XIX.—THE OSTEOLOGY OF AMIA CALVA: INCLUDING CERTAIN SPECIAL REFERENCES TO THE SKELETON OF TELEOSTEANS.

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The present paper will be divided into two parts; of these, Part I will consist of a translation of the admirable article of Dr. M. Sagemehl, entitled "*Beiträge zur vergleichenden Anatomie der Fische*," the first contribution given us being "I. *Das Cranium von Amia calva*, L." This carefully written essay appeared in the second part of the ninth volume of the *Morphologisches Jahrbuch*, for the year 1883. It is illustrated with one double-page, beautifully executed plate. The twelve figures in this plate I have had, through the kindness of Professor Baird, carefully copied by Mr. H. L. Todd, the artist of the Fish Commission and Smithsonian Institution. They appear in their proper places in the plates illustrating this article with their explanations set opposite to them.

In Part II it is my intention to review the conclusions arrived at by Bridge, after his study of the skeleton of this interesting form. This anatomist published his well known memoir in the Journal of Anatomy and Physiology (Vol. XI, 1877, pp. 605–622, Plate XXIII), six years before Dr. Sagemehl's results appeared in the *Jahrbuch*. In this part, too, I will bestow a passing glance upon the monograph of Henricus Franque,[1] and compare his figures with those given by the above authors. Beyond this, however, it is not my intention to pass further into the literature of the subject, as the short and unsatisfactory accounts given by the older writers would avail us nothing here. Finally, I propose to present a few observations of my own, which have been the result of an examination of a skeleton of *Amia*, carefully prepared from a specimen of this fish which I captured in the vicinity of New Orleans, La., during the summer of 1883. This preparation was done for me in the most skillful manner by Mr. J. L. Wortman, the anatomist of the Army Medical Museum, of Washington. A few figures will be presented in this part, illustrating points that do not appear in Dr. Sagemehl's article.

[1] *Amiæ Calvæ Anatomiam*, Berolini, 1847.

PART I.

Ever since 1845—when Carl Vogt[2] demonstrated that *Amia calva*, L. differed in the structure of its heart from all known bony fishes, being like the cartilaginous fishes in this respect; and since Johannes Müller,[3] noting this circumstance, separated this remarkable fish from the Clupeoids, with which it had formerly been classed, adding it to his and L. Agassiz's established sub-class of Ganoids—the attention of anatomists has been steadily directed towards this form.

A number of works touching upon nearly all parts of the anatomy of *Amia* have made their appearance, so its structure is at present better known than that of most bony fishes. It is quite remarkable that the cranial anatomy of this Ganoid has not received proper attention, as it is by no means a rare fish in collections. The memoir by Bridge,[4] published in 1877, is in my opinion the only one in which the subject has been at all fully described.

Upon the suggestion of Privy Counselor Professor Gegenbaur, I undertook the task of re-examining the crania of the Teleostei, especially in the Physostomi and the Anacanthini, and in looking for a form in which the various differences in the structure of the skull could best be judged, my attention was drawn to *Amia*. In fact, a careful study of the cranium of this fish showed that several diverging series of skull-types could easily be traced from it. On the other hand, the task of tracing the conditions of the cranium of the Teleostei from more simply constructed types—such as the Selachians offer—I found the *Amia* to be an excellent transitory form for the purpose. The careful descriptive work of Bridge, with whom I concur in the majority of points, so far as the actual conditions are concerned, does not suffice for this special purpose. Certain points of organization, which at the first glance appear to be incorrect, and the significance of which only become apparent after comparisons with other forms, he has left entirely unnoticed. Furthermore, in his descriptions he has kept strictly within the limits of his title, perhaps for lack of material, describing only the bones of the skull and entirely neglecting the surrounding soft parts, in which I recognize the necessary elements to complete the configuration of the skull. Finally, in my opinion, Bridge has not been fortunate in his descriptions of several of the bones of the skull in *Amia*.

Taking all this into consideration, I decided to present a comparative description of the skull of *Amia*. At the same time I believe I will be

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[2] *Annales des Sciences Naturelles*, T. IV, 1845. (I have changed the numbering of Dr. Sagemehl's foot-notes so as to accommodate them to the present article.—TRANS.)

[3] *Über den Bau und die Grenzen der Ganoiden. Abh. d. k. Akad. d. Wissenschaften z. Berlin vom Jahre* 1844. *Berlin*, 1846. *Nachschrift*, pag. 204.

[4] The Cranial Osteology of Amia calva. Journ. of Anatomy and Physiology, Vol. XI, 1877, pages 605–622.

able to discuss several questions of a more general nature, which are of prime importance when taken in connection with my work upon the crania of the Teleostei, soon to be undertaken. It only remains for me to justify myself for having confined myself in this work, as I will in those of the future, strictly to the cranium, and for having but touched lightly upon those parts of the visceral skeleton connected with it; and that, too, only so much of it as was necessary to complete the form of the skull. Such partiality would hardly be justifiable were one considering the forms the cranium assumes in the higher vertebrates.

This is entirely different in the class Pisces. The visceral skeleton here has, in so far as the cranium is concerned, preserved a certain independence, and in consequence its form has been much less influenced, less so than other organic systems, as for example the nervous system, the muscular system, and particularly the organs of sense.

There is yet another objection that might be brought forward, and that is, that I have paid but little attention to the literature of the subject, particularly the older literature. In my allusion to facts long known—and, as I assume, of facts well known—it seemed to me entirely superfluous to continually cite authorities. Such a course would have rendered my subject-matter diffuse and unwieldy, without adding anything useful. The literature relating to it, contained in the more recent and less known works, and which refers to the discussion of purely special points, I have in every instance conscientiously cited.

Through the unbounded liberality of Privy Counselor Mr. Gegenbaur, to whom I here express my profound thanks, I have been enabled to examine five specimens of *Amia*, the smallest of which was 36^{cm}, the largest 57^{cm} long.

In viewing an unprepared head of *Amia calva* one can already distinguish the superficial plates of bone that overlie the cranium, they being merely covered by an extremely thin cutis.[5]

The sculpturing of the superficies of these bony plates is quite characteristic, consisting of sharply-defined and numerous ridges, which start from the center of each bone, to radiate outwards to the peripheries. After the thin skin covering them has been carefully removed one recognizes the limits of the several bones with requisite distinctness. Three pairs of bony tables, situated one behind the other, first meet the eye, of which the foremost possesses the greatest and the hindmost the least longitudinal extension.

The foremost of these pairs of plates consists of two bones, each of a quadrilateral outline, being joined together mesially by a strong dentated suture. (Plate I, Fig. 1.) The lateral borders of these bones arch over

[5] If Bridge (*loc. cit.*, page 606) describes the surface of these bones as "highly polished," and further says "they are destitute of any covering of soft skin," he is in error. One can easily convince himself, from a microscopical examination, that all of these overlying plates of the skull in *Amia* are not only covered by an epidermis—which is also present is *Lepidosteus* and *Polypterus*—but undoubtedly also possesses a very thin covering of cutis.

the orbits, while their anterior lateral angles rest upon the autorbital processes. In view of this arrangement this pair of bones are characterized as the *frontalia*[6] [frontal plates].

Behind these two bones, follow two others of an approximately quadrilateral outline, which like the preceding pair are connected together in the middle line by a dentated suture. These are undoubtedly the *ossa parietalia* [parietal plates], which in *Amia*, as in several other bony fishes, are suturally united mesiad[7]. (Plate I, Fig. 1.)

On either side of the parietalia and of the posterior part of the frontalia is found a longitudinally placed bone (Plate I, Fig. 1, *Sq.*), which corresponds in all respects with the *os squamosum* of the Teleostei.[8]

Articulating with its hinder border with the squamosal on either side, and being situated at about the middle of the latter half of the frontal, we observe another osseous plate, with its long diameter placed longitudinally. It is the osseous plate that overlies the continuation of the post-orbital, and is the post-frontal (Plate I, Fig. 1, and Plate II, Figs. 5 and 6, *Psf.*). A similar, only smaller, bone-plate, extensively sculptured, articulates with the anterior lateral angle of the frontal, and is the superimposed plate that represents the prefrontal (Plate I, Figs. 1, 2, and 3, *Prf.*). While the bony plates just described are firmly articulated with one another, and are also in intimate relation with the true cranium beneath, or are even blended with it, the two rather small osseous plates (Plate I, Fig. 1, *Ex.*) situated behind the parietals and squamosals, and meeting each other in the middle line,[9] are connected only with the bones in front of them by means of dense ligamentous bands. Nor

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[6]As regards the determinations of these bones, I have adhered strictly to the names used for them by Gegenbaur. It is of course universally known that these names, now long in use, do not express any homology whatever with the correspondingly named bones of the higher vertebrated animals. I am of the opinion that a complete homology exists for only a very few of the bones of fishes when compared with those of the higher vertebrata. There is not positive proof for a single one of them at the present writing. The most rational thing to do under the circumstances would be to introduce, if possible, a new and neutral nomenclature for the bones of the skull in fishes; yet I did not think myself justified in introducing such an innovation, which at any rate, so long as an exhaustive knowledge of the bones of the skull in fishes is not complete, could only be provisional, and I have therefore contented myself with the old names.

[7]Bridge, on whose specimen this mesial suture between the *Paritalia* had worn away, bestows, in consequence, upon the blended bony plates the name of "dermo-supraoccipitale," a name which in any event is inadmissible. On seven specimens of *Amia*, examined by me for the special purpose of looking into this condition, I have invariably found the median suture to be present, agreeing in this particular with the descriptions given by Owen and Franque, and I must consider the condition as found by Bridge as an individual anomaly, to which no further significance need be attached.

[8]Bridge takes this pair of bones for the parietalia because they lie upon either side of his dermosupraoccipitale.

[9]If Bridge intends to convey the idea that these plates do not meet each other in the middle line, he is in error; his own drawing (Plate XXIII, Fig. 1) proves to the contrary.

have they anything whatever to do with the primoidal-cranium, and they are even separated from the exoccipitals by connective tissues, though they overlap these bones to some extent. The greater part of one of these bones laps over one of the bones of the shoulder girdle, which latter rests with a mesially-directed process upon the hinder border of the exoccipital, while its remaining process, directed forwards, is attached by a strong ligament to the intercalare. This bone (Plate I, Fig. 1, *Sc.*) corresponds in all respects with the suprascapula[10] found in nearly all of the Teleostei.

Among the Teleosteans one quite constantly finds, between the processes of the suprascapula, a very superficially-situated dermal bone, which was first differentiated by Stannius from the supratemporal bone, which articulates laterally with the squamosal, and has been termed the extrascapula. This bone usually is not very large, yet in a few cases, as for example in *Macrodon*, it attains quite a considerable size; it then resembles in a great measure the bone as just described for *Amia*, and it is only to be distinguished from it in that it does not meet its fellow in the middle line. One will therefore hardly go astray in regarding the bone in *Amia*, designated in Plate I, Fig. 1, as *Esc.*, as homologous with the extrascapula of the bony fishes.

The nasal region of *Amia* is covered by five small dermal bones, which are separated posteriorly from the frontal plates by a small transverse strip of cutis.

The dermal bone (Plate I, Fig. 1, *Eth.*), placed most anteriorly of this group, has the form of an equilateral triangle, with the apex directed backward, and with a somewhat spreading base. It lies more deeply seated in the skin than the rest of these bones that overlie the cranium, but nevertheless it shows traces of the sculpturing that characterizes them all. Posteriorly, and to either side of this unpaired osseous plate, lie a couple of small bones (Plate I, Fig. 1, *Na.*) of which the two medial ones are somewhat the larger pair. These are separated anteriorly by the azygos bone, just referred to, penetrating between them; behind, they meet each other in the median line. On either side of these dermal bones lie two smaller ones (Plate I, Fig. 1, *An.*), of which no special notice need be taken. The four bones just described, more especially the medial pair, form the covering to the nasal cavity. Among the three bones designated by *Eth.*, *Na.*, and *An.* there remains, where they come together anteriorly, a small opening which leads to the rhinal chamber, and corresponds to the anterior nasal aperture of *Amia*. The posterior nasal opening is far removed from the anterior, being situated at the posterior lateral angle of the bone designated by *Na.* The interpretation of the dermal plates just described is not difficult.

The two posterior medial dermo-bones, holding, as they do, a position in front of the frontals and above the narial depressions, correspond or answer to the nasal bones of osseous fishes. There is yet another con-

[10] Suprascapula of Cuvier; omolita of Geoffroy and Stannius.

dition of these bones that supports this statement, viz, their relation to the mucus canals of the head.[11]

Among the Teleostei the anterior branch of the mucus canal, imbedded in the frontal bone, begins with an opening which is situated to the inside of the anterior nasal aperture. Its course in the nasal is backwards, and then it passes through the frontal, in which it throws off several side branches.

This portion of the mucus canal bears exactly the same relations to the bones in question in *Amia* as in the nasal among the Teleosteans, as may be seen by referring to Plate I, Fig. 1.

The mucus canals can also be utilized in defining both lateral bones. The main branch of the mucus canal, imbedded in the same, unites with the canal of the suborbital arch, and only a small lateral branch anastomoses with the mucus canal of the frontal. This condition reveals the fact that the bone just mentioned must be the first piece of the suborbital arch somewhat removed from its usual position—the antorbital.

The middle non-parial piece can also be determined without difficulty. In it we see a rudimentary ethmoid which has abandoned its customary site and relations with the frontalia, owing to the unusually developed nasal bones. So Bridge has likewise considered it; in fact, one could hardly regard it in any other light, unless choosing the very improbable assumption that the ethmoid—very constant elsewhere—is entirely absent in *Amia*, and that this fish is provided with a peculiar prenasal bone that never occurs in other fishes. Our determination is undoubtedly correct, as we find in *Polypterus* an identically similar bone, though here it is connected with two small processes of the frontalia that enter in between the nasals.[12]

All of the bones just described that overlie the cranium, with the single exception of the prefrontal, are pierced by a system of mucus canals, which are worthy of a closer consideration (see Plate I, Fig. 1).

As already mentioned above, a large mucus canal commences, mesiad, by the anterior nasal aperture to follow a course first in the nasal, then through the entire length of the corresponding frontal, to terminate in the extreme anterior portion of the parietal, on the surface of which its mouth is to be found.

The right and left canal are connected anteriorly by means of a transverse anastomosis which passes through the ethmoid. During its course through the posterior part of the frontal the mucus canal just described throws off a lateral branch, which passes through the postfrontal, and, being confined between the bones of the orbital arch, passes around the

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[11] I desire to mention, at this point, that hitherto the relation of the mucus canals to the bones of the cranium have hardly been given a thought, and yet they deserve a closer study, as these relations are very constant, and in questionable cases they can be used to determine doubtful homologies.

[12] Cf. the representation of Müller, Structure and Limits (*Grenzen*) of the Ganoids, Pl. I, Fig. 1.

eye, reaches the preorbital, and terminates laterally near the anterior nasal aperture.

From the mucus canal leading to the orbital arch another canal takes origin, beginning in the frontal, passing through the entire length of the squamosal, to enter the extrascapula and suprascapula. After passing through the suprascapula it becomes the mucus canal of the lateral line, passing on to terminate at the tail. Both of these canals, just referred to, are united by a transverse anastomosis, which is imbedded in the substance of the extrascapula. During its course through the squamosal a branch directed laterally arises from this canal. This branch enters the preoperculum, passing through the entire length of this bone to enter the mandible beyond, and eventually join the fellow of the opposite side, which it meets at the symphysis. All these mucus canals send off numerous ramifications of smaller canals, arranged in several longitudinal rows, which terminate on the surface of the head in minute openings.

Taking into consideration their superficial location, the peculiar sculpturing of their surface, and the possession of mucus canals, the bones we have just described are unquestionably characterized as ossifications of the skin—as dermal bones. In making any attempt to remove these dermo-bones one recognizes the fact that their relations to the chondrocranium are very different.

The ethmoid, the nasals, and the preorbitals[13] do not come in contact at all with the same, but are separated from it throughout their entire extent by soft parts.

On a microscopical examination of cross-sections made from one of these bones (take for example the extrascapula) one can distinguish a superficial layer from a deep one. The latter consists of osseous lamellæ, which are piled up parallel with the bony plane, and which are interrupted by others, arranged concentrically around the Haversian canals.

This deeper bony layer gives passage to quite a number of capacious Haversian canals and is supplied pretty generously with bone corpuscles. The superficial layer of these dermal bones is characterized, when compared with the one just described, by a much denser tissue, by a small number of Haversian canals, by an almost entire absence of bone corpuscles, and, what is most important, by the existence of numerous and very minute dentine tubelets (*Dentinröhrchen*) which penetrate it from the surface of the bone. Yet I wish to explicitly state that one cannot make out the exact boundary between these two layers with any certainty.

The frontals, parietals, and squamosals are in more intimate relation with the skull. In part, these are quite closely connected with the cartilaginous cranium, and are separated from it simply by a layer of thin connective tissue. Histologically they remind one very much of the

[13] This applies also to the extrascapular, the suprascapular, and the supraclaviculas.

bones of the first group. The two osseous layers can also be distinguished in them, but the inferior one is better developed and more plentifully supplied with Haversian canals, so that it becomes quite spongy in character. As already stated, they are separated from the underlying cartilage by a thin layer of connective tissue, through which ramify a numerous set of vessels, and in which are found pigment cells.

Finally, the postfrontals and prefrontals present us true "primary" ossifications of the primoidal cranium, which cannot be removed without injury to it, and which only remind us of their original development as dermal bones by their superficial location and by their sculptured surfaces, the former also by their having mucus canals.

The conclusion which we arrive at after our examination of these two bones in *Amia*, and which they afford, is so unique and so unlike the usual conditions that characterize those specific differences between dermal bones and the ordinary ossifications of the true skeleton, that it is easily perceived how Bridge was induced to separate each of these bones into two components, and to distinguish the true—corresponding to the homologous bones of the Teleostei—prefrontal and postfrontal, as well as the "dermoprefrontal and dermopostfrontal," covering the same. An unprejudiced examination at once convinces us that the conclusions arrived at by Bridge do not agree with the actual condition of things. The plates of these bones, visible on the surface of the cranium, as well as the outer layer of all the other dermal bones, undoubtedly consist of a compact and very hard bony substance, while those parts which are more deeply situated are more cancellous in texture; still the transition of one to the other is gradual, and the superior plate cannot be removed without breaking the bone.

Here a rare case presents itself—up to the present time almost universally doubted—in which bones that on their surface present all the characteristics of dermal bones have acquired relations with the true skeleton through their more deeply situated parts or structure, and in consequence are in part dermal and in part true bones.

Another group of bones is to be seen—partly, also, without dissection—from the cavity of the mouth. Lying in the median line and longitudinally placed upon and belonging to the parasphenoid is an osseous strip that is entirely covered over with a growth of firmly implanted and small conical teeth.[14] Between these teeth the bone is covered by a very thin layer of mucous membrane, which is only to be discovered after careful search.

Situated anterior to these median bony strips, there is on either side a number (from 17 to 22) of strong conical teeth, which are supported by the vomer. As the interstices among these teeth are filled in by a thick mucous membrane, nothing can be seen of the bones from an

[14] When Bridge speaks of roughness (asperities) of the parasphenoid, he does not convey to us the correct idea or condition. This roughness is caused by these true teeth, and of this fact Franque was already cognizant.

external view. Similar bone-plates, provided with fine little teeth, such as those just described for the parasphenoid, are found upon the palatine, upon the three pterygoids, and upon the splenial of the mandible. After the excellent investigations of Leydig[15] and O. Hertwig[16] a particular reason is hardly required if I place the parasphenoid and the vomer, as ossifications of the mucous membrane of the mouth, opposite the dermal ossifications and the true ossifications of the skull.

In respect to this, it seems to me that the condition found to exist in *Polypterus* is of peculiar significance; in this form, according to Leydig's investigations, all the bones of the buccal cavity are covered over by the epithelial layer solely. The *Amia*, where the ossifications beneath the epithelium are likewise covered by a layer of connective tissue, constitutes an excellent example, so far as this condition is concerned, of the transition stage between this form and the majority of bony fishes, in which the parasphenoid and vomer are hidden beneath the thick mucous membrane of the mouth.

After the cranium has been skeletonized, the parasphenoid and the parial vomer can be easily discerned.

The *parasphenoid* (Plate I, Fig. 2, *ps.*) is a flat bone, having the form of a cross. Its stem extends from the hindermost extremity of the skull to the antorbital, and very near its middle it gives off two branches, which extend laterally and upward alongside the postorbital, and form the posterior boundary of the orbit.

The posterior extremity of the parasphenoid is deeply cleft, thus allowing a small triangular portion of the basi cranii, represented by the basioccipital, to come into view upon a basal aspect of the skull. That part of the bone which is provided with teeth, and which in different individuals varies with regard to its anterior and posterior extension, lies mesially between the two branches.

In front of the parasphenoid are found the two *vomers* (Plate I, Fig. 2, *vo.*), articulating with each other in the middle line. They are flat osseous plates, placed longitudinally, with their anterior thirds armed with stout teeth. Their posterior moiety covers the anterior part of the inferior aspect of the parasphenoid.

If the statement that the parasphenoid originally bore teeth over its entire surface be correct—and so many facts have been adduced in its favor that its correctness can hardly be doubted—the overlapping of the vomer on this bone must be a primitive state of affairs. In fact, if one compares this condition of *Amia*, with its parial vomer, with the arrangement in bony fishes, where the vomer is known to be always nonparial, hardly a doubt but that *Amia* represents the primitive condition remains.

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[15] W. Leydig, *Beitrag z. mikroskop. Anatomie v. Polypterus. Zeitschr. für wiss Zool.*, Bd. V.

[16] O. Hertwig, *Das Zahnsystem der Amphibien f. mikroskop. Anatomie.* Bd. XI, suppl.

Leaving entirely out of consideration the arguments that can be adduced in favor of a progressive development of *Amia* in the direction of the bony fishes, and that the division of a bone into several parts is an hypothetical process, the positive proof has been given us by Walther[17] that the vomer of the pike is a parial ossification. Yet the present position of the vomers in *Amia* is not the primitive one, and in order to get around all difficulties involved in this question we must assume that in still more pristine forms both these bones occupied a position more remote from the mesial line, on either side of the anterior extremity of the parasphenoid, as in many existing Amphibia.

The conclusion arrived at from these inferences—taken in connection with the fact that the vomerine and palatine teeth of fishes are situated in one and the same line, lying in the same arch—gives some coloring to the supposition that the vomers of fishes originally constituted the anterior overlapping segments of the palatine arch, as has been proven by Hertwig for the Amphibia.

To the "cover-bones" of the skull in *Amia* yet belongs another piece, that with other forms is not so intimately related to the primodal cranium. It is the *intermaxilla* (Plate I, Fig. 1, and Plate II, Fig. 6, *Sm.*).

This is to be seen extended upon the cartilaginous base of the rhinal chamber, proceeding backwards from its arched and compact alveolar process; this thin osseous plate encroaches to no small extent upon the antorbital region.

In the posterior portion of the nasal depression this plate is pierced by a large foramen for the passage of the olfactory nerve (Plate I, Fig. 1, *ol.*).

The integrity of the cartilaginous cover of the primoidal cranium of *Amia* is thoroughly preserved throughout, being devoid of fenestræ or other breaches in its substance of any kind whatever.

In outline it resembles a triangle placed longitudinally, with its apex cropped off anteriorly; it is generally level, and marked only by pit-like impressions at the posterior lateral angles, and by a number of projecting processes, which are more or less ossified. The two anterior ones are the antorbital processes (Plate I, Fig. 1), with their ossifications already described—the prefrontals. At about the middle of the skull-cover the postorbital processes project out laterally at each side, together with their ossifications, also described as the postfrontals (Plate I, Fig. 1).

The prominent posterior lateral angle of the primoidal skull is occupied by the intercalare [opisthotic] (Plate I, Fig. 1, *Jc.*).

As we proceed towards the median line from the angle formed by the intercalare we find rising on either side another process, situated not quite so far behind, that is formed by the exoccipital (Plate I, Fig. 1, *Ex.*). Between these processes, formed by the intercalare and exoccipital, ex-

[17] J. Walther, *Die Entwicklung der Deckknochen am Kopfskelet des Hechtes. Jenaische Zeitschrift f. Naturwiss.*, Bd. XVI, 1882.

tensive fossæ are found on the skull, that extend well anteriorly towards the frontal region (Fig. 1).

As the dermal bones, occupying their respective places, the squamosal and lateral margin of the parietal span this depression as the arch of a bridge, it gives rise to a cavity between the primoidal cranium and its cover-bone, the opening of which is upon the posterior aspect (Plate II, Fig. 6, *tg.*[18]) and into it enters, to be attached to the occiput on either side, a part of the muscle of the dorsum of the trunk.

This depression, which forms so striking a feature of the skulls in the Teleostei, I here propose to name the temporal fossa.[19]

Projecting from the middle line posteriorly there is a short cartilaginous process (Fig. 3, *Oc.*[20]) that occupies precisely the same position that the superoccipital does in the Teleostei. The last-mentioned bone is wanting in the Siluroids and Dipnoi. From the hinder boundary of the vault of the skull it is produced downwards and backwards, and finally is drawn out as a cylindrical prolongation of the same, in which is contained the posterior part of the medulla oblongata and the anterior commencement of the spinal cord.

The occipital region[21] of *Amia* is, so far as a comparison with bony fishes teaches us, remarkably drawn out longitudinally, and this prolongation, the cause and significance of which will be discussed further on, concerns chiefly the region posterior to the foramen for the vagus.

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[18] This is given in the text of the original as *Th.* and I here correct it to *tg.*—TRANS.

[19] This point is the proper one for us to take a careful look into the relations of the squamosal to the primoidal cranium. This bone rests by its lateral border only upon that crest of the primoidal skull which is directed upwards and outwards and forms the lateral boundary of the temporal fossa. Now, although the squamosal in *Amia*, as already stated, is a dermal bone, which appears only to be resting upon the primoidal cranium, it would be impossible to remove it without injury. This is the site it occupies: from the lateral margin of the bone are developed two osseous ridges, which are directed downwards and to some extent towards the median line, and have, when articulated, the two corresponding sharp cartilaginous crests of the skull inserted between them. The lateral ridge of the squamosal, of the two mentioned ones, is juxtaopposed to the lateral surface of the skull, and is carried from the margin of the bone downwards to the hyomandibular articulation. The remaining or mesial ridge lies in the temporal fossa. This condition is significant in so far that among the Teleostei it is only through the lateral margin of the squamosal, that the cartilages are wedged apart, and the firm union of the bone with the primoidal cranium takes place.

[20] This is *Co.* in the original text, and it has been corrected here to *Oc.* In either event it is not quite clear what Dr. Sagemehl intends to indicate, so *Oc.* has been omitted from my letters of reference, as I must believe he refers to *Ol.*—TRANS.

[21] It appears to me more to the point to consider the foramen for the glossopharyngeal and the posterior border of the petrosal as the extreme anterior boundary of the occipital region in the bony Ganoids and Teleostei, and not the foramen for the vagus, as Gegenbaur has done for the Selachians. In the fishes examined by us these two nerves are intimately related to each other, and in rare cases they may even have a common foramen of exit, so that placing them in this or that region would be quite arbitrary. Moreover, in the limitation proposed by me the confines of regions are almost without exception defined by the sutures between the bones, and therefore it becomes unnecessary to award a bone to different regions.

The base of the occiput is occupied by the *basioccipital* (Plate I, Figs. 2 and 3; Plate II, Figs. 4 and 5, *Ob.*). This bone has the form of a mussel-shell, not unlike *Cardium* or *Pecten*. Posteriorly it is shaped like the centrum of a vertebra, and presents for examination a tolerably even and conical excavation, into which the anterior end of the chorda enters. The margin of this excavation is connected by stout ligamentous bands to the centrum of the first vertebra, the anterior side of which appears slightly convex. Articulating with the lateral margins of the basioccipital are the *exoccipitals* (Plate I, Figs. 1 and 3 *Ol.*). These two bones, for the greater part of the posterior aspect of the primoidal cranium, assist in the formation of the lateral region only to a small extent. In large specimens of *Amia calva* they join together in the middle line over the medulla oblongata by means of a suture; in immature specimens they are separated throughout their entire extent by a strip of cartilage. They form no part of the articulation of the neural arch of the first vertebra, but they are separated from it by two bony arches, which rise upon the posterior portion of the basioccipital, having the form of a vertebral centrum, and which correspond in every respect with the neural arch of the vertebra, and shall be termed the occipital arches (Plate II, Figs. 4, 5, and 6, *Oc.* I and *Oc.* II).[22]

The anterior occipital arch is formed by two triangular osseous platelets, meeting together over the spinal cord, above which a non-paired oblong bone, directed upwards and backwards, is fastened by ligaments.[23]

The posterior arch is similarly fashioned, only both of its parts are of an oblong quadrangular shape, and develop on their posterior aspect a small articular facet for the arch of the first vertebra. Upon this arch is found also a pointed bone, directed upwards and backwards.[24]

The pointed bones resting upon the occipital arch are to be considered as spinal processes. At the same time, however, I will remark that inasmuch as they are situated in a line with the uppermost interspinous bones, which, indeed, no longer support the fins, one can just as well count them in with the latter. The boundaries between the fin-rays and the interspinous bones in *Amia* are not strictly defined, and the arrangement or condition they present us with in this form furnishes another proof that these formations originally had a genetic connection with each other. A good drawing of these conditions has been furnished us by Franque in Fig. 2 of his familiar treatise.

The occipital arches of Amia are not of uncommon occurrence, but are generally present either as independent arches, or reduced in various ways, or at-

[22] Reads *obg.* in original text.—TRANS.

[23] So I find the condition in the older specimens. In the younger individuals, from which the illustration is taken, each half of the occipital arch consists of three separate osseous portions—one lower triangular piece, and two upper ones resting upon it and situated behind one another. It is not possible to find an explanation for this state of things at present.

[24] In the older specimens of *Amia* the two pointed bones are blended into one osseous plate.

tached to the hinder extremity of the skull, as in the higher fishes which are provided with ossified skulls.

In *Polypterus* a free occipital arch has been described by Traquair. Franque has also observed the occipital arches of *Amia*, as would appear from his brief and not entirely lucid description, but their significance appears to have entirely escaped him. Bridge mentions them also. Here and there other authors have noticed them, without having, up to the present time, placed any weight upon the occurrence of precisely the same thing in bony fishes. I have been able also to convince myself that the occipital arch is not wanting in *Lepidosteus*. In this Sauroid I find both halves synosteologically joined together, as well as with the basioccipital, so that this latter bone appears to form by itself the periphery of the occipital foramen. Among the osseous fishes one finds in the pike free occipital arches beautifully developed, also in the Salmonidæ and Clupeidæ; but, as shall now be particularly mentioned, proof can be furnished that all Teleostei originally possessed occipital arches.

Over the occipitale laterale, and connected with it at one small point, is found the conical exoccipital (Plate I, Fig. 1, *Ex.*). It constitutes the boundary to the entrance of the temporal fossa, mesiad, and is partly covered on its superior surface by the posterior margin of the parietal.

The posterior lateral angle of the primoidal cranium is occupied by a thoroughly developed bone, which I, in concurrence with Bridge, can only take to be the intercalare (opisthotic) (Plate I, Figs. 1, 2, and 3, *Jc.*). It is also a conical bone, which is covered above by the posterior lateral angle of the squamosum, and which helps to form the lateral boundary of the entrance to the temporal fossa. It does not articulate with the exoccipital, but remains separated from it by a strip of cartilage lying at the base of the temporal fossa. Posteriorly and beneath it comes in contact with the occipitale laterale, and in some individuals also with the basioccipital. Below and anteriorly, the intercalare, though a very delicate process, meets and unites with a process from the petrosal. To the apex of this bone, chiefly projecting posteriorly, the inferior limb of the supraclavicular is attached, as already shown, by means of firm ligaments. Below, the intercalare meets with the cartilage of the primoidal cranium, at which point something of a protuberance is developed.

It is known that in most osseous fishes the intercalare is wanting, and in the minority, where it still exists, it is feebly developed, with the exception of the family Gadidæ.[25]

Yet a comparison of the condition in *Amia* with that of the *Gadidæ* leaves not a shadow of a doubt that the bone just described is really the intercalare, inasmuch as this very bone in the Gadidæ possesses

[25] Compare the careful description of the intercalare of the Gadidæ by Vrolick, "*Studien über die Verknöcherung und die Knochen des Schädels der Teleostei.*" *Niederländ. Archiv. f. Zoologie*, Bd. I, 1873.

precisely the same topographical relations to neighboring ossifications of the skull, to the suprascapula, and to the foramen for the exit of the vagus and the glossopharyngeal.

The nerve situated most anteriorly in the occipital region is the glossopharyngeal. Its foramen of exit is found where the intercalare, the petrosal, and the cartilaginous portion of the primoidal cranium come together, and below and between the basioccipital and petrosal (Plate I, Figs. 2 and 3, *gph.*). Immediately after its exit from the foramen the glossopharyngeal divides into its two well-known branches, the distribution of which is of no interest in the present connection.

Thoroughly separated from the glossopharyngeal foramen we find the foramen for the vagus is so located in the suture between the intercalare and the occipitale laterale that its periphery is formed by these two bones (Plate I, Figs. 2 and 3, *v.*[26]). The nerve itself exhibits essentially the same behavior after its exit as in the *Teleostei.*

While yet within the brain-case the vagus gives off a very minute branch, which, ascending upwards, perforates the cartilaginous skull-cover beneath the parietal, into which it enters, probably to supply its mucus canal. I should not have mentioned this little branch at all if the so-called *ramus lateralis nervi trigemini*, which is known to receive fibers from the trigeminus and from the vagus, did not quit the cranium at the same locality in many of the Teleostei. That this nerve in *Amia* also receives fibers through its anastomosis with cranial nerves that arise more anteriorly I have once been able to confirm, but, in consequence of the indifferent manner in which the specimen I examined had been preserved, it was impossible to ascertain from which nerve this anastomosis proceeded. While the occipital region of the Selachians[27] arrives at its posterior limits with the vagus, in fishes provided with ossified skulls several nerves of the occipital group, and of a character identical with the spinal nerves, are constantly to be found between the vagus and the first spinal nerve.

Amia, possessing the largest number hitherto observed of occipital nerves, furnishes us with three such for our consideration. The most anterior of these leaves the brain-case at a minute foramen in the occipitale laterale, and situated near its posterior border (Plate II, Fig. 4, *oc* I). It is of a smaller caliber than the two following, and also differs from them in that it only arises from the spinal cord by means of an anterior root. The nerve next in order arises by both an anterior and posterior root, between the hinder border of the occipitale laterale and the anterior occipital arch (Plate II, Fig. 5, *oc* II). Immediately after their exit these two roots unite in a common trunk, and in so doing carry out the character of a spinal nerve (Plate II, Fig. 5, *oc* III). The first spinal nerve in *Amia* quits the neural canal between the posterior occi-

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[26] Marked *vg.* in original text.—TRANS.

[27] As a matter of course only such Selachians are here taken into consideration whose crania are sharply defined from the vertebral column.

pital arch and the neural arch of the first vertebra, presenting us with nothing of particular note.

The three occipital nerves, together forming a group, run downwards in front of the shoulder-girdle, to finally ramify, and—probably together with the branch of the first spinal nerve, agreeing in this respect with the corresponding nerves in the Teleostei—to supply the muscles lying between the shoulder-girdle and the mandible. This I could not establish with certainty, for the reason that the specimen used by me for the examination of the nerves had already served for a dissection of the heart and great vessels. To complete the subject, a canal must yet be mentioned, the function of which I have been absolutely unable to discover. It commences on the lateral aspect of the bassioccipital, and on that portion of this bone which so much resembles a vertebra; it takes a course towards the median plane, turns at a right angle, and terminates at the inferior surface of the bone, between the posterior wings of the parasphenoid. This terminal opening is in close juxtaposition with the same opening of the canal of the opposite side, but no communication exists between them nor with the cavum cranii. The contents of this canal I found to be fibrous connective tissue and thin-walled vessels of some caliber (Plate I, Figs. 2 and 3, *cb.*).

The fact that free and independent neural arches are found upon the basioccipital, from between which emerge nerves of a structure like true spinal nerves, is of fundamental importance in the determination of skulls of the higher fishes, and admits of no other explanation than that which applies to the primoidal cranium, the best example of which we find in the Selachians, where we observe anchylosed together a still greater number of vertebræ, with the nerves that pertain to them making their proper exits.

A question still more difficult of determination is to define the number of vertebræ that enter into the composition of the cranium. In *Amia*, which for this purpose—of all the fishes with osseous skulls examined by me—possesses the best example of this primitive condition, I believe I am enabled to recognize the elements of three vertebræ. That the two occipital arches, with the nerves that pertain to them, represent the remains of what were originally distinct vertebræ, no reasonable doubt can exist; and the only question is whether we are to consider the first occipital nerve, which is very feebly developed and without a posterior [dorsal] root, as a rudimentary spinal nerve, or whether another interpretation is admissible.

If the first occipital nerve is not to be considered as a rudimentary spinal nerve, one can see in it—since it is absolutely inconceivable to have a generation of new nerves in the higher animals—but a branch of one of the two neighboring nerves, namely, of the vagus or of the second occipital nerve, that has branched and become independent. Now, the distribution of the first occipital nerve is such, that one cannot for an instant take it to be a branch of the vagus at all, and therefore the only possibility remains that it could belong to the second occipital nerve. Such a thing as the branches of nerves eventually becoming new and independent nerves does occur in fishes, and I would invite attention to the condition seen in the spinal nerves in the Gadidæ,[28] and to the condition seen in the *ramus palatinus nervi facialis* in many bony fishes. There are two factors to be taken into consideration that enter into such a divisional process. The first of these is that distal regions supplied by the nerve may grow apart, and become further and further separated from each other; and the second is, that the tendency of each nerve is to take a direct course to the part it supplies. Both of these conditions would eventually bring about a division of a nerve to its very origin. Therefore this division must begin at the distal end of the nerve, and, gradually progressing, must extend finally to the point of origin in the central nervous system.

Precisely the opposite condition is found in the first occipital nerve; distally it is united with the second occipital nerve, it being but partially separated from it. Therefore the only justifiable conclusion we have left us to adopt is that this nerve must be considered as a discrete spinal nerve, the survivor of a retrogressive process, and so in *Amia* we must assume that at least three vertebræ have merged into the cranium.

I have yet to invite more careful attention to a condition not remarked upon by me before. Upon closer scrutiny of the occipitale laterale one sees that the hindermost part of this bone, where it meets the anterior occipital arch, is thickened and consequently well defined from the other bones. The anterior border of this thickened strip is in immediate relation with the minute foramen of exit of the first occipital nerve, and consequently this thickened portion of the bone exactly corresponds in form as well as in its site to a third anterior semi-occipital arch that has merged into the occipitalia lateralia. Now that the proof has been furnished that vertebræ, originally separate, have blended with the skull, an explanation can be given for certain points for examination that are to be found upon the inferior aspect of the basioccipital, which have not been alluded to by me before, because their significance would not have been understood.

Between the two posterior limbs of the parasphenoid, immediately behind the two lower exits of the vascular canals described above, that pass through the basioccipital, one finds two small pieces of cartilage, quite superficially placed upon the surface of the bone. (Plate I, Fig. 2, *x*.) On viewing the vertebral column of this fish from beneath, one can satisfy himself that very similar pieces of cartilage are upon each vertebral centrum; indeed, in younger individuals these cartilages penetrate deeply into the substance of the centra, while in the older specimens only very thin cartilaginous pieces can be recognized resting superficially on the vertebræ.

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[28] Stannius, *Das peripherische Nervensystem der Fische*, pag. 119.

Without going any further into an explanation of these cartilaginous formations, which could only be done by a careful comparison of the vertebral column of *Amia* with that of other fishes, I feel called upon to invite attention to the remarkable—even in details—similarity of the posterior portion of the basioccipital to the centrum of a vertebra.

To make a comprehensive statement, the occiput of *Amia calva* reveals the elements of three vertebræ, which are co-ossified with it, and whose individual independence becomes less and less marked from behind forwards. The centrum of the hindmost vertebra, as well as the centra of the other two, is co-ossified with the basioccipital; it is, however, only in the posterior portion of this bone that the evident likeness to the centrum of a vertebra can be recognized. The neural arch of this vertebra cannot be distinguished from the neural arch of a trunk-vertebra, and it possesses also a well-formed spinous process; the corresponding nerve is stamped with all the characteristics of a typical spinal nerve. The middle vertebra, absorbed as it is by the cranium, is quite similarly formed, only that its neural arch has become broader and intimately blended with the cranium. The transformation and co-ossification of the anterior vertebra is the most complete. Both halves of its neural arch are blended with the occipitalia lateralia, and the nerve corresponding to it arises simply as a feeble anterior root [ventral]. This rudimentary nerve is really the only safe indication of the existence of this anterior vertebra, which has in other respects been completely appropriated by the skull; and should one imagine that this nerve was formed through a retrogressive process, or became blended with the occipital nerve, then nothing would remain to give us the slightest hint as to the original existence of this anterior vertebra. This is of importance in so far as it gives rise to the possibility that beyond this vertebra, the existence of which is still to be seen through its last faint traces, there existed other ones, which, however, have become thoroughly appropriated by the cranium so as not to be any longer distinguishable.

The number which I have indicated, then—that of three vertebræ co-ossified with the skull—can therefore only be the fewest of these segments to be recognized. The view that the original number of these vertebræ was greater is by no means to be precluded.

It is hardly worth while mentioning that the facts just discussed by me have nothing whatever to do with the question of the composition of the primoidal cranium out of like constituents—the so-called vertebral theory of the skull. The formation of the primoidal cranium in the Selachii—and maybe, too, in the Cyclostomata—has already been perfectly defined; and setting the question entirely aside as to whether any or how many metameres were contained in those skulls, my only aim was to establish that between the Selachian skull and that of the higher fishes no complete homology exists. The cranium of the higher fishes corresponds to the cranium of the Selachii, plus several (at least three) of the anterior vertebræ of the column.

I would also expressly state that the proof just given only applies to the higher fishes, and that every attempt to assume the same condition for the higher organized vertebrate animals also must be premature at least. I would not have mentioned this particularly if attempts had not been made recently to show that the atlas of the Amniota is co-ossified with the cranium in Amphibia.

Stöhr[29] first made the interesting discovery that the so-called odontoid process of the Amphibia is nothing more than the notochord becoming cartilaginous, and subsequently developing as an ossified process from the first vertebra. Upon this discovery[30] Wiederscheim has made the assertion, for which there is no foundation, that the atlas of the Amniota is to be looked for in the occipital part of the skull of the Amphibia, and that in consequence of this the first vertebra in these forms corresponds to the axis.

After considering that the arrangement of the nerves in the occipital region, and of the first spinal nerves in the Selachians and Amphibia, at least in the Urodela, is identical; that in both, the vagus is the last nerve given off by the brain; further, that the entire occipital region in the Amphibia appears extraordinarily rudimentary, weighty reasons arose in my mind discrediting the idea that we find in the Amphibia the skull appropriating one of the vertebra, and I rather believed that a complete homology of the skulls in the Amphibia and Selachians must be accepted. Wiederscheim's view has its origin in the one-sided comparison of the conditions of organization in the Amphibia with that in the Amniota. Existing Amphibia, so far as their crania go, form a very restricted group by themselves, their structure permitting certain comparisons to be made down the scale toward the Dipnoi and Selachians, but not upward toward the Amniota. Consequently, if one foregoes a direct comparison of the skull of the Amphibia with that of the Amniota, a phylogenetic interpretation of the ontogenetic facts discovered by Stöhr would not be difficult. In all fishes, particularly the Selachians, a conically-pointed piece of the chorda extends into the occipital region of the skull, and one need only imagine that this notochord be transformed to cartilage, and afterwards—developed from the first vertebra—to ossify, in order to arrive at exactly the same conditions as they exist in Amphibia.

Then, to be sure, the odontoid process of the Amphibia is not homologous with the structure bearing the same name in the Amniota, but only presents an analogous formation; yet the supposition of homology even does not seem to me at all probable, inasmuch as it can be easily shown

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[29] Ph. Stöhr, History of the Development of the Skulls of Urodela. *Zeitschrift f. wiss. Zoolog.*, Bd. 33. 1880.

[30] Wiederscheim, Comparative Anatomy of the Vertebrate Animals, page 60. It is not uninteresting that Albrecht (*Zoolog. Anzeiger*, 1880, Nos. 64 and 65), upon this same report, draws the opposite conclusion, and interprets the first vertebra of the Amphibia as his imaginary "pro-atlas" lying beyond the atlas, and the odontoid process of the Amphibia as the basioccipital separated from the cranium.

that the formation of the odontoid process out of the body of the atlas in the Amniota only begins among the reptiles.[31] In higher fishes it is very generally found that the anterior aspect of the first vertebra is not excavated, but slightly convex. Now, though it seems to me to be improbable that the conditions in Amphibia can be traced directly to these structures in fishes, yet here is a state of things that can be considered parallel with that of the Amphibia.

An explanation for the singular fact that in the higher fishes independent vertebra are co-ossified with the occiput is not difficult to find, and I believe the reason for this condition is to be found in the way and method in which the parasphenoid makes its appearance.

It has been fully and conclusively shown by Hertwig that teeth can be discovered upon all the bones of the buccal cavity, which arise from these osseous plates through sockets in their substance, and that the parasphenoid forms no exception to this rule, although teeth are found upon it far more seldom than on the other bones of the mouth. If we now know that the appearance of teeth in the Selachians is not confined to the cavity of the mouth, but that they also extend upon the mucous membrane of the fore-gut, as far as the gill slits, thus reaching far below the anterior extremity of the vertebral column, then the supposition will not be startling that the parasphenoid originally did not confine itself to the basis cranii, but extended far behind it upon the vertebral column. In fact, we meet with the parasphenoid occupying this very position in those fishes in which bone first begins to appear, in the cartilaginous Ganoids, and in the Dipnoi. As already known, the parasphenoid of Störs does not confine itself to the base of the true skull, but extends backwards to be applied to the inferior surface of the centra of about 7 or 8 vertebræ. According to Wiederscheim this is the arrangement in *Polypterus*, and Günther tells us that it also occurs in *Ceratodus*, only in these fishes the number of vertebræ covered by the parasphenoid is fewer. This also must have been the state of things in the direct ancestry of the existing bony Ganoids and Teleostei. Now, after the parasphenoid had ceased to be a tooth-bearing bone of the cavity of the mouth, a curtailment from behind took place, and at the same time a reduction in number and consolidation of the vertebræ resting upon this bone, which was already firmly connected with the cranium, set in, to replace the latter, a transformation the last traces of which can still be seen in bony Ganoids and Teleosteans.

The region of the labyrinth[32] is bounded posteriorly by the foramen

[31] Gegenbaur, *Grundzüge der vergl. Anatomie*, 2 Aufl., page 615.

[32] Labyrinth region, the term here used, applies more particularly to that space as seen in the Teleostei and bony Ganoids, which, by the way, it does not entirely include, as the labyrinth in these fishes generally extends beyond the confines given; moreover, all the bones enumerated by me as belonging to the occipital region may, under certain circumstances, serve for the inclosure of parts of this area. So I have retained the term simply to avoid a new name.

for the exit of the glossopharyngeus; anteriorly by the postorbital process and the posterior circumference of the orbit.

It forms the greater part of the lateral wall of the skull situated behind the orbits and includes the ossified petrosal and postfrontal.

The *petrosal* (Plate I, Figs. 2 and 3, *Pe*) is nearly circular in form, being connected behind and above by a small part of its periphery to the intercalare in a serrate suture.

It is separated from the surrounding bones by broad areas of cartilage, from the basioccipital posteriorly, the squamosal laterally and above, the postfrontal above and anteriorly, from the alisphenoid anteriorly, and from the petrosal of the opposite side by a mesial band of the same material.

Above the petrosal we find the long, flat, and longitudinally placed facet of articulation for the hyomandibular (Plate I, Figs. 2 and 3 *hm.*). This facet is entirely in cartilage, with the exception of the postero-superior angle, which is slightly overlapped by a thin piece of the squamosal.

Anteriorly and above the petrosal lies the ossified postorbital process —the *postfrontal* (Plate I, Figs. 2 and 3, *Psf.*). This bone has the form of a triangular pyramid, whose apex is directed laterally and upward. The superior aspect of this bone, which is stamped with all the characters of a dermal bone, has already been thoroughly described; of the two remaining sides, one faces outward and the other assists in forming the hinder part of the upper margin of the orbit. The ossification of the postfrontal does not reach through the entire thickness of the lateral cartilaginous skull wall, but remains separated from the brain cavity at all points by cartilage. Now, at the dividing line between the bone and the cartilage there lies a canal that commences at the lower margin of the bone at the side of the skull and makes its exit at the anterior angle of the temporal fossa. So far as I could satisfy myself, it contains vessels intended for the soft parts contained in the temporal fossa. This canal has no greater morphological significance, and I only mention it for the sake of making my description complete. Two openings are formed near the anterior margin of the petrosal; the upper and larger one is for the facial nerve and jugular vein (Plate I, Figs. 2 and 3 *fa.*), the smaller and lower one for the carotid (Plate I, Fig. 3 *ca.*). While still in the brain case the facial nerve gives off a branch which, running forward, enters the orbit at the posterior margin of the fenestra—to be spoken of further on—thence traversing the lower lateral margin of this cavity, to be distributed to the mucous membrane of the mouth.

This branch of the facial, which universally occurs in the Teleosteans, has always been referred to as the homologue of the *ramus palatinus* of the Selachians. If one considers that the *ramus palatinus* of the Selachians always arises extracranial from the facial, and from this origin runs anteriorly, while the nerve bearing the same name in *Amia* and bony fishes has an intracranial origin, the question of their homology becomes dubious. To render this homological comparison safe, we must have the positive proof, now missing, that this branch penetrates from the outer side of the skull to the inner in this series of fishes. The further distribution of the facial nerve after it quits the brain case is of no further interest in the present connection.

The orbital region is very definitely marked off. Its posterior boundary has already been alluded to; anteriorly the antorbital process, with its ossification, the prefrontal, divides it from the nasal region. In *Amia* the orbits are tolerably flat and oval depressions, separated from one another in the median plane by an antero-projecting process of the cavum cranii (Figs. 9 and 10); there is not a trace present in *Amia* of a bony or membranous interorbital septum, as we find in so many of the Teleostei.

The roof of the orbit is formed only to a limited extent by a cartilaginous, laterally-projecting ledge of the primoidal cranium, which one may consider as the last remnant of a cartilaginous orbital roof (Figs. 2 and 3), the greater part of this roof being furnished by the frontal bone. An orbital base is indicated by a feebly developed, winglike ledge projecting from the basis cranii, which is in contact with the parasphenoid beneath (Figs. 9 and 10).

The anterior third of the wall of the orbit is entirely cartilaginous,[33] while the posterior two-thirds are in part occupied by two ossifications. There is a large foramen found in the posterior part of the orbit, bounded above, behind, and in front by serrate edges of bone and below by cartilage, which opens into the brain case (Plate I, Figs. 2 and 3, *Op.*).

Posteriorly through this opening passes the optic and several other nerves out of the cranium, and through it the muscles of the eye reach the skull; anteriorly it is closed by a strong fibrous membrane. In many of the skulls of the Selachians one can see a fenestration of the lateral wall of the cranium, which is an extension of the foramen opticus, and it does not appear very improbable to me that the foramen I have just described in *Amia* is to be regarded as such a foramen opticus, much enlarged. At the boundary line between the labyrinth and orbital regions the cartilaginous base of the cranium is further pierced by a small foramen, which is covered by the parasphenoid, and which is only disclosed by removing that bone (Plate I, Fig. 3, *fh.*). This foramen in its position corresponds to the hypoplysis—to be described further on—and is to be compared in many bony fishes to that lengthened cleft at the base of the fossa for the muscles of the eye, which is closed by the parasphenoid.

The *alisphenoid*, constituting as it does the posterior ossification of the orbital region, is of a circular form, with a section cut from it below

[33] In a large specimen of *Amia* I saw the lateral, as well as the side foward the median plane—facing towards the cavum cranii—of this anterior orbital cartilage covered by a thin superficial layer of a brownish color, which at first sight looked like a very thin lamella of bone. A microscopical examination showed here that we had to deal with a calcification of the superficial layer of cartilage.

and anteriorly. This missing section is the foramen just described, and its outline depends upon it (Plate I, Figs. 2 and 3, *As.*).

Near its posterior margin the alisphenoid is perforated by a large circular foramen, intended for the second and third branch of the trigeminal. In large specimens of *Amia* the alisphenoid articulates above and posteriorly with the postfrontal; in younger individuals it is separated from the latter by a small zone of cartilage. Above the optic foramen, anteriorly, it is to a small extent suturally united with the orbitosphenoid.

Beyond the alisphenoid is found the *orbitosphenoid*, circular in outline and pierced behind and below for the optic foramen, of which nothing further will be remarked (Plate I, Figs. 2 and 3, *Os.*). It seems to me that at this point it would not be uninteresting to call attention to the circular form of so many of the ossifications of the primoidal cranium of *Amia*.

These forms are due to the fact that the centers of ossification start free in the cartilaginous matrix, and in their unhindered growth, which has been a proportionate increase of margin in all directions, they have but at a few places only been checked by contact with neighboring ossifications. In this respect, too, *Amia* has been preserved in a primitive condition, as compared with the Teleostei, in which the corresponding bones, owing to the fact of their contact at most points with their neighbors, exhibit a great irregularity of form.

The first branch of the trigeminus passes through the wall of the primoidal cranium at about the height of the anterior margin of the postfrontal, runs obliquely forwards and outwards, and quits the alisphenoid just above the large foramen for the second and third branch of the same nerve (Plate II, Fig. 6, *tr.*[34]).

During its course within the wall of the skull it gives off several minute branches, which ascend upward in the cartilage and pass to the mucus canals of the bones of the skull-cover. In the orbits these branches are two in number, and lie parallel to each other; just beneath the "cover;" they pass forward to reach the nasal depression to which they are distributed, and in doing so pass between the cartilaginous cover of the primoidal cranium and the frontal.

During its entire course through the orbit it gives off minute ascending branches, which in part perforate the cartilaginous roof, described above as the remains of the vault of the orbit, which is composed of this material, while another branch passes to be distributed to the mucus canals of the frontal bone.

The second and third branches of the trigeminus nerve pass from the skull cavity through the foramen in the alisphenoid already referred to, and are distributed in precisely the same manner as they are in the Teleosteans (Plate II, Figs. 4 and 5, *Tr.*).

[34] *Tr.* in the figure.—TRANS.

The oculomotorius and the trochlearis pass out through the large posterior foramen of the orbital region, at its posterior margin, the first-mentioned nerve above and the second beneath it.

Between these two nerves lies the group of straight eye muscles, of which the rectus externus is contained to some degree inside the cranium, and gives rise to the development of an eye-muscle canal.

Just anterior to the eye muscles, yet partly lying between them, we find the optic nerve, which in *Amia* is but feebly developed, owing to the small size of the eye. The ophthalmic artery, quite large in *Amia*, passes also into the bulbus with the optic. Between the last-named structures lies a strong fibrous cord, which arises at the posterior lower angle of the orbital cavity, to be inserted near the place of entrance of the optic on the bulbus. This cord corresponds in every respect to the *eye supports* in the Selachii. The two oblique muscles are inserted into the anterior angle of the orbit.

The nasal region of the primoidal skull of *Amia* is bounded behind by the antorbital processes, and has the shape of a triangular plate, bearing a superior median crest. With the exception of two small ossifications, the entire region is cartilaginous. On the inferior aspect of this region, situated mesially and in front of the antorbital processes, lie two oblong cartilaginous articulating facets for the anterior extremity of the palatine arch; the distal end of these touches the ossified part of this region, the *septomaxillare* (Plate I, Fig. 3, and Plate II, Fig. 5, *Smx.*). This is an osseous center that extends from the lower margin of the foramen for the nasal nerve to the lateral margin of the prenasal cartilage, and with which the maxillary is movably articulated at the latter place. The greater part of this small bone is covered above by the *intermaxillary*, and only becomes visible after this bone is removed. This bone has been declared identical by Bridge with the ossification at the base of the nasal capsule of the frog (the *septomaxillare*); and although I consider the homology thus assumed as at least improbable, still I did not introduce a new name.

It would appear to me more correct if Bridge had compared the two small ossifications known to us, which occur at the extremity of the cartilaginous rostrum of the Pike, with the septomaxillary of *Amia*, with which, indeed, they correspond in position as well as in their relation to the neighboring parts of the skeleton.

The cranial cavity is egg-shaped, with the apex directed forwards; that about the labyrinth region presents two niche-like depressions, for the concealment of the labyrinth, that are sharply defined as we proceed backwards towards the hinder extremity of the brain case. In *Amia*, as among the Selachii and Ganoids, this depression extends from the foramen magnum to the nasal fossæ. Not all of the ossifications of the primoidal cranium that are to be seen on the outer aspect are to be observed on the inner walls of the brain case or in the connecting spaces of the labyrinth; on the contrary, quite a number of them do not reach through the entire thickness of the skull wall, and therefore remain separated from the cranial cavity by a layer of cartilage.

The exoccipital, the intercalare, and the post- and prefrontal are found to be in this condition.

It is hardly worth while mentioning that the squamosal also belongs to this category, applied as it is, in most fishes, to bound a portion of the outer arch; a like condition obtains in *Amia*, where, as has been fully discussed, it retains the character of a cover-bone throughout life.

Within the cavum cranii the anterior part of the occipital region is very sharply defined by an elevation directed anteriorly and towards the median line, composed partly of cartilage and partly of membrane, which runs along the lateral wall from above downwards, forming the posterior wall of the niche of the labyrinth. The base of this region is formed by the basioccipital, by the lateral walls, and for the greater part also by the cover-bone of the occipitalia lateralia; the adjoining portion of the spinal canal, which is covered by the occipital arch posteriorly, does not lie in the same plane with the base of the brain cavity, but is found higher up on the posterior wall of the skull, so there remains a fossa in this locality, which terminates blindly behind and below, over which the medulla oblongata and the anterior end of the spinal marrow pass. This depression is filled in with the now recognized interdural lymphatic fat tissue,[35] most extensively found in the Teleosteans, and becomes interesting to us for the reason that in the family of Characinides, Cyprinoides, the Shads and Gymnotides, it is this very depression that is partitioned off from the rest of the skull cavity by the crests of the occipitalia lateralia, which meet mesially, and is utilized for the formation of the "atrium sinus imparis," which is connected with the swim-bladder by means of the apparatus of Weber. The broad foramen for the vagus is situated at the anterior margin of the occipitale laterale. The anterior border of the labyrinth region within the brain case is formed by the anterior margin of the petrosal which does not join with the anterior bounding ledge of the labyrinth niche, but runs a little before it. The exceedingly complicated structure of the labyrinth niche, with the canals for the arches, is for the most part cartilaginous; its lateral wall is only formed by the petrosal below and anteriorly. The labyrinth is divided by a medial and projecting cartilaginous elevation, running anteroposteriorly and from above downwards into two fossæ, the smaller one being situated anteriorly and above, the larger one posteriorly and below; the former contains the greater part of the utriculus, the latter is intended for the sacculus with the recessus cochlearis. The recess for the sacculus forms, as I have already had occasion to state, quite a prominence on the lateral wall of the skull, which is to be regarded as the commencement

[35] Usually this fat tissue of fishes is taken for the arachnoid in these forms. I have reserved my full reason for a dissenting view for a later work.

of the *bulla acoustica*, so extensively and in some cases excessively[36] developed in the Teleostei. I wish to state once more particularly that the canals intended for the arches, and bounded everywhere by cartilage, join with the labyrinth niche.

The anterior semicircular canal begins at the anterior upper portion of the utriculus inlet, courses laterally forwards and upwards, makes a turn in the vicinity of the postfrontal, running close beneath the cartilaginous skull cover, to be partly seen through it posteriorly and towards the median line, and finally terminates in the cavum cranii in an opening above the vestibule of the labyrinth (labyrinth niche). The outer semicircular canal takes its origin from the posterior portion of the utriculus, courses laterally and backwards, is barely seen just beneath the hyomandibular facet through the cartilaginous side wall of the skull, then proceeds backwards towards the median plane to find its exit, in common with the origin of the posterior canal, on the hinder boundary of the sacculus. During its course the outer canal approaches tolerably close to the intercalare. The posterior semicircular canal begins, as already stated, at the posterior margin of the sacculus, courses laterally backwards and upwards, comes almost in immediate contact with the exoccipital, then turns towards the median plane, forward, and makes its exit just above the vestibule of the labyrinth.

The description of the membranous labyrinth can be briefly presented. So far as I could convince myself from the specimens that were at my command, and really which were hardly suitable for a critical examination, it perfectly corresponds in its general structure with the labyrinth of the Teleostei, as we have learned from the admirable investigations made by Hasse.[37] It is described still more in detail by Retzius.[38]

The relation of the labyrinth to the cavum cranii in *Amia calva* shows a marked difference when compared with that of the Selachii. While in the Selachians the cavity of the labyrinth seems entirely isolated from the brain case, there exists in *Amia* and all other Ganoids and Teleosteans a more or less broad communication between these cavities. It would hardly be amiss if one would trace the causes of the varying size of the intercommunicating fenestra between the two cavities to the entirely disproportionate development and unfolding of the body of the labyrinth in the higher fishes, which has finally led to a stinted growth of the medial dividing wall of the same. The acusticus foramen has been in all probability the starting point for the fenestration of this wall. At least I think we are justified in assuming this from the position of this foramen of the labyrinth in *Amia* (when it is nothing more than the occurrence of absorption of the periphery of the foramen acus-

[36] In the *Scopelus* and *Gonostoma* I find a very extraordinary development of the bullæ acusticæ.

[37] C. Hasse, *Anatomische Studien*, Th. X. *Das Gehörorgan der Fische*. Leipzig, 1873.

[38] G. Retzius, *Das Gehörorgan der Wirbelthiere* [Vertebrates]. Th. 1. *Fische und Amphibien*, page 35. Stockholm, 1881.

ticus) as well as the fact that fenestrations in the skeleton in general are predisposed to proceed from the peripheries of the nerve foramina; as examples of which I would invite attention to the various foraminal perforations that occur at the points of exit of the cranial nerves in Selachians.

It is my wish now to make especial mention of certain important differences that exist between the labyrinth in *Amia* and that cavity in the Teleosteans. The more complete development of the labyrinth in osseous fishes has finally led to the belief that the still distinctly marked elevations that bound the labyrinth niches in *Amia*, where they occur in a rudimentary condition or are altogether absent, have resulted in a mergence of the cavity of the vestibule into the general cavity of the brain case, and that the labyrinth has really moved further backwards from its original position, appropriating parts that belonged to the occipital region, for its concealment. Besides, in the Teleostei the anterior arch has through a reduction in size of the broad cartilaginous strips, which in *Amia* separates it from the skull cavity, very frequently come to lie in the latter.

Finally, an important difference is seen in the fact that the almost entirely cartilaginous border of the labyrinth has in the Teleosteans been replaced for the greater part by a bony one. Underneath and behind the foramen for the facial, the petrosal throws off a horizontal lamella of bone, which in the middle line joins with the corresponding lamella of the opposite side, and forms the roof of a part of the cavum cranii that is closed posteriorly. It is the hindmost of the osseous part of the recess for the eye muscles, which is largely membranous in *Amia*, and of which an accurate description will be given further on.

While the limits of the separate regions of the skull are but feebly defined upon the skull-cover, quite a sharp definition takes place between the labyrinth and the orbital regions in the interior of the skull on its cover; this is through the means of a feebly-marked ledge, extending from one postorbital process to the other, and directed downwards towards the cavum cranii; here its lower edge meets the ascending epiphysis coming from below. This epiphyseal ledge of the skull-cover is constantly found in all Teleosteans, and represents in some individual cases the only remaining portion of the original cover of the primoidal skull.

The question which considers the channels through which the sound-waves of the surrounding medium reach the labyrinth in fishes has never, up to the present, been the subject of an exhaustive discussion. And yet the question deserves to be investigated, because quite a number of peculiar formations upon the skulls of fishes will become intelligible only after we have become acquainted with the nature of the sound-conducting channels. It does not demand any particular mention—inasmuch as an experiment is naturally out of the question—that the solution of this matter can only be brought about by critical investigations of the topographical relations of the labyrinth region in the skulls of fishes, and the determination of the sound-conducting channels according to pureiy physical principles. The prevailing idea at present is that, in fishes generally, no special channels for the conduction of sounds have been differentiated; that, on the contrary, an entirely evenly-proportioned conduction takes place through the bones of the skull, and above all through its cover-bones. Specialized auxiliary apparatus of the ear, intended for the conduction of the sound-waves to the labyrinth, with the least possible loss, are said to appear first in the class Amphibia; this is positively erroneous. A superficial review of the majority of fishes demonstrates the improbability of this assumption. In the vast majority of fishes the bones of the cranium at no place enter into contact with the surrounding medium, but are separated from it by extraordinarily poor sound-conductors, by a thick swardy skin, and frequently even by powerful layers of muscles, so that the conduction of the sound-waves directly through the bones of the head can be counted on in a comparatively very small number of fishes only, as in those whose heads are covered by naked bone-shields. The possibility that it takes place through a general conduction on the part of the bones must be absolutely set aside for the vast majority of fishes, and we will have to look about us for other channels of conduction.

Such a channel has been found for us by Hasse[39] in the Clupeidæ. He found that that portion of the auditory capsule, which bounds the sacculus laterally, forms the inner wall of the gill cavity, and so enables the sound-waves to infringe upon the sacculus through this space. These observations are correct, only that Hasse has erred in that he regards the intimate relations of the labyrinth to the gill cavity as confined to the Clupeidæ, whereas it occurs in the majority of osseous fishes. In a large number of these latter, representatives of the most widely separated families, I found almost without exception that the anterior superior apical recess of the gill cavity lies in close juxtaposition with the labyrinth region of the skull, consequently at this point the water present in the gill cavity is only separated from the thin, lateral osseous or cartilaginous wall of the labyrinth by a thin mucous membrane. In numerous cases, in which the sacculus with its otoliths is fully developed and forms a lateral jutting bulla on the skull, this bulla almost without exception projects into the gill cavity, and in many instances can be felt from the gill cavity by the finger with great ease. Yet I would have it distinctly understood that in most cases it is not the sacculus alone that has this relation to the gill cavity, but that the utriculus also enjoys a similar relation, and so it is not admissible here to

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[39] C. Hasse, *Anatomische Studien; Suppl. Die vergleichende Morphologie des häutigen Gehörgangs der Wirbelthiere*, 1873, page 53. [C. Hasse, Anatomical Studies; Suppl. The comparative morphology of the membranous auditory passage of the vertebrated animals, 1873, page 53.]

assume, as Hasse did, that we are dealing with a sound-conducting channel or medium specially intended for the sacculus. At present I cannot yet enter upon the details of the relations of the labyrinth to the gill cavity in the Teleostei, to which I must refer to special descriptions to be published later, upon the crania of separate families of osseous fishes.

Now that the grounds for the assumption have been demonstrated, that in bony fishes the sound-waves for the most part reach the labyrinth from the gill cavity, the remaining question presents itself as to how the sound-waves get into the gill cavity. There can be no doubt that the gill cleft plays an important part here; still I believe I am able to point out yet another channel which, according to physical principles, must be even better suited for the purpose. I mean the conduit which is presented in the bones of the opercular apparatus, especially by the operculum and sub-operculum. If one reflects that these bones are thin elastic plates in most Teleosteans, which through their broad surface are in contact with the water contained in the gill cavity, and covered as they are by a thin skin only, and at no time being covered by large masses of soft parts; then one must admit that an apparatus, thoroughly suited to the purpose, here presents itself for the conduction of the sound-waves from the outer medium to the body of water in the gill cavity. Should further investigations confirm this supposition, it would establish the statement formerly made by Geoffroy St. Hilaire who, as we are aware, declared that the opercular bones were ossicula auditus; to be sure in an entirely different sense from what this author meant. Although somewhat foreign to the subject of my paper, a comparison of the sound-conducting media of the bony fishes with those parts in other vertebrated animals, especially the Selachii, is of great interest, because such comparisons very well illustrate the position that the Teleosteans hold with respect to other vertebrates.

The common opinion is, that differentiated sound-conducting apparatuses first made their appearances in the Amphibia, more particularly among the Anura. It has already been sufficiently dwelt upon that this view is an erroneous one, and that in the majority of bony fishes no *general* conduction of the sound-waves to the labyrinth takes place; that, on the contrary, channels have been differentiated of a constant character. But osseous fishes are not the forms—in the vertebrate series—in which such auxiliary apparatuses to the organ of hearing first appear; contrivances for such purposes can already be demonstrated to exist in the Selachians, from which the apparatuses in the bony fishes were derived. The credit belongs to Johannes Müller[40] for being the first to truly recognize and appreciate these conditions in the Selachians;

[40] *Vergleichende Anatomie der Myxinoiden. Theil III. Das Gefässystem der Myxinoiden. Abhandt. d. Berlin. Akademie d. Wissenschaften von Jahre* 1843. [Comparative Anatomy of Myxinoids. Part III. The vascularsystem of the Myxinoids. Treat. of the Berlin Academy of Sciences, 1843.]

unfortunately his observations appear to have entirely passed into oblivion, at least I have not come across a single allusion to them in the writings of the more recent authors. The sound-conducting apparatus in the Selachians is the hyomandibular cleft. This starts, as we know, with a wide opening in the buccal cavity in a position nearer the median plane than the opening of the first gill cleft, and close to it, and then courses upwards between the hyomandibular and the palato-quadratum, making its exit either in an opening, the aforesaid hyomandibular cleft, behind and above the eye, or ending blindly beneath the skin. During its course this canal lies close to the labyrinth region, and in individual cases it even presents special blind diverticles, which adhere closely to it. This is the point in Selachians where the labyrinth is nearest the surrounding medium, and through this channel the sound-waves must reach it the least diminished in intensity. That they may be conducted, too, from the surface of the head, is by no means to be set aside—such general transmission, to a limited extent even taking place in man through parts of the skeleton of the head—yet the idea of such a conduction in the Selachians, if the parts concerned are investigated according to physical principles, must be utterly abandoned, when we come to compare this with the part played as a conductor by the hyomandibular cleft [*speitzloch canal*]. The sound-waves to only a limited degree can enter the hyomandibular cleft from the cavity of the mouth, and will at least in cases where there is a wide, open, external cleft existing, find their entrance through it.

The fact that the hyomandibular cleft of the Selachians being homologous with the tympanic cavity and the canals in the higher vertebrates, and exercising a similar function, is certainly very remarkable. This demonstration effects the removal of one difficulty, and that is the belief that the tympanic cavity and the canals first originated among the air-breathing vertebrates. In fact it was scarcely at all understood how for this purpose, a gill cleft, whose very existence depends upon its being constantly in water, could continue to exercise its true function, and still to some extent be subservient to the organ of hearing. This difficulty is completely set aside by the discovery that the sound-conducting function of the anterior gill cleft is not a new acquisition in land vertebrates, but that it also existed in their ancestors living in the water; and with these the reason [*ursächliche moment*] for this is also furnished, why this gill cleft could still survive, retaining its integrity to the very last and in the most advanced vertebrates in the scale of development, while the other gill clefts, originally provided with respiratorial functions, have disappeared without leaving a trace, having commenced in the Dipnoi and Amphibia with the development of a new respiratory organ.

After what we have just demonstrated, the fact that the Urodela and several of the Anura possess no tympanic cavities or Eustachian tubes, is to be differently construed from what it has been heretofore. Here, without doubt, a retrogressive process is presented us, as in the snakes; and the alternative proposition, that in these forms a middle ear has not yet developed, is untenable. In fact it would be incomprehensible, if the closed foremost gill cleft of the higher Amphibia were to reopen itself and re-enlist its functions in connection with the auditory apparatus. Equally unintelligible would be the occurrence of the columella in Urodela—a part of the skeleton whose origin is closely associated with the development of the middle ear, and if it existed by itself its need could not be understood, inasmuch as no function for it could be discovered.

The question now remains whether the apparatuses we have just described for the bony fishes and the Selachians originated entirely independently of each other, as appeared at the first glance, or whether there are not organs somewhere in existence which constitute the connecting links between them, and allow a genetic connection of these apparently entirely different formations to be entertained.

A direct comparison of the apparatuses in the Selachians with the Teleosteans leads to an unsafe result, inasmuch as the topographical appearances on the skulls of these forms are entirely different, and as a natural consequence the various relations of the parts cannot be compared with each other in detail; therefore it only remains for us to look about us for the intermediate forms and through them attempt the solution of the question. Such an absolutely intermediate form—of course only for the purpose mentioned—is *Polypterus*. While the cranium of this Sauroid, and particularly its maxillary apparatus and gill apparatus, very closely approach the Teleostean type, the *Polypterus* during life possesses a well-developed hyomandibular cleft, and in this respect reminds us of the Selachians. The inner, capacious opening of this cleft lies in the gill cavity; it is bounded mesially by the epibranchiæ of the first gill arch, posteriorly by the anterior margin of the hyomandibular, and laterally by the bones of the palatal arch. This wide hyomandibular cleft takes an upward direction, lying close to the labyrinth region of the skull, to make its exit at the upper and lateral margin of the cranium in a slit-like opening, that is covered by two small dermal bones, which act like valves. In *Polypterus* the conduction of the sound-waves to the labyrinth can scarcely take place through the outer opening, closed as it is by the small dermal bones just referred to, so we must believe that the sound-waves enter at the inner and least difficult opening, as this does not open into the buccal cavity—as in the Selachians—but into the gill cavity, which is in complete communication with the outer medium.

A comparison of the hyomandibular cleft in *Polypterus* with the blind apical recess lying close to the labyrinth region in bony fishes places it beyond all doubt that they are homologous structures, and that this recess of the gill cavity, which was alluded to when speaking of the Teleosteans, is nothing more than the hyomandibular cleft which has become widened and closed up at its dorsal aspect. An anatomical reason for this closure, I believe, must be looked for in the development of the hyomandibular in bony fishes. While in the Selachians this part of the skeleton is a slender cartilaginous rod; in osseous fishes it becomes more extensive, in conformity with the greater development and differentiation of the muscular system of the maxillary apparatus, so as to form a broad plate. Correlated with this, we also find the articular facet for this bone in Teleosteans, extending so far as the postorbital process, which extension anteriorily closes the hyomandibular cleft. The relations of the main trunk of the facial nerve—the *truncus hyoides mandibularis*—affords the strongest proof that this extension was in anterior direction, or towards the anterior extremity of the body. In Selachians this nerve passes close to the hyomandibular, coursing downwards in front of its anterior margin, while in the Teleosteans, in the majority of forms, it perforates the hyomandibular bone in order to reach the outer side. It requires no special demonstration to show that such an apparent perforation of the bone could only have been accomplished by its growth forwards, inclosing the nerve as it did so. At the same time the hyomandibular cleft had to be necessarily closed up and transformed into a blind recess in the gill cavity and with the same topographical relations with the labyrinth as we have described for it.

At the base of the orbital region, in the interior of the skull, there is a depression which is well defined both anteriorly and posteriorly, that reminds us to some degree of the sella turcica of the higher vertebrates (Plate II, Fig. 4). Posteriorly, this depression is continued beneath the processes of the petrosal bone, already referred to, where it terminates; anteriorly it is bounded by a bar of cartilage, which contains an osseous center at each lateral angle. At the base of this pit there is a breach in the primoidal cranium, already mentioned, which is closed in below by the parasphenoid. In the direction of the cavum cranii, speaking in a more limited sense, this pit is entirely closed by a strong membrane, which glistens like a tendon. This latter spans the space between the anterior sharp margin of the united and horizontal wings of the *ossa petrosa* to the foremost cartilaginous bar. This membrane extends far up the lateral walls of the skull, and becomes attached about half way up to a sharp bony crest that is developed downwards and mesially from the ali- and orbito sphenoid (Fig. 7, *Kl.*[41]). The posterior part of this upper extension of fascia ensheaths the trigeminal and facial nerves near their points of exit from the skull; the anterior part of this fascia is the membrane that closes the optic foramen.

This fascia divides off another space, situated below and somewhat laterally from the true cavity of the skull, which of course is intended for the brain. The greater part of this space is filled in with the well-known lymphoid fat tissue, found so extensively throughout the fishes, that is also contained in the remaining part of the cavum cranii in

[41] Dr. Sagemehl has failed to place these letters on his figure.—TRANS.

Amia; there are also nerves and muscles to be found in it. The facial, with its ramus palatinus, and the trigeminus course through the postero-lateral divisions of this space, as already stated, between the membrane and the bony lateral wall of the skull for some distance before they arrive at their foramina of exit. In the anterior part of this space the membrane is perforated by the opticus.

In the lower part of this cavity, which is separated as we have described from the brain case, are to be found the points of origin of the external rectus muscle. These arise near each other not far from the median line, close behind the cartilaginous transverse bar, already referred to above, that forms the anterior boundary of the sella turcica; anteriorly these muscles diverge from each other, each to enter an orbit through the optic foramen on either side. So we find in *Amia*, as in so many of the bony fishes, a subcranial canal, which to be sure is but feebly defined, lacking as it does a superior osseous partition to divide it from the cranial cavity. The nervus abducens perforates the fascia from above, and immediately passes into the substance of the external rectus muscle, so that it is not visible in the orbit proper. In addition to this, the principal branches of the carotid artery are to be found in this subcranial canal. Upon the membrane above this canal lie the *hypophysis cerebri* and the *lobus vasculosus* in a feebly developed funnel-shaped depression.

We will now turn our attention again to the two ossifications, found in the lateral angles of the anterior cartilaginous bar. These cannot be observed from the outside, and it is only in the dissected skull and after the fascia has been removed, that they are exposed to view. Bridge has called these parial ossifications the basisphenoidea and declares that they are homologous with the well-known Y-shaped basisphenoid of many of the osseous fishes.

This statement I fully indorse. If we bear in mind that besides the *recti externi*, the other muscles of the eye also make their appearance in the cavum cranii, then the cartilaginous partition lying between these two groups of muscles must necessarily be implicated, and the two centers of ossification already spoken of must through extension eventually meet and merge into each other, forming a non-parial bone, situated between the muscles of the right and left bulbus. It is then that we have the conditions presented to us seen in so many of the bony fishes.

If this explanation be not accepted, then we must see in *Amia* certain ossifications that occur in no other fish, and must deny *Amia* a bone of very frequent occurrence.

The next thing before us is to compare the subcranial canal, which lodges the muscles of the eye in *Amia* with that canal as found in osseous fishes, and endeavor to ascertain whether it cannot be traced to a known and similar structure in forms occupying a lower position in the scale. I will first briefly compare it with the canal as found in the Teleostei.

The principal difference between the subcranial canal for the eye muscles in *Amia* and that in bony fishes, is seen in the fact that in the latter it is separated from the brain case proper by an osseous partition, while in *Amia* this is composed only of membrane. In articles I have yet to publish, it is my intention to show how this osseous partition is developed in bony fishes from the neighboring bones, more particularly the petrosal, by their throwing out horizontal processes that meet to ossify in the median line of the skull. Commonly, too, this subcranial canal extends farther back in osseous fishes than it does in *Amia*, even to extend into the basioccipital. This results from the muscles of the eye being longer in these forms, and consequently a canal of proper length developes to accommodate them.

Concerning the phylogenetic origin of the subcranial canal, Gegenbaur conjectures that the *canalis transversus* of the Selachians is the subcranial canal of the Teleostei, in which the muscles of the eye find lodgment.[42] In the Selachians this canal passes from one orbit to the other, obliquely through the cartilaginous basis cranii, causing the two periorbital lymph sinuses to merge into one; in some cases it is separated from the brain case by membrane only. Immediately in front of this *canalis transversus* are found the openings for the carotids, which in some forms are separated from the former also only by membrane. In the orbits the recti muscles are inserted nearest to the anterior entrance of the subcranial canal. Quite close to this we also find—at least in several Selachians (*Hexanchus*)—the foramen of exit for the nervus abducens.

A great deal in the structure of the parts in question, so far as examined in *Amia*, goes to support this view. Above all, the fact must be noted that in *Amia* the canal separated from the cavum cranii is not entirely devoted to the eye muscles, as in the Teleostei, but is largely filled in by the lymphoid tissue.

Now, since we have not the least ground for assuming that *Amia* is descended from forms in which the muscles of the eye were far better developed, and filled the space alluded to entirely, there is but one hypothesis possible, that *Amia* has in this region a preformed lymphatic fossa situated at the basis cranii, into which the points of origin of the *recti externi* only moved secondarily. But this preformed lymphatic space—if we are to judge from homologous structure in inferiorly organized fishes—can only correspond to the *canalis transversus* of the Selachii, which, in *Amia*, is remarkably widened and spread out, and which has finally included the carotid canals and the surrounding nerves found near the exits of these vessels. At the same time its cartilaginous

[42] C. Gegenbaur, *Untersuchungen zur vergl. Anatomie d. Wirbelthiere. Heft III. Das Kopfskelet d. Selachier*, 1872, pag. 78. [C. Gegenbaur, Observations upon the Comparative Anatomy of Vertebrates. Part III. The skeleton of the head in Selachii, 1872, p. 78.]

roof was replaced by a membranous one. So long as such organizations exist and no intermediate forms are known to us between the primitive structures seen in the Selachians and the relatively and already widely differentiated organization of *Amia*, this view of Gegenbaur's must remain an hypothesis; an hypothesis, to be sure, that has much to support it. By accepting it, the survival of the transverse canal of the Selachii is accounted for in higher vertebrates, if nothing else, and one is not compelled to advance the dubious proposition that there exists in *Amia*, and in Teleosteans descended from *Amia*, a canal beneath the cavum cranii, unique in the sense of being without antecedents, and whose importance and homology would be quite enigmatical. The olfactory region presents for examination two spacious canals in the interior of the skull, running side by side, parallel and in an antero-posterior direction, which are separated from each other by a broad cartilaginous septum, and which end in the foramina olfactoria at the base of the nasal fossæ. In the canals, which are to be considered as the direct continuation of the cavum cranii, are to be found the very thick and firm olfactory nerves. They are composed of a strong neurilemma which surrounds a fasciculus of nerve fibers, some seven or eight in number, but loosely connected together, and among which, to all appearances, no anastomoses take place.

In fishes, as we are aware, two types can be distinguished, depending upon the relations existing between the nerve center of the olfactory organs and their terminal filaments. In one case the bulbi olfactorii of the olfactory mucous membrane lie close by, and are connected with the fore brain by a long tractus; a single olfactory nerve does not exist in this case, but rather, on the other hand, quite a number of short nerve fibers pass from the bulbus to the olfactory mucous membrane. In the other case the bulbi olfactorii are connected with the hemispheres of the cerebrum and arise as long and true olfactory nerves. At first sight it would appear as though the difference was not an essential one, and as though the bulbus olfactorius was no integral part of the brain, but simply a collection of ganglionic cells occurring in the course of the fibers of the olfactory, and could occupy divers positions. That it is, however, is clear when we see the typical, very characteristic, difference between the stout olfactory nerve, provided with a firm neurilemma, and distributed to the periphery from the bulbus, and the thin tractus, enveloped only in the delicate pia mater holding a central position with respect to the bulbus. This same fact was particularly dwelt upon by Stannius,[43] that these two specified conditions as regards the position of the bulbi olfactorii are always independently present, that there is either a bulbus adjacent to the brain or one annexed to the olfactory membrane; cases in which a centrally located bulbus occurs in connec-

[43] Stannius, *Das peripherische nervensystem d. Fische*, 1849, page 2. [Stannius, The Peripheral Nervous system of Fishes, 1849, p. 2.]

tion with ganglionic enlargements at the distal extremity of the olfactroy nervelets do not exist.

Besides, there are—though very rare—intermediate forms known between the two types we have indicated among fishes; cases, for instance, where the bulbus is placed half-way between the brain and the olfactory membrane, and where it is connected with the former by a thin, soft tractus; with the latter by a strong, firm nerve at least four times as thick. The only other case of this kind known up to the present time has been noticed by Stannius in the *Gadus raniceps fuscus;* and I find quite a similar condition in the Characinidæ, as in *Hydrocyon* and *Alestes*.

A mere superficial examination of these two types does not furnish us with sufficient data to judge from, and decide which is the primary form and which is the derived one. As in so many other cases, the question can only be decided by the systematic—based upon other conditions of organization—position of the forms that belong to one or the other type. We now find that the first type occurs in all Selachians, in Holocephals, and certain of the Teleostean groups, long known to us as the primitive forms, as in the Siluroids, the Cyprinoids, the Gadidæ, and, as I have found, also in the Mormyridæ.

The second type is extensively found in the Ganoids and in the great majority of the Teleosteans. With all this before us, no doubt can remain that the first type is the primitive one, and that from it the other type has developed by a gradual shortening of the tractus and a lengthening out of the nerve.

It appears that in the Teleosteans the development of the olfactory nerve is always brought about in the same way and with a uniform result. The enlargement of the orbits leads to a fenestration of the lateral orbital wall at its anterior angle near where the bulbus olfactorius was originally located, as one can see very well in the Characinides; this development extending further gives rise to an olfactory nerve, which must of necessity pass through the orbits. These conditions appear to be quite constant among the Teleosteans. Among a great number of very diverse forms I have always found either an olfactory nerve in the orbit or a long tractus extending directly from the brain case to the nasal pit.

In *Hydrocyon*, already referred to, the bulbus lies in a special elevation in the orbito-sphenoid; from it a nerve is given off that passes to the olfactory membrane, being free in the orbital cavity; and a long tractus lying within the cavum cranii to the fore-brain, so that in this case there is no exception to the general rule.

A remarkable exception to this rule is found in all the Ganoids. In these fishes a true olfactory nerve passes within the direct continuation of the brain case, and consequently proves to be a condition that must have arisen under circumstances to us nearly unknown and entirely different from those of the bony fishes, and, therefore, bears no genetic relation to the latter.

Lepidosteus alone seems to form an exception to this unvarying rule among the other Ganoids. The olfactory nerve in *Lepidosteus* at first passes into a tunnel-shaped osseous tube, formed by the alisphenoid. At the posterior part of the orbit it quits this tube and passes close beside the semicartilaginous, semimembranous interorbital septum; consequently at this point its course is free in the orbit. At the anterior part of the orbit both nerves enter a very long cartilaginous double tube, which corresponds to that portion of the long rostrum of this fish belonging to the primoidal cranium. At first glance we seem to have presented us here a method of development corresponding in every sense with that seen in the majority of bony fishes, yet this is by no means the case. As already stated, the fenestration of the lateral wall of the skull in the nasal region of bony fishes begins at the anterior part of the orbit, at the place where the bulbus olfactorius occupies a near position to the olfactory mucous membrane, and which leads to a marked separation of the same from the membrana olfactoria, and to the lengthening of the olfactory nerve. In *Lepidosteus* this long double tube, in which the nerves are contained, is to be considered as the original direct continuation of the skull cavity; therefore the development of an interorbital septum in this fish cannot have come about in the same way that it did in the bony fishes, nor can the necessity for the origin of the olfactory nerve be looked for in this fenestration. This nerve must have originally in *Lepidosteus*, as well as in the other Ganoids, been contained for its entire length in a continuation of the brain case, which was separated by a median dividing partition into two canals; subsequently the lateral partition in the posterior interorbital part of this septum disappeared, and in this way the olfactory nerve came to lie in the orbit.

In the course of this essay it would have been quite an easy matter for me, in more instances than one, to have pointed out the facts going to show that quite a number of the various structures in the bony fishes can be traced with tolerable certainty to *Amia*, and from this the opinion naturally arises that the same will apply to all the organs, and that *Amia* is in reality a direct ancestor of the family of Teleosteans.

For this reason I have the more eagerly seized upon the opportunity to point out the conditions referred to above with respect to the development of the olfactory nerve, in which particular *Amia* has decidedly reached a higher degree of organization than certain osseous fishes lower down in the scale.

In this place I will not omit the consideration of the morphological conditions of the peripheral olfactory organs of the Ganoids and Teleostei somewhat more critically, and compare them with corresponding conditions in the Selachians.

In the lowly organized Sharks, as, for example, the Notidanides and Acanthias, there exists upon the inferior aspect of the snout, on either side, a single nasal aperture, which is incompletely divided by two processes, the nasal flaps, which spring from its margin, and give rise in this way to a medial and a lateral entrance.

In the more highly organized Selachians, in the Scyllians, among the sharks, and in many rays, a more or less deep groove is found to extend from the medial entrance to the upper margin of the buccal aperture. This is the well-known naso-labial groove, which also appears in the ontogeny of the higher vertebrates, and for the closure of which the median nasal aperture is furnished with a valve, found on the margin of the upper lip and opening in the direction of the nasal cavity. This latter corresponds to the inner nasal opening of the Dipnoi, Amphibia, and Amniota. These structures have long since been described by Gegenbaur, and the question only concerns us with respect to the Teleosteans and Ganoids.[44] According to previous notions—still accepted by Gegenbaur—the two openings of the nasal pit in bony fishes and Ganoids correspond to the imperfectly separated nasal valves of the lowly organized Selachii. Balfour[45] has placed a different interpretation upon this. According to his views in the matter, the posterior nasal aperture of the higher fishes are homologous with the inner nasal apertures of air-breathing vertebrates, which by a gradual turning of the axis of the nasal capsule have shifted their position from the upper lip to the superior aspect of the head.

My observations upon fishes compels me to oppose this view, and adhere to the old opinion. There are two arguments that I must cite which conflict with Balfour's notion: one of comparative anatomy and one of the history of development. In a number of Teleostei, among others, all native Cyprinoids examined by me, I found in the immediate neighborhood of the nasal apertures and in the dermal bridge separating the anterior and posterior aperture, a small cartilage, that remained undescribed up to the present time, and that is strictly homologous with the nasal alar cartilage of the Selachians. This cartilage usually has the form of a figure 8, the two loops surrounding the nasal openings and the middle piece lying in the dermal bridge between the apertures. It is very intimately connected with the skin, so that it becomes a difficult matter to make a dissection simply trusting to the scalpel and forceps, but by the aid of a microscope, and carrying the incisions through the nasal region, one can very easily satisfy himself of its presence. It possesses the characteristics of hyaline cartilage and differs

[44] C. Gegenbaur, *Grundzüge der vgl. Anatomie, II Aufl.*, 1870, pag. 754, *und das Kopfskelet der Selachier*, 1872, pag. 97 *u* 216. [C. Gegenbaur, Elements of Comp. Anatomy, II Edit., 1870, page 754, and the skeleton of the Selachian head, 1872, pages 97 and 216.]

[45] F. M. Balfour, Manual of Comparative Embryology, 1881, Vol. II, page 477.

from the cartilage of the primoidal cranium, with which it is in no way connected, by its much denser cartilage cells.

In many cases among the Selachii, too, does the nasal alar cartilage encircle these apertures as a ring, sending out processes into the nasal valves. If one pictures to himself that the nasal valves of the Selachians have become merged with each other during their growth or development, and the cartilaginous processes contained within them become blended, there will result as a consequence a condition that can in no way be distinguished from the state of things as seen in the Teleostei. That this view is the correct one is shown by the history of the development of the nasal organ in the bony fishes.

In newly-born fishes there exists on either side a simple undivided nasal aperture, as I have observed in the *Lota vulgaris*, in the Pike, in the Trout, and in the *Chondostroma nasus*. It is not until these forms have passed the embryonic stage does there occur, sooner or later, a division of this aperture into anterior and posterior nares. Both the median and lateral periphery develops a small patch of skin, directed towards the center of the aperture. Very soon these processes that correspond to the nasal valves in the Selachii become contiguous, the lateral process being behind the median in all of the specimens examined by me. At this stage the nares in osseous fishes have reached the precise condition that remains permanently in Notidanides and *Acanthias*.

In a short time these two nasal valves of bony fishes blend together and the narial opening receives its definite shape, at least for those forms in which the two apertures are situated close to each other. Inasmuch as the primary conditions are not exactly so arranged in *Lota vulgaris*, whose anterior and posterior nares, after it has arrived at maturity, are far removed from each other, there must occur in this species a widening of the nasal bridge and a separation of the nasal apertures at a later period (unfortunately I lack the material to illustrate these stages). At any rate fishes with the anterior and posterior nares close together are to be considered as primitive forms, and from such, forms can be traced in which these apertures are far apart. Such forms, then, are to be considered as the highest in the scale of development in a certain direction, in which the narial apertures are far apart and are situated on the upper lip.

Such formations among bony fishes occur in *Ophisurus* and kindred forms,[46] in the family of Murænoids, and, in fact, they have at the first glance a certain resemblance to corresponding structures in Dipnoi and perennibranchiates, and it does not appear improbable to me that this peculiarity of the *Ophisurus* led Balfour to assert a homology of the

[46] Lütken, *Nogle Bemaerkninger om Naesceboreunes Stilling hos de i Gruppe med Ophisurus staaende Slaegter af Aale familien. Videnskabl. Meddelelser fra d. naturhistoriske Forening i Kjöbenhavn*, 1851.

posterior nasal aperture in osseous fishes with the posterior nares of the air-breathing vertebrates.

A comparison extended to a greater number of forms and the history of development clears up the actual state of affairs in this case also, and demonstrates that it is but an interesting case of "converging development" ["*konvergenten entwicklung*"]. The position held by those Teleosteans which permanently possess but one nasal aperture on either side, as for example *Belone*, the Pomacentrides, many Chromides, &c., is only to be determined with absolute certainty when we have a knowledge of the history of their development. If one, however, considers that the nearest kin to these fishes (Cyprinodonta, Labröidæ) exhibit the ordinary conditions, it will hardly be out of place to simply assume that the dividing dermal bridge between the nasal apertures in the form referred to has been secondarily reduced.

As in so many other structures, so in those of the nasal apertures, the lowly organized Selachii prove to be the starting point from which two diverging series can be traced; upon one side the higher fishes, on the other the air-breathing vertebrates.

As I have already mentioned, the anterior and posterior nares in *Amia* are far apart, and, consequently, *Amia* represents a form that must, as compared with the ordinary bony fishes, be accepted as possessing a higher state of development. The *nasal bone* is imbedded in the broad dermal bridge between the two nostrils. Under these circumstances it is not at all strange that, in spite of the careful search I made for it in this fish, I could not find the trace of a nasal alar cartilage in the vicinity of the nostrils. The nasal has taken upon itself the original function of the same, that is, to support the entrance to the nares, and thus rendered a nasal alar cartilage superfluous.

To conclude the present article it only remains for me to draw a comparison between the cranium of *Amia* and that of the Selachii, with which it may best be compared, and to particularize their resemblances and their differences. Taken as a whole the latter are fewer in number than one would at first suppose. The fundamental difference between the skull of *Amia* and that of the Selachians rests upon the appearance of the large connecting ossifications in the former. These ossifications either simply overlie the primoidal cranium, or they are connected very intimately with it, and without changing their form, replace structures in it that were originally cartilaginous.

The first appearance of the larger uniting masses of osseous tissue among fishes denotes one of the greatest and most far-reaching steps in the progress of the process of development of vertebrate animals. It indicates the first appearance of a tissue that, as a protective and supporting material, proves far more suitable than cartilage. A glance at a series of skulls of Selachians and Teleosteans will be sufficient at once to demonstrate the great significance of this "occurrence."

The entire organization has become changed. A pleasing, graceful structure has taken the place of the clumsy Selachian skull. The delicate and rounded contours of the latter are replaced by angular, and quite often by oddly-shaped skulls, on which the grooves for muscular attachment and tendon insertion are distinctly marked. The new material substituted for the building up of these structures far surpasses the old, not only in its capacity for resistance, but also is greatly superior to it in its fitness for plastic modelling. In this particular, one finds very marked gradations even among the higher fishes. In their rounded contours, and in the imperfectly developed muscular grooves and crests, the bony Ganoids and a number of the Physostoma remind one very much of the Selachians; and it is only in those groups of fishes exhibiting the highest development, more particularly Acanthopterygii, that the types of extreme differentiation come into bold relief.

Leaving out of consideration the fact that it partly consists of different material, the primoidal cranium shows but few points of difference from that of the Selachii. In the first place, by the co-ossification of several vertebræ, the occipital region in *Amia* has attained a distinct morphological value, differentiating it from the corresponding regions in the Selachians, without having its form essentially changed by the process. Compared with the Selachians it has increased considerably, but in length only, which is sufficiently accounted for by the circumstance just mentioned.

The posterior part of the skull cover, in the vicinity of the occipital region, presents a structure that already esssentially exists in the Selachii. The median, cartilaginous process, pointing posterially, is present in the Notidanides, being developed there as a cartilaginous crest. Nor is it difficult to recognize in the medial projections occupied by the exoccipitals in *Amia*, the cartilaginous elevations developed upon the projecting posterior arches of the Selachians. The posterior lateral angles of the skull, formed in *Amia* by the intercalare, are also very well developed already in some of the sharks, as, for example, in *Scyllium*. Between the crest of the posterior arch and the last-mentioned lateral projection of the skull in the Scyllia there can already be recognized a depression in the cranical vault, extending into the region of the postorbital process, which in *Amia* is bridged over by the overlying dermal bones, closing in the temporal fossæ. In the region of the labyrinth of the Selachians we find this cavity closed up on the side towards the cavum cranii; in *Amia* it is widely opened, probably a fenestration proceeding from the periphery of the acusticus foramen.

Upon the outer aspect of the labyrinth region, the changes occasioned by the presence of the articular facet for the hyomandibular, are the most striking. I have already availed myself of the opportunity to point out, in the higher fishes, the extension of the hyomandibular forwards as far as the postorbital process.

At this point I would remark, that in the matter of position of the hyomandibular articulation, it is the Notidanides among all the Selachians, that still most resembles *Amia* and the Teleostei.

The parietal grooves which occur in the skull cover of many Selachians, and which include the broad, blind terminal parts of the aquæducti vestibuli, are missing in all the Ganoids and Teleosteans. This has evidently something to do with the very imperfect development of the aquæducti in the higher fishes as compared with that structure in the Selachii.

At the base of the primoidal skull we invariably find in higher fishes a fenestration in the region of the hypophysis cerebri that is lacking in the Selachii.

Postorbital and antorbital processes occur in most of the Selachii as well as in *Amia* and most all the Teleostei.

The optic foramen of the Selachii—already exhibiting evidences of increasing size—is represented in the orbital region of *Amia* by an extensive vacuity.

The cartilaginous peduncle which supports the eye in many Selachians, is in *Amia* reduced to a fibrous cord. Only the merest traces exist in the orbits of *Amia* of that basal projecting ledge of the primoidal cranium and the vault as they occur in the Selachii.

The very characteristic vacuity which occurs in the prefrontal cover-bone of the primoidal skull in the Selachii is wanting in *Amia*, but appears to be present in certain families of osseous fishes, in Cyprinoids and Characinids.

Not a few differences in the structure of the nasal region between the Selachii and the higher fishes, including *Amia*, can be made out. While the nasal apertures in the Selachians are situated upon the lower aspect of the snout, in higher fishes they are without exception on the lateral or upper plain of the head; besides, the well-developed nasal capsules of the Selachii are reduced to quite flat pits in *Amia* and in the bony fishes.

A structure homologous with the nasal alar cartilage of the Selachians is entirely wanting in *Amia*, but can be pointed out, as demonstrated above, in certain bony fishes.

Still another, not unimportant, difference in the structure of the nasal region in the higher fishes and that of the Selachians is to be recognized in the fact, that in the former articular facettes for articulation with the anterior end of the palatine arch are developed on the inferior aspect of the region referred to.

The characteristic interrupted rostra, occurring in many Selachians, are wanting in the higher fishes, either entirely or are replaced by simple uninterrupted structures, that approach in this respect the rostra of the Notidanides.

The recapitulation of our investigations go to prove that there are several structures in the organization of *Amia* that cannot be regarded as having been derived through progressive development from existing structures in the Selachii.

To these belong the diverse courses of the ramus palatinus in the Selachians and in the higher fishes, the relations of which cannot be directly derived from one another. Yet it is not improbable that in this case we are dealing with a substitution of very different and appreciable nerve branches, as often happens in fishes.

In most of the plans of structure in the skull of Amia a direct progress in development can be discerned in parts from those that already exist in Selachii; and it is particularly the Notidanides—the least differentiated of the Selachians—which present the most evident relations to Amia for recognition.

It would be very difficult to specify the distinguishing characters between the cranium of *Amia* and that of the Teleostei. There are but very few characteristics to be found in the skull of *Amia* that could not be found in one or the other of the families of the Teleostei, and these few distinguishing characters are not restricted to *Amia*, but are also found in other Ganoids. In this category belongs the continuate, non-fenestrated, cartilaginous cover of the primoidal skull, in which, among the Teleostei, vacuities are always discoverable, but it has preserved its integrity in the Accipenserides among the Ganoids. A second important distinction is the absence of the supraoccipital in *Amia* and all the other Ganoids, while in the Teleostei it occurs quite constantly. The third distinction—already described above—refers to the course of the olfactory nerve in a direct prolongation of the brain case—is shared by *Amia* with all the other Ganoids.

POSTSCRIPT.—Just as this article had passed into the hands of the printer, I received a copy of the treatise by J. Van Wijhe, "Upon the visceral skeleton and the nerves of the Ganoids" (Netherlands Arch. f. Zoolog., Vol. V., Part III, 1882), in which the cranial nerves of *Amia* are described. I am glad that Van Wijhe agrees with me in all the essential points. I must also state that Van Wijhe has invited attention to the importance of the mucus canals in determining the bones that overlay the skull (*l. c.*, page 228).[47]

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[47] Dr. Sagemhel's paper is completed by a *résumé* of the lettering of the figures, or an "Explanation of figures in the plate," but I have omitted this, as the figures are separately described in their appropriate places here.—TRANS.