II. "On the Development of the Skull in *Lepidosteus osseous*." By W. K. Parker, F.R.S. Received November 3, 1881.

(Abstract.)

The materials for the present paper were kindly sent to me by Professor A. Agassiz; they were for the use of Mr. Balfour and myself, and consisted of *fifty-four* small bottles of eggs and embryos in various stages. These very valuable materials were obtained from Black Lake by Mr. S. W. Garman and Professor Agassiz, and many of the embryos were described and figured by the latter in the "Proceedings of the American Academy of Arts and Sciences," October 8, 1878.

Having received from my friend the author a copy of his important paper, I at once wrote to ask permission to work his materials out, thoroughly; suggesting that Mr. Balfour would undertake the embryological part of the work.

On receipt of my letter Professor Agassiz kindly acceded to my wish, and the results of our investigations are now ready for publication.

Mr. Balfour's part of the work has been done with the assistance of my son, Mr. W. N. Parker, and their joint labour will include the anatomy of various organs of the adult fish.

We have had additional materials from Professor Burt G. Wilder; these were larger young than those supplied by Professor Agassiz; Mr. Balfour also has obtained several adult fishes in spirit; and I am indebted to Professor Flower for an adult in the dry state.

Finding that we were in a condition to do some useful research on this important *Holostean Ganoid*, I pressed Dr. Traquair to take up the skull of the adult; this he consented to do; and I am daily expecting that his paper will be sent to the Royal Society.

My observations on the skull and visceral arches have been made on embryos and young, varying from one-third of an inch to $4\frac{1}{2}$ inches in length; I have (artificially) divided these into *six stages*. Cartilage was being formed in the smallest examined by me, but in my second stage, embryos five-twelfths of an inch long, this tissue was quite consistent, and I succeeded in dissecting out all the parts. The large notochord at this stage bends downwards under the swelling hind-brain, and then turns up a little at its free end; passing into the lower part of the fissure between the mid- and hind-brain, it reaches beyond the middle of the cranium, and just touches the infundibulum and *distinct* pituitary body.

The paired cartilages, "parachordals," that invest the notochord only cleave to its hinder *three-fifths;* these bands then diverge and

enclose a lanceolate space under the fore-brain ("thalamencephalon"). These somewhat flattened bands of cartilage become narrower up to the middle of this large primary "pituitary space," and then recover their former width in front, where they come in contact, having no notochord between them. All the cartilage that lies in front of the notochord is called *trabecular;* between the trabeculæ, in front, there is a small wedge of younger cartilage, the rudiment of the "inter-trabecula." The hinder, or *parachordal*, parts are somewhat scooped and bevelled above, and on their edge the auditory capsules rest. These are quite distinct, and have a cartilaginous coat, which, however, has a large oval deficiency below. As in the Batrachia, the fore part of the "palato-quadrate" cartilages is continuous with the trabeculæ in front; but the "pedicle" is free behind. The free "articulo-Meckelian" rod is quite in front of the eye-balls, and is nearly as long as the hind suspensorium, or proper quadrate region; this forward position of the hinge of the mandible is not temporary as in the frog, but is permanent. The uppermost element of the hyoid arch is an anvil-shaped cartilage from the first, and ossifies afterwards, as the hyo-mandibular and symplectic bones. As pointed out to me by Mr. Balfour, its dorsal end is continuous, *as cartilage*, with the skull (auditory capsule) above. The basi-hyal is not yet ossified, but distinct inter-cerato- and hypo-hyal segments are already marked out. Four larger and one small rods of cartilage are seen on each side, articulating with a median band; these are the branchial arches, which chondrify before they undergo segmentation. In this stage there are no osseous laminæ as yet formed.

Here, in this stage, in connexion with a large *pre-nasal* suctorial disk, we have three important generalised characters, namely, the continuity of the distal end of the mandibular pier and of the proximal end of the hyoid pier with the skull, and the forward position of the hinge of the jaw coupled with the horizontal direction of the suspensorium. The hyoid arch has its segments formed much earlier than in the Teleostei, and the "pharyngo-branchials" are not independent cartilages, as in the *Skate*.

The third stage—embryos two-thirds of an inch long—show a considerable advance in the development of the skull; the cartilage, generally, is more solid and more extensive, and new tracts have appeared. The apex of the notochord is now in the middle of the basis cranii, for the *pro*chordal tracts have grown faster than the *para*chordals. The large so-called pituitary space is now irregularly pyriform, and not lanceolate: the fore margin of the broad parachordal bands being now nearly transverse, whilst the prochordals (*trabeculæ*) are wide and fenestrate at first, then narrow, and then widening suddenly, they coalesce, forming a sharp anterior end to the pituitary space.

Behind, the parachordals have grown further along the thick notochord, and on each side they are now confluent with the auditory capsules, which have become irregularly ovoidal through the growth of the large semicircular canals within; their basal fenestra is still a round space under the partially floored "sacculus." The trabeculæ swell out where they are confluent, and then are narrower in front again. At their fore end each band passes insensibly into the corresponding palato-quadrate bar outside, whilst inside they are separated by a large pyriform wedge of cartilage, the intertrabecula. The thick, rounded, free fore end of this median cartilage is the rudiment of the great "nasal rostrum," and the rounded fore ends of the trabeculæ are the rudiments of their "cornua."

There is only a floor in the occipital region, but the *wall-plate* of the chondrocranium has begun as a styloid cartilage running forward from the fore end of each auditory capsule into the superorbital region. The palato-pterygoid band—continuous in front with the trabeculæ—is now longer than the proximal part of the suspensorium, the spatulate quadrate region whose dorsal end is the free "pedicle." The wide proximal part of each trabecula is now already forming an oblong facet, the "basi-pterygoid," for articulation with the facet of the "pedicle."

An oblong concavity is now seen under the outer edge of each auditory capsule, for the oblong head of the hyomandibular whose body is still solid, and the "symplectic" part merely a process growing downwards and forwards to get inside the lower margin of the suspensorium of the mandible. The epi-hyal region is still merely the top of the cerato-hyal; it is afterwards separate as a bony centre; the inter-hyal, hypo-hyal, and *double* basi-hyal are all now chondrified and distinct, but the branchial arches are not yet segmented. In this stage the skull is a curious compromise between that of a Salmon at the same stage and that of a Tadpole just beginning its transformation. The hind-skull is quite like that of a young Salmon, the fore-skull, with its non-segmented palato-quadrate, and its forwardly placed quadrate condyles and horizontal suspensorium, is very much like what is seen in the suctorial skull of the *Anurous larva;* a splint bone, the parasphenoid, as in the Tadpole, has now made its appearance.

The largest embryos reared by Messrs. Agassiz and Garman, which are about one inch in length, form my *fourth* stage; these are rapidly acquiring the characters of the adult.

This is the stage in which the chondrocranium of this Holostean type corresponds most closely with that of the Chondrostean Sturgeon, whose adult skull is similar to that of Garpike just as the latter begins to show its own special characters. This important difference is already evident, namely, that whilst in *Acipenser* the olfactory capsules remain in the *antorbital* position, those of *Lepidosteus* are already carried

forwards by the growing intertrabecula, and are even now in front of the relatively huge "cornua trabeculæ." Thus these regions are now well grown in front of the ethmoidal territory, which, instead of being, as in the last stage, in the front margin of the skull, is now fairly in its middle, and this change has taken place whilst the embryo has only become one-half larger—from two-thirds of an inch to an inch in length. It is the hypertrophy of cartilage in the three trabecular tracts that makes the "rostrum" of the Sturgeon so massive, even whilst only a few inches in length, and this state of things exists temporarily in the Garpike.

Each "cornu" is now like a thick succulent lanceolate leaf, coiled partly upon itself, downwards, at its outer edge; the middle bar, or intertrabecula, is now half as long as the skull, and projects forwards beyond the cornua, and between the distally-placed olfactory capsules. The cranial cavity is now relatively very large, and is covered by a cartilaginous "tegmen," before and behind; between these regions, over the huge mid-brain, there is a sub-circular "fontanelle," narrower in front than behind, and emarginate in front by some growth of cartilage in the mid-line.

The postorbital spike of cartilage has now grown into a narrowish superorbital band, bounding the upper fontanelle and enclosing between itself and the trabecula, below, a large "orbito-sphenoidal" fenestra. The floor is also still open, and this large pituitary space is spearhead-shaped, and is under-floored by the parasphenoid.

The basipterygoid processes are now well formed; the basal cartilages (parachordals) now embrace the huge notochord below, the flaps approaching, but not touching, each other. The notochord is now being formed into a "cephalostyle," but the bony sheath is imperfect. Above, the sphenotic, epiotic, and opisthotic projections of the auditory capsule are more evident, but are not ossified. Some slight bony deposit has appeared in the prootic region. The "cephalostyle" is the first *endo*-cranial bone, and the parasphenoid the first *ecto*-cranial centre; but the exoccipitals are just appearing also. The condyle of the quadrate is now still further behind the middle of the palato-quadrate arcade, the pterygopalatine part of which is now quite free in front, and has grown forwards parallel with the rostrum, as a long style, which reaches further *forwards* than the cornua trabeculæ. The "pedicle" of the suspensorium has a facet by which it articulates with the basipterygoid. The mandibular cartilage has also grown equally with the freed pterygopalatine rod, and has now a very large ear-shaped *coronoid* part in front of and above the articular part. The opercular process and fenestra of the hyomandibular are now formed, but this part is not ossified; the cerato-hyal diaphysis is present. It is the only *shaft-bone* in the hyoid arch as yet; the branchial arches are segmenting. The superficial bones can now be seen as fine films in the

transverse sections, and the *parosteal palatine* and pterygoid are large leaves of bone applied to the pterygopalatine bar; the mesopterygoid is only half as large as them, but is relatively much larger than in the adult.

Whilst doubling its length, the young *Lepidosteus* gains a cranium much more like that of the adult; this is my *fifth* stage. The general form is now intensely modified by the foregrowth of the rostrum: the "intertrabecula" is now *two-thirds* the length of the entire skull. The cornua trabeculæ now reach only *two-fifths* of the distance to the end of the beak, and the pterygopalatine arcade reaches but little further forwards. Owing to the "tegmen cranii" being much larger, the upper fontanelle is much smaller; it is now a short oval, its longer diameter being lengthwise. The bony matter of the "cephalostyle" is now aggregated towards the hinder half of the notochord; it is now the basi-occipital bone. The exoccipitals and prootics are growing larger, and there are now both sphenotics and alisphenoids. Also, below, the quadrate, metapterygoid, and articular "centres" have appeared; and behind the jaw there are the hyomandibular, symplectic, epi-hyal, cerato-hyal, and hypo-hyal centres; and the epi-, cerato-, and hypo-branchials have acquired a bony sheath.

In a young *Lepidosteus* $4\frac{1}{3}$ inches long (nearly), the approach to the adult state of the skull has been very great; the superficial bones can all be determined. The most remarkable of these are the small distal nasals and premaxillaries; the long *maxillary chain*, ending in an "os mystaceum and jugal"; the extremely long and slender "ethmo-nasals" and vomers; the small pre-opercular; and the huge angulated inter-opercular, which carries the large opercular and sub-opercular. The five mandibular splints are all present (as in most Sauropsida), the branchiostegals are only three in number, as in the Carp tribe.

The intertrabecula, which was merely a small tract of cells binding the trabeculæ together, in front, is now *three-fourths* the length of the entire skull; to it is due the length of the *beak*. The cornua trabeculæ are now merely short lanceolate leafy growths on the sides of the rostrum at its hind part. In the last stage there was a fine bridge of cells running across behind the pituitary body; this is now a small cartilaginous "post-clinoid" bar. The opisthotic and epiotic form now a scarcely divided tract of bone, all the other centres are developing, and a pair of additional bones have appeared in the funnel-shaped fore-end of the chondrocranium; these are the "lateral ethmoids." The bony matter of the basi-occipital has now retired to the hinder third of the notochord, which has much shrunken.

There are now two centres (as in *Amia calva*) in the articular region of the mandible; the quadrate and metapterygoid centres are much larger; the hyo-mandibular and symplectic are together only half

the size of the mandibular suspensorium; the basi-hyal is very large, is composed of two parallel pieces, and is very *Myxinoid*.

Brief and imperfect as this "Abstract" is, I trust it is sufficient to show the extremely interesting and suggestive nature of this type; anyhow, no clear understanding of the morphology of this type of skull can be had unless it be seen in the light derived from that of the Elasmobranchs, the Sturgeon, and the Anurous larva on one hand, and that of *Amia calva* and the Teleostei on the other.

III. "On the Structure and Development of *Lepidosteus*." By F. M. Balfour, LL.D., F.R.S., and W. N. Parker. Received November 24, 1881.

(Abstract.)

The authors commence this paper by thanking Professor Alexander Agassiz for the material, both embryological and adult, on which these researches were made.

The first section is devoted to the general development. In this section an account is given of the structure of the ripe ovum, of the segmentation, of the history of the germinal layers, of the first development of the principal organs, and of the external features of the embryo during embryonic and larval life. The more important points established in this section, are—

(1.) The ovum when laid is invested by a double covering formed of (*a*) a thick inner membrane, the outer zone of which is radially striated, and (*b*) an outer layer made up of highly refractive pyriform bodies which are probably metamorphosed follicular epithelial cells.

(2.) The segmentation is complete, though very unequal; the lower pole being very slightly divided into segments, and its constituent parts subsequently fusing together to form an unsegmented mass of yolk, like the yolk-mass of Teleostei.

(3.) The epiblast is divided into an epidermic and a nervous stratum, as in Teleostei.

(4.) The walls of the brain, of the spinal cord, and of the optic vesicles are formed from a solid medullary keel, like that found in Teleostei.

(5.) The lens, the auditory vesicle, and the olfactory pit, are wholly developed from the nervous layer of the epidermis.

(6.) The segmental or archinephric duct is developed, as in Teleostei, from a hollow ridge of the somatic mesoblast, which becomes constricted off, except in front; thus forming a duct with an anterior pore leading into the body cavity.