On the larval development of Amia calva.

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With Plates 9—11 and 17 figures in text.

The early developmental history of the Ganoids, *Lepidosteus, Acipenser* and *Amia,* forms an unbroken chain of evidence to connect what are essentially the embryonic characters of the Elasmobranchs with those of the Teleosts. Thus it is known that *Lepidosteus* [1]) is decidedly shark-like in its early developmental features; and that *Amia*, on the other hand [2]) is clearly Teleostean; — a range in early ontogeny which can at the least be regarded as providing the most interesting confirmation of the results of palaeontologists [3]) as to the phylogeny of the Teleostomes. The Ganoids, in short, have made good their claims to be regarded as an intermediate group: and from this standpoint the further study of their developmental characters might well be expected to demonstrate more definitely the relationships and the interrelationships of the Ganoids and to point out more clearly the lines of evolution of many of the puzzling processes in the specialized developmental type of the Teleost.

The sub-classes of Fishes are broadly separated in the characters

1) Dean, Early development of Gar-pike and Sturgeon, in: J. Morph., 1895, V. 11, No. 1, p. 1—62, tab. 1—4.

2) Dean, Early development of Amia, 1896, in: Quart. J. Micr. Sc., V. 38, p. 413—444, tab. 30—32.

3) Cf. Esp. Traquair, The Palaeoniscidae, in: Mem. Pal. Soc., 1876, and Smith Woodward, On the palaeontology of Sturgeons, in: P. Geol. Ass., 1889, V. 11, Nos. 1 and 2.

of their development: and indeed even within their sub-groups there occur such striking differences in ontogeny that a morphologist may well wonder to what degree may not adaptations be impressed upon the structures of the embryo. Within a single family like that of the *Cyprinidae* developmental differences may be found which according to older tenets must certainly be interpreted as of far greater significance than those existing between the classes of Reptiles, Birds and Mammals.

It has been noticed that differences in the adaptive characters of the different groups of fishes sometimes appear most strikingly in the stages of latest and earliest development. In the previous papers the writer has explained some of relationships of the most pronounced features of the early development of Ganoids: at present he would undertake to show that the later embryonic and the larval development of the most modern type of Ganoid demonstrates clearly marked transitions to the larval conditions of Teleosts, and that therefore no broad line can be drawn between the typical conditions in the Teleost and those of the most archaic form, *Lepidosteus*, as described by A. Agassiz.

The larval conditions of Ganoids it should be said in introduction are remarkably uniform during the first day after hatching in all forms examined; the larvae of *Lepidosteus*, *Acipenser* and *Amia* at this stage would not readily be distinguished were it not for the well marked difference in their size. In all forms the yolk sac is of the same relative form, and the degree of the differentiation of sense organs, trunk. fins, viscera, surprisingly uniform. But from this time onward the differentiation of the larvae takes place rapidly; on the second day the different forms have become dissimilar; and during the next two days the conditions already suggest those of the mature fish, of *Amia* on the third day, of *Acipenser* on the fourth and of *Lepidosteus* on the fifth to sixth. In tracing these developmental advances we cannot fail to be impressed with the greater precociousness [1]) of *Amia* in contrast with the other forms, a distinct nearing accordingly to the Teleostean.

The following arrangement has been made in describing the larval development of *Amia*:

1) The differences in the rate of development during the first days of development could not have been noteworthy; the larvae of all forms were hatched out and reared in rooms which could have varied but little in point of temperature.

A list of the literature on the embryology of the Ganoids has been given in the Journal of Morphology, V. 11 (1895), p. 54—55. To this is to be added the following titles:

Virchow, H., On the breeding habits and gill vessels of Lepidosteus, in: SB. Akad. Wiss. Berlin, 19. Jan. 1894, p. 33—44.
Furchungsbilder von Amia calva, in: SB. Ges. Nat. Fr. Berlin, 1896, No. 3, p. 41—42.
Nickerson, W. S., The development of the scales of Lepidosteus, in: Bull. Mus. Comp. Zool., Harvard 1893, V. 24, No. 5, p. 114—144.
Jungersen, H. F. E., Die Embryonalniere von Amia calva, in: Zool. Anz. 1894, No. 451.
Dean, Bashford, Spawning habits and early development of Amia, in: Quart. J. Micr. Sc., 1895, V. 13, p. 413—444.

In *Amia*, as in fishes generally, the distinctly larval period may be said to be initiated by the process of hatching and to be continued to the period of the ripening of the sexual products; usually, however, this period is looked upon as referring to the earliest weeks of the free-swimming existence of the fish, — since it is within this short time that nearly every growth process takes place. Thus in the case of *Amia* larvae of the fifth week, although as yet scarcely an inch in length, have attained practically their adult conditions, including the essential fin characters, scales and teeth. And it is to this point that the present outline has been carried: the further changes, those mainly of the genito-urinary system, body and fin proportions, coloration, have been practically omitted from the present discussion.

The later development of *Amia* was hitherto known from the classic memoir of E. P. Allis on the lateral line system, in: J. Morph., 1889, in which many larval stages were figured but not considered apart from the theme of the paper. The only additional account of *Amia*'s later development is the discussion by H. F. E. Jungersen of the larval excretory system, referred to above.

I. The larval habits of the Amia.

After hatching the young fish remains inactive for several days, during both day and night, at all events under the living conditions offered in an aquarium. There is a marked tendency for the larva to attach itself by its sucking disc, but rather curiously it does not appear to become attached to the surrounding stems and leaves of the water weeds; it sinks to the bottom, and there, lying on its side, rests attached to whatever may have been touched. In case no solid object comes in contact, the sucking disc functions nevertheless, becoming covered with sediment. Under natural conditions, as the writer has already noted, the larvae could not be found in the nest during the first days after hatching, and it is perhaps not impossible, as Mr. Kosmak suggested, that they may have been removed by the male fish, attached to him by their sucking disc.

The larvae of the second, third and fourth day exhibit considerable advances; they depend less upon their sucking disc, and occasionally exhibit a spasmodic activity; when touched, they wiggle about rapidly for a short distance, and then sink motionless, resting on their side. As in the younger stage there is a tendency to swim head downward.

The larvae of the fifth, sixth and seventh day have become notably active in their movements, are restless, and can with difficulty be kept even for a few minutes in a single spot. When not swimming they rest on their yolk sac in a normal position, but even then their large pectoral fins are in constant movement, as if serving as balancers. They dislike to be turned on their sides: they breathe with quick movements, the mouth and gill covers opening and shutting widely.

The larvae of the second week begin to attain the characteristic movements of the adult fish; they balance themselves with inconspicuous movements of the fins, pectorals and dorsals. Their firm movements in swimming are now in contrast to the wiggling motions of the younger stages. The caudal fin has become the main organ of propulsion. It is at this period that the young fish have been seen near the surface, attended by the male, in dense swarms often of several thousand. As previously noted by the writer the habits of the young fish under these conditions may be readily observed; the attendant male may be closely approached, and his movements followed; in a slow and cautious way he circles about now over and now under his swarming charges, watchful apparently that the stragglers shall be kept up to the rest; and in their turn the young fishes seem to fully realize that it is their duty to keep as close as possible to the guardian. It was found by the writer by no means easy to approach the male fish without attracting his notice; he appears to be constantly watchful, and when alarmed exhibits the greatest solicitude for his charges; sometimes he backs quietly into some reed-screened pool, hiding below in the shadow of floating weeds, his presence betrayed only by the black mass of larvae about him; at other times he will skulk cautiously away, drawing the swarm after him as rapidly as possible. His duty is clearly to care for his charges, and in the majority of cases when he finds that it is impossible to carry them off with him he will remain quietly and face the enemy. In one instance he was actually pushed away. There can be no question, the writer believes, that the feeling of alarm of the guardian may be transmitted to the young; for in case of need the swarm may be moved more rapidly, the young, excited in their movements, appearing to draw more closely together: under all circumstances they appeared to be careful not to disperse. When the male has been driven away the swarm sometimes becomes so dense that it may be taken almost to a fish by a single dip of a scap-net; if not interfered with it will gradually move away and take refuge among the floating weeds, often so perfectly that no traces of it can be noticed. Exactly to what period the larval *Amia* remains in company with the male fish has not seen determined exactly. The smallest which in any case the writer has observed measured $^5/_8$ inches (slightly younger than that of Pl. 10, Fig. 20), the largest 1 inch (Pl. 11, Fig. 25); and as these notes have been made from a large series of swarms, during a period of about two weeks, there is ground for believing that the time of the guardian's care of the movements of the young extends from — at least — the stage of the exhaustion of their yolk supply to that when the caudal fin and scales have attained the adult outlines; — a time certainly not less than four weeks [1]). The rate of growth of larvae of the same

1) The writer has recently learned from his friend Mr. F. B. Sumner that the period of the attendance of the male is much longer than at first supposed. In Minnesota Mr. Sumner records the taking of a swarm of *Amia* larvae of which the individuals measured 3—4 inches in length, and must have been about four months old; a remarkable fact in connection with them was that all of these young fishes

swarm has been observed to be approximately uniform, the individual differences depending rather upon size than upon actual developmental advances; larvae of apparently the same stage of development have varied in length as much as $^3|_8$ inches; in some cases, however, the range in development seems, as nearly as could be determined, to have been equivalent to a difference of two or three days.

Upon the dispersal of the swarm the larvae appear to make their way to the well-weeded shallows of the neighborhood; here they remain during the first summer, occasionally taken along adjacent shore reaches in the drawing of the minnow nets. Mr. Henry G. Meyer, to whom the writer has hitherto referred for his kindness during collecting trips, has stated that during the first summer many of the fishes will be taken in and near the mouths of the small streams which feed the lake chain of Pewaukee. It may at all events be surmised that the habits of the late larvae of *Amia* do not differ widely from those of the prevailing forms of the local Teleosts.

II. Description of larvae of *Amia*.

The latest embryonic stages of *Amia* correspond more closely to those of *Lepidosteus* than of *Acipenser*, the embryo's head and trunk lifting themselves sharply above the neighboring parietal zone and yolk.

Embryo surrounding 200° of the egg's circumference.

At about two days before hatching (138 hours), Pl. 9, Fig. 1, the embryo surrounds about 200° of the egg's circumference. Its trunk, a prominent whitish ridge, is of equal diameter from head to tail; it is sharply marked off from the yolk mass, which at this stage is elongated transversly to the axis of the body. The parietal zone, *p.z.*, is a distinct band, bordering on the one hand the line of the primitive segments and on the other the marginal yolk. The pericardial area, *p*, is now large in size and its distended sides may be seen on either side of the head. The tail is blunt ended, as yet unseparated from the yolk. The head is large; optic lobes are prominent, *o.l.*, overhanging a broad and deep fourth ventricle; sucking disc, nasal pits and auditory sacs are already defined; in the eyes

(females, therefore, as well as males — although no dissections were made to determine sex) had acquired the characteristic coloration of the male with the prominent orange and black spot on the caudal fin.

the lenses are forming; the two foremost gill slits are established, and the third and fourth already indicated. The pronephric duct, *p.n.*, passes tailward from its origin immediately behind the beginning of the myelon; unlike in *Acipenser*, it is inconspicuous, taking its position close to the trunk, as in Teleosts. Notes on the early structural conditions of the pronephros, brain, hypophysis, chorda, digestive tract and yolk are given below, pag. 654—668.

Embryo surrounding 225°.

A late embryo of 142 hours is figured in Pl. 9, Fig. 2. Its trunk is now a clearly defined ridge upon the egg's surface; it is no longer demarked from the yolk region by the parietal zone as a marginal trench. The pronephric ducts are most prominent at this stage, separate from the trunk region anteriorly, gradually converging tailward and passing within the margin of the trunk. The growth of the tail now separates it from the egg. This condition may well be seen in Pl. 9, Fig. 3, the ventral aspect of this stage. Here too may be seen the outline of the sucking disc, *s.d.*, its large size and distinctly paired character [1]): its uplifted rim consists on either side of about 4—6 papilla-like sucking organs. The heart, too, is also to be outlined in its thin walled and greatly dilated pericardial chamber; it is straight and tubular, showing at either end its diverging component elements. The mouth, *m*, is now a narrow, transversely widened pit, partly concealed by the sucking disc.

Embryo surrounding 240°.

In this stage, 148 hours, Pl. 9, Fig. 4, the trunk has risen vertically from the egg; the hinder trunk region, greatest in vertical width, is now separate from the egg; its terminal is blunt and rounded. Four gill slits are now apparent outwardly; as yet, however, the foremost two have alone broken through, and these but for a small proportion ($^1/_3$) of their length ventrally. The pericardial region is now becoming reduced in size, losing its transparency.

Embryo surrounding 290°.

The region of the hinder trunk in this stage, 160 hours, is seen

1) There can be no question that the figures of Allis, in: J. Morph., '89, V. 2, p. 463—566, are inaccurate in this regard; the paired character of the sucking disc is shown in surface view and sections from the time of its early appearance till the time of its absorption several weeks after hatching.

in Pl. 9, Fig. 5. The continued elongation of the tail in this stage, taking place within the egg membranes, is accompanied with the torsion of the hinder trunk; this, turning on its side, now grows flatwise, opposing (usually) its left side to the yolk-sac; and in its later growth it assumes a somewhat S-shaped position. Its terminal is still rounded. The entire trunk is whitish, pigmentless, semitransparent; toward its hinder part the somites become more and more difficult to distinguish.

Larva at hatching (Pl. 9, Fig. 6 and, in dorsal view, Fig. 7).

The embryo exhibits movements for nearly a day before hatching; these become especially noteworthy a few hours before the escape from the egg membranes, the tail writhing sometimes slowly, sometimes quickly and spasmodically, from side to side. The movements must undoubtedly be looked upon as the efficient cause of the escape of the embryo from the egg, although during the later stages a decided thinning and drying up of the membranes is to be noted. Upon detaching itself from its membranes the larva lies quietly on its side for some hours, rarely moving. Its head and trunk are whitish, still without pigment; the great rounded yolk sac is pale slate-coloured, in its region below the head a faint tinge of colour indicates the position of the heart. As seen in the figure, Pl. 9, Fig. 6, the body length is somewhat downbent, the tail drooping ventrally to the level of the base of the yolk sac. The conditions of the organs at this stage can readily be made out in the living larva an account of its transparency; the relatively large size of the optic lobes, the breadth and openness of the fourth ventricle are to be noted; the heart is as yet unbent, a short thick tube from whose hinder end diverge the omphalo-mesenteric veins; the mouth pit is just on the point of establishing its opening into the fore-gut, the proctodaeum, a sharp nick on the margin of the fin membrane, has not as yet its connection with the hind gut; the gill region is considerably flattened, dorso-ventrally, against the outswelling yolk; the fifth gill slit is determinable. In the eyes there are as yet but traces of pigment and the lens has not been completely formed. The body segments are to be traced into the hinder trunk but are not as yet differentiated near the bulbous tip of the tail; there is no post-anal gut; the unpaired fins are noticeable, but still inconspicuous; there is as yet little trace of the pectoral fins; the liver is now coming to be formed, distinguishable as a whitened tract on the yolk region at the left side of the trunk; the vitelline vessels become a prominent feature of the dorsal aspect of the yolk sac; the sucking disc is in this stage relatively at its largest size.

Larva of the second day (Pl. 9, Fig. 8).

The straightening of the trunk takes place during the second day, a change accompanied with a great development of the continuous unpaired fin; this now surrounds the entire hinder trunk, and in the caudal region develops a noticeable heterocercy. At the same time the pectoral fin becomes conspicuous, typically fin-fold-like in character, resembling the corresponding stage in the fin growth of the older Ganoids; it contains about seven (metameral) mesoblast buds. An elongation of the yolk sac accompanies these changes; and the entire head region has become distinct from the sac and greatly enlarged. At the side of the head the dermal operculum is enclosing the gill slits; the auditory vesicle is clearly defined; and the formation of the lens has taken place. There is a general loss of the transparency of the head and anterior trunk region; pigment patches become evident; the brain vesicles can no longer be distinguished through the head wall. The blood has now acquired a reddish colour and the pulsation of the heart can be followed; the long caudal vessel forms a broad band at the ventral margin of the somites of the trunk. Mouth and anus are established; the pronephric ducts are to be traced above the line of the hind gut, and may be seen to unite just above the anus; their common opening to the exterior appears to be on the point of formation. The head surface shows a faint outmapping of the sensory canals; the nervus lateralis vagi is seen to have pushed its way hindward along the side of the trunk to near the pectoral region (cf. Allis, op. cit.).

Larva of the third day (Pl. 9, Fig. 9).

The advances in this stage include: pigmentation, increased size and the distinctness from the yolk sac of head and trunk; enlargement of the pectoral fins and of the dermal operculum, which has now entirely overlapped the region of the gills; the U-shaped condition of the heart; the separation of the chin region from the yolk; the distinct appearance of the thickened tracts of sensory epiblast in the head surface; the progress of the nervus lateralis vagi to that portion of the mid-lateral line of the trunk immediately above the hind margin of the yolk sac.

Larva of the fourth day (Pl. 9, Fig. 10; dorsal aspect Pl. 9, Fig. 11; ventral aspect Pl. 9, Fig. 12).

In this larva there is an evident reduction in the size of the yolk sac, the latter's hinder end has now become pointed, its ventral side concave; anteriorly it is overlapped by the growth of the gular isthmus of the opercular flaps; these are now seen to open and shut, showing that the active process of breathing has begun; gill filaments are established, but as yet are small in size. The chin region is now prominent; conical teeth appear; the iris coming to be formed, shows on the ventral side a well marked break due to the connection of its growth with the choroidal fissure; the heart has completed its S-shaped course. The thickening of the ectodermal tracts of the head surface is now to be prominently noted; and the pushing of the nerve tract of the lateral line has progressed along the trunk region into the anterior part of the tail. The outline of the larval caudal fin is at this stage relatively largest; the pectorals, much enlarged in size, indicate that the fin axis has come to protrude from the body wall, and that it is already surrounded by the rapidly growing dermal margin of the fin. At this and earlier stages the pectorals are situated on the yolk sac close by the side of the trunk, their planes diverging somewhat tailward. In the ventral view of this larva, Pl. 9, Fig. 12, a remarkable arrangement of pigment may be seen in the chin and sucking disc, demarking in this region apparently the lines of the sensory tracts; especially striking is a cross line of pigment traversing both halves of the sucking disc.

Larva of the fifth day (Pl. 9, Fig. 13; dorsal view Pl. 9, Fig. 14).

A notable decrease in the size of the yolk sac characterizes this stage also; the sac's hinder end is now reduced to a pointed outgrowth, now no further from the body than the rim of the anal finfold. The size of the larva has on the other hand notably increased; its head is especially prominent; the mandible is now distinct, occasionally opening and closing; the nasal sac is prominent, its opening somewhat pear-shaped, — at its narrow end near the eye will be constricted off the posterior naris; the iris is now metallic in lustre, marked here and there with dark pigment. The mucous canal tracts are to be clearly followed on the head surface; the lateral line has passed into the region of the tail tip and has turned ventrally, as Allis has shown, into the position of the median line of the definitive caudal fin. The continued growth of the opercular folds has by this time enclosed the region of the heart, although their translucency still permits the heart's outline to be seen. The principal change in the fins is the increased growth of the pectorals; these have now a stout muscular base and exhibit their first movements. The caudal vessels, *c. v.*, are now less prominent on account of the enlargement and thickening of the muscle-plates in the ventral region of the trunk; a sub-intestinal vein, *s. i.*, is noted. The anal opening is now obscured by the longitudinal creasing at this point of the dermal fin; it is now, judging from surface view, that the pronephric ducts, *p. n.*, establish their outer opening.

Larva of the sixth day (Pl. 10, Fig. 15; dorsal aspect in Pl. 10, Fig. 16; outline of distal end of sucking disc in Pl. 10, Fig. 15a).

A general modelling of the head and yolk sac accompanies the size growth of this stage. In the head the brain is becoming surrounded by the cartilaginous cranium; this growth, however, is not as yet so complete as to obscure the profile of the fore-, mid- and hind-brain, as noted in the figures of the larvae of fifth, fourth, third and second days. The head contours are being filled in by the growth of the musculature of the opercula, gill arches and jaws. In the latter notable advances are present; the membrane bones, premaxillary and maxillary are forming, and give at once an *Amia*-like appearance to the young fish; their establishment has proceeded pari passu with the reduction in size of the sucking disc. Its distal outline at this stage is shown in Pl. 10, Fig. 15a. The lower jaw has also the beginning of its adult characters; its increased size becomes more conspicuous by its constant movements in breathing; the beginnings of the jugular plate, *jug.*, appear in the angle between its rami. A general outlining of the thickened epithelial tracts of the mucous canals can now be followed, especially in the temporal and supra-orbital regions, where the closing over process so admirably described by Allis is now taking place; this process has already occurred along the sides of the trunk and renders the lateral line less conspicuous in surface view. The great reduction in the size of the yolk sac gives the larva a tadpole-like appearance: around the sac's forward end the enlarged opercula have become neatly modelled. There is a noteworthy enlargement of the pectoral fin both in basal and dermal parts; it has at present somewhat the appearance of a shark's fin, a monoserial archipterygium, the dermal margin having made little advance is surrounding the hindward projecting fin axis.

Larva of the seventh day (Pl. 10, Fig. 17; dorsal aspect Pl. 10, Fig. 18).

The chondro-cranium is nearly completed at this stage, giving the frontal region somewhat its adult appearance. The sucking disc is reduced to a mere tubercle and is no longer functional; maxillae and premaxillae are established; the opercula have increased widely in outline, broadly enclosing the front of the yolk-sac region. The mucous canal tracts of the head are now mapped out most favorably; they have sunken into the skin as whitish lines and are gradually becoming darkened at various points by the overlapping tissue of the margining ledges. The pectoral fins have greatly increased in size and are in constant motion; they now suggest the archipterygial stage of the adult *Polypterus*, — especially interesting is this in its adverseness to GEGENBAUR[1]) in his last paper on the Archipterygial theory of the paired limbs, since it has been seen to have been preceded by the shark-like fin-form, and this in turn by the ptychopterygial type in its early dermal fold. At this stage the nasal opening, greatly constricted, is becoming divided into its anterior and posterior divisions by a dermal outgrowth of its anterior margin, an ontogenetic stage suggesting the adult conditions of sharks. The enlargement and strengthening of the muscle plates of the trunk should also be noted. The eyes, it is interesting to remark, are for the first time in constant movement, turning about on all sides in the most marked way, — the development of the eye muscles seeming to be accompanied by the need of their constant exercise, for at no later period are their movements so prominent.

Larva of the tenth day (Pl. 10, Fig. 19; jugular region in Pl. 10, Fig. 19a, sucking disc b).

From this stage onward the larva has to acquire but the minor characters of the adult. The general body outline has become established, the yolk sac largely absorbed, its walls now entirely surrounded by downgrowing muscle plates. The head region is distinctly that of the adult, its skeletal and muscular elements clearly modelled; mucous canal openings have now been formed by the process of enclosing the sensory tracts begun in the preceding stage; the mouth has its mature form and movements; the nasal openings are established;

1) Morph. Jahrb., V. 21, Heft 1, p. 119—160.

the beginnings of the opercular series of dermal bones have appeared. The sucking disc is greatly reduced, although it does not in fact disappear entirely (histologically) for several weeks; it remains as a small flattened pad, scarcely to be noticed in the profile of the head, although its distal surface, Pl. 10, Fig. 19b, still shows slight depressions. Its atrophy takes place first proximally, later marginally; the cells of its deepest tissue become greatly vacuolated and form a sponge-like mass, and the cell wall which here forms its outer boundary, gradually encroaches; the cells of the centro-distal region are the last to retain their early character. The anus appears in the now widely separated gap between the fin-folds of the abdominal and anal regions. Muscle plates are to be traced ventralward on the abdominal walls. The advances in the development of the fins include: the growth of the pectorals, the bases of which, changing from their crossopterygian character, are becoming less distinctly lobate as the dermal rays make their appearance; the origin of the ventral fins as minute dermal folds, arising independently, however, of the unpaired abdominal or anal; the appearance in the unpaired fins of supporting elements; these, the homologues of the radial cartilaginous fin supports of Wiedersheim, take their origin along the dorsal body wall in a continuous series, most prominent in the hindmost region and on the ventral side in those portions of the unpaired fin which will later become constricted off as anal and caudal fins; of these the outlines will be seen to be now suggested. These supporting elements make their appearance as in the Teleosts some time before dermal rays are to be determined, the latter when they come to arise seeming to bud out from their distal ends, spreading out like tapering fan rays toward the free margin of the fin. So closely are these elements then fused that it becomes impossible to determine their juncture; the histogenesis of the dermal rays appears to offer the same characters as demonstrated in Teleosts by Harrison [1]). Another interesting feature in the larval development of *Amia* is the mode of appearance of the jugular plate. This, although an unpaired structure, might reasonably on purely a priori grounds be expected to have had a paired origin, — that is if we accept the view that the jugular plates in the various sub-groups of the early Teleostomes have not been involved independently. It is accordingly of great interest that in this stage the jugular plate, Pl. 10, Fig. 19a *jug.*,

1) in: Arch. Anat., V. 32, p. 248—278.

is making its appearance as distinctly a paired structure. The ceratohyals, *ch.*, can be clearly made out passing from the jaw hinge to the hypobranchial region; a slight depression immediately behind the mandibular symphysis indicates the uplifting of the glossohyal; immediately behind, its posterior border slightly uplifted, the jugular may be seen to consist of two pairs of elements. These, however, are already closely apposed, forming together the shield-shaped mass, whose growth and dermal calcification will shortly give it the appearance of an unpaired structure. It follows, therefore, that there is no need of regarding the jugular plate of *Amia* as having had an independent origin from the paired structures of the early Teleostomes, — although one must acknowledge that it is decidedly remarkable that so ancient a feature of dermal armoring should have been retained in this most modern of Ganoids, while lost in the gar-pikes and sturgeons; its function must obviously have been an important one to have caused it not merely to be retained but to become enlarged and specialized. Its relation to the sensory canals of the lateral line system, as shown by Allis, is noteworthy in this connection.

Larva of about the fifteenth day (Pl. 10, Fig. 20; ventral aspect Pl. 10, Fig. 21).

A great advance in the conditions of the fins is apparent in this stage, and a corresponding growth in the breadth and thickness of the hinder trunk. The length of the dorsal fin is clearly indicated; the line of the dorsal fin-rays, *r.*, with their corresponding row of basal supporting elements, *b.*, terminate abruptly at a position which will mark the hindmost point of the dorsal fin of the adult. There is no trace of a series of larval fin supports surrounding the protocercal tail tip to connect the dorsal fin with the definitive caudal, as would naturally be supposed, if this, according to Shufeldt, were the ancestral condition in *Amia* (cf. U. S. Fish Commission Rep., 1883, Explanation of fig. 25). In the various fins the number of radialia which may now be counted are as follows: dorsal 57, caudal 20, anal 10, anterior anal — a larval element as yet persistent — 0, ventral 0 (?), pectoral 15. Comparison of these numbers and those of additional larval stages [1]) with the adult's leads to the conclusion

1) In the opposite table a general view may be had of the numerical increase (approximate only — i. e., as counted in surface view in single specimens) in radial fin supports at successive stages.

that the perfection in the fin supports takes place in the following order in time, 1) dorsal, 2) anal, 3) caudal, 4) pectoral, 5) ventral. In the pectoral fin the increase in the number of the radials takes place in the region of the ventral (i. e. posterior) fin margin, near the enlarged base of the fin. The ventrals, *v.*, are now elongated, lappet-like. In the head region the mucous canals exhibit but few advances; the tube-like outgrowth of the anterior naris, *a.n.*, is noteworthy; the enlarged size of the opercular flaps causes their broad overlap ventrally; in the gular region, however, they are overspread by the growth of the jugular plate, *jug.* This maintains at its distal

Radialia in larva of days	7	15	22	35	Adult
Dorsal	47	57	57	? 70	58
Anal	9	10	10	13	13
Caudal	16	20	20	21	24
Pectoral	14	17	19	22	22
Ventral	0	? 0	? 3	6	9

end dermal connection with the ridges of the ceratohyals. To this ridge are now appended the branchiostegal rays, a dozen in number as in the adult. These begin ventrally near the jugular region small, tapering, slender, and increase in size as their series passes lateral toward the opercula, with which, indeed, they appear in close serial homology. The exhaustion of the yolk material takes place during the final part of the larva's second week, and results outwardly in the closer modelling of the wall of the abdomen and that of the trunk.

Larva of about the twenty-second day (Pl. 11, Fig. 22; dorsal aspect Pl. 11, Fig. 23; ventral Pl. 11, Fig. 24).

The following advances characterize this stage: the marked outgrowth of the caudal fin, *c.*; the outlining of the definitive anal, and the reduction of the larval caudal-anal and pre-anal fin-fold, *c-a.* and *ant. an.*; the closer welding of the line of muscles of the basal fin supports with the muscles of the trunk; the distal broadening of the ventral fins; the first appearance of scales in the anterior region of the lateral line; the outlining of the pre-, sub- and interopercula. A broad transparent linea alba, *l.a.*, permits a glimpse of the ventral viscera, notably the ventricle and the conus and bulbus arteriosus.

Larva of about the thirty-fifth day (Pl. 11, Fig. 25; ventral aspect Pl. 11, Fig. 26).

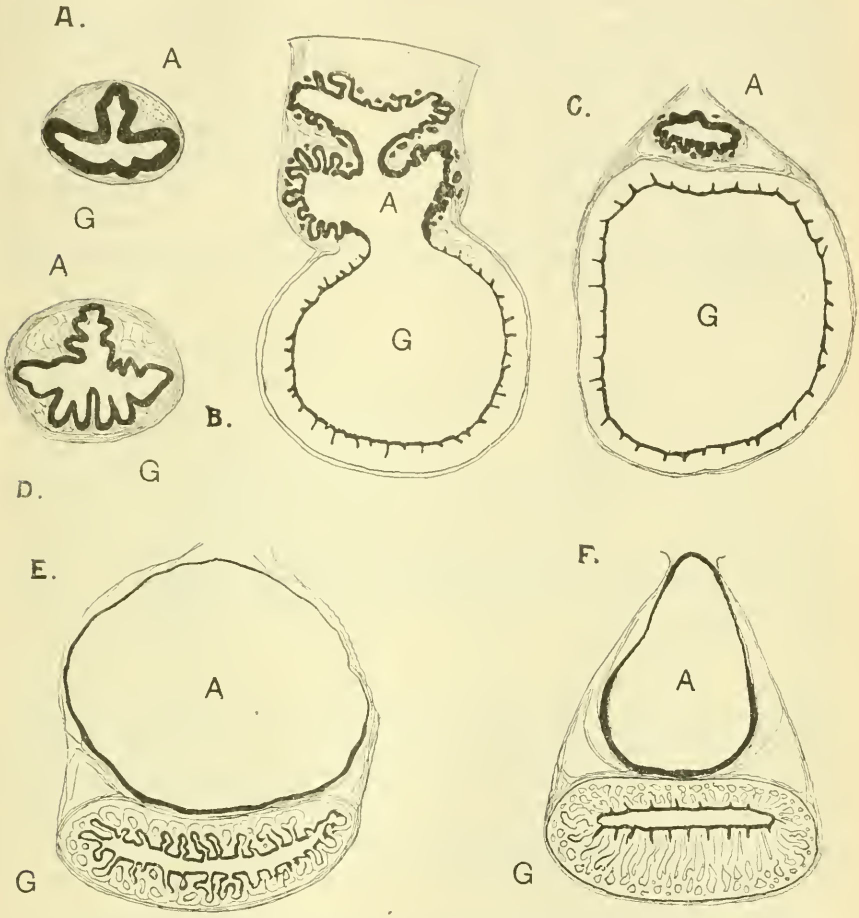
This stage, the latest to be figured in the present paper, has acquired the main outward features of the adult. The fins suggest clearly their mature forms; the intervening membranes of the larval unpaired fins have become greatly reduced, *c-a.*, that of the pre-anal abdominal region having entirely disappeared; the definitive caudal, *c.*, has now supplanted the larval caudal, and leaves it reduced to the condition of urostyle, *u.*, entirely separated anteriorly from the posterior margin of the dorsal. The outline of the mature ventral fin is now attained, and its basal portion suggested. In all fins dermal rays, *d. r.*, have made their appearance at the distal ends of the radials; to these their ontogenetic relations have not been determined, nor yet their subsequent outgrowth, and formation of splits and joints. In the entire trunk region the appearance of scales may now be noted although they have their greatest prominence in the region of the lateral line: unlike in *Lepidosteus* they do not exhibit cusp like outgrowths: they at once attain their oblong shape and their growth suggests closely that of the Teleost. The head growth is marked by the general outmapping of the dermal bones of the cranial roof, and by the definiteness of those of the opercular and orbital regions. To these, however, the relations of the mucous canals are as yet simple; for the subsequent growth of the mucous canals cf. Allis. The jugular plate, *jug.*, has now its characteristic position and proportions.

III. Notes on organogeny.

The general form-changes in the larval *Amia* have been briefly reviewed in the foregoing pages. Notes on several of the more important features of larval organogeny may now be added, derived from a study of serial sections: i. e., a) Mouth, teeth, gullet, swim bladder; b) anus, postanal gut, neurenteric canal, hinder excretory ducts; c) liver, yolk; d) pronephros; e) brain, neuromeres, hypophysis; f) sense organs, sucking organ, ciliation.

a) Mouth, teeth, gullet, swim-bladder.

The formation of the mouth in *Amia* differs little from that in *Lepidosteus*, Sturgeon and in Teleosts generally. The stomodaeum establishes its opening into the fore-gut earlier than in other Ganoids, about the same time in fact as in the sea-bass (H. V. WILSON); it is wide and slit-like at first, and becomes gradually pit-like and rounded.



Figs. A—F. Transverse sections of gut of larval *Amia* showing early conditions of the swim-bladder. Figs. A, B, C, Larva of about the tenth day sectioned through the opercula and through the anterior and posterior margins of the pectoral fins. Figs. D, E, F, Larva of about the twenty-second day, sectioned through corresponding planes.
A Air bladder, *G* gut.

At no time does it add evidence to the view that the mouth is of gill-slit origin [1]); nor does it show any traces of median asymmetry.

1) Cf. WILLEY, Amphioxus and the Ancestry of the Vertebrates, p. 281, summarizing the results of DOHRN, CLAPP and H. B. POLLARD.

Teeth take their origin at the bottom of deep tube-like insinkings of the mucosum: these are implanted irregularly in the dentigerous regions, without any apparent attempt at the production of a general dental trench. The pharynx of the early stages, Pl. 9, Figs. 1—8, is a well marked cavity although its dorsal and ventral walls are closely apposed; in the gullet the lumen is wanting, a secondary condition known to be of very general occurrence among fishes since the time of the studies of Balfour. The reopening of the gullet takes place at about the stage of Pl. 9, Fig. 10. And at nearly the same time the swim-bladder takes its origin as a crease-like invagination of its dorsal wall; its rapid growth has by the stage of Pl. 10, Fig. 19, given it the following characters: anteriorly, in the transverse plane of the opercules a narrow dorsal longitudinal slit, Fig. A; in the plane of the bases of the pectorals the swim-bladder's dorsal wall becomes enlarged, bilobed, although still retaining its opening to the gullet, Fig. B; in a plane immediately hindward of the tips of the pectorals it has become distinctly tubular. At the stage of Pl. 11, Fig. 22, the swim-bladder has assumed the following characters: in the transverse plane corresponding with that of Fig. A, its opening into the gullet is slit-like, its neighbouring mucous walls notably convoluted, Fig. D; shortly behind this position, in a plane still passing through the opercula, Fig. E, the swim-bladder is a large thin and smooth walled chamber, attached to the dorsal wall of the anterior portion of the stomach by connective tissue but otherwise unconnected with it; this attached condition the swim-bladder maintains as it passes down the mid-dorsal region of the visceral cavity, its diameter first increasing then diminishing till it terminates slightly in advance of the plane of the ventral fins. In its hinder region, Fig. F, it is somewhat deeper than wide, with thicker vascular walls. In this stage the adult conditions have practically been attained.

b) Anus, post-anal gut, neurenteric canal, hinder region of excretory ducts.

In Teleosts generally the anus is formed at a remarkably early period, — in *Serranus* (H. V. Wilson) before hatching. In the Ganoids its formation is later, at about the same time as the mouth opening, — in *Amia* at about the beginning of the second day. In Teleosts the abbreviation of the process is probably the cause of the formation of the anus directly, i. e., without proctodaeum; in *Amia*, on the other hand, a proctodaeum, although small, unquestionably occurs, as a nick in the margin of the ventral unpaired fin, Pl. 9, Fig. 6 *p*. A similar condition occurs in *Acipenser* and *Lepidosteus*.

A post-anal gut is suggested in the sagittal section of the tail of a late embryo (slightly earlier than that figured in the present paper in Pl. 9, Fig. 1) shown in Fig. G *PAG*. But throughout the early stages in the growth of the tail region there is no trace of a neurenteric canal. It will be remembered that in *Amia* the neural axis, as in Teleosts, is formed as a solid keel-like insinking of the ectoderm; and that its lumen is acquired at a later period — later than the blastopore's closure. A study of serial sections demonstrates that this lumen extends hindward into the outgrowing tail bud, as in Fig. G sepa-

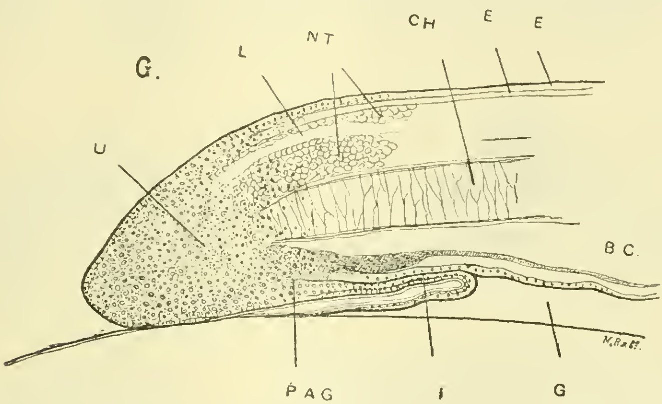


Fig. G. Sagittal section of the tail region of embryo surrounding about 195° of egg's circumference. *BC* body cavity, *CH* notochord, *E*, *E* inner and outer layer of epidermis, *I* intestine, *L* lumen of neural tube, *NT* neural tube, *PAG* region of post-anal gut, *U* undifferentiated tissue of tail.

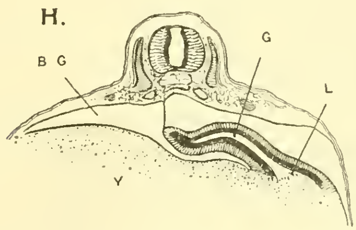
rate *I* and terminates blindly in the undifferentiated tissue of the caudal mass, *U*. No traces of a connection have been found between the cavity of the medullary tube and the virtual lumen of the post-anal gut, *PAG*. A similar condition has been described in *Lepidosteus*, although there can be no doubt that a truly shark-like neurenteric canal occurs in *Acipenser*.

The relation of the pronephric ducts to the hind gut and the position of their common opening in the region immediately behind the anus have already been noted. In their tailward growth the ducts, keeping close to the intestine, have been found to remain separate till they have attained a position slightly above and in front of the anal region (Pl. 9, Fig. 6); in this position they fuse, and, continuing their growth, they bend downward, tailward of the rectum and establish their outer opening. Very similar conditions have been described and figured in the Teleosts.

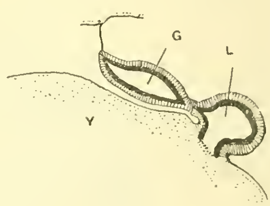
c) Liver, yolk.

The liver takes its origin in the stage of Pl. 9, Fig. 4, as a broad upwardly directed fold of the dorsal wall of the gut. In the stage of Pl. 9, Figs. 6, 7 *l*, it appears in surface view as a whitish mass lying on the dorsal wall of the yolk sac immediately at the left side of the trunk. It is now pocket-like, its blind end directed somewhat outward and forward, its hinder portion somewhat flattened, and communicating with the cavity of the gut through a narrow slit-shaped opening. These conditions are in part illustrated in Figs. H,

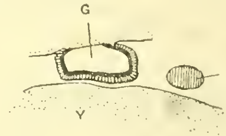
H.



J.



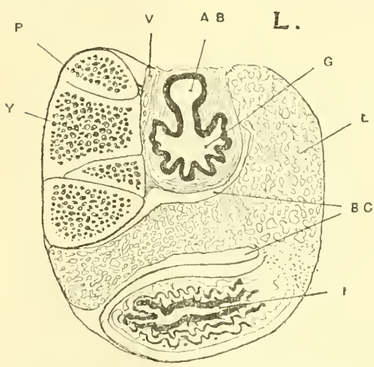
K.

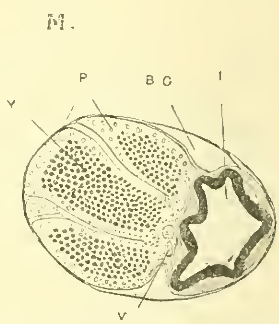


Figs. H—K. Transverse sections of *Amia* shortly before hatching. Fig. H through gut and hindmost portion of liver. Fig. J through gut and middle region of liver. Fig. K through gut and anterior tip of liver. *BC* Body cavity, *G* gut, *L* liver, *Y* yolk.

J, K, transverse sections through the region of the yolk sac of an embryo shortly before hatching; thus in Fig. H, the hindmost section, the position of the liver is shown at *L*: anteriorly the liver becomes a well marked diverticulum of the wall of the gut; in Fig. J the lumen of the liver, *L*, is separate from that of the gut, *G*, although it still is continuous ventrally with the yolk, *Y*; in the foremost section, Fig. K, passing through the anterior tip of the liver, the gut has become flattened dorso-ventrally, is broadly fused with the dorsal wall of the body cavity, and is separate, below from the yolk, and at the side from the liver. The subsequent growth of the liver is as follows: its cœcal condition becomes ramose, and the organ enlarges greatly in size, fitting itself into the space at the side of the visceral cavity, and between the stomach and intestine. In a transverse section of a larva of about the fourteenth day, Fig. L, the liver may be seen to occupy this position: inferiorly it is confluent with the intestine, *i*, in the region of the definitive gall duct; dorsally its finely ramose substance appears to be attached to the peritoneum, and between the gullet and the intestine it extends to the opposite visceral wall: it here becomes apposed to the ventral wall of the yolk sac, although not fusing with it.

The relation of the yolk sac to the alimentary canal may next be noted. The origin of the dorsal wall of the gut has been outlined in the writer's paper "On the early development of Amia." The lumen of the mid-gut appears to be formed by the gradual uplifting of the head region of the embryo, and the gut comes to be constricted off from before backward: thus at the stage of hatching the hinder gullet and the anterior region of the stomach, Figs. K, J, H, is entirely separated from the yolk; the hinder portion of the stomach, however, Fig. H, is confluent with the yolk. Hindward of this position the dorsal wall of the gut becomes constricted and more and more flattened, the lumen becoming reduced to a mere fissure. The outgrowth of the tail region causes an enlargement of the cavity of the gut, Fig. G, as well as giving rise to the evagination which is to form the hinder intestine, *I* and *PAG*; hindward of this evagination the wall of the gut flattens to the underlying yolk and shortly merges with it. It will thus be seen that the relations of the yolk to the alimentary canal differ but little from those of the typical meroblastic Vertebrates, the Teleosts in particular. From the latter, however, *Amia* differs broadly in the mode of its yolk absorption. In *Serranus* (H. V. Wilson) the liver becomes attached to the yolk-mass and aids directly in its absorption — a process, "probably akin to intercellular digestion", in which the liver "cells establishing a connection with the yolk, form a feeding or absorbing surface, which, as it incorporates new material on its yolk side, as constantly splits off new cells on its liver side". In *Amia*, on the contrary, the liver has no direct connection with the yolk, its growth being supplied largely by the vitelline (and intestinal) veins. That this condition may well prove ancestral in the evolution of bony fishes (*Serranus*) appears not unnatural when the following relations of the later yolk absorption in *Amia* are considered. In the larval *Amia* of seven days the transverse section of the liver region, Fig. L, already noted has shown that the yolk material has become largely absorbed: within three or four days, indeed, it will have entirely disappeared. In this section the yolk mass is seen to be closely apposed to the hindmost part of the gullet, enclosed in fact within its peritoneal investment; it has become broken into lobes, from whose translucent, periblastic margins the vitelline capillaries, nutriment laden, are passing liverward, uniting and enlarging till they become the vitello-intestinal veins, *V*. Hindward of this region the yolk mass has increased somewhat in size, but retained its intimate relation with the gut; in Fig. M, a transverse section through the hind gut, these conditions are illustrated; the yolk mass, *Y*, lies as before morphologically within the side wall of the gut, enclosed by its peritoneal sheathing; its substance is broken into lobes, along whose margins on the side of the gut the blood vessels are converging liverward, — these blood vessels in





Figs. L, M. Transverse sections of visceral region of larva of seven days. Fig. L through the gullet. Fig. M through the intestine. *AB* Air bladder, *BC* body cavity, *G* gullet, *I* intestine, *L* Liver, *P* periblast zone of the yolk, *Y* yolk.

turn arise in the vitelline capillaries which furrow the yolk segments and draw their nutriment from the yolk's peripheral zones (mainly from the sides away from the gut). It will thus be seen that the yolk-nutriment supply of *Amia* reaches the liver through vitelline veins which pass between the yolk mass and the gut; accordingly it follows that the conditions in *Serranus* would be attained without wide caenogenetic changes; for the growth of the liver occurring in Teleosts more precociously, could naturally cause the shortening of the length of the vessels connecting it with the yolk; by this process the liver would early become attached to the yolk and receive its vascular supply from the capillaries directly: these, shortened in turn by still more precocious development, would, it is evident, ultimately be replaced by the growing tissue of the liver —

as in *Serranus*. And it is further evident that the more intimate the relation of the yolk to the liver became, the less intimate would be its connection with the gut, — i. e., the earlier it would become separated from the wall of the digestive tube, — as the conditions in *Serranus* demonstrate.

A final word contrasting the mode of development of the liver in *Amia* and in Teleosts. In this regard the precociousness of *Serranus* is again to be noted. The liver here arises, not as a caecum, but as a solid outgrowth, which branches almost at once and later acquires a lumen through the dissociation of its cells.

That the periblast nuclei are directly concerned in the formation of blood cells the present writer has been unable to decide. In the Teleosts this disputed view certainly receives no confirmation, but in *Amia*, where the yolk material has still its primitive relations to the intestinal veins, the conditions appear to be worthy of more careful study. Although the writer has not attempted to follow the histogenesis of the blood cells, he has noted that cells occur in the peripheral periblast, that these especially on the side away from the gut, become greatly enlarged and then undergo division, and that their products, lying in the outermost periphery of the periblast zone, certainly resemble very closely the blood cells which fill the capillaries immediately adjoining.

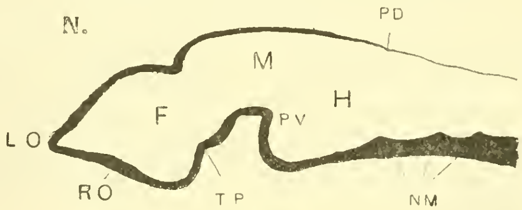
d) Pronephros.

Little can here be added to the studies of Jungersen on the pro- and mesonephros of larval *Amia*. The results of this author have been confirmed as far as the present observations have been carried. It has thus been found that 1) there are but two functional pronephric funnels at the time of hatching; 2) the segmental arrangement of the mesonephric tubules corresponds to that of the muscle plates; 3) the mesonephric tubules are not evaginations of the peritoneum, but are formed independently of it, in the neighborhood of the pronephric duct, into which they later establish their openings; 4) close relations exist between the larval excretory system of *Amia* and the Teleosts. The following is the only addition to the results of Jungersen which can now be given. In the stage 24 hours before hatching the pronephric duct is relatively wider than that shown by Jungersen in his first figure, and is lacking in snake-like twistings. The hinder portion of the duct is straight, its anterior division crook-shaped, bending inward and slightly downward. Its extreme tip opens into the body cavity through a loop-shaped perforation, the foremost (morphologically) pronephric funnel; a second opening is immediately behind (actually anterior to) it; and traces of a third immediately behind the second. By this is meant that the pronephric duct establishes temporarily a third connection with the coelomic wall, although the writer could not discover that a perforation subsequently occurred. This trace, however, seems noteworthy in view of the greater number of pronephric tubules of *Lepidosteus* and *Acipenser*. On the other hand the reduced number of the pronephric tubules is certainly of interest as a condition transitional to that of the Teleost.

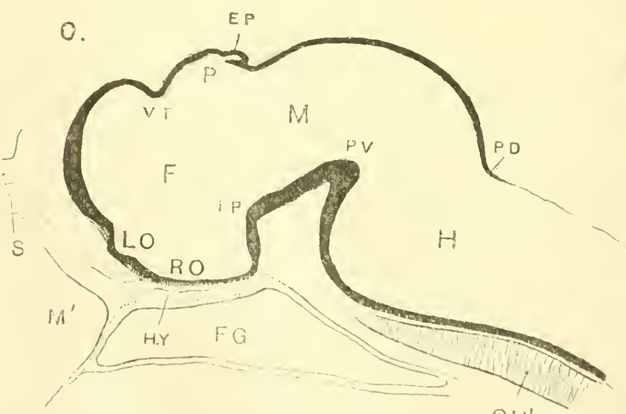
e) Brain, neuromeres, hypophysis.

In the account of the early development the brain and spinal cord have been shown to have had their origin in a solid ectodermic thickening. In a late embryo, slightly earlier than that of Pl. 9, Fig. 1,

N.

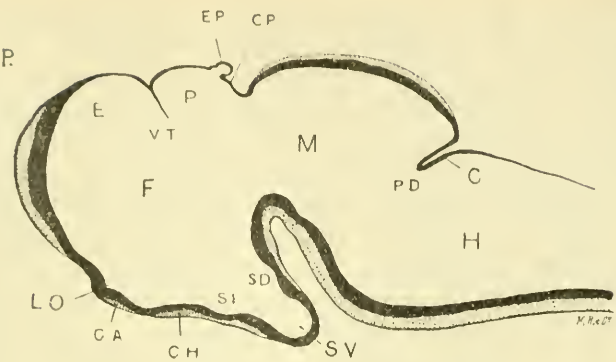


O.

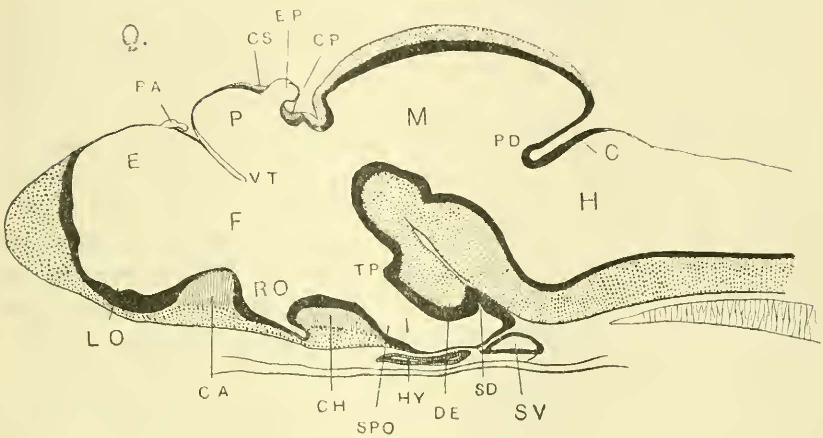


Figs. N—Q. Sagittal sections of brain of embryonic and larval *Amia*. Fig. R. Sagittal section of brain of *Salmo fario* at hatching. Fig. N of embryo surrounding about 195° of egg's circumference. Fig. O of larva at hatching. Fig. P of larva four days old. Fig. Q of larva four weeks old. *C* cerebellum, *CA* anterior commissure, *CH* chiasma, *CH'* notochord, *CP* posterior commissure, *CS* superior commissure, *DE* commissura debilis, *E* epencephalon (Kupffer), *EP* epiphysis, *F* forebrain, *FG* foregut, *H* hindbrain, *HY* hypophysis, *I* infundibulum, *LO* lobus olfactorius impar, *M* midbrain, *M'*

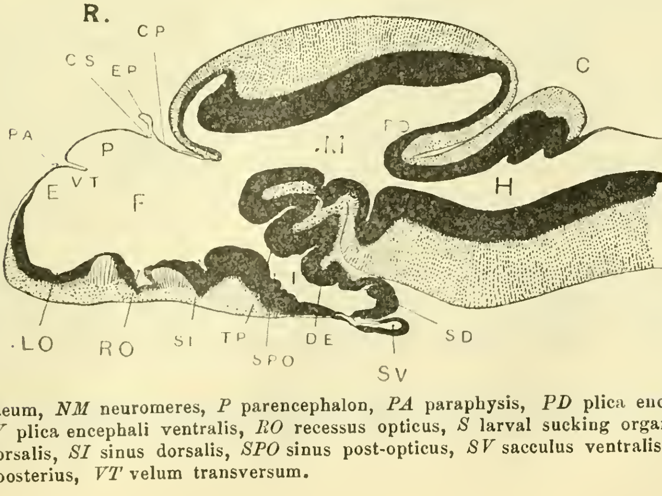
P.



Q.



R.



stomodaeum, *NM* neuromeres, *P* parencephalon, *PA* paraphysis, *PD* plica encephali dorsalis, *PV* plica encephali ventralis, *RO* recessus opticus, *S* larval sucking organ, *SD* sacculus dorsalis, *SI* sinus dorsalis, *SPO* sinus post-opticus, *SV* sacculus ventralis, *TP* tuberculum posterius, *VT* velum transversum.

the neural lumen has been fully acquired: the sagittal section of the brain at this stage, outlined in Fig. N, corresponds closely to that of a similar stage in *Acipenser*, as figured by v. KUPFFER [1]) (tab. 4, 5, figs. 14, 15). It differs from the latter mainly in the flatness of the brain wall in the region of the recessus opticus, *RO*, and in the more down turned position of the lobus olfactorius impar, *LO*. By this stage in *Amia* the lobus has already been separated from the formative epiblast for (about) 10 hours, relatively at an earlier period, therefore, than in *Acipenser*. The sagittal section of the brain of a newly hatched larva of *Amia*, Fig. O, corresponds with v. KUPFFER's tab. 6, fig. 17: its main differences include: a greater degree of flexure, a larger lumen anterior to the plica encephali ventralis, *PV*, a less degree of differentiation in the brain's ventral wall and in the commissures. A section of a four days' larva, Fig. P, contrasts with v. KUPFFER's tab. 5, fig. 18 as follows: it possesses a larger lumen in the anterior brain region, an almost obliterated recessus of the lobus olfactorius, a greater thickening of the anterior brain wall immediately dorsalward of the lobus, and a greater enlargement of this region, accompanied by the marked thinning away of the parencephalon, *P*, and of the epencephalon, *E*, in the neighborhood of the velum transversum, *VT*; also a less degree of differentiation of the cerebellum. A further contrast of the brains of *Amia* and *Acipenser* may be made by reference to Fig. Q, a sagittal section of a larval *Amia* of four weeks, and a similar section of a larval sturgeon of the same age in v. KUPFFER's tab. 8, fig. 19. It will thus be seen that in *Amia* have taken place by far the more striking changes, and that these have been confined largely to the anterior region of the brain. The anterior two thirds of the roof of the epencephalon (of v. KUPFFER) (measured from the lobus olfactorius to the margin of the velum transversum) has thus become greatly thickened, while its posterior third has become ependymatous; the recessus opticus is now sharply pit-like, the infundibulum narrow and tubular, its posterior wall elongated, its sacculus ventralis, *SV*, an almost separate cavity (later of the lobi inferiores).

Amia differs, therefore, from *Acipenser* in the mode of its brain development mainly in its tendency to differentiate the roof of the epencephalon, and to reduce the caliber of the infundibulum, features

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1) Studien zur vergleichenden Entwicklungsgeschichte des Kopfes der Cranioten. Die Entwicklung des Kopfes von Acipenser, München 1893.

which are clearly interpretable as specialized. But on the other hand it should be noted that the brain of *Acipenser* is in some of its features more specialized than that of *Amia*, *e.g.*, in the high degree of differentiation of the cerebellum, of the commissures, of the velum transversum. The relation of the brain type of *Amia* to that of the Teleost, however, is clearly to be traced, the elaborately specialized brain parts of the latter readily reducing to the simple conditions of *Amia.* This relationship may best be understood by comparison of the brain shown in Fig. Q with that of Fig. R, a sagittal section of a newly hatched trout, *Salmo fario.* Similar parts are clearly recognizable, but the divergences which the structures of the bony fish have undergone in the line of differentiation are most noteworthy. Broad changes have befallen the mid- and hind-brain, and the region of the infundibulum: in the mid-brain the lumen has become notably reduced, its roof greatly enlarged, thick walled, massive, its floor convoluted in adaptation to its greater size: of the hind-brain the floor is heavily thickened, the cerebellum large and convoluted: the infundibulum is also deeply convoluted, and the sacculus ventralis is relatively enlarged. It is, accordingly, evident that the brain of the bony fish has increased enormously in size hindward of the chiasma. In front of the chiasma, on the other hand, its conditions have come to differ but little from those of *Amia*; the anterior flexure of the brain has become slightly more marked, the lobus now appearing as if in the middle of the floor of the epencephalon; the anterior thickening of the roof of the latter is no longer prominent, and its ependymal portion, if anything, smaller[1]) in extent; the flattened roof of the parencephalon and the reduced depth of the velum transversum are finally to be noted as among the minor differences.

The foregoing comparison of the brains of *Amia* and a bony fish is not without a distinct phylogenetic interest: for it has shown that the transition between the Ganoïd and the Teleost in these structural regards is by no means as broad as has been generally believed. That the brain arises as a solid ectodermal thickening instead of as a tubular organ formed in the beginning by the overgrowth of the medullary folds, is a feature common as well to some of the Ganoids (*Lepidosteus* and *Amia*) as to the Teleosts. Nor can any distinction be grounded on the epithelial character of the roof of the Teleostean

1) In subsequent stages the ependymal portion becomes relatively larger.

forebrain, for precisely similar characters have been shown to occur in *Amia.* It is further evident that the brain of the bony fish is so closely Amioid that it may reasonably be looked upon as but a high degree of specialization of this neo-ganoidean type. The development of the brain of the Teleost is fully in keeping with the precocious growth rate of its other structures: by the time of hatching the brain, Fig. R, has assumed far more nearly its adult characters than has that of a month old *Amia*, Fig. Q.

The subject of the roof of the forebrain deserves a final word, especially in view of the unorthodox position of BEARD[1]). For, according to this writer, the pallium of lamprey and Teleostome was the homologue of the choroidal plexus of shark, lung-fish and amphibian; and it was, accordingly, taken as a most important character to separate two phyla of fishes. That this position is untenable is now evident from the studies of BURCKHARDT on the forebrain of fishes, especially as to the increase in its ependymal region, in which are traced well marked transitions from Selachian to Teleostean conditions. The results of BURCKHARDT[2]) are further confirmed by the study of the mode of development of the forebrain among the three types of Ganoids; for in these, as in a graded series, it may be shown that the ependymal region increases in size as the more modern type, *Amia*, is attained.

Neuromeres.

The recent memoir of LOCY[3]) has directed renewed attention to this subject. In *Amia* the discussion of neuromeres belongs more strictly to the period of later embryonic development and will not therefore be included in the present paper. Note should be made, however, of the very prominent neuromeres which appear in the floor of the hind brain, beginning immediately on either side of the sagittal plane, in the stages figured in Pl. 9, Figs. 1—7. These may be seen in the section of Fig. N, in which the hind brain has been cut in a favorable plane: five neuromeres are shown, the middle one the most prominent, the fore- and hindmost ones fading away into the region of the plica ventralis and cord respectively. Similar conditions, but

1) On the interrelationships of the Ichthyopsida, in: Anat. Anz., V. 5, 1890, p. 146—159.

2) in: Anat. Anz., V. 9, No. 12, p. 375—382.

3) in: J. Morph., V. 11, 1895, No. 3, p. 497—594.

not so favorably shown, have been seen by the writer in *Acipenser*, *Lepidosteus* and *Amiurus*, and they have also been noted in *Fundulus* by Dr. O. L. Strong.

Hypophysis.

The hypophysis is by no means as important an element in the development of the head in *Amia* as in the other Ganoids. Its appearance is late and inconspicuous. It has not been found in stages earlier than that of Fig. O, and even here its presence is not definite: at the most the position of its lumen can be recognized as the line, *HY*, formed by the arrangement of cells immediately below the region of the recessus opticus. These cells are apparently ectodermal for they are arranged in a continuous line with the cells of the formative epiblast of the dorsal wall of the stomodeum, but on the other hand their ventral limit cannot be distinguished from the entodermal cells roofing the foregut, *FG*. The tissue of the region of the hypophysis in *Amia* we may therefore conclude, has been brought into its definitive position at a relatively precocious period, and accordingly it has followed that abbreviated ontogeny has suppressed many phylogenetic stages. Thus the present writer has been unable to find that the hypophysis has at any time established an outer opening or in fact any fusion with the mouth roof: its wall has been entirely differentiated in situ, and its slender lumen formed. Its condition in a larva of one month is shown in Fig. Q at *HY*. The hypophysis of *Amia* will accordingly be seen to present well marked transitional features to that of the bony fishes.

f) Sense organs, sucking disc, ciliation.

The mode of development of the eye and of the nasal and olfactory capsules differs but little from that typical in the lower vertebrates generally. As already noted by Allis the nasal capsules, in their early stages, are connected with and closely correspond to the neighboring sensory pits of the mucous canal system. But on the other hand there appears to be no evidence that the auditory sac in *Amia* arises as in the Teleost *Serranus*. Here, according to H. V. Wilson, a common sensory furrow is the Anlage of the ear, the branchial sense organ, and the lateral line, — a condition which has been generally accepted as demonstrating a close genetic affinity in these associated structures. And close their affinity doubtless is, although the present writer cannot regard the evidence of *Serranus* as of undoubted phylogenetic value. For the process of shortening phylogenetic stages in the ontogeny of a bony fish has evidently progressed to such a degree that the ancestral relations of epiblastic organs might have become greatly obscured by the processes of precocious growth. To regard the evidence of the common sensory Anlage in *Serranus* as final and satisfactory evidence of the genetic kinship of these structures would, in the opinion of the present writer, be scarcely more conclusive than the homologizing of hypophysis and teeth on the ground of their having arisen in *Amia* as more or less solid structures in the epiblastic roof of the mouth.

Sucking disc.

The mode of origin of the sucking disc gives the most interesting evidence of how precociously embryonic and larval structures may be developed. As far as histological evidence goes there is certainly no difference between the enlarged thick-walled cup-shaped organs which arise on the snout of the late embryos of *Amia* or of *Lepidosteus*, and the typical pit organs, or sense buds, which later occur on other integumental regions. It is found in fact that a gradation in size exists which connects the huge sucking organs of the snout [1]) with the inconspicuous pit organs of the trunk. It is certain that these sucking organs, whether in the condition of little differentiated Haftscheibe (*Acipenser*), scattered sucking hillocks (*Lepidosteus*), or in groups as ring-shaped lobes (*Amia*), are purely larval structures, and that they occur (probably) only in Ganoids. They have evidently no place in the general study of the vertebrate head. But humble as their morphological rôle may be they yet throw a strong side light on the mode of evolution of structures not merely of the vertebrate head but of the entire vertebrate organism. For if a process of evolution can be made for so transient a purpose to produce sense buds in a definite locality enormously enlarged, and at a very early period, earlier not only than their kindred structures but even earlier than mouth, nose, liver, fins, gill slits, a similar process of evolution can even as evidently cause such sense organs as the nose, ear and eye to appear precociously in a definite region and in such enlarged and perfected form as to mask their genetic kinships. So too could brain parts or cranial nerves be precociously evolved, so that even at their

1) There is but little difference histologically between these and the neighboring nasal pits.

earliest stages they would give no definite clue as to their ancient form or relationships. And in like manner in the trunk region might the same principle be applied; thus at a definite point on the trunk wall could be produced fin structures at once large and perfected [1]) whose entire mode of growth should give little evidence of recapitulation.

Ciliation.

The ciliation of the body of the Amphibians, as recently described by ASSHETON [2]), does not appear to find a parallel among larval Ganoids. The present writer has been unable to find in *Amia* any tracts of ciliated epithelium other than those which form the mucous canals. The present observations, however, were made entirely upon preserved material, but this it may be noted was so favorably preserved that the cilia of the sensory canal regions and of the gut were clearly distinguished.

IV. Conclusions.

From palaeontological studies there can be little doubt that a series of transitional forms, closely Amioid, included in the families *Eugnathidae, Amiidae, Pachycormidae, Pholidophoridae* and *Leptolepidae*, provide the actual stepping stones from the Ganoids to the Clupeoid Teleosts. And as this genetic relationship of the Teleosts is now coming to be widely recognized it becomes less important to harmonize differences between the later and the older groups on the side of their embryonic and larval development. In the ontogeny of *Amia*, however, can now be found the final evidence of this genetic kinship — to serve both to confirm the palaeontological results, and to cause these to be accepted unhesitatingly by the embryologist. In the early stages of development the nearnesses of *Amia* to the Teleosts have already been shown, and in the present paper the larval stages of these forms have been found to possess many striking similarities, as in the development of the hinder digestive tract, post-anal gut, unformed neurenteric canal, hinder excretory ducts, liver and yolk, pronephros, brain, neuromeres, hypophysis.

But the especially suggestive feature which a study of the larvae of *Amia* has brought out is the matter of precocious development. We find, for example, that the organogeny of *Amia* progresses more

1) As in *Ceratodus*, as figured by SEMON.
2) in: Quart. J. Micr. Sc., V. 38, 1896, Part 4, p. 465—484.

rapidly than in *Lepidosteus*, yet not nearly as rapidly as in the Teleost. The shortening in the duration of the larval period, of which the transitional *Amia* provides so interesting an example, is clearly a developmental result which could hardly have been suggested on a priori grounds. For it certainly seems far more consistent with our preconceived ideas that the development of the older and simpler forms [1]) should be briefer than that of the forms derived from them: but in this case (*Amia*) we are given a well marked instance that the later forms have become specialized in the acquisition not merely of adult characters, but of developmental processes as well; that they have tended in their evolution to acquire their adult characters at an earlier period, to elaborate their conditions of yolk nutriment so that the growth processes might be shortened, and that the larva should more speedily be rendered self maintaining and self protecting. The shortening of the developmental, especially the larval period in the more recent forms, appears to bring with it a further and most interesting feature: for the shortening of the growth processes has produced a need for masking the stages of transformation. It would thus seem that a directive energy were making itself felt within tissues apparently undifferentiated, and giving them their definitive uses, long before they could have had the time to have performed even a part of the changes through which in phylogeny they have passed.

A comparison of the larvae of the Ganoids and Teleosts, Siluroids especially, brings to light with surprising clearness how perfect a range they present in transitional characters. Taking into account the forms of the early larvae, pigmentation, mouth and anus, gill characters, opercula, fin differentiation, yolk absorption, brain and sensory structures, all of these different types may readily be arranged in a gradational series. At the base of this series stands *Lepidosteus*, near it and in some ways even below it is *Acipenser*, next is *Amia*, next, and very closely related, is *Amiurus*, and finally are the many remaining forms of Teleosts.

Zoological Laboratory of Columbia College,
New York City, April 21, 1896.

1) In spite of the fact that among fishes it has generally been recognized that the shark's period of immaturity is longer than the lung fish's, the lung fish's than the Ganoid's, the Ganoid's than the Teleost's. This time relation might readily prove a caenogenetic one, dependent, for example, on richer yolk-supply.

Explanation of Plates.

Plate 9.

All figures of this plate have been drawn by the author from living material.

Fig. 1. Late embryo, surrounding about 200° of egg's circumference. 138 hours. × about 20.

Fig. 2. Late embryo, surrounding about 225° of egg's circumference. 142 hours.

Fig. 3. Late embryo of Fig. 2, shown in a somewhat ventral aspect.

Fig. 4. Late embryo, surrounding about 240° of egg's circumference. 148 hours. × about 18.

Fig. 5. Very late embryo, surrounding about 290° of eggs circumference. 160 hours. × about 20.

Fig. 6. Larva about time of hatching. 180 hours.

Fig. 7. Larva of Fig. 6, shown in dorsal aspect.

Fig. 8. Larva of about the beginning of the second day.

Fig. 9. Larva of about the middle of the third day.

Fig. 10. Larva of the fourth day. × 19.

Fig. 11. „ „ „ „ „ Dorsal aspect.

Fig. 12. „ „ „ „ „ Ventral aspect.

Fig. 13. Larva of the fifth day. × 16.

Fig. 14. „ „ „ „ „ Dorsal aspect.

au auditory sac, *gs* gill slit, *h* heart, *i* intestine, *l* liver, *ll* lateral line, *m* mouth, *n* nasal pit, *o* opercular dermal fold, *ol* optic lobes, *p* pericardium, *pc* post-cardinal (caudal) vein, *pf* pronephric duct, *pr* proctodaeum, *pz* parietal zone, *sd* sucking disc, *si* subintestinal vein.

Plate 10.

Figures 15—19 a drawn from the living larvae.

Fig. 15. Larva of the sixth day. × 16.

Fig. 15 a. „ „ „ „ „ Distal view of sucking disc.

Fig. 16. „ „ „ „ „ Dorsal aspect.

Fig. 17. Larva of the eighth day. × 16.

Fig. 18. „ „ „ „ „ Dorsal aspect.

Fig. 19. Larva of the tenth day. × 14.

Fig. 19 a. „ „ „ „ „ Jugular region.

Fig. 19 b. „ „ „ „ „ Sucking disc.

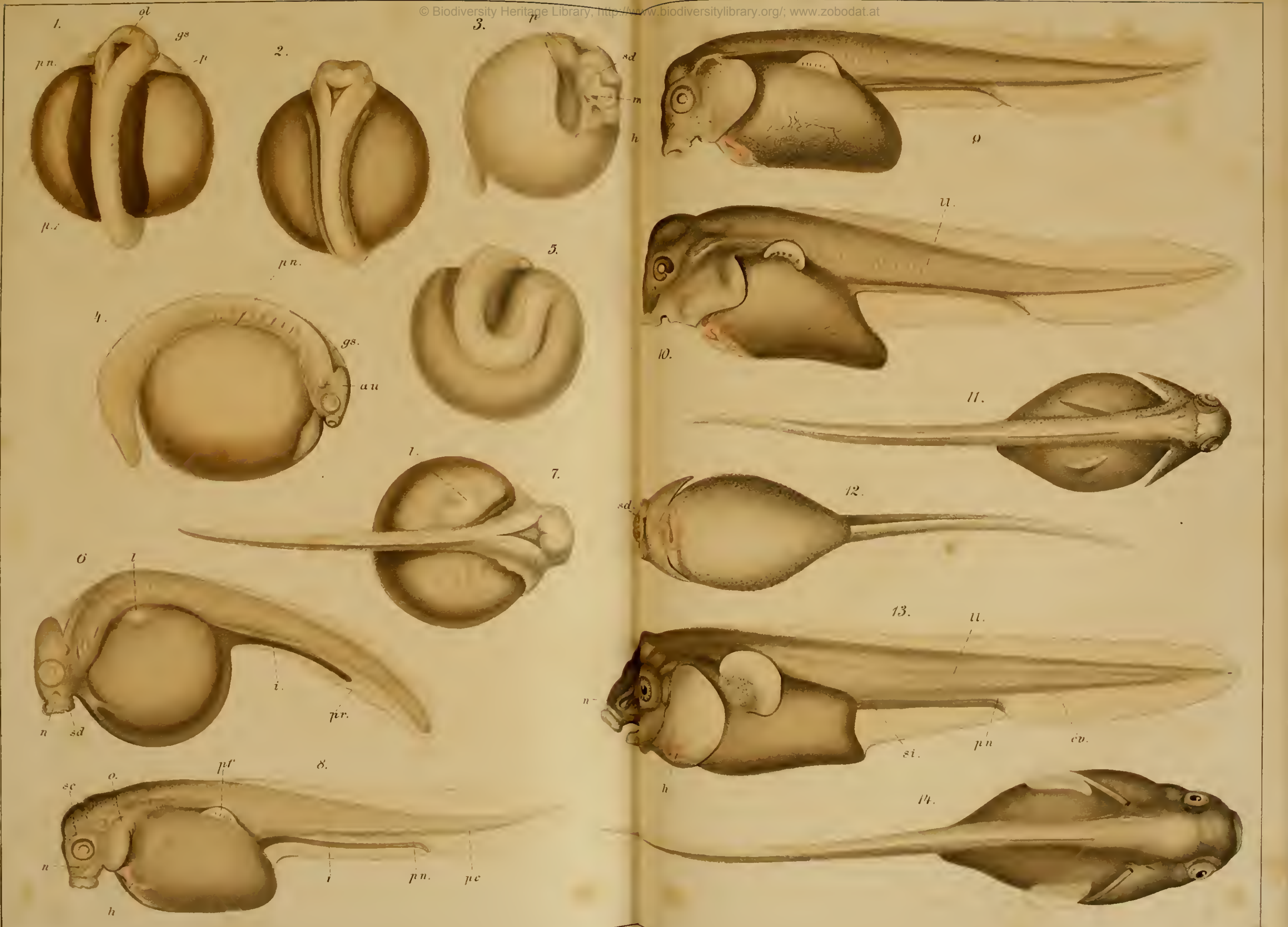
Fig. 20. Larva of about the fifteenth day. $\times$ 12.
Fig. 21. „ „ „ „ „ „ Ventral aspect.

a anal fin, *an* anterior naris, *ant. an.* anterior anal fin, *b* basal fin support, *brs* branchiostegal rays, *c* caudal fin, *ch* ceratohyal, *jug.* jugular plate, *o* operculum, *pn* posterior naris, *r* radial fin support, *v* ventral fin.

Plate 11.

Fig. 22. Larva of about the twenty-second day. $\times$ 7.
Fig. 23. „ „ „ „ „ „ Dorsal aspect.
Fig. 24. „ „ „ „ „ „ Ventral aspect.
Fig. 25. Larva of about the thirty-fifth day. $\times$ 7.
Fig. 26. „ „ „ „ „ „ Ventral aspect.

a anal fin, *an* anterior naris, *ant. an* anterior anal fin, *ao* anal opening, *brs* branchiostegal rays, *c* caudal fin, *c-a* membranous fin connecting caudal and anal, *dr* dermal fin rays, *io* interoperculum, *jug.* jugular plate, *la* linea alba, *o* operculum, *p* pectoral fin, *pn* posterior narial opening, *r* radial fin supports, *so* suboperculum, *ug* urinogenital eminence, *v* ventricle.



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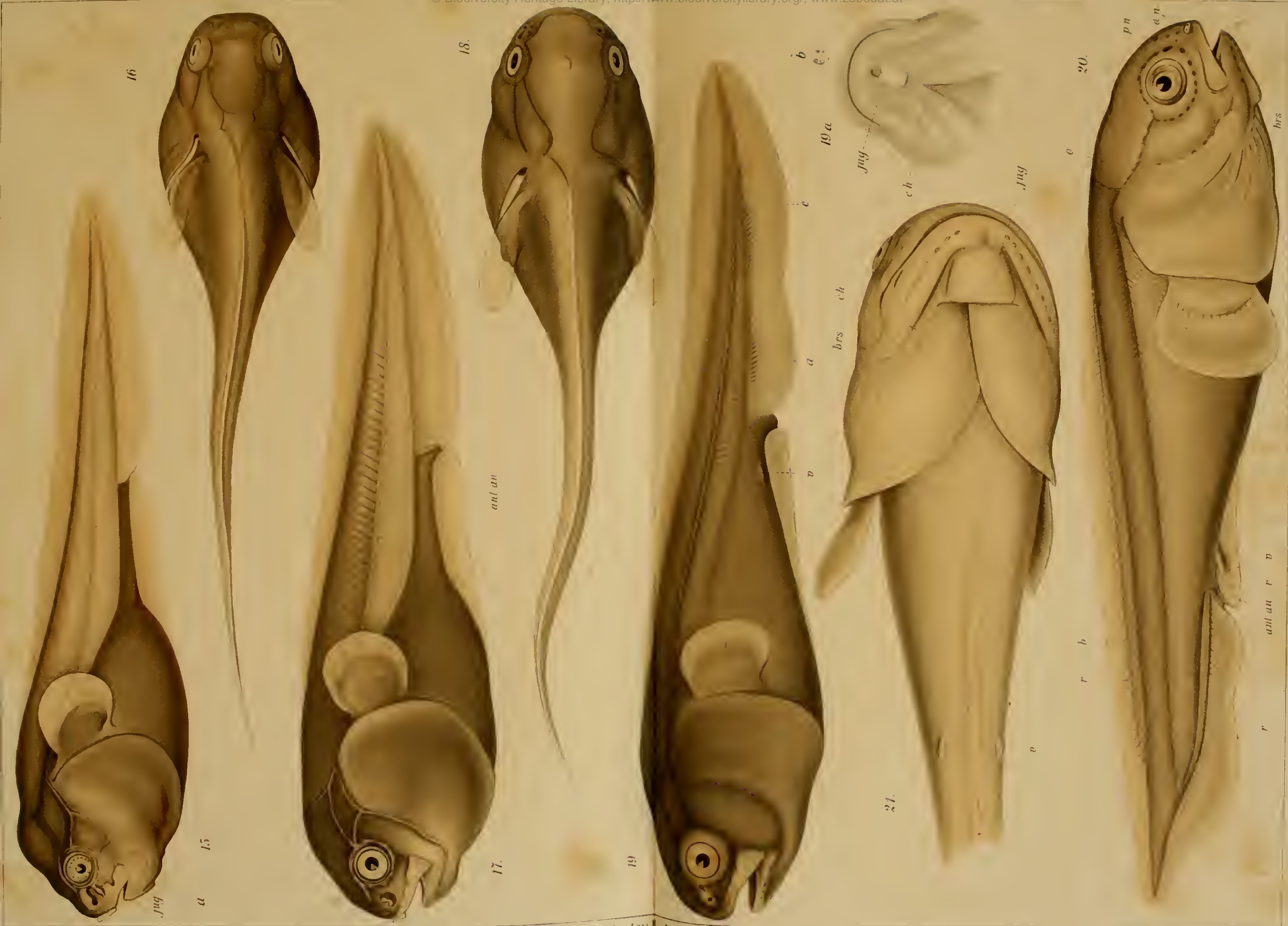

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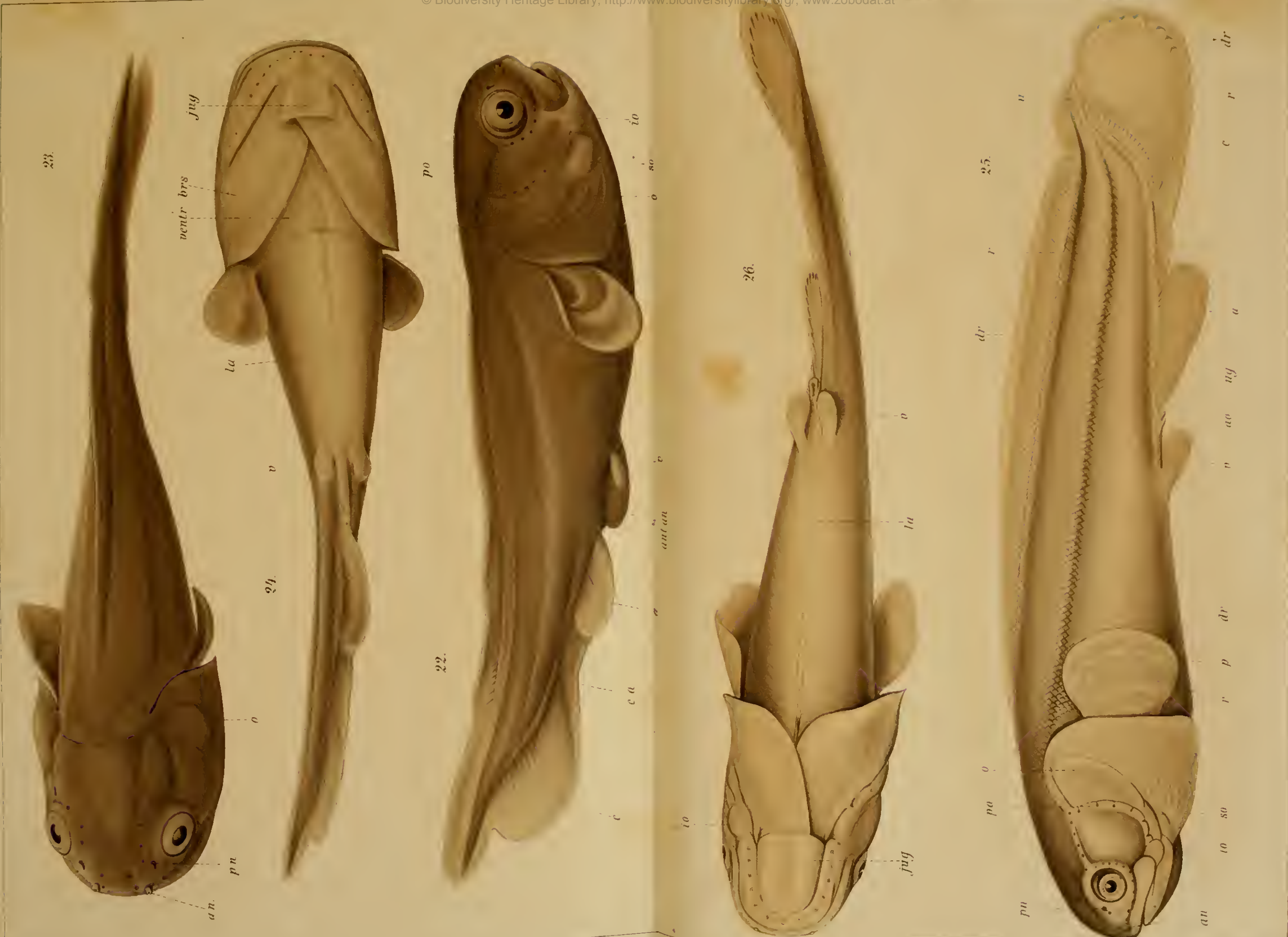

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