavity. Around the egg at this level there is a thick layer of small cells which abruptly thins out towards the margin of the small-celled area. It is at this stage, when the segmentation cavity has reached its maximum, that invagination begins.

Gastrulation.

A row of little depressions appears parallel to the equator and 8° to 10° below it (fig. 10, *invag.*). These become continuous, and form a line of invagination which may stretch through one-third of the circumference of the egg at this latitude. Sometimes the line of invagination may be continuous from the first and it may be comparatively short.

The line of indentation is placed along the edge of the small cell area which is here sharply marked. Round the rest of its extent the margin is less sharp, and this portion gradually sweeps over the surface of the egg, the small-celled area being continually added to by the splitting off of small superficial cells from the large underlying yolk cells. In accordance with the metabolic activity correlated with this, the yolk passes into a state of fine sub-division, where the splitting off is taking place, and the new cells appear white like the others. Along the line of indentation the margin of the small-celled area appears to remain stationary. Of an advance of this invagination lip over the yolk, such as one might expect, I am not able to offer any experimental evidence. Indeed, what evidence can be gathered from mere observation of the changes in external appearance is directly against such taking place, for if it did so one would expect the line of invagination, as it advanced and became part of a smaller and smaller circle of the sphere, to assume a more and more pronounced curvature downwards, *i.e.*, with its concave side below. Instead of this the contrary happens, and after only about 100° of the yolk remain uncovered the lip of the invagination begins to assume an upward curvature, *i.e.*, with its concave side towards the position in which the embryo will appear. The line of indentation rapidly deepens into a slit as the archenteron becomes formed. Reserving details for a later occasion, I may say that the archenteron appears to be formed by invagination of a type generally resembling that found in Urodela and in Petromyzon. The archenteron rapidly increases in size and as it does so obliterates the segmentation cavity. In stage 11, as can be seen in the whole egg (fig. 11s), the segmentation cavity has been much diminished, and by stage 12 it has almost completely disappeared. As the formation of the archenteron proceeds, its external opening assumes a definite curvature, with its concave side upwards. From being a slit, some 6 millims. in length, it shrinks up to a crescentic opening, measuring only 1·5 millims. from tip to tip. Meanwhile the margin of the small white-celled area has, except where stopped by the line of invagination, been sweeping over the surface of the salmon-coloured yolk, reducing as it does so the area of this exposed. At last only a faint flush of colour is to be seen on the posterior convex lip of the invagination opening; this too disappears, and as the small ectoderm cells are now continuous with the large cells lining the archenteron all round the invagination opening, we may refer to the latter as the completed blastopore. The blastopore being only now completed, one cannot regard the area of yolk remaining exposed in preceding stages as corresponding exactly with the so-called yolk-plug of Amphibia, for this is bounded all round by a slit of invagination; it projects in fact through the blastopore.*

* The area of yolk left still exposed in, *e.g.*, stage 13, is rather the equivalent of BALFOUR's "yolk blastopore" of the Selachian.

Development of the Embryo.

Already in stages 13 or 14 the first sign of the embryo may be seen as a very faint depression running forwards from the line of invagination. And a stage later (fig. 15, *emb.*), this becomes more obvious. The egg is now of a uniform straw-colour—the salmon-coloured yolk being completely covered over by the small-celled ectoderm. The blastopore is a small crescentic opening, marking the hind end of the future embryo. In front of the blastopore is the depression already mentioned, a space filled with fluid being between it and the capsule. This broad shallow depression in front of the blastopore becomes more obvious, and its edges and their forward prolongations rise up as two very faint ridges—the medullary folds. The extreme lowness of the medullary folds as compared with those of *Ceratodus*—in other words, the downgrowth of the rudiment of the central nervous system into the substance of the embryo rather than its upward growth above the surface—is very possibly to be correlated with the enclosure of the egg in a tightly-fitting capsule, as suggested by O. HERTWIG in the case of Cyclostomes and Teleosts. When they first become distinct (fig. 16) the folds are already fairly close together, except in front, where they enclose a wide valley, and behind, where they diverge, passing towards each end of the blastopore. The folds approach one another in the middle of their length, coming to lie close together, and their posterior continuations now become visible, passing back and uniting immediately behind the blastopore, in front of which they enclose a somewhat triangular area. The blastopore forms a slit still diminishing in length and still concave forwards. In front of it, on the floor of the space mentioned, there is no indication of the seam marking the anterior prolongation of the blastopore so distinct in *Ceratodus*, and in many Amphibia.

When the medullary folds have come to lie in close contact through the middle and greater portion of their length, although they have not yet fused, a very faint elevation may be detected on each side, and slightly in front of the middle of the embryo (fig. 17M, *p.n.*). These are caused by the underlying rudiment of the pronephros. At their front end the folds approach one another, and the broad valley separating them becomes narrowed. In the trunk region the closely apposed folds merge into one another. There is no obvious arching over to form a neural canal; the appearance is rather that of two waves meeting one another. It is only on examining transverse sections that one sees that there is a faint attempt at arching over, only very superficial cells taking part in the process. The cavity so enclosed is quite insignificant; it soon vanishes, and the central canal of the nervous axis arises secondarily.* The fusion of the two folds is completed first usually in the region just in front of what will become the hind-brain (fig. 18). In front of this a steep-sided trough persists for some time, while behind it a faint groove runs along the top

* There is no neurenteric canal.

of the neural ridge marking its dual nature. This disappears (fig. 19), the edges of the valley which occupies the position of the brain approach, and it too disappears, as shown in figs. 19 and 20. In many embryos of the latter stage a sharp constriction is present, marking off the hind from the mid-brain, but this varies much, and is often hardly visible. There is no further obvious division of the brain into regions. About the stage shown in fig. 19 one may detect faint indications of myotomes between the pronephric rudiment and the neural axis. A faint swelling (fig. 19M, *br.*) appears on each side in front of the pronephros. This is the rudiment of the group of branchial arches. Meanwhile the blastopore has been shortening up till it now forms a triangular opening. In front of it the medullary folds have approached close to one another. They remain for a time separated by a groove, which, however, gradually disappears from before backwards. At the stage shown in fig. 20 the pronephric elevation is seen to be increasing in length as the duct grows backwards. One may often at this early stage detect inequality in the rate of growth of the two ducts, as in the specimen figured.

In fig. 21 the main axis of the embryo is curved, though the embryo is otherwise normal. The chief new feature is the appearance of a slight swelling (*oc.*) on either side of the brain, indicating the optic outgrowths. The branchial eminence (*br.*) is increasing in size.

Up till now the contour of the head region has been determined practically entirely by the condition of the brain, but from now onwards, partly owing to the development of a head fold, partly to the accumulation of mesoblast, the outer contour no longer shows this correspondence with the shape of the brain (*cf.* fig. 22). The pronephric ducts have in stage 22 accomplished about half their growth backwards; they each form a narrower, more sharply-marked ridge than at first. At their anterior end each is beginning to show a characteristic comma-like curvature. The medullary folds have completely merged except at the extreme posterior end, where the faint groove between them still persists for a short distance in front of the blastopore. As already mentioned the head fold has appeared; the neural ridge in front of the blastopore begins to raise itself above the neighbouring egg surface, indicating the beginning of the tail fold. As the tail fold rises up the portion of the medullary folds lying behind the blastopore flatten out and disappear. It may be mentioned at this point that the blastopore becomes the cloacal opening. Of this there can be in *Lepidosiren* happily no question.

By stage 23 both head and tail folds are distinctly formed. The branchial eminence on each side shows a division by oblique grooves into three portions lying one behind the other. These correspond with Branchial arches I., II., and III. and IV., and the grooves between to the corresponding gill clefts. The pronephros is now distinctly comma-shaped, and the pronephric duct has completed about two-thirds of its backward growth.

To illustrate a slightly later stage, I have figured an embryo extracted from the

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egg and laid out in one plane (fig. 24). The head-fold and the contour of the head generally now stand out in bolder relief. There are obviously four branchial elevations on each side, the posterior one of the preceding stage having become divided into two by a groove parallel to those in front of it. Along the middle of the nervous axis the central canal is visible—widening out in front in the ventricles of the brain. But the most interesting feature of this stage is the curious crescentic body lying on the egg's surface beneath the head fold, and partially shown in fig. 24 *c.o.* This, in fact, is the rudiment of a cement organ exactly corresponding both in structure and function with that found so frequently in anurous Amphibia. The myotomes now show through the skin much more distinctly. There are about thirty-nine pairs of myotomes, but there is much variation amongst embryos of the same age, no two keeping abreast in all their features for any length of time. On the outer side of the myotomes the pronephric duct is seen to have completed its backward growth, and sections show that its opening into the hind end of the gut has been established. Consequently one may now talk of cloacal opening in place of blastopore.*

About four days before hatching the condition is reached shown in fig. 25. The head as a whole is rising definitely above the egg's surface. The external gills form four prominent knobs on each side, the third and fourth, however, incompletely separated. They correspond with the four branchial elevations already seen in the preceding stage. The external gills of *Lepidosiren* are thus situated on Branchial arches I., II., III., and IV., and consequently the anterior three pairs are the homologues of the External Gills of Urodeles. On looking down on the head from above, the fourth ventricle (*v.*iv.) is seen to be widely dilated. On each side of it a dark shadow indicates the cavity of the ear. The ear cavity, like that of the mouth and nose, as well as the central canal of the nervous axis, is formed by secondary excavation in an originally solid rudiment, and this accounts for the absence in *Lepidosiren* of the involutions of the outer skin to form these organs which are so conspicuous in most Vertebrates. In ventral view of the embryo at this stage, the most conspicuous feature is the curved cement organ (*c.o.*), now traversed by a longitudinal groove from end to end.

From now on till the time of hatching (figs. 26, 27), the external gills increase in size. The most prominent feature, however, is the very rapid folding off of the hind end of the body, which, as seen in fig. 27, is kept flexed somewhat obliquely over the ventral surface. The embryo is now of a yellowish salmon colour, the tinge of salmon less pronounced than in earlier stages. It makes occasional spontaneous movements within the eggshell, and when placed in an irritant solution the dorsal muscles contract vigorously. If the embryo is extracted from the shell under salt solution, and the impending yolk removed from its ventral side, the tail will bend once or twice to one side or the other.

* The pronephros has two nephrostomata, opening into an incompletely separated off portion of the cœlom containing the large glomerulus.

About two days after the first spontaneous movements are seen, hatching takes place. The horny eggshell, apparently undergoing digestion by some ferment secreted by the embryo, becomes quite soft. The creature makes violent attempts to move and eventually one of these causes rupture of the shell by an equatorial split, or often two or three splits running round the egg parallel to one another. Very often the young Lepidosiren remains for two or three hours or even longer stuck between the incompletely separated halves of the shell. At other times only the outer horny layer of the shell ruptures at first, the soft inner layer remaining for some time enclosing the embryo like a bag.

During the first day or two after hatching, the hind part of the body straightens out and the larva has a strikingly tadpole-like appearance. The resemblance is, however, only a superficial one, the apparent equivalent of the tail of the tadpole being here, not a tail, but the slender posterior portion of the body with the cloacal opening comparatively close to its tip (*cf. Petromyzon*). The larva is of a pale yellowish salmon colour and is without a trace of dark pigment. The cloacal opening (blastopore) closes up about the time of hatching and remains closed during about the first two weeks of larval life. Thus the temporary "closure of the blastopore" is in *Lepidosiren* very late, and only takes place after it has become a definite cloacal opening, by which both gut and pronephric ducts communicate with the exterior. During the first few days after hatching (*cf.* figs. 28, 29), the external gills rapidly increase in length, and about the third or fourth day a double row of little knobs along the outer surface of each indicates the commencing development of the pinnæ. The cement organ becomes more prominent above the surrounding surface.

A ten-day-old larva is shown in fig. 30. The gills are increasing in length and their pinnæ especially rapidly. About this stage the four gills of one side are beginning to be raised up on a common base. The cement organ is increasingly conspicuous in side view. The position of the mouth is indicated by a transverse groove (fig. 30 *v, m.*). At the hind end of the body, increase in length is taking place by the growth of the true tail region. Dorsally and ventrally the body is thinning out to form the median fin. Up till now the anterior end of the body has been much swollen up as compared with the posterior part, though already the difference is becoming less marked. The dorsal portions of the larva are white, the ventral part, except in the head and tail, yellow. The yellow lower part is, indeed, entirely made up of gut with its enormously thick yolk-laden walls. Pigment is now appearing in the pigment layer of the retina.

In the twelve to fifteen-day larva (fig. 31), in many cases scattered pigment cells had begun to appear over the dorsal side of head and anterior body region (*cf.* fig. 31*). The pinnæ of the external gills are growing rapidly. In the living larva one sees, ventral to the base of the external gills, the four vascular trunks that supply them running parallel to one another up the side of the neck, the fourth markedly smaller than the three in front of it. Below and in front of the base of the external gills a nearly vertical ridge appears—the rudiment of the opercular fold (fig. 31*, *op.*). The first rudiments of the paired limbs† are also now visible, the anterior one (fig. 31*, *f.l.*) a little elevation a short distance behind the last external gill, and the posterior one (fig. 31, *h.l.*) hardly yet rising perceptibly above the level of the neighbouring body surface.

The next larva I have figured is one killed twenty-four days after hatching (fig. 32). The living larva of this stage is a very fine object. The external gills are deep red, and with a lens one can see the current of corpuscles moving in regular jerks up one side of a pinna and down the other. The four branchial afferent vessels are conspicuous, running parallel to one another and close together up the side of the neck. The larvæ now occasionally swim a short distance, though they still rest most of the time. Their favourite position is amongst the loose vegetable *débris* at the bottom of the nest. They lie in a sloping position in this with just their heads sticking out with the external gills widely spread on each side. By now chromatophores are scattered conspicuously over the whole dorsal surface, and the eye is fully pigmented. The myotomes are ventrally increasing in length. The cement organ has increased greatly in size, and is actively functional, helping the larva to maintain the position above described without slipping down amongst the loose vegetable matter. The external gills have also become much larger. In the figure they are reflected upwards and forwards so as to show the fore limb and the opercular fold. The fore limb is increasing in size, and, as it does so, its base of attachment is undergoing a rotation, so that the main axis of the limb is assuming a backward, instead of an upward, direction—what was the anterior face of the rudiment becoming the upper edge of the limb. The opercular fold is now beginning its backward growth to enclose the opercular cavity. The gill slits are not yet perforated, though the mouth is in course of perforation, and a lumen has opened out in the gut as far back as the gill outgrowths. The cloacal opening (*cl.o.*) is now patent again, leading into a small cavity which receives the kidney ducts. Between this and the region of the gills the gut is for the most part solid—the lung outgrowth, however, being hollow.‡ The hind limb forms now a distinct papilla, whose base of attachment has also undergone a process of rotation. Whereas the anterior limb appeared first as a papilla looking upwards, the posterior limb papilla is situated on a surface looking outwards and downwards. In accordance with this the rotation of the attachment of the limb, in order to bring about a backward direction of its long axis, is in the opposite direction to what occurred in the case of the fore limb, and is such as to cause the originally posterior surface to become dorsal, the originally anterior surface becoming ventral. I was interested to observe in the living larva that the afferent part of the

† In *Ceratodus* the hind limb does not become visible till about a month later than the fore limb. SEMON, 'Zoologische Forschungsreisen,' Bd. I., p. 46.

‡ I may mention here that the lung in the earliest stage which I have so far examined, forms a median ventral outgrowth from the gut wall.

vascular loop supplying the limb was dorsal in the case of the fore limb, ventral in that of the hind limb. This curious circumstance is adequately explained by the rotation just mentioned. SEMON has recently described phenomena of a similar kind, though better marked in *Ceratodus*, and SCHNEIDER described the curious reversed position of undoubtedly homologous structures in the fore and hind limbs of *Protopterus*, doubtless due to a similar movement.*

The larva now increases rapidly in length (fig. 33). The median fin is becoming more conspicuous, especially in the tail region. The general shape alters by the absorption of the excess of yolk in the anterior part of the gut, so that the latter becomes uniformly tapering. At its posterior end a spiral groove appears, marking the beginning of the spiral valve. The pigment in the skin is increasing in quantity, and is spreading ventrally, keeping pace with the ventralward extension of the myotomes. Ventrally it tends to be arranged in bands parallel to the myotomes. The external gills are still increasing in size, as is also their common basal portion. In life they are voluntarily movable, and the larva frequently twitches one or other of them. The opercular fold is growing backwards, in the living larva conspicuously truncating the four branchial afferent vessels which run up the side of the neck parallel to one another. The cement organ, as in the preceding and succeeding stages figured, is enormously large, and is actively functional, secreting copious cement. The mouth is marked by a conspicuous groove: and sections show a split not yet quite continuous, extending from this into the buccal cavity. The limbs are increasing in length, and the hind limb is beginning to show its transient flattened shape.

In the next stage figured (fig. 34) the yolk is being rapidly absorbed. The whole animal is become more slender and lengthened out, and also more transparent. Dorsally the pigment has greatly increased. The cement organ is now at about its maximum, and the hind limb is comparatively broad and flat. The larva at this stage is becoming livelier, moving hither and thither every now and then with undulating movements, occasionally shooting backwards.

The larva of about a month old has the appearance of fig. 35. The tail is still increasing proportionally in length, but is becoming narrower from above downwards. The chromatophores are becoming much denser dorsally, so that the upper part of the larva is of a uniformally dark colour. Ventrally the pigment is bounded by a sharp line, which gradually sweeps over the ventral surface. In the head region the pigment was already over the ventral surface in the preceding stage. The cement organ is now rapidly atrophying, remaining functional, however, till quite small. The limbs, on the other hand, are increasing greatly in length, and the hind limbs much more rapidly than the fore limbs. The external gills have now attained their maximum. They are borne on a common stalk, the anterior gill being less removed from the body than the three posterior. Pigment cells do not spread on to the gills

* *Cf.* also *Amia*, DEAN, 'Zool. Jahrb.,' Abth. Systematik, vol. 9, Plate 9.

or their common stalk except just at its base. Since the first appearance of the rudiment of the fore limb differential growth has brought about an alteration in its position relative to the external gills, and instead of lying, as at first, well posterior to these, it now lies ventral or even slightly anterior to their point of attachment (*cf.* figs. 31* and 35*). In ventral view it is seen that the spiral valve groove has so increased in depth that the gut is divided by it into a coiled spiral. The larva of this stage when at rest lies no longer on its side, but back upwards, and holds its external gills curved forwards as shown in fig. 35 *v.*, with the pinnules behind. It, however, has become quite lively. It does not remain quiet for more than a few minutes at a time, but swims an inch or two in eel fashion, and then settles down again. As it swims forward the gills are pressed back against the sides of the body—the pinnules next it, and so protected. The larvæ are very sensitive to movement in the water, a slight tap on the edge of the dish at once setting its inhabitants in wild commotion. It was at this stage that respiration of air was first observed. A large number of larvæ had been left overnight in a rather small vessel, and next morning the contained larvæ were seen to be taking breaths of air. The larva would come to the surface, assume a vertical position, apparently by passing some air forward into its pharynx, give out a bubble of air, and then retire below the surface again. On dissection the larvæ were found to all have their lungs full of air. The examination of sections shows that the gut-cavity is now open as far back as the point of origin of the lungs, but behind this point, though occasional spaces have arisen, they are not continuous with one another. Through the greater part of its extent the gut is indeed quite solid, except quite posteriorly, where it has a definite lumen into which the pronephric ducts open. Only about this stage do the gill clefts become perforated.

METAMORPHOSIS. (Fig. 36.)

About six weeks after hatching the larva undergoes rapid changes, which one might almost designate by the name "metamorphosis." It has at this time a length of 40 to 50 millims. Circulation becomes sluggish in the external gills; they assume a white unhealthy appearance, portions drop off, and what is left rapidly atrophies. For some time little stumps persist, recalling the condition in *Protopterus* where similar vestiges persist till late in life. The pigment, whose still sharp boundary has nearly reached the ventral middle line, becomes much denser, and the general colour becomes a rich purplish-black. At the same time the young Lepidosiren becomes markedly livelier in its habits, cruising round and round the vessel, exploring in eel-like fashion.

A young Lepidosiren of 60 millims. in length is shown in fig. 37. The pigment margin has now swept over the ventral surface, and the general colour is rich brownish-black. In the dark ground colour are scattered minute yellowish spots. The margin of the conspicuous median fin is clear and transparent, the paired fins are patchy in colour. The general appearance is extraordinarily newt-like, and this is accentuated in a view from above by a slight lateral compression behind the head, simulating a neck. The hind limbs are strikingly long compared with the fore limbs. They are used a good deal in clambering about the water plants, etc., in irregular alternation. They can also be rotated about their point of attachment in an antero-posterior plane as for brushing off any foreign particle upon the skin. As the creature rests on the bottom, it balances itself by the two hind limbs, and under these circumstances they very commonly assume an S-like curvature, corresponding with the double flexure so characteristic of the pentadactyle limb. The latter is still more forcibly recalled by the occasional presence of a slight expansion at the tip suggesting the tendency towards the formation of a foot. The young Lepidosiren swims by lateral strokes of the hind part of the body, the hind limbs are then folded close to the body, the fore limbs are merely inclined backwards somewhat.

At about this stage the young Lepidosirens show a great tendency to jump out of their containing vessel, and in the wild state they probably now issue from the security of their nest into the general waters of the swamp. There they are very seldom seen. During many long watches in the swamp I only saw three young Lepidosirens away from their nest. These appeared at the surface of the water, took in a breath of air, lingered a few moments, and again disappeared into the depths. About this time the cornea, hitherto clear and transparent, begins to assume the white and unhealthy appearance which it has in the adult; and this we may probably correlate with the assumption of a free life doing away with the necessity of the young animal finding its way back to the nest after having taken a breath of air. Though their sight is becoming dim they are very sensitive to light, and are at once put into commotion by sudden exposure. Those kept in the light preferred to keep in the shadow of floating sheets of cork. At short intervals the young *Lepidosiren* takes a breath of air. It pushes the tip of its head vertically above the water's surface, first expires, and then takes a deep inspiration through the widely open mouth. A few seconds after withdrawing from the surface, one or two bubbles issue from the opercular opening, probably the surplus air in the mouth and pharynx which has not gone into the lungs.* Now that direct air-breathing has become so important, the Lepidosiren is able with impunity to withstand great impurity of the surrounding water. I had an interesting demonstration of this. The result of one day's collecting was brought back in one of my collecting jars. On reaching the laboratory I poured out the contents of the jar into one of my observation dishes, and then put into the jar a Lepidosiren head which had been already macerating some time. With a temperature of nearly 100° F. in the shade the water had soon become extremely foul and evil-smelling. What was my surprise next afternoon, as I sat working at my table, to see jump out of the jar a young Lepidosiren which had been inadver-

* At about this stage the anterior (hyo-branchial) gill cleft closes, leaving the four which remain open during life.

tently left behind the previous day. It appeared in no way the worse for its experience.

During the whole of the stay within the nest the young Lepidosiren subsists on the yolk stored in its gut-wall. I first observed evidence of a desire to feed at a period of from 70 to 90 days after hatching. In all probability in the swamp, feeding begins soon after leaving the nest. Those in my tanks ate the bodies of dead companions, and pieces of young Ampullarias, but seemed greatly to prefer small earthworms. Where a little blood had oozed out of a piece of earthworm, and lay on the bottom of the vessel, a passing Lepidosiren at once detected it and moved slowly about with its head bent down as it were sniffing up the blood. The piece of worm was seized and taken in by a succession of curious jerks, retained in the mouth and pharynx for a few minutes, and then rejected again in a series of similar jerks. On coming to examine young Lepidosirens, which I had been keeping in more natural conditions in a large pool, I found that their food had been mainly, if not entirely, of a vegetable nature—consisting of fragments of dicotyledonous plants.

Fig. 38 represents a Lepidosiren a month older than that last figured. The creature has now increased in length from 60 millims. to 77 millims. As compared with the preceding stage, the median unpaired fin has increased greatly in size; the colour shows a conspicuous change, the still brownish-black ground being now varied, not with small dots, but with large and numerous roughly circular yellow spots.

Figs. 38D and 38N are meant to illustrate the remarkable nightly change of colour alluded to on a previous page. As dusk sets in the black chromatophores, so abundant in the skin, draw in their processes and become almost invisible. The yellow chromatophores, on the other hand, remain expanded. As a result, the dark colour of the animal disappears, and it remains as a colourless, semi-transparent creature dotted with conspicuous yellow spots, the eyes, before hardly visible, standing out as conspicuous black beads, and many of the internal organs, liver, intestine, heart, etc., quite distinguishable. It is only on close examination that one notices the multitudes of tiny dots which represent the shrunk-up chromatophores. At dawn the reverse process begins—the chromatophores gradually push out their pseudopodia, and by sunrise the normal diurnal colour is resumed.

This stage marks the end of my continuous series of young Lepidosirens. I, however, figure yet one more—a stage of which I obtained several specimens, and which I took to represent the brood of the previous season, *i.e.*, to be about a year and a-half old. This stage measures about eighteen inches in total length. Traces of the yellow markings are still visible as irregular blotches. The scale areas are plainly marked, and so are the main branches of the lateral line systems.

General Remarks.

It now remains to make a few general remarks upon certain of the points referred to in the preceding pages.

Segmentation.

In its complete unequal segmentation, *Lepidosiren* belongs to the group of Vertebrates composed of the Lampreys, "Ganoids," Dipnoi and Amphibia,* and in the general features of segmentation there is a very marked resemblance to what occurs in Ganoids and Amphibians.

The first two furrows being vertical and meridional conforms with the general rule amongst the groups above named.

The furrows of the third cleavage phase vary between latitudinal and meridional (or vertical). Thus in Anura they are characteristically latitudinal; in *Petromyzon* they are usually so, but are occasionally vertical,† in Urodeles they vary much (*Amblystoma*—latitudinal;† *Triton* usually latitudinal, but occasionally vertical; *Salamandra* equally often latitudinal and meridional). In *Ceratodus* the furrows of this phase are vertical, and the group of "Ganoids" (excluding the still unknown Crossopterygians) seems specially characterised by their being meridional or vertical. In *Acipenser*‡ and in *Amia*§ the furrows of the third phase appear almost exactly as in *Lepidosiren*. In the meroblastic egg of Sauropsida‖ we again find a similar arrangement of the first three sets of furrows.

In the succeeding stages of segmentation the most noteworthy feature is the preponderance of meridional furrows for a time in the lower part of the egg. In this again there is a striking resemblance to what is known in *Acipenser* and *Amia*, and indeed also in the Meroblastic Sauropsidan egg with its radiating furrows at the edge of the blastoderm. This last mentioned feature, along with the vertical or meridional character of the third set of furrows, and also the early appearance of irregularities in segmentation, may well all be regarded as indications of an approach towards the meroblastic conditions.

Looking to the general course of segmentation in *Lepidosiren*, one sees that it approaches most closely that of Ganoids, and we may take this as at least indicating in it a similar distribution of living substance and yolk to that which characterises the eggs of the group mentioned.

Gastrulation.

In the phenomena of gastrulation, as far as they can be studied from merely external appearances, the most interesting point seems to lie in the much greater

* Gymnophiona in the present state of our knowledge appear to form an exception. There are certain points about BRAUER'S figures which, however, suggest that they too may turn out to be really holoblastic.

† EYCLESHYMER, 'Journ. Morph.,' vol. x., 1895, p. 351.

‡ SALENSKY (*A. ruthenus*), DEAN (*A. sturio*).

§ WHITMAN and EYCLESHYMER, DEAN.

‖ The eggs of Elasmobranchs still seem incompletely known in this respect. *Cf.* SOBOTTA, Merkel and Bonnet's 'Ergebnisse der Anatomie und Entwickelungsgeschichte,' Bd. vi., p. 560.

extension of the line of invagination at its first appearance, and its gradual shortening as invagination proceeds. In such a relatively primitive method of gastrulation as that occurring in *Amphioxus*, one portion of the blastula wall becomes pushed within the other, the boundary of the invaginated part, which I shall call the line of invagination, being co-extensive with the boundary between large and small cells, and forming a closed curve. With the hypertrophy of the large-celled part of the blastula wall through increased yolk storage, there comes about increase of the small-celled area through the addition to it of small cells split off from the surface of the large cells. At one point—corresponding to the posterior side—this epibolic growth of the small-celled area is inconspicuous, and here invagination takes place vigorously. Elsewhere, however, as the boundary between small and large cells passes further and further away from its original position, the tendency to invagination seems to become less and less intense, as is shown by the delay in the onset of invagination, and also by the comparatively slight extent to which it is carried out. In Amphibia the line of invagination, typically, still forms a complete circle, but only at its dorsal side is the invagination active, practically the whole of the archenteron taking its origin there. Round the rest of the circle there is, for a long time, merely a shallow groove, within whose periphery, only very late, the yolk plug disappears into the interior of the egg.

Lepidosiren shows a further stage to that of the typical Amphibian. Here no trace of invagination appears along the greater part of the small-large cell boundary. The first indications of invagination extend as described round about one-third of the extent of this boundary, but the terminal parts of the line of invagination flatten out, and the definitive invagination becomes more and more restricted to a small portion next to where the hind end of the embryonic rudiment will develop. Here the archenteric invagination takes place alone. The rest of the boundary between small and large cells gradually sweeps over the egg until at last it reaches right into the already formed archenteron without showing any trace of invagination. *Lepidosiren* may be taken as showing a transitional form between the method of gastrulation, characteristic of Amphibians, and that found in Elasmobranchs. In the latter group we may, I think, see a further development of the conditions seen in *Lepidosiren*. The proportion of yolk in the lower part of the egg has so increased, as compared with protoplasm and nuclei, that it does not segment at all in the ordinary sense; delaminational spreading of the epiblast over the yolk has greatly increased in extent, finally invagination is confined to a relatively very limited part of the boundary and between small cells and yolk.

Relations of Medullary Folds and Anus.

In 1884 SEDGWICK showed how in an early stage of the development of *Peripatus capensis* the gastrula mouth formed an elongated slit stretching along the neural surface of the body and surrounded by the continuous nerve rudiment. He explained this curious stage in the development of the creature on the hypothesis of a Cœlenterate-like ancestor, with an elongated slit-like mouth, tending to close except at its two ends, as in Actinians, so as to give rise to a definite mouth and anus, and surrounded by a continuous band of nervous epithelium. He * extended such hypothetical ancestry to Annelids, Molluscs, and Vertebrates, as well as to Arthropods. BALFOUR had already suggested the possibility of deriving the central nervous system of Chætopoda, Mollusca, and Arthropoda, with its supra-œsophageal and supra-rectal commissures in such primitive forms as *Chiton*, *Peripatus*, etc., from a primitive continuous nerve ring such as that of a Medusa.

Were the above-mentioned hypothesis a true theory of the homologies of the central nervous system of Vertebrates, we should expect to find in their ontogeny more or less distinct traces of a stage corresponding to that described above in *Peripatus*.

One of the most striking features in recent embryological work on the Vertebrata is the accumulation of evidence of the fusion of the lips of the blastopore along the middle line of the medullary plate. In *Lepidosiren*, perhaps in correlation with the thickening of the floor of the medullary groove associated with the peculiar mode of development of the neural canal, there is no external evidence of the presence of the blastoporic, or, as I should prefer to call it, protostomal † seam (*Urmundnaht*) marking this line of fusion. In *Ceratodus*, on the other hand, where with a less amount of yolk and the absence of a close-fitting rigid egg-shell the medullary groove attains its full development, such a seam is, as SEMON has shown, very distinct. In other Vertebrata the fact of the existence of traces of blastopore along the back is supported by a large mass of observations, certain of the facts being concisely expressed by the so-called theory of concrescence (HIS, RAUBER, MINOT), while a more general view of them is taken by the "Urmundtheorie" (*vide* O. HERTWIG, 'Lehrbuch der Entwickelungsgeschichte,' 6th edition, 1898, pp. 151–169).

We have only to associate this generally admitted extension of the blastopore

* 'Q. J. Micr. Sci.,' vol. 24, 1884, "On the Origin of Metameric Segmentation."

† It would much conduce to clearness were Embryologists, as urged by SEDGWICK (*op. cit.*, p. 52), to use separate names for the "definite blastopore," and for the original Gastræa- or Gastrula mouth (*Urmund*). It would seem most convenient to adopt for the latter the name *Protostoma*. Adopting this term, in the Vertebrate embryo, the mouth, neurenteric canal, and anus, are morphologically persisting portions of the protostoma, while the structures known as primitive streaks indicate regions where its lips are fused. While the relations of mouth to protostoma have become obscured (*cf.*, however, the below-cited observation by Miss JOHNSON), those of neurenteric canal and anus are more distinct (*cf.* in "Anura," v. ERLANGER, 'Zool. Jahrb. Anat. Abt.,' Bd. iv., 1891; and for "Urodela," SCHANZ ('Jena. Zeitschr.,' xxi., 1887), and MORGAN ('Studies Biol. Lab. Johns Hopkins,' iv., 1890)). much of the obscurity involving the discussion of the "fate of the blastopore" seems to have been due to the confusion under this name of different parts of the protostoma, *e.g.*, in *Amphioxus* the conspicuous blastopore is the neurenteric section of the protostoma; in *Lepidosiren* it is the anal portion, while in *Amphibia urodela* both portions are distinct.

along the back in Vertebrates with the persistence of its posterior portion in *Lepidosiren* as the anus, and the continuity behind this* of the medullary folds, to recognise in these the elements that go to make up a stage in ontogeny corresponding extremely closely with that of SEDGWICK in *Peripatus capensis*. In each we have a long slit-like blastopore stretching along the neural surface of the body, and running parallel with this the rudiment of the central nervous system, its two moieties being continued into one another behind the posterior expanded end of the slit—the anus.

There is, indeed, only one grave difference.† In the Vertebrate the more obvious vestiges of the protostomal seam are not described as passing forwards so far as the mouth, and so far I am not aware of any instance where the medullary folds are at any time continued into one another in front of the mouth.

These difficulties are greatly lessened by, firstly, the fact that in the newt the "primitive groove" has been seen‡ to be continued right forwards to the position where the mouth will appear, and secondly, by the following considerations :—

1. That in the great majority of Vertebrates the post-anal portions of the medullary folds, with no career of usefulness in front of them, remain obscure or invisible, and the anus seems to develop right behind the neural rudiment.
2. That, probably in correlation with the stored-up food supply, and later on with the vascular skin, the formation of the definite mouth becomes greatly deferred in the typical Vertebrate as compared with that of the anus (the earlier opening of the latter being retained possibly in relation with excretory needs), and that consequently one is much more likely to find traces of its primitive relations in the case of the former than in that of the latter.

The first of the above-mentioned considerations, together with the manner in which in *Lepidosiren* the post-anal portion of the medullary folds flatten out and disappear, certainly suggests that a similar process may have taken place at the anterior end of the body, the pre-oral portion of the nerve rudiment, *i.e.*, the part which would correspond with supra-œsophageal ganglia and para-œsophageal connectives, being suppressed. Thus would be explained the failure to establish definite homologues of these in the brain of the Vertebrate.

* There can be little doubt that a similar post-anal continuity of the medullary folds occurs in many other of the more primitive Vertebrates. SEMON shows that they are distinctly continuous in *Ceratodus* behind the blastopore, and it seems probable that the anus arises either directly from, or at least in the position of the posterior part of, the blastopore. A figure of BELLONCI (Mem. Acc. Lincei, xix., 1884) indicates that a similar state of affairs holds for a time in the case of the Axolotl.

† SEDGWICK has shown that the early traces of the mouth in the Selachian are in the form of a longitudinal slit, which would, as he has pointed out, accord well with its being a part of the longitudinal protostoma. 'Q. J. Micr. Sci.,' vol. 33, 1892.

‡ *Cf.* Miss JOHNSON, 'Q. J. Micr. Sci.,' vol. 24, 1884.

Neural Rudiment.

The central nervous axis in *Lepidosiren* combines, in its development, features characteristic of the more usual method, where the neural folds rise up and overarch the neural canal, with others characteristic of the method found in Teleosts, *Lepidosteus*, and *Petromyzon*, where the neural rudiment forms a solid keel in which a central canal arises by secondary excavation. In the latter group of forms there are apparent vestiges of the process of involution present in the faint medullary groove of *Petromyzon* and *Lepidosteus*. In *Lepidosiren* these vestiges are more strongly marked, for definite medullary folds and grooves are present, and overarching of the groove does take place to a slight extent.

Enteron.

One point in the external appearances during the development of the gut, which I wish to draw special attention to, relates to the origin of the spiral valve. I have already pointed out that the gut passes through a phase in which it may be said to be coiled up in a tight spiral. The turns of the spiral becoming later fused together, give rise to the spiral valve.

RÜCKERT* has shown that in Selachians the spiral valve has a similar origin.

What I wish to draw attention specially to is the suggestion this gives as to the morphological significance of the spiral valve. The ordinary explanation of this structure is that it is an exaggerated Typhlosole.† Upon such a view its development is difficult to understand. It appears to me to be suggested very strongly that the origin‡ of the spiral valve is to be sought rather in the region of Morphology than in that of Physiology, and that it is a relic of a once-coiled gut, a witness to the transition of the gut from a long coiled condition to a short and straighter one, such a transition as is correlated in the frog with change from vegetable to animal diet. It is interesting in this connection to refer to *Ichthyophis*, where the mass of yolk becomes, as it were, carved out into a long, irregularly contorted gut in very similar manner to that in which the spirally-coiled one arises in Lepidosiren. The gut in *Ichthyophis*, with later development, becomes relatively shorter, but is simply straightened out (SARASINS).§

In regard to the Enteron generally, I may mention in passing what has not come out very clearly from my description before: that the gut cavity disappears temporarily during development throughout its whole extent, except at its extreme posterior end. This portion into which the pronephric ducts have already opened at

* 'Arch. f. Entwick. Mech.,' vol. 4, 1896.

† *Cf.* T. J. PARKER, 'Trans. Zool. Soc. London,' vol. 11, 1880.

‡ The origin of the spiral valve being so explained, its further development might well be in accord with physiological advantage.

§ 'Ergebnisse Naturwissenschaftlicher Forschungen auf Ceylon,' vol. 2.

the time the rest of the gut becomes solid, remains, probably in correlation with this, patent throughout.

Gill Slits.

Little has been said of gill slits. They do not enter at all indeed into views from the exterior, as they do not become perforated until a period at which the operculum has completed its backward growth* (stage 35). There are six conspicuous gill outgrowths from the gut. Of these the first (hyomandibular) never becomes perforated, the second does, but becomes closed about stage 36, and the four remaining ones remain open in the adult.

Just after the gill slits have become perforated the young Lepidosiren has, besides the general skin surface, no less than three sets of special repiratory organs:—external gills, internal gills, and lungs.

External Gills

As we have seen, *Lepidosiren* during its development shows large external gills at the dorsal ends of Branchial arches I., II., III., IV. The external gills in the Amphibia are typically three in number on each side, and they are situated on Branchial arches I., II., and III. So far as I am aware, *Lepidosiren* is the first Vertebrate known to possess an external gill on the fourth branchial arch, though one would gather from ORR's account that *Amblystoma* (sp. inc.) shows a rudiment of one. Crossopterygians possess an external gill on the Hyoid arch. In the development of various Urodeles the conspicuous structures known as "balancers" are present. At an early stage in this research these structures attracted my attention, and closer investigation disclosed the probability of their being serially homologous with the external gills. I soon found that this view was not a new one. Both ORR† and MAURER‡ have adduced evidence that the balancer is really the external gill of the mandibular arch, and I think we may pretty safely accept this. Occurring as they do in three independent, and on the whole very primitive groups of Gnathostomata (Crossopterygians, Dipnoi, and Amphibians), we may fairly consider the external gills as in all probability very ancient organs inherited at least from the common ancestor of the three groups mentioned. It is true that no traces of true external gills are known to occur in Selachians, but this may well be due to the fact that here the large yolk sac, with its richly vascular wall, provides a structure which must necessarily, in addition to its nutrient function, act as an extremely efficient organ of respiration. The same explanation would apply to the more highly developed

* In this *Lepidosiren* agrees with *Ceratodus*. *Cf.* SEMON, 'Zoologische Forschungsreise,' vol. 1, part 1.

† 'Q. J. Micr. Sci.,' vol. 29, p. 316.

‡ 'Morph. Jahrb.,' vol. 14.

Teleostomes.† To reject the true Homology of the epidermal gills in the three groups named and to regard them as merely homoplastic is hardly possible in view of their identity, both in general structure and in their connections with deeper lying structures. The view might be held with MAURER that the gill arches would be most likely places for specially respiratory portions of the skin to develop, especially in forms where the perforation of the gill slits is delayed, on account of the comparatively superficial position of the gill arches. But taking into account the general respiratory property of the skin, and the extraordinarily constant position of the external gill with regard to the branchial arch, I cannot but feel that some more deeply seated explanation must be sought after. It being granted that the external gills are homologous structures, then we have evidence which at least suggests the former existence of a pair to each visceral arch from the first to the sixth inclusive.‡

I would direct attention to figs. 31* and 35*, showing the relative positions of opercular fold, external gills, and anterior limb rudiment, in stages 31 and 35 respectively. The striking differential growth in the region of those structures is well indicated, the external gills projecting from the body wall in the older larva, at a point dorsal to or even slightly behind the root of the fore limb. This gives the explanation of the curious position of the vestigial external gills in the case of *Protopterus*—immediately over the pectoral girdle.

Tail.

The tail throughout development is diphycercal. It has been held§ that the tail in Dipnoi is secondarily diphycercal (gephyrocercal). Both in *Lepidosiren* and in *Ceratodus* (SEMON) the external features of development fail to lend any support to this view.

† *Cf.* MAURER, 'Morph. Jahrb.,' vol. 14, p. 207; who also associates the absence of external gills in Teleostei with the former possession of a large yolk sac.

‡ I may perhaps be permitted, in the comparative obscurity of a foot-note, to draw attention to a bearing which the question of external gills seems to me to have on the general theory of the limbs of the Vertebrata. As is well known, the theory of GEGENBAUR, which there is a general tendency to accept at present, consists of two main theses, (1) the derivation of the limb girdles from modified branchial arches, (2) the derivation of the skeleton of the limb itself through the stage of an archipterygium from the gill rays. As regards the latter of these, apart from points emphasising the resemblances of the ichthyopterygium of Selachians and Crossopterygians with the archipterygium, surprisingly little confirmatory evidence has been obtained, so little that it forms evidence of considerable weight against the view. It is quite different with the first thesis, however, the great difficulty, viz., that of the very extensive migration of the gill arch along the body to form the pelvic girdle, being to a great extent done away with by the researches of BRAUS and others, which make it extremely probable that such a migration has actually taken place in Phylogeny. Now what I desire to point out is that assuming the derivation of the limb girdles from branchial arches, we have in the presence of an external gill upon the arch, *just* such a projection from the body wall as would afford material for the manufacture of a paired fin.

§ BALFOUR, W. N. PARKER, DEAN, and DOLLO.

Cement Organ.

One of the most conspicuous features represented in the accompanying series of figures is the cement organ, which, appearing at a stage slightly older than that corresponding with fig. 23, increases in size and prominence until nearly the close of larval life, when it rapidly atrophies. This structure completely corresponds with the so-called "sucker," so characteristic an organ in the larvæ of most Anura which develop free in the water. It is interesting to notice that here, too, in its early stages, the organ has identically the same crescentic form so usually passed through by the structure in Anura, and which persists during the functional career of the organ in the larva of the ordinary toad (*Bufo vulgaris*). In *Lepidosiren* the cement organ appears much later than in Anura, where it usually appears before the closure of the medullary folds.*

Summary of the More Salient Developmental Facts Established in the foregoing Paper.

1. The cœlomic egg of Lepidosiren measures 6 millims. to 7 millims. in diameter, and is of pale salmon colour, with a white germinal cap covering about 100° at one pole.
2. It is surrounded by a transparent capsule about 1 millim. in thickness.
3. The eggs are laid in an underground burrow in the peaty soil at the bottom of the swamp.
4. The fertilised egg taken from the nest is surrounded by a thin horny capsule, round which is occasionally a loose, jelly-like envelope, resembling that which surrounds the egg of *Rana temporaria.*
5. Segmentation is complete and unequal—closely resembling that of *Amia*
6. Invagination begins over about one-third of the entire extent of the boundary between small and large cells, but as the process goes on, the lateral portions of the line of invagination flatten out and disappear, and the ultimate blastopore is only about a quarter as long as the original invagination.
7. The gastrula ultimately formed closely resembles that of *Petromyzon.*
8. The medullary folds are distinct but quite low, and the neural axis arises mainly by a solid keel-like downgrowth. At the same time there is a faint attempt at overarching, though the canal so enclosed apparently disappears.
9. The medullary folds are continuous behind the blastopore, which becomes directly the cloacal opening.
10. There is no trace externally of a dorsal seam running along the floor of the medullary groove.

* *Cf.* Thiele, 'Zeits. Wiss. Zool.,' vol. 46, 1888.

11. Nor is there a neurenteric canal.
12. As the tail fold appears, the portions of the medullary folds behind the blastopore (cloacal opening) flatten out and disappear.
13. Four external gills, whose rudiment appears very early, are developed upon Branchial arches I., II., III., and IV.
14. A cement organ, exactly corresponding with that of the larvæ of Anura, appears, though at a later stage in development.
15. Auditory and nasal sacs, and stomodæum, are formed by secondary excavation of originally solid rudiments.
16. The just hatched larva is superficially tadpole-like.
17. The cloacal opening, close to the tip of the apparent tail, closes temporarily, and remains closed for some time after hatching.
18. Up till the second week after hatching the larva remains, as was the egg, completely devoid of dark pigment. This first appears in the pigment layer of the retina, and soon afterwards in scattered cells on the dorsal surface of the head and anterior body region.
19. The external gills when fully formed are large and pinnate, and are raised upon a common stalk.
20. The fore and hind limbs undergo a similar rotation to those of *Ceratodus*, so that the upper side of either is homologous with the lower side of the other.
21. Differential growth causes the group of external gills on each side to become situated directly above or even slightly behind the root of the fore limb.
22. The origin of the spiral valve is in a deep incision which passes spirally round the solid mass of yolk forming the gut rudiment.
23. Pulmonary breathing was first noticed at a period when the external gills were still at their full development.
24. The branchial clefts become perforate long after they are completely overgrown by the opercular fold.
25. About the sixth week after hatching the external gills are lost, the colour becomes darker, and the habits more lively.
26. The young Lepidosiren is remarkably newt-like in general appearance. It uses its hind limbs in clambering about the vegetation.
27. The young Lepidosiren shows a colour change with change in surrounding condition of light and darkness, the black chromatophores retracting their pseudopodia in the dark, while the yellow ones remain unaffected.

Description of Plates.

The following drawings have been made from specimens for the most part preserved in formalin, which, when carefully used, I found to produce marvellously little post-mortem alteration in naked eye appearance. Some have been made from alcohol material fixed in various ways. Drawings from formalin specimens are indicated by the letter F in the explanations of the Plates; those from alcohol specimens by the letter A. The few rough sketches which I was able to make on the spot I have not used otherwise than as an occasional check upon the drawings from preserved material.

The two figures of adult *Lepidosiren* have been drawn by Mr. EDWIN WILSON from photographs, the details such as scale areas being traced direct from the photograph.

As regards the eggs and embryos the following method was employed. I drew them in outline by means of an Abbe camera lucida under a Steinheil lens of low power ("magnification 8"). Then Mr. WILSON worked up the drawing, either upon my outline or on a tracing of it, with the embryo before him, and, of course, under my own supervision. In this way I hope to have secured both absolute accuracy and artistic effect.* Certain of the drawings which were drawn by Mr. WILSON without the camera tracing I indicate by a star prefixed to the number.

* I regret to say that this has been to a great extent lost in the lithographed reproductions of the drawings. It is necessary to point out that in the following points the lithographs are inaccurate:—

In figs. 9–14 the effect of perspective upon the small segments of the egg towards the margin of the figures is ignored.

In Plate 2 the various elevations on the surface of the egg are too sharply marked, giving the impression that they are much more prominent than they really are.

Fig. 37 should be darker in shade than fig. 36, and fig. 36 darker than fig. 35.

In fig. 38N the dots representing the chromatophores are too large and too conspicuous.

In Plate 5, fig. E, the rudimentary papillæ are too strongly marked.

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PLATE 8.

All the figures on this plate were drawn under a magnification of eight diameters, and were reduced by the lithographer to $\frac{2}{3}$ the size of the original drawing. The actual magnification in the figures is therefore slightly over five diameters ($5\frac{1}{3}$). Where more than one figure of the same egg is given, *a* affixed to the number indicates view from above (*i.e.*, from the animal pole aspect), *s* view from the side, and *b* view from below.

b.p. Blastopore.
cap. Egg capsule.
emb. First indication of medullary plate.
ep.e. Growing edge of epiblast.
ger. "Germinal cap."
invag. Line of invagination.
seg. cav. Segmentation cavity.
yk. Yolk cells.

Fig. 1. Unfertilized egg from cœlom, still enclosed in its capsule. F. 1.
Fig. 2. Egg showing first segmentation furrow. A. XV Per. A.
Fig. 3. Egg with two primary furrows, seen from above. F. XVIII β.
Fig. 4. Egg after the appearance of the furrows of the Third phase. F. XV Per. β.
Fig. 5. An egg of similar stage showing irregularity induced by one of the furrows of the Third phase (γ) being latitudinal. F. XVIII.
Fig. 6. F., IV γ.
Fig. 7. F., IV α.
Fig. 8. F., XX.
Fig. 9. F., fr. XVII.
(Figs. 6–9) Illustrating the further progress of segmentation. In fig. 9*a* the segmentation cavity is indicated by a dark shadow.
Fig. 10. Egg showing the commencement of invagination. F. fr. XVIII.
Fig. 11. Slightly later stage seen from behind. In the side view the diminishing segmentation cavity is indicated by a shadow.
Fig. 12. F., fr. 3*
Fig. 13. F., XXX B.
Fig. 14. F., XXXVII C.
(Figs. 12–14) These figures illustrate the shortening up of the line of invagination, and the covering in of the yolk by the small superficial cells.

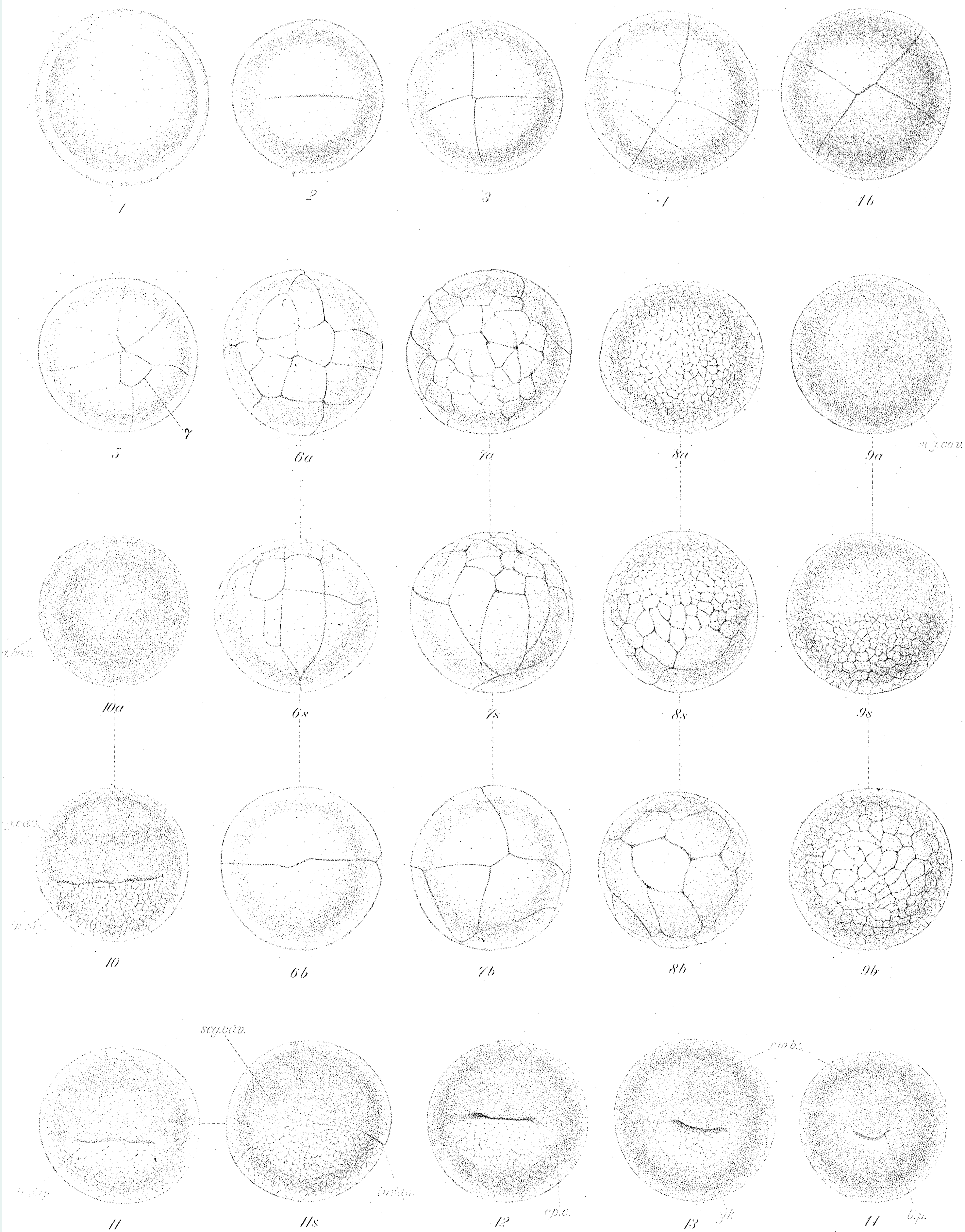

1
2
3
4
4b
5
6a
7a
8a
9a
seg.cav.
10a
6s
7s
8s
9s
10
6b
7b
8b
9b
seg.cav.
11
11s
12
13
14
emb.

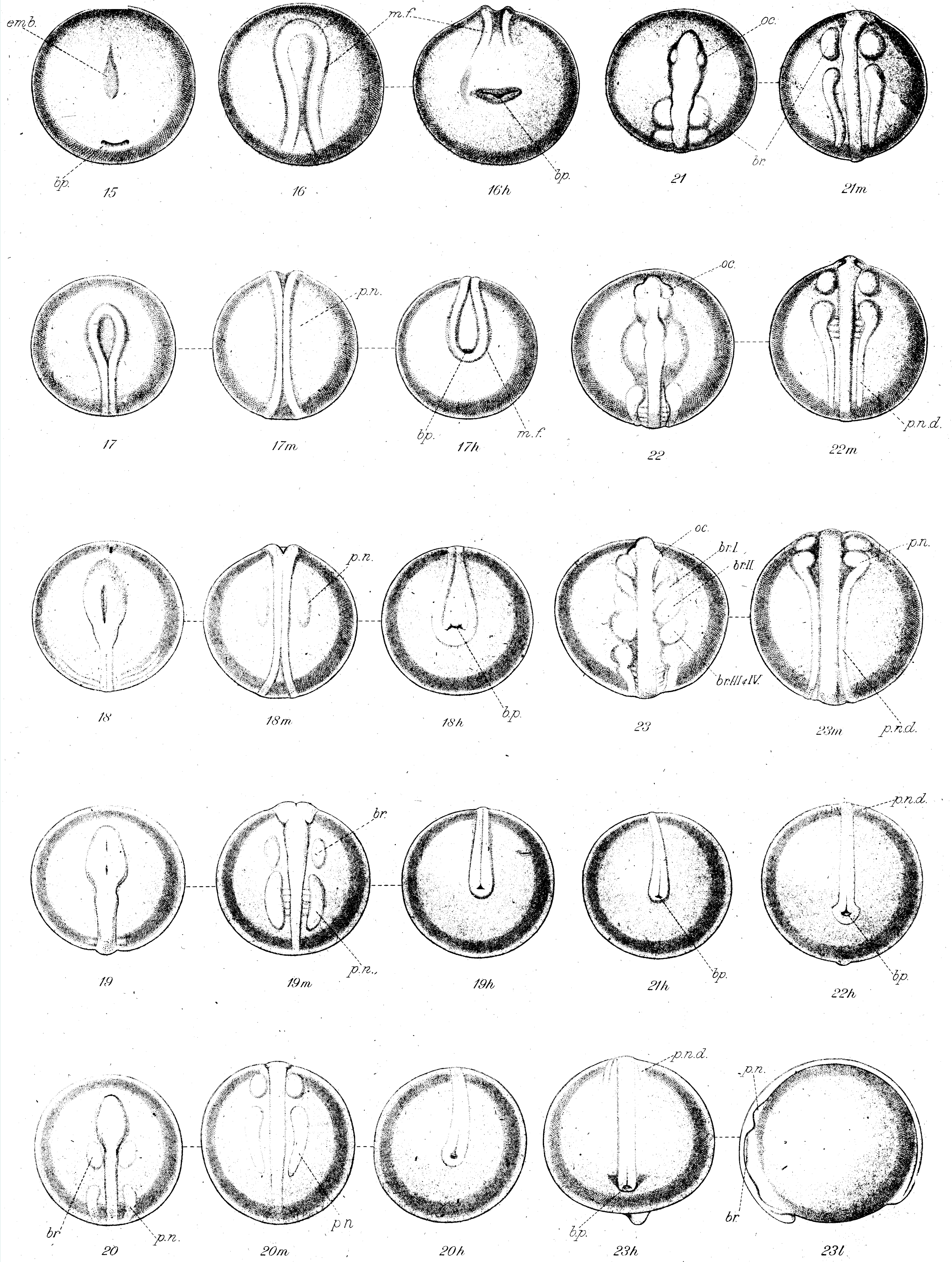
PLATE 9.

Magnification as in Plate 8.

The letters affixed to the numbers of the figures on this Plate signify :—*h*, view from behind; *m*, view looking down on middle of trunk region of the embryo from the dorsal side; *l*, view from the side.

bp. Blastopore.
br. Branchial eminence.
br. I, II, &c. Branchial arches.
emb. Depression over medullary plate.
m.f. Medullary folds.
oc. Optic outgrowth from brain.
p.n. Pronephros.
p.n.d. Pronephric duct.

Fig. 15. Egg slightly more advanced than that of fig. 14. F. fr. XVI.
Fig. 16. Egg in which the medullary folds have appeared. F. XXXVII A.
Fig. 17. Egg in which the medullary folds have become closely apposed in the mid-trunk region, and showing the continuity of the medullary folds behind the blastopore. F. XXI β.
Fig. 18. Egg showing commencing fusion of the medullary folds. F. XXXVIII α.
Fig. 19. Egg with the medullary folds nearly completely fused, and with first trace of the branchial eminence on each side. F. XIX E.
Fig. 20. Egg in which the fusion of the medullary folds is completed. F. fr. XXXII.
Fig. 21. A somewhat later stage in which the optic outgrowths have appeared. F. XXXIV β.
Fig. 22. An egg in which the head fold of the embryo is beginning to develop. F. XXIX Δ.
Fig. 23. Showing the segmentation of the branchial eminence, and the commencing development of the tail fold. F. fr. 9*.



Edwin Wilson del. et lith. Cambridge.

PLATE 10.

Magnification as in Plates 8 and 9.

br. I., II, &c. Branchial arches.
c.c. Central canal.
c.o. Cement organ.
cl. Position of cloacal opening, at present closed by membrane.
cl.o. Cloacal opening.
E.g. I, II, &c. External gills.
Ext. gill I and IV. Cut roots of external gills.
f.l. Rudiment of fore limb.
h.l. Rudiment of hind limb.
m. Groove in position of mouth.
op. Operculum.
pigt. Pigment cells in skin of antero-dorsal region.
p.n.d. Completed pronephric duct.
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Fig. 28. A larva three days after hatching. A. 69.

Fig. 29. A more advanced larva (also three days after hatching, the weather however being warmer than in the case of the larva of fig. 28). The pinnæ are beginning to develop on the external gills. A. 90.

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Fig. 30*v*. Ventral view of the same specimen, to show the cement organ, and the groove in the position where the mouth will appear. A. 93.

Fig. 31. A larva thirteen days after hatching, showing the first trace of the hind limb. A. 103.
Fig. 31*. Anterior portion of a larva of the same stage from which the external gills have been cut away, to show the position of their roots in relation to the fore limb and to the rudiment of the operculum. A. 103*.

Fig. 32. A larva twenty-four days after hatching. A. 111 A.

Fig. 33. A larva twenty-five days after hatching but considerably more advanced than that shown in fig. 32, showing the backward growth of the operculum, and the first traces of the spiral valve groove. F. 19* A.


c.o.
v.IV
I
II
III
IV
c.c.
o.n.d.
24
25v
v.IV.
E.g.IV.
E.g.I.
25
E.g.II.
25l
26
E.g.I.
28
E.g.I.
29
c.o.
30
cl.
m.
27z
c.l.
27
30v
h.l.
31
E.g.I.
cl.o.
h.l.
op.
32
f.l.
Ext.gill I-IV.
pigt.
op.
31*
c.o.
27y
c.l.o
33

PLATE 11.

The magnification is :—in figs. 34 and 35, four diameters ; in figs. 36 and 37 three diameters, and in fig. 38 two diameters ; fig. 39 is reduced to one-half natural size.

c.o. Cement organ. *e.g.* External gills.
s.v.g. Groove marking rudiment of spiral valve.

Fig. 34. A larva twenty-seven days after hatching. F.

Fig. 35. A larva thirty days after hatching, showing the external gills at their maximum development. They are drawn in the position they are in when the larva is moving forwards. The cement organ is in process of atrophy.

Fig. 35*v*. Ventral view of the same specimen showing the spiral valve groove. The external gills are here drawn as they are when the larva is at rest. F.

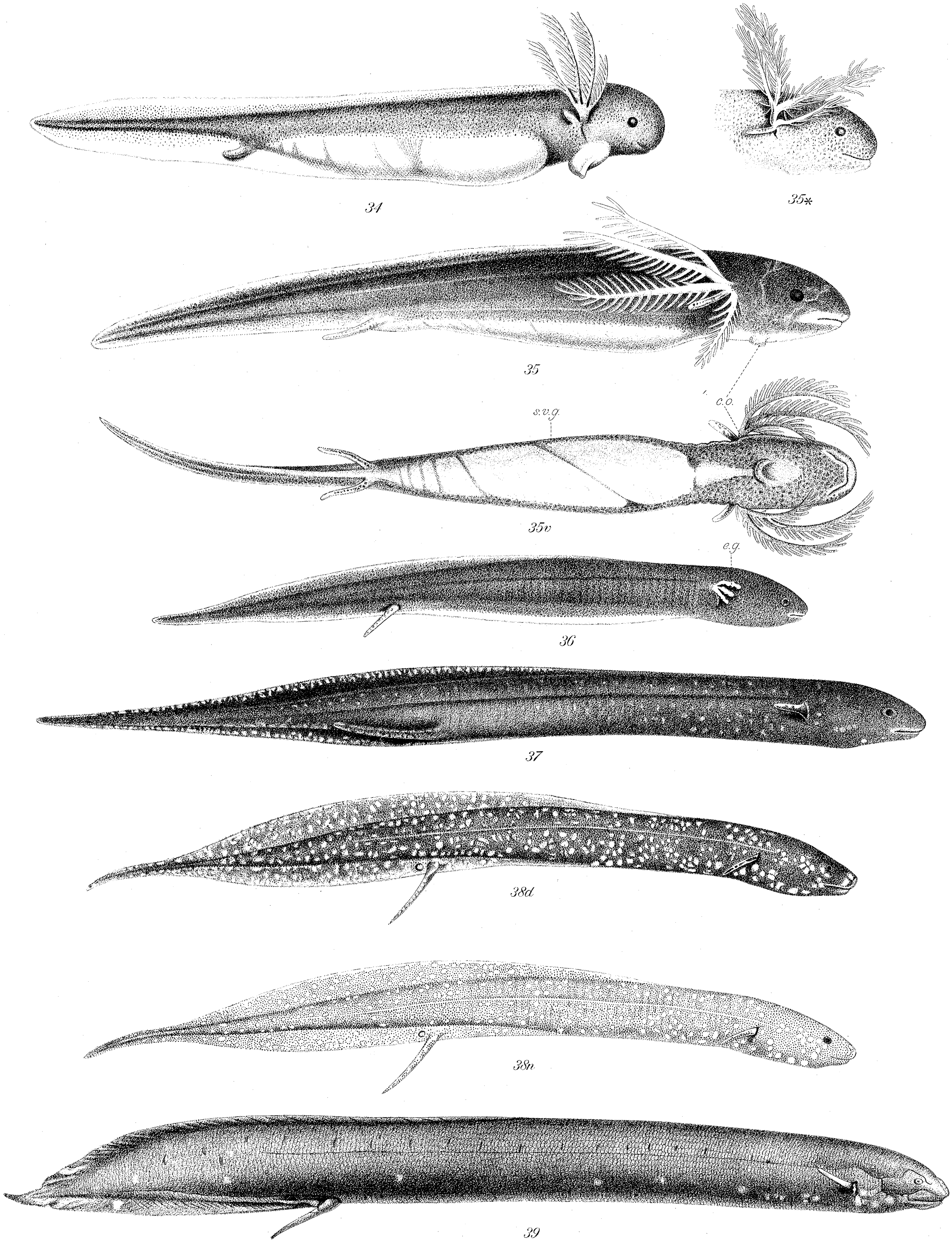
Fig. 35*. The anterior portion of a larva of the same stage, to show the relative positions of the roots of the external gill and of the fore limb. F. 25*.

*Fig. 36. A larva forty days after hatching, showing the shrivelled vestiges of the external gills. F.

Fig. 37. A young Lepidosiren about two months after hatching. F. 31.

*Fig. 38. A young Lepidosiren about three months after hatching ; 38*d* showing the appearance by day (2 P.M.), 38*n* the appearance by night (9 P.M.). F.

*Fig. 39. A Lepidosiren probably about eighteen months old. F.



Edwin Wilson del. et lith. Cambridge.

PLATE 12.

Figs. 1 and 2 are one quarter natural size ; figs. A, B, C, D, E are natural size.

Fig. 1. Male Lepidosiren during the breeding season, showing the filaments on the hind limb.

Fig. 2. Female Lepidosiren.

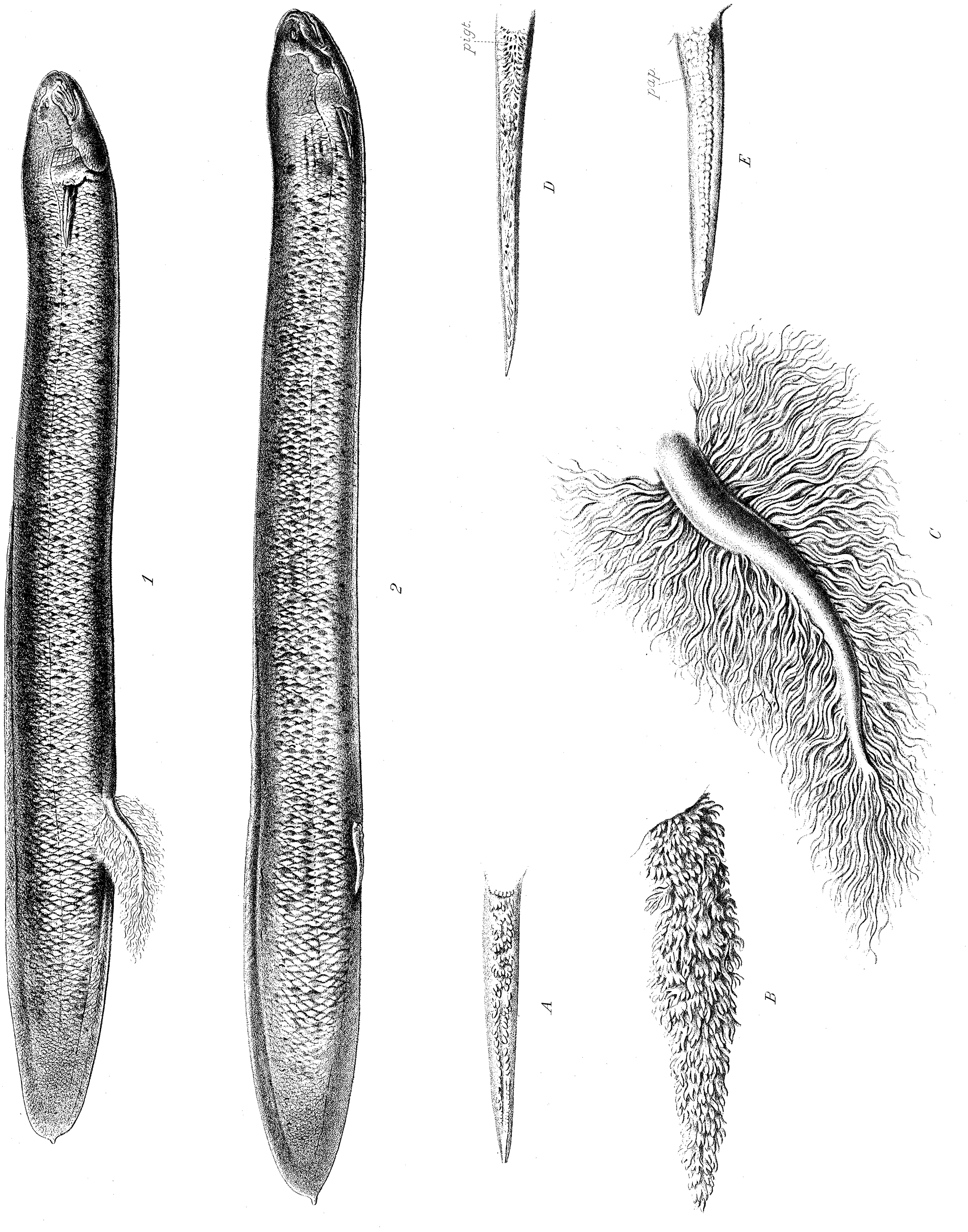
Fig. A. Postero-median aspect of hind limb of male some months before the breeding season, showing the papillæ in the resting condition.

Fig. B. A similar view of a hind limb just before the breeding season, while the papillæ are in course of rapid growth.

Fig. C. External view of the hind limb during the height of the breeding season, when the branches of the tree-like processes have grown out into long vascular filaments.

Fig. D. Postero-median view of hind limb of male, after the close of the breeding season. The filaments have disappeared except short stumps, about which there is an accumulation of black pigment (*pigt.*).

Fig. E. Similar view of the hind limb of a female, showing the rudimentary papillæ (*pap.*) which occasionally occur.



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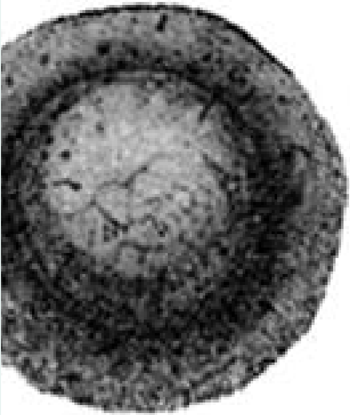
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Fig. 2.



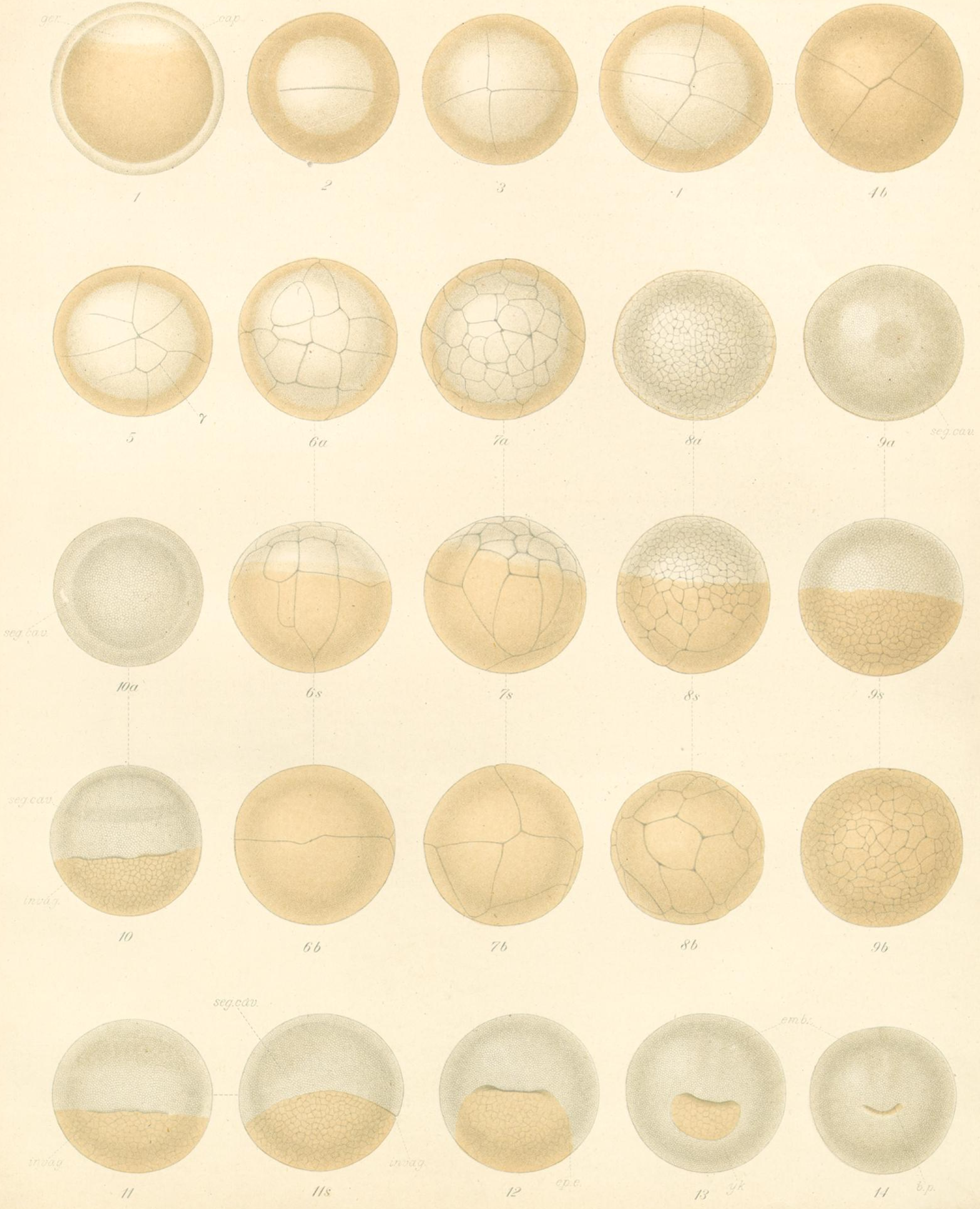


PLATE 8.

All the figures on this plate were drawn under a magnification of eight diameters, and were reduced by the lithographer to $\frac{2}{3}$ the size of the original drawing. The actual magnification in the figures is therefore slightly over five diameters ($5\frac{1}{3}$). Where more than one figure of the same egg is given, *a* affixed to the number indicates view from above (*i.e.*, from the animal pole aspect), *s* view from the side, and *b* view from below.

b.p. Blastopore.
cap. Egg capsule.
emb. First indication of medullary plate.
ep.e. Growing edge of epiblast.
ger. "Germinal cap."
invag. Line of invagination.
seg. cav. Segmentation cavity.
yk. Yolk cells.

Fig. 1. Unfertilized egg from cœlom, still enclosed in its capsule. F. 1.
Fig. 2. Egg showing first segmentation furrow. A. XV Per. A.
Fig. 3. Egg with two primary furrows, seen from above. F. XVIII β.
Fig. 4. Egg after the appearance of the furrows of the Third phase. F. XV Per. β.
Fig. 5. An egg of similar stage showing irregularity induced by one of the furrows of the Third phase (γ) being latitudinal. F. XVIII.
Fig. 6. F., IV γ.
Fig. 7. F., IV α.
Fig. 8. F., XX.
Fig. 9. F., fr. XVII.
(Figs. 6–9:) Illustrating the further progress of segmentation. In fig. 9*a* the segmentation cavity is indicated by a dark shadow.
Fig. 10. Egg showing the commencement of invagination. F. fr. XVIII.
Fig. 11. Slightly later stage seen from behind. In the side view the diminishing segmentation cavity is indicated by a shadow.
Fig. 12. F., fr. 3*
Fig. 13. F., XXX B.
Fig. 14. F., XXXVII C.
(Figs. 12–14:) These figures illustrate the shortening up of the line of invagination, and the covering in of the yolk by the small superficial cells.

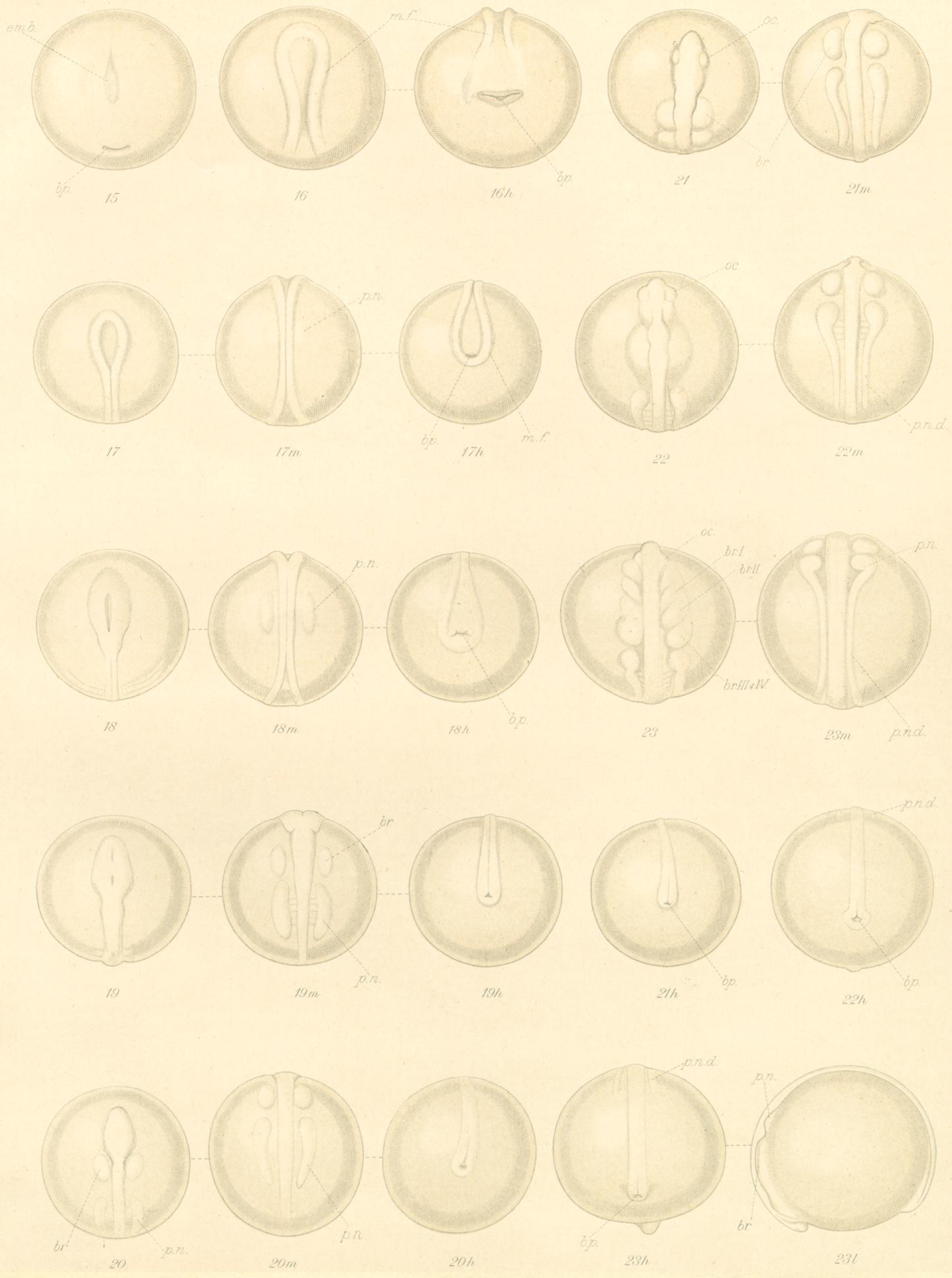


PLATE 9.

Magnification as in Plate 8.

The letters affixed to the numbers of the figures on this Plate signify:—*h*, view from behind; *m*, view looking down on middle of trunk region of the embryo from the dorsal side; *l*, view from the side.

bp. Blastopore.
br. Branchial eminence.
br. I, II, &c. Branchial arches.
emb. Depression over medullary plate.
m.f. Medullary folds.
oc. Optic outgrowth from brain.
p.n. Pronephros.
p.n.d. Pronephric duct.

Fig. 15. Egg slightly more advanced than that of fig. 14. F. fr. XVI.

Fig. 16. Egg in which the medullary folds have appeared. F. XXXVII A.

Fig. 17. Egg in which the medullary folds have become closely apposed in the mid-trunk region, and showing the continuity of the medullary folds behind the blastopore. F. XXI β.

Fig. 18. Egg showing commencing fusion of the medullary folds. F. XXXVIII α.

Fig. 19. Egg with the medullary folds nearly completely fused, and with first trace of the branchial eminence on each side. F. XIX E.

Fig. 20. Egg in which the fusion of the medullary folds is completed. F. fr. XXXII.

Fig. 21. A somewhat later stage in which the optic outgrowths have appeared. F. XXXIV β.

Fig. 22. An egg in which the head fold of the embryo is beginning to develop. F. XXIX Δ.

Fig. 23. Showing the segmentation of the branchial eminence, and the commencing development of the tail fold. F. fr. 9*.

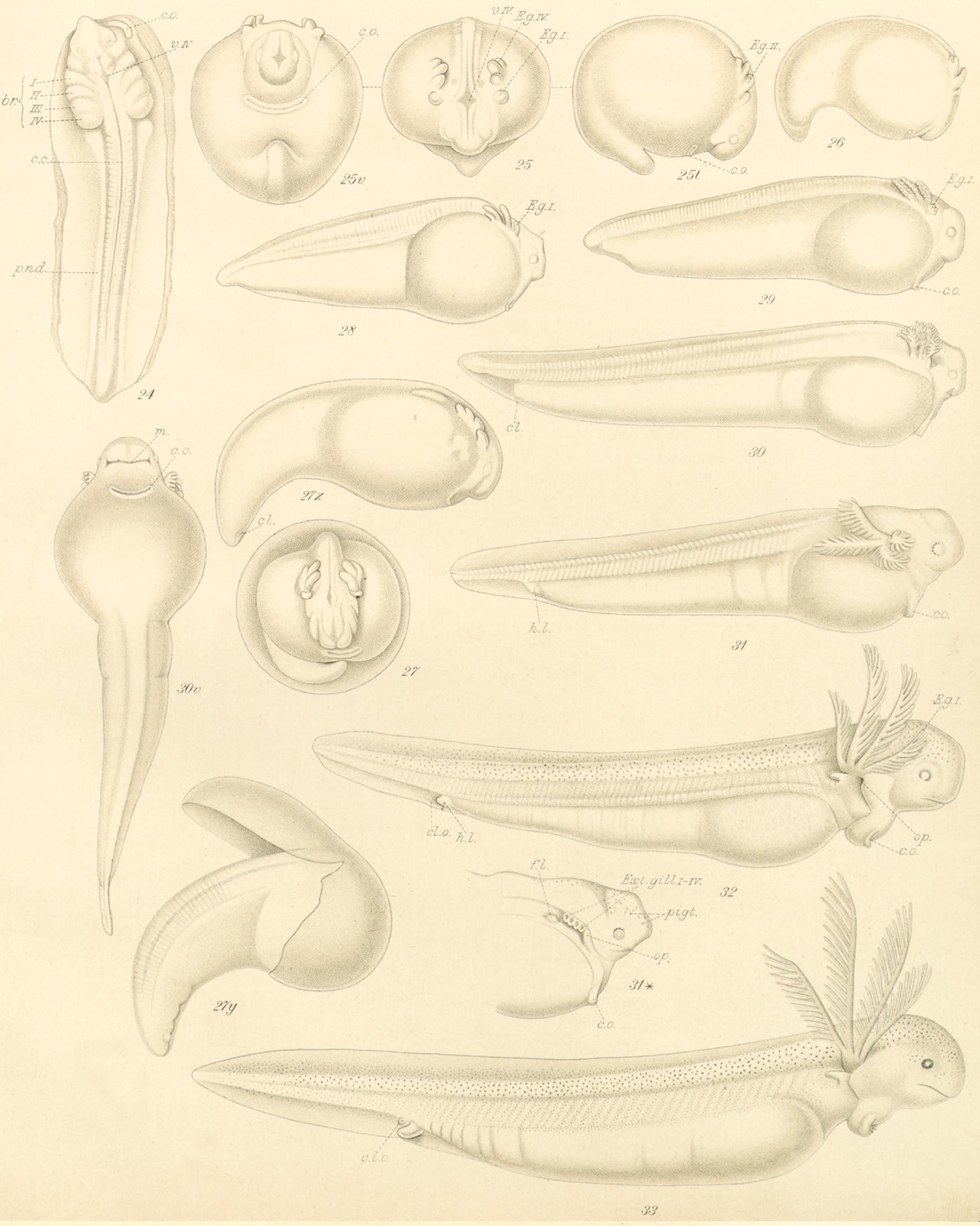


PLATE 10.

Magnification as in Plates 8 and 9.

br. I., II, &c. Branchial arches.
c.c. Central canal.
c.o. Cement organ.
cl. Position of cloacal opening, at present closed by membrane.
cl.o. Cloacal opening.
E.g. I, II, &c. External gills.
Ext. gill I and IV. Cut roots of external gills.
f.l. Rudiment of fore limb.
h.l. Rudiment of hind limb.
m. Groove in position of mouth.
op. Operculum.
pigt. Pigment cells in skin of antero-dorsal region.
p.n.d. Completed pronephric duct.
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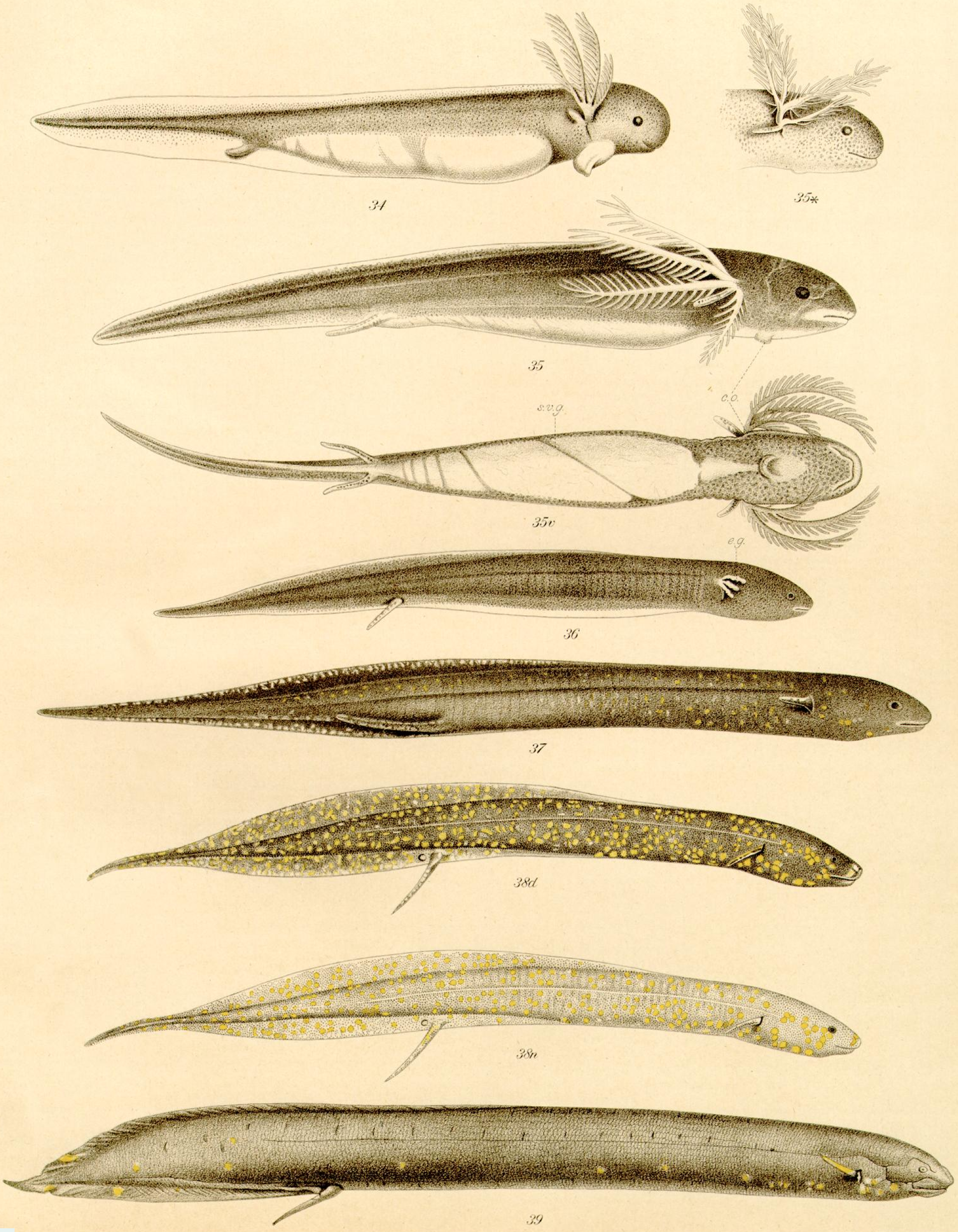

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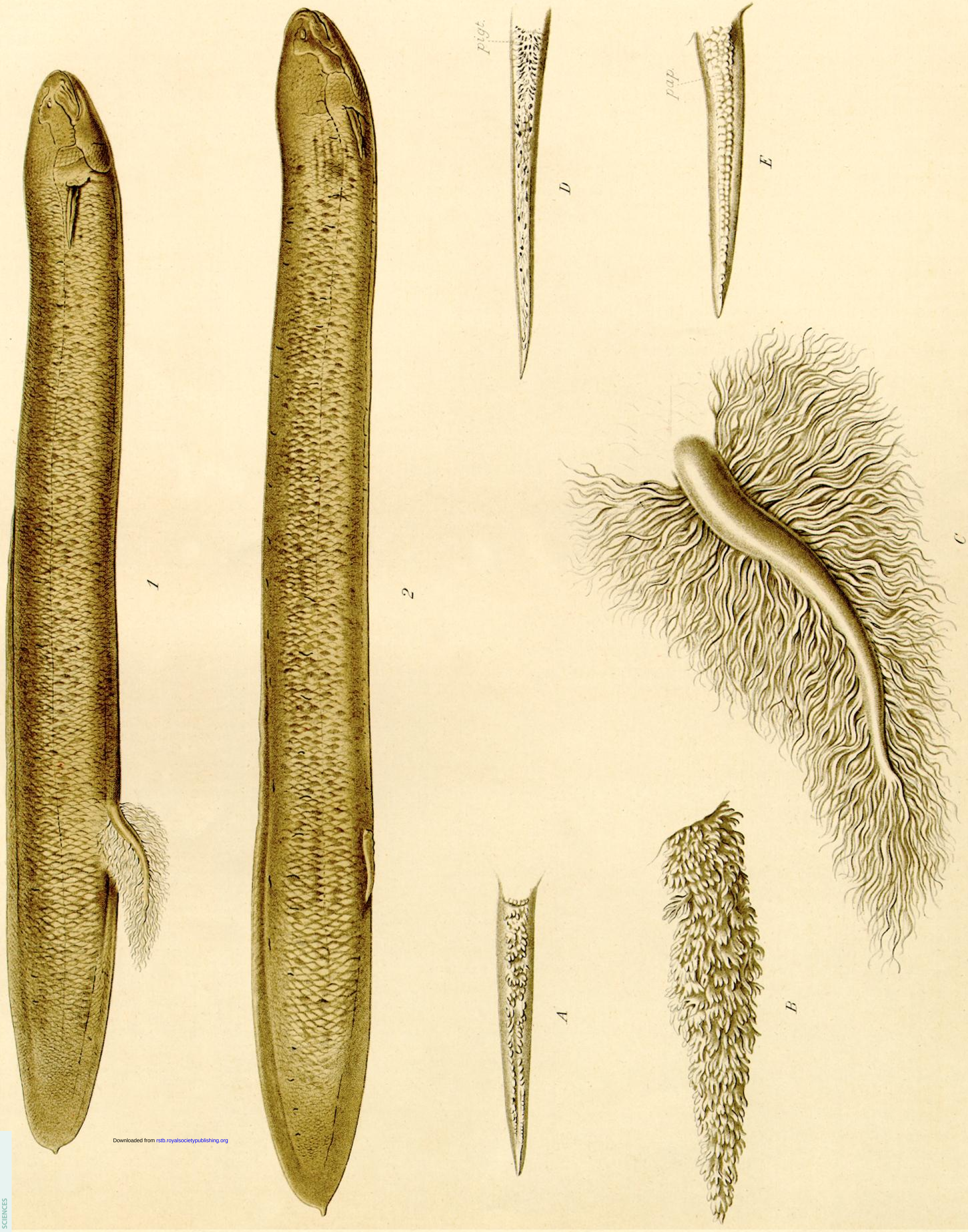

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