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NOTES

ON THE

NORTH AMERICAN GANOIDS,

AMIA, LEPIDOSTEUS, ACIPENSER, AND POLYODON,

WITH THREE PLATES,

BY BURT G. WILDER, M. D.,

PROFESSOR OF COMPARATIVE ANATOMY AND ZOÖLOGY IN THE CORNELL UNIVERSITY, ITHACA, N. Y.

(From the Proceedings of the American Association for the Advancement of Science, Detroit Meeting, August, 1875.)

SALEM, MASS.
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CONTENTS.

NOTES ON THE NORTH AMERICAN GANOIDS, AMIA, LEPIDOSTEUS, ACIPENSER AND POLYODON. By BURT G. WILDER, of Ithaca, N. Y.

(With three plates.)

I.—THE RESPIRATORY ACTIONS OF AMIA AND LEPIDOSTEUS.

The respiratory actions of *Lepidosteus* have been described by Prof. L. Agassiz and by Prof. Poey. The observations of the latter (27)[1] are reproduced by Duméril (4, II, 306).

Prof. Agassiz' remarks are reported as follows:

"This fish is also remarkable for the large quantity of air which escapes from its mouth. The source of this Prof. Agassiz had not been able to determine. At certain times it approaches the surface of the water and seems to take in air, but he could not think that so large a quantity as is seen adhering in the form of bubbles to the sides of the gills, could have been swallowed, nor could he suppose that it could be secreted from the gills themselves" (2).

During the past summer the ten young *Lepidosteus* mentioned in another part of this paper, were observed by me for about three weeks. They seemed to prefer keeping near the surface, probably for convenience of aërial respiration. In emitting the bubble of air they raised the anterior end of the body a little, but I could not be sure that they intentionally protruded the head from the water. At the same moment the whole body was suddenly rolled on one side, and one or more bubbles of air escaped from the mouth. Within a second or two after assuming the horizontal position, other and smaller bubbles escaped from the opercular orifice.

With the smallest gar ($63^{mm.}$, about $2\frac{1}{2}$ in. long), these respiratory movements occurred pretty regularly at intervals of $\frac{1}{2}$ to $\frac{3}{4}$ of a minute. It rolled almost invariably upon the right side so as to emit the bubbles from the left. The ordinary branchial respiratory movements of the jaws and opercula were 95 per minute.

Very often these young individuals of *L. osseus*, and more frequently the adults of the smaller species (*L. platystomus*), would protrude the snouts from the water in the respiratory act; but the

[1] See list of works referred to, at the end of this paper. The first figure designates the number of the work on the list; the last, the page; the middle, when it occurs, the volume.

length of the jaws made it impossible to determine whether this was intentional and for the purpose of inhaling as well as of exhaling the air.

Inasmuch, however, as the exhalation could be as well accomplished at any depth, the uniform approach of the gars to the surface goes to show that air is taken in as well as given out.

More satisfactory observations upon this point were made upon adult and uninjured individuals of the mud-fish, *Amia*, which, like *Lepidosteus* has a very cellular and vascular air-bladder with large air-duct, and upon the respiratory actions of which nothing has been published so far as I am aware.

Amia seems to prefer the darker parts of the aquarium and to remain at or near the bottom, but like *Lepidosteus* it comes to the surface at intervals to breathe. One or two very large bubbles of air escape from the mouth, and on descending, some lesser ones from the operculum.

When at the surface the movement of the jaws seemed to be two-fold, first to permit the escape of air, and second to take in a fresh supply. But the whole was so rapidly executed that I could not be certain.

The following method was adopted for determining this point.

The fish was gradually accustomed to the contact of the hand, gently embracing the body at about the middle. After a time it would swim slowly in the tank with no apparent agitation on account of the contact, and come to the surface at the usual intervals to discharge a bubble of air.

Having been thus prepared, the fish was permitted to move to and fro at about six inches below the surface, but prevented from rising. It became uneasy and after a few not very violent efforts to disengage itself, emitted a large bubble of air which rose to the surface.

If this emission were all it required we may suppose that it would have been content. On the contrary, after a second or two of quiet (perhaps resulting from the habit of being satisfied after the respiratory action), the fish became more and more uneasy; moved rapidly to and fro, turned and twisted, and lashed with its tail, and finally escaped from the hand. It rose at once to the surface, and, *without emitting any bubble whatever, opened the jaws widely and apparently gulped in a large quantity of air.* It then descended and remained quiet for the usual interval. This experiment was several times repeated, always with the same result.

There seems no doubt from the above, that with *Amia* there is a true inspiration as well as expiration of air. The same may be considered probable though not yet proved, with *Lepidosteus*. The escaping air should be chemically examined. But there can be little doubt that in these two genera, in *Polypterus*, and in the Dipnoans, all having cellular and vascular air-bladders, there is effected an interchange of oxygen and carbonic acid, as in the lungs of aërial Vertebrates.

Amia and *Lepidosteus* have no spiracle and it is small in *Polypterus*. The three genera have the space between the rami of the lower jaw occupied (by plates or folds of skin with underlying muscle) so as to better prevent the egress of air than would be the case with most Teleosts. But, as already stated, some air escapes from the opercular orifice of *Amia* and *Lepidosteus* after the fish has descended, and while, probably, the air is being forced backward so as to enter the air-duct.

Amia and *Lepidosteus* were observed to perform the acts of respiration above described more frequently when the water was foul or had not been changed.

It was noticeable that they survived removal from the water for a much longer time than *Acipenser* or *Polyodon*, whose air-bladders are simple and but slightly vascular.

II. — The transformations of the tail of the gar-pike, *Lepidosteus*.

That the tail of the young *Lepidosteus* is unlike that of the adult has been observed by Prof. Louis Agassiz. But although he repeatedly called attention to the transformation, little notice has been taken of it; it is not mentioned in any systematic work in the English language.

This neglect may have been due partly to the absence of figures from Prof. Agassiz's descriptions, and partly to their brief and, to some extent, contradictory nature.

The observations of Prof. Agassiz are here reproduced.

"Zadock Thompson has described a young specimen under the name of *Lepidosteus lineatus*. . . . . I have ascertained, by a series of specimens, that the detached lobe formed by the upper raylets of the caudal fin is gradually united with the lower rays," (Agassiz, 1, 263.)

"In the immature state these fishes [the species of *Lepidosteus*] have the upper region of the caudal separate from the lower as a distinct lobe, the body is scaleless, and the pectorals consist of membrane arising from a fleshy tubercle; . . . . they have mostly a broad longitudinal black band along the middle line," (Agassiz, 9, 360.)

"The young gar-pikes are remarkable as possessing certain embryological characters. The most conspicuous of these is the prolongation of the vertebral column in the shape of a fleshy filament, distinct from the caudal fin, which [the filament] had at times a vibratory motion, involuntary, and quite distinct from the motions of the body itself, as is seen in some embryos."

"This singular formation shows that the caudal fin is properly an appendage to the lower surface of the dorsal column, a true second anal, and not the proper termination of the column.")Agassiz, 2, 48.)

It will be noted that in this later account Prof. Agassiz speaks of the filament as *single* and not as the upper raylets, as in the passage first quoted. But he does not here correct the erroneous statement, that it is "gradually united with the lower rays."

"In the adult state, the *Lepidosteus* has a large rounded caudal at the extremity of the tail; in the young, the entire caudal is placed below the extremity of the vertebral column, as a second anal, and the vertebral column is prolonged as a detached lobe, along the superior border of the caudal. That conformation persists until the fish is .200, (2 decimeters, about 8 inches) in length." (Agassiz, 3, 57.)

Dumeril (4, 319) calls attention to these descriptions by Agassiz, and figures (Pl. 24, fig. 4) the tail of what is stated to be a very small specimen, but which, judging from the size of the figure and the shortness of the filament, was probably at least $200^{mm.}$ (about 8 inches) long.

My own observations relate to the form of the tail in the very young, before it assumed the character described by Agassiz; the manner of formation of the caudal fin; the gradual disappearance of the filamentary end of the body; its representation in the tail of the adult fish.

The material at my disposal is as follows:—

A. Young *Lepidosteus* brought to me in alcohol by Master Edward Steers (nephew of the late Prof. Evans of Cornell University), who took them from the Red River, near Shreveport, La.[2]

The smallest of these is shown (enlarged 5 diameters) in fig. 1. It is 18 millimeters (about ¾ of an inch) long. The largest is 44$^{mm.}$ (about 1¾ inches) long.

B. Ten young *Lepidosteus* (probably *L. osseus*) obtained by me in the Illinois River, at Peoria, during July, 1875. These were kept alive by me and carefully watched for from three weeks to a few days each. The smallest is 63$^{mm.}$ (about two and a half inches) long; the largest is 300$^{mm.}$ (about twelve inches) long.

C. Numerous specimens and preparations of adult and partly grown *L. osseus* and *L. platystomus* in the Museum of the Cornell University.

The smallest *Lepidosteus* in my possession (it is apparently much smaller than any that have hitherto been examined) is 18$^{mm.}$ (a little less than three-fourths of an inch) in length. In figure 1 it is enlarged 5 diameters. Unlike most young specimens it is almost colorless.[3]

The head is rather short and depressed like that of *Polypterus*. The eyes are large and dark. The nostrils are easily seen; the anterior openings look upward and outward instead of downward and forward as in the adult. The branchiostegal membranes are separate as far forward as the transverse fold which exists in all *Lepidosteus*.[4]

The ventral fins have not yet appeared. The pectorals are very large and prominent, and consist of a central lobe with a thin border or fringe. The significance of this will be discussed hereafter; see page 166.

A median fin extends from the middle of the length to the vent,

[2] Several of these were handed by me to the late Prof. Agassiz. Unfortunately his failing health and pressing avocations prevented any examination of them, and they have been kindly loaned to me by Mr. Alex. Agassiz, Curator of the Museum of Comparative Zoology.

[3] This is the case with two small specimens about 5$^{mm.}$ long, taken from the stomach of a small *Lepidosteus*. They are probably newly hatched gars, but are not capable of determination.

[4] I think there are reasons for regarding this fold as homologous with the hinder border of the gular plate of *Amia*. But as this question involves the homology of some other parts now undetermined, I reserve it for another occasion.

and thence to the end of the tail. A similar primordial fin extends along the hinder third of the body above. This fin is quite deep and consists of a delicate membrane supported by very numerous and slender rays in close apposition; they incline slightly backward.

The tip of the tail is unfortunately missing from this specimen, so that its exact form can only be inferred. The larger specimens show a gradual sharpening of the caudal extremity, whence we may infer that in the earliest stage the end is not very acute.

Near its hinder extremity the body has a slight *downward* inclination. In all the larger individuals the body is either nearly horizontal or inclined upward at its hinder extremity.

The primordial median fin presents four points of special alteration, two dorsal and two ventral. They are nearly opposite each other, but the ventral one of each pair is a little anterior to the dorsal.

They appear to be somewhat thicker than the surrounding parts of the fin, and darker from a greater or less deposition of pigment granules, especially near the margin of the body.

The anterior pair (*D*, *A*), dorsal and ventral, occupy the portion of the dorsal and anal fins of the adult. But no large rays, or other structures than the delicate rays of the primordial fin, are to be seen.

The hinder dorsal spot (*X*) is very faint and would hardly be noticeable but for its more pronounced character in larger specimens. It has no large rays and later disappears entirely.[5] It may possibly represent the second dorsal of *Glyptolœmus;* but more probably the upper lobe of the caudal fin of *Undina* and *Macropoma*. This correspondence will be referred to hereafter.

The spot (*C*) on the lower lobe of the caudal of the young *Lepidosteus* is evidently a developing fin. It is thicker than the rest of the primordial fin. In the centre of the thickened space are dimly seen four or five larger rays pointing obliquely downward and backward. Their attachment to the margin of the body is indicated by its thickening and by a crescentic emargination. This emargination resembles that on the lower part of the tail of *Calamoichthys;* but in this genus the fin so indicated is probably the true anal; the infra-caudal lobe not being differentiated.

[5] This transitory fin is comparable with the temporary anals of the young skate as described by Wyman (11, 35); one of which, however, attains quite a large size before its disappearance.

The specimen above described, represents, so far as I am aware, the earliest known stage of *Lepidosteus*. But there can be no doubt that at a still earlier stage the tail was simple and undifferentiated like that of *Amphioxus*.

A second very small specimen is no longer than the one above described, but seems to be more developed. It is darker colored; the belly being almost black while the upper half of the body is brownish. The four median fins are indicated by decided though irregular blotches, and the rays of the infra-caudal are more distinct.

White longitudinal elevations show where the ventral fins (*Ve*) are about to appear.

The difference in the color of these two smallest specimens is very marked. The white one is apparently the younger although a trifle the longer. But it cannot be determined at present that the color is developed only after the attainment of a certain size or stage of growth.

The specimen next figured (Fig. 2) presents the following features. Its length is 23$^{mm.}$ Its colors are darker than the one first described, but less decided than in the second small specimen referred to.

The ventral fins (*Ve*) are little white buds opposite the anterior extremity of the primordial fin (1). This latter has changed but little. It seems rather thinner and its borders are ragged, as if in process of removal by both absorption and abrasion.

In addition to the interruption for the vent, the primordial fin now presents three emarginations, as follows:—1. About mid-way between the spots representing the dorsal and the supra-caudal fins. 2. Behind the spot representing the anal fin. 3. Between the primordial fin (3) on the lower border of the tail and the infra-caudal lobe, which now projects slightly and is supported by eight or ten rays split at their tips but reaching the border of the fin.

In this specimen we see the beginning of the changes which are to result in the total disappearance of the tail proper and the taking of its place and office by the greatly enlarged infra-caudal lobe.

Passing over intermediate sizes in which the head is progressively lengthened, and the ventrals enlarged we come to the specimen represented in fig. 3.

Like the one first described this is a pale individual. Its total length is $44^{mm.}$ From the tip of the snout to the middle of the eye, $9^{mm.}$; from the eye to the vent, $21^{mm.}$; from the vent to the tip of the tail $14^{mm.}$

The primordial fin has disappeared excepting on the border of the filament (*fi*) which is the elongated and slender termination of the body. The pectoral fins are still distinctly lobate, the thin border not being more than one-half as broad as the fleshy central lobe.

The anal and dorsal fins are distinct, and have each seven rays. The ventrals are still very small.

The rays of the infra-caudal are distinct. They are more nearly in line with the body than in the younger specimens, while the tail is slightly elevated. Both the filament and the infra-caudal lobe have increased in length. But the latter has also become wider, while the former is so slender as to merit the name filament. It projects about $1.5^{mm.}$ beyond the infra-caudal lobe.

The specimen last described is the largest of those from the Red River. The smallest of the specimens from the Illinois River has a total length of $63^{mm.}$; $13^{mm.}$ from muzzle to middle of eye; $28^{mm.}$ from eye to vent, and $22^{mm.}$ from vent to tip of filament.

As in most of the Red River specimens and all of those from the Illinois, the dark lateral stripe is strongly contrasted with the white belly and brownish back. The border of the pectoral is now equal to the lobe. The tip of the caudal filament is very slender and projects $3^{mm.}$ beyond the infra-caudal lobe.

At the base of the filament, just behind the tip of the dorsal, are two pairs of slight elevations, one behind the other, and looking backward. These are the first representatives of the *fulcra;* a series of strong spine-like plates which, in the adult gar, cover the anterior part of the upper and lower borders of the tail.

In a specimen $108^{mm.}$ long, the tips of the filament and the infra-caudal lobe coincide. Both have increased in length and width, but the lobe more rapidly than the filament.

The outlines of scales appear on the sides of the hinder half of the body, and there is an increase in the size and number of the fulcra.

In a specimen measuring $142^{mm.}$ from tip of head to tip of caudal lobe, this latter projects $8^{mm.}$ beyond the filament. Its rays, that is, the central ones, are in direct line with the axis of the body, while the base of the filament is crowded upward. There are now five pairs of fulcra, the hindermost of which extends backward as far as the point of separation between the filament and the lobe. Behind this point the filament is apparently undergoing structural degeneration and removal. It is thin, slender and ragged at the edges.

But there is evidently considerable variation as to the period of this removal. For of two specimens about 190$^{mm.}$ in length, one has the filament equal to the lobe, and in the other it is but 3$^{mm.}$ shorter.

The largest specimen in which the filament is preserved, is about 300$^{mm.}$ long. The lobe projects 15$^{mm.}$ beyond the filament. The free part of the latter is much attenuated, and, during life, was but feebly and occasionally employed. The tail of this specimen is shown in fig. 4.

In imagination we may readily supply the stages intermediate between that last described and the tail as usually represented, where the free part of the filament has wholly disappeared, and its base, covered by the fulcra, seems to form only the upper border of the functional tail. This latter, however, from a morphological point of view, is really an appendage of the filament.

The movements of the filament have been well described by Agassiz. He, however (2), speaks of it as "involuntary." By this he may have meant only that, as with other very rapid vibrations, a separate volition is not required for each individual movement. In fact, during vibration, the filament is invisible. But the motion is not involuntary as is that of cilia or unstriped muscular fibres. For at times the filament is wholly at rest; it may be elevated or depressed, curved strongly to the one side or to the other, and more or less rapidly vibrated in any of these positions.

The movement may be compared to that of the wings of most insects and of the humming-bird. Still more closely with that of the tail of *Crotalus*.[6]

On each side of the cartilaginous rod, in its whole length, is a band of *striated* muscular fibre.

It would be interesting to ascertain whether the nervous supply comes from the cord within the filament or from the permanent

[6] **Many of the *Colubridæ*, under strong excitement, will vibrate the tail as does the rattlesnake.**

portion of the cord anterior to the point of its separation from the infra-caudal lobe.

The representation of the filament in the adult tail. Agassiz' figure of the tail of *Lepidosteus* (5, tome II, tab. A), was probably made from a dry preparation, and his description (tome I, part II, 23), does not mention any cartilaginous prolongation of the bony vertebral column. I am not aware of any other figures or description of the tail of *Lepidosteus*.

Figure 5 represents (reduced ½) the dissected tail of a medium sized *L. platystomus*. It will be noted that the outline of the caudal fin (the infra-caudal lobe of the foregoing descriptions) is nearly though not quite symmetrical; the lower rays being a little shorter than the uppermost.

In the figures of Agassiz and Duméril the outline is much more oblique. This however, may be due in part to the fact that the upper rays are usually less separated than the lower, so as to cover less area than the lower.

Probably too, there is specific variation in this respect. I am inclined to think also that the same species presents different characters at different ages. But for the determination of these questions a large number of individuals should be compared after their species have been ascertained. At present the taxonomy of *Lepidosteus* is in a very confused state.[7]

The outline of the base of the fin presents a double curve like an elongated letter *f*. The fulcra cover the anterior two-thirds of the dorsal border and three-fourths of the ventral border. Both series are closely attached to the uppermost and lowermost caudal ray respectively. These rays not only divide and subdivide like the fin rays of *Malacopteri*, but also consist of two lateral halves[8] which are often not exactly applied to each other, as seen in fig. 6.

The lateral halves of the uppermost caudal ray are separated from each other excepting at their lower border, and between them lies a tapering cartilaginous rod, whose upper surface is covered by the bases of the dorsal fulcra. The relation of parts

[7] The same is true of many other American forms which are not readily obtainable, in large numbers, by European naturalists; as, for instance, the American Sturgeons, the Petromyzontidæ, and the tailed Batrachians.

[8] Goodsir (13, II, 106) and Humphrey (8, 59) have called attention to the fact that the rays of median fins consist of two lateral halves. The latter author regards it as one of the grounds for considering each lateral fin to correspond to a lateral factor of a median fin. I find, however, that in *Lepidosteus* the rays of the ventral fins are likewise double.

is seen in fig. 6, which represents a vertical section of the upper border of the tail about the middle of the series of fulcra.

Posteriorly the rod may be traced to beneath the hindermost fulcra, this point corresponding nearly with the point of separation of the filament and infra-caudal lobe in the young. Anteriorly it descends gradually to become continuous with the hindermost vertebra.

The cartilaginous rod above described is called notochord by Huxley (7, 20). A cross-section, however, shows that it really represents the whole spinal axis, as seen in fig. 6. The notochord (*N*) is surrounded below and on the sides by the cartilaginous and unsegmented basis of the vertebræ (*CS*) which, above, separates into two laminæ enclosing the neural canal and the spinal cord (*SC*).

The structures above described are readily seen in the tail of the adult *Acipenser* and *Polyodon*. After maceration in weak spirits for some months, the notochord of these genera may be withdrawn from the surrounding cartilage as a membraneous tube, the contents of which may be washed out.

In *Polyodon* the fibres of this membraneous notochordal sheath are arranged in a peculiar net-work permitting considerable extension, with contraction of the caliber, or shortening with corresponding increase in diameter.

In *Amia* the cartilaginous sheath is thicker in proportion, but the true notochord and the spinal cord may be traced to the extremity.

The whole structure is much shorter than that of *Lepidosteus*, but in several specimens prepared by me, it comes much nearer the upper border of the fin than in the figure by Huxley, (7, fig. 6). The rod is not represented by Franque (10).

The tail of the adult *Amia* has, therefore, essentially the same structure as has that of *Lepidosteus*. Nothing is as yet known of the earlier stages of its development. Through the kindness of Prof. H. A. Ward, of Rochester, I have recently obtained two small specimens, respectively 70$^{mm.}$ and 100$^{mm.}$ (about three and four inches) long, which have the characteristic tail of the adult[9]

[9] These specimens will be described upon another occasion. For the present I will only mention that in both the markings on the body and fins are more distinct than in the adult, and that the smallest presents two decided black stripes on each side of the head, one of which runs across the eye, as in the young *Lepidosteus*, while the other descends obliquely backward from the eye toward the margin of the operculum.

with an even more decided upward inclination of the upper caudal rays, in strong contrast with the figures of Franque (10) and Huxley, (7, Fig. 6).

Nevertheless, so nearly does the tail of the adult *Amia* resemble that of *Lepidosteus*, that I cannot avoid inferring that it passes through a similar series of transformations. And I would suggest to those who live near the breeding places of *Amia*, the importance of making a complete study of its development.

As the most teleosteoid of Ganoids (its ganoid nature being in fact denied by Lütken, 16, 336), its embryology will be especially valuable.

The stages through which the *Lepidosteus* passes are comparable with the adult conditions of various living and fossil forms.

But this parallelism is rarely or never exact in regard to more than one of the features under consideration, the direction of the spinal axis and the subdivision of the primordial median fin.

As already stated the first stage is not represented among the specimens. But, judging from all analogy, we may infer that the young *Lepidosteus* of about $10^{mm.}$ in length, has a continuous median fin with no differentiation of color or thickness, and with no sign of subdivision into separate fins; and that the posterior end of the body is horizontal or slightly deflected downward, separating the equal or nearly equal upper and lower caudal lobes.

In the earliest of the stages here described the spinal axis is still nearly horizontal, but the median fin shows signs of subdivision.

In both the tail would be described as truly homocercal by most authors, as diphycercal by McCoy and Huxley, and as protocercal by Wyman.

I do not wish, on this occasion, to discuss the general subject of the nomenclature of tails. But it seems to me that all the arguments of Huxley in favor of diphycercal for homocercal[10] as applied to tails like that of *Polypterus*, apply with even greater force toward substituting protocercal for both. For the latter term indicates that the structure under consideration exists in the earliest known stages of development of Selachians and Ganoids;

[10] Cope (17) has proposed "isocercal" for the same form of tail. But he applies this term to the eel (*Anguilla*), in which, according to Huxley (15, 42), the arrangement is really heterocercal as in most if not all other osseous fishes. The whole subject, however, needs a special revision by comparison of several stages of development of the tail in all forms of aquatic vertebrates.

in certain very ancient Ganoids (as *Glyptolæmus* and *Gyroptychius*); and in the generalized forms *Lepidosiren* and *Ceratodus*.

I have not been able, however, to find the word used elsewhere than in Wyman's paper on the Development of *Raia batis* (11).

Upon the general subject see Huxley (6, 7, and 15), with other papers therein referred to.

This stage of the *Lepidosteus* may be compared with *Amphioxus*, the lowest known Vertebrate, with *Lepidosiren*, *Protopterus* and *Ceratodus*,[11] where, however, the primordial fin-rays seem to have been replaced by stronger and permanent rays; *Myxine*, *Bdellostoma* and *Petromyzon*, where the rays are cartilaginous;[12] (in some species of *Petromyzon* the median fin is continuous, with slight undulations indicating the subdivisions in other species); and with *Menobranchus* and *Menopoma*, where, as in the larvæ of Anoura, there are no fin-rays at all.

The cartilaginous prolongation of the vertebral column of *Polypterus* is not shown by Agassiz (5, II, tab. C). It is figured by Huxley and described (7, 20), as hardly at all bent up.

In a *Calamoichthys* in my possession a line drawn vertically across the tail over the end of the cartilaginous rod intersects twelve fin-rays. Four of these lie above the rod and eight below. Still the upward inclination of the rod is very slight, perhaps not enough to prevent the recognition of these two genera as protocercal. Some other form would have been better, however, for illustration.

Among fossil forms with apparently protocercal tails are probably included the extinct species of *Ceratodus* described by Newberry and Cope.

In all the above excepting *Polypterus* and *Calamoichthys*, the median fin is continuous as if formed by direct enlargement of the whole primordial fin.

But in other fossil forms, as in the two genera above named, parts of the primordial fin are differentiated and bear the names dorsal and anal.

The most instructive of these is *Glyptolæmus*, a Devonian fish described and figured by Huxley (6, fig. 1, and plates I and II). "There are two dorsal fins placed in the posterior half of the

[11] Commonly known as Dipnoans, but included among the Ganoids by Günther (19) Gill (12) and others.

[12] Perfectly distinct, although these have been called Dermopteri by Owen.

body. The ventral fins are situated under the first dorsal and are succeeded by a single anal. The caudal fin, whose contour is rhomboidal, is divided into two equal lobes by the prolonged conical termination of the body; in other words, the fish is diphycercal or truly homocercal" (Huxley 6, 3).

Huxley states that the head, body and fin, of *Gyroptychius* might be described in the terms which have just been applied to *Glyptolæmus*.

Both these genera are comparable with the first stage of *Lepidosteus*. The tail is strictly protocercal (or "diphycercal"). Moreover there are two dorsals. If the anterior be the homologue of the single dorsal of the adult *Lepidosteus*, then the posterior may, perhaps, represent a development of the transitory posterior dorsal of the young *Lepidosteus*. If the anals correspond in the two, then the infra-caudal lobe of *Lepidosteus* is not differentiated from the rest of the tail in *Glyptolæmus*, or *Gyroptychius*.

But it may be that another interpretation is more nearly correct. Certain other fossil forms, as *Undina*, and probably *Macropoma*, have a continuation of the vertebral column between the two equal lobes of the caudal fin, and the prolongation of the caudal extremity beyond it as a filamentary appendage (Huxley 6, 15). Leaving out of the comparison the advanced anterior dorsal of *Undina*, the posterior dorsal may be compared with the true dorsal of *Lepidosteus*; the anals are apparently homologous. There are then an upper and a lower caudal lobe of nearly equal size, the filament projecting between. The lower lobe may naturally be homologized with the permanent infra-caudal of *Lepidosteus*, while the upper lobe represents a similar development of the transitory appearance (*X*) of *Lepidosteus*.

Which of these interpretations is correct will hardly be determined before the general affinities of all these forms, fossil and living, are better understood than at present. Meantime I venture to call attention to the facts, well known but not always borne in mind, that all median fins are differentiations of a single continuous primordial fold; that even in nearly allied forms they present considerable diversity of size and position; and that no such taxonomic significance is probably to be assigned to them as to the lateral fins, of which there are never more than two pair.

Leaving out of the comparison the degree of subdivision of the median fin, the stages 3, 4, and 5, represented in figs 2, 3, and 4, have their more or less accurate counterparts among various living and fossil Ganoids and Sharks.[13]

Alopias has a long upper lobe (so-called).[14]

In *Polyodon* and some species of *Acipenser* and in most Sharks, the upper lobe is but little the longer; in *Lamna* the lower lobe nearly equals the upper. I am not acquainted with any Ganoid or Selachian where the lower lobe is the longer, as in the sixth stage of *Lepidosteus* (Fig. 5).[15]

The last stage (7, fig. 6), exists in *Amia* alone among living Ganoids, and, so far as I am aware, is not presented by any palæozoic forms; their tails being either protocercal (as in *Glyptolæmus*) or obviously heterocercal as in *Palæoniscus*, etc.

But among mesozoic forms the amioid tail is not unusual; and a series may easily be formed, as, for instance, of *Lepidotus*, *Megalurus* and *Thrissops* by which the truly heterocercal tail is apparently converted into the apparently homocercal form. Indeed the tail of *Megalurus*, as figured by Agassiz (5, tab. E, fig. 4), might almost be taken for that of *Amia*.[16]

[13] Several species of *Loricaria* have the upper caudal ray greatly prolonged so as to form a filament. In an adult examined by me there is no prolongation with it of the notochord. It would be interesting to examine the young in this genus. The filament adds another to the analogies between the Goniodonts of South America and the Sturgeons of the Northern hemisphere which have been pointed out by Agassiz (20, 30; 21, 212, 299; 22, 351).

[14] I use the term upper lobe because it is commonly employed. Strictly speaking, however, it is not a lobe of the caudal fin in any such sense as is the lower lobe here called infra-caudal. It is the prolongation of the body and is really a gigantic *filament*. The tail of *Chimera* is even more exaggerated.

Something like a reversed representation of the changes in the tail of *Lepidosteus* occurs with the developing skate. The dorsals of *Raia batis* were found by Wyman (11, 43) to "change position from the middle to the end of the tail. At the time of hatching, however, there is still a slender terminal portion of the tail which is afterwards either absorbed or covered up by the enlarged dorsals as they extend backward."

In a young skate taken from the egg-case and measuring 70mm. in length, I find projecting beyond the second dorsal a slender filament about 10mm. long, which is atrophied as compared with the rest of the tail, and apparently in process of removal. (In *Uraptera*, as remarked by Wyman, this slender tail is persistent). After its removal the hinder dorsal of the skate occupies toward the end of the body the same position, morphologically, as if it were a supra-caudal lobe or differentiation of the primordial fin, corresponding to the infra-caudal lobe of Lepidosteus. The end of the vertebral column is not, however, bent downward so as to allow the dorsal to be strictly terminal: perhaps in adaptation to its frequenting the bottom.

[15] There seems to be no reason why such a form should not exist, a reversed counterpart of *Alopias* as *Hemirhamphus* is of *Xiphias*.

[16] In the diagrammatic restoration of *Megalurus* above referred to, the scales are represented as rhombic. But they are really cycloid, as in *Amia*, in all the four species shown by Agassiz in Plates 51 and 51a of the same work. May not *Megalurus* be a fossil representative of the Amiadæ? Huxley, however, (7, 127), says that "it is not certain that any member of the group occurs in a fossil state;" and Lütken (16, 336), thinks "there is no positive reason for arranging the Megaluri (which he regards as Teleostei) with the Amiadæ."

Since Huxley (15) has shown the probability that the tails of most if not all Teleostei, are really strongly heterocercal, it is not difficult to imagine a series by which the tail of *Amia* should become that of one of the Clupeoids with which Cuvier had placed it. Indeed there are fossil Ganoids (*Thrissops*, *Aspidorhynchus*, etc.) whose tails are apparently as perfectly homocercal as those of any *Salmo* or *Scomber*, but which, by analogy, we may suppose to have been, in the earlier stages of development, distinctly heterocercal, or, perhaps, even protocercal.

But the transition is still better illustrated by the changes which occur in *Gasterosteus* as described by Huxley (15) and as lately seen by me in a Siluroid.

For in the young *Gasterosteus* the cartilaginous rod (called notochord by Huxley) is not only strongly bent upward but also reaches the upper angle of the tail, nearly as in *Lepidosteus*. But in the half-grown fish, by the growth of the fin rays the end of the notochord "no longer reaches, by a long way, to the posterior superior angle of the caudal fin;" this is the condition of things in *Amia*.

It may be said, therefore, that the Teleostean tail does not simply begin where the Ganoid tail leaves off, but actually overlaps it; the two earlier stages of the former being represented by the tails of *Lepidosteus* and *Amia*, the latter genus, as has been already stated, being regarded as the most teleosteoid of Ganoids.

Lütken has remarked (16, 332) that "in general an evident progress from the heterocercal to the so-called homocercal or fan-like tail may be observed running parallel to the progress of the geological epochs."

The transformation of the tail of *Lepidosteus* so far as already known, would have furnished an embryological parallel to the structural and geological series; while the earlier condition here first described enables us to extend the comparison to the protocercal forms of which some are among the oldest known fishes and others, now living, are either the lowest of vertebrates or manifest such striking relations with other classes as to have received the name "generalized Ganoids."

III.—The transformations of the pectoral fins of Amia and Lepidosteus.

Rafinesque[17] described a small gar-pike under the name *Sarchi-*

[17] Journ. ac. nat. sci., Philad., 1818, vol. I, part II, p. 418.

rus because the pectorals consisted of a membrane rising from a fleshy lobe.

Agassiz (9, 360; 3, 58) has shown that this form of pectoral is characteristic of the young *Lepidosteus*. Duméril (4, 320) quotes Agassiz' observations but makes no comment upon them. No other systematic work, so far as I know, contains any reference to the fact.

Since Huxley (6, 24), has proposed a new sub-order of Ganoids, Crossopterygia, mainly "in consideration of the peculiar manner in which the fin rays of the paired fins (the pectorals and usually the ventrals) are arranged so as to form a fringe round a central lobe," it is desirable to ascertain whether the early stages of other Ganoids exhibit similar features.

This is certainly the case with all the young *Lepidosteus* above described, including the largest. Moreover, in any minute description of the adult *L. platystomus*, the pectoral fins would be distinguished from the ventrals by the existence of a decided fleshy rounded lobe at their base.

In the smallest gar (Fig. 1, P) the fringe forms little more than one-third the whole length of the fin. As the fish grows the lobe becomes rather longer and narrower, but the fringe increases so much more rapidly as to render the former comparatively inconspicuous in the adult.

The pectorals of *Amia*, even the adult, have a fleshy lobe. In the smallest specimen already alluded to, the length of the whole fin is $10^{mm.}$ and the basal lobe forms one-fifth of this, $2^{mm.}$

So far as regards external form alone, both *Amia* and *Lepidosteus* must be regarded as having lobate or fringed pectoral fins.

But the significance of this fact depends largely upon two other considerations. 1. Is the structure of the fin identical with that of *Polypterus* and the other forms included among the Crossopterygia? 2. Is the lobe necessarily covered by scales?

It is so covered in *Polypterus* and, as I infer, in the fossil genera. But I have not found scales upon the lobe in even the adult *Amia* and *Lepidosteus*.

Since, however, all those forms, like the young *Lepidosteus*, were probably scaleless when young, it would seem that not much weight should be assigned to the lack of scales in the adult.

IV.—On the brains of Amia, Lepidosteus, Acipenser and Polyodon.

There is a wide difference of opinion among zoölogists respecting the limits of the group commonly known as Ganoids, and its relations with the other fishes, and the higher Vertebrates. To the group as originally defined by Agassiz and Müller, including, with many fossil forms, the living *Lepidosteus*, *Polypterus* and sturgeons (*Acipenser*, *Scaphyrhynchus* and *Polyodon*), *Amia* was soon added, and Agassiz was even inclined to adjoin the Siluroids, the Plectognaths and Lophobranchs. Prof. Gill (12) considers that "the Polypterids (Crossopterygia of Huxley) and Dipnoans" (*Lepidosiren*, *Protopterus* and, probably, *Ceratodus*) exhibit so many characters in common that they are not even entitled to subclassical distinction. Dr. Gunther (19) considers the Dipnoi as a sub-order of Ganoids, and unites these with the Selachians as a sub-class of fishes, Palæichthyes. Lütken (16) goes to the other extreme and excludes from the Ganoids not only the sturgeons but also *Amia*.[18] Cope (17, 582) does not recognize the group at all.

It will be observed that, for determining the limits and relations of Ganoids, naturalists have appealed to the scales, to the dermal ossifications upon the head, to the skull and skeleton in general, to the limbs, to the spiral intestinal valve, and the multivalvular and rhythmically contractile bulbus arteriosus.

The embryology of the typical Ganoids is wholly unknown, and this most valuable aid in classification is, therefore, not at present available.

The only brain character which has entered into the discussion is the chiasma of the optic nerves. In this the Ganoids differ from the Teleosts and Myzonts, and agree with the Selachians and higher Vertebrates; but the general aspect of the brain is more nearly that of the Teleosts.

It does not appear however that any detailed comparisons have been made between the brains of Ganoids and those of other fishes and the higher Vertebrates; and Prof. Gill who alludes (12) to "the superior taxonomic value of modifications of the brain and

[18] Lütken makes no reference to the brain, and his characters seem to be in other respects defective. But (p. 336) he admits the possibility that future discoveries may some day demonstrate to us unknown bonds.

heart in other classes of Vertebrates," does not refer to any other feature than the optic chiasma already mentioned.

Having reasons,[19] other than those derived from the extreme diversity of conclusions already referred to, for believing that a careful study of their brains will throw light upon the limits and classification of Ganoids, I have this summer (1875) made numerous preparations of the brains of the four American genera, *Amia*, *Lepidosteus*, *Acipenser* and *Polyodon*, comparing them with each other and with the figures and descriptions of Ganoid brains to which I have had access.

Since, in comparison with the preparations, none of the published figures and descriptions are wholly satisfactory, I here refer to them in detail.

Apparently the earliest figure of a ganoid brain is that by Stannius (32) of the sturgeon's brain. It seems to be a correct representation, and fairly indicates the features, which, according to the views I have reached, are characteristic of the brains of all Ganoids. But no especial attention is drawn to them, and the nomenclature of the two anterior pairs of lobes has not been accepted by later authors. Stannius calls the first pair, from which arise the olfactory nerves, the *olfactory tubercles*, and the second pair, which most authors call hemispheres (but which I believe to be specially developed portions of the thalami), the *olfactory lobes*. He thus recognizes no cerebral hemispheres at all, and makes no comparison between the sturgeon's brain and those of other fishes, or the higher Vertebrates.

It is to be noted that this nomenclature of the two anterior pairs of lobes corresponds with that which Gottsche had applied to the brains of osseous fishes, in 1835. This author (30, 445) enumerates the various names which had been given to the hinder and larger pair, and concludes that they are the olfactory lobes, the anterior pair being olfactory tubercles. Gottsche cites Desmoulins and Serres as regarding the so-called olfactory lobes as cerebral lobes, which name has since been more commonly employed. Gottsche makes no definite allusion to the brains of other fishes than the Teleosts.

[19] Based upon the probability that such an organ as the brain would be most exempt from modifications by external agencies in the progress of evolution, and would thus manifest more uniformity of structure throughout the more comprehensive groups than would the digestive organs, the skeleton or limbs. Compare Agassiz, 49, II, 302).

In 1844 Johannes Müller figured (18) the brain of *Polypterus* from above, from below, from the side and in single cross section, through the pair of lobes next to the anterior.

There can be no better illustration of the slight importance ascribed at that time to the brain for taxonomic purposes than the insufficient of figures and very brief descriptions, which the great ichthyologist devoted to the brain of a typical Ganoid. He says (p. 139) "Das Gehirn der Ganoiden ist eigenthumlich und unterscheidet sich von dem der Knochenfische und Plagiostomen." Yet his description of the brain (p. 140) and résumé of the characters (p. 141) give us only the optic chiasma, a feature which the Plagiostomes share with the Ganoids. (See also 41, 24.)

Müller enumerates the cerebellum and the optic lobes, the "lobus ventriculi tertii" (corresponding to the thalamus of higher vertebrates) the hemispheres, olfactory lobes and olfactory nerves. Although commenting upon the general resemblance of the brain to that of the sturgeon he does not call attention to the different determination which he makes of the two anterior pairs of lobes.

In the following year Busch (29) published figures of several Ganoid brains.

This work I have not been able to obtain. But if the figures of the brains of the sturgeon and the *Chimera*, copied by Owen (24, I, figs. 173 and 179), are fair examples, the work did not materially advance the knowledge of either the form, the structure, or the homology of the ganoid brain.

The paper of Hollard (34) admits three types of brains, the *teleostean*, the *plagiostome* and the *cyclostome*. It is not clear to which of these types he would refer the ganoid brain.

In 1848, a pupil of Müller, H. Franque, figured (10) the brain of *Amia* from above and below with separate views of the optic chiasma. He makes no comparisons with other brains, and his description is a simple enumeration of the lobes according to the usual nomenclature, the two anterior pairs being olfactory lobes and hemispheres respectively.

Duméril (4, pl. 20), copies from Phillippeaux and Vulpian figures of a sturgeon's brain from above and below. He makes no original observations. The so-called hemispheres are shown as solid rounded masses without eversion of the dorsal borders, and the olfactory lobes as solid without even the orifices distinctly portrayed, though not interpreted, by Stannius and Busch.

In 1864, Mayer (40) published figures of a large number of fishes' brains, as illustrations of his idea that by the relative size and more or less intimate connections of the brain-lobes, fish-like forms could be divided into Pisces Mesencephali (Teleosts), and Pisces Proëncephali (all others including Dipnoans). The eighty-four figures of Teleost brains are mostly original; they usually present only the upper surface and vary in the degree of their accuracy, judging by comparison with preparations of the same species.

The Myzont brain is represented by Müller's figures of *Myxine* and *Bdellostoma*, and by an original and very good figure of *Petromyzon marinus*. His interpretation of the parts differs from both Müller's and my own.

Among Selachian brains are copies of *Galeus* and *Callorhynchus* from Busch, and of *Torpedo* from Savi; the author adding a fœtal *Galeus*, a *Zygœna*, *Squatina*, *Raia Scymnus* and *Chimera;* all are shown from above, *Chimera* alone shows the olfactory lobes; the separation of these from the rest of the brain in the figure is not referred to in the text or regarded by others who have copied the figure.

The brain of *Protopterus* is seen from the side in a copy of Owen's figure and from above in that of Peters.

Mayer copies Busch's figure of the brain of *Lepidosteus semiradiatus*, and by its side gives an original figure of that of *L. osseus* without commenting upon the great difference and form and relative size of parts; both are inaccurate.

Similar unexplained discrepancies appear between the original figures of the brains of *Acipenser sturio* and *Ruthenus*, while that of *Polyodon* agrees neither with them nor with the preparations made by me. There are copies of Müller's figure of the brain of *Polypterus* and of Franque's of that of *Amia*. None of these figures indicate the existence of a lateral ventricle or a foramen of Monro.

The Ganoids together with the Dipnoans are called Hemiepencephali. The Holo-ganoidei include *Acipenser* and *Lepidosteus*, while the Hemi-ganoidei embrace *Amia*, *Polypterus*, *Protopterus* and *Polyodon*.

While sympathizing with Mayer in his attempt to follow out the earlier suggestion of Carus, and make the brain the basis for a subdivision of fishes, I am compelled to say that his determination of homologies and discrimination of groups, as founded upon the external aspect of preparations (some of which certainly are badly preserved) do not stand the test of a careful structural comparison. A smaller number of figures of sections or dissections of a few typical forms would have more materially aided our comprehension of the brains themselves and of the zoölogical relations of the fish-like Vertebrates.

In 1868 appeared a paper upon the comparative anatomy and development of the brain by Miklucho-Maclay (41).[20]

This author regards the brain of Selachians as typical, and bases his determination of homologies upon the comparison of vertical longitudinal sections of the brains of an embryo shark (*Heptanchus*) and a goat. He concludes that the cerebellum of the shark is a narrow bridge; that the convoluted mass just in front, which is usually regarded as the cerebellum, represents the optic lobes; that the optic lobes are really the thalami (zwischenhirn); and that the hemispheres (vorderhirn) are only partly separated from each other.

Remarking, in passing, that Miklucho-Maclay offers no sufficient reason for the interpretation of the hinder lobes of the brain, I would call attention to the fact that the embryo shark was 130$^{mm.}$ (more than 5 inches) in length, and that, as shown by the figure, the so-called vorderhirn had already nearly filled up.

His diagram of a typical brain (Fig. 1) is not readily or closely comparable with any fish-brain, as it seems to me; and since the author adopts Müller's statement respecting the slight extent of the ventricles in the Myzonts, and neither describes nor figures any part of the brain of a Ganoid or Teleost, we are compelled to regard his interpretation of homologies throughout the branch as open to doubt, on account of the statement that the hemispheres of Ganoids and Teleosts are wholly separated (p. 560); this not being the case in any fish-brain excepting that of *Protopterus*, where the true hemispheres are separate as in Batrachians.

Owen (24, I, figs. 173 and 174) figures from above the brains of a sturgeon copied from Busch, and of *Lepidosteus* apparently original and very imperfect. In both, the masses just in front of the optic lobes are called prosencephala (hemispheres). But, as there figured, the outward aspect of the two brains is so dissimilar

[20] This paper was not obtained by me until February, 1876. The delay in publication of this paper enables me to insert a comment upon it.

and so little indicative of their real structure, that the eminent author seems not to have thought of making any comparison between them. The openings which I shall show to be the "foramina of Monro" are represented in the sturgeon's brain even too distinctly, but there is no reference to them in the text. The cerebellum of the sturgeon is described as a "simple commissural bridge or fold" according to its outward appearance, whereas, by its downward projection into the optic ventricle as a thick keelshaped mass, the cerebellum has a very considerable bulk. The cerebellum of the gar-pike is figured as smooth and described as solid, whereas it is really hollow and presents two longitudinal depressions.

The manual of Gegenbaur (14) contains several figures of fishes' brains. Three represent vertical longitudinal sections of the brains of embryo shark, snake and goat, which are apparently original, although the first resembles that of Maclay. Figures of the brain of *Polypterus* are copied from Müller, and of the brain of a shark from Busch.

Like many continental anatomists, Gegenbaur subdivides the brain into nach-, hinter-, mittel-, zwischen- and vorder-hirn. We have no good English equivalent for *zwischenhirn*, nor do the other names seem to aid the comprehension of the brain type any better than the ancient and convenient latin terms, *cerebellum*, *lobi optici*,[21] *hemispheræ*, *thalami*, etc.

In the present case the nomenclature of the several brains is not homogeneous, even according to the common interpretation that the hemispheres of the frog and other aërial Vertebrates are represented in fishes by the pair of solid lobes in front of the optic lobes, or in sharks by the single median mass from which arise the olfactory crura. The optic lobes of the shark are called zwischenhirn, and those of *Polypterus* mittelhirn; and in the section of the brain of the embryo shark the term mittelhirn is applied to the larger and folded anterior portion of the cerebellum, while the hinder border is named hinterhirn.

Huxley (7, fig. 38), figures the brain of *Lepidosteus osseus* from above and from below. In accordance with the plan of the "Manual" it is not stated whether the figure is original.

Huxley follows the usual nomenclature in making the two pair of lobes in front of the optic lobes respectively hemispheres and

[21] The ponderous phrase *corpora quadrigemina* is rarely employed by comparative anatomists.

olfactory lobes. But he does not refer to the figure in the text, nor does he mention the brain as likely to aid either at present or in the future in the discrimination between the Ganoids and the other fishes.

The figures and descriptions of the brains of Myzonts (Marsipobranchs), Teleosts, and Sclachians (Elasmobranchs) are hardly more satisfactory. With none of them is any effort made to ascertain, by a structural comparison, the extent to which they conform to the type of brain commonly recognized among the air-breathing Vertebrates.

This is the more noteworthy because by far the clearest presentation of this type is furnished by the figures and descriptions in the earlier pages of the same work. For these diagrams indeed, as for so many others which bring orderly knowledge out of chaotic detail, the anatomist is greatly indebted to Prof. Huxley.

In this brief historical survey, considering the general desire to ascertain the extent to which Ganoids form a natural group separable from other fish-like forms, one is struck with the absence of both any attempt to characterize the group by means of the brain and of the supposition that such characterization is possible.

Evidently the first step in such characterization should be the identification of parts, if possible, with those which uniformly exist in the brain of all air-breathing Vertebrates, the Batrachians, Reptiles, Birds and Mammalia.

The ganoid brains upon which this paper is based, were all prepared by myself from fish just taken from the water. The difference between these preparations and some previously made from specimens which had been transported for some distance or kept for a time in spirit before the heads were opened, has convinced me that, for the determination of doubtful points of structure, the brain should be hardened in strong alcohol before the fish has been twenty-four hours out of water.

The published figures and descriptions of ganoid brains with which I am acquainted appear to have been made from poorly preserved specimens. Moreover, none of them inclnde all the views (from the side and from below as well as from above) and sections (mesio-longitudinal, and transverse at several points) which are necessary to the presentation of the real structure of a brain. With no other organ is it less safe to trust to the external form and appearance of the several lobes.

How far this is true of the brains under consideration, may be seen by a comparison of the representation (Plate II, fig. 7) of the mesial surface of the brain of *Lepidosteus osseus* with the figures of Huxley (7, fig. 38), or of Owen (24, I, fig. 174), both of which seem to have been made from poorly preserved preparations.[22]

The gar-pike from which was taken the brain here represented, was a female, 1.3 meters (about four and one-half feet) in length. The brain, as is usual with this species, and, so far as I know, with all adult Ganoids, was covered by a layer of connective tissue. This envelope is fatty and yellowish in *Acipenser;* jet black and very abundant in *Polyodon*, the brain of which does not nearly fill the cavity; moderate in amount, and light colored in *Amia* and *Lepidosteus*. In the young of these latter, less than 120mm. long, no envelope exists, the brain quite filling the cerebral cavity. It would be interesting to ascertain at what period commences the increase in the brain case of *Polyodon*.

The brain is represented enlarged two diameters.[23]

The description of the brain of *Lepidosteus* will be more readily followed if we first refer to the general type of brain as found in Batrachians, Reptiles, Birds and Mammals.

The best figures and descriptions of this type of vertebrate brain, are those of Huxley (24, figs. 19 and 20), which, with unimportant changes are reproduced on figure 15.[24]

According to Huxley's description the brain begins as three median vesicles, whose cavities are continuous with the central canal of the spinal cord. The hinder vesicle thickens below to become the *medulla oblongata* (*M*). It opens above to form the fourth *ventricle* (4) and a bridge over the anterior part of this ventricle is the *cerebellum* (*C*). The middle vesicle becomes the *optic lobes* ("corpora quadrigemina" of anthropotomy); its cavity may, as in Batrachians, remain as a wide space, the *optic ventricles*, or be narrowed to a mere "aqueduct of Sylvius" or passageway (*I*) from the fourth ventricle behind to the third ventricle in front.

[22] It is not strange that Europeans have been obliged to content themselves with imperfectly preserved brains of American fishes. But it is little to the credit of our native zoölogists that they have not long ago investigated the structure and development of the forms peculiar to this continent.

[23] Some parts would be more advantageously shown upon a still larger scale. Most fishes' brains can hardly be understood if figured of the natural size.

[24] For the use of these figures I am indebted to Messrs. Estes and Lauriat of Boston.

This third ventricle is the cavity of the anterior vesicle, and its lateral walls become the *thalami* (*Th*). But from each side in front there is produced a hollow bud which enlarges so as to become the *cerebral hemisphere* (*H*). From the front of each hemisphere a second bud is produced, the *olfactory lobe* (*Ol*). The cavity of each hemisphere is a *lateral* (first or second) *ventricle*, (*LV*) and the cavity of the olfactory lobe is the *olfactory ventricle*. The constricted communication between each lateral ventricle and the median third ventricle is known as the "*foramen of Monro*" (*FM*). Median dorsal and ventral outgrowths from the thalamus vesicle become respectively *conarium* ("pineal body," *Co*) and *infundibulum*, the connection of which with the hypophysis (*Hy*) is now regarded as secondary (43, 92).

The thin anterior wall of the anterior vesicle between the hemisphere-buds, remains as the *lamina terminalis* (*Lt*) the "lamina cinerea" of anthropotomy. The *corpus striatum* is a thickening of the outer walls of the hemisphere (*CS*). The various transverse and longitudinal commissures *corpus callosum*, *anterior commissure*, *fornix* and *pons Varolii*, probably do not exist in fishes and need not here be described.

Taking for granted the sequence of principal ganglia, medulla, cerebellum, optic lobes, thalami, hemispheres and olfactory lobes, no difficulty is met in recognizing the three first named in the brain of *Lepidosteus*. But the appearance of these in the section differs considerably from the idea conveyed by the figures of the brain from above and below. The fourth ventricle (IV) extends farther back, and has no bridge across its anterior end as in Huxley's figure. In this species the hinder end is quite sharply pointed. But in a smaller gar from Wisconsin, not yet identified, the ventricle is shorter, its borders are raised and everted, and the hinder extremity less sharp. The borders also approach each other quite nearly, just behind the cerebellum, which, with a poorly preserved preparation, might lead an artist, not an anatomist, to regard them as normally continuous.[25]

If figure 7 be held with the olfactory lobe upward, then the section of the entire cerebellum may be compared to a letter S, the lower curve larger and its substance thicker than the upper.

The lower, or, if the figure be replaced in the horizontal posi-

[25] Huxley's figure purports to be of the brain of *L. semiradiatus*, Ag. Günther regards this as a synonym of *L. osseus*.

tion, posterior curve, represents the cerebellum proper. The anterior curve corresponds to the "valve of Vieussens" of anthropotomy, and to the "fornix of Gottsche" referred to by Huxley in his description of the brain of Teleosts (7, 142).

This part is about one-half the thickness of the cerebellum itself, and it becomes an exceedingly thin lamina where it joins the overhanging posterior border of the optic lobes. The cerebellar ventricle is quite extensive, its vertical diameter being more than twice and its longitudinal diameter more than thrice, the thickness of the lamina by which it is surrounded.

About midway between the posterior rounded border of the cerebellum and the free thin edge of its anteverted portion upon the ventral aspect, is a low ridge. Laterally this is in apposition with a corresponding everted edge of the medulla.

The dorsal surface of the cerebellum presents on each side a rather deep furrow separating the median rounded portion from the peduncle on each side.

The "aqueduct of Sylvius" (*AS*) is a rather contracted passage from the fourth ventricle to the ventricle of the optic lobes.

The dorsal aspect of the optic lobes inclines downward and forward at about the same angle as that at which the cerebellum inclines backward. The thickness of the cut surface is about the same as that of the "fornix of Gottsche," but the anterior margin is slightly thickened and rounded. At this point the expanded optic ventricle (*OV*) opens forward by a contracted aperture surrounded by a flaring lip. The conarium or pineal body (*C*) lies just in front of this aperture.

So far there seems no reasonable cause for doubting the correctness of the commonly accepted nomenclature. But the anterior half of the brain of *Lepidosteus* presents serious difficulties in the way of strict comparison with the brains of the higher Vertebrates.[26]

The form and connections of the parts marked 2, 3, 4, cannot be well indicated without more figures, especially cross-sections. These I hope to present upon another occasion.

The third ventricle (III) opens downward into a cavity with walls thicker before and behind but thin upon the sides. It ex-

[26] To say nothing here of the brains of the Myzonts, Selachians and Teleosts, with which considerable rectification is required, as will be shown hereafter.

tends under nearly the whole width of the brain and opens downward by a median slit into what seems to be a plexus of vessels.

The hollow lateral lobes are what Owen calls "hypoaria" and Huxley, with most authors, "lobi inferiores." The lower solid vascular mass corresponds to what is commonly called the pituitary body or hypophysis. It is easily detached, and is not, so far as I am aware, represented in any figure of a Ganoid brain.

Pending an examination of the brain of *Lophius*, the hypophysis of which lies far in front of the brain connected with its usual attachment by a very long infundibulum, I am inclined to regard the lobi inferiores as lateral expansions[27] of what is called in anthropotomy the *tuber cinereum*.

There remain to be described the two pair of masses which, in *Lepidosteus* as in most Teleosts, are placed just in front of the optic lobes. They are at the present time usually regarded as representing respectively the hemispheres and olfactory lobes.

According to the type of brain as described by Huxley and generally accepted, the hemispheres should be lateral masses separate from each other and each containing a cavity, the lateral ventricle, communicating with the median or third ventricle through a foramen of Monro.

Yet, so far as I am aware, no such condition of things has been figured or described with respect to the brain of any fish-like form excepting Protopterus and Lepidosiren.[28] (See Appendix.)

In the brain of the adult *Lepidosteus*, the lateral mass marked *PTh* is a solid lamina with its upper or dorsal border everted, as seen in the transverse section (Fig. 11). The mesial surface of its rounded dorsal aspect presents two furrows. It is joined with its fellow of the opposite side by a large commissure (*B*)[29] and by a thinner lamina reaching back to the optic chiasma.

[27] Dr. Cleland (38, 203) regards the hypoaria of osseous fishes as the thalami, and states that "in various fishes, the optic nerves arise from them as well as from the optic lobes." Dr. Cleland's learning and accuracy are such that I would not reject his view upon less grounds than those here presented. But I have not observed the origin of the optic nerves from the hypoaria in any fish.

[28] Tiedemann frankly admits (35, 264), that "we find no trace of lateral ventricles in the osseous fishes;" he regarding the so-called hemispheres as the corpora striata (p. 230). Contrast this with the loose statement of Vulpian (31, 821), "on trouve parfois des rudiments de ventricules lateraux dans les lobes cérébraux" of osseous fishes.

The so-called ventricles of Selachians will be shown hereafter to be remnants of the third ventricle; not rudiments of the first and second.

[29] This is apparently what Gottsche called in osseous fishes, "commissura interlobularis."

Just in front of each of these lobes is a rounded orifice opening obliquely outward and forward into the base of the anterior or olfactory lobes.

This orifice is wholly invisible from above or below or from the outer side, and, although figured by Stannius in the sturgeon, seems to have attracted no attention from those who have studied Ganoid brains.

It leads into a cavity which extends the whole length of the so-called olfactory lobe, and is about 1$^{mm.}$ in diameter.

As this is the only lateral opening from the median ventricle there seems to be no escape from the conclusion that it is the "foramen of Monro," and that the cavity into which it leads is, wholly or in part, the lateral ventricle.

Where then are the hemispheres?

The mesial border of the foramen of Monro is slightly raised, so as to be distinguishable upon close inspection from the olfactory lobe. Still it is very small, and upon a poorly preserved specimen, or under a brief examination it might escape notice altogether.

But if the corresponding parts of other Ganoid brains be carefully examined, they will be seen to present the same foramen, while in all of them the anterior lip is decidedly broader, presenting the appearance of a separate lobe. See figures 8, 9, 10.

Shall we conclude that the hemisphere and olfactory lobe are undifferentiated, or regard the lip already described as a rudimentary hemisphere. This latter is the conclusion to which I am inclined.

It involves, as a corollary, the interpretation of the lateral masses between the optic lobes and those just described, as representing the whole or some part of the *thalami*, or *lobi ventriculi tertii*.

In *Lepidosteus* one would be inclined to regard the lateral masses as the whole thalamus. But in *Amia* the distance between the front of the optic lobes and the hinder surface of these masses equals that of the masses themselves. In *Polypterus* likewise, as figured by Müller, it is considerable. In *Chimera* what seems to be a corresponding region is very much elongated. In most Selachian brains it is quite extensive.

For the sake of distinction therefore, we may call the anterior lateral masses *prothalami*, and the portion connecting them with the brain behind the *crura thalami*. These latter seem to correspond to the thalami of the higher Vertebrates; the third ventricle lies between them, the conarium above and the hypophysis below.

Aside from the adverse opinions of all authors (which, however, are of less importance in view of the imperfection of the material at their disposal) the only objection to this view is, that it makes the hemispheres so much smaller than either the thalami or the olfactory lobes.

It is to be remembered, however, that mere size is of no value for the determination of homologies. The cerebellum is recognized as such in the lamprey and the salamander because it is a bridge over the fourth ventricle, although it is so much smaller than the corresponding organ of the bird or mammal.

The hemispheres are hardly larger than the optic lobes in some Batrachians, while in man they overshadow all the other parts.

Now the hemispheres are, by development, mere buds from the thalami, yet, as may happen with human families, the offspring are larger than the parents. In like manner, in the Ganoid brain, the hemispheres themselves are surpassed in size by their buds, the olfactory lobes.

But while regarding the view here advanced as based upon sound morphological grounds, the large size and convoluted surface of the thalami suggests the idea that they may in some way *functionally* represent the hemispheres.

For the determination of this the brain should be examined microscopically and the fibres from the medulla should be traced forward into the several lobes as has been done with the frog by Wyman and Stieda. They should also be experimented upon by injury, ablation and galvanic stimulation.

To complete the evidence we should find, at least in young specimens, something like a *lamina terminalis*, connecting the rudimentary hemispheres just in front of the foramina of Monro. No such has been found by me in *Amia* or *Lepidosteus*, but the sturgeon and *Polyodon* present a transverse curtain with foldings upon the deep surface resembling those of the curtain over the fourth ventricle of Batrachians and lamprey-eels. Though not, apparently, of nervous tissue, it may nevertheless, represent the lamina terminalis. For there is reason to believe that, in the course of development, many parts of the roof of the primary vesicles may become merely connective and vascular tissue.

In a young *Lepidosteus* $151^{mm.}$ long, the dorsal borders of the prothalami are not everted as in the adult. For reasons which will be understood when the brains of Selachians and Myzonts are described, I am inclined to think that at an earlier period of development the dorsal borders were united.

Detailed descriptions of the brains of the other Ganoids are deferred until figures can be presented. That of *Amia* closely resembles that of *Lepidosteus*, especially in the cerebellum. The infundibulum is more folded. The crura thalami are considerably longer.

The brain of *Acipenser*[30] and *Polyodon* are very similar in both structure and general appearance. In both the cerebellum is apparently a narrow bridge, but, as seen in the figure of Stannius, it really extends far forward into the optic ventricle, as an exaggerated fornix of Gottsche. The walls of the optic lobes are thicker in *Polyodon* than in *Acipenser*. The brain of *Scaphyrhynchus* was not obtained for examination. There is no reason for supposing it to differ essentially from that of *Acipenser*.

Müller's figures and descriptions of the brain of *Polypterus* do not allude to the communication between the median ventricle and the olfactory ventricles, but the figures are quite insufficient, and pending its examination with reference to this point, we may infer that it agrees with *Lepidosteus* in this respect as in the eversion of the thalami.

The brain of *Calamoichthys* is not known to me. We may even more naturally infer its agreement with that of *Polypterus*.

Provisionally, at least, the seven genera, *Amia* and *Lepidosteus*, *Polypterus* and *Calamoichthys*, *Acipenser*, *Scaphyrhynchus* and *Polyodon*, may be associated as having *rudimentary hemispheres in the form of slightly raised borders of the foramina of Monro and much smaller than the olfactory lobes; large prothalami connected below by a commissure but having their dorsal borders free and more or less everted; an optic chiasma; a rythmically contractile and multivalvular bulbus arteriosus.*

Fig. 12 shows a mesial section of what seems to me to be a typical Ganoid brain with cross sections at characteristic points.

Let us now see whether the above definition includes any other Vertebrates.

30 Three species of this genus were examined, *rubicundus*, *oxyrhynchus*, and one as yet undetermined.

Amphioxus appears to have only a medulla with a fourth ventricle. The part in front of the ventricle may be regarded as an undifferentiated representative of the brain of the higher Vertebrates (Langerhans (44, 297) says he finds a small olfactory lobe).

In *Myxine* and *Bdellostoma*, Joh. Müller (37), found no ventricle in front of the fourth, and no cerebellum. In a somewhat injured preparation of the brain of *Myxine*, I find what seems to be a thin and rudimentary cerebellum; and a median ventricle which extends forward to the base of the anterior pair of lobes, which Müller and all other authors regard as the olfactory lobes. On each side at this point is a slit-like orifice leading into the cavity of the olfactory lobe. These can be no other than the foramina of Monro and lateral ventricles. The hemispheres are hardly distinguishable from the olfactory lobes. The larger pair of lobes just behind, since they form the walls of a median ventricle must be regarded as the undifferentiated prothalami and thalami. They differ from those of Ganoids in being connected above as well as below. But behind them are the conarium and the orifice of the optic ventricle just as in the brain of *Lepidosteus*. In *Petromyzon* Müller found (37) the third ventricle only. In several well preserved preparations of the brain of the large sea-lamprey (*P. marinus*, var. *Americanus*), I find at the anterior extremity of this median cavity, as in *Myxine*, a foramen of Monro leading into the olfactory or lateral ventricle. The thalami are closed above as in *Myxine*. The distinct lobes which project just behind the olfactory lobes are probably hemispheres. (See Appendix.)

Müller describes the optic nerves of the Myzonts as not crossing at all. Upon this ground, as by the non-separation of the thalami above and the lack of several rows of valves in the bulbus arteriosus, they differ from the Ganoids. In figure 13 (*M*) is represented a cross section of the brain of *Petromyzon* through the thalami. (See Appendix.)

The Selachians (here restricting the term to the sharks and skates) have a brain which is really only a complex modification of the Lamprey's. In an embryo shark (*Mustelus canis*) 37$^{mm.}$ (about 1½ inches) in length, that part which gives rise to the olfactory crura and which has been variously interpreted as hemispheres alone, hemispheres and thalami, and thickened lamina terminalis, is a large vesicle with thin walls and a single cavity. This communicates behind with the optic ventricle and on each side in front with the cavity of a little bud which is in contact with the nasal sack. The vesicle is evidently the expanded prothalamus closed above as in the Myzonts. In the adult Selachians (as I hope to show by a series of figures at a future time) we must suppose the original median cavity to have gradually filled up so as to leave only two slender passages, near the lower wall, which start from opposite the optic foramen behind, and diverge to enter the olfactory ventricles in front. The degree of differentiation of the crura thalami, and the hemispheres, will be more fully described hereafter. In some forms the hemispheres are distinctly constricted from the sides of the nearly solid prothalamus. Although, therefore, the optic chiasma and multivalvular and contractile bulbus and some other characters are common to Ganoids and Selachians, the prothalamus is open in the former and closed in the latter. In these and some other respects the contrast between the two groups is noteworthy. In figure 13, *ES* represents a cross section of the prothalamus of an embryo shark and *AS* that of an adult.

The Holocephali (*Chimera* and *Callorhynchus*) are commonly arranged with or near the Selachians. They have many features in common and the intromittent organs upon the ventral fins are usually regarded as very important. Being a purely sexual apparatus we may question whether their taxonomic value is equal to that of the brain. Not having had the opportunity of examining a brain[31] I can only judge from the figure by Busch, copied by

[31] Just as this goes to press I am enabled, through the kindness of Mr. Alex. Agassiz, to expose and examine the brain of a well-preserved male *Chimera* in the Museum of Comparative Zoology. The cerebellum is very large and covers the optic lobes, but is not folded transversely as in most, if not all, adult sharks and skates. The crura thalami are very long and thin and united ventrally by a delicate membrane apparently only pia mater. Anteriorly each crus expands into a prothalamus, the dorsal border of which is thin and slightly everted. This prothalamus, however, instead of forming the principal anterior mass as in Ganoids, is overlapped outside by a large and elongated hemisphere about 8mm. in height and 15mm. in length. On the hinder third of the mesial surface is a large rounded foramen of Monro, 4mm. in diameter. The lateral ventricle extends forward into the olfactory lobe. Into the foramen, and occupying its entire area, projects a thickening of the outer wall of the hemisphere which may represent a primordial corpus striatum. Just in front of the foramen the ventral borders of the hemispheres are connected by a transverse commissure. I greatly regret not having been able to examine this brain before presenting this paper. It seems to furnish an actual form intermediate between the apparently distinct types represented by the brains of Selachians, Ganoids and Dipnoans. If I correctly interpret the appearance of a partial subdivision of the elongated mass behind the olfactory lobe the Chimera's brain presents a more equal proportion of hemisphere and prothalamus than exists in Ganoids or Teleosts, where the former seems to be reduced to a rudiment hardly recognizable as such.

Owen (24, fig. 179). The cerebellum appears like that of the sharks and skates. But the elongated crura thalami, and what seem to be somewhat expanded prothalami, and the rudimentary hemispheres, indicate a close similarity with the Ganoid type. The brain should be carefully reëxamined, and that of a very young embryo would be especially valuable.

The figure of the brain of *Protopterus* (Owen, 25 and 24) might be taken for that of *Menopoma* or *Menobranchus*. It has no apparent resemblance to either the Ganoid or the Selachian type. There are also true nostrils, and, according to Huxley (7, 147), a small pulmonary auricle. These characters united with those of the brain seem to offer strong grounds against the association of the Dipnoi with the Ganoids, excepting as a very generalized type combining Ganoid and Batrachian features. The brain of *Ceratodus* has not been described.[32]

Of fish-like forms there remain the Teleostei. They may at once be distinguished from all others by the non-rythmically contractile bulbus provided with a single row of valves and by the decussation of the optic nerves without a chiasma.[33]

A sufficient number of Teleost brains has not yet been carefully examined to enable us to generalize with safety. But so far as they are known we may characterize them as having solid lateral masses (prothalami), their dorsal borders separate and sometimes everted, and with the olfactory lobes sometimes in contact with the prothalami, sometimes in contact with the olfactory sacks and connected with the prothalami by more or less elongated crura.

Since this paper was presented I have found small foramina of Monro and ventricles in *Perca flavescens*, *Anguilla Bostoniensis* and *Scomber vernalis*. They, however, are much smaller

[32] In "Nature" for Jan. 6th, 1876, it is stated that Prof. Huxley described, for the first time, the brain of *Ceratodus* at the meeting of the Zoological Society, Jan. 4th; that he showed how closely it resembled that of *Lepidosiren*, and that in some points it resembled the Selachian rather than the Ganoid type. He laid especial stress upon the affinities of the animal with *Chimera*.

Zoölogists will look with great interest for this paper on account of the description and figures of the brain of a form which has aroused so much discussion, and also for the morphological and taxonomic considerations which can hardly fail to throw great light upon the relations of the fish-like Vertebrates.

[33] Gottsche (30, 476, and fig. xxxiii), refers to a remarkable variation of the optic nerves described by Weber (Meckel's Archiv, 1872, p. 317). In an example of *Clupea harengus* the nerve of the left eye was pierced by that of the right. The *structure* of the chiasma of Ganoids and Selachians should be carefully examined to ascertain how completely the fibers cross, or intermingle, or connect the eyes and lobes of the two sides together.

than in Ganoids, and I give a provisional figure (Fig. 14) mainly for the purpose of calling attention to the point where they are to be looked for. Probably they are proportionally larger in embryo brains. They may become wholly obliterated in some adults, especially those with olfactory crura. They should be looked for in large species, as *Esox*, *Xiphias*, *Hippoglossus*, etc., where the olfactory lobes are sessile.[34]

The following table exhibits the above mentioned characters in a more condensed form. But it must not be inferred that the order of names indicates my belief respecting either their rank, their affinities, or geological succession. In the first place no linear arrangement can do this. In the second, while the Teleosts seem to most perfectly and abundantly embody the *fish idea* and their geological relations and the structure of some parts would lead us to place them highest in the fish series, yet the non-mingling of the optic nerves and the very embryonic condition of the kidneys as compared with those of Selachians,[35] seem to place them next the Myzonts.

The air-breathing Vertebrates are added in order to complete the series.

Provisional Arrangement of Vertebrates according to Cerebral and Cardiac Characters.

Leptocardii. (*Amphioxus*). Brain not differentiated from medulla. Heart a contractile tube.

Myzonts. (Marsipobranchii). Optic nerves do not cross (Müller). Single median nostril. Hemispheres smaller than olfactory lobes. Thalamus and prothalamus not distinctly separated. Thalamus closed forward and dorsad. Cerebellum a narrow and thin lamina; perhaps wanting in Myxinoids. (See Appendix.)

Selachians. (Elasmobranchii.) Optic chiasma. Rhythmically contractile bulbus arteriosus, with several rows of valves. Olfactory lobes pedunculated. Hemispheres smaller than olfactory lobes. Prothalami and thalami distinct; the latter as crura. In

[34] The brains must be well preserved.
[35] As recently studied by Balfour (39, 30).

embryo the prothalamus a thin-walled vescicle, with a single cavity which, in adult, is reduced to two canals diverging forward. Prothalamus remains closed forward and dorsad. Nostrils in pairs, but do not enter mouth. Cerebellum folded transversely.

HOLOCEPHALI. Brain combines characters of Selachians, Ganoids and Batrachians. Crura thalami much elongated. True hemispheres, larger than prothalami or olfactory lobes. Foramen of Monro very large. (The last two sentences have been added since this paper was read. See notes 31 and 36.)

GANOIDS. Optic chiasma. Rhythmically contractile bulbus arteriosus with several rows of valves. Hemispheres rudimentary. Olfactory lobes sessile. Prothalami separate forward and dorsad, and more or less everted. Cerebellum with no transverse folds. Foramina of Monro large.

TELEOSTS. Optic nerves cross but form no chiasma. Bulbus arteriosus not rhythmically contractile and has a single series of valves. Olfactory lobes sessile or pedunculated. So-called hemispheres are probably prothalami; more or less everted as in Ganoids, and separate forward and dorsad. True hemispheres rudimentary or absent. Foramina of Monro and lateral ventricles small or, perhaps in some, obliterated. (Last sentence added since this paper was read.)

DIPNOANS. Hemispheres larger than olfactory lobes. Heart trilocular. True nostrils. Optic chiasma. (Should probably be arranged with or near Batrachians in the Series of air-breathing Vertebrates).

BATRACHIANS. Hemispheres larger than olfactory lobes. Heart trilocular. Optic chiasma. No corpora striata or commissures. Walls of brain thin and ventricles large. True nostrils.

REPTILES. True hemispheres. True nostrils. Corpora striata and anterior commissure. Heart trilocular or quadrilocular. Right and left aortic arches persistent.

BIRDS. Same brain characters as in Reptiles. Heart quadrilocular. Right aortic arch persistent. (Birds seem to be an aberrant group of Sauropsida.)

MAMMALS. Corpora striata. Anterior commissure. Corpus callosum. Fornix. Pons varolii. Heart quadrilocular. Left aortic arch persistent.

By characters of the brain alone the Ganoids are readily separable from all other vertebrates. From the Teleosts they differ in respect to the optic chiasma; also, so far as now known, on account of the greater size of the lateral ventricles and foramina of Monro.[36] But differences of size alone are not reliable; and our knowledge of the structure of the Teleost brain must be much extended before final generalizations can be made. Meantime it is interesting to note that some cerebral characters seem to associate the Ganoids with the Teleosts, while others, with cardiac characters, link them with the Selachians. The Teleosts are apparently an aberrant group, like the Birds.

Minor modifications of the brain, together with those of the tail and air-bladder, will probably furnish the basis for subdivision of the Ganoids. The brains of *Amia* and *Lepidosteus* are very nearly alike, and both seem to agree in all essential respects with that of *Polypterus*, and, by inference, *Calamoichthys*. The brains of the Sturgeons resemble one another more closely than they do those of the other genera, but all agree in the rudimentary hemisphere, the enlarged prothalami, and the position of the foramen of Monro.

Reserving for the present any discussion as to the separation of Dipnoans from Batrachians, and of Birds from the other Sauropsida, the groups seem to readily fall into five categories. The first and lowest includes *Amphioxus* alone. The second the Myzonts and Selachians, whose brains are differentiated, but have not yet assumed the distinctive features of either the true aquatic or the aërial Vertebrates. They have the form and habit of fishes, but their brains are more readily comparable with those of Batrachians. For the hemispheres are distinct, though small, and the thalamus remains closed, instead of being separated forward and

[36] At the time this paper was presented I had not been able to find these openings in any Teleostean brain, and therefore supposed that their existence in the Ganoids formed a sharp distinction between the two groups.

dorsad, as in the Teleosts, the Ganoids and Holocephali. The Holocephali cannot yet be fully characterized. The brain presents a very generalized condition. These and the other characters may be more distinctly presented in tabular form.

Series V. Hemispheres well developed; larger than olfactory lobes. Pulmonary auricle. True nostrils.

Mammals.
Birds.
Reptiles.
Batrachians.
Dipnoans.

Series IV. Hemispheres rudimentary or absent; smaller than olfactory lobes. Prothalamus open forward and dorsad. Dorsal borders of prothalami more or less everted. Heart bilocular. Nostrils do not enter mouth.

Teleosts.
Ganoids.

Series III. Holocephali. Brain presents a condition intermediate between Series II, IV and V.

Series II. Hemispheres distinct but smaller than olfactory lobes. Thalamus not open forward or dorsad. Heart bilocular. Nostrils do not enter mouth.

Selachians.
Myzonts.

Series I. Brain not differentiated from medulla. Heart tubular.

Amphioxus.

To such an arrangement of vertebrates as the above the palæontologist would naturally object upon the ground that it includes no osteological characters by which fossil forms may be collocated with the living.

To this I plead guilty, but urge in extenuation the following:

1. The *argumentum ad hominem*. For the classifications now in vogue make little or no reference, or that of the most unsystematic kind, to the brain; and osteological characters alone would not enable us to define embryos, Myzonts, or *Amphioxus* at all.

2. The above does not pretend to be a complete or final arrangement. It is an effort to show how far cerebral and cardiac characters concur with each other and with the results of a previous consideration of all systems of organs. Such an effort could hardly be successful before the brains of fishes were structurally homologized with those of the air breathing Vertebrates.

3. I should be willing to have it shown that I had made some

mistakes as to both fact and interpretation, for the sake of the advantages which I am confident will attend the careful and systematic reconsideration of our present methods of classification. These last are almost purely empirical. They have, as in the case of the Ganoids, led to the most diametrically opposite conclusions. Would it not be worth while to enquire whether, from both analogy and experience, cerebral and cardiac characters are not more trustworthy for the discrimination of larger groups, and whether characters drawn from the skeleton, teeth, digestive and reproductive systems are not likely to serve us better if restricted to the determination of orders, families and genera.

When the limits of classes and sub-classes have been once ascertained by the study of the heart and the brain, most of the fossil forms may, by the correlations of their hard parts be assigned to places in them. At present, on account of the greater availability of hard parts for preparation and preservation, we practically depend upon them almost entirely, or tacitly assume that they are of greater taxonomic value than the soft parts, and that the latter are, therefore, readily correlated with the former.

SUMMARY. 1. The smallest *Lepidosteus* here described (18$^{mm.}$ long), has a primordial median fin extending over the hinder third of the body above, and its hinder half below, interrupted at the vent.

2. The locations of the dorsal, the anal and the infra-caudal fins are marked by coloration and thickening of the primordial fin.

3. A fourth or supra-caudal fin is also indicated, though less decidedly. This fin is not functionally developed.

4. The tail of this smallest *Lepidosteus* is nearly protocercal, the end of the body inclining slightly downward.

5. The end of the body proper is gradually forced upward by an increase of the infra-caudal lobe, and becomes the "filament" already known in the young gar-pike.

6. The movements of this filament are extensive, and vibratory, and wholly voluntary.

7. The filament exists, though evidently in process of removal, in a young *Lepidosteus osseus* 300$^{mm.}$ long.

8. The infra-caudal lobe becomes the functional tail of the adult.

9. The vertebral column is then continued obliquely upward and backward as a tapering cartilaginous rod which terminates at a point corresponding with the previous separation of the filament

from the infra-caudal lobe. This point coincides with the hindermost of the dorsal fulcra.

10. This rod comprises the notochord, the spinal cord and two lateral cartilaginous pieces.

11. The tail of the adult *Amia* presents a similar structure, excepting that the rod is shorter and there are no fulcra.

12. It seems probable that the tail of *Amia* passes through stages like those of *Lepidosteus*, but the smallest specimen here described (70$^{mm.}$ long) shows no sign of the filament.

13. The two earlier stages of the tail of *Lepidosteus* may be compared with the protocercal (or diphycercal) and the ordinary heterocercal tails of other living and fossil forms. The *masked* heterocercal tail of *Amia* and *Lepidosteus* probably existed in *Megalurus* and some other mesozoic forms, but is not known among the palæozoic fishes. It likewise exists in the embryo of certain Teleosts, as *Gasterosteus* and the Siluroids.

14. The pectoral fins of *Lepidosteus* attain considerable size before the appearance of the ventrals.

15. The latter are not lobed, but the former consist of a fleshy lobe and a thin fringe or border.

16. In the smallest *Lepidosteus* the branchiostegal membranes are separate farther forward than in the adult. The point of their junction in the young becomes a transverse fold, which may correspond with the hinder border of the jugular plate of *Amia*.

17. The "foramina of Monro" and lateral ventricles have been found by me in the following Ganoids:—*Amia*, *Lepidosteus*, *Acipenser* and *Polyodon;* and in the following Teleosts:—*Perca*, *Scomber*, *Anguilla;* in *Chimera;*[37] in the following Selachians:—*Mustelus*, *Carcharias;* and in the Myzont genera *Myxine* and *Petromyzon*. There is good reason to believe that *Scaphyrhynchus*, *Polypterus* and *Calamoichthys* have the same parts; and that they exist in other Teleosts, but less easily seen than in Ganoids, or perhaps wholly obliterated in the adults of some species. In both Ganoids and Teleosts the foramen of Monro seems to open into the base of the anterior or olfactory lobe on each side.

18. Aside, therefore, from the difference in general aspect and in size of the foramina and ventricles, the Ganoid and Teleost brains, as heretofore, are most readily distinguished by the *chiasma* which exists in the former group.

[37] As stated on previous pages the foramina were found in *Chimera* and the Teleosts after this paper was presented.

19. We may regard, provisionally, the seven genera, *Amia*, *Lepidosteus*, *Polypterus*, *Calamoichthys*, *Acipenser*, *Scaphyrhynchus* and *Polyodon* (together with such fossil forms as are obviously allied to them) as constituting a natural group (class or sub-class) characterized by an *optic chiasma; a rhythmically contractile bulbus arteriosus with several rows of valves; large prothalami separate above but united below; rudimentary hemispheres;* and the *foramina of Monro opening apparently into the base of the sessile olfactory lobes.*

20. It seems probable that by features of the brain and heart alone, all of the primary subdivisions of Vertebrates may be accurately characterized.

21. The Dipnoans, hitherto regarded as fishes and usually arranged with or near the Ganoids, agree with the Batrachians in cerebral and cardiac and other characters. This group seems to furnish a case for testing the relative taxonomic value of characters derived from the brain and heart on the one hand and from the skeleton, limbs and digestive organs on the other. In like manner the brain of Holocephali would indicate that they belon nearer the Ganoids than the Selachians, perhaps as a transition between the two.

22. While the facts and considerations presented in this paper cause me to doubt the correctness of all classifications of fish-like Vertebrates hitherto proposed, they do not seem to justify the framing of another system. Nor is it probable that any phyllogenetic arrangement can be proposed which shall either advance science or reflect credit upon the propounder, until our knowledge of the embryology, of the brains and of fossil forms is much more extensive than at present.[38]

APPENDIX.—Just as this goes to press I have been able to consult the admirable paper of Paul Langerhans, "Untersuchungen über *Petromyzon Planeri*," pp. 114, 16mo, 10 Tafeln. Freiburg, 1873. This author figures and describes (p. 83) the lateral and olfactory ventricles of *Petromyzon*. He also states (p. 95) that an *optic chiasma does exist*. These statements must be considered in connection with paragraphs upon pages 178, 182, 185 of this paper.

[38] As this paper is passing through the press, I have seen in the "Zoölogical Record" for 1872, page 86, an abstract of a memoir by Panceri and De Sanctis "Sopra alcuni organi della *Cephaloptera*, Napoli," 1869, 4to. The authors recognize four types of brain besides that in *Amphioxus*; namely, in Cyclostomata; in Teleosts; in four Selachian genera, *Dicerobatis*, *Zygæna*, *Myliobatis*, *Trygon*; and in all other Selachians and Ganoids.

No mention is made of the lateral ventricles or foramina of Monro, and, so far as indicated by the abstract, the conclusions are very different from those here presented.

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EXPLANATION OF PLATE I.[*]

Fig. 1. Young *Lepidosteus* 18mm. in length, enlarged 5 diameters. The tip of the tail is missing, and its supposed form is indicated by the dotted outline. *N*, the nostrils of the left side; the anterior one is more nearly upon the upper surface than in the adult. In the margins of the jaws appear slight elevations, probably teeth. *O*, the operculum; *P*, the pectoral fin consisting of a rounded fleshy lobe *L* and a thin fringe *F*; 1, 2, 3, 4, 5, regions of the primordial median fin. *V*, the vent. *C*, the commencement of the infra-caudal lobe. The commencing anal is seen between *V*, and *L*. *D*, the commencing dorsal fin; *X*, indicates a slight and transitory modification of the primordial fin like a second dorsal, or, more probably, supra-caudal lobe. The ventrals have not appeared. The lines above figures 1, 2, 3 indicate the actual length of the young *Lepidosteus*.

Fig. 2. Tail of young *Lepidosteus* 22mm. in length, enlarged 4 diameters. The lettering as in fig. 1. The infra-caudal (*C*) begins to project beyond the outline of the primordial fin. *V's* the ventral fin.

Fig. 3. Tail of young *Lepidosteus* 44mm. in length, enlarged 2 diameters. Lettering as in fig. 2. The primordial fin exists only upon the borders of the filamentary termination of the body (*Fi*) which is now crowded up by the increasing infra-caudal lobe.

Fig. 4. Tail of young *Lepidosteus osseus* 300mm. long, natural size. The infra-caudal lobe now occupies its permanent place as the functional tail, while the filament (*Fi*) has nearly disappeared. Its base is protected by six pair of fulcra (*DF*) and a similar series covers the anterior half of the lower border of the tail (*VF*).

Fig. 5. Dissected tail of medium sized *Lep. platystomus*. The filament has disappeared and the fulcra extend backward to a point nearly corresponding with its separation from the caudal fin. To this point may be traced a cartilaginous rod (*N*), the prolongation of the vertebral column (*VC*), and previously continued into the filament. This rod consists of the notochord, the spinal cord (*SC*), and a cartilaginous sheath. *NC*, neural canal laid open. *HC*, hæmal canal, laid open.

Fig. 6. Section of the upper margin of the tail of *L. platystomus* at a point about mid-way between the base of the fin and the last pair of fulcra; enlarged. *N*, notochord; *SC*, spinal cord; *CS*, cartilaginous sheath, in which the vertebræ are afterward developed. *F''*, points of the upper fulcra; *F'*, cut surfaces of the next lower fulcra; *F*, cut surfaces of the lowest fulcra which are separated so as to embrace the upper half of the cartilage. *CR'*, cut surface of the uppermost caudal fin ray, the two halves being separated above to enclose the lower part of the cartilage. The dark line crossing the section indicates the commencing splitting of the ray into two. *CR*, the halves of the second fin ray not quite perfectly apposed, and joined by a double membrane to the rays above and below.

[*] All the figures were drawn, from specimens and preparations, by Mr. Philip Barnard.

Fig. 1. Young Lepidosteus, enlarged 5 diameters.

Fig. 2. Tail of young Lepidosteus, enlarged 4 diameters.

Fig. 3. Tail of young Lepidosteus, enlarged 2 diameters.

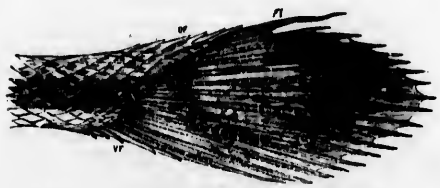

Fig. 4. Tail of young Lepidosteus, natural size.

Fig. 5. Tail of adult Lepidosteus platystomus, one-half natural length; dissected.

Fig. 6. Section of notochord and the surrounding parts.

Fig. 7. Lepidosteus. Mesial, vertical, longitudinal section of brain, enlarged two diameters.

Fig. 8. Amia.

Fig. 9. Acipenser.

Fig. 10. Polyodon.

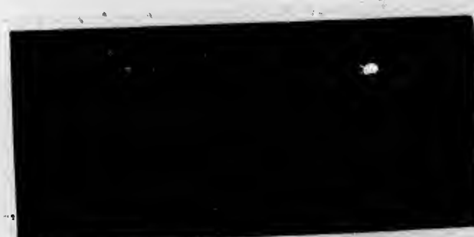

Fig. 11. Cross sections of Prothalami of Ganoids.

EXPLANATION OF PLATE II.

Fig. 7. Vertical longitudinal section of the brain of *Lepidost us osseus*. The specimen was a female, about four and one-half feet long. The ure is enlarged two diameters. The cut surfaces are dotted. *SC*, spinal cord; *M*, medulla oblongata; *IV*, fourth ventricle; *Cb*, cerebellum; *CV*, ventricle of the cerebellum; 1, anteverted posterior border of the cerebellum; behind this is seen the low ridge referred to in the text; *AS*, aqueduct of Sylvius, or passage from the fourth ventricle into that of the optic lobes; *OL*, optic lobe; *OV*, optic ventricle; *C*, conarium or pineal body just in front of the opening of the optic ventricle; *III*, third ventri opening downward into the hypoaria or *lobi inferiores*, which may represent the *pora cinerea* of anthropotomy; 2, the thickened hinder wall of this cavity; 3, the hypophysis or pituitary body, apparently vascular and easily detached; a narrow longitudinal slit communicates with the cavity above; 4, the optic chiasma, forming part of the anterior wall of the hypoarian ventricle; *ON*, the right optic nerve; *PTH*, the right prothalamus (usually called hemisphere): 5, commissure connecting the prothalami; it is connected with the optic chiasma by a thin lamina forming part of the floor of the ventricle; *FM*, the foramen of Monro; *H*, a raised margin of this orifice, which is more apparent in the other brains, and may be a rudimentary hemisphere; *OlL*, olfactory lobe, containing a ventricle which communicates through the foramen of Monro with the third or median ventricle between the prothalami of opposite sides. In *Amia*, *Acipenser* and *Polyodon* the optic lobe is connected with the prothalamus by a lower rounded crus thalami on each side; but as the ganoid nature of these genera is denied by some, I chose the brain of *Lepidosteus*, although it is less well adapted to display all the parts.

Figs. 8, 9, 10. Mesial surface of the right olfactory lobe and nerve, the hemisphere, foramen of Monro and anterior part of the prothalamus of *Amia*, *Acipenser* and *Polyodon*; enlarged two diameters. The letters as in Fig. 7.

Fig. 11. Transverse sections of the prothalami enlarged two diameters. These figures are somewhat diagrammatic, but they indicate the facts that the lateral masses (*C*) are solid, with dorsal borders (*D*) more or less everted, so as to form an external concavity (*E*); that they are connected by a ventral commissure (*B*) and that between them (*A*) is a space, the median or third ventricle. 5, *Polypterus* (from Müller); 3, *Amia*; 4, young *Amia*, 70mm. in length; 1, *Lepidosteus osseus*; 2, young *Lepidosteus*, 300mm. in length; 6, *Polyodon*; 7 and 8, *Acipenser rubicundus*, at two different points and angles.

EXPLANATION OF PLATE III.

Fig. 12. Diagrams intended to represent the structure of a ganoid brain as seen in longitudinal mesial section and in transverse sections through several parts. The letters as in Fig. 7.

Fig. 13. Diagrams representing the cross-section of the prothalami of Myzonts (*M*) and Selachians and of the hemispheres of Batrachians. The prothalamus of the adult Myzont is closed above, as in the embryo Selachian (*ES*). In the adult Selachian, by a deposition of matter the single cavity is filled up, excepting two lateral canals which converge backward to meet opposite the optic forsmen, and diverge forward to enter the olfactory crura through the small hemispheres. In Ganoids, as seen in Fig. 11, the prothalamus is open above. Likewise in many, if not all, Teleosts, in which, however, the optic nerves form no chiasma. In Batrachians, as in the Dipnoans, the place of the prothalami is taken by a pair of true hemispheres, each containing a lateral ventricle.

Fig. 14. Anterior part of prothalamus of a perch (*Perca flavescens*), with the olfactory lobe and nerve, and the small foramen of Monro. (The dotted line makes the ventricle larger than it is really.) Enlarged ten diameters. The existence of the foramen in some Teleosts was ascertained after the paper was read. See page 184.

Fig. 15. Diagrams, slightly altered from Huxley, to indicate the typical structure of the brain in Batrachians, Reptiles, Birds and Mammals. The upper is a horizontal, the lower a vertical section. See page 175.

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Fig. 12. Diagram of ganoid brain.

Fig. 13.

Fig. 14. Perca.

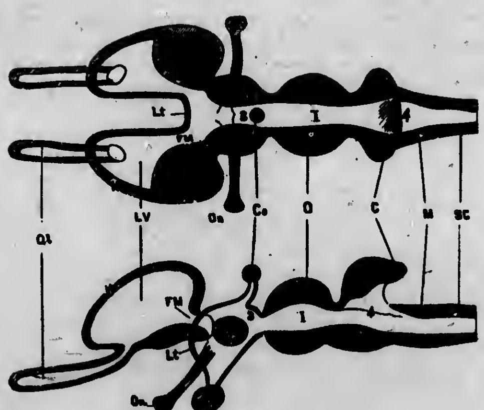

Fig. 15.